

SYNTHESIS

Global patterns of resilience decline in vertebrate populations

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Abstract

Maintaining the resilience of natural populations, their ability to resist and recover from disturbance, is crucial to prevent biodiversity loss. However, the lack of appropriate data and quantitative tools has hampered our understanding of the factors determining resilience on a global scale. Here, we quantified the temporal trends of two key components of resilience—resistance and recovery—in >2000 population time-series of >1000 vertebrate species globally. We show that the number of threats to which a population is exposed is the main driver of resilience decline in vertebrate populations. Such declines are driven by a non-uniform loss of different components of resilience (i.e. resistance and recovery). Increased anthropogenic threats accelerating resilience loss through a decline in the recovery ability—but not resistance—of vertebrate populations. These findings suggest we may be underestimating the impacts of global change, highlighting the need to account for the multiple components of resilience in global biodiversity assessments.

KEYWORDS

biodiversity, conservation, extinctions, fauna, global change, long-term time-series, multiple stressors, wildlife

INTRODUCTION

Global change is eroding life on earth at an unprecedented rate and scale (Butchart et al., 2010; Díaz et al., 2019; Tittensor et al., 2014). Species extinctions have accelerated over the last decades (Barnosky et al., 2012; Ceballos et al., 2015), with the concomitant loss of the functions and services they provide (Boyce et al., 2020; Dirzo et al., 2014; Estes et al., 2011). A general assumption is that this current loss of global biodiversity is paralleled by a decrease in the resilience of ecological systems (Côté & Darling, 2010; Hughes et al., 2005)—their ability to resist and recover from disturbances (Hodgson et al., 2015). As such, preserving resilience has become a major international conservation target (CBD 2010; United Nations General Assembly, 2015). However, global

assessments of temporal changes in resilience, and the factors (e.g. taxonomic groups, system) determining such trends, are thus far absent, rendering the assumption of global resilience loss untested.

Despite recent calls for global resilience analyses (e.g. Willis et al., 2018), most of our current understanding of resilience stems from experimental (Dai et al., 2012), modelling (Bozec & Mumby, 2015) or field (Ling et al., 2009) studies. While these have significantly contributed to better understand the resilience of determined systems, the knowledge that they provide is often spatially and temporally limited. Moreover, most studies usually focus on a single component of resilience (e.g. resistance; reviewed in Donohue et al., 2016; Kéfi et al., 2019). Yet, resilience encompasses at least two separate processes, resistance and recovery (Hodgson et al., 2015; Ingrisch

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& Bahn, 2018); where resistance represents the capacity of a system to absorb the impact of a particular stressor, and recovery describes the ability to return to the undisturbed state (Hodgson et al., 2015; Ingrisich & Bahn, 2018). Neglecting the multifaceted nature of resilience risks underestimating the impacts of global change (Donohue et al., 2013), as the effects on resistance can be different than on recovery (de Vries et al., 2012; White et al., 2020).

Another challenge for global assessments of resilience has been the lack of coherent ways to measure resilience (Pimm et al., 2019; Willis et al., 2018). Fortunately, recent studies have developed frameworks to quantify and compare resilience across different systems (Hodgson et al., 2015; Ingrisich & Bahn, 2018). At the population level, resilience can be estimated by measuring changes in the population growth rate (r) (Figure 1; Capdevila et al., 2020; Larios et al., 2017). Population decreases ($r < 0$) and increases ($r > 0$) are natural process that result from the continuous changes in the environment and demographic stochasticity (Lande et al., 2017), and they represent the intrinsic resilience of the population (Capdevila et al., 2020). Because resistance represents the ability of the system to remain unchanged after a disturbance (Hodgson et al., 2015), it can be linked with negative values of r . The more negative the value is, the less resistant the population is to a given disturbance (Capdevila et al., 2020; Larios et al., 2017). On the other hand, given that recovery represents the rate of return to the undisturbed state (Hodgson et al., 2015), it can be linked to positive r values. The more positive the r is, the faster the recovery is (Capdevila et al., 2020; Larios et al., 2017). Thus, the natural dynamics of populations can be explicitly linked to resilience theory through the processes of resistance and recovery.

In this study, we use a global data set of vertebrate population time-series, the Living Planet Database (LPD; Loh et al., 2005), to evaluate the temporal trends of the resilience components, resistance and recovery

(Figure 2). Population increases ($r > 0$) and decreases ($r < 0$) are natural process that result from the continuous changes in the environment and demographic stochasticity (Lande et al., 2017), representing the intrinsic resilience of a population (Capdevila et al., 2020; Larios et al., 2017). So rather than defining resilience to a particular disturbance, here we estimate the intrinsic resilience of the populations. In this scenario, we assume that if we partition the growth rates into resistance (all the time steps where $r < 0$) and recovery (all the time steps where $r > 0$) we should expect no trend in resistance or recovery over time, as fluctuations are approximately symmetrical around the mean growth rate of 0—that is, the population is showing no declines in either component of resilience. In this study, we hypothesised that if the resilience of vertebrate populations is in decline, we should observe a negative trend either in resistance, or recovery, or both (Figure 1). On the contrary, if the resilience of vertebrate populations is not affected, no trend in their resistance or recovery should be observed. More specifically, we test the effect of different factors on temporal trends of resistance and recovery to determine: (1) whether mean trends in resistance and recovery of vertebrate populations differ between marine, terrestrial and freshwater systems; (2) how these trends vary among the major vertebrate groups and (3) whether these trends are affected by the number of threats a population is impacted by.

MATERIALS AND METHODS

Data

To quantify the change in the resilience of vertebrate populations, we used the largest global population monitoring database currently available, the Living Planet Database (LPD; Loh et al., 2005). The LPD includes

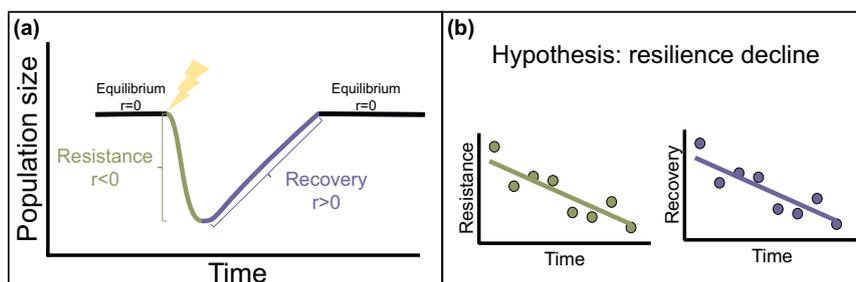


FIGURE 1 Conceptual summary of population resistance and recovery, and the main hypothesis tested in this study. (a) Conceptual representation of the resistance and recovery after a punctual disturbance affecting a population. In a population context, the system state is defined as the population size (y axis). The lightning represents a disturbance affecting a population. The stable state of the population is when the population growth rate (r) is 0. In this case, resistance represents the ability of the system to remain unchanged after a disturbance. Therefore, negative values of r can be associated with a lack of resistance, the more negative r is, the less resistant the population is. On the other hand, recovery represents the rate of return to the undisturbed state. Then, positive values of r represent proxies of the recovery of the population, the more positive the value of r the faster the rate of recovery. (b) Graphical summary of the main hypothesis of this study. Here we hypothesise that if the resilience of vertebrate populations is decreasing over time, we should observe declines in resistance (negative r) and/or recovery (positive r) over time

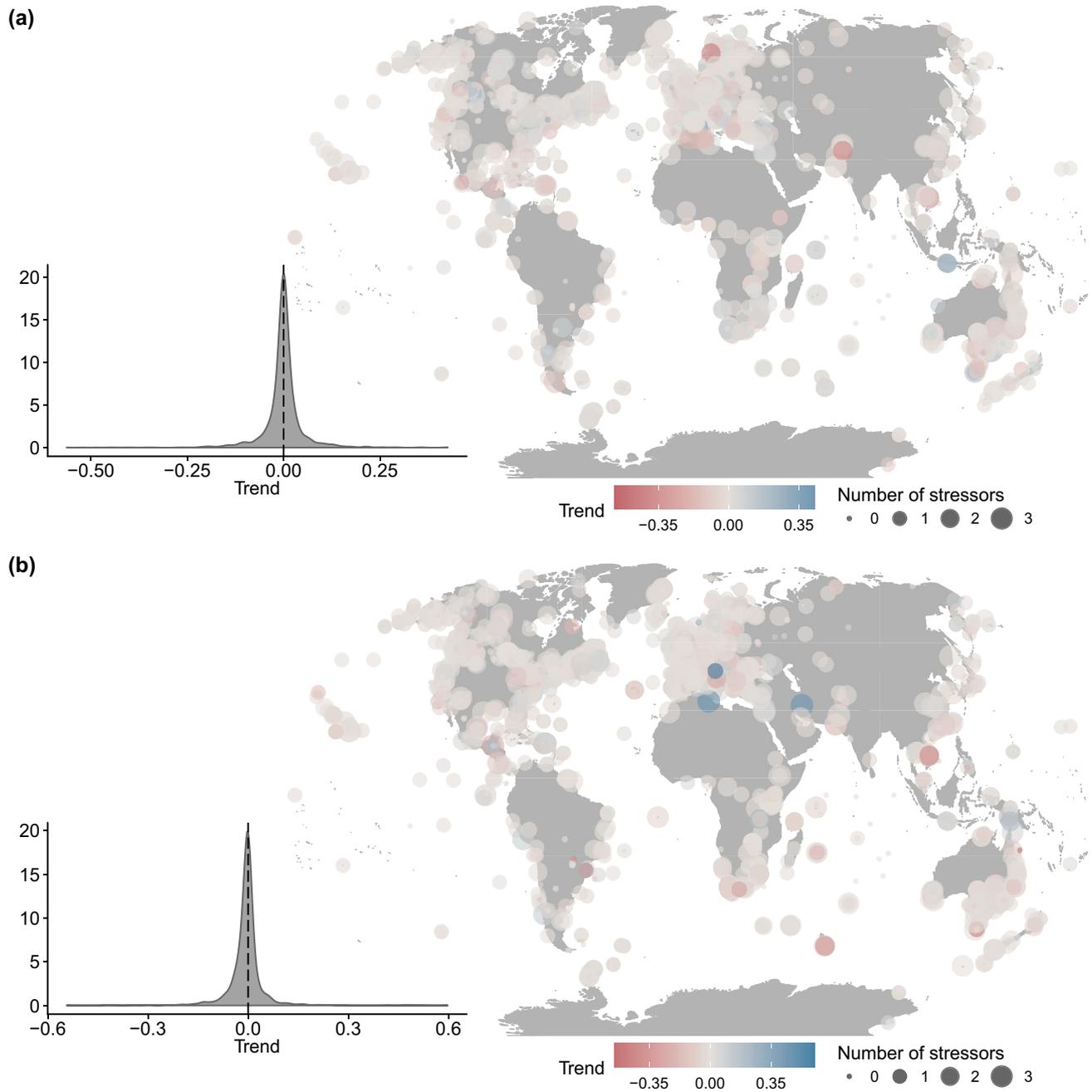


FIGURE 2 Trend estimates of changes in recovery and resistance of vertebrate populations according to the number of threats that they are exposed to. The recovery and resistance trend estimates of each population were derived from the state-space models of the population growth rates estimated from the Living Planet Database (see Methods). The size of the dots represents the number of threats at which each population was exposed to. (a) Spatial distribution of the resistance trends of 2364 resistance time-series from 1068 species, and the number of threats at which each population was exposed to. Resistance trends represent the temporal change in the ability of populations to absorb disturbance, measured as the negative population growth rates ($r < 0$). The more negative, the less resistant the population is. Most of the populations showed a trend close to zero [bottom left inset]. (b) Spatial distribution of 2434 recovery time-series from 1059 species, and the number of threats at which each population was exposed to. Recovery trends represent the temporal change in the ability of populations to rebound after disturbance, measured as the positive population growth rates ($r > 0$). The more negative, the lower the recovery ability. Most of the populations showed a trend close to zero [bottom left inset]

20,811 population time-series of 4392 species, each time-series has repeated monitoring surveys of the population abundance in a given area. These data are collated from a variety of sources, including peer-reviewed literature, grey literature, online databases and data holders (Loh et al., 2005). Of these, 7827 population time-series

contain information on whether the populations were exposed to known threats (Figure 2). Threats were identified as direct or indirect human activities or processes that impacted the populations for at least 50% of the surveyed years, according to the original source of the time-series. Threats were classified into broad categories:

climate change, invasive species, habitat loss/degradation, exploitation pollution and diseases, following the Red List threat classification (Threats authority file Version 2.1; IUCN 2006a). For this study, we focused on how the number (rather than identity) of threats affects components of resilience, allowing comparison between patterns of resilience loss across different taxa and systems. Therefore, we classified each time-series according to the number of threats it was exposed to, from zero to three. We only considered a maximum of three threats because very few studies reported more than three. Our results thus represent the first assessment of resilience change at the global scale in the face of single or multiple stressors.

From these data, we estimated the population growth rate (r) as a proxy of resistance ($r < 0$) or recovery ($r > 0$) (Figure 3; see also Figure S1 for worked examples). To estimate the resistance and recovery trend, we used state-space models (Dennis et al., 2006; Humbert et al., 2009), from population time-series of 5 years or greater in length. This resulted in two data sets, one for resistance (2364 time-series) and one for recovery (2434 time-series) (Figure 1; Table S1). Resistance time-series included 1068 species of amphibians (59), birds (905), fishes (797), mammals (457) and reptiles (146) populations, covering freshwater (433), marine (1043) and terrestrial (888) systems. While recovery time-series included 1059 species of amphibians (53), birds (975), fishes (720), mammals (522) and reptiles (164) populations, covering freshwater (433), marine (1044) and terrestrial (957) systems. It should be noted that fishes were included as a broad category containing the taxonomic classes Holocephali, Elasmobranchii, Myxini, Cephalaspidomorphi, Actinopterygii and Sarcopterygii. The duration of both data sets varied between five and

63 years, covering a period between 1951 and 2017 and all the continents of the world (Figure 2). The time span included in our analyses encompasses the period of Great Acceleration, a period of dramatic increase in the influence of human activities on earth natural systems (Steffen et al., 2015).

Resistance and recovery estimation

To define resilience we followed the definition provided by Hodgson et al. (2015), where resilience is defined as the result of two processes, resistance to and recovery from disturbance (Hodgson et al., 2015; Ingrisch & Bahn, 2018). In our case, resistance represents the ability of a population to avoid a decrease in abundance after a disturbance, and recovery is the rate at which a population returns at its previous state after a disturbance. To capture these two natural processes in our time-series, we estimated the population growth rates (r) from abundance data of each population time-series as

$$r_t = \log\left(\frac{N_{t+1}}{N_t}\right), \quad (1)$$

where N_t is the population abundance at time t and N_{t+1} is the population abundance for the next time step $t+1$, creating a time-series of r estimates for each population. r is an index that indicates whether a population is increasing ($r > 0$), decreasing ($r < 0$) or stable ($r = 0$). Resistance and recovery need to be defined relative to a reference (non-disturbed) state (Capdevila et al., 2020; Ingrisch & Bahn, 2018). Here, we consider that the reference state for an undisturbed population would be when

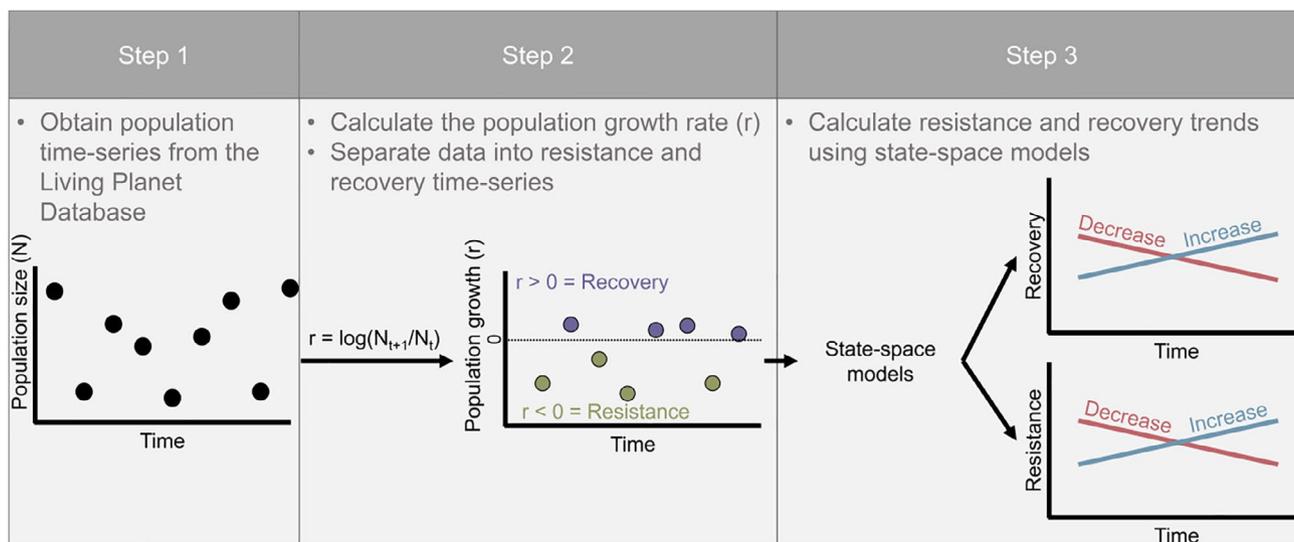


FIGURE 3 Workflow of the methods used to calculate the resistance and recovery trends. We analysed population time-series in the Living Planet Database including population-level information on how many threats were impacting each of the populations at the time of the study, according to the original source. For each time-series we calculated the population growth rate (r) at each time step, where positive values of r represent the recovery of those populations and negative values of r represent the resistance. Then, we used state-space models (Humbert et al., 2009) to calculate the trend in resistance and recovery

$r = 0$. Because resistance represents the ability of the system to remain unchanged after a disturbance (Hodgson et al., 2015), $r < 0$ can be associated with a lack of resistance (Capdevila et al., 2020; Larios et al., 2017). On the other hand, given that recovery represents the rate of return to the undisturbed state (Hodgson et al., 2015), $r > 0$ is linked to recovery (Capdevila et al., 2020; Larios et al., 2017). Then, to obtain the resistance and recovery time-series, we separated the population growth rates into negative values (resistance) and positive values (recovery).

Estimates of resistance and recovery trends

To estimate trends of resistance and recovery over time we fitted state-space models to the resistance and recovery time-series (Dennis et al., 2006; Humbert et al., 2009). We used state-space models as they allowed us to estimate resistance and recovery trends (μ) while accounting for the variance in the trends caused by process error (σ^2) and observation or measurement error (τ^2) (Dennis et al., 2006; Humbert et al., 2009). Our state-space models take the general form:

$$r_t = r_{t-1} + \mu + E_t, \quad (2)$$

where r_t represents the resistance or recovery at time t and r_{t-1} is the resistance or recovery from the previous year ($t-1$), and the process noise is $E_t \sim \text{gaussian}(0, \sigma^2)$. Observation errors were added to each r_t :

$$Y_t = r_t + F_t, \quad (3)$$

where Y_t is the estimate of the true resistance or recovery value, and the measurement error was $F_t \sim \text{gaussian}(0, \tau^2)$.

Following (Daskalova et al., 2020a, b), we substituted r_t value into Equation 2:

$$Y_t = Y_{t-1} + \mu + E_t + F_t, \quad (4)$$

We then used Equation 4 to estimate the resistance and recovery trends for each of the time-series (see Figure 3 and Figure S1 for more details).

Statistical analyses

To quantify the effects of the number of threats, system and major taxonomic groups, we developed a set of Bayesian hierarchical models, using resistance and recovery trends as response variables. The number of threats was included as a categorical fixed effect with four levels (0–3), according to the number of threats each population was recorded as being exposed to. System was a fixed effect with three levels: freshwater, marine or terrestrial; and the taxonomic group was a fixed effect

with five levels: amphibians, birds, fishes, mammals and reptiles.

We tested the effects of each of the aforementioned factors on resistance or recovery trend by fitting six separate models for each of the factors and response variables. We also explored the interaction of the number of threats with the taxonomic group (number of threats:taxon group) and systems (number of threats:system), using four separate models. To account for the non-independence of repeated measurements for each species, we included a random intercept for each species. Each model was fitted with a zero intercept to allow us to determine the absolute effect of each category of the factors tested on resistance and recovery trends.

The general structure of the models was as follows:

$$y_{i,j} = \text{Normal}(\mu_{i,j}, \sigma^2), \quad (5)$$

$$\mu_{i,j} = \beta_0 \text{Species} + \beta_1 \text{Factor}, \quad (6)$$

where $\beta_0 \sim \text{Normal}(\alpha, \sigma_{\text{species}})$; $y_{i,j}$ is the estimate for change in resistance/recovery for i th time-series and j th species. β_0 represent intercepts and β_1 represent slopes. We accounted for the error associated with the resistance and recovery trends derived from the state-space models by including the measurement error (τ^2) in our models. *Factor* represents the different factors that we tested, which were the number of threats, system and taxonomic group. For the interactive models of the number of threats and system/taxonomic group, the model exclusively incorporated the interaction between them.

We set weakly informed priors:

$$\alpha \sim \text{Normal}(0, 1), \quad (7)$$

$$\beta_1 \text{Factor} \sim \text{Normal}(0, 1), \quad (8)$$

$$\sigma \sim \text{Exponential}(1), \quad (9)$$

$$\sigma_{\text{Species}} \sim \text{Exponential}(1). \quad (10)$$

All models were fitted using the brms package v2.1.0 (Bürkner, 2017) in R v4.0.0 (R Core Team, 2020). Models were run for 10,000 iterations, with a warm up of 1000 iterations. Convergence was assessed visually by examining trace plots and using Rhat values (the ratio of the effective sample size to the overall number of iterations, with values close to one indicating convergence). To evaluate the outcomes of the model we also used the overlap of the confidence intervals of the posterior distribution with zero. We interpreted that when the 95% or the 80% confidence interval were larger/smaller than zero there was a strong or moderate evidence for the trend observed respectively. We also estimated the conditional and marginal Bayesian R^2 as a proxy of the variance explained for each of the models (Gelman et al., 2019), using the

function *r2_bayes* from the package *performance* v0.7.3 (Lüdecke et al., 2021).

Robustness of the analyses

Populations increasing towards their carrying capacity (K) could show decreasing trends in recovery and/or resistance, given that as a population approaches K its r decreases (e.g. Lande et al., 2017). These cases have the potential to bias our interpretation of the recovery trends. Overall, these re-analyses confirmed that the results presented in our manuscript were robust to the removal of increasing populations (Figures S2–S4), with the only difference between the analyses being an increase in the confidence intervals. This pattern is likely due to the decrease in the sample size of the data set when excluding increasing populations, which changed from 2364 (original data set) to 1293 (decreasing populations data set) for resistance, and from 2434 to 993 for recovery. These results provide evidence of the robustness of our analyses to some particular cases, such as populations getting close to carrying capacity.

Because the life-history strategies of the species could have influenced their resistance and recovery trajectories (e.g. Capdevila et al., 2020), we also analysed the effect of adult body mass (g) and the evolutionary history. Overall, we did not find any clear interaction between body mass, taxonomic group and the resistance or recovery trends (Figure S5). In addition, none of the taxonomic groups included in this study showed a clear influence of phylogeny on their resistance and recovery trends (Figure S6).

Finally, short time-series are known to produce less reliable population trajectories (Dennis et al., 2006; Humbert et al., 2009). Although state-space models are supposed to produce robust population trends when time-series have a minimum of five years (Dennis et al., 2006; Humbert et al., 2009), the minimum temporal length considered in this study, we also tested the robustness of our analyses to the duration of the time-series. We found that the duration of time-series did not have a clear effect on the resistance trends (Figure S6a), but that longer time-series have more positive recovery trends (Figure S6b). However, the length of the time-series was negatively correlated with the year the monitoring began (Figure S7). Finally, when we explored the resilience trends over the different decades, we observed that the loss of recovery was more evident during recent years (Figure S8). Taken together, these results suggest that the effect of time-series length was related to the intensification of anthropogenic threats that has occurred over the last decades (Díaz et al., 2019; Scheffer et al., 2015), rather than a methodological artefact (Leung et al., 2020).

RESULTS

Our results show that resistance and recovery trends over time were system- and taxa-specific. The state-space

models from the resistance and recovery time-series showed that for 50% of the populations' resistance was declining over time, while 59% showed a decrease in recovery over time (Figure 2). Hierarchical Bayesian models suggested there was no clear trend for resistance for any of the systems (Figure 4a and Table S2). Conversely, there was strong evidence that recovery trends were negative across terrestrial, marine and freshwater systems (Figure 4d and Table S3). Similarly, resistance did not show any clear trend across the different taxonomic groups (Figure 4b and Table S2), while recovery trends were strongly negative for birds and fishes, with no clear trend for amphibians, reptiles, or mammals (Figure 4e and Table S3). Terrestrial amphibians were the system/taxonomic group with the strongest decline in resistance, with freshwater fishes and marine reptiles showing signs of positive resistance trends (Figure S10a). Most system/taxonomic group showed recovery declines, with the most clear ones being freshwater amphibians, but with terrestrial amphibians and mammals showing positive recovery trends (Figure S10b). These complex patterns of resistance and recovery trends among systems and taxonomic groups mirror previous findings of similar analyses of vertebrate populations trends worldwide (Daskalova et al., 2020b; Leung et al., 2020).

The number of threats to which a population was exposed proved a strong predictor of recovery trends. Resistance did not show any clear trend when populations were exposed to multiple threats, although the median trend changed from positive to negative as the number of threats increased (Figure 4c and Table S2). On the contrary, recovery trends showed an increased negative trend as the number of threats the populations were exposed to increased (Figure 4f and Table S3). These results suggest that accounting for the number of threats is crucial to understand the patterns of resilience loss, and highlights the need to consider multiple components of resilience simultaneously (Bozec & Mumby, 2015; Capdevila et al., 2020).

The impacts of cumulative threats across systems also differed between resistance and recovery trends. Only in terrestrial systems, the increase in the number of threats decreased the resistance trend, while marine species showed a positive trend in resistance when impacted by two threats (Figure 5a and Table S4). However, the increase in the number of threats always decreased the recovery ability of populations across systems (Figure 5b and Table S5).

The impact of the number of threats on resistance and recovery trends was also taxon-specific. Birds, fishes and amphibians were the taxonomic groups most affected by the number of threats (Figure 6). Birds showed a progressive decline of resistance and recovery as the number of threats increased (Figure 6, Tables S4 and S5). A similar pattern was observed in amphibians but with lower certainty (Figure 6, Tables S4 and S5). Fishes resistance trend was positive for populations exposed

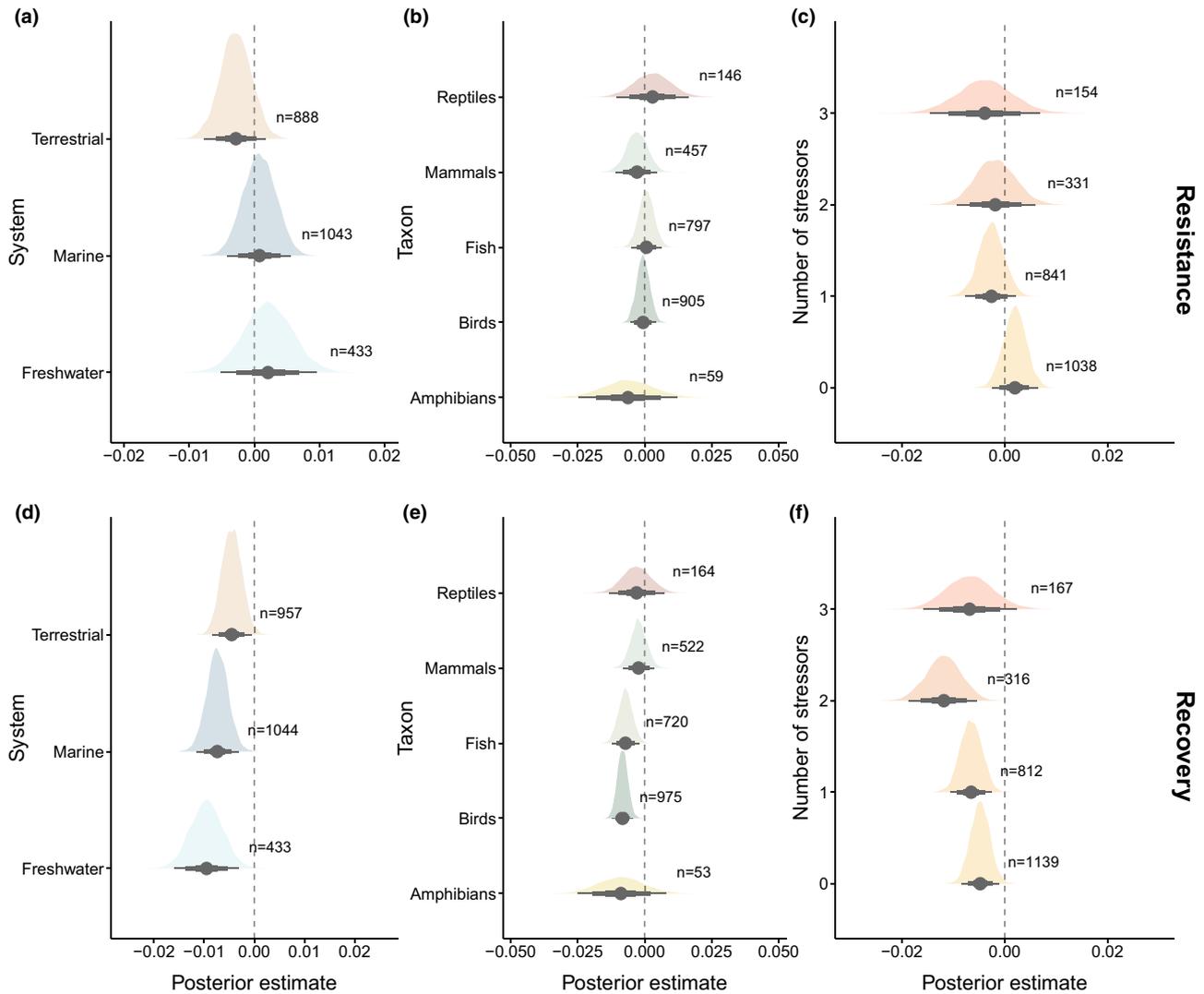


FIGURE 4 Resistance and recovery trends of populations according to the system, the taxonomic group and the number of threats. Density plots of posterior distributions for study-level slope estimates of resistance (a, b, c) and recovery (d, e, f) grouped by the system (a, d), the major taxonomic group (b, e) and the number of threats (c, f). The dashed vertical line shows the zero-slope—that is no effect of the factors. Each density plot is based on 1000 samples from the posterior distribution of the slope estimates. The reported values are the highest posterior density median values (circles), with 50% (thickest bars), 80% and 95% (thinnest bars) uncertainty intervals

to two threats, while recovery was more negative as the number of threats increased (Figure 6, Tables S4 and S5). However, these patterns were less clear in mammals and reptiles, with no clear trends for any of these two taxonomic groups (Figure 6, Tables S4 and S5). This general lack of resistance or recovery trends is in line with recent findings of no net decline of vertebrate populations worldwide (Daskalova et al., 2020b), indicating that both decreases and increases of resilience are taking place across the studied taxonomic groups (Bolam et al., 2021; Duarte et al., 2020; Lotze et al., 2011).

DISCUSSION

Our analyses of >2000 vertebrate populations time-series demonstrate that the planetary scale of human impacts to

wildlife is also accelerating resilience loss across systems and taxonomic groups. We show that such loss is, however, not driven by uniform declines in all components of resilience. The resilience of vertebrate populations is declining mostly through a decrease in their ability to recover, rather than their resistance, with the number of threats being the main driver of such loss. Therefore, our results highlight the need to consider multiple components of resilience simultaneously if we are to avoid biasing our understanding of biodiversity change (Donohue et al., 2013, 2016; White et al., 2020).

Our findings of clear resilience declines in populations exposed to one or multiple threats, challenge recent suggestions of no population declines for vertebrate populations worldwide (Daskalova et al., 2020b; Leung et al., 2020). We believe that such contrasting results are due to the inherent biases in global population databases.

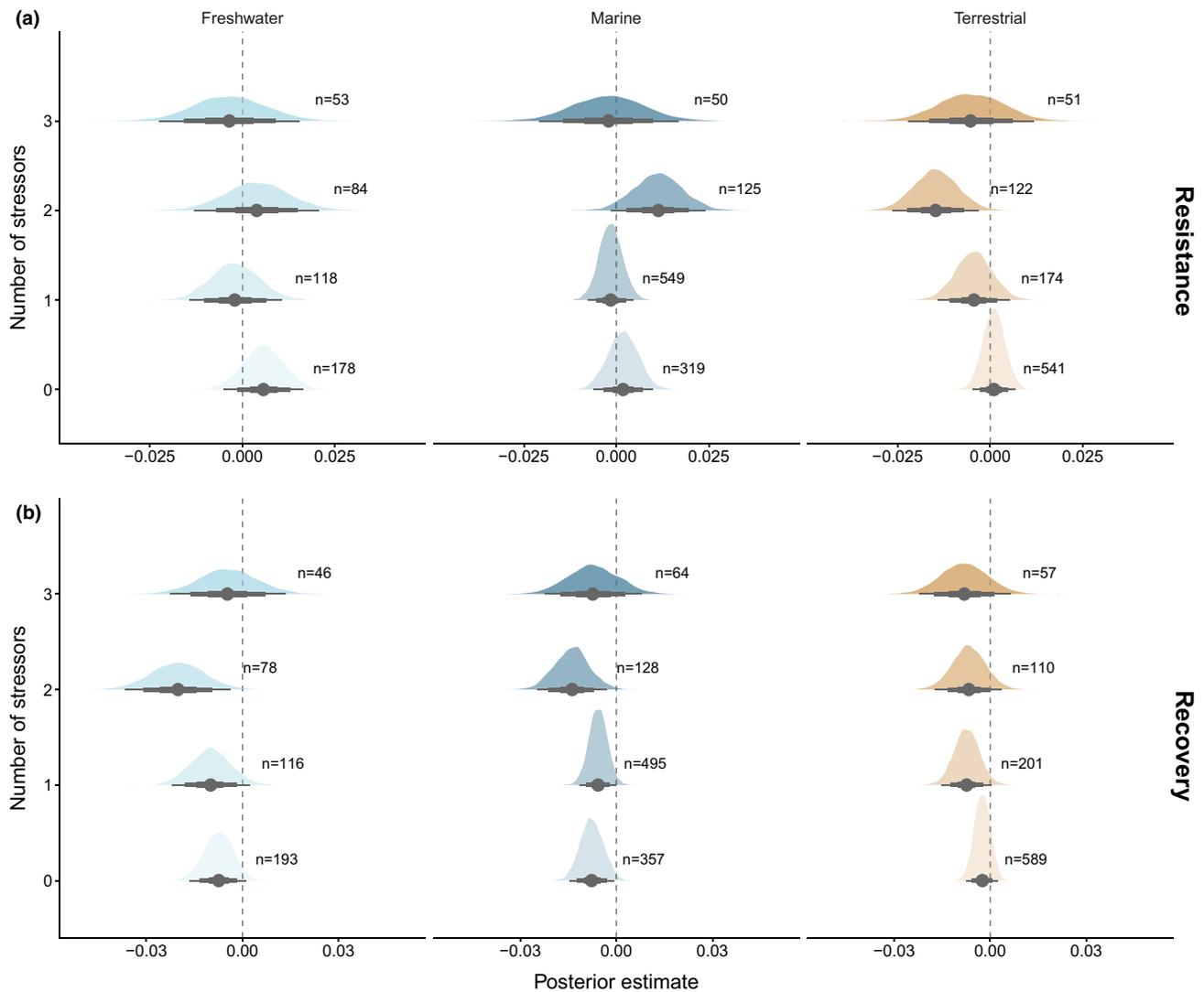


FIGURE 5 Interactive effects of the number of threats and system on the recovery and resistance trends of vertebrate populations. Density plots of posterior distributions for study-level slope estimates of resistance (a) and recovery (b) according to the system in which the species inhabits. The dashed vertical line shows the zero-slope expected when there is no effect of the fixed factors. Each density plot is based on 1000 samples from the posterior distribution of the slope estimates. The reported values are the highest posterior density median values (circles), with 50% (thickest bars), 80% and 95% (thinnest bars) uncertainty intervals

For instance, a large proportion of the available wildlife monitoring programmes used in global analyses of population trends come from protected/managed areas and developed countries (Loh et al., 2005; Römer et al., 2021), two known factors favouring population growth (Amano et al., 2018; Barnes et al., 2016). As such, drawing general conclusions from these data sets risks biasing our knowledge about biodiversity trends. Most importantly, the threats impacting the populations at the time of data collection are not usually considered (Leung et al., 2020), or are estimated based on global threats data that does not necessary reflect local-scale patterns (Daskalova et al., 2020b). In our study, accounting for the impact of multiple threats and studying resistance and recovery trends separately a the key factors to detect resilience loss. Resilience mostly shows signs of decline in populations exposed to one or more threats through a

decrease in their recovery trends. These findings suggest that focusing on mean population abundance trends and neglecting the number of threats may overlook the incipient loss of resilience, risking to ignore populations approaching a period of instability and potential collapse (Hughes et al., 2013; Kuussaari et al., 2009). Failure to recognise these resilience trends over time may lead to a false sense of security, effectively concealing mismanagement and providing little warning for future population collapses.

Despite the unequal distribution of global threats to species across the planet (Bowler et al., 2020), the signals of recovery loss were consistent across terrestrial, freshwater and marine systems. These results contrast with previous suggestions that marine systems are still relatively unimpacted compared to the millennia-long defaunation of terrestrial and freshwater systems

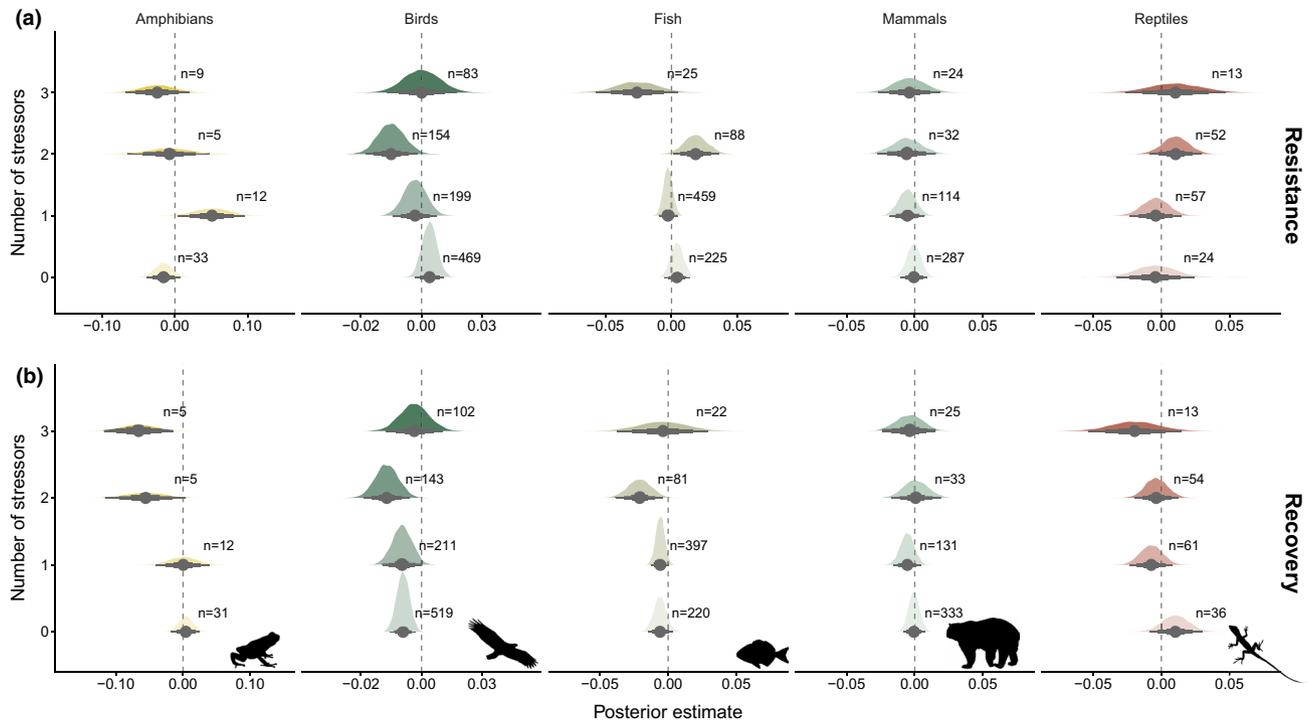


FIGURE 6 Interactions between the number of threats and taxonomic groups on the recovery and resistance trends of populations. Density plots of posterior distributions for study-level slope estimates of resistance (a) and recovery (b) according to the major taxonomic groups. The dashed vertical line shows the zero slope expected from no effect of the factors. Each density plot is based on 1000 samples from the posterior distribution of the slope estimates. The reported values are the highest posterior density median values (circles), with 50% (thickest bars), 80% and 95% (thinnest bars) uncertainty intervals. Silhouettes were obtained from <http://phylopic.org/>

(McCauley et al., 2015; Van Der Kaars et al., 2017). The main taxonomic groups showing signs of recovery decline were amphibians, birds and fishes exposed to one or more threats. These findings mirror previous reports on the global population trends of amphibians, birds and fishes, where multiple threats have shown direct consequences for their survival (Pounds et al., 2006; Anchukaitis & Evans, 2010; Worm et al., 2009). For example, the extinction of the golden toad (*Incilius periglenes*) in Costa Rica was attributed to the concurrent impacts of chytrid fungus (*Batrachochytrium dendrobatidis*) and an exceptionally strong El Niño event (Anchukaitis & Evans, 2010). Our findings, reinforce the vulnerability of these taxa and suggest that in addition to declining populations and range contractions (Almond et al., 2020; Ceballos et al., 2020) they are becoming more vulnerable to future threats.

Not all taxa showed resilience declines over time, with mammals and reptiles showing no clear trends. The contrasting trends among the distinct taxonomic groups studied here provide further evidence for the need to account for local population dynamics to further understand the causes of biodiversity change (Daskalova et al., 2020b; Leung et al., 2020). For instance mammal populations have shown recent signs of recovery in Europe (Cimatti et al., 2021), also suggesting that their resilience might be increasing. Such taxon-specific responses to global change could be attributed to non-random

susceptibility among clades due to differences in their life history (Cardillo et al., 2005; Fisher & Owens, 2004). Yet, we did not find a clear effect of body mass—a key indicator trait for vulnerability to threats and extinction (Fisher & Owens, 2004; Ripple et al., 2017)—on resistance or recovery trends (Figure S5). Also, the phylogenetic signal of the resistance and recovery trends was weak across all the different taxonomic groups (Figure S6).

Other properties of the threats can also influence the rate of resilience decline. While here we only focused on the number of threats, their type (e.g. exploitation, habitat loss), intensity and/or frequency might also affect the resilience of populations (Radchuk et al., 2019). That is, different threats, or the same threat with different intensity and/or frequency, might decrease the resistance or delay the recovery times to future threats (Dai et al., 2015; DeSoto et al., 2020; Hughes et al., 2019). In addition, the timing (when threats impacted the population over the time-series) and the synchrony (the overlap on time between multiple threats) of the threats likely plays a key role in determining resistance and recovery trends (Jackson et al., 2021; Johnstone et al., 2016). While here we did not account for these different properties of threats affecting populations, they might explain the wide variety of resistance and recovery trends among the different studied populations. Future explorations of the effects of threats of

different nature, intensity and frequency will be crucial to identify further drivers of resilience declines (Gladstone-Gallagher et al., 2019; Jentsch & White, 2019).

Overall, our study reveals a global loss of resilience across vertebrate populations, driven by unequal declines in resistance and recovery, a pattern intensified by increasing numbers of anthropogenically derived threats. These results also demonstrate that by focusing on mean population trends, rather than resilience, previous studies might have underestimated the extent of biodiversity loss. Therefore, our results emphasise the importance of accounting for the loss of resilience and its multiple components in future biodiversity projections to avoid underestimating the impacts of global change.

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AUTHORS' CONTRIBUTION

P.C. and C.C. conceived the idea with inputs from all the authors. P.C. and C.C. performed the analyses. N.N., L.M. and R.F. collected the data. P.C. and C.C. wrote the manuscript with contributions from all authors.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The Living Planet Database (excluding confidential records) is available at: www.livingplanetindex.org/data_portal. Data and code used in this manuscript is available in Zenodo at <https://doi.org/10.5281/zenodo.5647088>.

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