Rarity and conservation status do not predict vertebrate population trends

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Data accessibility statement:

We will make all R code for the analyses and data publicly available on GitHub and will include the relevant DOIs and links.

Abstract

Species' attributes such as rarity and conservation status are often assumed to predict population change which in turn can influence conservation decision-making; however, there are very few empirical tests across taxa and biomes. We use a database of 9284 vertebrate populations from 2084 species in the UK and globally to quantify population change across rarity, Red List status, biomes and taxa. In the UK, rarity metrics (geographic range, population size and habitat specificity) did not explain trends, but greater fluctuations were more likely for smaller populations. There was no consistent pattern of net declines with increasing Red List status in the UK and globally. We found taxonomic but not geographic patterning of population change at global scales. Our findings suggest that rarity metrics and conservation status are poor predictors of vertebrate population trends, but that rare species were nevertheless more likely to fluctuate, potentially increasing their extinction risk.

Introduction

Species' attributes such as rarity, conservation status, distribution and taxon are often assumed to predict variation in extinction risk (Purvis *et al.* 2000; Olden *et al.* 2007; Fritz *et al.* 2009; Ripple *et al.* 2017) and in population change (Julliard *et al.* 2004; Shultz *et al.* 2005). Population trends (Hutchings & Reynolds 2004) and population fluctuations (Melbourne & Hastings 2008) have both been frequently linked with a higher likelihood of a species' extinction. For decades, conservation efforts have focused on protecting rare species (Pigott 1977; Gunn 1980; Longton & Hedderson 2000; Povilitis 2001; Gaston & Fuller 2008), those with restricted geographic extents, small population sizes or high habitat specificity, as these species are thought to be more likely to be threatened with extinction. However, there are very few empirical tests of the influence of rarity and conservation status on population change and extinction risk (e.g., Purvis *et al.* 2000; O'Grady *et al.* 2004; Ripple *et al.* 2017), and those that exist mostly focus on either specific taxa (Jones *et al.* 2003; Cardillo *et al.* 2004; Fritz *et al.* 2009) or on population declines alone (Purvis *et al.* 2000; Fritz *et al.* 2009; Gilroy *et al.* 2016; Hefley *et al.* 2016; Ceballos *et al.* 2017), and not population change across taxa and geographic regions. Quantifying the variation in trends and fluctuations of populations around the world can provide valuable insight for conservation policy and decision-making by testing the processes that ultimately lead to community reassembly (Batt *et al.* 2017) and by determining the drivers of population change (Ehrlén & Morris 2015; Hefley *et al.* 2016).

Understanding what factors best explain population change and extinction risk across species has been a key focus in population ecology and conservation biology, with possible measures including species' attributes and traits, such as rarity (Gaston &

Blackburn 1995; Owens & Bennett 2000; Purvis *et al.* 2000; Cardillo *et al.* 2004; O'Grady *et al.* 2004; Olden *et al.* 2007; Collen *et al.* 2009; Ripple *et al.* 2017). Extinction risk, the likelihood that a species will go extinct within a given time frame (Mace *et al.* 2008), is widely assumed to increase when species are rare (i.e., they have small geographic ranges (Jones *et al.* 2003), small population sizes (Green 2003) and are very specialized (Gilroy *et al.* 2016)). Rare species with small populations are more likely to undergo stochastic fluctuations that could lead to extinction at any given point as per population dynamics theory (Lande 1993; Melbourne & Hastings 2008). Population declines can lead to local and eventually potentially global species extinction (Ceballos *et al.* 2017). Small populations are also more vulnerable to demographic stochasticity and inbreeding (Kareiva 1990; Hanski 1998). Allee effects, the positive relationship between population growth rate and population density, further increase the likelihood of declines due to lack of potential mates and low reproductive output once populations reach a critically low density (Dennis *et al.* 2016; Sun 2016). Thus, small populations from rare species are thought to be more likely to experience population declines (McKinney 1997; Purvis *et al.* 2000; Manne & Pimm 2001; Hutchings & Reynolds 2004).

Investigating population change over time in relation to rarity can provide insights into species' extinction risk. Rabinowitz (1981) defined 'seven forms of rarity' based on the combinations of the extremes of three characteristics: geographic range (small vs. large), habitat specificity (generalist vs. specialist), and local population size (small vs. large). Rarity can be either a state in which species naturally occur, or a state to which they are driven following external perturbations to populations (Magurran & Henderson 2003). However, previous analyses of the influence of rarity

101 on population trends and extinction risk have shown mixed results. Geographic range
102 did not correlate with species' vulnerability to extinction in 45 bird and mammal taxa
103 from all continents except Antarctica (O'Grady *et al.* 2004) and the minimum viable
104 population size did not vary with geographic range and population size in 629
105 invertebrate, 529 vertebrate and 30 plant species (Brook *et al.* 2006). In contrast, in
106 bats, geographic range was found to be the most important predictor of extinction risk
107 (Jones *et al.* 2003). Thus, a generalizable relationship between rarity and population
108 declines and increased extinction risk across taxa and geographic regions remains
109 unquantified. However, simplifying the concept of rarity so that it can be modelled as
110 a predictor of population change remains a considerable challenge (Magurran 2013;
111 Batt *et al.* 2017).
112
113 Investigations of potential factors that predispose species to population change
114 across geographic and taxonomic scales (e.g., from country to biome level, and from
115 population to taxa level) are particularly valuable for guiding conservation decision-
116 making (O'Grady *et al.* 2004; Ehrlén & Morris 2015; Hefley *et al.* 2016; Batt *et al.*
117 2017). Conservation actions are predominantly implemented on smaller, country-
118 specific, regional or local scales (Mills *et al.* 2010; Guerrero *et al.* 2013), yet policy
119 may be determined for larger regions or broader taxonomic groups (Agardy 2005;
120 Pressey *et al.* 2007). Similarly, overall species' Red List status is determined on a
121 global scale based on multiple criteria (Mace *et al.* 2008), but on a local scale,
122 populations may vary in the direction and magnitude of experienced change (Ehrlén
123 & Morris 2015; Lawson *et al.* 2015; Gilroy *et al.* 2016; van Strien *et al.* 2016; Leung *et*
124 *al.* 2017). Population time-series data from the Living Planet Database (LPD),
125 complemented by extensive occurrence data from the Global Biodiversity Information

Facility (GBIF) and information on species habitat preferences and conservation status from the IUCN Red List, provide a unique opportunity to test which species attributes explain global and country-specific population trends.

Here, we addressed the research question: Is variation in vertebrate population change explained by differences in species attributes, such as rarity metrics and conservation status? We investigated two types of population change – population trends and population fluctuations. We combined open source data from the LPD, GBIF and IUCN to examine population change in the UK, a country with high-quality monitoring and abundance data, and global population change across species' Red List status, biomes, systems (freshwater, marine, terrestrial) and taxa. We considered rarity to be the state in which species exist if their geographic range is small vs. large, their local population size is low vs. high, or they are habitat generalists vs. specialists. Thus, we quantified rarity through these three individual metrics - geographic range extent, mean population size, habitat specificity, and additionally species' Red List status. We tested the following hypotheses: (1) in the UK, rare species are more likely to be experiencing negative population trends than common species; (2) on a global scale, declining populations are more likely for species from more threatened Red List categories, (3) there are geographic and taxonomic patterns in vertebrate population trends and fluctuations (e.g., hotspots of declines, increases or fluctuations in abundances in specific regions and in specific taxa) and (4) rare species or those with a higher Red List status are more likely to experience greater population fluctuations.

Methods

Population data

To quantify vertebrate population change, we extracted the abundance data of all populations monitored at more than five different time points from the LPD (LPI 2016), resulting in 9284 populations from 2084 species for our system, biome, taxa and conservation status analysis (global scale) and 508 populations from 237 species for our rarity analysis (UK scale, but note that habitat specificity data were only available for 402 populations from 206 species, Table S1). Monitoring duration differed among populations; however, in our analysis, we retained all populations that had at least five time points of monitoring data (Figures S1 and S2). Before analysis, we scaled the abundance of each population to a common magnitude between zero and one, because the populations were monitored using different metrics of abundance (e.g. population indices vs. number of individuals). This allowed us to explore trends among populations relative to the variation experienced across each time series.

Rarity metrics data

We defined rarity following a simplified version of the 'seven forms of rarity' model (Rabinowitz 1981), and thus consider rarity to be the state in which species exist when they have a small geographic range, low population size, or narrow habitat specificity. We combined publicly available data from three sources: (1) population records for vertebrate species from the LPD (LPI 2016), (2) occurrence data from the Global Biodiversity Information Facility (GBIF 2017), and (3) habitat specificity and Red List classification data for each species from the International Union for Conservation (IUCN 2017). Extracting the necessary data and calculating the rarity metrics was challenging and computationally-intensive, thus we did not estimate

rarity metrics for all species globally. Instead, we focused on analyzing rarity effects for species from the UK, a country with intensive and detailed biodiversity monitoring of vertebrate species.

To estimate range, we calculated a km^2 square occurrence area for each UK vertebrate species with available population data in the LPD based on the maximum and minimum latitudes and longitudes of species' GBIF occurrence data cleaned for outliers by excluding records at sea for terrestrial species and records on land for marine species (GBIF 2017, accessed between Feb 2016 and Apr 2017). Latitude-longitude polygons were transformed to km^2 using the WGS84 Coordinate Reference System (CRS) from the package *geosphere* (Hijmans 2016). We did not use IUCN range maps, as they were not available for all of our study species, and previous studies using GBIF occurrences to estimate range have found a positive correlation between GBIF-derived and IUCN-derived geographic range (Phillips *et al.* 2017).

We calculated mean population size across the monitoring duration for each population using the raw population data. To create an index of habitat specificity, we extracted the number of distinct habitats a species occupies from the online IUCN profiles for our study species between Jan and Apr 2017 (IUCN 2017). We included both breeding and non-breeding habitats to determine distinct habitat preferences for each species (Table S2). We obtained global conservation status data for all study species through the IUCN Red List classification (IUCN 2017).

Population change modelling

As the first stage of our analysis, we modeled population change to produce a population trend (slope and variance of population change over time). We used state-space models that model abundance over time (freely-varying intercept) to calculate the amount of overall population change experienced by each population (*mu*), following Dennis *et al.* (2006) and Humbert *et al.* (2009). State-space models account for process noise and observation error and thus deliver reliable estimates of population change when working with large datasets where records were collected using different approaches (Knape *et al.* 2011; Pedersen *et al.* 2011; Leung *et al.* 2017). Not accounting for process and measurement error could lead to over-estimation of population declines (Rueda-Cediel *et al.* 2018). Positive *mu* values indicate population increase and negative *mu* values indicate population decline. We calculated the error around *mu* for each population ((upper 95% confidence limit – lower 95% confidence limit) / 2), with larger errors indicating populations that have experienced more fluctuations (variance in abundance metrics) overtime.

Population trends across rarity metrics and species' Red List status in the UK

To test the influence of rarity metrics (geographic range, mean population size and habitat specificity) and species' Red List status on variation in population trends in the UK, we conducted a second stage analysis using four Bayesian linear models (one per metric) based on Markov Chain Monte Carlo Bayesian inference (Hadfield 2010). The response variable was population trend (*mu* values from state-space models), and fixed effects were geographic range (log transformed), mean population size (log transformed), habitat specificity (number of distinct habitats occupied) and Red List status (categorical). We used weakly informative priors for all coefficients (an inverse Wishart prior for the variances and a normal prior for the fixed effects),

225 and we refer to predictors as ‘significant’ when the 95% credible interval for the
226 corresponding parameter in the fitted models did not overlap zero. We did not include
227 random effects in the Bayesian models (e.g., a species or region random intercept),
228 because only a very small proportion of the studied species had more than three
229 monitored populations and spatial replication was low (Table S1).
230
231 *Global population trends across species’ Red List status*
232 To investigate the relationship between population trends and species’ Red List
233 status on a global scale, we modelled population trends from the first stage of the
234 analysis (state-space models) as a function of Red List status using a Bayesian linear
235 model.
236
237 *Global population trends across latitude, biomes, systems and taxa*
238 To investigate the geographic and taxonomic patterns of population trends, we
239 estimated population trend from the first stage of the analysis (state-space models)
240 as a function of (1) latitude and biome (as defined by the ‘biome’ category in the LPD,
241 e.g. ‘temperate broadleaf forest’, Olson & Dinerstein 2002), (2) system (freshwater,
242 marine, terrestrial), and (3) taxon (*Actinopterygii*, bony fish; *Amphibia*, amphibians;
243 *Aves*, birds; *Mammalia*, mammals; *Reptilia*, reptiles). Each categorical model from
244 this second stage of our analyses was fitted with a zero intercept to allow us to
245 determine if net population trends differed from zero for each of the categories under
246 investigation.
247
248 *Population fluctuations across systems, taxa, Red List status and rarity metrics*

To test whether rare species fluctuate more than common species and whether there is geographic and taxonomic patterning in population fluctuations, we modelled the error around *mu* (half of the 95% confidence interval) as a response variable across systems, taxa, Red List status and rarity metrics.

Monitoring duration and units

To assess the influence of monitoring duration on population trends, we used a Bayesian linear model (Figures S1 and S2). We modelled population trend (*mu*) as a function of monitoring duration (years) for each population, fitted with a zero intercept, as when duration is zero, no population change has occurred. The units of population monitoring across the LPD varied with 1368 different categorical levels (e.g., population index, nest counts, numbers of individuals). Variation in population trends were not explained by sampling method across the five most commonly used units (Figure S3). We estimated population change using state-space models specifically because of their suitability for analyses of large databases where records were derived using different methods (Humbert *et al.* 2009; Leung *et al.* 2017).

Comparison of modelling approaches

We conducted the following supplementary analyses: in the second-stage Bayesian models estimating population trends across systems, biomes, taxa and rarity metrics, 1) we weighed *mu* values by the square of *tau*, the observation error estimate derived from the state-space models, 2) we used slopes of linear model fits of abundance (scaled at the population level) instead of the *mu* estimates from state-space models, 3) we modelled the standard error around the slope values of the linear models and the standard deviation of the raw population data for each time-series as additional

metrics of population fluctuations. All different analytical approaches yielded very similar results (see main text and Figures S6 and S7, Table S3).

All statistical analyses were conducted using R (version 3.4.2, R Core Team 2017). Code and data are publicly available on GitHub (link to be added at time of publication).

Results

Population trends across rarity metrics and species' Red List status in the UK

Across monitored vertebrate populations in the UK, species with smaller ranges, smaller population sizes, or narrower habitat specificity (i.e. rare species) and species with more threatened Red List status were not more prone to population declines than common species (Figure 1a-f, Table S3). Over the monitoring duration for each population, species classified as least concern and near threatened had a positive population trend (LC: slope = 0.01, CI = 0.005 to 0.02; NT: slope = 0.03, CI = 0.01 to 0.05), whereas vulnerable, endangered and critically endangered populations did not experience directional change (Figure 1d, f and Table S3). For example, one monitored colony for the common species grey seal (*Halichoerus grypus*) in Scotland increased by 158% over a 17-year period going from 25,824 to 66,522 individuals; whereas, a population of the vulnerable species Atlantic horse mackerel (*Trachurus trachurus*) remained stable across a 21-year monitoring period.

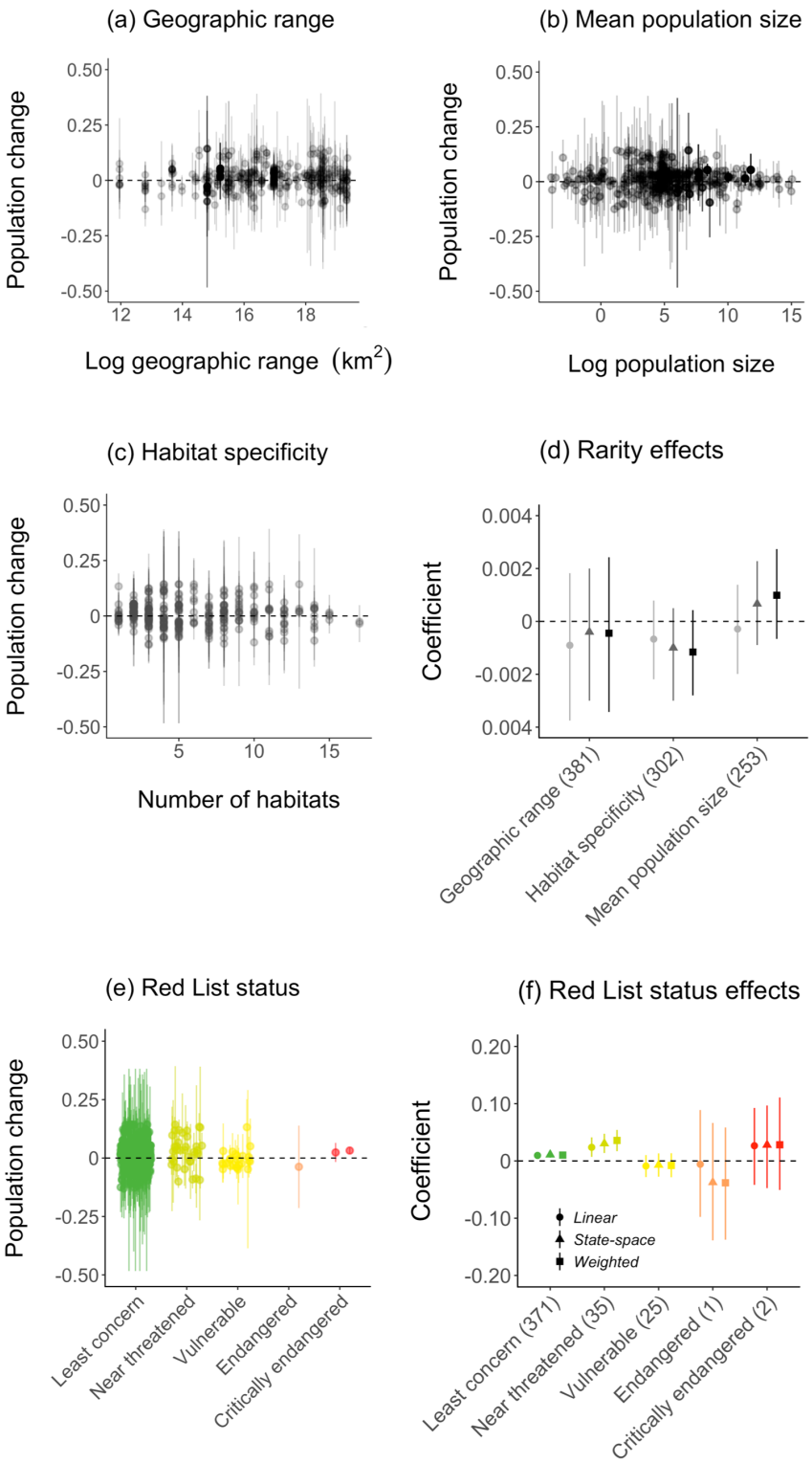

Figure 1. Effects of rarity metrics (geographic range, mean population size and habitat specificity, plots a-d) and of Red List status (plots e and f) on population trends of UK species. Results include 508 populations from 237 species in the UK. The *mu* values (plots a-c, e) are state-space model fits of changes

in abundance over the monitoring duration for each population. Effect sizes (plots d and f) are population trends calculated using state-space and linear models, and population trends (*mu*) weighted by *tau*, the observation error estimate from the state-space models. Error bars show confidence intervals around population trend (*mu,* plots a-c, e) and credible intervals for *mu* across rarity metrics and Red List status (plots d and f). The numbers on the x axis show the sample size in each category (plot d, e, f). See Table S3 for full model outputs.

Global analysis of population trends across Red List status

Globally, we found increasing, decreasing and stable populations across all Red List categories of conservation status. For example, a population of the least concern species red deer (*Cervus elaphus*) in Canada declined by 68% over 7 years going from 606 to 194 individuals and a population of the critically endangered Hawksbill sea turtle (*Eretmochelys imbricate*) from Barbados increased by 269% over 7 years going from 89 to 328 individuals. Populations from least concern species were more likely to increase (slope = 0.006, CI = 0.005 to 0.007), whereas populations from vulnerable and endangered species did not experience net directional change (Figure 2a). Populations from near threatened and critically endangered species were more likely to decline (NT: slope = -0.005, CI = -0.01 to -0.001; CR: slope = -0.01, CI = -0.02 to -0.001). Across all categories, there was no consistent pattern of greater population declines with increasing Red List status (Table S3). Most of the populations in the LPD that were monitored at more than five time points were from species categorized as least concern (Figure 2b).

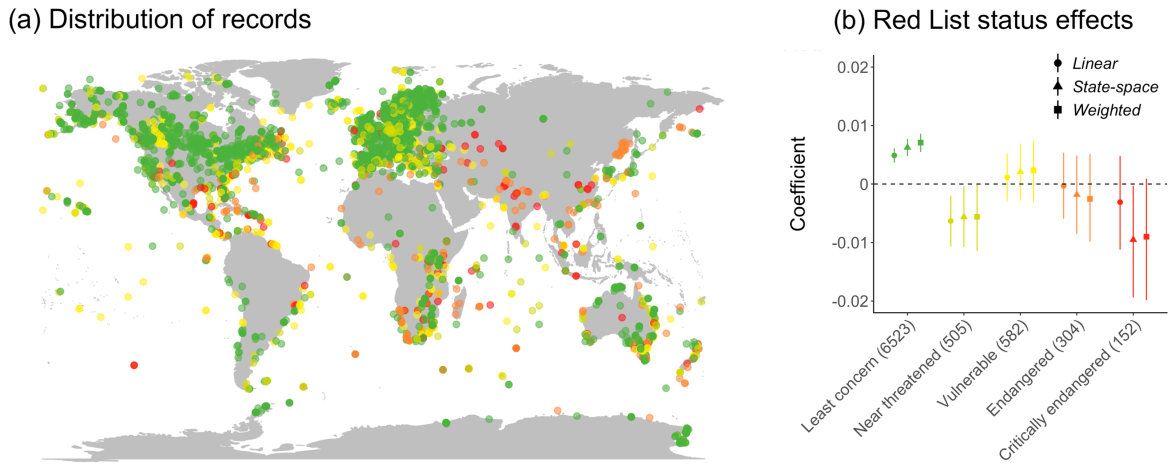

Figure 2. Distribution of population records by Red List status (plot a) and global vertebrate population trends across species' Red List status (plot b). Results include 8064 populations from 1702 species. Effect sizes (plot b) include the population trend (*mu*) calculated using state-space and linear models, and population trend (*mu*) weighted by *tau*, the observation error estimate from the state-space models. The numbers on the x axis show the sample size in each Red List category (plot b). Error bars show 95% credible intervals (plot b). See Table S3 for full model outputs.

Global population trends across latitude and biomes

Global vertebrate population trends did not show distinct geographic patterning, as increasing, stable and declining populations were present on all continents and across all latitudes (Figure 3a and b). Populations in Mediterranean forests, montane grasslands, polar freshwaters, temperate wetlands, tropical forests and tropical coral biomes were more likely to increase, whereas populations from the remaining studied biomes were not more likely to be increasing versus decreasing (Figure 3c and Table S3). The lack of biogeographic patterning in vertebrate population trends was also apparent on a UK scale (Figure S4 and Table S3).

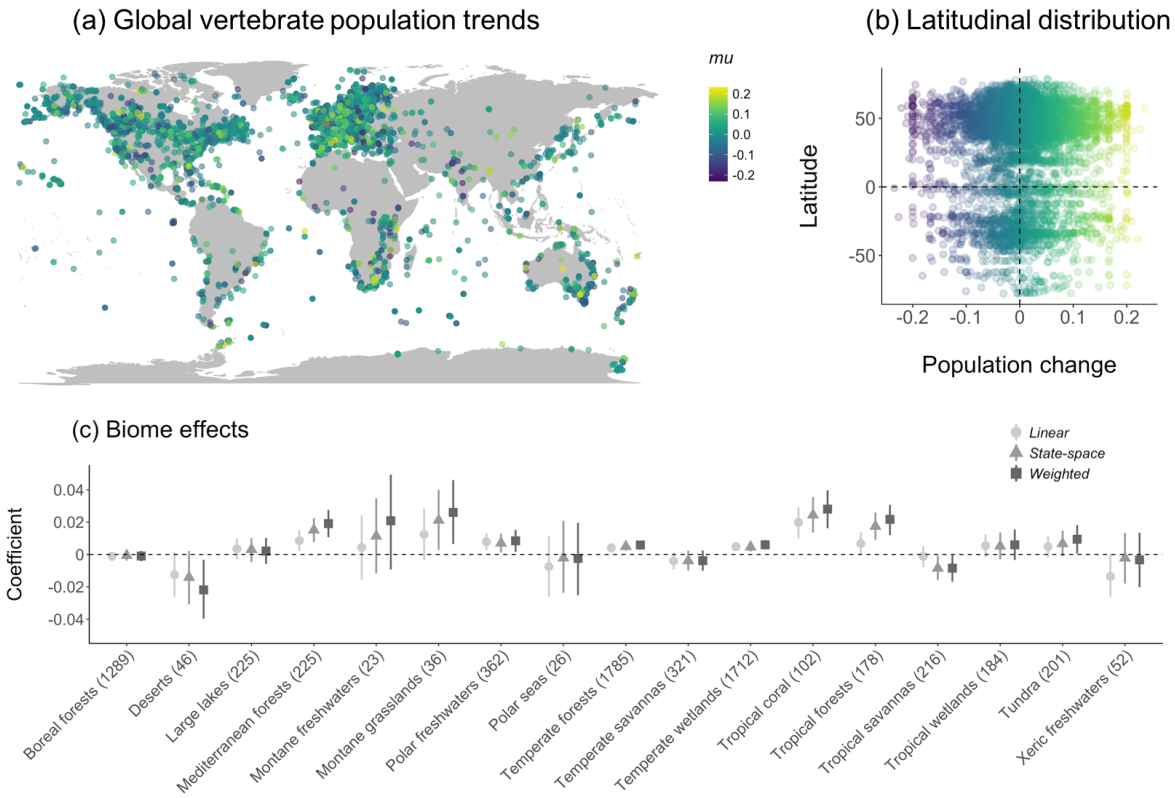

Figure 3. Lack of biogeographic patterning in global vertebrate population trends (plot a), latitudinal distribution of population trends (plot b), and population trends across biomes (plot c). Results include 9284 populations from 2084 species. Effect sizes (plot c) include population trend (*mu*) calculated using state-space and linear models, and population trend (*mu*) weighted by *tau*, the observation error estimate from the state-space models. The numbers on the x axis show the sample size for each biome category (plot c). Error bars show 95% credible intervals (plot c). See Table S3 for full model outputs.

Global population trends across systems and taxa

Globally, monitored vertebrate populations experienced population increases in all three studied systems (freshwater slope = 0.005, CI = 0.002 to 0.01; marine slope = 0.004, CI = 0.002 to 0.01; terrestrial slope = 0.003, CI = 0.001 to 0.005, Figure 2a-b,

Table S4). In freshwater and terrestrial habitats, there was a bimodal distribution of population change (Hartigans' dip test, $D = 0.04$, $p < 0.01$, Figure S5a). Amphibian populations were more likely to decline (slope = -0.01, CI = -0.02 to -0.005), whereas birds, mammals and reptiles were more likely to increase (slope = 0.004, CI = 0.003 to 0.01; slope = 0.01, CI = 0.01 to 0.01; slope = 0.02, CI = 0.01 to 0.02). Bony fish were not more likely to increase or decline (slope = -0.001, CI = -0.004 to 0.002). The distribution of *mu* values in bird populations was bimodal (Hartigans' dip test, $D = 0.04$, $p < 0.01$, Figure S5b).

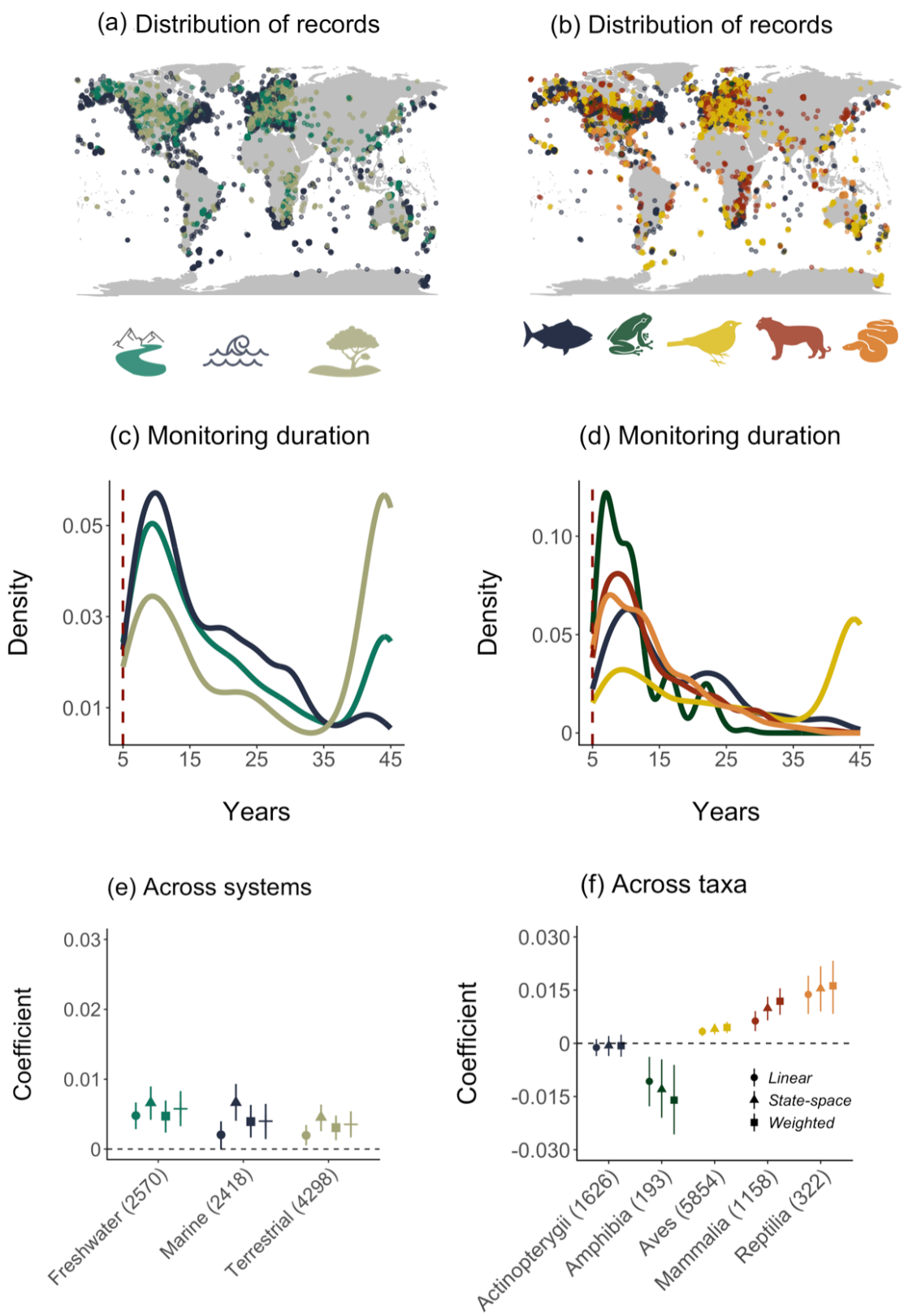

Figure 4. Distribution of records across (plot a) freshwater, marine and terrestrial systems and (plot b) bony fish, amphibians, birds, mammals and

reptiles, monitoring duration (plots c and d) and their respective population trend (*mu*) effect sizes (plots e and f). Results include 9284 populations from 2084 species. Effect sizes are population trend (*mu*) calculated using state-space and linear models, and population trend (*mu*) weighted by *tau*, the observation error estimate from the state-space models (plots e and f). The numbers on the x axis show the sample size for each taxa category (plots e and f). Error bars show 95% credible intervals (plots e and f). See Table S3 for full model outputs.

Population fluctuations across systems, taxa, Red List status and rarity metrics

Global population fluctuations (variation in population abundance over time) did not show distinct geographic patterning (Figure 5a-b). Populations that experienced more fluctuations had a smaller mean population size (slope = -0.008, CI = -0.01 to -0.004) and were more likely to be generalists in their habitat preferences (slope = 0.005, CI = 0.001 to 0.01, Figure 5c). On a global scale, population fluctuations were more common with increasing Red List status (LC: slope = 0.11. CI = 0.11 to 0.12; CR: slope = 0.17, CI = 0.15 to 0.19, Figure 5d, see Table S3 for all model outputs). Across the three studied systems, terrestrial populations experienced lower population fluctuations (slope = 0.10, CI = 0.10 to 0.11, Figure 5e). Across taxa, fluctuations were most common for amphibian populations (slope = 0.22, CI = 0.20 to 0.23, Figure 5f).

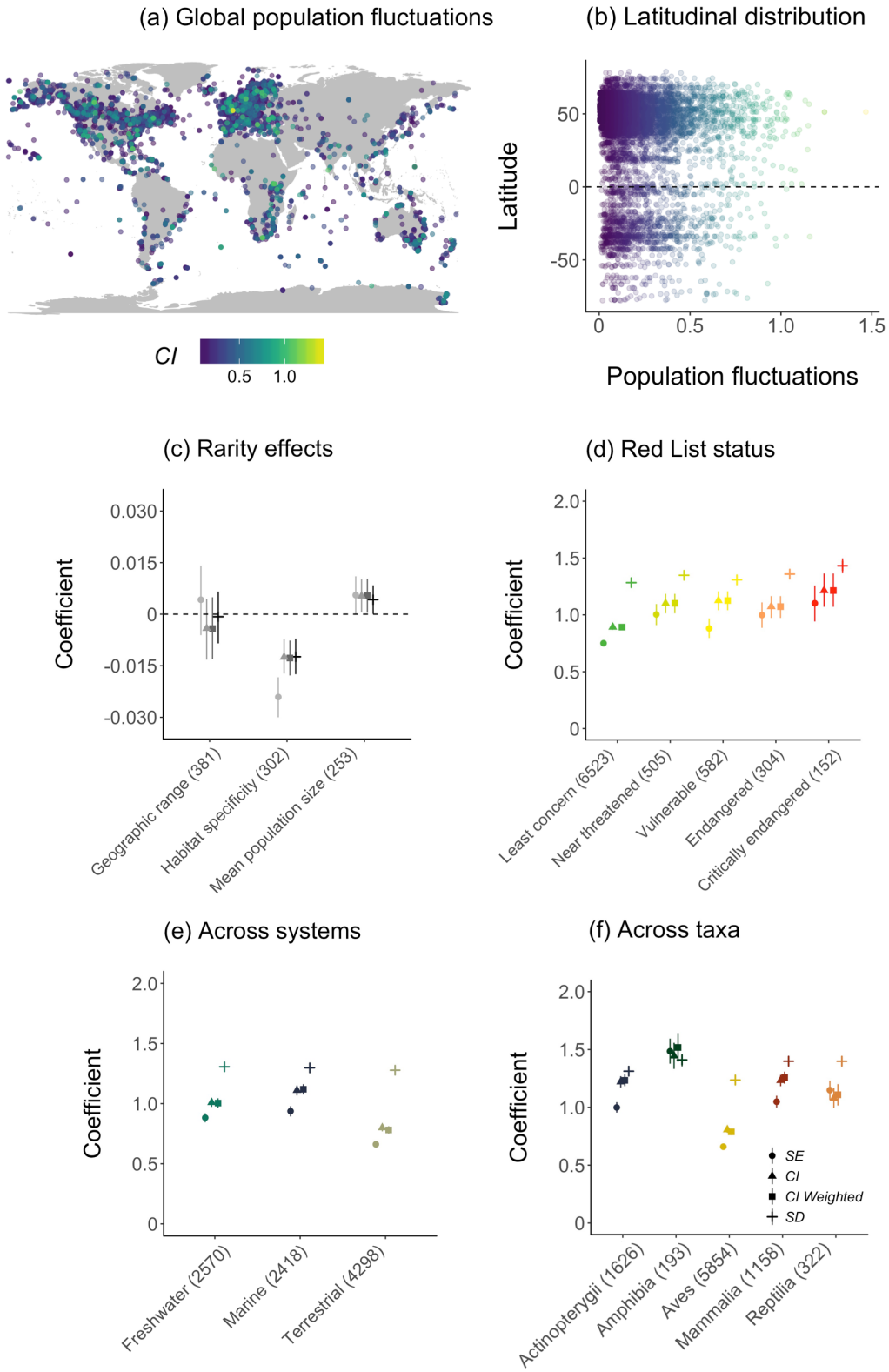

Figure 5. Global population fluctuations in vertebrate species (plot a) across latitude (plot b), rarity metrics (UK scale, plot c), Red List status (global scale, plot d), systems (plot e) and taxa (plot f). Results include 508 populations from

237 species in the UK and 9284 populations from 2084 species globally. The response variables in the models were: 1) the standard error around the slope estimates of the linear model fits of abundance versus year, 2) half of the 95% confidence interval around the *mu* value of population change, 3) half of the 95% confidence interval around *mu* weighted by *tau*, the observation error estimate from the state-space models, and 4) the standard deviation of the raw data for each population time-series. Larger errors indicate more population fluctuations. Effect size coefficients (c-f) were standardized by dividing the effect size by the standard deviation of the corresponding input data. Error bars show 95% credible intervals (c-f). See Table S3 for full model outputs.

Global population trends across monitoring duration

Monitoring duration was weakly positively related to vertebrate population trends, with slightly more increasing populations found for longer duration studies (Figure S6, Table S3).

Discussion

Across monitored vertebrate populations in the UK, rarity metrics (geographic range, population size and habitat specificity) and species' Red List status did not explain variation in population trends (Figures 1 and 2). There was no consistent pattern of greater population declines with increasing Red List status in either the UK or globally (Figures 1e,f and 2). There was no biogeographic patterning of population trends and fluctuations, as populations increased, remained stable and declined across different biomes on all continents (Figure 3). Among taxa, birds, mammals and reptiles increased, bony fish did not experience net directional change and amphibians were

418 the only taxon with overall declines, as well as the taxon that experienced the most
419 population fluctuations (Figures 4-5). Fluctuations were more likely for species with
420 smaller population sizes and broader habitat preferences (Figure 5). Our findings do
421 not support the application of rarity metrics as generalizable predictors of population
422 trends in well-monitored vertebrate populations, but rare species were nevertheless
423 more likely to fluctuate, potentially increasing their extinction risk.
424
425 *Population change across rarity metrics and species' Red List status*
426 The power of rarity metrics and Red List status to explain population trends could be
427 mediated by the type of threats to which populations are exposed (Schemske *et al.*
428 1994), as well as whether species are naturally rare, or have become rare due to
429 external drivers in recent time (de Lange & Norton 2004; Robbirt *et al.* 2006; Harrison
430 *et al.* 2008). Geographic range, population size and habitat specificity may be of
431 lesser importance in human-dominated landscapes where threats such as habitat
432 change, pollution and exploitation are more prevalent (Newmark 1996; Purvis *et al.*
433 2000; O'Grady *et al.* 2004; Brook *et al.* 2006, Sullivan *et al.* 2016 but see Owens &
434 Bennett 2000 and Julliard *et al.* 2004). For UK vertebrate populations, the lack of
435 rarity effects on population trends (Figure 1) could be related to urbanization,
436 intensive land management and to the high investment in conservation (Keith *et al.*
437 2015), which may be contributing to the observed increases in species classified as
438 near threatened by the IUCN (Figure 1f). Populations with smaller mean population
439 size experienced more fluctuations (Figure 5c), which is in line with population
440 dynamics theory, suggesting that even though rarity metrics did not predict
441 population trends, they might still be good indicators of extinction risk, as greater

fluctuations could in time lead to extinction (Lande 1993; Melbourne & Hastings 2008).

Global population change across Red List status

Across all Red List status categories, there was no consistent pattern of net declines with increasing threat (Figure 2). Populations from vulnerable and endangered species did not experience directional change, suggesting that local scale conservation actions might have stabilized populations for species which are declining on a global scale (Saterson *et al.* 2004; Vickery *et al.* 2004; Gillings *et al.* 2005; Hoffmann *et al.* 2010). The threats and mitigation actions to which populations with more threatened Red List statuses are exposed on a local scale are likely heterogeneous across different biomes (Pereira *et al.* 2012; Maxwell *et al.* 2016). The finding that populations from species with higher Red List status were more likely to fluctuate (Figure 5d) relates to one of the Red List criteria – number of breeding individuals (Mace *et al.* 2008). Because of Allee effects, extinction risk is higher when there are very few breeding individuals (Dennis *et al.* 2016; Sun 2016). Thus, although we did not find evidence to support the hypothesis that species with a higher Red List status are more likely to be declining, those populations did experience higher population fluctuations, suggesting that species of concern might still have a higher risk of extinction.

Global population change across latitude, biomes and systems

Global vertebrate population trends varied among taxa but did not show distinct geographic patterning (Figures 3-4). Some biomes like Mediterranean forests were more likely to include increasing populations, whilst populations in other biomes did

467 not experience directional population change (Figure 3 and Table S3). Similar
468 heterogeneity in the patterns of population trends across habitats has been
469 documented in the Netherlands (van Strien *et al.* 2016) and in temperate North
470 America and Europe (Leung *et al.* 2017) also using the LPD, suggesting that local
471 scale environmental factors or proximity to anthropogenic drivers of change may be
472 better predictors of population trends (Brook *et al.* 2006; Fritz *et al.* 2009, but see
473 Phillips *et al.* 2017). The lack of distinct geographic patterning of population
474 fluctuations around the world (Figure 5a, b and e) suggests that these well-monitored
475 vertebrate populations are likely influenced by both stochastic and deterministic
476 processes (Kareiva 1990; Lundberg *et al.* 2000). Our findings go beyond previous
477 studies (Ceballos *et al.* 2017; Davidson *et al.* 2017) by quantifying the full spectrum of
478 population change, including positive, negative and stable trends and fluctuations
479 (Figures 3-5), which is critical for disentangling the pathways from population change
480 to biodiversity change (Primack *et al.* 2018; Yoccoz *et al.* 2018).
481
482 *Global population change across taxa*
483 Taxon-specific factors including reproductive strategy, trophic level, generation time,
484 life history traits (Purvis *et al.* 2000; Cardillo *et al.* 2004), or sampling effects
485 (Magurran *et al.* 2010) could explain why some taxa were more likely to increase
486 (birds, mammals and reptiles), whereas others were more likely to decline
487 (amphibians) or remain stable (bony fish), (Figure 4 and Table S3). Amphibians were
488 the only taxa to experience net population declines as well as greater population
489 fluctuations among monitored vertebrate species in the LPD (Figure 4f and 5f). The
490 global amphibian decline (Houlahan *et al.* 2000), also demonstrated with this dataset
491 at the temperate North American and European scale (Leung *et al.* 2017), has been

linked to the spread of a fungal disease (chytrid fungus, *Batrachochytrium dendrobatidis*), facilitated by global warming (Pounds *et al.* 2006), as well as habitat loss and Allee effects in small populations (Green 2003).

Study limitations

Our study is limited by three main factors: 1) the gaps in global monitoring of populations, 2) challenges in estimating geographic range and habitat specificity, and 3) overrepresentation of common species. The LPD under-represents populations outside of Europe and North America (Pereira & Cooper 2006; Proença *et al.* 2016; McRae *et al.* 2017) and includes different species abundance measures across populations that have been monitored for different durations (Figures S1, S2 and S6). The GBIF database includes sub-optimal representation of some species and occurrence outliers (Yesson *et al.* 2007; Boakes *et al.* 2010), despite being the largest international open source database of species locality data (Yesson *et al.* 2007). In addition, we used a static measure of geographic range, which does not account for changes in species distributions over time. For example, species could naturally have a small range or the small range size could be due to historic habitat loss (Magurran & Henderson 2003; Prendergast *et al.* 1993). In addition, UK populations included in the LPD are predominantly from species with wide geographic ranges (Table S4). The relationship between population change and geographic range could differ for highly endemic species with restricted distribution that are not monitored or included in the LPD dataset.

Conclusion

In summary, rarity metrics did not explain vertebrate population trends in the UK and

we did not find a consistent pattern of net declines with increasing Red List status in the UK and globally. We found taxonomic but not geographic patterning of population change around the world. Vertebrate populations experienced different magnitudes of net change and population fluctuations, which in the future may lead to shifts in community composition as some species become locally extinct and others expand into new habitats. Our findings caution the use of rarity metrics for the prediction of future global population trends, but suggest that such metrics are nevertheless indicators of population fluctuations, which might ultimately link to increased species extinction risk.

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Supplementary Information

Table S1. Number of species and populations included in analyses.

Scale	Analysis	Number of species	Number of populations	Number of species with >3 populations
UK	Geographic range	167	381	32
	Population size	112	253	19
	Habitat specificity	150	302	29
	Red List status	153	364	31
Global	System	2074	9284	834
	Biome	2074	9284	834
	Taxa			
	- *Actinopterygii*	544	1626	151
	- *Amphibia*	78	193	21
	- *Aves*	968	5852	538
	- *Mammalia*	306	1158	94
	- *Reptilia*	110	322	16
	Red List status	1702	8064	708
	Latitude	2074	9284	834
	Duration	2074	9284	834

759 **Table S2. Key used to determine habitat specificity for 194 species with**

760 **populations in the UK in the LPD.** We extracted the habitats in which each species

761 occurs from their IUCN profiles (http://www.iucnredlist.org/).

Habitat	Considered to be the same as:	Considered to be different to:
Rural park	Suburban park, urban park, rural garden, suburban garden, urban garden	
Lake	Big lake, small lake, pond, pool, dam, oxbow lake, reservoir	
Bog	Swamp, bogland	Lagoon
Coastal cliff	Island cliff	
Shingle beach	Pebble beach, rock beach	Sandy beach
Stream	River	Weir
Fruit Tree Plantation	Fruit Garden, orchard	
Thicket	Copse, grove, small stand	
Forest		Woodland
Glade	Forest Clearing	
Broadleaf	Deciduous	
Urban	Suburban	
River margin	Various types of river margins	
Tidal Creek		Estuary
Harbor	Dock, jetty, pier	
Bush lands	Shrublands	
Irrigation channel	Ditch	
Heath	Moorland	
Sandy beach	Spit, dune	Shingle beach, pebble beach, rock beach
Crag	Rocky outcrop, cliff, rocky slope	
Marsh	Wet meadow	
Islet	Island	

762

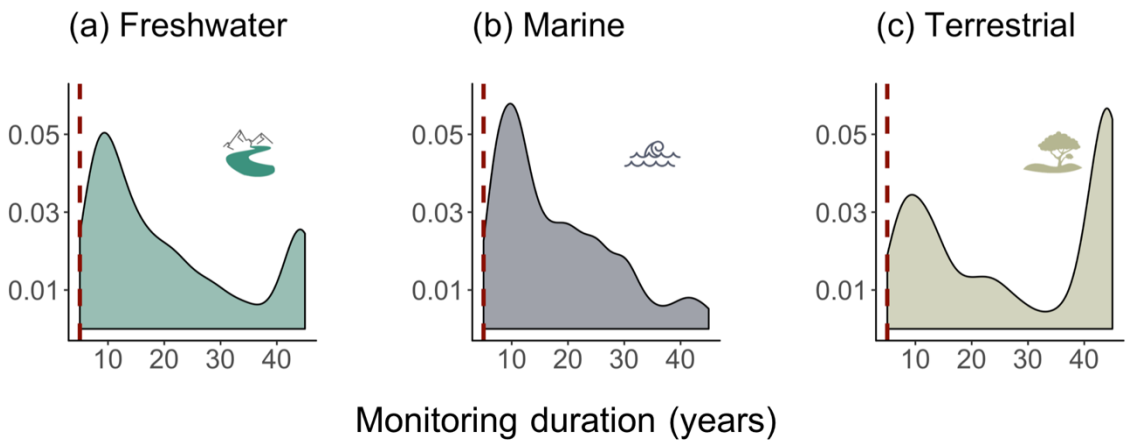

Figure S1. Distribution of monitoring duration across (a) freshwater, (b) marine and (c) terrestrial systems. Results include 9284 populations from 2084 species.

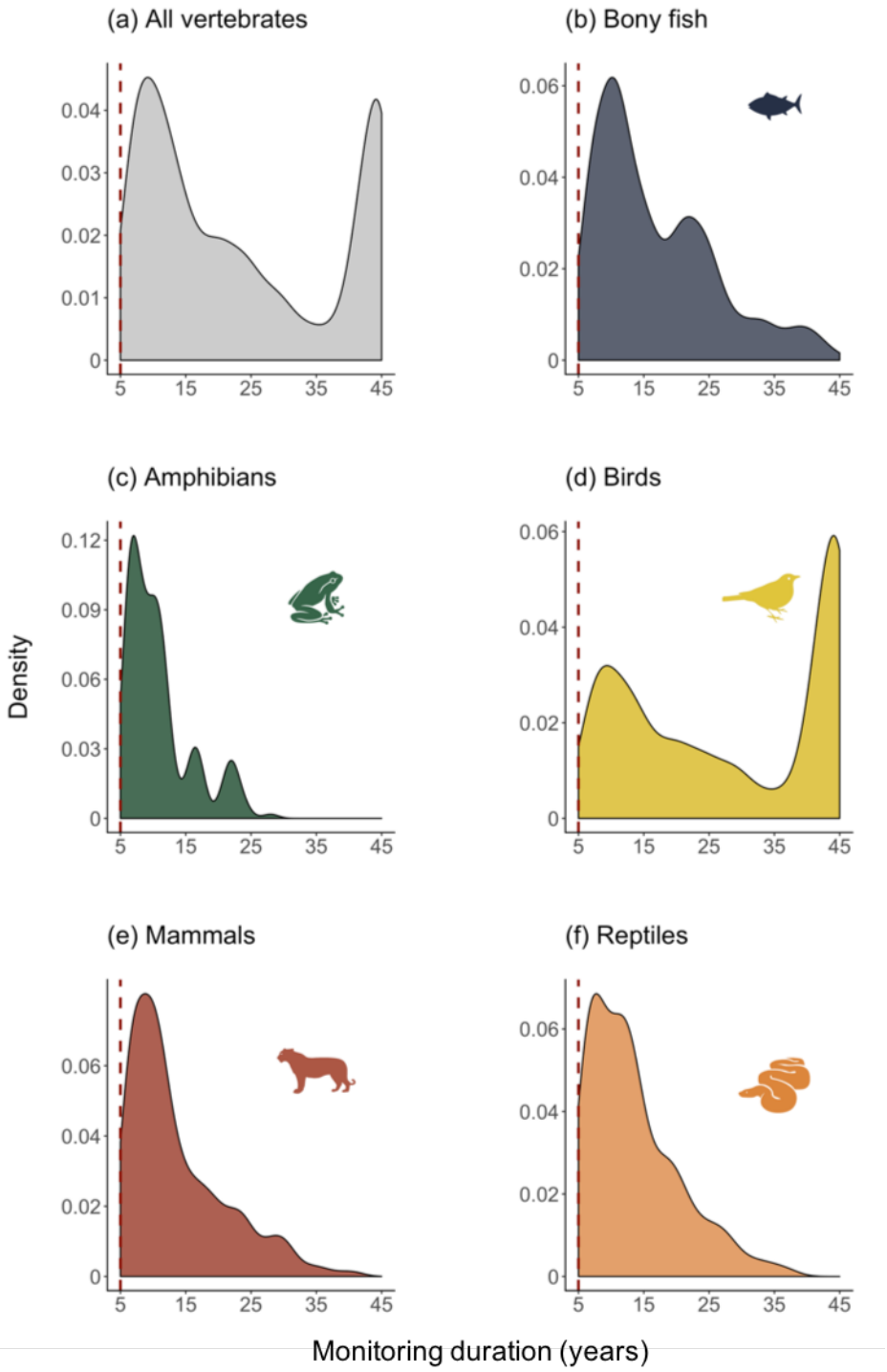

Figure S2. Distribution of monitoring duration across all monitored vertebrate populations (plot a), bony fish (plot b), amphibians (plot c), birds (plot d), mammals (plot e) and reptiles (plot f). See Table S1 for sample sizes of each group.

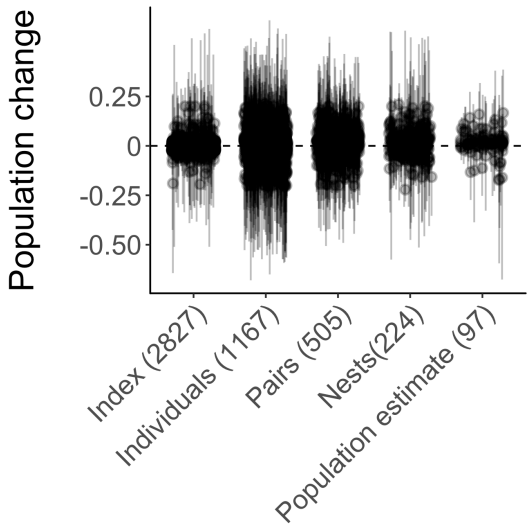

Figure S3. Population change (*mu* values from state-space models) across the five most commonly used units in the subset of the LPD we analyzed. Numbers on the x axis correspond to sample size in each category.

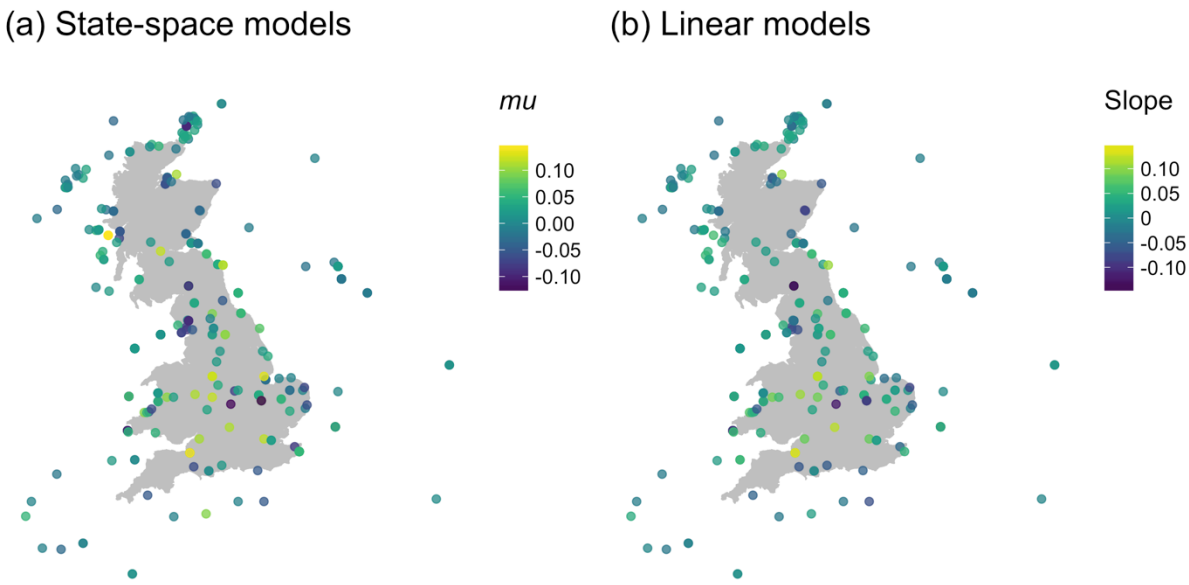

Figure S4. Geographic distribution of vertebrate population change in the UK, from state-space models (plot a) and linear models (plot b). Results include 508 populations from 237 species in the UK.

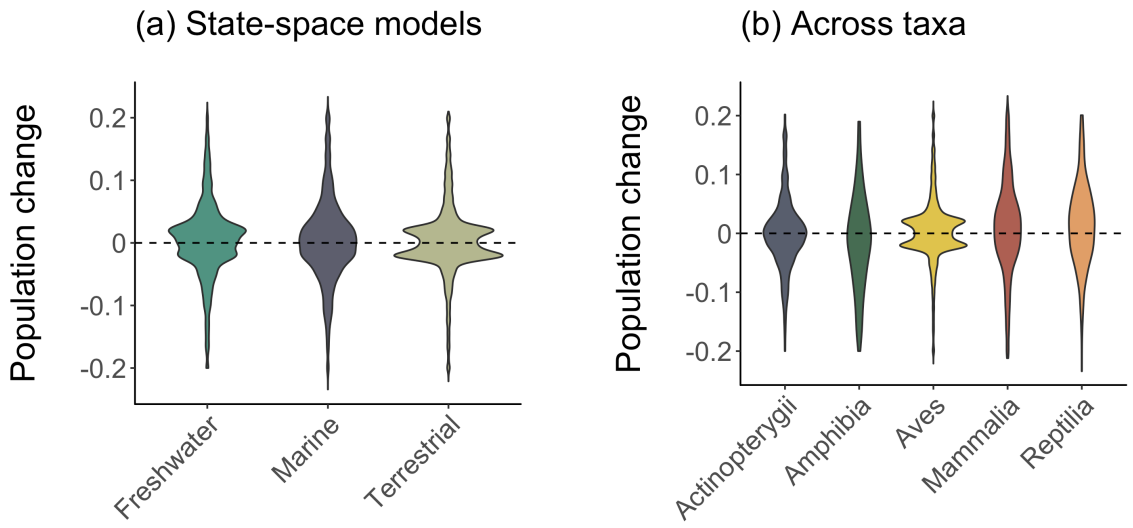

Figure. S5. Distribution of population change (*mu*) values from state-space models of vertebrate abundance over time across systems (plot a) and across taxa (plot b). See Table S1 for sample sizes.

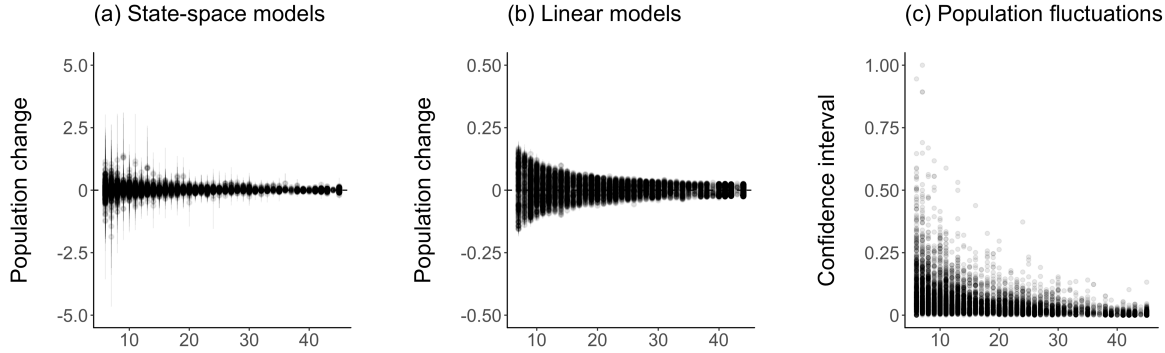

Figure S6. Vertebrate population trends across monitoring duration. Results are for 9284 populations from 2084 species. Population trends (*mu*) were estimated for all populations monitored for more than five time points using state-space models (plot a) and linear models (plot b). Population fluctuations (plot c) were estimated using the confidence interval (half of the 95% confidence interval) of the *mu* values (see also Figure 5). Error bars show 95% confidence intervals.

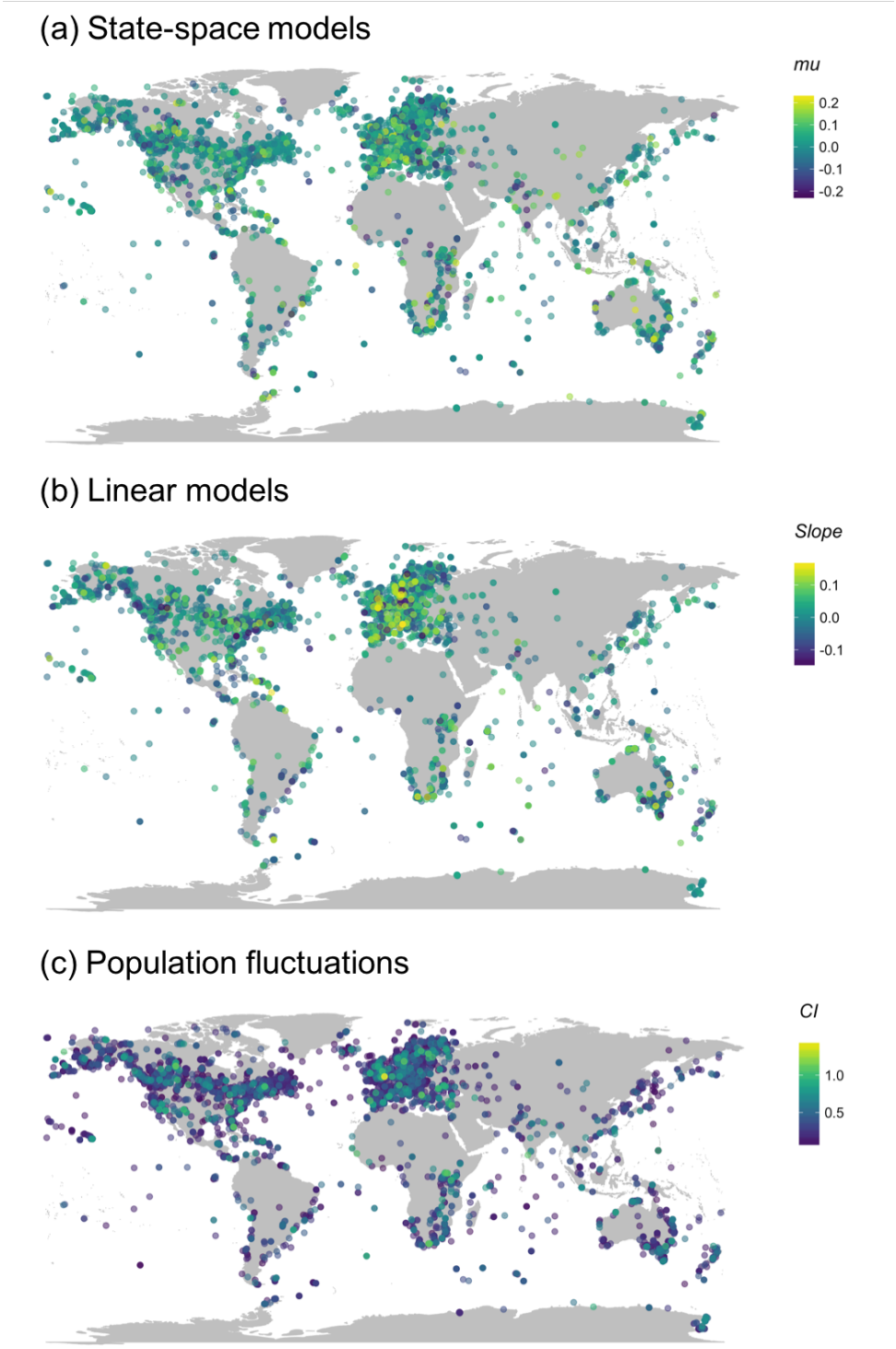

Figure S7. Geographic distribution of population change, calculated using state-space models (plot a), linear models (plot b), and using the confidence interval (half of the 95% confidence interval) of the *mu* values (plot c). Results include 9284 populations from 2084 species. Larger confidence intervals on (c) correspond to populations that have experienced more fluctuations.

Table S3. Model outputs from UK and global analyses. Sigma is the overall model residual variance. Net population change is estimated using *mu* values derived from state-space models of population abundance versus time and slopes of linear models of population abundance versus time. The weighted *mu* models included *mu* as a response variable, weighted by *tau*, the observation error estimate derived from the state-space models. The fluctuation models included half of the 95% confidence interval around the *mu* value of population change, the standard error around the slopes of linear models of population abundance versus time, and the standard deviation of the raw time-series data for each population. Larger confidence intervals correspond to populations that experienced more fluctuations. The weighted fluctuation models were weighted by *tau*, the observation error estimate derived from the state-space models.

Model name	Variable	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	pMCMC	Effect
			UK scale analyses				
Geographic range - mu	(Intercept)	0.02	-0.03	0.06	18,000	0.45	fixed
	log(km2_range)	-0.0004	-0.003	0.002	18,000	0.79	fixed
	sigma	0.003	0.002	0.003	17,265		residual
Geographic range - slope	(Intercept)	0.02	-0.02	0.07	18,937	0.32	fixed
	log(km2_range)	-0.001	-0.004	0.002	19,025	0.52	fixed
	sigma	0.002	0.002	0.003	17,450		residual
Geographic range - weighted	(Intercept)	0.02	-0.03	0.07	18,000	0.47	fixed

	log(km2_range)	-0.0004	-0.003	0.002	18,000	0.76	fixed
	sigma	0.003	0.002	0.003	18,000		residual
Geographic range – fluctuations (SE)	(Intercept)	0.12	-0.05	0.29	18,000	0.17	0.12
	log(km2_range)	0.004	-0.01	0.01	18,000	0.42	0.004
	sigma	0.03	0.03	0.04	18,000		0.03
Geographic range – fluctuations (CI)	(Intercept)	0.25	0.10	0.39	18,000	0.001	fixed
	log(km2_range)	-0.004	-0.01	0.004	18,000	0.37	fixed
	sigma	0.03	0.02	0.03	18,000		residual
Geographic range – fluctuations weighted (CI)	(Intercept)	0.25	0.10	0.40	18,000	0.001	fixed
	log(km2_range)	-0.004	-0.01	0.005	18,000	0.37	fixed
	sigma	0.03	0.02	0.03	18,313		residual
Geographic range – fluctuations (SD)	(Intercept)	0.35	0.23	0.48	18,000	0.0001	0.35
	log(km2_range)	-0.001	-0.01	0.01	18,000	0.84	-0.001
	sigma	0.02	0.02	0.02	18,000		0.02
Mean population size - mu	(Intercept)	0.004	-0.01	0.02	18,549	0.53	fixed
	log(meanpop)	0.001	-0.001	0.002	18,000	0.41	fixed
	sigma	0.003	0.002	0.003	18,000		residual

Mean population size - slope	(Intercept)	0.01	-0.003	0.02	18,000	0.17	fixed
	log(meanpop)	-0.0003	-0.002	0.001	18,000	0.74	fixed
	sigma	0.003	0.002	0.003	18,000		residual
Mean population size - weighted	(Intercept)	0.001	-0.01	0.01	18,000	0.91	fixed
	log(meanpop)	0.001	-0.001	0.003	18,000	0.26	fixed
	sigma	0.003	0.002	0.003	18,000		residual
Mean population size – fluctuations (SE)	(Intercept)	0.34	0.30	0.38	17,499	0.0001	fixed
	log(meanpop)	-0.02	-0.03	-0.02	18,000	0.0001	fixed
	sigma	0.03	0.03	0.04	18,000		residual
Mean population size – fluctuations (CI)	(Intercept)	0.26	0.23	0.30	18,000	0.0001	fixed
	log(meanpop)	-0.01	-0.02	-0.01	18,000	0.0001	fixed
	sigma	0.03	0.02	0.03	18,000		residual
Mean population size – fluctuations weighted (CI)	(Intercept)	0.27	0.23	0.30	17,575	0.0001	fixed
	log(meanpop)	-0.01	-0.02	-0.01	18,000	0.0001	fixed
	sigma	0.03	0.02	0.03	18,000		residual

Mean population size – fluctuations (SD)	(Intercept)	0.48	0.45	0.52	18,000	0.0001	fixed
	log(meanpop)	-0.01	-0.02	-0.01	18,000	0.0001	fixed
	sigma	0.03	0.02	0.03	17,812		residual
Habitat specificity - mu	(Intercept)	0.02	0.01	0.03	18,000	0.002	fixed
	hab_spec	-0.001	-0.003	0.0005	18,000	0.16	fixed
	sigma	0.003	0.003	0.003	18,000		residual
Habitat specificity - slope	(Intercept)	0.01	0.001	0.02	18,000	0.04	fixed
	hab_spec	-0.001	-0.002	0.001	18,172	0.38	fixed
	sigma	0.003	0.002	0.003	18,412		residual
Habitat specificity - weighted	(Intercept)	0.02	0.01	0.03	18,000	0.003	fixed
	hab_spec	-0.001	-0.003	0.0004	18,000	0.15	fixed
	sigma	0.003	0.002	0.003	18,000		residual
Habitat specificity – fluctuations (SE)	(Intercept)	0.18	0.14	0.22	17,681	0.0001	fixed
	hab_spec	0.01	-0.0002	0.01	18,000	0.05	fixed
	sigma	0.04	0.03	0.04	18,510		residual
Habitat specificity – fluctuations (CI)	(Intercept)	0.16	0.13	0.20	18,000	0.0001	fixed

	hab_spec	0.01	0.001	0.01	18,553	0.03	fixed
	sigma	0.03	0.03	0.03	18,000		residual
Habitat specificity – fluctuations weighted (CI)	(Intercept)	0.16	0.13	0.20	18,000	0.0001	fixed
	hab_spec	0.01	0.0004	0.01	18,000	0.04	fixed
	sigma	0.03	0.03	0.03	18,000		residual
Habitat specificity – fluctuations (SD)	(Intercept)	0.36	0.33	0.39	18,000	0.0001	fixed
	hab_spec	0.004	0.0001	0.01	18,000	0.05	fixed
	sigma	0.02	0.02	0.03	18,503		residual
Red List status - mu	Least concern	0.01	0.01	0.02	18,000	0.0001	fixed
	Near threatened	0.03	0.01	0.05	18,000	0.001	fixed
	Vulnerable	-0.01	-0.03	0.01	18,000	0.48	fixed
	Endangered	-0.04	-0.14	0.06	18,000	0.47	fixed
	Critically endangered	0.03	-0.05	0.10	16,574	0.45	fixed
	sigma	0.003	0.002	0.003	18,000		residual
Red List status - slope	Least concern	0.01	0.004	0.01	18,000	0.001	fixed
	Near threatened	0.02	0.01	0.04	18,000	0.005	fixed
	Vulnerable	-0.01	-0.03	0.01	18,000	0.37	fixed
	Endangered	-0.01	-0.10	0.09	18,000	0.91	fixed

	Critically endangered	0.03	-0.04	0.09	18,000	0.43	fixed
	sigma	0.002	0.002	0.003	18,000		residual
Red List status - weighted	Least concern	0.01	0.005	0.02	18,000	0.0002	fixed
	Near threatened	0.04	0.02	0.05	17,614	0.0001	fixed
	Vulnerable	-0.01	-0.03	0.01	18,000	0.46	fixed
	Endangered	-0.04	-0.14	0.06	18,000	0.45	fixed
	Critically endangered	0.03	-0.05	0.11	18,000	0.49	fixed
	sigma	0.003	0.002	0.003	18,000		residual
Red List status – fluctuations (SE)	Least concern	0.19	0.17	0.21	18,523	0.0001	fixed
	Near threatened	0.28	0.22	0.35	17,404	0.0001	fixed
	Vulnerable	0.16	0.09	0.24	18,000	0.0002	fixed
	Endangered	0.18	-0.19	0.54	18,000	0.33	fixed
	Critically endangered	0.09	-0.17	0.34	17,758	0.51	fixed
	sigma	0.03	0.03	0.04	18,000		residual
Red List status – fluctuations (CI)	Least concern	0.18	0.16	0.20	18,000	0.0001	fixed
	Near threatened	0.21	0.16	0.27	18,000	0.0001	fixed
	Vulnerable	0.16	0.09	0.22	18,000	0.0001	fixed
	Endangered	0.41	0.08	0.73	18,000	0.01	fixed

	Critically endangered	0.06	-0.18	0.29	18,000	0.64	fixed
	sigma	0.03	0.02	0.03	18,000		residual
Red List status – fluctuations weighted (CI)	Least concern	0.18	0.16	0.20	18,000	0.0001	fixed
	Near threatened	0.21	0.16	0.27	18,000	0.0001	fixed
	Vulnerable	0.16	0.09	0.23	18,000	0.0001	fixed
	Endangered	0.40	0.07	0.73	19,079	0.02	fixed
	Critically endangered	0.06	-0.18	0.29	18,000	0.63	fixed
	sigma	0.03	0.02	0.03	17,569		residual
Red List status – fluctuations (SD)	Least concern	0.38	0.37	0.40	18,000	0.0001	fixed
	Near threatened	0.37	0.32	0.43	18,000	0.0001	fixed
	Vulnerable	0.27	0.21	0.33	18,000	0.0001	fixed
	Endangered	0.24	-0.06	0.55	18,000	0.12	fixed
	Critically endangered	0.32	0.14	0.51	18,000	0.001	fixed
	sigma	0.02	0.02	0.03	18,043		residual
System - mu	Freshwater	0.01	-0.01	0.02	18,000	0.39	fixed
	Marine	0.004	-0.002	0.01	18,000	0.23	fixed
	Terrestrial	0.03	0.02	0.03	18,000	0.0001	fixed
	sigma	0.003	0.002	0.003	18,000		residual

System - slope	Freshwater	0.01	-0.002	0.02	18,000	0.11	fixed
	Marine	0.004	-0.002	0.01	18,395	0.22	fixed
	Terrestrial	0.02	0.01	0.03	18,000	0.0001	fixed
	sigma	0.002	0.002	0.003	17,258		residual
System - weighted	Freshwater	0.001	-0.01	0.01	18,000	0.86	fixed
	Marine	0.01	-0.002	0.01	18,000	0.15	fixed
	Terrestrial	0.02	0.02	0.03	18,000	0.0001	fixed
	sigma	0.002	0.002	0.003	18,000		residual
Taxa - mu	Actinopterygii	-0.01	-0.02	0.001	18,000	0.09	fixed
	Amphibia	-0.02	-0.05	0.01	18,000	0.15	fixed
	Aves	0.02	0.01	0.02	18,000	0.0001	fixed
	Mammalia	0.02	0.01	0.03	18,000	0.0001	fixed
	Reptilia	-0.02	-0.09	0.05	19,343	0.52	fixed
	sigma	0.003	0.002	0.003	18,000		residual
Taxa - slope	Actinopterygii	-0.01	-0.02	0.0004	18,000	0.07	fixed
	Amphibia	-0.02	-0.05	0.01	18,000	0.13	fixed
	Aves	0.01	0.004	0.02	18,000	0.001	fixed
	Mammalia	0.03	0.02	0.04	18,000	0.0001	fixed
	Reptilia	-0.04	-0.10	0.02	18,000	0.21	fixed
	sigma	0.002	0.002	0.002	18,000		residual
Taxa - weighted	Actinopterygii	-0.01	-0.02	-0.0003	18,000	0.05	fixed

	Amphibia	-0.04	-0.07	-0.002	18,000	0.04	fixed
	Aves	0.01	0.01	0.02	18,000	0.0001	fixed
	Mammalia	0.02	0.01	0.03	18,000	0.0001	fixed
	Reptilia	-0.05	-0.13	0.04	18,862	0.31	fixed
	sigma	0.002	0.002	0.003	18,000		residual
Global scale analyses							
System - mu	Freshwater	0.005	0.002	0.01	18,000	0.0001	fixed
	Marine	0.004	0.002	0.01	18,587	0.001	fixed
	Terrestrial	0.003	0.001	0.005	18,000	0.001	fixed
	sigma	0.003	0.003	0.004	18,000		residual
System - slope	Freshwater	0.005	0.003	0.006	17544	0.0001	fixed
	Marine	0.002	0.001	0.004	18,000	0.04	fixed
	Terrestrial	0.002	0.001	0.003	17,374	0.01	fixed
	sigma	0.002	0.002	0.003	18,175		residual
System - weighted	Freshwater	0.01	0.003	0.01	18,390	0.0001	fixed
	Marine	0.004	0.001	0.01	18,000	0.002	fixed
	Terrestrial	0.004	0.002	0.01	18,000	0.0004	fixed
	sigma	0.003	0.003	0.003	18,000		residual
System – fluctuations (SE)	Freshwater	0.12	0.12	0.13	18,000	0.0001	fixed
	Marine	0.12	0.11	0.12	17,506	0.0001	fixed
	Terrestrial	0.09	0.08	0.09	18,000	0.0001	fixed

	sigma	0.02	0.02	0.02	18,000		residual
System – fluctuations (CI)	Freshwater	0.13	0.13	0.14	18,000	0.0001	fixed
	Marine	0.13	0.13	0.14	18,000	0.0001	fixed
	Terrestrial	0.10	0.10	0.10	18,000	0.0001	fixed
	sigma	0.02	0.02	0.02	18,000		residual
System – fluctuations weighted (CI)	Freshwater	0.13	0.13	0.14	18,000	0.0001	fixed
	Marine	0.14	0.13	0.14	18,550	0.0001	fixed
	Terrestrial	0.10	0.09	0.10	18,590	0.0001	fixed
	sigma	0.02	0.02	0.02	18,000		residual
System – fluctuations (SD)	Freshwater	0.39	0.39	0.40	19,118	0.0001	fixed
	Marine	0.40	0.40	0.41	18,000	0.0001	fixed
	Terrestrial	0.37	0.37	0.38	18,136	0.0001	fixed
	sigma	0.02	0.02	0.02	18,000		residual
Biome - mu	Boreal forests/taiga	-0.001	-0.004	0.002	18,000	0.72	fixed
	Deserts and xeric shrublands	-0.01	-0.03	0.003	18,000	0.10	fixed
	Trop. and subtrop. grasslands savannas and shrublands	-0.01	-0.02	-0.001	17,414	0.03	fixed
	Large lakes	0.003	-0.004	0.01	18,665	0.43	fixed

	Mediterranean forests woodlands and scrub	0.02	0.01	0.02	17,081	0.0001	fixed
	Montane freshwaters	0.01	-0.01	0.04	17,409	0.34	fixed
	Montane grasslands and shrublands	0.02	0.002	0.04	18,000	0.03	fixed
	Polar freshwaters	0.01	0.001	0.01	18,002	0.02	fixed
	Polar seas	-0.002	-0.02	0.02	18,000	0.85	fixed
	Temperate forests	0.005	0.002	0.01	18,000	0.0003	fixed
	Temperate wetlands and rivers	0.005	0.002	0.01	18,000	0.001	fixed
	Temperate grasslands savannas and shrublands	-0.004	-0.01	0.002	16,766	0.22	fixed
	Tropical wetlands and rivers	0.01	-0.003	0.01	18,000	0.22	fixed
	Tropical and subtropical forests	0.02	0.01	0.03	16,634	0.0002	fixed
	Tropical coral	0.02	0.01	0.04	18,000	0.0001	fixed
	Tundra	0.01	-0.001	0.01	19,359	0.10	fixed
	Xeric freshwaters and endorheic basins	-0.002	-0.02	0.01	18,000	0.77	fixed
	sigma	0.003	0.003	0.003	18,000		residual
Biome - slope	Boreal forests/taiga	-0.001	-0.004	0.002	18,686	0.41	fixed

Deserts and xeric shrublands	-0.01	-0.03	0.002	18,000	0.08	fixed
Trop. and subtrop. grasslands savannas and shrublands	-0.001	-0.01	0.01	18,000	0.72	fixed
Large lakes	0.004	-0.003	0.01	18,000	0.28	fixed
Mediterranean forests woodlands and scrub	0.01	0.002	0.01	18,000	0.01	fixed
Montane freshwaters	0.004	-0.02	0.02	18,000	0.66	fixed
Montane grasslands and shrublands	0.01	-0.003	0.03	17,697	0.12	fixed
Polar freshwaters	0.01	0.003	0.01	18,015	0.002	fixed
Polar seas	-0.01	-0.03	0.01	18,000	0.44	fixed
Temperate forests	0.004	0.002	0.01	18,000	0.001	fixed
Temperate wetlands and rivers	0.005	0.002	0.01	18,000	0.0001	fixed
Temperate grasslands savannas and shrublands	-0.004	-0.01	0.001	20,175	0.14	fixed
Tropical wetlands and rivers	0.01	-0.002	0.01	18,000	0.13	fixed
Tropical and subtropical forests	0.01	-0.0005	0.01	17,482	0.06	fixed
Tropical coral	0.02	0.01	0.03	18,000	0.0001	fixed

	Tundra	0.005	-0.002	0.01	18,393	0.17	fixed
	Xeric freshwaters and endorheic basins	-0.01	-0.03	0.0001	18,000	0.04	fixed
	sigma	0.002	0.002	0.002	18,000		residual
Biome - weighted	Boreal forests/taiga	-0.001	-0.004	0.002	18,000	0.56	fixed
	Deserts and xeric shrublands	-0.02	-0.04	-0.003	18,000	0.02	fixed
	Trop. and subtrop. grasslands savannas and shrublands	-0.01	-0.02	-0.0005	18,000	0.04	fixed
	Large lakes	0.002	-0.01	0.01	18,000	0.60	fixed
	Mediterranean forests woodlands and scrub	0.02	0.01	0.03	18,000	0.0001	fixed
	Montane freshwaters	0.02	-0.01	0.05	18,829	0.17	fixed
	Montane grasslands and shrublands	0.03	0.01	0.05	18,000	0.01	fixed
	Polar freshwaters	0.01	0.002	0.02	18,000	0.01	fixed
	Polar seas	-0.002	-0.03	0.02	18,685	0.83	fixed
	Temperate forests	0.01	0.003	0.01	18,000	0.0001	fixed
	Temperate wetlands and rivers	0.01	0.003	0.01	18,000	0.0002	fixed
	Temperate grasslands	-0.004	-0.01	0.003	18,699	0.24	fixed

	savannas and shrublands						
	Tropical wetlands and rivers	0.01	-0.003	0.02	18,000	0.22	fixed
	Tropical and subtropical forests	0.02	0.01	0.03	18,000	0.0001	fixed
	Tropical coral	0.03	0.02	0.04	16,691	0.0001	fixed
	Tundra	0.01	0.001	0.02	18,000	0.04	fixed
	Xeric freshwaters and endorheic basins	-0.003	-0.02	0.01	18,000	0.70	fixed
	sigma	0.003	0.003	0.003	18,000		residual
Biome – fluctuations (SE)	Boreal forests/taiga	0.06	0.06	0.07	18,000	0.0001	fixed
	Deserts and xeric shrublands	0.21	0.17	0.25	19,592	0.0001	fixed
	Trop. and subtrop. grasslands savannas and shrublands	0.11	0.09	0.13	18,342	0.0001	fixed
	Large lakes	0.09	0.07	0.11	17,588	0.0001	fixed
	Mediterranean forests woodlands and scrub	0.16	0.14	0.17	18,000	0.0001	fixed
	Montane freshwaters	0.15	0.10	0.21	18,000	0.0001	fixed
	Montane grasslands and shrublands	0.11	0.07	0.15	18,000	0.0001	fixed

	Polar freshwaters	0.14	0.12	0.15	18,000	0.0001	fixed
	Polar seas	0.08	0.03	0.13	17,192	0.002	fixed
	Temperate forests	0.08	0.08	0.09	17,721	0.0001	fixed
	Temperate wetlands and rivers	0.11	0.11	0.12	18,000	0.0001	fixed
	Temperate grasslands savannas and shrublands	0.07	0.06	0.09	18,000	0.0001	fixed
	Tropical wetlands and rivers	0.21	0.19	0.23	18,385	0.0001	fixed
	Tropical and subtropical forests	0.15	0.13	0.17	17,658	0.0001	fixed
	Tropical coral	0.18	0.16	0.21	18,000	0.0001	fixed
	Tundra	0.13	0.11	0.14	18,000	0.0001	fixed
	Xeric freshwaters and endorheic basins	0.13	0.09	0.16	18,000	0.0001	fixed
	sigma	0.02	0.02	0.02	18,518		residual
Biome – fluctuations (CI)	Boreal forests/taiga	0.07	0.07	0.08	18,000	0.0001	fixed
	Deserts and xeric shrublands	0.22	0.18	0.26	18,000	0.0001	fixed
	Trop. and subtrop. grasslands savannas and shrublands	0.21	0.19	0.23	18,000	0.0001	fixed
	Large lakes	0.11	0.09	0.12	18,725	0.0001	fixed

	Mediterranean forests woodlands and scrub	0.15	0.13	0.16	18,000	0.0001	fixed
	Montane freshwaters	0.14	0.09	0.19	18,000	0.0001	fixed
	Montane grasslands and shrublands	0.17	0.13	0.21	18,000	0.0001	fixed
	Polar freshwaters	0.14	0.12	0.15	18,000	0.0001	fixed
	Polar seas	0.16	0.11	0.20	18,000	0.0001	fixed
	Temperate forests	0.09	0.09	0.10	18,000	0.0001	fixed
	Temperate wetlands and rivers	0.13	0.12	0.13	18,000	0.0001	fixed
	Temperate grasslands savannas and shrublands	0.08	0.07	0.09	17,497	0.0001	fixed
	Tropical wetlands and rivers	0.20	0.19	0.22	18,000	0.0001	fixed
	Tropical and subtropical forests	0.20	0.18	0.21	18,000	0.0001	fixed
	Tropical coral	0.16	0.14	0.19	18,000	0.0001	fixed
	Tundra	0.11	0.09	0.13	18,000	0.0001	fixed
	Xeric freshwaters and endorheic basins	0.18	0.14	0.21	18,000	0.0001	fixed
	sigma	0.02	0.01	0.02	18,440		residual
Biome – fluctuations	Boreal forests/taiga	0.07	0.06	0.08	18,000	0.0001	fixed

weighted (CI)							
	Deserts and xeric shrublands	0.23	0.19	0.27	18,000	0.0001	fixed
	Trop. and subtrop. grasslands savannas and shrublands	0.22	0.20	0.23	18,000	0.0001	fixed
	Large lakes	0.11	0.09	0.12	18,000	0.0001	fixed
	Mediterranean forests woodlands and scrub	0.15	0.13	0.16	18,000	0.0001	fixed
	Montane freshwaters	0.16	0.10	0.21	18,404	0.0001	fixed
	Montane grasslands and shrublands	0.17	0.13	0.21	18,000	0.0001	fixed
	Polar freshwaters	0.14	0.13	0.15	17,400	0.0001	fixed
	Polar seas	0.16	0.11	0.21	18,000	0.0001	fixed
	Temperate forests	0.09	0.08	0.10	18,000	0.0001	fixed
	Temperate wetlands and rivers	0.12	0.12	0.13	18,000	0.0001	fixed
	Temperate grasslands savannas and shrublands	0.08	0.06	0.09	18,000	0.0001	fixed
	Tropical wetlands and rivers	0.20	0.18	0.22	18,000	0.0001	fixed

	Tropical and subtropical forests	0.20	0.18	0.22	18,000	0.0001	fixed
	Tropical coral	0.17	0.14	0.19	18,575	0.0001	fixed
	Tundra	0.10	0.09	0.12	17,153	0.0001	fixed
	Xeric freshwaters and endorheic basins	0.18	0.15	0.22	18,000	0.0001	fixed
	sigma	0.02	0.01	0.02	18,683		residual
Biome – fluctuations (SD)	Boreal forests/taiga	0.33	0.32	0.34	18,000	0.0001	fixed
	Deserts and xeric shrublands	0.45	0.41	0.49	18,000	0.0001	fixed
	Trop. and subtrop. grasslands savannas and shrublands	0.47	0.45	0.48	18,000	0.0001	fixed
	Large lakes	0.37	0.35	0.38	18,000	0.0001	fixed
	Mediterranean forests woodlands and scrub	0.44	0.43	0.46	18,000	0.0001	fixed
	Montane freshwaters	0.43	0.37	0.48	18,000	0.0001	fixed
	Montane grasslands and shrublands	0.44	0.40	0.49	18,000	0.0001	fixed
	Polar freshwaters	0.39	0.37	0.40	17,812	0.0001	fixed
	Polar seas	0.39	0.34	0.44	18,000	0.0001	fixed
	Temperate forests	0.36	0.36	0.37	18,000	0.0001	fixed

	Temperate wetlands and rivers	0.39	0.38	0.39	18,000	0.0001	fixed
	Temperate grasslands savannas and shrublands	0.34	0.33	0.36	18,000	0.0001	fixed
	Tropical wetlands and rivers	0.45	0.43	0.47	18,000	0.0001	fixed
	Tropical and subtropical forests	0.48	0.46	0.50	18,000	0.0001	fixed
	Tropical coral	0.47	0.44	0.49	18,391	0.0001	fixed
	Tundra	0.38	0.36	0.39	18,000	0.0001	fixed
	Xeric freshwaters and endorheic basins	0.39	0.36	0.43	18,000	0.0001	fixed
	sigma	0.02	0.02	0.02	18,831		residual
Taxa - mu	Actinopterygii	-0.001	-0.003	0.002	18,000	0.66	fixed
	Amphibia	-0.01	-0.02	-0.005	18,000	0.002	fixed
	Aves	0.004	0.003	0.01	18,000	0.0001	fixed
	Mammalia	0.01	0.01	0.01	18,000	0.0001	fixed
	Reptilia	0.02	0.01	0.02	18,000	0.0001	fixed
	sigma	0.003	0.003	0.004	18,743		residual
Taxa - slope	Actinopterygii	-0.001	-0.004	0.001	18,082	0.33	fixed
	Amphibia	-0.01	-0.02	-0.004	18,000	0.002	fixed
	Aves	0.003	0.002	0.005	18,000	0.0001	fixed
	Mammalia	0.01	0.003	0.01	18,000	0.0001	fixed

	Reptilia	0.01	0.01	0.02	18,000	0.0001	fixed
	sigma	0.002	0.002	0.003	18,000		residual
Taxa - weighted	Actinopterygii	-0.001	-0.004	0.002	18,000	0.67	fixed
	Amphibia	-0.02	-0.03	-0.01	18,000	0.001	fixed
	Aves	0.004	0.003	0.01	18,000	0.0001	fixed
	Mammalia	0.01	0.01	0.02	18,000	0.0001	fixed
	Reptilia	0.02	0.01	0.02	18,000	0.0001	fixed
	sigma	0.003	0.003	0.003	17,290		residual
Taxa – fluctuations (SE)	Actinopterygii	0.14	0.13	0.14	18,000	0.0001	fixed
	Amphibia	0.24	0.23	0.26	18,000	0.0001	fixed
	Aves	0.08	0.07	0.08	18,503	0.0001	fixed
	Mammalia	0.15	0.14	0.16	18,000	0.0001	fixed
	Reptilia	0.19	0.18	0.20	17,583	0.0001	fixed
	sigma	0.02	0.02	0.02	18,000		residual
Taxa – fluctuations (CI)	Actinopterygii	0.15	0.14	0.16	18,000	0.0001	fixed
	Amphibia	0.22	0.20	0.24	18,000	0.0001	fixed
	Aves	0.09	0.09	0.10	17,773	0.0001	fixed
	Mammalia	0.17	0.17	0.18	18,000	0.0001	fixed
	Reptilia	0.17	0.15	0.18	18,000	0.0001	fixed
	sigma	0.01	0.01	0.02	17,064		residual
Taxa – fluctuations	Actinopterygii	0.15	0.15	0.16	16,986	0.0001	fixed

weighted (CI)							
	Amphibia	0.23	0.21	0.25	18,000	0.0001	fixed
	Aves	0.09	0.09	0.09	18,000	0.0001	fixed
	Mammalia	0.18	0.17	0.19	18,000	0.0001	fixed
	Reptilia	0.17	0.16	0.19	18,000	0.0001	fixed
	sigma	0.01	0.01	0.02	18,000		residual
Taxa – fluctuations (SD)	Actinopterygii	0.41	0.40	0.41	18,000	0.0001	fixed
	Amphibia	0.48	0.46	0.50	18,650	0.0001	fixed
	Aves	0.36	0.36	0.36	18,000	0.0001	fixed
	Mammalia	0.45	0.45	0.46	18,000	0.0001	fixed
	Reptilia	0.44	0.43	0.46	17,470	0.0001	fixed
	sigma	0.02	0.02	0.02	18,000		residual
Red List status - mu	Least concern	0.01	0.005	0.01	18,731	0.0001	fixed
	Near threatened	-0.01	-0.01	-0.0003	18,000	0.03	fixed
	Vulnerable	0.002	-0.003	0.01	18,000	0.41	fixed
	Endangered	-0.002	-0.01	0.005	18,000	0.61	fixed
	Critically endangered	-0.01	-0.02	-0.0001	18,000	0.05	fixed
	sigma	0.004	0.003	0.004	18,000		residual
Red List status - slope	Least concern	0.005	0.004	0.01	17,042	0.0001	fixed

	Near threatened	-0.01	-0.01	-0.002	18,000	0.004	fixed
	Vulnerable	0.001	-0.003	0.01	18,374	0.58	fixed
	Endangered	-0.0003	-0.01	0.01	18,000	0.91	fixed
	Critically endangered	-0.003	-0.01	0.005	18,387	0.45	fixed
	sigma	0.003	0.002	0.003	18,000		residual
Red List status - weighted	Least concern	0.01	0.01	0.01	18,000	0.0001	fixed
	Near threatened	-0.01	-0.01	0.0000	18,000	0.05	fixed
	Vulnerable	0.002	-0.003	0.01	18,000	0.39	fixed
	Endangered	-0.003	-0.01	0.01	18,000	0.51	fixed
	Critically endangered	-0.01	-0.02	0.001	18,000	0.09	fixed
	sigma	0.003	0.003	0.004	18,000		residual
Red List status – fluctuations (SE)	Least concern	0.10	0.10	0.10	18,506	0.0001	fixed
	Near threatened	0.13	0.11	0.14	18,000	0.0001	fixed
	Vulnerable	0.11	0.10	0.12	18,000	0.0001	fixed
	Endangered	0.13	0.12	0.15	17,738	0.0001	fixed
	Critically endangered	0.15	0.13	0.17	18,000	0.0001	fixed
	sigma	0.02	0.02	0.02	18,000		residual
Red List status –	Least concern	0.11	0.11	0.12	16,941	0.0001	fixed

fluctuations (CI)							
	Near threatened	0.14	0.13	0.15	18,000	0.0001	fixed
	Vulnerable	0.14	0.13	0.15	17,556	0.0001	fixed
	Endangered	0.16	0.15	0.17	18,000	0.0001	fixed
	Critically endangered	0.17	0.15	0.19	18,000	0.0001	fixed
	sigma	0.02	0.02	0.02	17,523		residual
Red List status – fluctuations weighted (CI)	Least concern	0.11	0.11	0.11	18,000	0.0001	fixed
	Near threatened	0.14	0.13	0.16	18,000	0.0001	fixed
	Vulnerable	0.14	0.13	0.15	18,000	0.0001	fixed
	Endangered	0.16	0.15	0.18	17,504	0.0001	fixed
	Critically endangered	0.17	0.15	0.19	18,000	0.0001	fixed
	sigma	0.02	0.02	0.02	18,000		residual
Red List status – fluctuations (SD)	Least concern	0.38	0.38	0.38	18,000	0.0001	fixed
	Near threatened	0.42	0.41	0.43	18,406	0.0001	fixed
	Vulnerable	0.40	0.39	0.41	17,595	0.0001	fixed
	Endangered	0.44	0.42	0.45	18,000	0.0001	fixed
	Critically endangered	0.47	0.44	0.49	16,838	0.0001	fixed

	sigma	0.02	0.02	0.02	18,000		residual
Latitude - mu	(Intercept)	0.004	0.002	0.01	18,000	0.0001	fixed
	Decimal.Latitude	-0.0000	-0.0000	0.0000	18,000	0.89	fixed
	sigma	0.003	0.003	0.004	18,000		residual
Duration - mu	Duration	0.0000	0.0000	0.0001	18,000	0.04	fixed
Duration - mu	sigma	0.003	0.003	0.004	18,469		residual

Table S4. List of species included in the UK scale analysis of population change across rarity metrics.

Species name	Number of populations
Acrocephalus schoenobaenus	1
Acrocephalus scirpaceus	1
Agonus cataphractus	1
Alca torda	4
Anarhichas lupus	1
Anas acuta	1
Anas crecca	1
Anas platyrhynchos	2
Anser albifrons	4
Anser fabalis	1
Anthus pratensis	2
Ardea cinerea	1
Arenaria interpres	1
Argentina silus	1
Argentina sphyraena	1
Arnoglossus laterna	1
Asio flammeus	1
Aythya ferina	4
Aythya fuligula	2
Botaurus stellaris	14
Branta bernicla	54
Branta canadensis	1
Branta leucopsis	3
Brosme brosme	1
Bucephala clangula	1
Bufo bufo	1
Burhinus oedicnemus	1
Buteo buteo	1
Calidris alba	1
Calidris alpina	1
Calidris canutus	2
Calidris maritima	2
Callionymus maculatus	1
Capreolus capreolus	3

Carduelis cannabina	2
Cepphus grylle	2
Cervus elaphus	2
Cetorhinus maximus	1
Cettia cetti	1
Charadrius hiaticula	1
Chelidonichthys lucerna	2
Circus aeruginosus	1
Circus cyaneus	1
Clupea harengus	2
Columba oenas	1
Coronella austriaca	1
Corvus corax	1
Corvus corone	1
Corvus monedula	1
Crex crex	1
Cyclopterus lumpus	1
Cygnus columbianus	3
Cygnus cygnus	1
Cygnus olor	1
Delphinus delphis	2
Echiichthys vipera	1
Egretta garzetta	1
Emberiza cirlus	1
Emberiza citrinella	1
Emberiza schoeniclus	3
Eptesicus serotinus	1
Esox lucius	2
Falco peregrinus	1
Falco tinnunculus	1
Fulica atra	1
Fulmarus glacialis	7
Gadus morhua	7
Glyptocephalus cynoglossus	1
Haematopus ostralegus	2
Haliaeetus albicilla	1
Halichoerus grypus	52
Hippoglossus hippoglossus	1
Lagopus lagopus	3

Larus argentatus	1
Larus canus	1
Larus fuscus	1
Larus melanocephalus	1
Lepidorhombus whiffiagonis	2
Lepus timidus	1
Limosa lapponica	2
Limosa limosa	2
Lissotriton vulgaris	5
Lophius budegassa	1
Lophius piscatorius	2
Lullula arborea	1
Melanogrammus aeglefinus	9
Meles meles	1
Mergus serrator	1
Merlangius merlangus	8
Merluccius merluccius	2
Micromesistius poutassou	1
Milvus milvus	3
Molva molva	1
Morus bassanus	4
Muscicapa striata	1
Myotis nattereri	1
Natrix natrix	1
Netta rufina	1
Numenius arquata	2
Nyctalus noctula	1
Oenanthe oenanthe	1
Orcinus orca	1
Oriolus oriolus	1
Oryctolagus cuniculus	6
Oxyura jamaicensis	2
Pandion haliaetus	1
Parus major	2
Passer domesticus	1
Passer montanus	1
Perca fluviatilis	3
Perdix perdix	1
Phalacrocorax aristotelis	8

Phoca vitulina	28
Phrynorhombus norvegicus	1
Pipistrellus pipistrellus	1
Pipistrellus pygmaeus	1
Platichthys flesus	1
Plecotus auritus	1
Plectrophenax nivalis	2
Pleuronectes platessa	6
Pluvialis apricaria	2
Pluvialis squatarola	1
Podiceps cristatus	1
Pollachius pollachius	1
Pollachius virens	3
Prunella modularis	1
Puffinus mauretanicus	2
Pyrrhula pyrrhula	1
Raja brachyura	1
Raja clavata	1
Raja microocellata	1
Raja montagui	1
Rhinolophus ferrumequinum	2
Rhinolophus hipposideros	4
Rissa tridactyla	9
Salmo salar	1
Salmo trutta	1
Scomber scombrus	2
Scyliorhinus canicula	1
Sitta europaea	1
Sprattus sprattus	1
Stenella coeruleoalba	1
Stercorarius parasiticus	3
Sterna dougallii	5
Sterna hirundo	1
Sterna paradisaea	1
Sternula albifrons	1
Streptopelia turtur	1
Strix aluco	1
Sturnus vulgaris	1
Sylvia communis	1

Syngnathus rostellatus	1
Tachybaptus ruficollis	1
Tadorna tadorna	1
Thalasseus sandvicensis	2
Trachurus trachurus	2
Tringa nebularia	1
Tringa totanus	1
Trisopterus esmarkii	2
Trisopterus luscus	1
Trisopterus minutus	1
Triturus cristatus	5
Turdus philomelos	1
Tursiops truncatus	4
Uria aalge	10
Vanellus vanellus	3
Xiphias gladius	1