Rare and common vertebrates span a wide spectrum of population trends

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Abstract

The Earth's biota is changing over time in complex ways. A critical challenge is to test whether specific biomes, taxa or types of species benefit or suffer in a time of accelerating global change. We analysed nearly 10 000 abundance time series from over 2000 vertebrate species part of the Living Planet Database. We integrated abundance data with information on geographic range, habitat preference, taxonomic and phylogenetic relationships, and IUCN Red List Categories and threats. We found that 15% of populations declined, 18% increased, and 67% showed no net changes over time. Against a backdrop of no biogeographic and phylogenetic patterning in population change, we uncovered a distinct taxonomic signal. Amphibians were the only taxa that experienced net declines in the analysed data, while birds, mammals and reptiles experienced net increases. Population trends were poorly captured by species' rarity and global-scale threats. Incorporation of the full spectrum of population change will improve conservation efforts to protect global biodiversity.

Main text

Ecosystem-level change is currently unfolding all around the globe and modifying the abundances of the different species forming Earth's biota. As global change continues to accelerate[1,2], there is a growing need for comprehensive assessments of the factors explaining the variation in ecological changes observed across taxa and biomes[3]. However, existing empirical studies of the predictors of the abundance of individuals of different species (hereafter, population change) mostly focus on either specific taxa[4] or on population declines alone[2,5]. A critical research challenge is to disentangle the sources of heterogeneity across the full spectrum of population change for available population data. Recent compilations of long-term population time series, extensive occurrence, phylogenetic, habitat preference and IUCN Red List Category data[6–8] provide a unique opportunity to test which species- and population-level attributes explain variation in population trends and fluctuations among the world's well-monitored vertebrate species. Population change is the underlying process leading to community reassembly[9] and the resulting changes to biodiversity are vitally important for ecosystem functions and services[10].

The distributions of global change drivers such as land-use change, habitat change, pollution, invasion by non-native species and climate change show distinct clustering across space[11–13]. Spatial clustering has also been documented for biodiversity trends derived from assemblage time series, with the marine realm emerging as a hotspot for rapid changes in community composition[14]. Since assemblages are made up of populations, the biogeographic patterns at the assemblage level suggest similar clustering might occur at the population level as well[15]. In addition to geographic patterns in exposure to anthropogenic activities, species' vulnerability can also influence population abundance over time[16]. Species traits can moderate population responses to natural and anthropogenic environmental change[16], and across evolutionary time,

63 certain clades have been more vulnerable to declines and extinctions[6–8]. Building on known
64 variability in species' vulnerability[16–18], we expected taxonomic and phylogenetic signals in
65 population trends and fluctuations (e.g. greater declines, increases or fluctuations in abundance
66 for specific taxa and among specific clades). Understanding which biomes, taxa and types of
67 species are experiencing the most acute changes in abundance over time could provide key
68 insights for conservation prioritization.
69
70 Conservation efforts often focus on protecting rare species - those with restricted geographic
71 extents, small population sizes or high habitat specificity - as they are assumed to be more likely
72 to decline and ultimately go extinct[19–21]. Species with a smaller geographic range might have more
73 concentrated exposure to environmental change, with less opportunities to find refugia or
74 disperse, thus increasing the likelihood of declines[1,9]. As per population dynamics theory[22,23] and
75 Taylor's power law[24], species with small populations are more likely to undergo stochastic
76 fluctuations that could lead to pronounced declines, local extinction and eventually global species
77 extinction[5]. Small populations are also more likely to decline due to inbreeding, but note that there
78 are also instances of naturally small and stable populations[25,26]. Allee effects, the relationship
79 between individual fitness and population density, further increase the likelihood of declines due
80 to lack of potential mates and low reproductive output once populations reach a critically low
81 density[27,28]. Furthermore, environmental change might have disproportionately large effects on
82 the populations of species with high habitat specificity, as for these species persistence and
83 colonization of new areas are limited by strict habitat preferences[1,29]. The fossil record indicates
84 that on millennial time scales, rare species are more likely to decline and ultimately go extinct[30],
85 but human actions have pushed Earth away from traditional geological trajectories[31], and the
86 relationships between rarity and population change across the planet have yet to be tested across
87 the Anthropocene.

On a global scale, species are exposed to a variety of threats, among which habitat change, resource exploitation and hunting dominate as key predictors of extinction risk[32]. Species' IUCN Red List Categories are often used in conservation prioritisation and more threatened species tend to be the focus of conservation initiatives[33]. At more local scales, there might be variation in how populations are changing over time in different locations, in isolation from their overall conservation status[4,34]. Testing population change across species' IUCN Red List Category allows us to link contemporary changes in abundance with long-term probability of extinction[35]. Determining how local-scale population trends vary across species' IUCN Red List Categories has practical applications for assessing species' recovery which is useful for the proposed IUCN Green List of Species[36].

Here, we asked how the trends and fluctuations of vertebrate populations vary with biogeography, taxa, phylogenetic relationships and across species' rarity metrics and IUCN Red List Categories and threat types from the species' IUCN Red List profiles. We tested the following predictions: 1) There will be biogeographic patterns in population trends and fluctuations across the planet's realms and biomes, in line with particular regions of the world experiencing high rates of environmental change (e.g., tropical forests[37]). 2) Populations of rare species will be more likely to decline and fluctuate than the populations of common species. 3) Populations of species with a higher number of threats are more likely to decline and fluctuate than the populations of least concern species and those exposed to a lower number of threats. We quantified differences in population trends and fluctuations across latitudes and biomes within the freshwater, marine and terrestrial realms to test the presence of distinct hotspots of declines and increases. Additionally, we used data from the VertLife and BirdLife Databases[6–8] to assess taxonomic and phylogenetic signals, in the patterns of population change to determine if specific groups experience

113 pronounced changes over time. We investigated whether the heterogeneity in population change
114 globally is explained by differences in species' rarity and IUCN Red List Categories. We measured
115 rarity using three separate metrics – geographic range derived from GBIF records, mean
116 population size (number of individuals that were recorded during monitoring for each population
117 in the Living Planet Database) and habitat specificity derived from the species' IUCN Red List
118 profiles. In a *post-hoc* analysis, we compiled threat types and number of threats derived from the
119 species' IUCN Red List profiles to determine how threats influence local-scale population change.
120 Using the largest currently available compilation of population records over time, we conducted a
121 global synthesis of population trends and fluctuations to provide key empirical evidence for the
122 management, conservation and prediction of ecological changes across the Anthropocene.
123
124 We analysed 9286 vertebrate population time series from 2084 species part of the Living Planet
125 Database (133 092 records) over the period between 1970 and 2014. These time series represent
126 repeated monitoring surveys of the number of individuals in a given area (species' abundance
127 over time), hereafter called "populations". We focus on two aspects of population change – overall
128 changes in abundance over time (population trend, μ) and abundance variability over time
129 (population fluctuations, σ^2). In the first stage of our analyses, we quantified trends and
130 fluctuations for each population using state-space models that account for observation error and
131 random fluctuations[38] (Figure S1). In the second stage, we modelled the population trend and
132 fluctuation estimates from the first stage across latitude, realm, biome, taxa, rarity metrics,
133 phylogenetic relatedness, species' IUCN Red List Category and threat type using a Bayesian
134 modelling framework (Figure S2). We included a species random intercept effect to account for
135 the possible correlation between the trends of populations from the same species (see table Table
136 S1 for sample sizes). As sensitivity analyses, we additionally used variance weighting of the
137 population trend estimates (μ) by the observation/measurement error around them (τ^2) and

138 population trend estimates from linear model fits (slopes instead of μ) as the input variables in the
139 second stage models, as well as several different fluctuations estimates. We also repeated our
140 analyses on a single-country scale, using only populations within the United Kingdom, where
141 monitoring efforts are particularly rigorous and extensive. All different analytical approaches
142 yielded very similar results and are described in further detail in the methods.
143
144 **Results**
145 We found a broad spectrum of population trends across vertebrate populations within the Living
146 Planet Database. Across the time series we analysed, 15% (1381 time series) of populations
147 were declining, 18% (1656 time series) were increasing, and 67% (6249 time series) showed no
148 net changes in abundance over time, in contrast to a null distribution derived from randomised
149 data (Figure S6b). Trends were considered statistically different from no net change when the
150 confidence intervals around the population trend estimates did not overlap zero. Our results were
151 similar when we weighted population trends by the state-space model derived observation error
152 (Figures 1-4 and Tables S2-3).
153
154 **Biogeographic patterns of population trends and fluctuations**
155 We found that globally, population increases, declines and fluctuations over time occurred across
156 all latitudes and biomes within the freshwater, marine and terrestrial realms, with no strong
157 biogeographic patterning and no specific hotspots of population declines (Figure 1, Table S2).
158 Across realms, monitored vertebrate populations experienced net population increases
159 (freshwater slope = 0.005, CI = 0.002 to 0.01; marine slope = 0.004, CI = 0.002 to 0.01; terrestrial
160 slope = 0.003, CI = 0.001 to 0.005, Figure 1d-e). In the freshwater and terrestrial realms, there
161 was a bimodal distribution of population trends, driven largely by terrestrial bird species showing
162 small increases and decreases over time (Hartigans' dip test, $D = 0.04$, $p < 0.01$). Across biomes,

163 populations in Mediterranean forests, montane grasslands, polar freshwaters, temperate
164 wetlands, tropical forests and tropical coral biomes were more likely to increase, whereas
165 populations from the remaining studied biomes experienced no net changes (Figure 1h, Table
166 S2). Population fluctuations were less pronounced in the terrestrial realm (slope = 0.02, CI = 0.018
167 to 0.021, Figure 1f-g), but those populations were also monitored for the longest duration across
168 systems (average duration – 28 years for terrestrial, 18 years for marine and 21 years for
169 freshwater populations, Figure S1, Table S2).

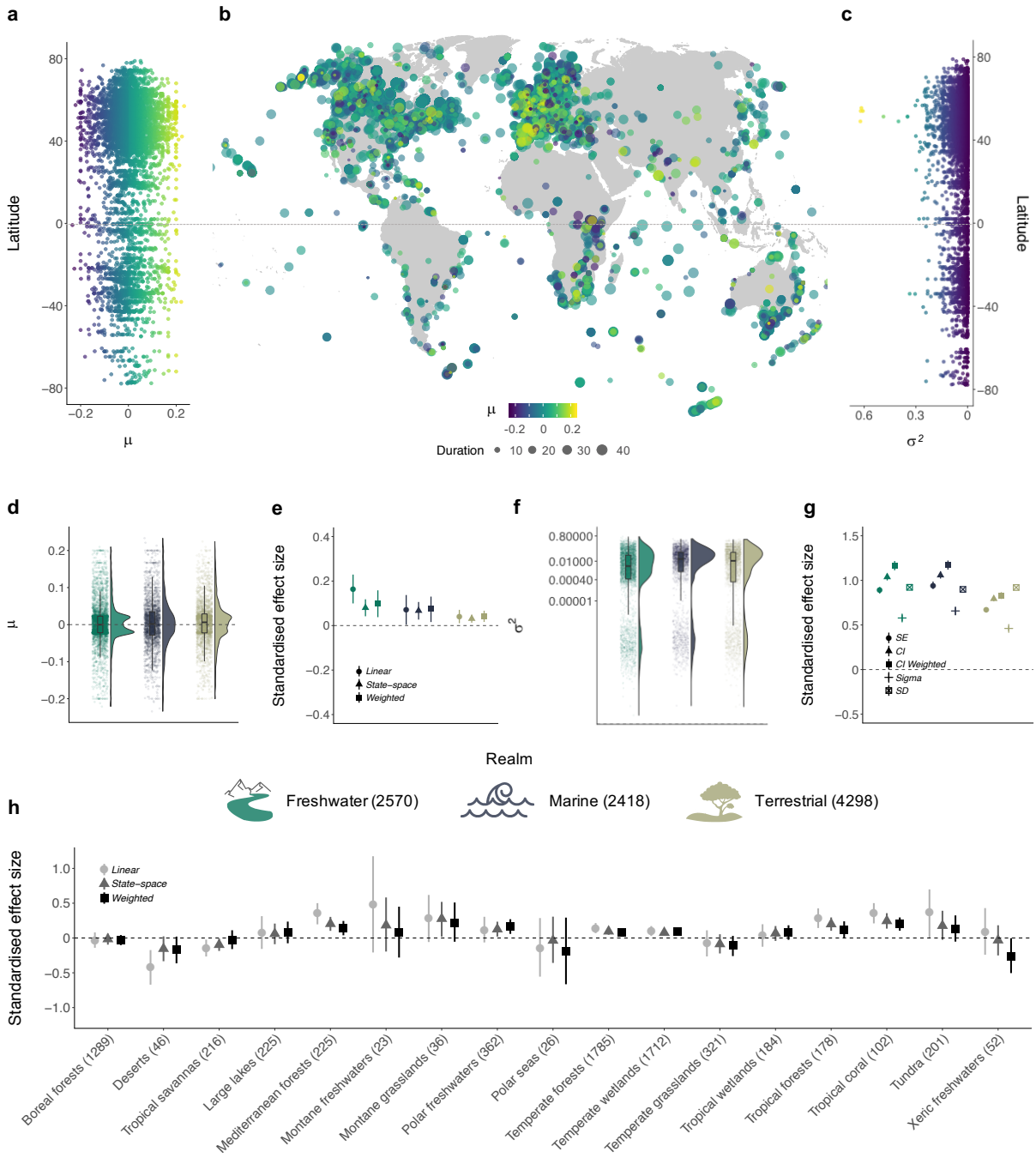

Figure 1. Population declines, increases and fluctuations over time occur across all latitudes and biomes within the freshwater, marine and terrestrial realms. Results include 9286 populations from 2084 species. The lack of biogeographic patterning in vertebrate population trends was also apparent on a UK scale (Figure S6 and Table S2). The numbers in

175 the legend for plots **d**-**g** and on the x axis in plot **c** show the sample sizes for realms and biomes,
176 respectively. The μ values of population trend (plots **a**-**b**, **d**-**e**, **h**) and the σ^2 values of population
177 fluctuation (plots **c**, **f**-**g**) were derived from state-space model fits of changes in abundance over
178 the monitoring duration for each population. Plots **d** and **f** show the density distribution of
179 population trends across realms, the raw values (points) and boxplots with the mean, first and
180 third quartiles and boxplot whiskers that indicate the distance that covers 1.5 times the
181 interquartile range. Plots **e**, **g** and **h** show the effect sizes and the 95% credible intervals of
182 population trends (**e**, **h**) across realms and biomes, and fluctuations across realms (**g**). For
183 variation in fluctuations across biomes, see SI Figure S9. The three estimates for each
184 realm/system in plots **e** and **h** refer to different analytical approaches: population trends calculated
185 using linear models (circles), state-space models (μ, triangles), and population trends (μ)
186 weighted by τ^2, the observation error estimate from the state-space models (squares). The five
187 estimates in plot **g** refer to different analytical approaches, where the response variables in the
188 models were: 1) the standard error around the slope estimates of the linear model fits of
189 abundance versus year (circles), 2) half of the 95% confidence interval around the μ value of
190 population change (triangles), 3) half of the 95% confidence interval around μ weighted by τ^2, (full
191 squares), 4) the process noise (σ^2) from the state-space models, and 5) the standard deviation of
192 the raw data for each population time series (empty squares). Effect sizes were standardized by
193 dividing the effect size by the standard deviation of the corresponding input data. The process
194 noise is the total variance around the population trend minus the variance attributed to observation
195 error. Error bars in plots **e**, **g** and **h** show 95% credible intervals. See Table S2 for model outputs.
196

197 **Taxonomic and phylogenetic patterns of population trends and fluctuations**

198 We found taxonomic, but not phylogenetic patterns, in population trends and fluctuations over
199 time among nearly 10 000 populations from over 2000 vertebrate species, with amphibians

200 emerging as the taxa experiencing pronounced declines (Figure 2, Table S2). Amphibians
201 experienced net declines over time (slope = -0.01, CI = -0.02 to -0.005), whereas birds, mammals
202 and reptiles experienced net increases (slope = 0.004, CI = 0.003 to 0.01; slope = 0.01, CI = 0.01
203 to 0.01; slope = 0.02, CI = 0.01 to 0.02), with birds having a bimodal trend distribution indicating
204 greater numbers of increasing and decreasing trends (Hartigans' dip test, $D = 0.04$, $p < 0.01$,
205 Figure 1a, see Figures S6, S7 and S13). Bony fish population trends were centred on zero (slope
206 = -0.001, CI = -0.004 to 0.002, Figure 1a-b) and sharks and rays showed net declines, but the
207 credible intervals overlapped zero (slope = -0.01, CI = -0.02 to 0.01). Fluctuations were most
208 common for amphibian populations (slope = 0.04, CI = 0.036 to 0.049, Figure 2d), which were
209 monitored for the shortest time period on average (11 years, Figure S1, Table S2). We did not
210 detect finer scale species-level phylogenetic clustering of population change (both trends and
211 fluctuations) within amphibian, bird and reptile classes (Figures 2 and S16, Table S4). Similarly,
212 species identity within amphibian, bird and reptile classes did not explain variation in population
213 trends or fluctuations (Figures 2 and S16, Table S4). There were no distinct clusters of specific
214 clades that were more likely undergo increases, decreases or fluctuations in population
215 abundance (Figure 2).
216

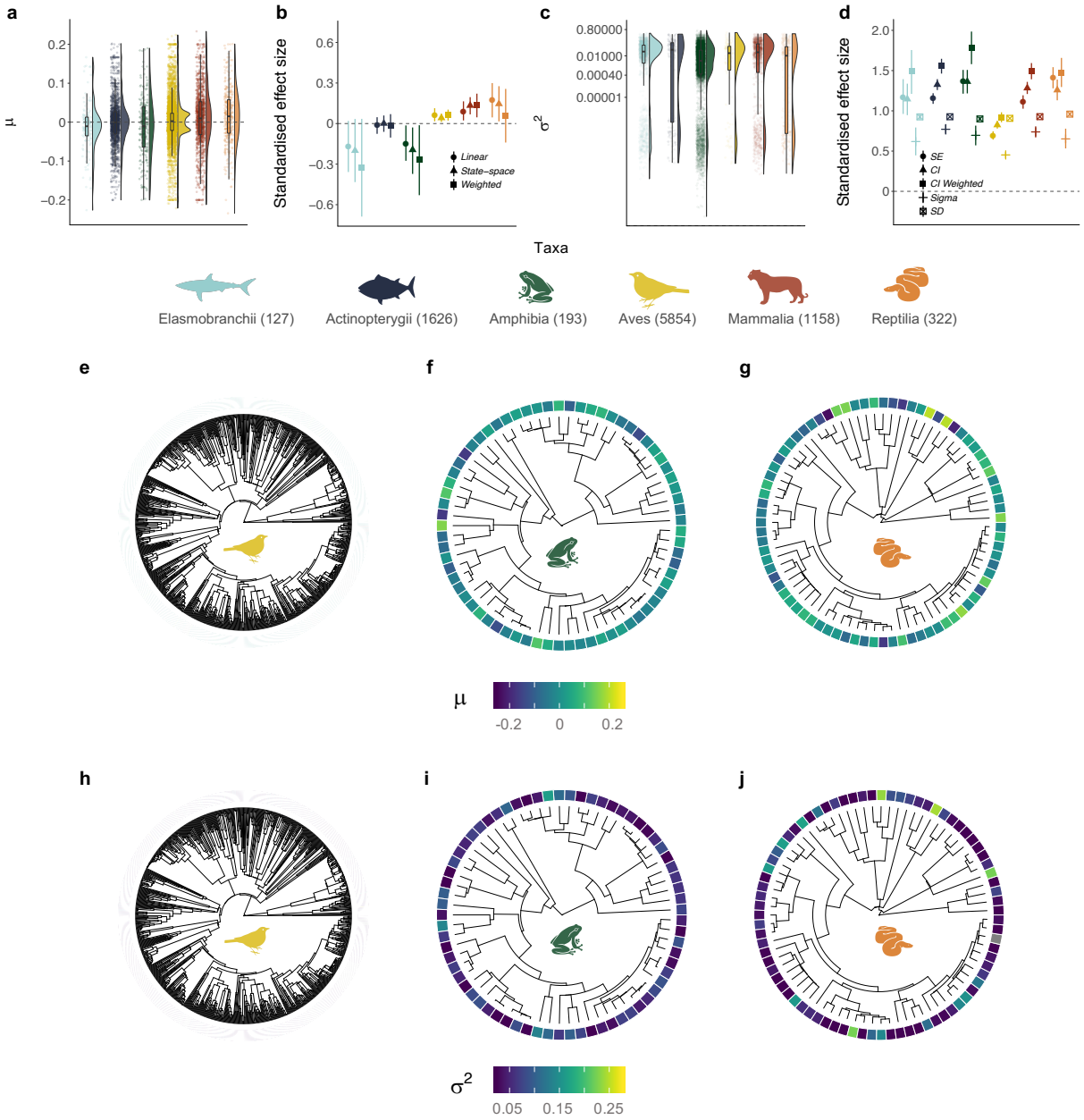

Figure 2. Population trends and fluctuations varied more among, rather than within, taxa, with amphibians being the only group showing pronounced declines over time. There were no distinct phylogenetic patterns in population trends and fluctuations (plots **e**-**j**). For details on phylogenetic models, see methods. Grey colour in the heatmap in plot h shows species for which no population trend data were available. The numbers in the legend for plots **a**-**d** show sample size for each taxon. The μ values of population trend (plots **a**-**b**, **e**-**g**) and the σ^2 values of

224 population fluctuation (plots **c-d**, **h-j**) were derived from state-space model fits of changes in
225 abundance over the monitoring duration for each population. Plots **a** and **c** show the density
226 distribution of population trends across taxa, the raw values (points) and boxplots with the mean,
227 first and third quartiles and boxplot whiskers that indicate the distance that covers 1.5 times the
228 interquartile range. Plots **b** and **d** show the effect sizes and the 95% credible intervals of
229 population trends (**b**) and fluctuations (**d**) across the five studied taxa. Effect sizes (plots **b** and **d**)
230 were standardized by dividing the effect size by the standard deviation of the corresponding input
231 data. Error bars in plots **b** and **d** show 95% credible intervals. See Figure 1 caption for further
232 details on effect sizes and Tables S2 and S4 for model outputs.
233

234 **Population trends and fluctuations across rarity metrics, IUCN Red List Categories and**
235 **threats**

236 Species-level metrics, such as rarity and global IUCN Red List Category, did not explain the
237 heterogeneity in trends of monitored populations in the Living Planet Database. Both rare and
238 common species experienced declines, increases and fluctuations in population abundance over
239 time (Figures 3 and 4). Across these time series, species with smaller ranges, smaller population
240 sizes, or narrower habitat specificity (i.e., rare species) were not more prone to population
241 declines than common species (Figure 3, Table S2). Populations that experienced more
242 fluctuations had smaller mean population sizes on average (slope = -0.001, CI = -0.001 to -0.001,
243 Figure 3f). We found increasing, decreasing and stable populations across all IUCN Red List
244 Categories (Figure 4a). For example, a population of the Least concern species red deer (*Cervus*
245 *elaphus*) in Canada declined by 68% over seven years going from 606 to 194 individuals and a
246 population of the critically endangered Hawksbill sea turtle (*Eretmochelys imbricate*) from
247 Barbados increased by 269% over seven years going from 89 to 328 individuals. We found more
248 fluctuations (Least concern: slope = 0.022, CI = 0.021 to 0.023; Critically endangered: slope =

0.035, CI = 0.028 to 0.041), but not more population declines, with increasing IUCN Red List Category (Figure 4, Table S2). Populations from species with a higher number of threats from the species' IUCN Red List profiles did not experience greater declines when compared to those categorised with a smaller number of threats (Figure 4f). There were no distinct signatures of threats from the species' IUCN Red List profiles that were associated with predominantly declining local trends of monitored populations (Figure 4e) and there were increasing, decreasing and stable trends across all threat types.

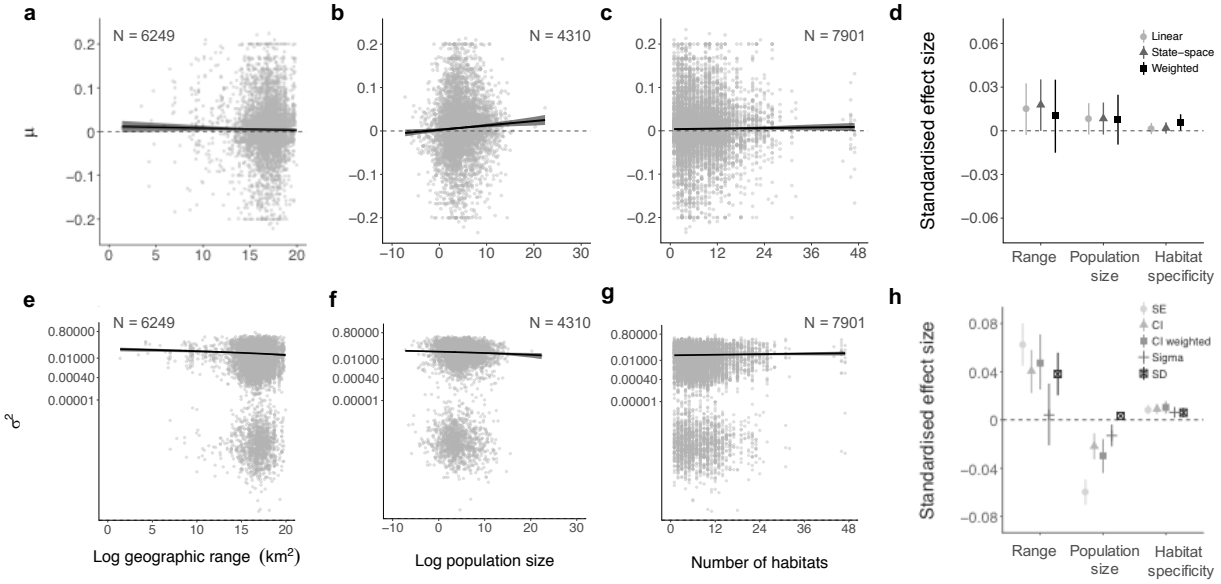

Figure 3. Rarity metrics do not explain heterogeneity in local population trends, and both rare and common species experienced declines and increases over time, whereas smaller populations fluctuated more over time. Numbers on plots show sample size for each metric. Rarity metrics were calculated for all species for which information was available and cover all taxa represented in the Living Planet Database, with the exception of geographic range, which refers to the global range of only bird and mammal species in the global Living Planet Database (plots **a**-**e**). The μ values of population trend (plots **a**-**d**) and the σ^2 values of population fluctuation

(plots **e**-**h**) were derived from state-space model fits of changes in abundance over the monitoring duration for each population. Plots **d** and **h** show the effect sizes and the 95% credible intervals of three rarity metrics on population trends (**d**) and fluctuations (**h**). Effect sizes (plots **d** and **h**) were standardized by dividing the effect size by the standard deviation of the corresponding input data. Error bars in plots **d** and **h** show 95% credible intervals. Lines on **a**-**c** and **e**-**g** show model fits and 95% credible intervals. See Figure 1 caption for further details on effect sizes and Table S2 for model outputs.

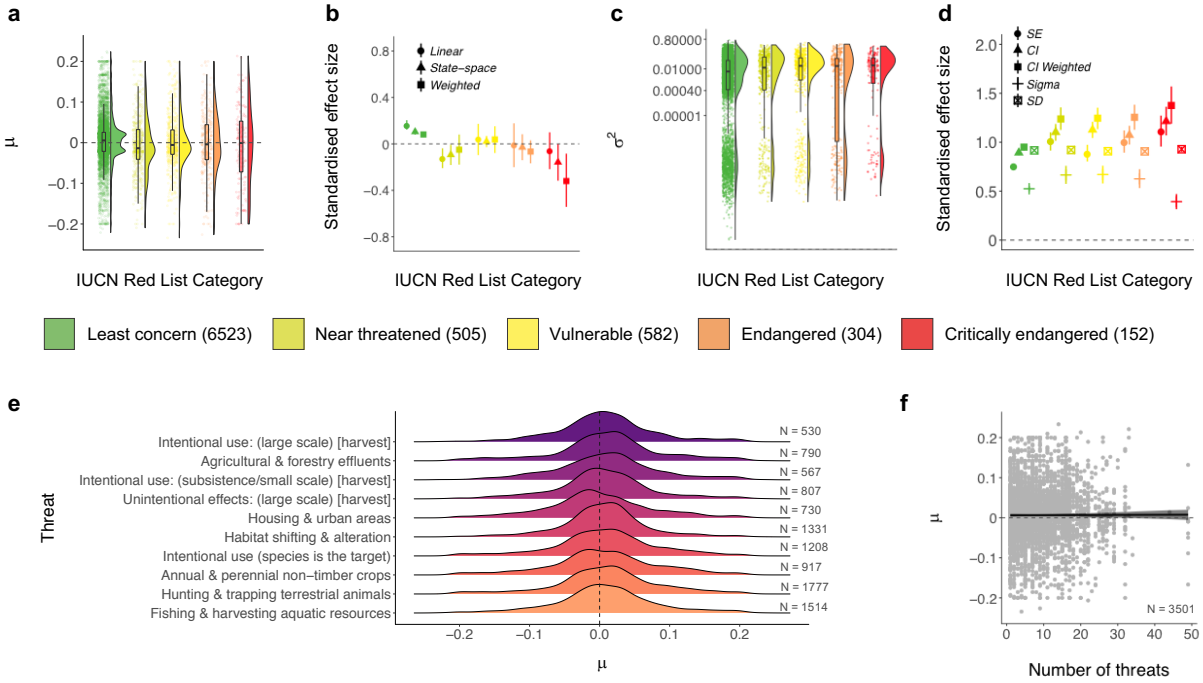

Figure 4. On local scales, there are increasing, decreasing and stable populations across the full spectrum of the globally-determined species' IUCN Red List Category and anthropogenic threat type from the species' IUCN Red List profiles. Numbers in the legend for plots **a**-**d** and in plots **e**-**f** show sample size for each metric. Plots **a** and **c** show the density distribution of population trends across Red List status, the raw values (points) and boxplots with the mean, first and third quartiles and boxplot whiskers that indicate the distance that covers 1.5

times the interquartile range. Plots **b** and **d** show the effect sizes and the 95% credible intervals of population trends (**b**) and fluctuations (**d**) across Red List status categories. The μ values of population trend (plots **a**, **e**-**f**) and the σ^2 values of population fluctuation (plots **c**) were derived from state-space model fits of changes in abundance over the monitoring duration for each population. For the relationships between type and number of threats and population fluctuations, see Figure S19. Plots **b** and **d** show the effect sizes and the 95% credible intervals for population trends (**b**) and fluctuations (**d**) across IUCN Red List Categories. Effect sizes (plots **b** and **d**) were standardized by dividing the effect size by the standard deviation of the corresponding input data. Error bars in plots **b** and **d** show 95% credible intervals. Plot **e** shows the distributions of population trends across different threats that the species face globally, with the central tendencies of all distributions overlapping with zero. Lines in plot **f** show model fit and 95% credible intervals, where "number of threats" refers to the number of different threats that each species, whose populations are locally monitored, are exposed to on a global scale. See Figure 1 caption for further details on effect sizes, Methods for details on deriving the number and types of threats and Table S2 for model outputs.

Discussion

Taken together, our analysis of nearly 10 000 vertebrate population time series using a state-space modelling approach demonstrated ubiquitous alterations in vertebrate abundance over time across all biomes on Earth. We revealed that population change includes both increasing and decreasing populations and spans a wide spectrum of magnitudes, and while anthropogenic impacts have accelerated in recent decades, our results highlight that vertebrate species span a wide spectrum of population change across variation in the number and types of threats to which species might be exposed. Against a backdrop of no biogeographic patterning of population trends and fluctuations (Figure 1), we uncovered distinct taxonomic signals, with amphibians

representing the only taxa that exhibited pronounced net declines, while birds, mammals and reptiles on average became more abundant over time (Figure 2). Within amphibian, bird and reptile taxa, there was no distinct phylogenetic clustering of closely-related species experiencing similar population trends or fluctuations (Figure 2). We found that both rare and common species experienced the full spectrum of population change, from declines to no net changes and increases. Species' geographic range, mean population size and habitat specificity did not explain variation in population trends, but species with smaller population sizes were nevertheless more likely to fluctuate, potentially increasing their extinction risk (Figure 3). There was no consistent pattern of greater population declines with increasing IUCN Red List Category (Figure 4). On a global scale, the vertebrate species in the Living Planet Database are exposed to a variety of threats according to the species' IUCN Red List profiles, but on more local scales, none of the threats were characterized by predominantly declining populations (Figure 4), testifying to the diverse ways in which populations are likely responding to threats across the Anthropocene.

Contrary to our initial predictions, we did not find a distinct geographic patterning of population change around the world, nor a consistent trend of increasing declines in population abundance with increasing IUCN Red List Category (Figures 1 and 4). Similar lack of biogeographic signal has been documented in regional studies of population change from the Netherlands[34] and in temperate North America and Europe[39]. Coarsely represented biogeographic regions and global-scale species' IUCN Red List Categories and threat types might not capture the drivers acting in the locations of the specific populations we studied[32,40–42]. Furthermore, the same driver can have opposing effects on population abundance at different sites[43]. A lack of biome-specific directional trends in population change, despite a spatial clustering of human pressure around the world[12], can also arise due to differences in species traits and vulnerability to environmental change within biomes[16–18]. Accounting for divergent responses of species to global change is key when

translating global policy, such as the upcoming post-2020 planetary biodiversity strategy[44], into conservation actions implemented on scales much finer than biogeographic realms.

Our results highlight variation in population change among taxa, with amphibians emerging as the taxa experiencing the most pronounced declines in the Living Planet Database. The remaining taxa showed either stable or increasing net changes in abundance over time (Figure 2). Such taxonomic patterns could be driven by different taxon-specific factors including reproductive strategy, trophic level, generation time and life history traits[45,46]. For amphibians, population declines have been linked to the spread of a fungal disease (chytrid fungus, *Batrachochytrium dendrobatidis*), facilitated by global warming[47], as well as habitat loss and Allee effects in small populations[48]. Within bird, amphibian and reptile taxa, phylogenetic relatedness and species-level taxonomic classification did not explain variation in population trends and fluctuations. A similar lack of phylogenetic dependencies has been detected for the population growth rates of migratory birds[49]. While phylogenetic clustering might be lacking in contemporary trends, there is evidence that phylogenetic relatedness predicts extinction, a process occurring over much longer time scales[6,7]. Over shorter time periods, species' traits and ability to persist, reproduce and disperse in ever changing landscapes might be influencing local abundance[16], which has created a mix of winners and losers across all taxa[15]. We demonstrate ongoing alterations in the abundances of six vertebrate taxa which over time, may lead to shifts in community composition and ultimately alter ecosystem function as some species become locally extinct whilst others become more abundant[9,10].

Surprisingly, our results indicate that despite decades of conservation focus on rare species[19–21], both rare and common species in the Living Planet Database experienced declines and increases in population abundance over the period of monitoring. The lack of rarity effects on population

trends can be explained by theory and empirical evidence demonstrating that small populations do not necessarily have a higher likelihood of experiencing declines and some species are able to persist in small, but stable populations[50]. The power of rarity metrics to predict population trends could also be mediated by whether species are naturally rare, or have become rare due to external drivers in recent years[51,52]. Naturally rare species might be more likely to persist over time, whereas species that have more recently become rare might be more likely to decline in response to environmental disturbance. Furthermore, the timing and magnitude of past and current disturbance events influence population trends[43,53] and there could be temporal lags in both positive and negative abundance changes over time[43,54]. However, disentangling the processes leading to rarity over time remains challenging, and across the 2084 species we studied, there are likely cases of both natural and human-driven vertebrate population change. We found that species with small populations were, nevertheless, more likely to fluctuate (Figure 3f), which may increase their probability of extinction, a process that could play out over longer time-scales than found for most population monitoring time series to date[22,23,55]. Our results highlight that rarity metrics alone do not capture the heterogeneity in local population change over time, and common species should not be overlooked in conservation prioritization decisions as they could be as likely to decrease in abundance over time as rare species.

Our finding that declines are not universal, or even predominant, for vertebrate populations monitored for longer than five years in the Living Planet Database contrasts with reports of an overall decline in the Living Planet Index[56], a weighted summary of population change across all abundance time series in the Living Planet Database. Consistent with our results, the Living Planet Reports[56–58] also document that the numbers of declining and increasing species are similar across this database, but the Living Planet Reports document a larger magnitude of population declines relative to increases. The calculation of the Living Planet Index involves

differential weighting of population trends derived using logged abundance data, geometric means and generalized additive models, which could explain the discrepancies between our study findings and those of the Living Planet Reports[59]. The Living Planet Index is hierarchically averaged from populations to species, taxa and realm and is also weighted by the estimated and relative number of species within biomes, which influences the direction and magnitude of the Living Planet Index[59,60]. In contrast, our analysis explores the heterogeneity in local trends and fluctuations of monitored species from the raw population abundance data, and thus, we did not use an index with weightings and we did not aggregate population trends to a species-level. Rather than summarising trends with an index, our goal was to explain variability in abundance over time across better monitored vertebrates around the world. We detected net population declines at local scales over time only in the amphibian taxa, in contrast with the overall negative trend of the aggregate weightings of the Living Planet Index[56]. We caution that distilling the heterogeneity of local population change at sites around the world into a simple metric may hide diverging trends at local scales, where we found both increases and declines among species.

The magnitude and strength of population trends could be influenced by how long populations are monitored[61], as well as whether monitoring began during a population peak or a population trough[62]. While overall, we did not find a strong effect of duration on the detected population trends in the Living Planet Database (Figures S7-8, Table S2), our findings demonstrated that for reptiles, time series with longer durations are more likely to capture declines (Table S2). We also found a bimodal pattern of weak population increases and decreases in time series with longer durations particularly for terrestrial bird species with the monitoring unit being an index (Figure S13). Seven key challenges have been identified when drawing robust inference about population trends over time: establishment of the historical baseline, representativeness of site selection, robustness of time series trend estimation, mitigation of detection bias effects, and ability to

405 account for potential artefacts of density dependence, phenological shifts and scale-dependence
406 in extrapolation from sample abundance to population-level inference[63]. New methods to
407 rigorously account for different sources of uncertainty in time series monitoring will allow the
408 analyses of available population data to better inform global estimates of net trends across taxa.
409
410 The strength of documented relationships between population dynamics and global change could
411 be influenced by how well-monitored populations capture the full range of variation in driver
412 intensity. To attribute population trends and fluctuations to site-specific anthropogenic drivers, we
413 need to go beyond previous studies that have focused exclusively on declines and extinctions[5,64].
414 We require attribution analyses that statistically test the links between observed changes in
415 ecosystems and the experienced extrinsic pressure[3]. Through attribution studies that encompass
416 the full spectrum of population change, including positive, negative and stable trends[43,65], we can
417 better understand the variety of ways in which climate change, land-use change and other drivers
418 are altering global biodiversity. For a subset of the bird populations in the Living Planet Database,
419 greater warming of temperatures corresponded with a higher likelihood of population declines
420 over time[65], which could be caused by worldwide and cross-biome phenological mismatches
421 between breeding and resource availability[66]. Across terrestrial species represented in the Living
422 Planet Database, peak forest loss was associated with accelerations in both population increases
423 and decreases in the period following habitat alteration[43]. There is evidence from the marine realm
424 that when species are simultaneously exposed to multiple drivers, the resulting biodiversity effects
425 are antagonistic and could produce patterns of no net biodiversity changes[67]. The next critical
426 step is to test how multiple global change drivers together[12] influence populations across both
427 terrestrial and marine realms and determine how these relationships are mediated by species'
428 traits and vulnerability to extrinsic threats[68].
429

In summary, our global analysis reveals the ubiquitous nature of population change over time across monitored vertebrate species. We show that in a time of accelerating global change, there were as many increases as there are decreases in population abundance over time. Among this heterogeneity, we uncovered pronounced declines in amphibian abundance as well as net abundance increases for birds, mammals and reptiles in the Living Planet Database. The taxonomic patterning of population change highlights amphibians as a conservation priority, especially as their declines can have further cascading effects across trophic levels within ecosystems. Rarity metrics, specifically geographic range, mean population size and habitat specificity, as well as IUCN Red List Categories, threat types and numbers, and evolutionary history, did not explain the heterogeneity in population change across the data analysed in this study. Our findings caution the use of rarity metrics as a proxy for future global population trends, but suggest that such metrics, in particular mean population size, are nevertheless indicators of population fluctuations, which might ultimately be related to increased species extinction risk. On a global scale, both rare and common vertebrate species face numerous threats due to resource exploitation and habitat change. As human activities continue to accelerate, the next key step is to determine how intrinsic factors, such as rarity attributes and threats, interact with extrinsic global change drivers and together influence the persistence of Earth's biota. Capturing the complexity of species' population dynamics will improve our estimates of shifts in community composition and ultimately the impact of altered ecosystem functions and services around the world.

Methods

All data syntheses, visualization and statistical analyses were conducted using R version 3.5.1[69]. For conceptual diagrams of our workflow, see Figures S1 and S2.

455 **Data sources**

456 *Population data*

457 To quantify vertebrate population change (trends and fluctuations), we extracted the abundance
458 data for 9286 population time series from 2084 species from the publicly available Living Planet
459 Database[70] (http://www.livingplanetindex.org/data_portal) that covered the period between 1970
460 and 2014 (Table S1). These time series represent repeated monitoring surveys of the number of
461 individuals in a given area, hereafter called "populations". Monitoring duration differed among
462 populations, with a mean duration of 23.9 years and a mean sampling frequency of 23.3 time
463 points (Figure S1, see SI Figures S7 and S8 for effects of monitoring duration on detected trends).
464 In the Living Planet database, 17.9% of populations were sampled annually or in rare cases
465 multiple times per year. The time series we analysed include vertebrate species that span a large
466 variation in age, generation times and other demographic-rate processes. For example, from
467 other work that we have conducted, we have found that when generation time data were available
468 (approximately 50.0% or 484 out of 968 bird species, and 15.6% or 48 out of 306 mammal
469 species), the mean bird generation time is 5.0 years (min = 3.4 years, max = 14.3 years) and the
470 mean mammal generation time is 8.3 years (min = 0.3 years, max = 25 years)[43]. Thus, we believe
471 that most vertebrate time series within the LPD capture multiple generations.

472

473 In our analysis, we omitted populations which had less than five time points of monitoring data,
474 as previous studies of similar population time series to the ones we have analysed have found
475 that shorter time series might not capture directional trends in abundance[61]. Populations were
476 monitored using different metrics of abundance (e.g., population indices vs. number of
477 individuals). Before analysis, we scaled the abundance of each population to a common

478 magnitude between zero and one to analyse within-population relationships to prevent conflating
479 within-population relationships and between-population relationships[71]. Scaling the abundance
480 data allowed us to explore trends among populations relative to the variation experienced across
481 each time series.
482
483 *Phylogenetic data*
484 We obtained phylogenies for amphibian species from https://vertlife.org[4], for bird species from
485 https://birdtree.org[8], and for reptile species from https://vertlife.org[6]. For each of the three classes
486 (*Amphibia*, *Aves* and *Reptilia*), we downloaded 100 trees and randomly chose 10 for analysis (30
487 trees in total). Species-level phylogenies for the classes *Actinopterygii* and *Mammalia* have not
488 yet been resolved with high confidence[72,73].
489
490 *Rarity metrics, IUCN Red List Categories and threat types*
491 We defined rarity following a simplified version of the 'seven forms of rarity' model[74], and thus
492 consider rarity to be the state in which species exist when they have a small geographic range,
493 low population size, or narrow habitat specificity. We combined publicly available data from three
494 sources: 1) population records for vertebrate species from the Living Planet Database to calculate
495 mean population size, 2) occurrence data from the Global Biodiversity Information Facility[75]
496 (https://www.gbif.org) and range data from BirdLife[76] (http://datazone.birdlife.org) to estimate
497 geographic range size, and 3) habitat specificity and Red List Category data for each species
498 from the International Union for Conservation[77] (https://www.iucnredlist.org). The populations in
499 the Living Planet Database[70] do not include species that have gone extinct on a global scale. We
500 extracted the number and types of threats that each species is exposed to globally from their
501 respective species' IUCN Red List profiles[77].
502

503 **Quantifying population trends and fluctuations over time**

504 In the first stage of our analysis, we used state-space models that model abundance (scaled to a
505 common magnitude between zero and one) over time to calculate the amount of overall
506 abundance change experienced by each population (μ, [38,78]). State-space models account for
507 process noise (σ^2) and observation error (τ^2) and thus deliver robust estimates of population
508 change when working with large datasets where records were collected using different
509 approaches, such as the Living Planet Database[39,79,80]. Previous studies have found that not
510 accounting for process noise and measurement error could lead to over-estimation of population
511 declines[81], but in our analyses, we found that population trends derived from state-space models
512 were similar to those derived from linear models. Positive μ values indicate population increase
513 and negative μ values indicate population decline. State-space models partition the variance in
514 abundance estimates into estimated process noise (σ^2) and observation or measurement error
515 (τ^2) and population trends (μ):

516 $$X_t = X_{t-1} + \mu + \varepsilon_t, (1)$$

517 where X_t and X_{t-1} are the scaled (observed) abundance estimates (between 0 and 1) in the present
518 and past year, with process noise represented by $\varepsilon_t \sim gaussian(0, \sigma^2)$. We included measurement
519 error following:

520 $$Y_t = X_t + F_t,$$

521 where Yt is the estimate of the true (unobserved) population abundance with measurement error:

522 $$F_t \sim gaussian(0, \tau^2).$$

523 We substituted the estimate of population abundance (Y_t) into equation 1:

524 $$Y_t = X_{t-1} + \mu + \varepsilon_t + Ft.$$

525 Given $X_{t-1} = Y_{t-1} - F_{t-1}$, then:

526 $$Y_t = Y_{t-1} + \mu + \varepsilon_t + F_t - F_{t-1}.$$

527 For comparisons of different approaches to modelling population change, see *Comparison of*
528 *modelling approaches* section.
529
530 **Quantifying rarity metrics**
531 We tested how population change varied across rarity metrics – geographic range, mean
532 population size and habitat specificity – on two different but complementary scales. In the main
533 text, we presented the results of our global scale analyses, whereas in the SI, we included the
534 results when using only populations from the UK – a country with high monitoring intensity, Thus,
535 we quantified rarity metrics for species monitoring globally and in the UK.
536
537 *Geographic range*
538 To estimate geographic range for bird species monitored globally, we extracted the area of
539 occurrence in km^2 for all bird species in the Living Planet Database that had records in the BirdLife
540 Data Zone[76]. For mammal species' geographic range, we used the PanTHERIA database[82]
541 (http://esapubs.org/archive/ecol/E090/184/). To estimate geographic range for bony fish, birds,
542 amphibians, mammals and reptiles monitored in the UK (see Table S5 for species list), we
543 calculated a km^2 occurrence area based on species occurrence data from GBIF[75]. Extracting and
544 filtering GBIF data and calculating range was computationally-intensive and occurrence data
545 availability was lower for certain species. Thus, we did not estimate geographic range from GBIF
546 data for all species part of the Living Planet Database. Instead, we focused on analysing range
547 effects for birds and mammals globally, as they are a very well-studied taxon and for species
548 monitored in the UK, a country with intensive and detailed biodiversity monitoring of vertebrate
549 species. We did not use IUCN range maps, as they were not available for all of our study species,
550 and previous studies using GBIF occurrences to estimate range have found a positive correlation
551 between GBIF-derived and IUCN-derived geographic ranges[83].

552

553 For the geographic ranges of species monitored in the UK, we calculated range extent using a
554 minimal convex hull approach based on GBIF[75] occurrence data. We filtered the GBIF data to
555 remove invalid records and outliers using the *CoordinateCleaner* package[84]. We excluded records
556 with no decimal places in the decimal latitude or longitude values, with equal latitude or longitude,
557 within a one-degree radius of the GBIF headquarters in Copenhagen, within 0.0001 degrees of
558 various biodiversity institutions and within 0.1 degrees of capital cities. For each species, we
559 excluded the lower 0.02 and upper 0.98 quantile intervals of the latitude and longitude records to
560 account for outlier points that are records from zoos or other non-wild populations. We drew a
561 convex hull to most parsimoniously encompass all remaining occurrence records using the *chull*
562 function, and we calculated the area of the resulting polygon using *areaPolygon* from the
563 *geosphere* package .

564

565 *Mean size of monitored populations*

566 We calculated mean size of the monitored population, referred to as population size, across the
567 monitoring duration using the raw abundance data, and we excluded populations which were not
568 monitored using population counts (i.e., we excluded indexes).

569

570 *Habitat specificity*

571 To create an index of habitat specificity, we extracted the number of distinct habitats a species
572 occupies based on the IUCN habitat category for each species' profile, accessed through the
573 package *rredlist*[86]. We also quantified habitat specificity by surveying the number of breeding and
574 non-breeding habitats for each species from its online IUCN species profile (the 'habitat and
575 ecology' section). The two approaches yielded similar results (Figure S3, Table S2, key for the

576 profiling method is presented in Table S4). We obtained global IUCN Red List Categories and
577 threat types for all study species through the IUCN Red List profiles[77].
578
579 **Testing the sources of variation in population trends and fluctuations**
580 In the second stage of our analyses, we modelled the trend and fluctuation estimates from the
581 first stage across latitude, realm, biome, taxa, rarity metrics, phylogenetic relatedness, species'
582 IUCN Red List Category and threat type using a Bayesian modelling framework through the
583 package *MCMCglmm*[87]. We included a species random intercept effect in the Bayesian models
584 to account for the possible correlation between the trends of populations from the same species
585 (see Table S1 for sample sizes). The models ran for 120 000 iterations with a thinning factor of
586 ten and a burn-in period of 20 000 iterations. We assessed model convergence by visually
587 examining trace plots. We used weakly informative priors for all coefficients (an inverse Wishart
588 prior for the variances and a normal prior for the fixed effects):

589 $$Pr(\mu) \sim N(0, 10^8)$$

590 $$Pr(\sigma^2) \sim Inverse\ Wishart\ (V = 0, nu = 0)$$

591
592 *Population trends and fluctuations across latitude, biomes, realms and taxa*
593 To investigate the geographic and taxonomic patterns of population trends and fluctuations, we
594 modelled population trends (μ) and population fluctuations (σ^2), derived from the first stage of our
595 analyses (state-space models), as a function of 1) latitude, 2) realm (freshwater, marine,
596 terrestrial), 3) biome (as defined by the 'biome' category in the Living Planet Database, e.g.,
597 'temperate broadleaf forest'[88] and 4) taxa (*Actinopterygii*, bony fish; *Elasmobranchii*, sharks and
598 rays; *Amphibia*, amphibians; *Aves*, birds; *Mammalia*, mammals; *Reptilia*, reptiles). We used

separate models for each variable, resulting in four models testing the sources of variation in trends and four additional models focusing on fluctuations. Each categorical model from this second stage of our analyses was fitted with a zero intercept to allow us to determine if net population trends differed from zero for each of the categories under investigation. The model structures for all models with a categorical fixed effect were identical with the exception of the identity of the fixed effect, and below we describe the taxa model:

$$\mu_{i,j,k} = \beta_0 + \beta_{0j} + \beta_1 * taxa_{i,j,k},$$

$$y_{i,j,k} \sim gaussian(\mu_{i,j,k}, \sigma^2),$$

where $taxa_{i,j,k}$ is the taxa of the *ith* time series from the *jth* species; β_0 and β_1 are the global intercept (in categorical models, $\beta_0 = 1$) and the slope estimate for the categorical taxa effect (fixed effect), β_{0j} is the species-level departure from β_0 (species-level random effect); $y_{i,j,k}$ is the estimate for change in population abundance for the *ith* population time series from the *jth* species from the *kth* taxa.

Population trends and fluctuations across amphibian, bird and reptile phylogenies

To determine if there is a phylogenetic signal in the patterning of population change within amphibian, bird and reptile taxa, we modelled population trends (μ) and fluctuations (σ^2) across phylogenetic and species-level taxonomic relatedness. We conducted one model per taxa per population change variable – trends or fluctuations using Bayesian linear mixed effects models using the package *MCMCglmm*[87]. We included phylogeny and taxa as random effects. The models did not include fixed effects. We assessed the magnitude of the random effects (phylogeny and species) by inspecting their posterior distributions, with a distribution pushed up against zero indicating lack of effect, since these distributions are always bounded by zero and have only positive values. We used parameter-expanded priors, with a variance-covariance

structure that allows the slopes of population trend (the *mu* values from the first stage analysis using state-space models) to covary for each random effect. The prior and model structure were as follows:

$$Pr(\mu) \sim N(0, 10^8),$$

$$Pr(\sigma^2) \sim Inverse\ Wishart\ (V = 1, nu = 1),$$

$$\mu_{i,k,m} = \beta_0 + \beta_{0k} + \beta_{0m},$$

$$y_{i,k,m} \sim gaussian(\mu_{i,k,m}, \sigma^2),$$

where β_0 is the global intercept ($\beta_0 = 1$), β_{0l} is the phylogeny-level departure from β_0 (phylogeny random effect); $y_{i,k,m}$ is the estimate for change in population abundance for the *ith* population time series for the *kth* species with the *mth* phylogenetic distance.

To account for phylogenetic uncertainty, for each class, we ran ten models with identical structures but based on different randomly selected phylogenetic trees. We report the mean estimates and their range for each class.

Population trends and fluctuations across rarity metrics

To test the influence of rarity metrics (geographic range, mean population size and habitat specificity) on variation in population trends and fluctuations, we modelled population trends (μ) and fluctuations (σ^2) across all rarity metrics. We conducted one Bayesian linear models per rarity metric per model per scale (for both global and UK analyses) per population change variable – trends or fluctuations. The response variable was population trend (μ values from state-space models) or population fluctuation (σ^2 *values from state-space models*), and the fixed effects were

645 geographic range (log transformed), mean population size (log transformed) and habitat
646 specificity (number of distinct habitats occupied). The model structures were identical across the
647 different rarity metrics and below we outline the equations for population trends and geographic
648 range:

649 $$\mu_{i,k,n} = \beta_0 + \beta_{0k} + \beta_1 * geographic\ range_{i,k,n},$$

650 $$y_{i,k,n} \sim gaussian(\mu_{i,k,n}, \sigma^2),$$

651 where *geographic range*$_{i,k,n}$ is the logged geographic range of the *kth* species in the *ith* time
652 series; β_0 and β_1 are the global intercept and slope estimate for the geographic range effect (fixed
653 effect), β_{0j} is the species-level departure from β_0 (species-level random effect); $y_{i,k,n}$ is the
654 estimate for change in population abundance for the *ith* population time series from the *jth* species
655 with the *nth* geographic range.

656

657 *Population trends across species' IUCN Red List Categories*

658 To investigate the relationship between population change and species' Red List Categories, we
659 modelled population trends (μ) and fluctuations (σ^2) as a function of Red List Category
660 (categorical variable). We conducted one Bayesian linear model per population change metric
661 per scale (for both global and UK analyses). To test variation in population trends and fluctuations
662 across the types and number of threats to which species are exposed, we conducted a post-hoc
663 analysis of trends and fluctuations across threat type (categorical effect) and number of threats
664 that each species is exposed to across its range (in separate models). The model structures were
665 identical to those presented above, except for the fixed effect which was a categorical IUCN Red
666 List Category variable.

667

668 The analytical workflow of our analyses is summarized in conceptual diagrams (Figures S1 and
669 S2) and all code is available on GitHub ((https://github.com/gndaskalova/PopChangeRarity, DOI
670 10.5281/zenodo.3817207).

671 **Data limitations**

672 *Taxonomic and geographic gaps*

673 Our analysis is based on 9286 monitored populations from 2084 species from the largest currently
674 available public database of population time series, the Living Planet Database[70]. Nevertheless,
675 the data are characterized by both taxonomic and geographic gaps that can influence our findings.
676 For example, there are very few population records from the Amazon and Siberia (Figure 1b) –
677 two regions currently undergoing rapid environmental changes due to land-use change and
678 climate change respectively. Additionally, birds represent 63% of all population time series in the
679 Living Planet Database, whilst taxa such as amphibians and sharks where we find declines are
680 included with fewer records (Figures 2 and S5). On a larger scale, the Living Planet Database
681 under-represents populations outside of Europe and North America and over-represents common
682 and well-studied species[60]. We found that for the populations and species represented by current
683 monitoring, rarity does not explain variation in population trends, but we note that the relationship
684 between population change and rarity metrics could differ for highly endemic specialist species
685 or species different to the ones included in the Living Planet Database[89]. As ongoing and future
686 monitoring begins to fill in the taxonomic and geographic gaps in existing datasets, we will be able
687 to re-assess and test the generality of the patterns of population change across biomes, taxa,
688 phylogenies, species traits and threats.
689

690 *Monitoring extent and survey techniques*

691 The Living Planet Database combines population time series where survey methods were
692 consistent within time series but varied among time series. Thus, among populations, abundance
693 was measured using different units and over varying spatial extents. There are no estimates of
694 error around the raw population abundance values available and detection probability likely varies
695 among species. Thus, it is challenging to make informed decisions about baseline uncertainty in
696 abundance estimates without prior information. We used state-space models to estimate trends
697 and fluctuations to account for these limitations as this modelling framework is particularly
698 appropriate for analyses of data collected using disparate methods[39,79,80]. Another approach to
699 partially account for observer error that has been applied to the analysis of population trends is
700 the use of occupancy models[34]. Because the precise coordinates of the polygons where the
701 individual populations were monitored are not available, we were not able to test for the potential
702 confounding effect of monitoring extent, but our sensitivity analysis indicated that survey units do
703 not explain variation in the detected trends (Figure S13).
704
705 *Temporal gaps*
706 The population time series we studied cover the period between 1970 and 2014, with both
707 duration of monitoring and the frequency of surveys varying across time series. We omitted
708 populations which had less than five time points of monitoring data, as previous studies of similar
709 population time series data have found that shorter time series are less likely to capture directional
710 trends in abundance[61]. In a separate analysis, we found significant lags in population change
711 following disturbances (forest loss) and that population monitoring often begins decades to
712 centuries after peak forest loss has occurred at a given site[43]. The findings of this related
713 Daskalova *et al.* (in press) study suggest that the temporal span of the population monitoring does
714 not always capture the period of intense environmental change and lags suggest that there might
715 be abundance changes that have not yet manifested themselves. Thus, the detected trends and

716 the baseline across which trends are compared might be influenced by when monitoring takes
717 place and at what temporal frequency. Challenges of analysing time series data are present
718 across not just the Living Planet Database that we analysed, but more broadly across population
719 data in general, including invertebrate datasets[63]. Nevertheless, the Living Planet Database
720 represents the most comprehensive compilation of vertebrate temporal population records to
721 date, allowing for the most comprehensive analyses possible into the patterns of vertebrate trends
722 and fluctuations around the world.
723

724 *Time series with low variation*

725 Eighty populations (<1% of the 9286 time series) had very little variance (see Table S7 for full
726 references for those studies). The majority of those studies are for bird species and come from
727 the North American breeding bird survey with a measurement unit of an index[90]. We have also
728 observed some time series that appear to show logistic relationships with little natural variance
729 (e.g., time series 468, 10193, 17803, see Table S8 for full references). Inspecting the raw data
730 showed that some populations have abundances which follow an almost perfect linear or
731 logarithmic increase over time, as could be the case for modelled, versus raw field data. We
732 provide the references for these studies and cannot definitely attribute the low variance to a
733 particular cause across all studies. Some of these studies are reported in units that are an index
734 which may not capture variation in the same way as other raw units of population data. Some of
735 these time series may represent modelled population data based on demographic information
736 rather than only direct observations of populations (e.g., time series 1355[91]). We chose to not
737 remove studies that may not be raw observation time series based on visual inspection of trends
738 to avoid introducing bias against populations with naturally low variation into our analysis.

739

740 *Clustering in the values of population trends and fluctuations*

741 We found a clustering of population trend and fluctuations values in some parts of the population
742 change spectrum. For example, we found two peaks – in small increases and in small decreases
743 over time – which were most prevalent in terrestrial bird studies and species which were monitored
744 using an index (Figure 2, Figure S13). Overall 11.4% of time series had trend values between
745 0.02 and 0.03 and 11.6% of time series had trend values between -0.03 and -0.02. There was
746 also a similar, but smaller, clustering around trends of 0.25 and -0.25. All reported population
747 trends are from models that converged successfully, and visual inspection indicated to us that the
748 μ values are appropriate estimates for the individual time series (Figure S7e). We investigated
749 the population time series where the value of the population trends over time were estimated to
750 be the same value and found that they came from a variety of taxa, locations and survey methods
751 (Figure S7e). We hypothesise that there might be a publication bias against publishing no net
752 change studies, which could explain the trough in μ values of around zero in long-term studies.
753 The clustering of values for some time series may sometimes be associated with the same time
754 series that also have low variance (Figure S7e, see discussion above). With the information
755 available in the Living Planet Database metadata, we cannot fully explain the clustering in
756 population trends. We advocate for more detailed metadata in future versions of the Living planet
757 database to allow researchers to filter the database appropriately for individual analyses.

758

759 *Challenges in estimating geographic range*

760 Estimating geographic range across taxa, and specifically for species that are not birds or
761 mammals, remains challenging due to data limitations. We used a static measure of geographic

range, which does not account for changes in species distributions over time. Furthermore, species could naturally have a small range or the small range size could be due to historic habitat loss[92]. The UK populations included in the Living Planet Database are predominantly from species with wide geographic ranges (Table S3), and our global scale analysis of the relationship between population change and geographic range is based on mammal and bird data. As data availability improves, future research will allow us to test the effect of geographic range on the trends of other taxa, such as amphibians and sharks.

Sensitivity analyses

Trends relative to null expectation

We tested whether the number of increasing and decreasing populations trends differed from a null expectation using a data randomisation approach (Figure S6b). We used linear models to estimate trends in the data and randomized data with identical structure to the Living Planet Database. We found that there were over 10 times more population declines and increases in the real data relative to the randomised data (2.29% of trends were declining and 2.30% were increasing in the randomised data, versus 28.9% and 32.5% of time series which had significant negative and positive slopes in the real data, respectively).

Monitoring duration, sampling methods and site-selection bias

To assess the influence of monitoring duration on population trends, we used a Bayesian linear model. 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. Monitoring duration was weakly positively related to vertebrate population trends, with slightly greater population increases found for longer duration studies (Figure S7, Table S2). There was a similar weakly positive effect of number of time points within time series (Table S2).

787 Additionally, we tested if monitoring duration influenced the relationships between population
788 trends across systems, and population trends across taxa. We found that duration did not
789 influence those relationships, with the exception of reptiles, where declines were more frequent
790 as monitoring duration increased (Table S2). Variation in population trends was not explained by
791 sampling method across the five most commonly used abundance metrics (population index,
792 number of individuals, number of pairs, number of nests and population estimate, Figure S13).
793 Following Fournier *et al.* 2019[62], we tested the time series that we analysed for site-selection bias.
794 Removing the first five survey points reduces the bias stemming from starting population surveys
795 at points when individual density is high, whereas removing the last five years reduces the bias
796 of starting surveys when species are very rare. The distribution of population trend values across
797 time series was not sensitive to the omission of the first five (left-truncation) or the last five years
798 (right-truncation) of population records (Figure S6a). Additionally, we used a data randomisation
799 approach to compare the distribution of trends from the real data to a null distribution and found
800 different patterns (Figure S6b). Overall, our sensitivity analyses suggest that our findings are
801 robust to the potential confounding effects of differences in monitoring duration, sampling method
802 and site-selection.
803
804 *Comparison of modelling approaches*
805 We conducted the following supplementary analyses: in the second-stage Bayesian models
806 estimating population trends across systems, biomes, taxa and rarity metrics, 1) we weighed *mu*
807 values by the square of *tau*, the observation error estimate derived from the state-space models[38],
808 2) we used slopes of linear model fits of abundance (scaled at the population level, centered on
809 zero and with a standard deviation of one)[71] instead of the *mu* estimates from state-space models,
810 3) we modelled the standard error around the slope values of the linear models, the error around
811 *mu* (half of the 95% confidence interval) and the standard deviation of the raw population data for

each time series as additional metrics of population variability. To allow comparison, we scaled the different metrics of population variability to be centred on zero and with a standard deviation of one before they were used as response variables in models. All different analytical approaches yielded very similar results (see main text and Figures S6, S7 and S10, Table S2).

Data availability

Code for all data processing and analyses and summary datasets are publicly available on GitHub[93]. Raw data are available from the following websites: for population time series[70] - http://www.livingplanetindex.org/data_portal, GBIF occurrences[75] - https://www.gbif.org, bird geographic ranges[76] - http://datazone.birdlife.org, mammal geographic ranges[82] - http://esapubs.org/archive/ecol/E090/184/, species' habitat preferences, threat types and IUCN Red List Categories[77] - https://www.iucnredlist.org, and phylogenies[6–8] - https://vertlife.org and https://birdtree.org.

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Author contributions

GND and IMS conceived the idea and conducted the statistical analyses. JLG contributed to the calculation of geographic range estimates. All authors contributed to the integration of the LPI, GBIF and IUCN databases, which GND led. GND created all figures with input from IMS. GND wrote the first draft of the manuscript and all authors contributed to revisions. IMS supervised the research as a senior author.

Competing interests

The authors declare no competing interests.

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