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More losers than winners: investigating Anthropocene defaunation through the diversity of population trends

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ABSTRACT

The global-scale decline of animal biodiversity ('defaunation') represents one of the most alarming consequences of human impacts on the planet. The quantification of this extinction crisis has traditionally relied on the use of IUCN *Red List* conservation categories assigned to each assessed species. This approach reveals that a quarter of the world's animal species are currently threatened with extinction, and ~1% have been declared extinct. However, extinctions are preceded by progressive population declines through time that leave demographic 'footprints' that can alert us about the trajectories of species towards extinction. Therefore, an exclusive focus on IUCN conservation categories, without consideration of dynamic population trends, may underestimate the true extent of the processes of ongoing extinctions across nature. In fact, emerging evidence (e.g. the *Living Planet Report*), reveals a widespread tendency for sustained demographic declines (an average 69% decline in population abundances) of species globally. Yet, animal species are not only declining. Many species worldwide exhibit stable populations, while others are even thriving. Here, using population trend data for >71,000 animal species spanning all five groups of vertebrates (mammals, birds, reptiles, amphibians and fishes) and insects, we provide a comprehensive global-scale assessment of the diversity of population trends across species undergoing not only declines, but also population stability and increases. We show a widespread global erosion of species, with 48% undergoing declines, while 49% and 3% of species currently remain stable or are increasing, respectively. Geographically, we reveal an intriguing pattern similar to that of threatened species, whereby declines tend to concentrate around tropical regions, whereas stability and increases show a tendency to expand towards temperate climates. Importantly, we find that for species currently classed by the IUCN *Red List* as 'non-threatened', 33% are declining. Critically, in contrast with previous mass extinction events, our assessment shows that the Anthropocene extinction crisis is undergoing a rapid biodiversity imbalance, with levels of declines (a symptom of extinction) greatly exceeding levels of increases (a symptom of ecological expansion and potentially of evolution) for all groups. Our study contributes a further signal indicating that global biodiversity is entering a mass extinction, with ecosystem heterogeneity and functioning, biodiversity persistence, and human well-being under increasing threat.

Key words: population declines, conservation category, sixth mass extinction, IUCN Red List, vertebrates, insects.

CONTENTS

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I. INTRODUCTION

Animal populations and whole species are declining across the tree of life, making the Anthropocene defaunation crisis one of the most alarming syndromes of human impacts on environments globally (Ceballos, García & Ehrlich, 2010; Ceballos, Ehrlich & Dirzo, 2017; Dirzo *et al.*, 2014; Pimm *et al.*, 2014; Young *et al.*, 2016). The widespread loss of biodiversity has reached unprecedented degrees of ecosystem degradation at rapid timescales (ongoing extinction rates are 1000–10,000 higher than 'background' extinction rates), leading to the growing consensus that life on Earth is entering its sixth mass extinction (Barnosky *et al.*, 2011; Kolbert, 2014; Ceballos *et al.*, 2015; McCallum, 2015; Cowie, Bouchet & Fontaine, 2022). However, compared with the previous five such events, this mass extinction is the first directly induced by a single species – humans.

The traditional approach employed to estimate levels of extinction risk across nature has focused on the International Union for Conservation of Nature (IUCN) *Red List* conservation categories that are assigned to each assessed species (IUCN, 2022*b*). These categories are based on the assessment of multiple species features (e.g. geographic range size, population size, and levels of fragmentation: IUCN, 2012) that combined suggest the most likely level of threat. At the time of assessment, species can be classed as 'threatened' with extinction [categories Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW)], 'non-threatened' [categories Least Concern (LC), Near Threatened (NT)], Data Deficient (DD) or unassessed (NA). While these categories capture the range of factors that underlie extinction risk across species with available data at a given time (Purvis *et al.*, 2000; Fisher & Owens, 2004), the case of DD and NA groups is a cause for concern given that they lack conservation focus. Yet, high proportions of such species have been suggested to be threatened (Borgelt *et al.*, 2022). Moreover, while conservation categories have been a pivotal instrument for developing conservation sciences and guiding priorities (Rodrigues *et al.*, 2006; Hoffmann *et al.*, 2008; Brooks *et al.*, 2015; Chichorro, Juslén & Cardoso, 2019; Betts *et al.*, 2020), actual allocation of conservation investment may be taxonomically and geographically biassed irrespective of extinction risk level (Rodrigues *et al.*, 2006; Mammola *et al.*, 2020; Adamo *et al.*, 2022).

In recent years, the focus on conservation categories as proxies for extinction risk has been expanded with the incorporation of the assessment of changes in population sizes over time ('population trends' hereafter). The underlying rationale for the use of population trends is that processes of extinction are underpinned by the onset of demographic collapses that initiate progressive declines within a species, subsequently leading to extinction (Ceballos *et al.*, 2010, 2017; Collen *et al.*, 2011; Stein, 2020). Importantly, given that millions of populations have disappeared within the past 100 years alone (Dirzo *et al.*, 2014; Ceballos *et al.*, 2017; Ceballos, Ehrlich & Raven, 2020; Hallmann *et al.*, 2017), declines in populations provide a more dynamic measure of endangerment through time, whereas conservation categories can be seen as 'snapshots' of species endangerment. Consequently, population trends may be used as a powerful additional proxy for extinction risk (Ceballos & Ehrlich, 2002; O'Grady *et al.*, 2004; Ceballos *et al.*, 2017; Pincheira-Donoso *et al.*, 2023). Given the advantages of this approach, it has already been used to identify biological, ecological, climatic and threatening factors in common among declining species (e.g. Murray & Hose, 2005; Collen *et al.*, 2011; Murray *et al.*, 2011, 2014; González-Suárez, Lucas & Revilla, 2012). Likewise, large-scale analyses of population trends over time can be used to indicate from an alternative perspective the state of global biodiversity, such as the *Living Planet Report*'s average 69% decline in population abundance between 1970 and 2018 (WWF, 2022), and the 'biological annihilation' of global vertebrate populations (Ceballos *et al.*, 2017). In fact, in the most comprehensive study based on species population trends to date, Ceballos *et al.* (2017) revealed that 32% (out of >27,000) of included land vertebrate species were declining. Importantly, these authors show two main signals of the severity of the defaunation crisis. Firstly, almost a third of species identified to be declining were classed as non-threatened by the IUCN. Secondly, while tropical species-rich regions host hotspots of declining species when measured as absolute numbers of species, these patterns shifted towards temperate regions when the figures of declining species were calculated as proportions. Collectively, their findings reveal that declines are ubiquitous across species and geographical regions, irrespective of endangerment levels or hotspot status.

An evident limitation of studies exclusively reporting patterns of species undergoing population declines is that the significant proportions of species that have remained stable over time, or which have even undergone increasing population sizes, are neglected. As such, criticism is growing towards large-scale aggregations of trends failing to identify not only 'losers' but also 'winners' [e.g. for the *Living Planet Report* (Dornelas *et al*., 2019; Leung *et al*., 2020)]. In addition, the reporting of widespread biodiversity loss and the public attention that these patterns can often gain have been criticised for their effects in the delivery of partial 'big pictures' (Leung *et al*., 2020). Thus, global-scale studies integrating the diversity of population trends to draw planetary patterns of declines, stability and increases across the tree of life remain a significant gap. Holistic consideration would provide a true representation of the state of current biodiversity – a means by which to inform both the scientific community and the broader public.

Here, we provide the first comprehensive global-scale overview of all four categories of population trends (decreasing, stable, and increasing, as well as species for which they remain unknown) for vertebrates and insects. Through both geographic and taxonomic space, the patterns of population trends across animal taxa are assessed comparatively to draw an integrative picture of how vertebrate and insect populations, and their proportions, are changing over time. Our overview expands the pioneering advances made in previous large-scale studies (e.g. Ceballos *et al*., 2017) by considering all population trends, utilising newly released and updated species data available from the IUCN *Red List*, and by incorporating additional taxonomic groups (fishes and insects). We advocate that quantification and forecasting of the spatial and phylogenetic distribution of extinction risk are underpinned by incorporating these different measures of demographic trends through time.

II. THE DEMOGRAPHIC TRAJECTORIES THAT LEAD SPECIES TO EXTINCTION

Extinctions are the outcome of progressive processes of population declines until a 'tipping point' where the degree of demographic collapse that prevents a species from recovering is reached (Cardillo *et al*., 2005; Sinervo *et al*., 2010; Collen *et al*., 2011; Hoffmann & Sgró, 2011; Chaparro-Pedraza, 2021; Pincheira-Donoso *et al*., 2021). The circumstances that trigger the onset of these processes of decline can be multiple, but they have in common an alteration in the interactions between environmental conditions and the traits that species have evolved to face those conditions (Ferriere, Dieckmann & Couvet, 2004; Hoglund, 2009; Hoffmann & Sgró, 2011; Pincheira-Donoso *et al*., 2021), i.e. when patterns of natural selection change at rates that exceed a species' ability to respond or adapt to such changes (Parmesan, 2006; Brook, Sodhi & Bradshaw, 2008; Dirzo *et al*., 2014; Murray *et al*., 2014; Chaparro-Pedraza, 2021). Extinctions are, therefore, a demographically progressive process that can be anticipated based on the signatures that population trends leave in species through time (Collen *et al*., 2011; Chaparro-Pedraza, 2021), in contrast with conservation categories. Overall, using population trends to inspect the demographic progression of species towards extinction provides an ideal tool to reinforce predictions about the future status of species. Population increases may indicate recovery in species currently classed as threatened, whereas population decreases may signal progression towards future extinction risk in non-threatened species (Collen *et al*., 2011; Ceballos *et al*., 2017).

III. METHODS

(1) Taxonomic estimates

All data on population trends and conservation categories were sourced from the IUCN *Red List* using their advanced search criteria portal (IUCN, 2022*b*; available at www.iucnredlist.org). Population trend data can be defined as one of four groups: decreasing, stable, and increasing population sizes, in addition to species for which population trends remain unknown/NA. To account for species with unknown population trends in our taxonomic estimates, we adapted previous methods used for accounting for taxa classed as Data Deficient (DD) in calculations of proportions of threatened species (Schipper *et al*., 2008; Hoffmann *et al*., 2010; Böhm *et al*., 2013; IUCN, 2022*a*). We calculated the proportion of species with decreasing populations as: $\text{PropDecr} = \text{Decrease}N/(N - \text{Unknown}N)$ where Decrease$N$ is the number of decreasing species, Unknown$N$ is the number of unknown-trend species, and N is the total number of species across all four trend categories. We also calculated the lower and upper bounds of this proportion. The lower bound $\text{PropDecr}_\text{L} = \text{Decrease}N/N$ assumes that no unknown-trend species are decreasing, while the upper bound $\text{PropDecr}_\text{U} = (\text{Decrease}N + \text{Unknown}N)/N$ assumes all unknown-trend species to be decreasing. We also calculated this midpoint and lower and upper bounds for species with stable populations. We did not calculate lower and upper bounds for species with increasing populations, as given the low overall numbers of these species the likelihood that all unknown-trend species actually would be increasing was very low. Therefore, only the midpoint values for species with increasing populations are reported below.

For calculating the proportion of species classified within 'threatened' conservation categories, we again followed previous studies (e.g. Schipper *et al*., 2008; Hoffmann *et al*., 2010; Böhm *et al*., 2013; IUCN, 2022*a*). Importantly, the explicit recommendations from the IUCN denote that while Extinct species should be excluded from 'threatened' categories, Extinct in the Wild (EW) should be integrated into analyses given that any successful reintroduction of such species would result in their classification within a 'threatened' category (IUCN, 2022*a*). Therefore, to account for both DD and EW we calculated the proportion threatened as PropThreat = (EW + CR + VU + EN)/(N − DD), a lower bound as PropThreat_L = (EW + CR + VU + EN)/N and upper bound as PropThreat_U = (EW + CR + VU + EN + DD)/N.

(2) Habitat systems

We obtained data on habitat type for each assessed species with a documented population trend (decreasing, stable, increasing, unknown) from the IUCN *Red List* using their advanced search criteria portal (IUCN, 2022*b*; available at www.iucnredlist.org). Species that lacked a habitat type and had an NA population trend were excluded. Habitats were classed as one of the following categories: terrestrial, freshwater, marine, terrestrial and freshwater, terrestrial and marine, freshwater and marine, terrestrial freshwater and marine. These were then grouped into two taxonomic groups: vertebrates (mammals, birds, amphibians, reptiles and fishes) and insects. Proportions of species reported for each habitat in Section IV.1 were calculated for exclusively terrestrial, freshwater and marine species.

(3) Spatial mapping

For mammals, birds, amphibians, fishes and insects we sourced all available distribution data for the included species with a known population trend (decreasing, stable, increasing or unknown) from the IUCN *Red List* (IUCN, 2022*b*; available at www.iucnredlist.org) advanced search criteria portal using the 'download range file' option. This portal allows for selecting a specific taxonomic group and specific population trend to download all available data matching those criteria. Each taxonomic group thus had four associated shapefiles of distributional data. For reptiles we sourced data from Roll *et al.* (2017), and each species' respective population trend from the IUCN *Red List*. We sourced a list of known global invasive species from the IUCN invasive species database (ISSG, 2015; available at http://www.iucngisd.org/gisd/) and removed these species from our shapefiles. These were omitted given that invasive species represent one of the most prevalent drivers of biodiversity loss (Brook *et al.*, 2008; Bellard, Cassey & Blackburn, 2016; Young *et al.*, 2016). Therefore, their inclusion would reflect areas where historical human-induced species invasions have occurred, biassing our interpretation of global regions where naturally occurring species are truly 'succeeding' in the Anthropocene. All maps were made using R version 4.1.0 (R Core Team, 2022). Each shapefile was re-projected from its original standard WGS84 to a Behrmann's equal area projection using the *sf* package (Pebesma, 2018). We created a global grid covering the world with 1° × 1° grid cell size using the *rnaturalearth* (available at: https://CRAN.R-project.org/package=rnaturalearth) and *sf* packages. We joined each shapefile individually to a grid and summarised number of species per grid cell to obtain species richness counts.

IV. GLOBAL PATTERNS OF ANIMAL POPULATION TRENDS IN THE ANTHROPOCENE

(1) Taxonomic patterns of population trends

In contrast with the overall global estimates of biodiversity erosion arising from IUCN *Red List* conservation categories [28% of assessed species classed as threatened (IUCN, 2022*b*; available at www.iucnredlist.org)], the levels of biodiversity degradation revealed by the analysis of population trends across over 71,000 species spanning all vertebrate groups and insects is much more severe. Globally, 48% (23–76%) of included animal species are undergoing population declines, 49% (23–76%) remain stable, and only 3% of species are undergoing population increases (Fig. 1; see online Supporting Information, Table S1). The proportions of each of these three population trends (plus the unknown category) differ across animal groups (Fig. 1; Table S1). A consistent pattern across all groups was that the proportion of species undergoing population increases was considerably lower than any other population trend within each taxon (Fig. 1). While not as consistent, we also found that in four (mammals, birds, amphibians and insects) out of the six groups, the proportion of species undergoing

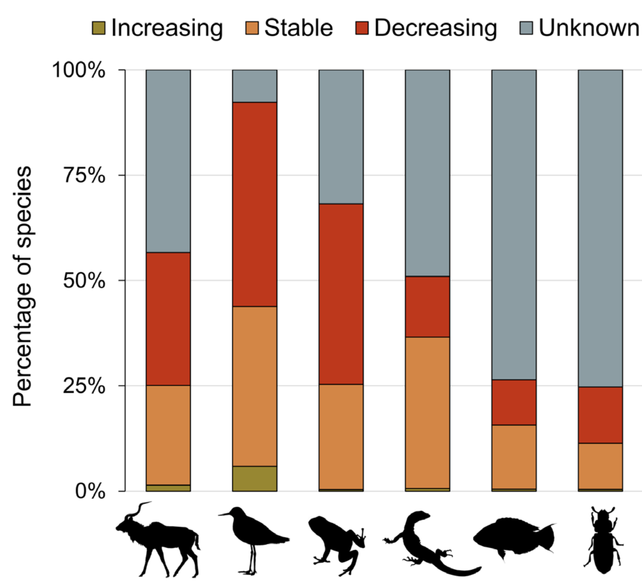


Fig. 1. Percentage of species per taxonomic group which have decreasing, stable, increasing or unknown/unassessed (NA) population trends. Each group is represented by a silhouette from left to right; mammals (N = 5969), birds (N = 11,162), amphibians (N = 7316), reptiles (N = 10,150), fishes (N = 24,356) and insects (N = 12,161). Data were sourced from the IUCN Red List (www.iucnredlist.org).

decreases in population size was higher than the combined proportion of species with populations that have remained stable or are increasing (Fig. 1). This was particularly severe for amphibians (Fig. 1). By contrast, a higher proportion of species appear to have stable populations among reptiles and fishes (Fig. 1). Lastly, we found a high proportion of species with unknown population trends for mammals (43%), reptiles (49%), fishes (74%) and insects (75%); in the latter two groups, the proportions of unknown population trends were greater than their combined proportions of decreasing, stable and increasing population trends (Fig. 1). Overall, these observations show that only a small number of species show increasing populations and that a high proportion of species with decreasing populations within groups is the norm across animals for which these data are currently available.

Despite the tendencies revealed by population trends, it is important to acknowledge that the use of data of this nature may come with drawbacks. For example, IUCN population trends are calculated from the combined total of all populations of a species, which may make them susceptible to overinflation by trends from larger populations – a similar weakness to the previously discussed susceptibility of the *Living Planet Report* to strong fluctuations or strong population declines (Westveer *et al*., 2022). Our findings both agree and conflict with recent work using time-series population data for over 2000 vertebrate species, wherein amphibians were also found to be undergoing net population declines (combined net decrease in abundance estimated from state-space models), but mammals, birds and reptiles showed net population increases (combined net increase in abundance estimated from state-space models), for the period 1970–2014 (Daskalova, Myers-Smith & Godlee, 2020). However, whereas population data based on changes in abundance (e.g. time-series data) may offer important advantages, the global-scale coverage of IUCN population trends remains unmatched by any other proxy of demographic quantification over time. Moreover, caveats due to assessment bias towards certain taxonomic groups, and the drive to expand the taxonomic scope of assessments being at odds with updating of existing but outdated (10-year-old) assessments, are well recognised (Rondinini *et al*., 2014; Brummitt *et al*., 2015; Bachman *et al*., 2019).

Another important aspect to highlight is that population trend data from the IUCN, like conservation category data, still remain limited, with many species included in the 'unknown' population trend group (Stein, 2020). The proportions of species for which the population trend was classified as 'unknown' are high for all groups (ranging from 32% to 75%), except birds for which 8% of species are so classified (Fig. 1; Table S1). This is important to recognise when comparing our work to that of Ceballos *et al*. (2017), as their study included 'unknown' trends in their total counts (G. Ceballos, personal communication), thus providing a conservative estimate of population declines. Below, we discuss proportions of species calculated following previous methods used to include DD species in 'threatened' estimates (Schipper *et al*., 2008; Hoffmann *et al*., 2010; Böhm *et al*., 2013; Pincheira-Donoso & Hodgson, 2018; IUCN, 2022*a*). We provide a mid-point estimate with upper and lower bounds for the proportions of species decreasing and remaining stable (see Section III.1). Due to the small numbers of species with increasing population trends we do not calculate the upper and lower bounds for these trends as it was felt unlikely that the 'unknown' trends would represent population increases.

(*a*) *Vertebrates*

Amphibians had the highest proportion of species with decreasing populations at 63% (43–75%), and the lowest proportions of stable populations at 37% (25–57%) and increasing populations at 1% (Fig. 1; Table S1). These alarming figures are consistent with the widely known proportion of amphibian species classified as threatened by the IUCN *Red List* (>40% species; Pincheira-Donoso & Hodgson, 2018; Pincheira-Donoso *et al*., 2021), and add further evidence that global amphibian biodiversity is declining at accelerating rates (Stuart *et al*., 2004; McCallum, 2007; Collins & Crump, 2009). While no other group of vertebrates matches the level of amphibian declines, the proportions of mammals with decreasing populations at 56% (32–75%) and birds at 53% (48–56%) outweigh that of their proportions remaining stable, at 42% (24–67%) and 41% (38–46%), respectively (Fig. 1; Table S1). Birds have the highest proportion of species recorded to be increasing (6%, followed by only 2% in mammals and fishes). In contrast to other vertebrates, the proportion of species with stable population trends is the highest for reptiles at 70% (36–85%) and fishes at 58% (15–89%), whereas the proportion of decreasing populations in these taxa is 28% (14–63%) and 41% (11–84%), respectively (Fig. 1; Table S1).

Importantly, patterns of population trends may vary considerably across habitat systems. For example, the recent *Living Planet Report* revealed freshwater vertebrates to be the most impacted, with an average 83% decline in population abundances (WWF, 2022). Grouping species by habitats thus may provide a more accurate representation of relative susceptibility to declines, and assist better-informed conservation planning. In a comparison of species inhabiting solely terrestrial, marine or freshwater habitats, we found similar proportions of vertebrate species with decreasing population trends for terrestrial species at 47% (32–64%) and freshwater species at 45% (15–82%), and a slightly lower proportion for marine species at 36% (8–86%) (Table S2). However, given the wide ranges calculated for freshwater and marine species, we stress that these mid-point estimates are unlikely to be representative of these habitat systems globally.

Collectively, these findings expand our understanding of the global state of vertebrate population trends. The inclusion of species with stable and increasing population trends in our analyses provides a more accurate representation of current biodiversity, allowing us not only to identify variation in population erosion among 'losers' (e.g. which lineages are more threatened than others), but to also have a comprehensive global overview of 'winners' (species that have maintained demographic stability through time despite the extent of environmental degradation). We note that the high proportions of 'unknown' population trends (Fig. 1) highlights an evident gap in our knowledge, but accounting for them by calculating upper and lower bounds limits the risks of either overestimating or downplaying biodiversity loss (Loreau *et al.*, 2022).

(*b*) *Insects*

The limited available information suggests that insects show similar patterns to most tetrapods, with the proportion of species undergoing population decreases estimated at 54% (13–89%) (Fig. 1; Table S1). Only 2% of species were found to be undergoing population increases. Not surprisingly, given the enormous estimated global species diversity of these invertebrates (Stork, 2018; García-Robledo *et al.*, 2020), which represent one of the dominant proportions of planetary biomass among animals worldwide (Bar-On, Phillips & Milo, 2018), available data on insects reveal the highest proportion of species with unknown population trends, at 75% (Fig. 1; Table S1). Interestingly, in contrast to vertebrate declines across habitats (WWF, 2022), accumulating evidence suggests that terrestrial insects may be experiencing greater declines than aquatic insects (e.g. van Klink *et al.*, 2020). In a comparison of the three habitat types, the proportion of terrestrial species showing population declines was 66% (17–91%), far exceeding that of freshwater species at 12% (1–93%) (Table S2), although note the very wide ranges, and therefore these mid-point values may not be considered representative globally.

While large-scale studies of human-induced insect declines have provided critical insights for decades (Parmesan *et al.*, 1999; Hill *et al.*, 2002; Wilson *et al.*, 2004, 2005), a review by Sánchez-Bayo & Wyckhuys (2019) led to heated discussion on estimating the extent of the extinction crisis in this taxon. Based on a review of 73 long-term insect population-monitoring reports, Sánchez-Bayo & Wyckhuys (2019) suggested that around 40% of global insect species may become extinct in the coming decades. Their conclusions have been widely questioned based on methodological issues, geographic, taxonomic, and declining species bias and misuse of IUCN *Red List* categories, among other aspects (Cardoso & Leather, 2019; Cardoso *et al.*, 2019; Komonen, Halme & Kotiaho, 2019; Thomas, Jones & Hartley, 2019). Our calculations suggest that populations are in decline for 54% (13–89%) of insect species included in the *Red List* (3006 species with known population trends; Table S1). More than a million insects have been described to date, with estimates that an additional 4.5–7 million species are yet to be named (Stork, 2018; García-Robledo *et al.*, 2020). Moreover, insect data are generally scarce in the *Red List*, and are geographically and taxonomically biassed (Stein, 2020). Therefore, we are inclined to agree that any global estimates of the severity of the insect extinction crisis derived from the limited existing data must be interpreted cautiously.

(2) Geographic patterns of population trends

While the geographic distribution of 'hotspots' of species with decreasing (Fig. 2), stable and increasing population trends (Fig. 3) varies considerably across taxonomic groups, some patterns emerge from the data. We find a relatively consistent pattern that decreasing vertebrate species tend to be concentrated around the tropics (Fig. 2). This tropical signal of declines is similar to previous findings for tetrapods (Ceballos *et al.*, 2017), for vertebrates in the recent *Living Planet Report* (WWF, 2022), and for threatened conservation category species (Hoffmann *et al.*, 2010; Dirzo *et al.*, 2014; Pimm *et al.*, 2014; Cox *et al.*, 2022). However, this pattern is very weak in reptiles and insects, with high concentrations of decreasing species limited to tropical islands or multiple areas in temperate regions (Fig. 2).

The distribution of stable populations among vertebrates also shows higher concentrations within the tropics, but with a tendency for a more widespread pattern extending to temperate regions (Fig. 3). Additionally, tropical South America appears to be a shared hotspot of stable populations across all four tetrapod groups (Fig. 3). Finally, the distribution of increasing populations is highly variable and based on small sample sizes (except for birds), but there appears to be a slight tendency for higher concentrations of increasing populations in the temperate Northern Hemisphere (except in the case of amphibians and reptiles; Figs 3 and 4).

Collectively, while these observations suggest that the greatest magnitude of demographic declines are concentrated within tropical regions, spatial patterns both within and among population trends vary considerably by taxonomic group. This may explain why no biogeographic patterns were identified in a study combining spatial distributions in cross-taxa population time-series data (Daskalova *et al.*, 2020). Aggregating broad taxonomic groups which differ in global macroecological organisation (e.g. endotherms and ectotherms) may mask taxon-specific spatial signals.

(*a*) *Macroecological patterns of population declines*

Our assessment shows that the highest concentrations of species with decreasing population trends occur within tropical regions (Figs 2 and 4). Multiple parallels emerge with previous work on tetrapods (Ceballos *et al.*, 2017). Firstly, there appear to be hotspots of decline in tropical rainforests, and most notably, in tropical mountain systems along the Andes, East Africa highlands and south of the Himalayas (Figs 2 and 4). Secondly, we find a similar distribution of patterns of declines among mammals and birds (Fig. 2). Thirdly, spatial distributions of these patterns of declines for mammals and birds differ from those of amphibians and reptiles, with the latter having fewer declining species in temperate regions (Fig. 2). However, we did identify more declines for reptiles

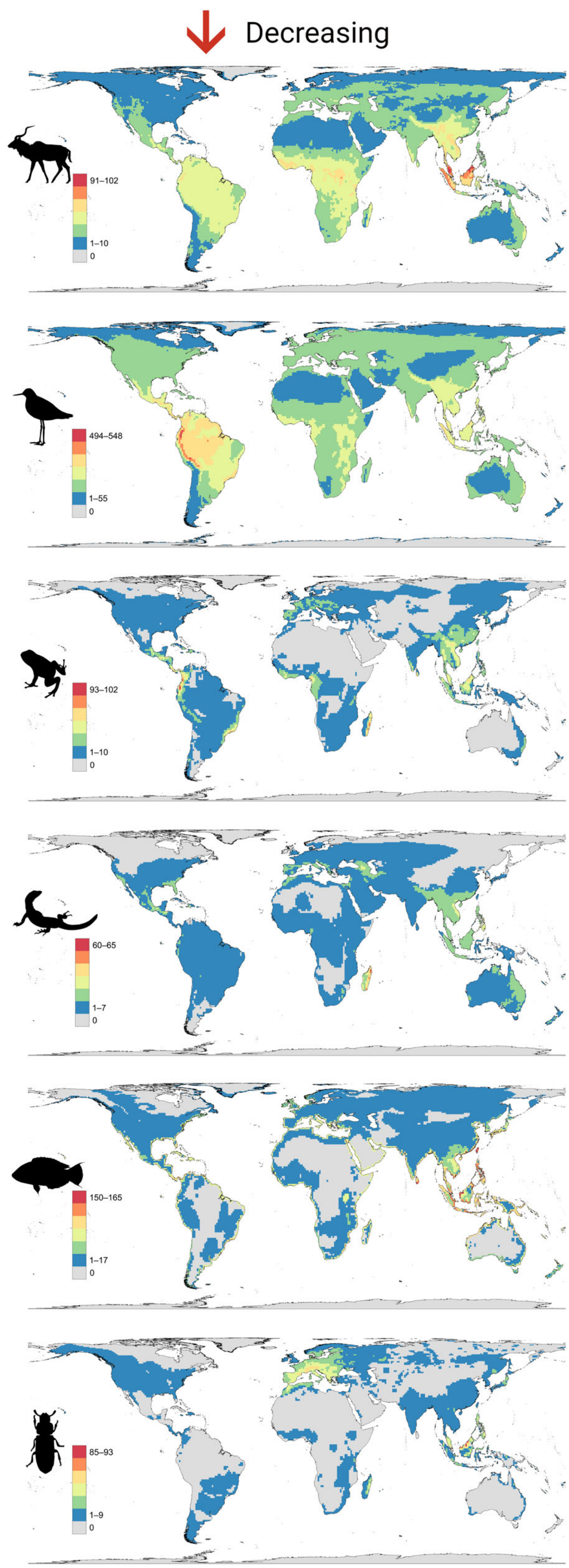


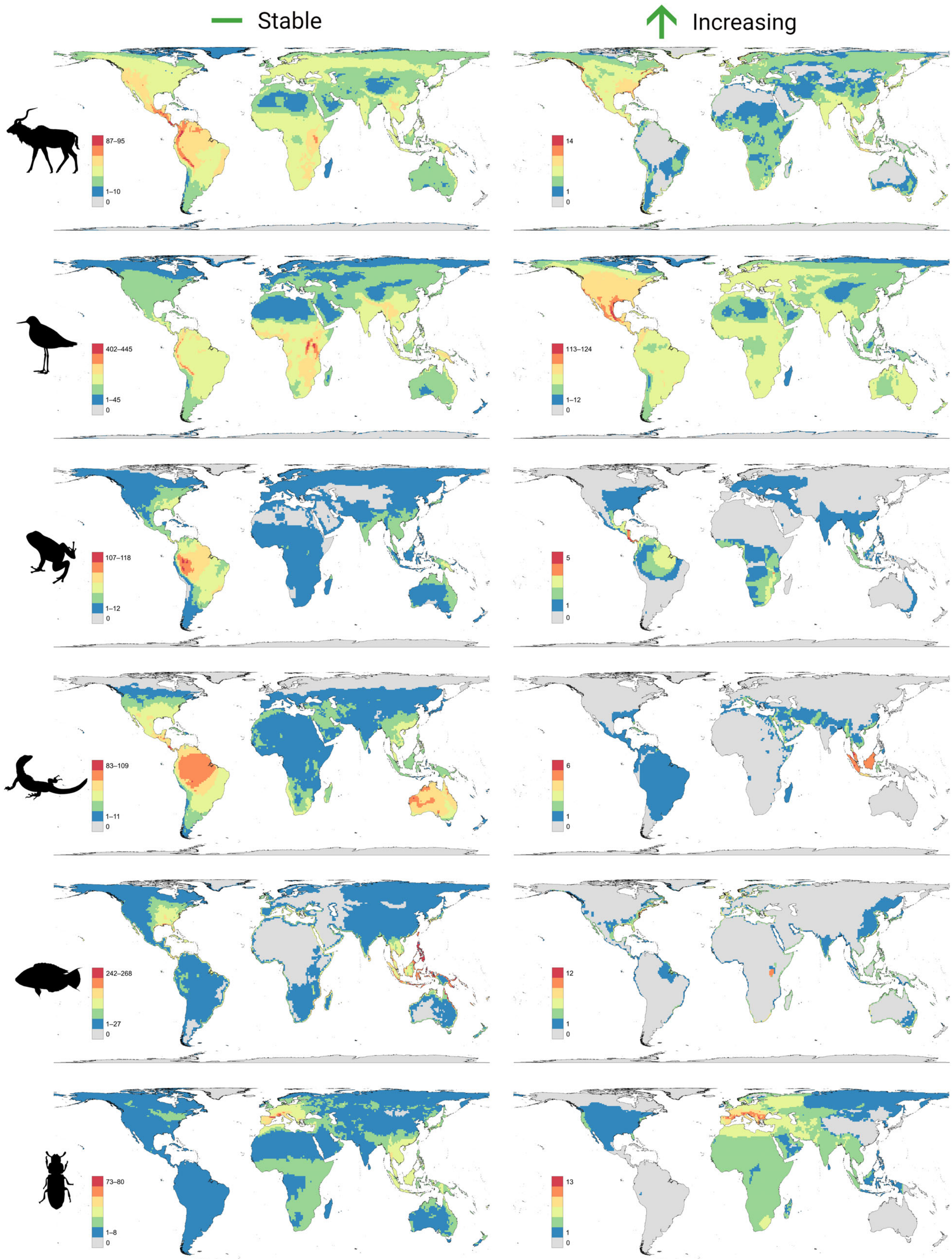
Fig. 2. The global distribution of animals with decreasing populations. Each taxonomic group is mapped individually. Numbers of species were counted within each 1° × 1° grid cell covering the globe, using a Behrmann's equal area projection.

and amphibians in temperate regions than reported by Ceballos *et al.* (2017), with amphibians also showing declines in Africa and across Eurasia (Fig. 2). Moreover, Ceballos *et al.* (2017) did not include fishes or insects in their analyses. For fishes we identified a similar spatial signal for declines in the tropics, most notably in Southeast Asia (Fig. 2). In the case of insects, while high concentrations of declines are reported in Borneo, they appear to differ from other groups, with high concentrations of declines in western, central and eastern Europe (Fig. 2). However, note that the extremely limited data available for insects in comparison to overall richness mean that these patterns should be interpreted cautiously.

These spatial patterns of decreasing populations are in concordance with spatial analyses on the distribution of hotspots of threatened vertebrates (Dirzo *et al.*, 2014; Pimm *et al.*, 2014), which tend to be concentrated across tropical rainforests in Central and South America (the Andes, Amazon basin and Atlantic forest), west African forest, east African highlands, Madagascar and across South and Southeast Asia (Hoffmann *et al.*, 2010). For groups that have been assessed individually, the distribution of threatened mammals, birds, amphibians (Pimm *et al.*, 2014) and reptiles (Böhm *et al.*, 2013; Cox *et al.*, 2022), show similar spatial patterns to those found here for decreasing populations. However, our results suggest that declines are occurring across greater geographical extents and across larger numbers of species (Figs 1 and 2). Interestingly, Madagascar does not host high concentrations of threatened amphibians and reptiles, yet we find this region to be a hotspot for declines in these groups (Fig. 2). In the case of insects, little is truly known about the global distribution of threatened species due to the scarcity of data and a research bias towards Europe and the USA – which host only around 20% of insect species diversity globally (Dirzo *et al.*, 2014; Stork, 2018).

(*b*) *Macroecological patterns of stable and increasing populations*

Considering all groups, the spatial distribution of species with stable populations again tends to be concentrated in the tropics, but with a greater spread into temperate regions than was the case for species with decreasing populations (Figs 3 and 4). This pattern can be seen for all four tetrapod groups. For mammals and birds, stable populations are concentrated across the tropics, but extend to most geographical regions (Fig. 3). Stable populations of amphibians and reptiles tend to be concentrated across the Americas, and for reptiles also in Australia (Fig. 3). For fishes, the distribution of stable populations is in some respects similar to that of population declines, with the highest values across Southeast Asia, but in addition there are high values in North America (Fig. 3). In the case of insects, the limited data imply that stable populations are found across Europe (similar to their pattern of declines), but with additional concentrations across Africa, Southeast Asia and Australia (Fig. 3).



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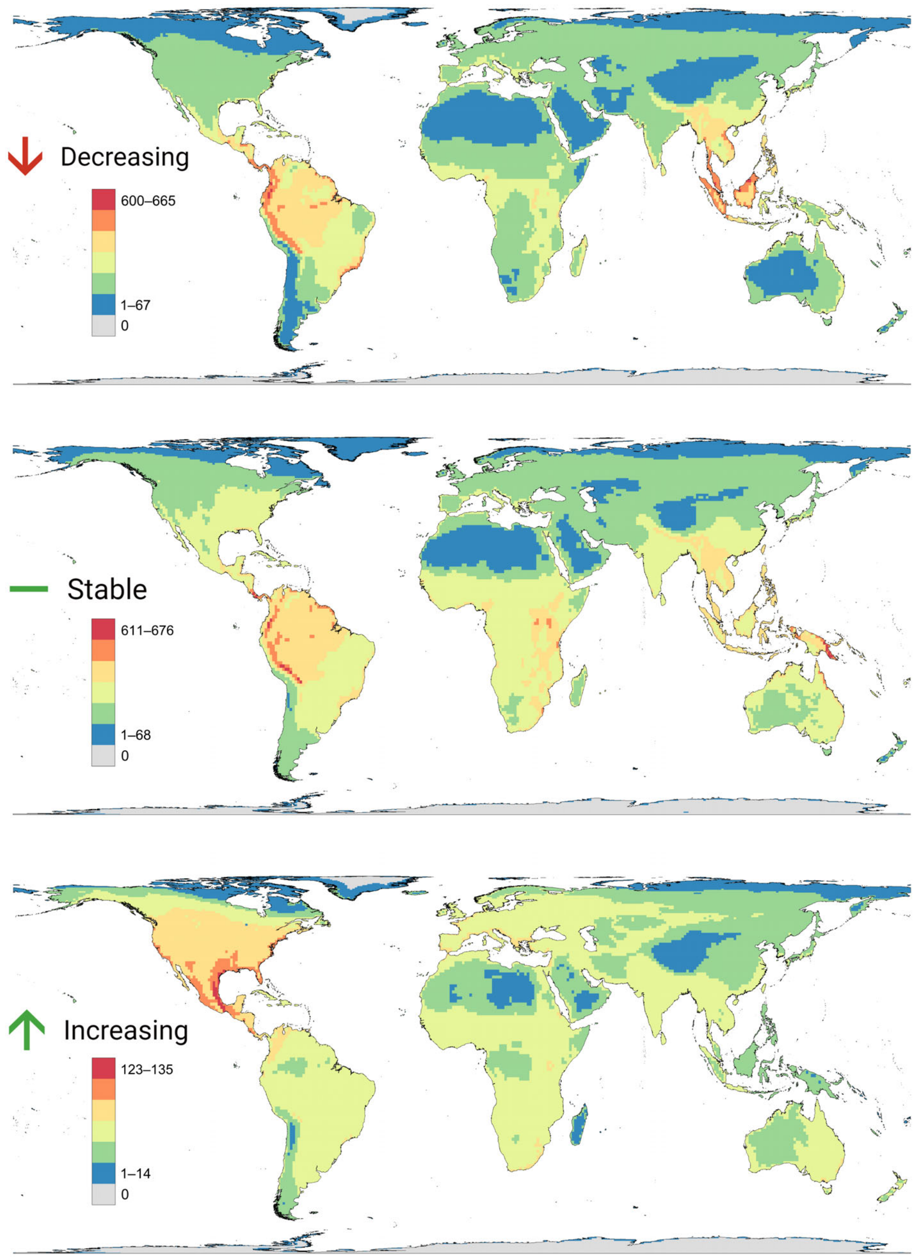

Fig. 4. The global distribution of animals with decreasing (top), stable (middle) or increasing (bottom) populations combining data from all taxonomic groups. Numbers of species were counted within each 1° × 1° grid cell covering the globe, using a Behrmann's equal area projection.

For all taxa combined, there is a tendency for increasing populations to be concentrated in sub-tropical to temperate regions, especially across Central to North America (Fig. 4). However, there was much variation across taxonomic groups (Fig. 3). The most consistent pattern is seen between mammals and birds (both endotherms) for which the highest concentrations of species with increasing populations are in Central and North America (Fig. 3). Increasing population trends for amphibians were concentrated in Central and South America and southeast Africa, while for reptiles increasing population

(Figure legend continued from previous page.)
Fig. 3. The global distribution of animals with stable (left) and increasing (right) populations. Each taxonomic group is mapped individually. Numbers of species were counted within each 1° × 1° grid cell covering the globe, using a Behrmann's equal area projection.

trends occur mostly in Southeast Asian islands (Fig. 3). Increasing population trends in fishes occur predominantly along North America's east coast, and in Europe, South Africa and Lake Victoria (Fig. 3). Intriguingly, for insects, similar to the spatial patterns of decreasing and stable populations, increasing populations are concentrated in western, central and eastern Europe (Fig. 3). However, sampling bias of long-term insect monitoring towards these regions is well recognised (Cardoso & Leather, 2019; Thomas *et al.*, 2019), and these patterns may be an artefact of this. Moreover, note that the numbers of species showing population increases per grid cell are low for all groups except birds (e.g. compare keys in Fig. 3, a maximum of six reptiles compared to 124 for birds). Therefore, the patterns observed for birds will be driving the patterns for all taxa combined (Fig. 4).

Collectively, our findings appear to show that higher numbers of species with stable and increasing populations are found in temperate regions compared with the patterns of species with decreasing populations. This agrees broadly with findings that vertebrate populations in temperate regions (Mediterranean forests, montane grasslands and temperate wetlands, but not tropical rainforests) were more likely to increase (Daskalova *et al.*, 2020). However, observed spatial patterns of extinction risk differ among studies investigating species undergoing population declines (Ceballos *et al.*, 2017) and those that are classed under threatened categories (Böhm *et al.*, 2013; Cox *et al.*, 2022). Future analyses of data sets including a larger number of species may enable a more detailed assessment of global spatial patterns of extinctions.

(*c*) *Knowledge gaps*

Species included in the *Red List* with currently unknown population trends tend to be concentrated in the tropics (Fig. 5). This is consistent with the predominant patterns of latitudinal diversity gradients (Gaston, 2000; Roll *et al.*, 2017), perhaps indicating that the numbers of species with unknown population trends are roughly proportional to their regional biodiversity. However, the hotspots of knowledge gaps do vary among taxa, as do the numbers of species involved (Fig. 5). Across all groups, the distribution of species with unknown population trends is not spatially congruent with that of species with decreasing, increasing or stable population trends (Figs 3–5), with the possible exception that the patterns for mammals (concentrated in Central and South America and tropical Africa), birds (concentrated in tropical Andes, Atlantic forest, East Africa, India, Himalayas and Southeast Asia) and fishes (concentrated in Southeast Asian islands) are to some extent congruent with their decreasing and stable distributions. Collectively, these findings show that species for which population trends are unknown tend to be found in the tropics, and based on the patterns for other species, the likelihood that these populations will be increasing is low.

The geographic deficiencies in our knowledge of population trends reflect important socioeconomic disparities in global conservation investment. On the one hand, the money spent by a nation and the funding it receives for conservation both increase with GDP (McKinney, 2002; Hickey & Pimm, 2013). This is a fundamental problem in the distribution of conservation resources, given that biodiversity concentrations occur within some of the lowest-income countries (Giam *et al.*, 2010; Lenzen *et al.*, 2012). This unequal distribution of global wealth and investment is mirrored in the patterns of knowledge gaps we report herein, with the highest concentrations of species with unknown population trends found in countries with low GDP (e.g. tropical and savannah Africa, parts of South America, the Indo-Burma region and Papua New Guinea: Fig. 5; IMF, 2022). It is increasingly recognised that conservation implementation is frequently incongruent with conservation priorities [e.g. threatened species (Rodrigues *et al.*, 2006; Mammola *et al.*, 2020; Adamo *et al.*, 2022)]. For example, Waldron *et al.* (2017) found that 32% of threatened mammals are found in the 40 most underfunded countries globally. Likewise, while tropical moist forests have been denoted as 'conservation consensus areas' (Hickey & Pimm, 2013), many hotspots of species with unknown population trends also occur in such systems – particularly in those known to represent biodiversity hotspots (tropical Andes and Choco/Darien hotspot, Sundaland and Wallacea hotspot and Papua New Guinea, Amazon and Atlantic forest, Indo-Burma hotspot). While this may simply reflect both higher diversity and incomplete knowledge, it also raises questions regarding funding allocation. For example, although conservation funding generally increases with GDP globally, within a region it is often the lowest GDP countries that receive greater funding (e.g. Europe, Latin America), irrespective of biodiversity importance (Hickey & Pimm, 2013). This has been suggested to result from investment in biodiversity conservation with an underlying goal of poverty reduction (Scherl *et al.*, 2004). While unarguably important, biodiversity priorities are only one of multiple factors (e.g. wealth, cost and effectiveness, political stability, international relations and donor bias) involved in funding allocation (Grenyer *et al.*, 2006; Bode *et al.*, 2008; Waldron *et al.*, 2013; Hickey & Pimm, 2013). Collectively, disparities in global wealth and the distribution of funds will contribute towards geographic biases in our knowledge of progressive declines in biodiversity.

V. ARE THREATENED SPECIES DECLINING AND NON-THREATENED SPECIES SAFE?

The underlying premise of this and previous studies (e.g. Collen *et al.*, 2011; Dirzo *et al.*, 2014; Ceballos *et al.*, 2017), is that to tackle the biodiversity crisis holistically we must integrate proxies of extinction. A sole focus on threatened categories as indicators of the state of global biodiversity may underestimate the severity of the crisis. For example, for the majority of taxa, the percentage of species experiencing population declines greatly outweighs the percentage of

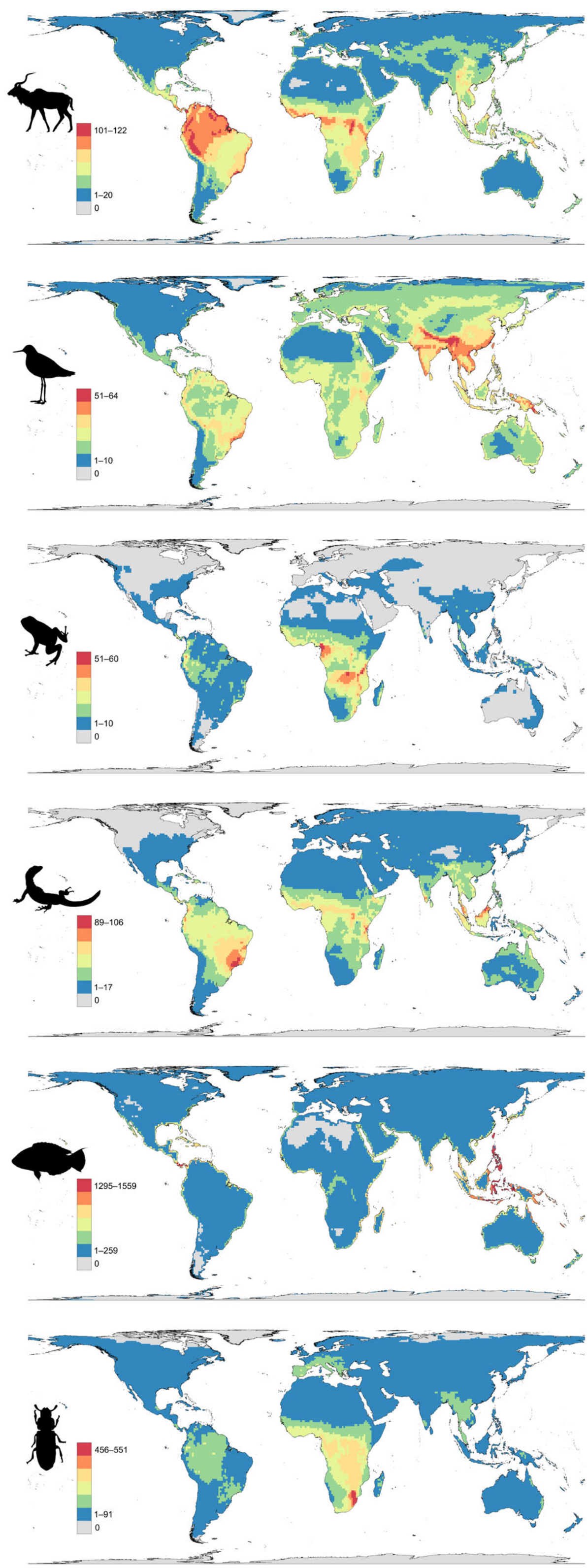

Fig. 5. The global distribution of animals with unknown population trends. Each taxonomic group is mapped individually. Numbers of species were counted within each 1° × 1° grid cell covering the globe, using a Behrmann's equal area projection.

species currently classified as 'threatened' (Table S3). While 56% (32–75%) of mammals, 53% (48–56%) of birds, 63% (43–75%) of amphibians, 41% (11–84%) of fishes, and 54% (13–89%) of insect species in the *Red List* are undergoing population declines, only 27% (23–37%), 13% (13–13%), 41% (35–51%), 18% (15–34%) and 26% (19–45%) of species in those groups, respectively, are classified as threatened (Table S3). Values are more similar for reptiles, where 28% (14–63%) of species are undergoing population decreases, in contrast to 21% (18–33%) classed as threatened (Table S3).

We can also contrast proxies of extinction against each other. This is a critical need only addressed by a handful of studies. For example, Stein (2020) found that of the 15,649 globally threatened species (plants, animals, fungi, and chromists) for which the IUCN *Red List* tracks population trend data, populations of 90% of species were decreasing, 9% were stable, and only 1% were increasing. Similarly, we find that for threatened vertebrates and insects, 91% (60–94%) are decreasing, 8% (5–39%) are stable and only 1% are increasing (Table S4). Importantly, Stein (2020) suggested that if 90% of the threatened species in their study are declining, a similar magnitude of decline may apply for the estimated 1 million species potentially threatened with extinction on Earth (IPBES, 2019).

We expand on this existing work by calculating that for all taxa 33% (17–65%) of non-threatened species are declining, with this being considerably higher for some groups [e.g. 47% (44–51%) for birds], or lower for others [e.g. 12% (7–48%) for reptiles], while 64% (33–81%) remain stable and 3% are increasing (Fig. 6A; Table S4). Moreover, considering these non-threatened categories individually, we additionally calculate that 81% (55–88%) of NT species and 27% (14–63%) of LC species are declining (Table S5). In the case of NT species, if unabated, these progressive declines could result in an additional 2136 species becoming classed as threatened (Fig. 6B; Table S5). Similarly, an unabated progressive decline of LC species could result in an additional 5785 becoming NT (Table S5). Our findings that declines are spreading across non-threatened species agree with recent work revealing that IUCN categories do not explain heterogeneity in population changes (Daskalova *et al.*, 2020). Overall, our analyses based on population trends (see also Ceballos *et al.*, 2017) suggest that the magnitude of the Anthropocene biodiversity crisis is considerably more severe than suggested by analyses based on IUCN *Red List* conservation categories.

VI. PROGRESSIVE DEFAUNATION

The trajectory of global defaunation continues at accelerating rates, and despite growing calls for immediate biodiversity loss mitigation (Cardinale *et al.*, 2012; Dirzo *et al.*, 2014; Kolbert, 2014; Ceballos *et al.*, 2015, 2017; McCauley *et al.*, 2015; Steffen *et al.*, 2015; Young *et al.*, 2016; Sánchez-Bayo & Wyckhuys, 2019; Cowie *et al.*, 2022), the onset of a

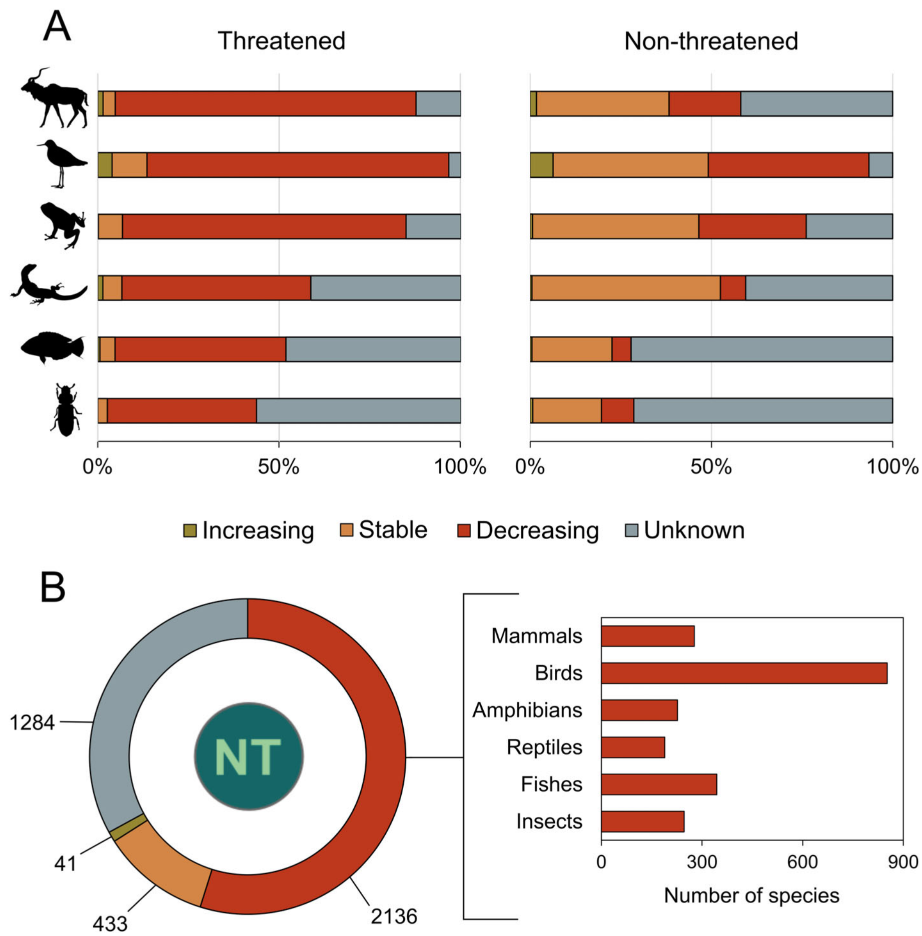

Fig. 6. (A) Percentage of species with decreasing, stable, increasing or unknown/unassessed (NA) population trends split across threatened [left: Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW)] and non-threatened [right: Least Concern (LC), Near Threatened (NT)] conservation category groups. Each group is represented by a silhouette from top to bottom; mammals, birds, amphibians, reptiles, fishes and insects. (B) The population trends (decreasing, stable, increasing and unknown) of species currently classified as Near Threatened, with numbers representing number of species (left), and graph showing the numbers of Near Threatened species with decreasing population trends per taxon (right). Data were sourced from the IUCN Red List (www.iucnredlist.org).

mass extinction remains underway [with 48% (23–76%) of species with known population trends undergoing declines, which includes a staggering 33% (17–65%) of species currently classified as non-threatened in the IUCN *Red List*]. Collectively, our findings reinforce the warning that biodiversity is on the brink of an extinction crisis. This crisis will have extensive ecological and ecosystemic consequences, given that ecological functioning is severely impacted by population declines and the resulting changes in community compositions (Ceballos & Ehrlich, 2002; Gaston & Fuller, 2008; Hooper *et al.*, 2012; Dirzo *et al.*, 2014; Young *et al.*, 2016).

Slowing the rate of biodiversity declines must therefore be a global priority, and now is a critical time to increase efforts towards pre-emptive conservation – protecting species before they become threatened (Rockström *et al.*, 2009*a*,*b*; Steffen *et al.*, 2015; O'Neill *et al.*, 2018). For example, one species-based approach has focussed on 'extinction models' which aim to identify characteristics in common among threatened species, ultimately defining the 'type' of species likely to be at risk (Purvis *et al.*, 2000; Fisher & Owens, 2004; Cardillo *et al.*, 2008; Kuussaari *et al.*, 2009). Small geographic range size, low fecundity and body size (the direction of effect differing by taxonomic group and size-selective environmental threats) are frequently used predictors of extinction risk across taxa (Pimm, Jones & Diamond, 1988; Cardillo *et al.*, 2005; Dirzo *et al.*, 2014; Murray *et al.*, 2014; Verde Arregoitia, 2016; Ripple *et al.*, 2017; Ruland & Jeschke, 2017; Chichorro *et al.*, 2019; Pincheira-Donoso *et al.*, 2021). However, given that the majority of these studies utilise conservation categories as proxies of extinction risk, we still need to learn more about the traits associated with population declines (but see Collen *et al.*, 2011; Murray *et al.*, 2011) – traits that could be indicators of future extinction risk, given that populations decline before a species becomes threatened. For example, using amphibian population trend data from the Global Amphibian Assessment database, Sodhi *et al.* (2008) identified additional life-history predictors of decline (e.g. habitat, reproductive strategy and parental care) which conservation-category-based models did not. These traits could be used to pre-emptively identify species at risk before they become threatened.

Likewise, in the case of area-based conservation (e.g. identifying and protecting regions hosting high metrics of biodiversity and experiencing extensive human impacts), while a fundamental aspect of biodiversity conservation (Myers, 2003, 1988; Mittermeier *et al.*, 2011; Marchese, 2015), we must consider what 'aspects' of biodiversity are being conserved. While protected areas directed towards hotspots of threatened species will protect species currently classified by the IUCN *Red List* as threatened (e.g. Mi *et al.*, 2023), these areas may not encompass species experiencing progressive declines (e.g. >2100 NT species) and that are likely to be threatened in the future. Likewise, while the drivers of overall biodiversity loss are well recognised (Pimm *et al.*, 1988; Brook *et al.*, 2008; Cahill *et al.*, 2013; Dirzo *et al.*, 2014; Newbold *et al.*, 2015; Urban, 2015; Bellard *et al.*, 2016; Young *et al.*, 2016), whether the initial drivers of population declines are the same as those resulting in a species becoming threatened remains unexplored. For example, the global-scale threats influencing IUCN *Red List* extinction risk status may not explain the likelihood of population declines (e.g. Daskalova *et al.*, 2020). Importantly, it is recognised that the type of threat – or synergies between threats – may determine the initial severity of population responses (i.e. mortality rate) (Mace *et al.*, 2008; Murray *et al.*, 2014), while the downward spiral to extinction is the outcome of mutual reinforcement between demographic, genetic and environmental factors (Brown, 1995; Lande, 1999; O'Grady *et al.*, 2004). As such, the initial stressors stimulating demographic alterations may be de-coupled from those ultimately driving extinction. Mitigation of threats stimulating initial declines could allow pre-emptive conservation of species before they become threatened.

More widely, the loss of populations must be considered in a threshold context. How many population extinctions are too many? What level of population loss warrants definition as a global crisis? For example, mass extinction events are typically defined as ~75% of species going extinct (Jablonski, 1994; Sepkoski, 1996; Barnosky *et al.*, 2011). While our modern crisis has not yet reached this point, we need to provide evidence to identify such events unfolding, and to define warning thresholds to alert proactively, rather than defining the crisis as already having occurred. For example, the Planetary Boundaries (PB) framework defines the limits of environmental changes which can occur beyond which the stability of human societies may be at risk (Rockström *et al.*, 2009*a*,*b*). Out of the nine currently defined boundaries, four have already been crossed, with biodiversity loss/biosphere integrity (based on genetic and functional diversity) being one of these (Steffen *et al.*, 2015). Genetic diversity – the long-term ability for biodiversity persistence (Mace *et al.*, 2014) – has also crossed its boundary, based on the classic signal of current extinction rates (Rockström *et al.*, 2009*b*; Steffen *et al.*, 2015). Functional diversity describes the functioning of the biosphere based on organismal functional traits, which relates to population abundances (Díaz & Cabido, 2001; Mace *et al.*, 2014; Steffen *et al.*, 2015). However, this aspect remains severely under addressed and the status of this component remains virtually unknown at a global scale. Moreover, the PB framework itself has not been without criticism, particularly in relation to whether biodiversity loss can in fact have a 'tipping point', and the applicability of metrics that could be used to define global functional diversity (Montoya, Donohue & Pimm, 2018*a*,*b*). However, what this growing body of work does highlight is the limited knowledge we have on estimating changes in population abundances at a global scale, limiting our ability to determine whether the current rate of population losses are as severe, or worse, than the disparity between current *versus* background extinction rates.

VII. CONCLUSIONS

(1) The comprehensive, global-scale overview of the unfolding Anthropocene defaunation crisis revealed by the analysis of animal population trends presented in this paper provides a considerably more alarming picture than the estimates derived from the use of IUCN *Red List* conservation categories of threat. We show that 48% (23–76%) of species included in our analyses are undergoing population declines, while 49% (23–76%) remain stable. Only 3% are increasing in population size. This pattern varies across taxonomic groups, with some lineages being more impacted [63% (43–75%) of included amphibians are decreasing] than others [e.g. 28% (14–63%) of included reptiles are decreasing]. We also find major deficiencies in our knowledge of population trends, particularly for fishes and insects (e.g. ~75% of included species had unknown population trends). Importantly, our results show that biodiversity is undergoing a period of demographic imbalance, whereby the level of species experiencing decreasing populations outweighs that of population increases by an alarming margin. The scenario shown by these demographic trajectories is a major cause for concern as it represents actual loss in biodiversity, rather than a turnover. Given the unprecedented speed at which global environments are being degraded by human activities, the number of populations that are collapsing in response to these rapid environmental changes (i.e. species are failing to adapt) is far higher than the number of species that are adaptively 'catching up' with those rapid changes.

(2) We find spatial signals in species' demography, with decreasing populations tending to be concentrated in the tropics, while population stability and increases are found more in temperate regions. However, these patterns vary across taxonomic groups, highlighting that spatial generalisations cannot always be made especially across groups which differ greatly in the way they interact with their environments (e.g. endotherms and ectotherms). The patterns we identify are determined by data availability, currently a major

constraint for certain organisms (e.g. insects and fishes). We find a tendency for species with unknown population trends to be found in the tropics, but specific hotspot regions vary considerably among taxonomic groups.

(3) A focus on IUCN *Red List* threatened categories runs a risk of downplaying the severity of biodiversity loss. We found that populations of 33% (17–65%) of non-threatened species are currently decreasing. Additionally, for NT species currently defined as experiencing population declines, if such trends remain unabated, an additional 2136 species could become threatened in the near future.

(4) Holistic approaches to tackling biodiversity loss must be based on the integration of multiple proxies for defining likelihood of extinction. Combining measures representing current status (conservation categories) and dynamic changes (population trends) allows predictions of future trajectories of extinction risk levels. Incorporating such approaches into methods already employed in conservation (e.g. extinction models, hotspot identification) could advance how we conserve biodiversity pre-emptively.

(5) Whether species and their populations can survive the Anthropocene defaunation will depend on their intrinsic traits, their adaptive potential, and also the research and management we dedicate towards preventing their disappearance. Based on the signals of the current biodiversity crisis, the time to recognise this phenomenon as occurring has already passed, and now is the pivotal time to protect the future integrity of biodiversity, and thereby the persistence of humanity.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Number of species with decreasing, stable, increasing or unknown/unassessed (NA) population trends across taxonomic groups.

Table S2. Number of vertebrates (mammals, birds, amphibians, reptiles and fishes) and insects with decreasing, stable, increasing or unknown/unassessed (NA) population trends split across habitat types.

Table S3. Percentage, range and number of species currently classified as threatened [Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW)] *versus* those classified as decreasing.

Table S4. Number of species classified as within threatened [Vulnerable (VU), Endangered (EN), Critically Endangered

(CR), Extinct in the Wild (EW)] or non-threatened [Least Concern (LC), Near Threatened (NT)] categories in the IUCN *Red List* with decreasing, stable, increasing or unknown/unassessed (NA) population trends.

Table S5. Number of species classified in the IUCN *Red List* as Near Threatened (NT) or Least Concern (LC) with decreasing, stable, increasing or unknown/unassessed (NA) population trends.

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