

**TITLE:** Examining the relationship between local extinction risk and position in range

Elizabeth H. Boakes<sup>1,\*</sup>, Nicholas J.B. Isaac<sup>2,\*</sup>, Richard A. Fuller<sup>3</sup>, Georgina M. Mace<sup>1</sup>, Philip J.K. McGowan<sup>4</sup>

<sup>1</sup>Centre for Biodiversity and Environment Research, University College London, Gower Street, WC1E 6BT, UK.

<sup>2</sup>NERC Centre for Ecology and Hydrology, Wallingford, Oxfordshire, OX10 8BB, UK.

<sup>3</sup>School of Biological Sciences, University of Queensland, Brisbane, QLD 4072, Australia.

<sup>4</sup>School of Biology, Newcastle University, Newcastle upon Tyne, NE1 7RU, UK.

\*These authors contributed equally to this work.

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## ABSTRACT

Over half of globally threatened animal species have experienced rapid geographic range loss. Identifying the parts of species' distributions most vulnerable to extinction would benefit conservation planning. However, previous studies give little consensus on whether ranges decline to the core or edge. Here we build on previous work by using empirical data to examine the position of recent local extinctions within species' geographic ranges, addressing range position as a continuum and exploring the influence of environmental factors. We aggregated point locality data for 125 species of galliform birds across the Palearctic and Indo-Malaya into equal area half degree grid cells and used a multi-species dynamic Bayesian occupancy model to estimate the rates of local extinctions. Our model provides a novel approach to identify loss of populations from within species ranges. We investigated the relationship between extinction rates and distance from range edge, examining whether patterns were consistent across biogeographic realm and different categories of land-use. In the Palearctic, local extinctions occurred closer to the range edge in both unconverted and human-dominated landscapes. In Indo-Malaya, no pattern was found for unconverted landscapes but in human dominated landscapes extinctions tended to occur closer to the core than the edge. Our results suggest that local and regional factors over-ride any general spatial patterns of recent local extinction within species' ranges and highlight the difficulty of predicting the parts of a species' distribution most vulnerable to threat.

## INTRODUCTION

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Substantial geographic range loss has occurred in over half of the ~12,000 species of animals currently listed by the IUCN as globally threatened (Criterion B: IUCN 2016). An ability to forecast which parts of species' geographic range (hereafter range) are most at risk of local extinction would improve predictions of both global extinction probability and the consequences for ecosystems where those local extinctions take place. However, while the general spatial pattern of range change, specifically whether ranges decline toward the core or edge, has been the subject of much theoretical discussion and empirical research (e.g. Hanski 1982; Channell & Lomolino 2000a; Sagarin et al. 2006; Pironon et al. 2015), little consensus has emerged. Some studies conclude that species decline toward their range core (Nathan et al. 1996; Donald & Greenwood 2001; Yackulic et al. 2011) and others toward their periphery (Channell & Lomolino 2000a; Farnsworth & Ogurcak 2006; Fisher 2011).

Many studies have focussed on understanding the evolutionary mechanisms behind range change, for example by determining the distribution of abundance (e.g. Blackburn et al. 1999; Sagarin & Gaines 2002) or genetic diversity (e.g. Hampe & Petit 2005; Eckert et al. 2008) across species' ranges. However, the recent scale of anthropogenic processes driving biodiversity loss may now overwhelm any such natural patterns (Yackulic et al. 2011; Lucas et al. 2016). Drivers of change such as coastal settlement or deforestation that move contagiously across the landscape could lead to increased vulnerability of range edges (Boakes et al. 2010a). Alternatively, since species' ranges and ecosystem boundaries are often not identical, and with the spatial reach of anthropogenic

disturbance larger than ever before (Sanderson et al. 2002), species might be equally vulnerable across their entire range.

Understanding the spatial patterns of range change raises a significant practical challenge; our actual knowledge of species' distributions is much less comprehensive than range maps might suggest. Studies of geographic range change are restricted and biased by data availability (Boakes et al. 2010b) and thus information on changes in range extent is likely to be of uneven quality. Previous studies of decline to core versus periphery (e.g. Channell & Lomolino 2000a, b) have used generalised distribution maps to analyse loss of species' historic ranges in comparison with contemporary distributions. While these studies have provided insights into past range decline, the coarse spatial resolution of the historic ranges and often dichotomous measure of position in range (i.e. edge or core) limit statistical power and the conclusions that can be drawn. For example, since many species occur in only a small fraction of their extent of occurrence (EOO; (Gaston & Fuller 2009)), assessments of range loss using EOO polygons may identify range loss in places where the species never occurred or may overlook significant fragmentation within occupied areas. It would thus be preferable to examine patterns of range loss at a finer spatial resolution whilst addressing range position as a continuum based on observations (Yackulic et al. 2011). Historical data on the occurrence of species are widely scattered in museums, published literature and unpublished reports but intensive and directed data gathering can provide comprehensive information on species occurrences over time and space (e.g. Boakes et al. 2010b; Turvey et al. 2015).

Here we use multi-species dynamic occupancy modelling to analyse a compilation of point locality data that record the presence of galliform birds over the last two centuries (see Boakes et al. (2010b)). We explore links between position in a range and local extinction risk for the 125 European and Asian species of Galliformes. Specifically, we test the hypothesis that local extinction rates are affected by distance to range edge, and investigate whether effects are consistent between a) the Palearctic and Indo-Malayan biogeographic realms, b) human dominated versus unconverted land-use types and c) species.

## **METHODS**

### **Distributional data**

The data include 125 species of Galliformes (pheasants, quails, grouse etc) in the Palearctic and Indo-Malay biogeographic realms, see Supporting Information (S1). Historical distribution data for the Galliformes are of relatively high quality owing to their long association with humans through hunting and religious symbolism (McGowan & Garson 2002) and their attraction for collectors and ornithologists. Almost all species are resident, making range delimitation more tractable. Over 25% of Galliformes are threatened (IUCN 2016) and many local extinctions have been reported (BirdLife International 2015).

Point locality data, at a resolution of  $\leq 30$  minutes ( $\sim 50$ km) were collected from museum collections, journal articles, personal reports and letters, banding records, ornithological atlases and birdwatching trip-report websites (see Boakes *et al.* (2010b) for detailed description of sources). Records were included if they could be dated to within  $\pm 10$  years or were known to be pre- or post-1980. Records from non-native parts of species' ranges (determined from range maps in McGowan (1994)) were not included other than as a measure of survey effort. (See Boakes *et al.* (2010b) and McGowan *et al.* (1999) for full details). The final database contained 158,714 locality records, dating from 1727 to 2008, with a median year of 1981 (see Supporting Information (S2)). Although the dataset was compiled as comprehensively as possible, record coverage was unavoidably uneven with the last three decades showing a strong bias towards threatened species and protected areas (Boakes *et al.* 2010b) and countries rated as more 'peaceful' (Global Peace Index: Institute for Economics and Peace 2015) (Boakes *et al.* 2016). We aggregated the point locality data into a Behrmann equal area projection, using a grid with cells measuring 48.24 x 48.24 km, i.e.  $\sim 30$  minute resolution. Grid cell size was chosen to maximise spatial resolution within the constraints of the spatial coverage of our data. The dataset contained 8,551 cells with at least one native species observation (Figure 1).

### Measuring distance from range edge

No single measure can encapsulate all aspects of geographic range change, e.g. contraction from one edge, fragmentation, collapse to the core. Even defining the edges and core of a range is difficult. Exact range margins do not exist in the sense of a strict border (Gaston 1994). If margins

are drawn to exclude outliers, their delineation will be arbitrary but ranges encompassing all occurrences are disproportionately affected by a few outliers (Quinn et al. 1996). Distance to range edge can be estimated in ovoid ranges by measuring distance from the centroid. However, irregularly-shaped ranges present conceptual and practical problems: the centroid can fall close to, or even outside, the inferred range. (Sagarin et al. 2006); for examples see Supporting Information (S3). We therefore employed a continuous measure of distance to range edge that is not based upon the range centroid nor the range border.

To measure distance from range edge, we calculated  $D_o$ , the geometric mean distance from the centroid of a cell to the centroids of all other cells containing that species (excluding introductions) (following Blackburn *et al.* (1999)). We derived a species' historical distribution by aggregating the grid cells in our database with the range polygon from Orme et al. (2005) (see Supporting Information S4). There are instances where occurrence records which we are confident are within the native range fall close to but outside these range polygons. This is to be expected since range maps are approximations and the Orme et al. polygons are compiled from relatively recent sources (Orme et al. 2005).

In order that measures of distance to range edge could be compared across species,  $D_o$  values must be standardised (Fortin et al. 2005): for each species  $D_o$  values were divided by the largest value of  $D_o$  for that species yielding the standardised  $D^*$ . A  $D^*$  value close to one indicates that a cell is near the range edge although, depending on range shape, some edges are 'edgier' than others. For extremely small-ranged species, the gridded data meant that all cells are almost equally 'edgy' and

thus all have values of  $D'$  close to 1 (see Supporting Information S4). These ranges are thus effectively treated as having no core – the centre of a small range is closer to the range edge than the centre of a large range. An alternative option would be to force the scaling of the distance to edge measure to run from 0 to 1 but we decided against this since it would vastly over inflate the variance of the distance to edge measure for small-ranged species.

### **Biogeographic realm and landscape type**

The Palearctic biogeographic realm has a longer history of anthropogenic disturbance than Indo-Malaya (Ellis et al. 2010) thus we hypothesised that the two realms might exhibit different spatial patterns of range loss. We assigned cells to realm as defined by Olson et al. (2001), using the cells' centroids.

To investigate whether ranges follow the same pattern of decline in unconverted and human-dominated landscapes we classified cells into 'unconverted' and 'human-dominated' using a threshold of one third of land having been converted for human use before 1970 using the HYDE 2.0 Land Use Data (Klein Goldewijk 2001) – the closest approximation of anthropogenic disturbance available for 1980 - (unconverted = land class categories 5-18; human-dominated = land classes 1-2, see Supporting Information (S5)). It has been suggested that increasingly rapid loss of biodiversity occurs following landscape conversion of over 30% (Andr n 1994) and this threshold has the additional advantage of a similar number of cells in the two sets (1319 human dominated cells; 1199



unconverted cells). We note that the uncertainty associated with historical modelled land use data (Klein Goldewijk & Verburg 2013) is small for recent decades.

### **Multispecies Occupancy Model**

Estimating extinction is a major challenge as an absence of sightings does not necessarily indicate extinction, especially if search effort or species' detectability is low (Boakes et al. 2015). Most of our data were derived from opportunistically collected presence-only data (as opposed to systematic presence-absence survey data) and there are likely to be many pseudo-absences – cases where a species was not recorded in a grid cell at which it was in fact present. The opportunistic nature of these observations leads to spatial and temporal biases in presence-only datasets (Isaac & Pocock 2015). Hierarchical Bayesian occupancy-detection (BOD) models are robust to these biases if they contain parameters to describe the data collection process (van Strien et al. 2013; Isaac et al. 2014). These models are hierarchical in that the occupancy of each grid cell (presence or absence) is separated statistically from the data collection process (detection vs non-detection): specifically, observations are conditional on the species being present.

Our modelling framework required us to define a temporal resolution at which to estimate occupancy, and within which repeated surveys can be identified. After examining the data, we decided to work with two time periods with 1980 as the cutoff (this is the median year of observation). A larger number of time periods would have reduced the precision of our occupancy

estimates for each time period and therefore our ability to infer patterns of local extinction risk. Having defined this threshold, we excluded grid cells that contain no information about relative extinction rates (3511 cells with no observations after 1980 and 2,528 cells lacking data before 1980). Our analysis is based on 2,512 cells with observations on both time periods. These cells encompassed records from 123 species. Two species, the Arabian Chukar (*Alectoris melanocephala*) and Philby's Rock Partridge (*Alectoris philbyi*) were excluded from further analysis since there were no cells containing records of these species from both time periods. We used a temporal precision of one year to define repeat surveys within grid cells. Our final dataset contains 18,492 surveys, which equates to an average of 3.68 surveys per grid cell per time period (standard deviation = 4.88).

We employed a multispecies dynamic BOD model similar to that employed by Woodcock et al (2016). The model is 'dynamic' (Royle & Dorazio 2008), in that persistence and colonization of individual grid cells is modelled explicitly (equation 1), and 'multispecies' (Ruiz-Gutierrez et al. 2010), in that we fitted a single model to the full dataset, with species-specific parameter estimates. The model consists of two sub-models: "state" and "detection". The state sub-model defines the occupancy (presence-absence) of 123 species on 2,512 grid cells in each of the two time periods. We included only the 14,256 species-cell combinations within the range polygon of each species (i.e. the state sub-model has 28,512 elements). The detection sub-model defines the probability, per survey, of detecting a species that is in fact present. The data are 112,485 binary observations (one per survey-species combination) on whether the species was detected or not: the model then estimates the distribution of parameters that is most likely, given both the data and the condition that species can only be detected if present.

In the model, the expected value of  $z_{i,j,2}$  (occupancy of species  $i$  in grid cell  $j$  in the second time period, i.e. after 1980) was modelled as a function of occupancy in the first time period,  $z_{i,j,1}$ .

Unoccupied cells could be colonized with species-specific probability  $\gamma_i$ , while occupied cells persisted with a probability  $\phi_{i,j}$  (extinction rates can be inferred as  $1 - \phi$ ). Occupancy in the second time period is a Bernoulli trial with an expected value defined by equation 1:

$$E[z_{i,j,2}] = z_{i,j,1} * \phi_{i,j} + (1 - z_{i,j,1}) * \gamma_i \quad (1)$$

Population persistence,  $\phi_{i,j}$ , was modelled as a linear function of position in range,  $D^*$ , and two parameters,  $\alpha_{i,j}$  and  $\beta_{i,j}$ :

$$\text{logit}(\phi_{i,j,t}) = \alpha_{i,j} + \beta_{i,j} \cdot (D^*_{i,j} - 0.5) \quad (2)$$

We subtracted 0.5 from the  $D^*$  scores in order to avoid confounding our estimates of intercept ( $\alpha_{i,j}$ ) and slope ( $\beta_{i,j}$ ) effects. Thus,  $\beta_{i,j}$  is the difference in persistence between the range edge and centre;  $\alpha_{i,j}$  is the persistence rate at some notional point in between. Both  $\alpha_{i,j}$  and  $\beta_{i,j}$  are composites, made up of components for: realm, conversion-status and species:

$$\alpha_{ij} = \alpha_0 \cdot (1-R_j) + \alpha_1 \cdot R_j + \alpha_2 \cdot (1-R_j) \cdot C_j + \alpha_3 \cdot R_j \cdot C_j + u_i \quad (3)$$

$$\beta_{ij} = \beta_0 \cdot (1-R_j) + \beta_1 \cdot R_j + \beta_2 \cdot (1-R_j) \cdot C_j + \beta_3 \cdot R_j \cdot C_j + v_i \quad (4)$$

$R_i$  takes the value 0 for cells in the Palearctic and 1 in Indo-Malaya;  $C_i$  takes the value 0 for unconverted cells and 1 for human-dominated ones. Thus  $\alpha_0$  and  $\alpha_1$  are intercept terms measuring the log-odds of persistence for the average species at unconverted cells in Palearctic ( $\alpha_0$ ) and Indo-Malaya ( $\alpha_1$ ) that are midway between the range edge and core ( $D = 0.5$ ). The  $\beta$  parameters define slopes, i.e. the difference between range core and edge in the log-odds of persistence):  $\beta_0$  and  $\beta_1$  are the slopes (for unconverted cells in Palearctic ( $\beta_0$ ) and Indo-Malaya ( $\beta_1$ )). Positive slopes indicate higher persistence at the range edge (i.e. extinction is concentrated in the centre) and negative values indicate the converse (extinction is edge-prone). Parameters  $\alpha_2$  and  $\beta_2$  are the difference in intercept and slope, respectively, between human-dominated and unconverted cells in the Palearctic;  $\alpha_3$  and  $\beta_3$  are equivalent terms for Indo-Malaya;  $u$  and  $v$  are species-specific random effects (normally-distributed with a mean of zero). Thus, parameters  $\beta_0 - \beta_3$  are relevant to our hypotheses about the degree to which the “edge proneness” of extinction varies with respect to biogeographic realm and conversion status; the values of  $v_i$  are relevant to our question about the degree to which edge-proneness varies among species (see below).

Our detection sub-model states that the  $k$ th survey to a cell occupied by species  $i$  will yield an observation with probability  $p_{i,k}$ . We define a survey as the set of unique records from a particular

cell:year combination. We modelled this probability as a function of the total number of species recorded on that survey, since this provides a convenient measure of sampling effort (Szabo et al. 2010; van Strien et al. 2013). Specifically,  $p_{i,k}$  is a function of two binary variables indicating whether the survey produced a short (2 or 3 species) or long (>3 species) list (van Strien et al. 2013):

$$\text{logit}(p_{i,k}) = \delta_t + \delta_{1i} + \delta_{2i} * \text{Short}_k + \delta_{3i} * \text{Long}_k \quad (5)$$

Parameter  $\delta_1$  is the probability that a single-species list is a survey of the focal species; parameters  $\delta_2$  and  $\delta_3$  estimate how the detection probability changes with survey effort and  $\delta_t$  estimates the difference in detectability before and after 1980. This formulation treats short lists, long lists and single species surveys as separate datasets with different statistical properties (van Strien et al. 2013) and does not assume that all surveys record ‘complete lists’ of what was present (Isaac & Pocock 2015). Parameters  $\delta_1 - \delta_3$  carry the subscript  $i$ , indicating that species are allowed to vary in their detection probability as random effects.

We fitted the model described by equations 1-5 in a Bayesian framework, in the BUGS language implemented in JAGS (Plummer 2014) via the R package ‘jagsUI’ (Kellner 2014). The BUGS code describing the model above can be found in the Supporting Information (S8) and a model validation exercise in Supporting Information (S6). We used minimally informative priors and ran the model for 25,000 iterations following a burn-in of 250,000, on three chains with a thinning rate of 10. Gelman-Rubin statistics indicated satisfactory convergence by this point (all Rhat values < 1.05 for all

parameters, and  $R_{hat} \ll 1.01$  for the vast majority). We report three types of statistics to describe our model parameters: i) the mean of the posterior distribution, ii) its standard deviation, and iii) the proportion of the posterior distribution that has the same sign as the mean. This value, referred to as  $f$ , is our confidence that the parameter is either positive or negative. It always lies in the range  $0.5 \leq f \leq 1$ : a value of 0.67 indicates that two thirds of the posterior lies one side of zero and one third on the other side (i.e. the odds of the parameter taking a particular sign are 2:1).

### **Species' range size and edge-proneness of local extinctions**

We investigated whether species' extinction risk and the degree to which extinctions are concentrated at the range edge ("edge-proneness":  $v_i$ ) varies with range size. Larger ranges might confer more protection on their core than smaller ranges. In the seven instances where the IUCN (2016) taxonomy differed from Orme et al. (2005), we amended Orme et al.'s distribution maps.

Species' average extinction risk (after controlling for biogeographic realm and conversion history) is measured as  $1 - u_i$  (equation 3); edge-proneness is measured as  $v_i$  (equation 4), with positive numbers indicating that extinctions are concentrated towards the range centre (compared with the average species, and after controlling for realm and conversion history); negative numbers indicating that extinctions have been concentrated towards the range edge.

We did not conduct a formal test of the interrelationship between  $u_j$ ,  $v_j$  and geographic range size because the test would be subject to multiple forms of non-independence. In addition to the phylogenetic non-independence associated with interspecific comparative tests, our estimates of  $u_j$  and  $v_j$  derive from a model in which  $D^*$  is the independent variable, and  $D^*$  is not independent of range size. Moreover, the main axes of variation in extinction risk (biogeographic realm and conversion history) have been removed, so the test statistic would be misleading. Rather, we make a qualitative comparison in order to identify species with unusual combinations, especially those species experiencing high rates of extinction that are concentrated in one part of the range.

## RESULTS

Actual values of distance to range edge,  $D^*$ , ranged from 0.199 to 1 with a mean of 0.564 ( $SD=0.171$ ) and median of 0.537. Values of  $D^*$  for the different species co-occurring within a cell can vary considerably (Supporting Information S7).

Overall, persistence rates were much higher in the Palearctic than Indo-Malaya ( $\alpha_0 \gg \alpha_1$ : Table 1 and Figure 2). The effect of landscape conversion on average persistence was small compared with the difference between realms ( $\alpha_2 \ll \alpha_0$ ;  $\alpha_3 \ll \alpha_1$ ). In unconverted landscapes, extinctions occurred closer to the range edge in the Palearctic ( $\beta_0$  is negative: table 1), but was more-or-less independent of range position for Indo-Malayan cells ( $\beta_1$  is small and we have low confidence that the effect is different from zero: Table 1). Human dominated landscapes in the Palearctic were edge-prone to a similar degree as unconverted landscapes ( $\beta_2$  is small and we have low confidence that the effect is

different from zero: Table 1), but human-dominated landscapes in Indo-Malaya had higher extinction rates near the centre of the range ( $\beta_3$  is large and positive: Table 1). The impact of these effects is visualised in Figure 2. The estimated changes in species richness for each cell and the associated uncertainty are shown in Figure 3. High relative extinction rates can be seen in the Himalayas and the Malay Archipelago.

There is a weak relationship, at best, between species' edge-proneness and geographic range size (Figure 4), although species with relatively high extinction rates are all moderately widespread Palearctic species (note that extinction rates are low in the Palearctic, in absolute terms). However, the relationship identifies some key species with interesting dynamics. The Red Grouse (*Lagopus lagopus*) is a good example of a widespread species that appears to be declining within its range. It is the bluest point on Figure 4: the extinction is relatively high (for the Palearctic) and it has the overall highest value of  $v_j$ , indicating that extinction events are concentrated at the centre of the range. By contrast, the Necklaced Hill-partridge (*Arborophila torqueola*), whose geographic range size is close to the overall median, is the reddest point on Figure 4 because it has the lowest value of  $v_j$ , indicating that any extinctions it does suffer are concentrated at the edge of the range. Whilst it has one of the lowest relative extinction rates, it should be borne in mind that it's restricted to Indo-Malaya, where the absolute extinction rates are high (Figure 2).

## DISCUSSION



Our study of the relationship between spatial properties of species ranges and local extinction rates has shown that the nature of the relationship differs between biogeographic realms and, in Indo-Malaya, between unconverted and human-dominated landscapes. Relative extinction rates do not appear to be affected by geographic range size although species with particularly high relative extinction rates tended to have relatively large geographic ranges.

Our findings raise several important issues for conservation. Firstly, local extinctions in human-dominated landscapes occurred closer to the edge in the Palearctic and either with no pattern or further from the edge in Indo-Malaya, dependent on landscape. The two biogeographic realms have different histories of anthropogenic transformation; by 1700, Europe was already mostly transformed, and Asia was beginning to undergo transformation into the intensive cropland and village anthromes that would later predominate in the 20<sup>th</sup> century (Ellis et al. 2010). The intensity of extinction drivers differs between the realms with wildlife extraction in Southeast Asia estimated to be at six times the sustainable rate (Bennett 2002) and current deforestation continuing at exceptionally high rates (Sodhi et al. 2004). One explanation of the difference between realms thus might be that local extinctions are mainly central during the early stages of decline and switch to the edge later. Alternatively the difference might reflect spatial patterns in the drivers of range loss or the severity of threatening processes. The realms' different biome compositions might also be a factor, a previous study finding biome to be a better predictor of vulnerability to local extinction than position in range (Yackulic et al. 2011). Additionally, Indo-Malaya has a more complex geometry with many instances of coastal edge occurring in the centre of a species geographic range; our measure of  $D'$  may have been less representative of range edge in these cases (see Supporting Information S4).

Within Indo-Malaya, species' range change differed between land-use type. In unconverted landscapes, no pattern was seen but in human-dominated landscapes local extinctions tended to occur further from the range edge. Differences in the distribution and intensity of anthropogenic pressures may explain why patterns of range change differed between landscapes. Hunting is more likely to be focussed on areas of high species abundance, which are generally scattered across a species' range (Sagarin & Gaines 2002) and thus one might not expect local extinctions caused by hunting to show a pattern with respect to distance to edge. In contrast, habitat loss might be more likely to cause contraction from an edge inwards. More research is needed regarding the placement of threats and their position in a species' range - mapping the intensity of threats across species ranges would be extremely valuable.

The relationship between landscape conversion history, range position and local extinction rate was more complicated than we anticipated. In the Palearctic, the relationship conformed to our expectation that human-dominated landscapes experience higher extinction rates, but that the spatial pattern (the relationship with position in range) would be the same in both types of landscape. By contrast, the pattern in Indo-Malaya was that overall extinction rates were similar (although slightly lower in human-dominated landscapes), but concentrated at range centres in human-dominated landscapes. Our finding of similar extinction rates in both landscapes has implications for models in which land-cover type (known/measured or inferred) is used as a proxy for species occurrence or extinction risk, e.g. species distribution modelling, protected area planning

and IUCN Red List assessments that use habitat loss as a surrogate for population decline. We urge further work at a finer grain to progress understanding of this issue.

Our study showed no apparent relationship between relative extinction rate and range size (Figure 4). However, it is worth noting that the Palearctic species undergoing the highest relative extinction rates were all non-threatened, wide ranging species, several of which (e.g. Red Grouse, Black Grouse (*Lyrurus tetrix*), Western Capercaillie (*Tetrao urogallus*) and Barbary Partridge (*Alectoris barbara*)) had high positive values of 'edginess' meaning extinctions tended to occur away from the range edge. Such declines in more central parts of species' ranges will, of course, not be picked up by measures of EOO (Gaston & Fuller 2009) and thus monitoring programmes for wide-ranged species need to be sensitive to central range loss. The three species suffering the highest relative extinction rates in Indo-Malaya were the Black Francolin (*Francolinus francolinus*), the Common Quail (*Coturnix coturnix*) and the Rock Bush-quail (*Perdica argoondah*). In contrast to the predominate pattern in Indo-Malaya, these species all showed had high negative 'edginess' values meaning extinctions tended to occur near the range edge and, along with the Necklaced Hill-partridge, thus correspond to the classical 'contraction to the centre' paradigm. Like their Palearctic counterparts, these species with the highest relative extinction rates are not considered threatened. It is essential that such declines are not overlooked, lest today's common species become tomorrow's threatened species.

Identifying the 'core' and 'edge' of an irregular shaped range is not easy. The measure we chose treated the 'core' of small ranges as being close to the range edge which we believe is broadly sensible. However, there were many range shapes for which a relatively low  $D^*$  occurred at or near a

range edge. One alternative would have been to measure the distance to the nearest border but, as we explain in the methods, defining such a border is in itself problematic and, as our measure shows, some edges can be viewed as 'less edgy' than others. How to deal with complex range shapes remains an open question as indeed does the effect of range shape on a species' vulnerability.

In light of our finding that the pattern of range loss is affected by the local factors of biogeographic realm and by land-use type, the discrepancy between the conclusions of previous studies of range loss (e.g. Channell & Lomolino (2000a); Fisher (2011) versus Donald & Greenwood (2001); Yackulic *et al.* (2011)), which did not all control for these factors, is unsurprising. Should patterns of decline be scale dependent, as suggested by Thomas *et al.* (2008), discrepancies between studies would also be expected. Indeed vulnerability to extinction is almost certainly even more complex than the interactions between position in range, biogeography and land-use type that our study has revealed. For example, Dos Anjos *et al.* (2010) found the interaction of endemism and position in range to predict vulnerability whilst Yackulic *et al.* (2011) found biome to be a better predictor of vulnerability than position in range. There is much scope for further research in this area.

Our analysis was limited by the distribution of our point locality data, particularly a lack of recent observations from eastern Europe, northern Asia and central India (Figure 1). Additionally, we could not model extinctions of species that were observed after 1980 but subsequently became extinct. This lack of baseline data on many species will make understanding of future range or abundance changes extremely difficult. Biodiversity data collection and curation needs a radical new direction.

Technological advances coupled with the development of statistical methodologies that can cope with opportunistic and noisy data mean that citizen science is being used in an increasing variety of ways to a) document species distributions and abundances and b) apply such data to ecological research (August et al. 2015; Powney & Isaac 2015). We encourage the use of citizen science in addressing issues of spatial and taxonomic bias in biodiversity data globally.

Our model provides a template for exploring how extinction risk varies with position in range and other patterns. Our approach is particularly valuable for identifying widespread species that may be suffering high rates of population loss within the core of the range. We found no overall tendency towards either of the dominant paradigms of range collapse, suggesting that local factors predominate in determining local extinction risk (Cowlshaw et al. 2009). However, we were limited to studying losses of whole populations from grid cells: changes in occupancy are likely to lag behind changes in abundance (Rodriguez 2002), so research to understand the spatial patterns of trends in abundance should be a priority.

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## LITERATURE CITED

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## TABLES

Table 1. Posterior distribution of parameter values from the Dynamic Occupancy model. Parameters  $\alpha_0$ - $\alpha_3$  and  $\beta_0$ - $\beta_3$  relate to persistence probabilities (equations 2-4);  $\gamma$  relates to the colonization probability (equation 1) and  $\delta$  parameters relate to the conditional probability of detection (equation 5). Both  $\gamma$  and  $\delta$  are reported as means across species.

Parameter	Mean	sd	2.5%	97.5%	Rhat	f
$\alpha_0$	9.067	0.997	7.335	11.128	1.048	1
$\alpha_1$	1.821	0.499	0.943	2.891	1.014	1
$\alpha_2$	-0.856	0.325	-1.503	-0.224	1.018	0.996
$\alpha_3$	0.882	0.314	0.291	1.526	1.001	0.998
$\beta_0$	-7.719	3.309	-13.919	-1.051	1.004	0.989
$\beta_1$	1.429	2.215	-2.776	5.970	1.007	0.737
$\beta_2$	0.766	1.292	-1.825	3.242	1.013	0.734
$\beta_3$	4.425	2.040	0.500	8.589	1.002	0.984
$\gamma$	0.487	0.324	-0.123	0.272	0.477	0.941
$\delta_t$	0.076	0.020	0.038	0.115	1.002	1

$\delta_1$	-1.487	0.084	-1.651	-1.322	1.000	1
$\delta_2$	1.041	0.068	0.908	1.178	1.000	1
$\delta_3$	2.188	0.100	1.994	2.386	1.000	1

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$\hat{R}$  is the Gelman-Rubin convergence statistic and  $f$  is the proportion of the posterior distribution that has the same sign as the mean.

#### FIGURE LEGENDS

Figure 1. The distribution of the 8551 cells where Galliformes were recorded at least once. Black cells – recorded in both time periods (2512 cells), light grey cells – first time period only (3511 cells), dark grey cells – second time period only (2528 cells).

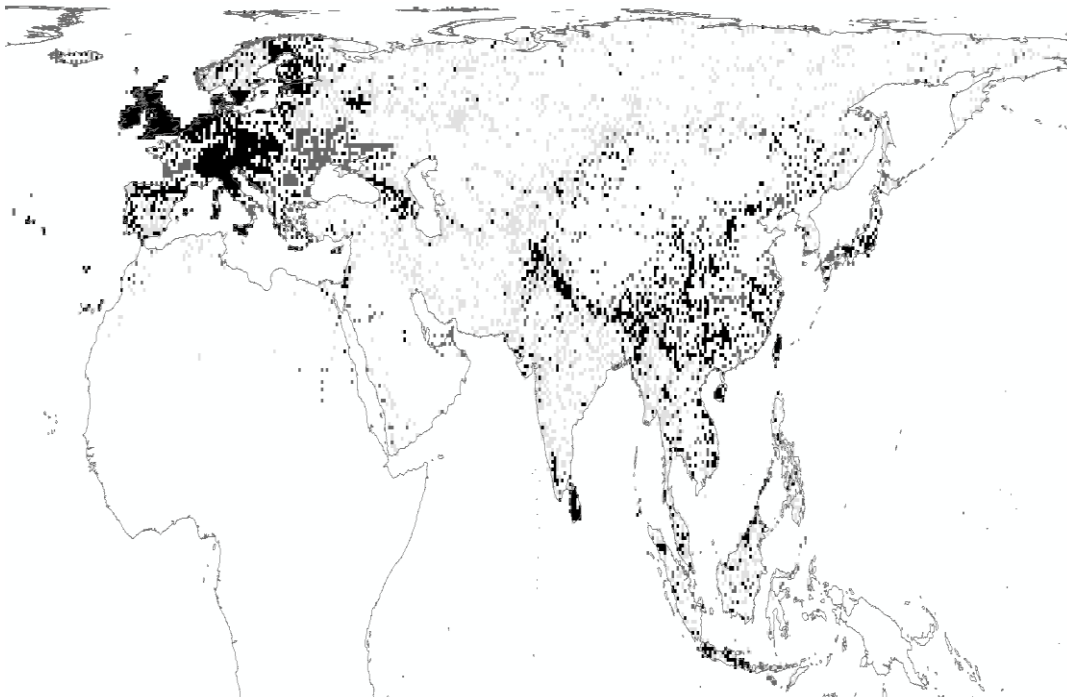


Figure 2. The relationship between extinction rates and position in range,  $D'$  varies among realms (PA=Palearctic; IM=Indo-Malaya) and according to whether the habitat was converted prior to 1970.

The data are fitted values from our multispecies dynamic occupancy model and represent the average species' response. The lines show the median of the posterior distribution; the ribbons delimit 80% credible intervals. Note that the figure shows extinction rates, calculated as 1-persistence rates.

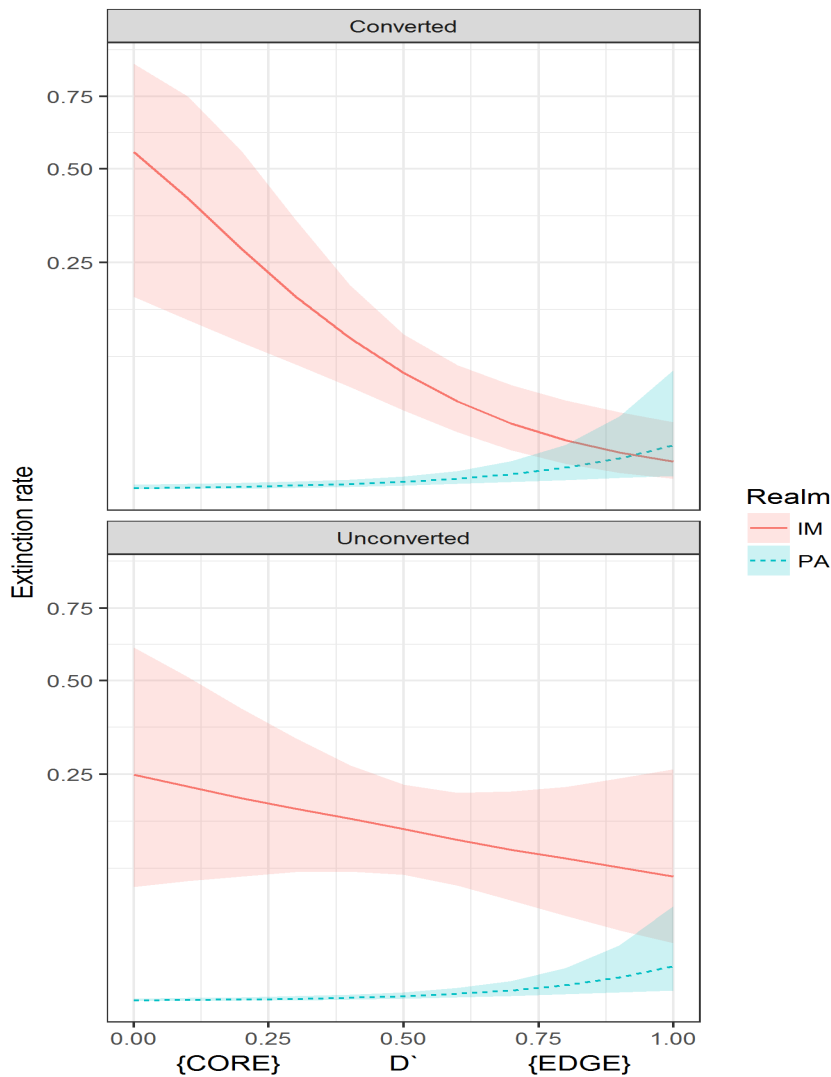


Figure 3. a) Map showing estimated changes in species richness for each grid cell. Data were extracted from our multispecies dynamic occupancy model. For each grid cell we extracted a distribution of species richness values before and after 1980: from this we calculate the change in richness (values shown here are the means of these posterior distributions). Red colours indicate losses of species richness, blue indicates gains. b) Map showing spatial variation in uncertainty associated with changes in species richness. We calculated species richness for each grid cell in each iteration of the model: from these data we calculated the proportion of iterations in which species richness was higher after 1980 than before. This gives a continuous measure for our confidence about changes in species richness. Values close to zero (red colours) indicate high confidence for net loss of species; high values (darker blue colours) indicate high confidence for gains.

Figure 3a

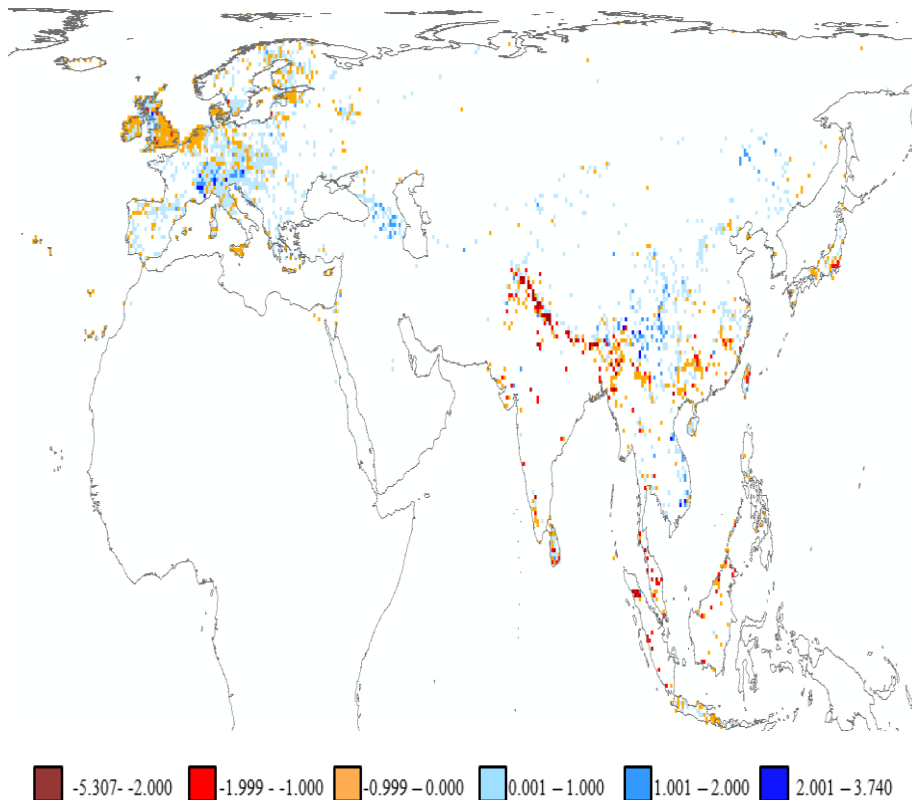


Figure 3b

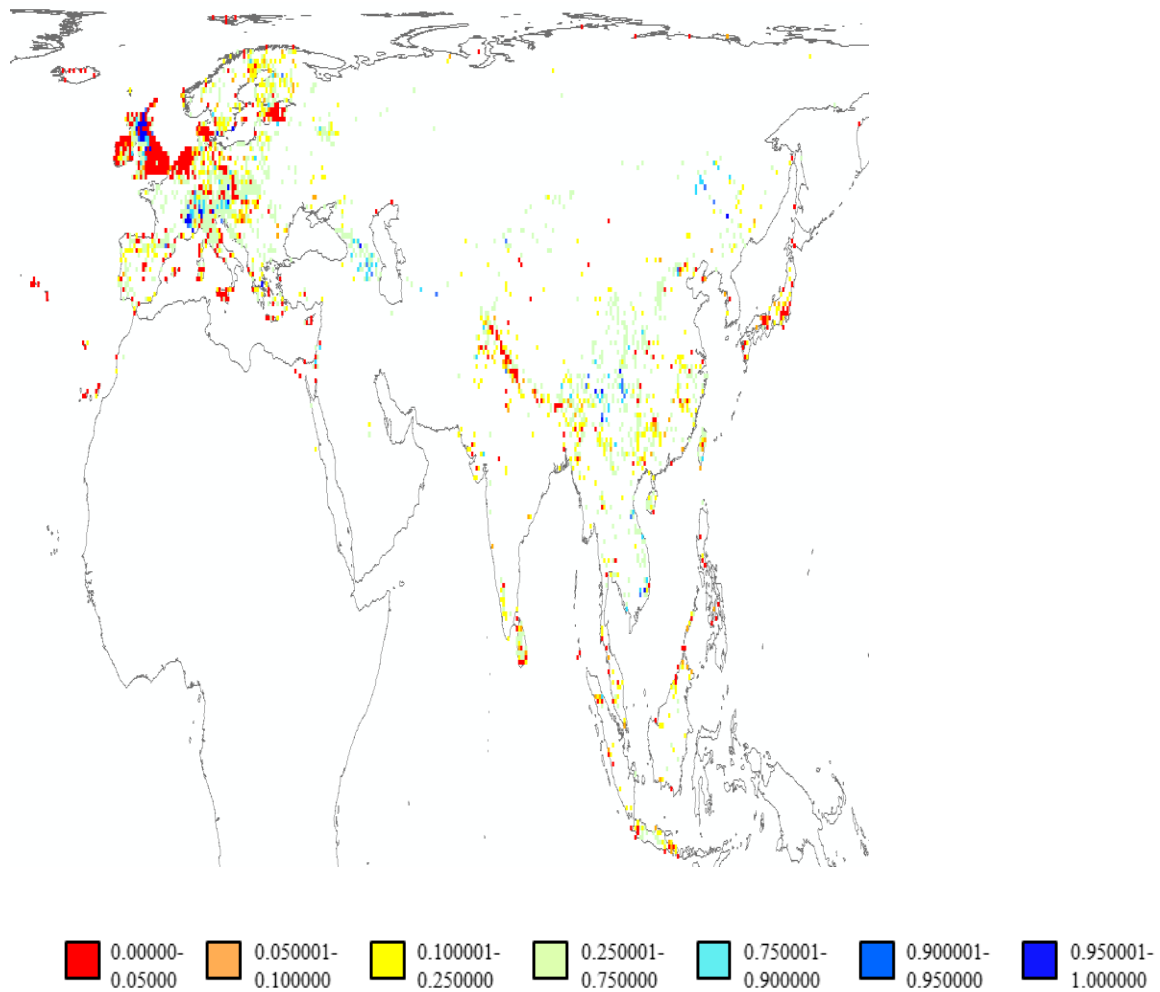


Figure 4. Relative extinction rates ( $1 - u_j$ ) against species' geographic range size and coloured by the edge-proneness of species' extinctions ( $v_j$ ), with positive values indicating that extinctions are concentrated towards the range centre. Note that  $u_j$  and  $v_j$  are both estimated as departures from the overall relationships shown in Figure 2. Figure 1

