All is not decline across global vertebrate populations

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Abstract

The populations of Earth's species are changing over time in complex ways, creating a mixture of winners and losers in a time of accelerating global change. A critical research challenge is to test if there are specific biomes, taxa or types of species that are experiencing rapid alterations in abundance over time. We conducted an analysis of the Living Planet Database using a state-space modelling approach including nearly 10,000 abundance time-series from over 2,000 vertebrate species. We integrated the population abundance data with information on geographic range, habitat preference, taxonomic and phylogenetic relationships, conservation status and threats from occurrence, phylogenetic and conservation assessment data. We found that 15% of populations were declining, 18% were increasing, and 67% showed no net changes in abundance 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 analyzed data, while birds, mammals and reptiles on average became more abundant over time. The continuum of abundance changes over time was poorly captured by species' rarity and global-scale threats. Capturing the full spectrum of abundance change of species around the planet will inform conservation efforts and improve projections of biodiversity and ecosystem function change under the accelerating influence of the Anthropocene.

Main text

Alterations to ecosystems currently unfolding all around the globe are modifying the abundances of the different species forming Earth's biota. As global change continues to accelerate[1,2], the need for comprehensive assessments of the factors explaining the variety of ecological changes observed across taxa and biomes is also growing[3]. However, existing empirical studies of the predictors of 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. Recent compilations of long-term population time-series, extensive occurrence, phylogenetic, habitat preference and conservation status data[6–8] provide a unique opportunity to quantify population trends and fluctuations among the world's well-monitored vertebrate species and test which species- and population-level attributes explain variation in population change. 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 distribution of global change drivers such as such as land-use change, habitat change, pollution, invasion by non-native species and climate change[11–13] shows distinct clustering across space. Thus, we predicted biogeographic patterning of 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[14]). 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[15]. 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. 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, certain clades have been more vulnerable to declines and extinctions[6–8]. Building on known variability in species' vulnerability[16–18], we expected taxonomic and phylogenetic signals in population trends and fluctuations (e.g. greater declines, increases or fluctuations in abundance for specific taxa and among specific clades). Understanding which biomes and taxa are experiencing the most acute changes in abundance over time could provide key insights for conservation prioritization.

Conservation efforts often focus on protecting rare species, those with restricted geographic extents, small population sizes or high habitat specificity, as they are assumed to be more likely to decline and ultimately go extinct[19–21]. Thus, we predicted that the populations of rare species are more likely to decline and fluctuate than the populations of common species. Species with a smaller geographic range might have more concentrated exposure to environmental change, with less opportunities to find refugia or disperse, thus increasing the likelihood of declines[1,9]. As per population dynamics theory[22,23] and Taylor's power law[24], species with small populations are more likely to undergo stochastic fluctuations that could lead to pronounced declines, local extinction and eventually global species extinction[5]. Small populations are also more likely to decline due to inbreeding[25,26]. Allee effects, the relationship between individual fitness 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[27,28]. Furthermore, a high habitat specificity means that environmental change might have disproportionately large effects on the populations of rare species, as their persistence and colonization of new areas are limited by strict habitat preferences[1,29]. The fossil record indicates that on millennial time scales, rare species are more likely to decline and ultimately go extinct[30], but human actions have pushed Earth away from

93 traditional geological trajectories[31], and the relationships between rarity and population change
94 across the planet have yet to be tested across the Anthropocene.
95

96 On a global scale, species are exposed to a variety of threats, among which habitat change,
97 resource exploitation and hunting dominate as key predictors of extinction risk across the planet's
98 species[32]. We predicted that the populations of species with more threatened conservation status
99 and more species-level threats are more likely to decline and fluctuate than the populations of
100 least concern species and those exposed to a smaller number of threats. Species' IUCN
101 conservation status levels are often used in conservation prioritization and threatened species
102 tend to be the focus of conservation initiatives, but on the local scale, there might be variation in
103 how species abundance is changing over time in different locations[4,33]. Testing population change
104 across species' IUCN conservation status allows us to link contemporary changes in abundance
105 with long-term probability of extinction[34]. Determining how local-scale population trends vary
106 across species' IUCN conservation status has practical applications for assessing species'
107 recovery which is useful for the proposed IUCN Green List of Species[35].

108

109 Here, we asked how the trends and fluctuations of vertebrate populations vary with biogeography,
110 taxa, phylogenetic relationships and across species' rarity metrics and IUCN conservation and
111 threat categories. We quantified differences in population trends and fluctuations across latitudes
112 and biomes within the freshwater, marine and terrestrial realms to test the presence of distinct
113 hotspots of declines and increases. Additionally, we assessed taxonomic and phylogenetic
114 signals in the patterns of population change to determine if specific groups experience
115 pronounced changes over time. We investigated whether the heterogeneity in population change

116 globally is explained by differences in species' rarity and IUCN conservation status. We measured
117 rarity using three separate metrics – geographic range, mean population size (number of animals
118 that were recorded by monitoring) and habitat specificity. In a *post-hoc* analysis, we categorized
119 each population based on the global IUCN threat categories to determine how the number and
120 type of threats influences local-scale population change. Using the largest currently available
121 compilation of population records over time, we conducted a global synthesis of population trends
122 and fluctuations to provide key empirical evidence for the management, conservation and
123 prediction of ecological changes across the Anthropocene.
124
125 We analyzed vertebrate population time-series from the Living Planet Database (133,092
126 records) covering the period between 1970 and 2014. These time-series represent repeated
127 monitoring surveys of the number of individuals in a given area (species' abundance over time),
128 hereafter called "populations". We focus on two aspects of population change – overall changes
129 in abundance over time (population trend) and abundance variability over time (population
130 fluctuations). In the first stage of our analyses, we quantified trends and fluctuations for each
131 population using state-space models that account for observation error and random fluctuations[36]
132 (Figure S1). In the second stage, we modelled the population trend and fluctuation estimates from
133 the first stage across latitude, realm, biome, taxa, rarity metrics, phylogenetic relatedness,
134 species' conservation status and threat type using a Bayesian modelling framework (Figure S2).
135 We included a species random intercept effect to account for the possible correlation between
136 the trends of populations from the same species (see table Table S1 for sample sizes). As
137 sensitivity analyses, we additionally used variance weighting of the population trend estimates (μ)
138 by the observation/measurement error around them (τ) and population trend estimates from linear
139 model fits (slopes instead of μ) as the input variables in the second stage models, as well as
140 several different fluctuations estimates. We also repeated our analyses on a single-country scale,

using only populations within the United Kingdom, where monitoring efforts are particularly rigorous and extensive. All different analytical approaches yielded very similar results and are described in further detail in the methods.

Results

Biogeographic patterns of population trends and fluctuations

Globally, population increases, declines and fluctuations over time occurred across all latitudes and biomes within the freshwater, marine and terrestrial realms, with no strong biogeographic patterning and no specific hotspots of population declines (Figure 1, Table S2). Across all time-series, 15% of populations were declining, 18% were increasing, and 67% showed no net changes in abundance over time. Across realms, monitored vertebrate populations experienced net population increases (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 1d-e). In the freshwater and terrestrial realms, there was a bimodal distribution of population trends (Hartigans' dip test, $D = 0.04$, $p < 0.01$). Across biomes, 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 experienced no net changes (Figure 1h, Table S2). Population fluctuations were less pronounced in the terrestrial realm (slope = 0.02, CI = 0.018 to 0.021, Figure 1f-g), but those populations were also monitored for the longest duration across systems (average duration – 28 years for terrestrial, 18 years for marine and 21 years for freshwater populations, Figure S1, Table S2).

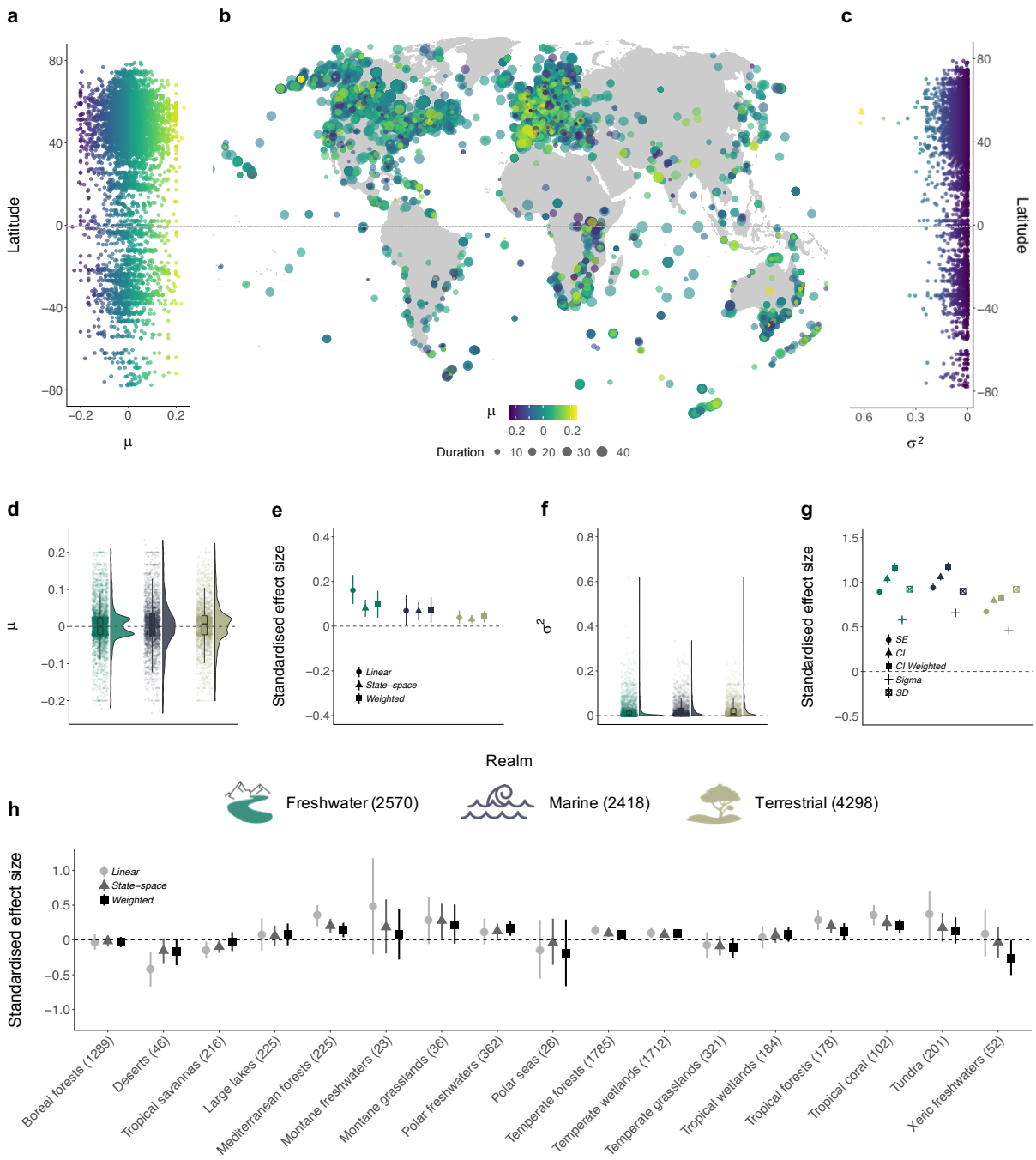

Figure 1. Population declines, increases and fluctuations over time occur across all latitudes and biomes within the freshwater, marine and terrestrial realms. Results include 9286 populations from 2084 species. The lack of biogeographic patterning in vertebrate population trends was also apparent on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

the legend for plots **d**-**g** and on the x axis in plot **c** show the sample sizes for realms and biomes, respectively. The μ values of population trend (plots **a**-**b**, **d**-**e**, **h**) and the σ^2 values of population fluctuation (plots **c**, **f**-**g**) were derived from state-space model fits of changes in abundance over the monitoring duration for each population. Plots **d** and **f** show the density distribution of population trends across realms, 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 **e**, **g** and **h** show the effect sizes and the 95% credible intervals of population trends (**e**, **h**) across realms and biomes, and fluctuations across realms (**g**). For variation in fluctuations across biomes, see SI Figure S9. The three estimates for each realm/system in plots **e** and **h** refer to different analytical approaches: population trends calculated using linear models (circles), state-space models (μ, triangles), and population trends (μ) weighted by τ^2, the observation error estimate from the state-space models (squares). The five estimates in plot **g** refer to different analytical approaches, where the response variables in the models were: 1) the standard error around the slope estimates of the linear model fits of abundance versus year (circles), 2) half of the 95% confidence interval around the μ value of population change (triangles), 3) half of the 95% confidence interval around μ weighted by τ^2, (full squares), 4) the process noise (σ^2) from the state-space models, and 5) the standard deviation of the raw data for each population time-series (empty squares). Effect sizes were standardized by dividing the effect size by the standard deviation of the corresponding input data. The process noise is the total variance around the population trend minus the variance attributed to observation error. Error bars in plots **e**, **g** and **h** show 95% credible intervals. See Table S2 for model outputs.

Taxonomic and phylogenetic patterns of population trends and fluctuations

We found taxonomic, but not phylogenetic patterns, in population trends and fluctuations over time among nearly 10,000 populations from over 2,000 vertebrate species, with amphibians

192 emerging as the taxa experiencing pronounced declines (Figure 2, Table S2). Amphibians
193 experienced net declines over time (slope = -0.01, CI = -0.02 to -0.005), whereas birds, mammals
194 and reptiles experienced net increases (slope = 0.004, CI = 0.003 to 0.01; slope = 0.01, CI = 0.01
195 to 0.01; slope = 0.02, CI = 0.01 to 0.02), with birds having a bimodal trend distribution (Hartigans'
196 dip test, D = 0.04, $p < 0.01$, Figure 1a). Bony fish population trends were centered on zero (slope
197 = -0.001, CI = -0.004 to 0.002, Figure 1a-b) and sharks and rays showed net declines, but the
198 credible intervals overlapped zero (slope = -0.01, CI = -0.02 to 0.01). Fluctuations were most
199 common for amphibian populations (slope = 0.04, CI = 0.036 to 0.049, Figure 2d), which were
200 monitored for the shortest time period on average (11 years, Figure S1, Table S2). We did not
201 detect finer scale species-level phylogenetic clustering of population change (both trends and
202 fluctuations) within amphibian, bird and reptile classes (Figures 2 and S16, Table S4). Similarly,
203 species identity within amphibian, bird and reptile classes did not explain variation in population
204 trends or fluctuations (Figures 2 and S16, Table S4). There were no distinct clusters of specific
205 clades that were more likely undergo increases, decreases or fluctuations in population
206 abundance (Figure 2).
207

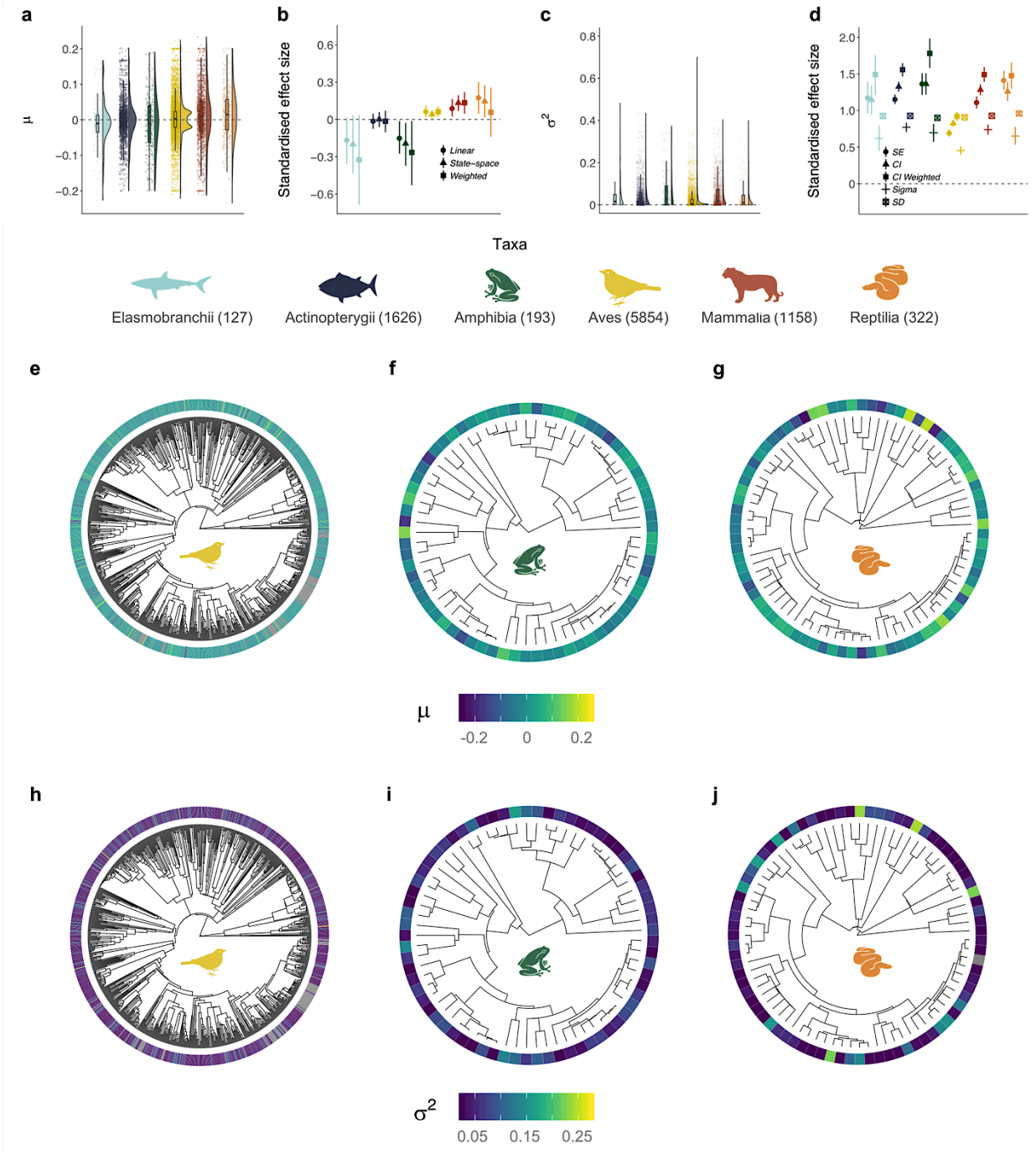

Figure 2. Population trends and fluctuations varied more among, rather than within, taxa, with amphibians being the only group showing pronounced declines over time. There were no distinct phylogenetic patterns in population trends and fluctuations (plots **e-j**). For details on phylogenetic models, see methods. Grey color 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 population fluctuation (plots **c**-**d**, **h**-**j**) were derived from state-space model fits of changes in abundance over the monitoring duration for each population. Plots **a** and **c** show the density distribution of population trends across taxa, 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 the five studied taxa. The three estimates for each metric in plot **b** refer to different analytical approaches: population trends calculated using linear models (circles), state-space models (μ, triangles), and population trends (μ) weighted by τ^2, the observation error estimate from the state-space models (squares). The five estimates in plot **d** refer to different analytical approaches, where the response variables in the models were: 1) the standard error around the slope estimates of the linear model fits of abundance versus year (circles), 2) half of the 95% confidence interval around the μ value of population change (triangles), 3) half of the 95% confidence interval around μ weighted by τ^2, (full squares), 4) the process noise (σ^2) from the state-space models, and 5) the standard deviation of the raw data for each population time-series (empty squares). Effect sizes (plots **b** and **d**) were standardized by dividing the effect size by the standard deviation of the corresponding input data. The process noise is the total variance around the population trend minus the variance attributed to observation error. Error bars in plots **b** and **d** show 95% credible intervals. See Tables S2 and S4 for model outputs.

Population trends and fluctuations across rarity metrics, conservation status and threats

Species-level metrics, such as rarity and global conservation status, did not explain the heterogeneity in trends of monitored populations in the Living Planet Database, and both rare and

common species experienced declines, increases and fluctuations in population abundance over time (Figures 3 and 4). Across monitored vertebrate populations globally, species with smaller ranges, smaller population sizes, or narrower habitat specificity (i.e., rare species) were not more prone to population declines than common species (Figure 3, Table S2). Populations that experienced more fluctuations had smaller mean population sizes on average (slope = -0.001, CI = -0.001 to -0.001, Figure 3f). We found increasing, decreasing and stable populations across all Red List categories of conservation status (Figure 4a). For example, a population of the Least concern species red deer (*Cervus elaphus*) in Canada declined by 68% over seven 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 seven years going from 89 to 328 individuals. We found more 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 conservation status (Figure 4, Table S2). Populations from species that were exposed to a larger number of threats on a global scale based on the species' IUCN threat categorizations did not experience greater declines when compared to those categorized with a smaller number of threats (Figure 4f). There were no distinct signatures of global species threats which were associated with predominantly declining local trends of monitored populations (Figure 4e) and there were increasing, decreasing and stable trends across all threat types.

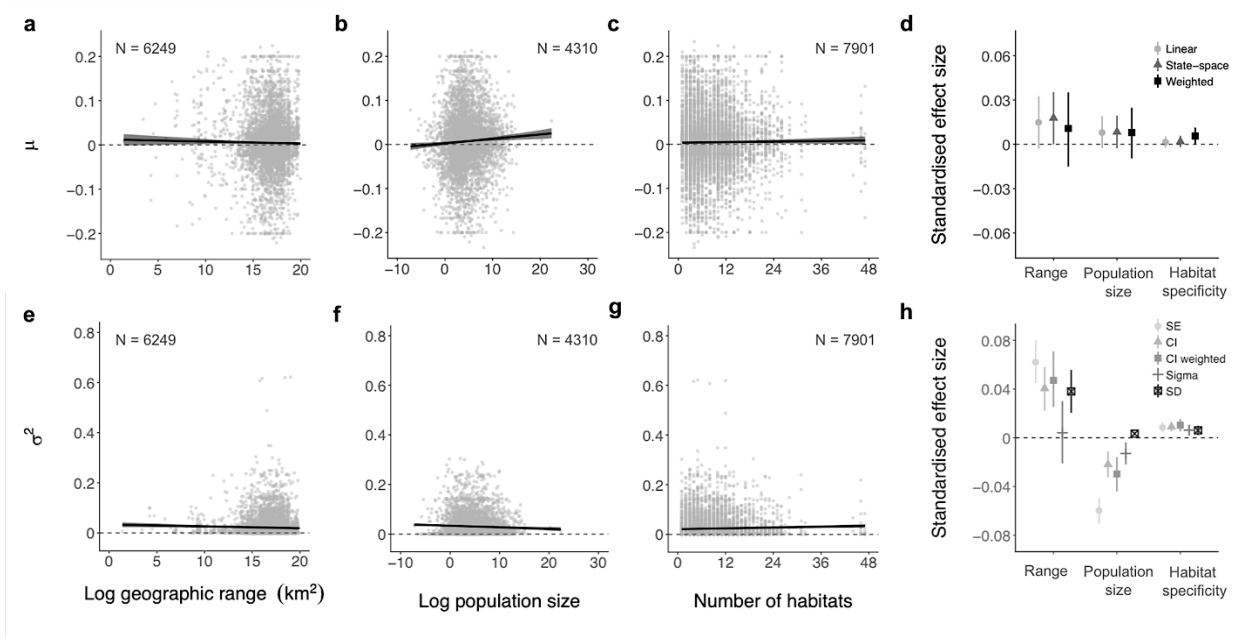

Figure 3. Rarity metrics do not explain heterogeneity in local population trends, and both rare and common species experienced declines and increases over time, whereas smaller populations fluctuated more over time. Numbers on plots show sample size for each metric. Rarity metrics were calculated for 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**). The three estimates for each metric in plot **d** refer to different analytical approaches: population trends calculated using linear models (circles), state-space models (μ, triangles), and population trends (μ) weighted by τ^2, the observation error estimate from the state-space models (squares). The five estimates in plot **h** refer to different analytical approaches, where the response variables in the models were: 1) the standard error around the slope estimates of the linear model fits of abundance versus year

(circles), 2) half of the 95% confidence interval around the μ value of population change (triangles), 3) half of the 95% confidence interval around μ weighted by τ^2, (full squares), 4) the process noise (σ^2) from the state-space models, and 5) the standard deviation of the raw data for each population time-series (empty squares). Effect sizes (plots **d** and **h**) were standardized by dividing the effect size by the standard deviation of the corresponding input data. The process noise is the total variance around the population trend minus the variance attributed to observation error. 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 Table S2 for model outputs.

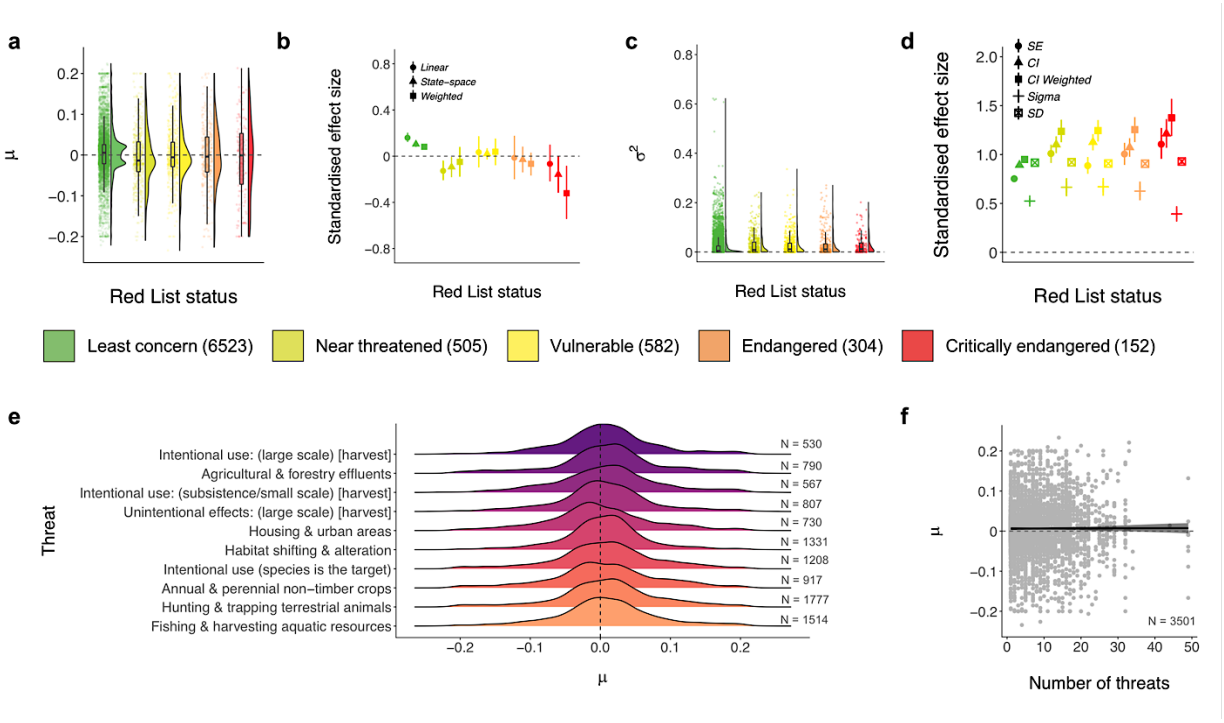

Figure 4. On local scales, there are increasing, decreasing and stable populations across the full spectrum of the globally-determined species' conservation status and anthropogenic threats (IUCN Red List Index). Numbers in the legend for plots **a**-**d** and in plots **e**-**f** show sample size for 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 conservation status across the IUCN Red List categories. The three estimates for each metric in plot **b** refer to different analytical approaches: population trends calculated using linear models (circles), state-space models (μ, triangles), and population trends (μ) weighted by τ^2, the observation error estimate from the state-space models (squares). The five estimates in plot **d** refer to different analytical approaches, where the response variables in the models were: 1) the standard error around the slope estimates of the linear model fits of abundance versus year (circles), 2) half of the 95% confidence interval around the μ value of population change (triangles), 3) half of the 95% confidence interval around μ weighted by τ^2, (full squares), 4) the process noise (σ^2) from the state-space models, and 5) the standard deviation of the raw data for each population time-series (empty squares). The process noise is the total variance around the population trend minus the variance attributed to observation error. 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 Methods for details on deriving types of threats and Table S2 for model outputs.

Discussion

Taken together, our analysis of the Living Planet Database using a state-space modelling approach demonstrated ubiquitous alterations in vertebrate abundance of monitored populations 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 all is not declines across vertebrate species. 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 conservation status (Figure 4). On a global scale, the vertebrate species in the Living Planet Database are exposed to a variety of threats, 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 changing 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

338 with increasing threat level (Figures 1 and 4). Similar lack of biogeographic signal has been
339 documented in regional studies of population change from the Netherlands[33] and in temperate
340 North America and Europe[37]. Coarsely represented biogeographic regions and global-scale
341 species' IUCN status and threat categories might not capture the drivers acting in the locations of
342 the specific populations we studied[32,38–40]. Furthermore, the same driver can have opposing
343 effects on population abundance at different sites[41]. A lack of of biome-specific directional trends
344 in population change, despite a spatial clustering of human pressure around the world[12], can also
345 arise due to differences in species traits and vulnerability to environmental change within
346 biomes[16–18]. Accounting for divergent responses of species to global change is key when
347 translating global policy, such as the upcoming post-2020 planetary biodiversity strategy[42], into
348 conservation actions implemented on scales much finer than biogeographic realms.
349
350 Our results highlight variation in population change among taxa, with amphibians emerging as
351 the taxa experiencing the most pronounced declines in the Living Planet Database. The remaining
352 taxa showed either stable or increasing net changes in abundance over time (Figure 2). Such
353 taxonomic patterns could be driven by different taxon-specific factors including reproductive
354 strategy, trophic level, generation time and life history traits[43,44]. For amphibians, population
355 declines have been linked to the spread of a fungal disease (chytrid fungus, *Batrachochytrium*
356 *dendrobatidis*), facilitated by global warming[45], as well as habitat loss and Allee effects in small
357 populations[46]. Within bird, amphibian and reptile taxa, phylogenetic relatedness and species-level
358 taxonomic classification did not explain variation in population trends and fluctuations. A similar
359 lack of phylogenetic dependencies has been detected for the population growth rates of migratory
360 birds[47]. While phylogenetic clustering might be lacking in contemporary trends, there is evidence
361 that phylogenetic relatedness predicts extinction, a process occurring over much longer time
362 scales[6,7]. Over shorter time periods, species' traits and ability to persist, reproduce and disperse

363 in ever changing landscapes might be influencing local abundance[16], which has created a mix of
364 winners and losers across all taxa[48]. We demonstrate ongoing alterations in the abundances of
365 six vertebrate taxa which over time, may lead to shifts in community composition and ultimately
366 alter ecosystem function as some species become locally extinct whilst others become more
367 abundant[9,10].
368
369 Surprisingly, our results indicate that despite decades of conservation focus on rare species[19–21],
370 both rare and common species experienced declines and increases in population abundance over
371 the period of monitoring. The lack of rarity effects on population trends can be explained by theory
372 and empirical evidence demonstrating that small populations do not necessarily have a higher
373 likelihood of experiencing declines and some species are able to persist in small, but stable
374 populations[49]. The power of rarity metrics to predict population trends could also be mediated by
375 whether species are naturally rare, or have become rare due to external drivers in recent
376 years[50,51]. Naturally rare species might be more likely to persist over time, whereas species that
377 have more recently become rare might be more likely to decline in response to environmental
378 disturbance. Furthermore, the timing and magnitude of past and current disturbance events
379 influence population trends[41,52] and there could be temporal lags in both positive and negative
380 abundance changes over time[41,53]. However, disentangling the processes leading to rarity over
381 time remains challenging, and across the 2084 species we studied, there are likely cases of both
382 natural and human-driven population change. We found that species with small populations were,
383 nevertheless, more likely to fluctuate (Figure 3f), which may increase their probability of extinction,
384 a process that could play out over longer time-scales than found for most population monitoring
385 time-series[22,23,54]. Our results highlight that rarity metrics alone do not capture the heterogeneity
386 in local population change over time, and common species should not be overlooked in

387 conservation prioritization decisions as they could be as likely to decrease in abundance over
388 time as rare species.
389
390 Our finding that all is not declines for vertebrate populations monitored for longer than five years
391 contrasts with reports of the overall decline in the Living Planet Index (LPI)[55], a weighted summary
392 of population change across all abundance time-series in the Living Planet Database. The LPI
393 reports[55–57] also document that the numbers of declining and increasing species are similar across
394 this dataset but that the magnitude of declines is larger than the magnitude of increases. The
395 calculation of the index used involves differential weighting of population trends derived using
396 logged abundance data, geometric means and generalized additive models[58]. The LPI is
397 hierarchically averaged from populations to species, taxa and realm and is also weighted by the
398 estimated and relative number of species within biomes, which influences the direction and
399 magnitude of the index[58,59]. Our analysis explores the heterogeneity in local trends and
400 fluctuations of monitored species from the raw population abundance data, and thus, we did not
401 use an index with weightings and we did not aggregate population trends to a species-level. We
402 detected net population declines at local scales over time only in the amphibian taxa, in contrast
403 with the overall negative trend of the aggregate weightings of the LPI[55]. Our results were similar
404 when we weighted population trends by the state-space model derived observation error (Figures
405 1-4 and Tables S2-3). We caution that distilling the heterogeneity of local population change at
406 sites around the world into a simple metric may hide diverging trends at local scales, where we
407 found both increases and declines among species.
408
409 To attribute population trends and fluctuations to site-specific anthropogenic drivers, we need to
410 go beyond previous studies that have focused exclusively on declines and extinctions[5,60].
411 Attribution analyses statistically test the links between observed changes in ecosystems and the

experienced extrinsic pressure[3]. Through attribution studies encompassing the full spectrum of population change, including positive, negative and stable trends[41,61], we can better understand the variety of ways in which climate change, land-use change and other drivers are altering biodiversity. For a subset of the bird populations in the Living Planet Database, higher temperature warming corresponded with a higher likelihood of population declines over time[61], which could be caused by worldwide and cross-biome phenological mismatches between breeding and resource availability[62]. Across terrestrial species represented in the Living Planet Database, peak forest loss was associated with accelerations in both population increases and decreases in the period following habitat alteration[41]. The strength of documented relationships between population alterations and global change could be influenced by how well-monitored populations capture the full range of variation in driver intensity as well as whether monitoring began during a population peak or a population trough[63]. Additionally, there is evidence from the marine realm that when species are simultaneously exposed to multiple drivers, the resulting biodiversity effects are antagonistic and could produce patterns of no net biodiversity changes[64]. The next critical step is to test how multiple global change drivers together[12] influence populations across both terrestrial and marine realms and determine how these relationships are mediated by species' traits and vulnerability to extrinsic threats[65].

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 uncover a pronounced net decline in amphibian abundance as well as net abundance increases for birds, mammals and reptiles. 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

437 geographic range, mean population size and habitat specificity, as well as conservation status
438 and evolutionary history, did not explain the heterogeneity in population change across the data
439 analyzed in this study. Our findings caution the use of rarity metrics for the prediction of future
440 global population trends, but suggest that such metrics, in particular mean population size, are
441 nevertheless indicators of population fluctuations, which might ultimately link to increased species
442 extinction risk. On a global scale, both rare and common vertebrate species face numerous
443 threats due to resource exploitation and habitat change. As human activities continue to
444 accelerate, the next key step is to determine how intrinsic factors, such as rarity attributes and
445 threats, interact with extrinsic global change drivers and together influence the persistence of
446 Earth's biota. The ongoing alterations in the abundances of species around the world may lead
447 to shifts in community composition and ultimately alter ecosystem functions and services.
448

449 **Methods**

450 All data syntheses, visualization and statistical analyses were conducted using R version 3.5.1[66].
451 For conceptual diagrams of our workflow, see Figures S1 and S2.
452

453 **Data sources**

454 *Population data*

455 To quantify vertebrate population change (trends and fluctuations), we extracted the abundance
456 data for 9284 population time-series from 2084 species from the publicly available Living Planet
457 Database[67] (http://www.livingplanetindex.org/data_portal) that covered the period between 1970
458 and 2014 (Table S1). These time-series represent repeated monitoring surveys of the number of
459 individuals in a given area, hereafter called "populations". Monitoring duration differed among
460 populations (Figure S1, see SI Figures S6 and S7 for effects of monitoring duration on detected
461 trends). In our analysis, we retained only populations that had at least five time points of

462 monitoring data, as that is a considered a long enough period to detect a directional population
463 trend (if one exists) in 80-90% of cases[68]. Populations were monitored using different metrics of
464 abundance (e.g., population indices vs. number of individuals). Before analysis, we scaled the
465 abundance of each population to a common magnitude between zero and one to analyze within-
466 population relationships to prevent conflating within-population relationships and between-
467 population relationships[69]. This allowed us to explore trends among populations relative to the
468 variation experienced across each time series.
469
470 *Phylogenetic data*
471 We obtained phylogenies for amphibian species from https://vertlife.org[4], for bird species from
472 https://birdtree.org[8], and for reptile species from https://vertlife.org[6]. For each of the three classes
473 (*Amphibia*, *Aves* and *Reptilia*), we downloaded 100 trees and randomly chose 10 for analysis (30
474 trees in total). Species-level phylogenies for the classes *Actinopterygii* and *Mammalia* have not
475 yet been resolved with high confidence[70,71].
476
477 *Rarity metrics, conservation status and threat data*
478 We defined rarity following a simplified version of the 'seven forms of rarity' model[72], and thus
479 consider rarity to be the state in which species exist when they have a small geographic range,
480 low population size, or narrow habitat specificity. We combined publicly available data from three
481 sources: 1) population records for vertebrate species from the Living Planet Database to calculate
482 mean population size, 2) occurrence data from the Global Biodiversity Information Facility[73]
483 (https://www.gbif.org) and range data from BirdLife[74] (http://datazone.birdlife.org) to estimate
484 geographic range size, and 3) habitat specificity and Red List classification data for each species
485 from the International Union for Conservation[75] (https://www.iucnredlist.org). The populations in
486 the Living Planet Database[67] do not include species that have gone extinct on a global scale, and

487 we use species' Red List conservation status as a proxy for extinction risk[75], an approach used
488 recently in other studies[76]. We extracted the number and types of threats that each species is
489 exposed to globally from their respective IUCN profiles[75].
490
491 **Quantifying population trends and fluctuations over time**
492 In the first stage of our analysis, we used state-space models that model abundance (scaled to a
493 common magnitude between zero and one) over time to calculate the amount of overall
494 abundance change experienced by each population (μ, [36,77]). State-space models account for
495 process noise (σ^2) and observation error (τ^2) and thus deliver robust estimates of population
496 change when working with large datasets where records were collected using different
497 approaches, such as the Living Planet Database[37,78,79]. Previous studies have found that not
498 accounting for process noise and measurement error could lead to over-estimation of population
499 declines[80], but in our analyses, we found that population trends derived from state-space models
500 were similar to those derived from linear models. Positive μ values indicate population increase
501 and negative μ values indicate population decline. State-space models partition the variance in
502 abundance estimates into estimated process noise (σ^2) and observation or measurement error
503 (τ^2) and population trends (μ):
504 $$X_t = X_{t-1} + \mu + \varepsilon_t, \quad (1)$$
505 where X_t and X_{t-1} are the scaled (observed) abundance estimates (between 0 and 1) in the present
506 and past year, with process noise represented by $\varepsilon_t \sim gaussian(0, \sigma^2)$. We included measurement
507 error following:
508 $$Y_t = X_t + F_t,$$
509 where Yt is the estimate of the true (unobserved) population abundance with measurement error:
510 $$F_t \sim gaussian(0, \tau^2).$$

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

512 $$Y_t = X_{t-1} + \mu + \varepsilon_t + Ft.$$

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

514 $$Y_t = Y_{t-1} + \mu + \varepsilon_t + F_t - F_{t-1}.$$

515 For comparisons of different approaches to modelling population change, see *Comparison of*
516 *modelling approaches* section.

517

518 **Quantifying rarity metrics**

519 We tested how population change varied across rarity metrics – geographic range, mean
520 population size and habitat specificity – on two different but complementary scales. In the main
521 text, we presented the results of our global scale analyses, whereas in the SI we included the
522 results when using only populations from the UK – a country with high monitoring intensity, Thus,
523 we quantified rarity metrics for species monitoring globally and in the UK.

524

525 *Geographic range*

526 To estimate geographic range for bird species monitored globally, we extracted the area of
527 occurrence in km^2 for all bird species in the Living Planet Database that had records in the BirdLife
528 Data Zone[74]. For mammal species' geographic range, we used the PanTHERIA database[81]
529 (http://esapubs.org/archive/ecol/E090/184/). To estimate geographic range for bony fish, birds,
530 amphibians, mammals and reptiles monitored in the UK (see Table S5 for species list), we
531 calculated a km^2 occurrence area based on species occurrence data from GBIF[73]. Extracting and
532 filtering GBIF data and calculating range was computationally-intensive and occurrence data
533 availability was lower for certain species; thus, we did not estimate geographic range from GBIF
534 data for all species part of the Living Planet Database. Instead, we focused on analyzing range
535 effects for birds and mammals globally, as they are a very well-studied taxon and for species

536 monitored in the UK, a country with intensive and detailed biodiversity monitoring of vertebrate
537 species. We did not use IUCN range maps, as they were not available for all of our study species,
538 and previous studies using GBIF occurrences to estimate range have found a positive correlation
539 between GBIF-derived and IUCN-derived geographic ranges[82].
540
541 For the geographic ranges of species monitored in the UK, we calculated range extent using a
542 minimal convex hull approach based on GBIF[73] occurrence data. We filtered the GBIF data to
543 remove invalid records and outliers using the *CoordinateCleaner* package[83]. We excluded records
544 with no decimal places in the decimal latitude or longitude values, with equal latitude or longitude,
545 within a one-degree radius of the GBIF headquarters in Copenhagen, within 0.0001 degrees of
546 various biodiversity institutions and within 0.1 degrees of capital cities. For each species, we
547 excluded the lower 0.02 and upper 0.98 quantile intervals of the latitude and longitude records to
548 account for outlier points that are records from zoos or other non-wild populations. We drew a
549 convex hull to most parsimoniously encompass all remaining occurrence records using the *chull*
550 function, and we calculated the area of the resulting polygon using *areaPolygon* from the
551 *geosphere* package .
552
553 *Mean size of monitored populations*
554 We calculated mean size of the monitored population, referred to as population size, across the
555 monitoring duration using the raw abundance data, and we excluded populations which were not
556 monitored using population counts (i.e., we excluded indexes).
557
558 *Habitat specificity*
559 To create an index of habitat specificity, we extracted the number of distinct habitats a species
560 occupies based on the IUCN habitat category for each species, accessed through the package

561 *rredlist*[85]. We also quantified habitat specificity by surveying the number of breeding and non-
562 breeding habitats for each species from its online IUCN profile (the 'habitat and ecology' section).
563 The two approaches yielded similar results (Figure S3, Table S2, key for the profiling method is
564 presented in Table S4). We obtained global conservation status and threat data for all study
565 species through the IUCN Red List classification[75].
566
567 **Testing the sources of variation in population trends and fluctuations**
568 In the second stage of our analyses, we modelled the trend and fluctuation estimates from the
569 first stage across latitude, realm, biome, taxa, rarity metrics, phylogenetic relatedness, species'
570 conservation status and threat type using a Bayesian modelling framework through the package
571 *MCMCglmm*[86]. We included a species random intercept effect in the Bayesian models to account
572 for the possible correlation between the trends of populations from the same species (see Table
573 S1 for sample sizes). The models ran for 120 000 iterations with a thinning factor of ten and a
574 burn-in period of 20 000 iterations. We assessed model convergence by visually examining trace
575 plots. We used weakly informative priors for all coefficients (an inverse Wishart prior for the
576 variances and a normal prior for the fixed effects):

577 $$Pr(\mu) \sim N(0, 10^8)$$

578 $$Pr(\sigma^2) \sim Inverse\ Wishart\ (V = 0, nu = 0)$$

579
580 *Population trends and fluctuations across latitude, biomes, realms and taxa*
581 To investigate the geographic and taxonomic patterns of population trends and fluctuations, we
582 modelled population trends (μ) and population fluctuations (σ^2), derived from the first stage of our
583 analyses (state-space models), as a function of 1) latitude, 2) realm (freshwater, marine,

terrestrial), 3) biome (as defined by the 'biome' category in the Living Planet Database, e.g., 'temperate broadleaf forest'[87] and 4) taxa (*Actinopterygii*, bony fish; *Elasmobranchii*, sharks and 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*[86]. We included phylogeny and taxa as random effects. The models did not include fixed effects. We assessed the magnitude of the random effects

608 (phylogeny and species) by inspecting their posterior distributions, with a distribution pushed up
609 against zero indicating lack of effect, since these distributions are always bounded by zero and
610 have only positive values. We used parameter-expanded priors, with a variance-covariance
611 structure that allows the slopes of population trend (the *mu* values from the first stage analysis
612 using state-space models) to covary for each random effect. The prior and model structure were
613 as follows:

614 $$Pr(\mu) \sim N(0, 10^8),$$

615 $$Pr(\sigma^2) \sim Inverse\ Wishart\ (V = 1, nu = 1),$$

616 $$\mu_{i,k,m} = \beta_0 + \beta_{0k} + \beta_{0m},$$

617 $$y_{i,k,m} \sim gaussian(\mu_{i,k,m}, \sigma^2),$$

618 where β_0 is the global intercept ($\beta_0 = 1$), β_{0l} is the phylogeny-level departure from β_0 (phylogeny
619 random effect); $y_{i,k,m}$ is the estimate for change in population abundance for the ith population
620 time-series for the kth species with the mth phylogenetic distance.
621
622 To account for phylogenetic uncertainty, for each class, we ran ten models with identical
623 structures but based on different randomly selected phylogenetic trees. We report the mean
624 estimates and their range for each class.
625
626 *Population trends and fluctuations across rarity metrics*
627 To test the influence of rarity metrics (geographic range, mean population size and habitat
628 specificity) on variation in population trends and fluctuations, we modelled population trends (μ)
629 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 geographic range (log transformed), mean population size (log transformed) and habitat specificity (number of distinct habitats occupied). The model structures were identical across the different rarity metrics and below we outline the equations for population trends and geographic range:

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

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

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

Population trends across species' IUCN conservation status

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

654 fixed effect which was a categorical IUCN conservation status variable. The analytical workflow
655 of our analyses is summarized in conceptual diagrams (Figures S1 and S2) and all code is
656 available on GitHub (link to public repository to be added at time of publication).
657
658 **Data limitations**
659 *Taxonomic and geographic gaps*
660 Our analysis is based on 9286 monitored populations from 2084 species from the largest currently
661 available public database of population time-series, the Living Planet Database[67]. Nevertheless,
662 the data are characterized by both taxonomic and geographic gaps that can influence our findings.
663 For example, there are very few population records from the Amazon and Siberia (Figure 1b) –
664 two regions currently undergoing rapid environmental changes due to land-use change and
665 climate change respectively. Additionally, birds represent 63% of all population time-series in the
666 Living Planet Database, whilst taxa such as amphibians and sharks where we find declines are
667 included with fewer records (Figures 2 and S5). On a larger scale, the Living Planet Database
668 under-represents populations outside of Europe and North America and over-represents common
669 and well-studied species[59]. We found that for the populations and species represented by current
670 monitoring, rarity does not explain variation in population trends, but we note that the relationship
671 between population change and rarity metrics could differ for highly endemic specialist species
672 that are not included in the Living Planet Database. As ongoing and future monitoring begins to
673 fill in the taxonomic and geographic gaps in existing datasets, we will be able to re-assess and
674 test the generality of the patterns of population change across biomes, taxa, phylogenies, species
675 traits and threats.
676
677 *Monitoring extent and survey techniques*

678 The Living Planet Database combines population time-series where survey methods were
679 consistent within time-series but varied among time-series. Thus, among populations, abundance
680 was measured using different units and over varying spatial extents. There are no estimates of
681 error around the raw population abundance values available and detection probability likely varies
682 among species. We used state-space models to estimate trends and fluctuations to account for
683 these limitations as this modelling framework is particularly appropriate for analyses of data
684 collected using disparate methods[37,78,79]. Because the precise coordinates of the polygons where
685 the individual populations were monitored are not available, we were not able to test for the
686 potential confounding effect of monitoring extent, but our sensitivity analysis indicated that survey
687 units do not explain variation in the detected trends (Figure S13).
688
689 *Temporal gaps*
690 The population time-series we studied cover the period between 1970 and 2014, with both
691 duration of monitoring and the frequency of surveys varying across time-series. We only included
692 populations with more than five survey points in time in our analyses, because this amount of data
693 has been found to be enough to detect directional trends in 80-90% of cases[68]. In a separate
694 analysis, we found significant lags in population change following disturbances (forest loss) and
695 that population monitoring often begins decades to centuries after peak forest loss has occurred
696 at a given site[41]. The findings of this related study suggest that the temporal span of the population
697 monitoring does not always capture the period of intense environmental change and lags suggest
698 that there might be abundance changes that have not yet manifested themselves. Thus, the
699 detected trends and the baseline across which trends are compared might be influenced by when
700 monitoring takes place and at what temporal frequency. Nevertheless, the Living Planet Database
701 represents the most comprehensive compilation of temporal population records to date, allowing

for the most comprehensive analyses possible into the patterns of vertebrate trends and fluctuations around the world.

Challenges in estimating geographic range

Estimating geographic range across taxa, specifically species that are not birds or 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[88]. 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

Monitoring duration, sampling methods and site-selection bias

To assess the influence of monitoring duration on population trends, we used a Bayesian linear model (Figures S6). 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 S9, Table S2). Variation in population trends was not explained by sampling method across the five most commonly used abundance metrics (population index, number of individuals, number of pairs, number of nests and population estimate, Figure S13). Following Fournier *et al.* 2019[63], we tested the time-series that we analyzed for site-selection bias. Removing the first five survey

727 points reduces the bias stemming from starting population surveys at points when individual
728 density is high, whereas removing the last five years reduces the bias of starting surveys when
729 species are very rare. The distribution of population trend values across time-series was not
730 sensitive to the omission of the first five (left-truncation) or the last five years (right-truncation) of
731 population records (Figure S8). Overall, our sensitivity analyses suggest that our findings are
732 robust to the potential confounding effects of differences in monitoring duration, sampling method
733 and site-selection.
734
735 *Comparison of modelling approaches*
736 We conducted the following supplementary analyses: in the second-stage Bayesian models
737 estimating population trends across systems, biomes, taxa and rarity metrics, 1) we weighed *mu*
738 values by the square of *tau*, the observation error estimate derived from the state-space models[36],
739 2) we used slopes of linear model fits of abundance (scaled at the population level, centered on
740 zero and with a standard deviation of one)[69] instead of the *mu* estimates from state-space models,
741 3) we modelled the standard error around the slope values of the linear models, the error around
742 *mu* (half of the 95% confidence interval) and the standard deviation of the raw population data for
743 each time-series as additional metrics of population variability. To allow comparison, we scaled
744 the different metrics of population variability to be centered on zero and with a standard deviation
745 of one before they were used as response variables in models. All different analytical approaches
746 yielded very similar results (see main text and Figures S6, S7 and S10, Table S2).
747
748 **Data availability**
749 Code for all data processing and analyses and summary datasets are publicly available on GitHub
750 (link to be added at time of publication). Raw data are available from the following websites: for
751 population time-series[67] - http://www.livingplanetindex.org/data_portal, GBIF occurrences[73] -

752 https://www.gbif.org, bird geographic ranges[74] - http://datazone.birdlife.org, mammal geographic
753 ranges[81] - http://esapubs.org/archive/ecol/E090/184/, species' habitat preferences, threats and
754 conservation status[75] - https://www.iucnredlist.org, and phylogenies[6–8] - https://vertlife.org and
755 https://birdtree.org.
756

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770

771 **Author contributions**

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

Competing interests

The authors declare no competing interests.

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