Non-linearity and temporal variability are overlooked components of global population dynamics

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Abstract

Aim.

Population dynamics are usually assessed through linear trend analysis, quantifying their general direction. However, linear trends may hide substantial variations in population dynamics that could reconcile apparent discrepancies when quantifying the extent of the biodiversity crisis. We seek to determine whether the use of non-linear methods and the quantification of temporal variability can add value to the linear approach by offering a more complete representation of global population changes. In addition, we seek to determine how these components are distributed among biogeographical regions and taxonomic groups.

Location.

Global.

Methods.

We analysed 6,437 population time series from 1,257 species from the Living Planet Database over the period 1950-2020. We modeled populations through the use of second order polynomials and classified trajectories according to their direction and acceleration. We modeled and classified these same populations using a more common linear trend analysis. We quantified temporal variability using three metrics, the coefficient of variation, the mean squared error and the consecutive disparity index. We then used chi-squared tests and linear mixed-effects models to test potential sources of heterogeneity in non-linear trajectories and temporal variability.

Results.

Non-linear models were a better fit for 44.8 % of the analyzed time series, and temporal variability was higher among trajectories classified as linear. Linear models missed meaningful information by misclassifying recent declines or recovery signals. Marine populations were highly variable, and all taxonomic groups or IUCN categories exhibited variability in their degree of non-linearity and temporal variability.

Main conclusions.

Non-linearity and temporal variability reveal usually overlooked dramatic declines or recovery signals in global population dynamics. Thus, moving beyond linearity can help reduce the risk of misleading conclusions and better inform conservation decisions. In particular, population usually classified as « stable » can hide informative non-linear and variable changes to integrate in more advanced global biodiversity assessment.

Keywords: population dynamics, non-linearity, temporal variability, biodiversity crisis, conservation biogeography

1 | Introduction

Quantifying and understanding global biodiversity changes are critical research challenges. A commonly used approach to quantifying global biodiversity changes is to rely on the linear trend in global indices derived from the combination and collation of local monitoring data distributed across realms and groups (e.g. Living Planet Index (McRae et al., 2017; WWF, 2022)). More recently, the widespread availability of open-access large datasets (e.g. BiotTIME (Dornelas et al., 2018)), has revealed contrasting results depending on the scale or metric considered (Blowes et al., 2019; Daskalova et al., 2020). In particular, “no net loss” in the number of species or “no net change” in population abundances have been reported (Vellend et al., 2013; Primack et al., 2018). While such conclusions raised many questions and caused controversies within the scientific community (Cardinale, 2014; Gonzalez et al., 2016; Loreau et al., 2022; Kuczynski et al., 2023), they revealed that global biodiversity changes are complex and heterogeneous, and cannot be encapsulate in a single metric (Dornelas et al., 2023).

However, the majority of empirical studies tracking temporal changes in the abundance of individuals of different species over time rely on linear regressions (Dornelas et al., 2019) or assimilated models (e.g. state-space models (Daskalova et al., 2020)). By focusing solely on the general direction of population trajectories (i.e. the sign of the slope) and its magnitude (i.e. the value of the slope), these models could miss critical information for describing population dynamics, such as how fast and when changes occur (Rigal et al., 2020). For instance, a convex trajectory for the population size of a threatened species (Fig. 1) can testify of a successful conservation strategy and a recent improvement of its population status. On the contrary, an accelerated decrease in the population size of a species (Fig. 1) can indicate an increasingly worsening situation. Such non-linear dynamics are expected to occur substantially in population dynamics given that the drivers of population trajectories themselves follow non-linear patterns. For instance, many global change pressures have accelerated synchronously in the 1980s, often labelled as a "great acceleration" in the Anthropocene (Steffen et al., 2015). Besides, non-linearity has already been observed at large spatial and temporal scales in populations of arthropods (Duchenne et al., 2022), birds(Rigal et al., 2020) or fishes (Pélissié et al., 2023) or in community dynamics (Penny et al., 2023). Yet, the extent and distribution of non-linear trajectories of populations at global scale has been, to our knowledge, largely overlooked.

Besides non-linear trajectories, temporal variability is another overlooked aspect of global biodiversity dynamics. Temporal variability is a common estimator of ecological stability, a multifaceted concept with many alternative definitions including resistance to environmental change and resilience (Pimm, 1984; McCann, 2000; Donohue et al., 2016). Increase in variability has been long identified as a loss of stability in ecological systems (Grimm and Wissel, 1997) or even a signature of abrupt ecological collapse (Scheffer et al., 2009; Hughes et al., 2013). Thus, population variability was proposed as a proxy for vulnerability (Mrowicki et al., 2016) yet is not captured by the slope or the shape of the trajectory (even if non-linear) of a population. For instance, an apparent absence of change in regard of the overall trajectory may mask strong variations (Fig. 1), and therefore a potential risk of extinction, especially if the population's abundance is small and exposed to demographic, environmental or genetic stochasticity (Caughley, 1994). Although temporal variability has been studied at global scale (Leung et al., 2017; Capdevila et al., 2022), how it is coupled with non-linear population trajectories remains unclear.

Overall, a complete understanding of global biodiversity changes based upon the complete description of trajectories (beyond usual linear trends) and their associated temporal variability (beyond usual estimates of model fit) is missing. Such comprehensive description could have implications for conservation biogeography. Testing which habitat types, geographical regions and/or taxonomic groups are facing specific patterns of change in population abundance over time could provide key insights for improving conservation prioritization. For instance, Global IUCN Red List Categories are often used for conservation prioritization, yet they are based, among other factors, on simple linear population trends (IUCN, 2022). Global IUCN Red List Categories could be refined by integrating recent abrupt changes within populations dynamics revealed by non-linear models or strong temporal variability exposing specific species to increasing vulnerability.

In this paper, we analyze population data from the Living Planet Database and describe their non-linear trajectories and temporal variability. We test three predictions on those two components. 1) We assume that there would be biogeographic patterns in population non-linear trajectories and temporal variability across the planet's habitat types, regions and realms, in line with particular regions of the world experiencing high rates of environmental change (e.g., tropical forests (Barlow et al., 2007), Arctic (IPCC, 2021)). The clustered distribution of global change drivers in space has been proven to lead to hetereogeneous patterns (Blowes et al., 2019; He et al., 2019), we therefore expect regions particularly under pressure to express more non-linearity through accelerated declines and concave trajectories, given that the rate at which the changes occur is not linear. Similarly, high environmental changes are expected to result in stronger temporal variability in populations (Lawson et al., 2015). 2) We expect populations from species with life history traits related to high vulnerability to global change to express higher non-linearity and variability. Species with different life history traits may respond to the environment differently or may intrinsically differ in a way that results in more non-linearity and more variable population dynamics, and this may be seen in the different taxonomic groups. In particular, amphibians (Houlahan et al., 2000; Blaustein et al., 2011) are expected to express more non-linearity and temporal variability than the other groups. We expect higher non-linearity and especially a higher diversity in its form, as non-linearity may be expressed either through dramatic declines (accelerated declines or concave trajectories), along with high variability, or through recovery signals (decelerated declines, convex trajectories) if conservation actions were implemented and successful. 3) As for more vulnerable taxonomic groups, we also expect populations from species with a high IUCN Red List Category (being a proxy of high extinction risk) to be more likely to express non-linearity and temporal variability than the populations of least concern species.

2 | Methods

2.1 | Ecological time series data

We used population time series from the Living Planet Database (LPD). The current public version contains 32,211 population time series distributed worldwide, with populations that were monitored using different metrics of abundance or proxy of abundances (e.g., number of individuals vs. number of nests); and time series ranging from 1950 to 2020. We omitted populations which had less than twenty time points of monitoring data, as previous studies have found that shorter time series might not capture biologically meaningful directional trends in abundance (Wauchope et al., 2019). For each population time series, habitat type (Terrestrial, Marine or Freshwater), region (e.g. Africa, North America, Europe) and taxonomic group (e.g. Birds, Mammals) is provided in the LPD. Additionally, we extracted IUCN Red List Category data for each species from the International Union for Conservation of Nature (IUCN).

2.2 | Modeling population dynamics

We fitted both linear and non-linear models in order to compare the resulting classifications. Before analysis, we log transformed the abundance of each population in order to make them comparable. Ecological data are often log-transformed prior to statistical analysis as variance has the tendency to increase with the mean abundance, and because log-transformation allows the reduction of the outliers’ weight (Cottingham et al., 2001).

We first fitted each population time series (log transformed abundance through time) with a linear regression model to qualify the overall linear direction of the trajectory. We distinguished increasing trajectories (significantly positive slope), decreasing trajectories (significantly negative slope), and trajectories with no significant trend, classified as "no trend".

For the main analysis (non-linear modeling), we adopted the framework proposed by Rigal et al. (2020). We fitted each population time series with a second order polynomial model to qualify the non-linear shape of the trajectory through:

$$Y(t)=\alpha_0+\alpha_1 t+\alpha_2 t^2+\varepsilon(t)$$

Where Y is the log transformed abundance estimate (we added 1 to every population count, to account for estimates of zero abundance in a given year), t the time in years, and the process error is represented by $\varepsilon \sim N(0,\sigma^2)$. We used orthogonal polynomials so that the correlation between the first and second order variables is removed (Rigal et al., 2020). The significance of each coefficient (α_1 for first order and α_2 for second order) is therefore used to test whether the second order significantly improves the regression compared to the first order. Second order polynomials can discriminate trajectories with no net changes – stationary processes – (if α_1 and α_2 are not significant); linear – or monotonous – trajectories (if only α_1 is significant); and non-linear – or non-monotonous – trajectories (if α_2 is significant).

2.2.1. Classifying population trajectories

We used the direction and the acceleration to classify the different types of trajectories. **The direction** (increase, decrease or null) is null if there is no net changes, and equal to α_1 if the trajectory is linear. If the trajectory is non-linear (if α_2 is significant), the direction is determined by the slope of the tangent given by the linearisation around the center of the time series. **The acceleration** is given either by the sign of the second order coefficient α_2 or by the sign of $\dot{\gamma}$, the derivative of the curvature function. When the direction is null, the acceleration refers to the convexity or concavity of the trajectory and only the sign of α_2 is needed to describe it (convex if $\alpha_2 > 0$, concave if $\alpha_2 < 0$). When the direction is an increase or a decline, the sign of $\dot{\gamma}(\alpha_2)$ is used to determine if the process is accelerated ($\dot{\gamma}(\alpha_2)<0$) or decelerated ($\dot{\gamma}(\alpha_2)>0$) (see Rigal et al., 2020 for details). Using the combination of direction and acceleration, one can classify any trajectory as belonging to one of the nine following trajectory types: linear decrease, accelerated decrease, decelerated decrease, no trend (linear), concave (down), convex (up), linear increase, decelerated increase and accelerated increase (Fig. 2 shows examples of each trajectory type).

2.2.2. Estimating temporal variability

Once we fitted the non-linear models, we statistically estimated the temporal variability around the calculated trajectories. We considered the temporal variability of a population to reflect the fluctuations around the overall trajectory (i.e. the second order polynomial), that we assume to be the "equilibrium". We then used three ways to estimate temporal variability. Using the three metrics was necessary to cover different and complementary aspects of variability:

a. The coefficient of variation ($CV = standarddeviation * mean^{-1}$), which is one of the most common metric used to assess temporal variability, despite being known to present several drawbacks (e.g. mean dependance, insensitivity to the chronological order of time series) (Fernández-Martínez et al., 2018).

b. The mean squared error (MSE), measured as:

$$MSE = \frac{1}{n} \sum_{t=1}^{n} \left(Y_t - \widehat{Y}_t \right)^2$$

where Y_t corresponds to the log transformed abundance value at time t and $\widehat{Y}_t$ to the corresponding estimated value from the second order polynomial fit. As the MSE is calculated from the residuals of the fitted model, it allows to account for variability around the main trajectory and presents therefore a reduced dependance to the mean compared to the CV.

c. The consecutive disparity index (D), introduced by Fernández-Martínez et al. (2018), and previously used to estimate interannual climatic variability (Meseguer-Ruiz et al., 2017) and population and community temporal variability (Dallas and Kramer, 2022). It is measured as:

$$D = \frac{1}{n-1} \sum_{t=1}^{n-1} \left| \ln \left(\frac{Y_{t+1} + k}{Y_t + k} \right) \right|$$

where Y_t corresponds to the log transformed abundance at time t, n is the length of the time series, and k is a constant used to reduce the influence of zeroes on the calculation of D. As suggested in Fernández-Martínez et al. (2018), we considered k to be 1% of the time-series mean, to make estimates of D comparable across different time series. The D metric calculates temporal variability within each time step and is thus sensitive to the chronological order of the time series. Similarly to the MSE, it presents a reduced dependance to the mean compared to the CV (Fernández-Martínez et al., 2018).

2.3 | Identifying sources of variation in population trajectories and temporal variability

To determine if non-linearity was expressed differently across habitat types, regions, realms, taxonomic groups, and IUCN Red List Categories, we performed chi-square tests of independence for each factor (e.g. we ask if the habitat types influence the proportion of non-linearity). When the chi-square tests showed significant variations among categories, we performed two-proportions z-tests to test whether the proportions of non-linearity in each category differed from the overall proportion of non-linearity in all populations. We used the *prop.test* function from the “stats” package and compared the proportion within each category (e.g. Marine habitats) to the calculated overall proportion of non-linearity among all populations.

To determine if population temporal variability varied according to biogeographic and taxonomic patterns, we used a generalized linear mixed-effects model (GLMM) framework. We took either the mean squared error (MSE), the coefficient of variation (CV) or the consecutive disparity index (D) as the response variables and habitat types, regions, realms, taxonomic groups, IUCN Red List categories and trajectory types as the explanatory variables in separate models. We treated each factor individually and not all together to account for the effects within factors and not among factors. Each model included species as a random effect to account for the possible correlation between populations from the same species. For example, the model to test whether the MSE varies among regions is structured as followed:

$$MSE_{i,j,k}=\beta_0+\beta_k Region_{i,j,k}+\mu_{0,j}+\varepsilon_{i,j,k}$$

where $MSE_{i,j,k}$ is the mean squared error for the i^{th} population time series from the j^{th} species from the k^{th} region, $Region_{i,j,k}$ is the geographic region of the i^{th} time series from the j^{th} species, β_0 the global intercept, β_k the global slope estimates for the k^{th} region (fixed effect), $\mu_{0,j}$ is the species-level departure from 0 (random effect), and $\varepsilon_{i,j,k}$ is the random error (unreliable measurements, random fluctuations).

We examined the significance of fixed effect terms by examining the likelihood ratio of including each term versus a null model (containing only the random effects terms). All mixed-effect models were fitted using maximum likelihood as implemented in the R package “lme4” (Bates et al., 2015). When differences were detected, we performed post-hoc tests using the *ghlt* function from the “multcomp” package in order to distinguish groups that expressed significantly different temporal variability from others (Hothorn et al., 2008).

All tests outputs are presented in the appendix (SM3 and SM4).

3 | Results

3.1 | Estimating non-linear trajectories and temporal variability among global population dynamics

We analyzed 6,437 population time series from 1,257 species extracted from the Living Planet Database over the period between 1950 and 2020, which reflects almost 20% of the entire database. The remaining 80% were not selected because of their small length (<20 years). These time series represent repeated monitoring surveys of the number of individuals in a given area (species’ abundance over time). The temporal, geographical and taxonomic extents of the database we analyzed are presented in appendix SM1.

3.1.1. Classification of population dynamics into trajectory types

We applied both the linear and non-linear classification methods on 6,437 population time series. We found a broad spectrum of trends and trajectories among the studied populations. Across the time series we analyzed, 36% (2,338 time series) of populations were declining, 34% (2,164 time series) were increasing and 30% (1,935 time series) showed no trend in population change over time according to the linear framework. When classifying the trajectories following the non-linear framework, we found that 3,550 were linear while for the other 2,887 (i.e. 44.8 % of the 6,437 trajectories) a second order polynomial was a better fit (Fig. 2). However, the proportion of non-linearity found was conditioned by the number of years sampled and the starting year of the time series used. The detected proportion of non-linearity seemed to increase with the number of years sampled and to decrease with the starting year (see appendix SM2).

Among the 2,887 non-linear trajectories, concave (curved downwards) and convex (curved upwards) cases were the most represented, accounting for almost half of all non-linear trajectories (47.7%, 1,378 time series) (Fig. 2E, 2H). Non-linear declines and non-linear increases were represented in similar proportions (respectively 26.6% and 25.6% of non-linear trajectories). Among the 6,437 population trajectories, 1,939 (i.e. 30.1%) were classified as declining of which 554 were decelerated, 215 accelerated and 1,170 were linear. 1,783 (i.e. 27.7%) were classified as increasing of which 276 were decelerated, 464 accelerated and 1,043 were linear. Finally, 2,715 (i.e. 42.2%) were neither declining or increasing, of which 757 were concave, 621 were convex and 1,337 showed no trend.

3.1.2. Cross-comparison of linear and non-linear classifications

Interestingly, when comparing the linear vs. the non-linear classifications, we found that among the 2,338 populations that were classified as decreasing according to the linear framework, only 1,161 were classified as linearly decreasing according to the non-linear framework (Fig. 3A). The other (representing 18% of the total) were classified either as (i) decreasing non-linearly (N=768, i.e. 32.8% of the 2,338 classified as decreasing); (ii) concave trajectories (N=201, 8.6%), i.e. trajectories showing a recent decrease after an increase; or (iii) convex trajectories (N=203, 8.7%), i.e. trajectories showing a recent increase after a decrease (Fig. 3A). Similarly, among the 2,164 populations that were classified as increasing according to the linear framework, only 1,040 were classified as linearly increasing according to the non-linear framework (Fig. 3C). The others were showing a mix of non-linear decreases, concave and convex trajectories (Fig. 3C). Among the 1,935 populations classified as “stable” by the linear framework, only 1,329 showed no trend according to the non-linear framework, the rest 606 (31%) experiencing mostly concave or convex trajectories (Fig. 3B).

3.1.3. Distribution of temporal variability among population trajectories

We investigated how temporal variability was distributed among the different trajectory types through three different metrics. No matter the metric, temporal variability differed among the different population trajectory types (MSE: χ^2 = 116.89, df = 5, p-value < 0.001; D: χ^2 = 400, df = 5, p-value < 0.001; CV: χ^2 = 472, df = 5, p-value < 0.001). Figure 4A shows the variability of D values within the different trajectory types (results for CV and MSE can be found in SM4). In particular, Figure 4A shows that populations that were categorized as “no trend linear” were having significantly higher temporal variability relative to the other trajectory types. The second group of trajectory that had a high temporal variability was constituted of the linear trajectories (both increases and decreases) and of the “no trend non-linear” trajectories. Non-linear increases and non-linear decreases had the lowest temporal variability compared to other trajectory types. These results were also consistent when the CV or the MSE were used as proxy for temporal variability (Fig. 4B). Overall, populations whose trajectories were classified as “no trend linear” always showed significantly more temporal variability than populations experiencing other types of trajectories, and linear trajectories expressed higher variability than non-linear ones.

3.2 | Biogeographical distribution of non-linear trajectories and temporal variability in population dynamics

Overall non-linearity was expressed in non-anectodic proportions across habitats and regions (Fig. 5A, 5B). The proportion of non-linearity was significantly different from one habitat type to another (χ^2 = 48.8, df = 2, p-value < 0.001) (Fig. 5A), with populations living in marine environments showing a lower proportion of non-linearity (39.8%) than those in terrestrial (48.4%) and freshwater (48.9%) environments. The different regions represented in our dataset also showed varying proportions of non-linearity (χ^2 = 191.05, df = 7, p-value < 0.001) (Fig. 5B). There was a very low proportion of non-linear trajectories in the time series populations from Oceania (27.1%) compared to the overall proportion (44.8%). In contrast, populations from North America, Europe and International Waters showed significantly high proportions of non-linear trajectories compared to the overall proportion (respectively 48.2, 49 and 56%). Beyond the variability in the percentage of non-linearity, we observed variability in the relative proportions of the different trajectory types within different habitat types and regions (see appendix SM3). In particular, terrestrial and freshwater habitats showed higher proportions of non-linear increases than marine habitats (respectively, 16.5%, 16.9% and 4.4%); and marine populations exhibited a majority of no trend trajectories, either linear (30.1% of marine populations) or non-linear (26.7%). Among regions, North America had approximately equivalent proportions of each trajectory type for instance, while Oceania had a large majority of trajectories with no trend (44.2%) and concave or convex (18.9%).

Temporal variability also differed among the different habitat types, no matter the metric (for MSE: χ^2 = 47.6, df = 2, p-value < 0.001) (Fig. 5C). Marine populations exhibited significantly higher temporal variability than terrestrial and freshwater populations. Based on previous results, one might expect this propensity for high variability to be explained by the high proportion of “no trend linear” trajectories in marine habitats, since we have shown that this type of trajectory is particularly prone to variability (Fig. 4A). However, when examining the variability between different habitat types within the different types of trajectory taken separately, we found that in the majority of cases marine populations still showed higher variability, even when comparing similar types of trajectories (see appendix SM4). This confirms that time series retrieved from marine habitats are more variable than in other habitat types. Differences existed among regions as well (χ^2= 101.99, df=7, p-value < 0.001), in particular populations monitored in Oceania were more variable compared to populations from other regions (Fig. 5D). Again, this could be linked to the high proportion of “no trend linear” trajectories within populations monitored in Oceania (44.2%, Fig. S3.1).

3.3 | Non-linearity and temporal variability among taxonomic groups and IUCN categories

The proportion of non-linearity varied significantly among taxonomic groups (χ^2 = 26.5, df = 5, p-value < 0.001) (Fig. 6A), with mammals being the only group showing a significantly higher proportion of non-linearity than the overall mean (53.0%). Even though the proportion of non-linearity varied among IUCN Red List Categories (χ^2 = 88.49, df = 6, p-value < 0.001), we did not detect a straightforward link between non-linearity and IUCN Categories (Fig. 6B). For instance, “Least Concern” populations showed a higher proportion of non-linearity (47.6%) than “Endangered” populations (34%). Similarly to biogeographical patterns, the proportions of each type of trajectory within taxonomic groups and IUCN categories were variable (see appendix SM3). The high proportion of non-linearity in mammals’ populations was largely due to non-linear concave and convex trajectories (28.8% of the 473 mammals populations analyzed) and to non-linear increases (21.1%). Amphibians did not show any non-linear decreases nor a high proportion of concave or convex trajectories (16%), which we could have expected following a scenario where their more recent dramatic declines or recovery would be visible in the LPD database.

Depending on the metric used, we found either differences or no differences in temporal variability between the different taxonomic groups. In particular, the use of the MSE as temporal variability showed no differences between groups (χ^2 = 10.51, df = 5, p-value = 0.06), unlike the use of the CV (χ^2 = 12.12, df = 5, p-value = 0.03) or the D metric (χ^2 = 63.51, df = 5, p-value < 0.001). Rather than major differences in temporal variability between the different taxonomic groups, it seems that differences were expressed more among populations within the different groups (Fig. 6C). Even though the temporal variability differed among Red List Categories (for MSE: χ^2 = 16.3, df = 5, p-value = 0.006), it did not increase with the extinction risk (Fig. 6D). Only the populations from “Least Concern” species were less variable than populations from “Near Threatened” species, but no significant differences in temporal variability was detected between higher Categories (i.e. higher extinction risk). These results were consistant no matter the metric of temporal variability that was used.

4 | Discussion

In this work, we studied non-linear trajectories and temporal variability in the dynamics of 6,437 populations in the last 70 years across the globe, representing 1,257 unique species, and we tested how these two components of populations dynamics were distributed among habitats, regions, taxonomic groups and conservation status. Overall, our findings reveal that adopting linear approaches and ignoring temporal variability to characterize population dynamics could mask discrepancies among biogeographical regions or habitats and taxonomic groups.

4.1 | The need for integrating non-linearity and temporal variability in conservation biogeography

We show that non-linear models better explain the trajectory patterns for almost 45% of all analyzed populations, expressed through a broad range of patterns - decelerating, accelerating, concave and convex. Cross-analysis of population classification (linear vs. non-linear) reveals that the commonly-used linear approach misses some key information from a conservation perspective. We show that almost 18% of populations showing linear decreasing trends are in fact exhibiting recent flat or reversing curves, which may reflect successful conservation strategies. Conversely, in numerous cases a linear approach fails to reflect sharp declines in populations, such as accelerated declines or concave trajectories, which may require urgent conservation interventions.

Our results also emphasize that temporal variability in population dynamics is a complementary component to characterize populations’ status. Temporal variability is expressed differently across types of trajectories. In particular, population trajectories that have been classified as “no trend linear” show more variability than other types of trajectories, and in general linear trajectories show more variability than non-linear ones. We suspect this result to partly emerge from the difficulty to detect any type of trajectory in highly noisy population time series. Yet, the absence of a trend within certain populations does not necessarily imply high variability. In fact, our results indicate a wide range in the magnitude of variability within populations categorized as exhibiting "no trend linear" trajectories. Furthermore, even if we cannot 100% rule out that high variability could be due to a statistical artefact, it is crucial to emphasize that, from a conservation point of view, the mere fact that some populations show highly variable abundances over time warrants special attention.

This reinforces the need to consider non-linearity and variability together in conservation biogeography. Indeed, variability is expected to be a signal of instability or even a signal preceding ecological collapse, being either at the population (Dai et al., 2012), community (Carpenter et al., 2011), or ecosystem (Scheffer et al., 2009) level. As a result, considering only population trajectories through their trends is not sufficient to detect vulnerable populations. For instance, populations with increasing but highly variable trajectories may become extinct, if they fail to settle permanently. Moreover, the impact of environmental stochasticity and the probability to be exposed to extinction increases when the population sizes become smaller (Soulé, 1987). Therefore, instead of relying on unified approaches of population trajectories for policy making, it’s more likely that a cautious intermixing of both non-linear trajectories and temporal variability might well lead to improved conservation strategies.

4.2 | Heterogeneous population dynamics at local scales can be masked by global biogeographic or taxonomic groupings

Our results show that there is a wide range of variability across biogeographic regions, testifying to the diversity of ways in which populations are likely to respond to global change. In particular, marine populations are subject to greater fluctuations in abundance over time, no matter the types of trajectories identified. This complements previous findings where the marine communities emerged as a hotspot for rapid changes in composition (Blowes et al., 2019). Contrary to our expectations, we have not found any clear geographic or taxonomic patterns in global population changes, that we assumed would reflect regions and groups even more vulnerable to global changes. The broad groupings into major taxonomic groups and biogeographical regions on a global scale may not reflect the drivers shaping the trajectories of the specific populations we studied (Brook et al., 2006; Pereira et al., 2012), a warning that was also flagged by studies investigating changes through linear analyses (e.g. Daskalova et al., 2020). Alternatively, our results show that dramatic declines and high variability are observed across diverse regions and groups, which indicates that these particular attributes are not localized but have the potential to impact all groups and regions.

Furthermore, while threatened species tend to be the focus of conservation initiatives (Martín-López et al., 2011), we show that at local scales there are variations in how populations are changing over time, in isolation from their overall conservation status. Species' IUCN Red List Categories are determined at species level hence at a global scale, meaning that IUCN status might be unrelated to the abundance trajectories and temporal variability of individual populations at local scales. This decoupling further highlights the heterogeneity in local-scale population trends. Plus, this scale dependency has led to strong debates for particular groups (e.g for Storks (Gula et al., 2023b; Gula et al., 2023a)). As a result, implementing global policies, such as the post-2020 Biodiversity Framework, necessitates to focus on the diversity of responses not only at the level of species and regions, but also at finer scales such as that of populations.

4.3 | Major weaknesses in global biodiversity changes assessments

Analyzing time series data presents caveats that are present across population data in general, including taxonomic and geographic gaps (Cordier et al., 2021; Tekwa et al., 2023). The lack of taxonomic signals might undoubtedly reflect the lack of long-term information on the least studied taxa. Indeed, only limited numbers of amphibian and reptile populations were available in our data selection, and no invertebrate population was recorded. The patterns we identify, either in the biogeographical or taxonomic distributions of the dynamics, are likely influenced by the overrepresentation of certain groups (Birds) and regions (Europe and North America) and do not extend to the overlooked parts, notably tropical populations which comprise the species that may be at the greatest risk of decline and extinction (Butchart et al., 2010; WWF, 2022). The proportion of non-linearity as the relative proportion of the different trajectories detected could be influenced as well by how long populations are monitored (White, 2019) and by the period at which monitoring began (Mihoub et al., 2017; Duchenne et al., 2022). Our findings demonstrate that non-linear models were more likely to be a better fit for time series with longer durations (see appendix SM2). Such result is consistent with previous studies showing that trend estimates could be improved by increasing time series length (Wauchope et al., 2019). As long-term data are accumulating worldwide, this stresses even more the importance of the non-linear assessment of population changes in future research.

5 | Conclusion

This paper supports the view that the ongoing biodiversity crisis is far more complex than just a global decline, but in no way refute the existence of global biodiversity erosion. The same way it has been shown that the species composition of natural ecosystems is changing at an unprecedented rate (Dornelas et al., 2014), we show that biodiversity dynamics at population level are changing in complex ways. We urge to consider this complexity, and to resist the temptation to over-interpret results showing equal amounts of positive and negative trends as being positive or synonymous of an “equilibrium”. Our intention is not to question the fundamental value of the numerous studies of global biodiversity changes using linear approaches. We rather claim that estimating non-linear trajectories and quantifying the temporal variability of population dynamics can enhance existing findings. Not only such approach clarifies how populations decline and how they increase, it also refines our approach to population "stability".

Overall, we demonstrate that the general perception that a population is "stable" or "healthy" when its dynamics cannot be characterized by a linear decline is misleading. While declines are obviously a primary concern, our study reinforces the importance of nuance and the need to take multiple parameters into account when studying species status in conservation biogeography. Even apparently no-changing populations should not be overlooked in conservation. Monitoring species locally, regardless of their global status, should be of primary concern. Describing the full spectrum of complex population changes, including positive, negative and stable trends, but also accelerating, decelerating and variable trajectories, will improve our understanding of global biodiversity changes and should help to capture the variety of ways in which climate change, land-use change, and other anthropogenic pressures are altering global biodiversity.

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Data Accessibility Statement

Raw data are available from the following websites : for population time series — https://www.livingplanetindex.org/data_portal, for IUCN Red List Categories — https://www.iucnredlist.org. Code for data processing, analyses and vizualisation are publicly available on a GitHub respository (https://github.com/MaelysBoennec/Non-linearity-and-variability-in-global-population-dynamics/) and archived on Zenodo (DOI:10.5281/zenodo.10406601).

Figures

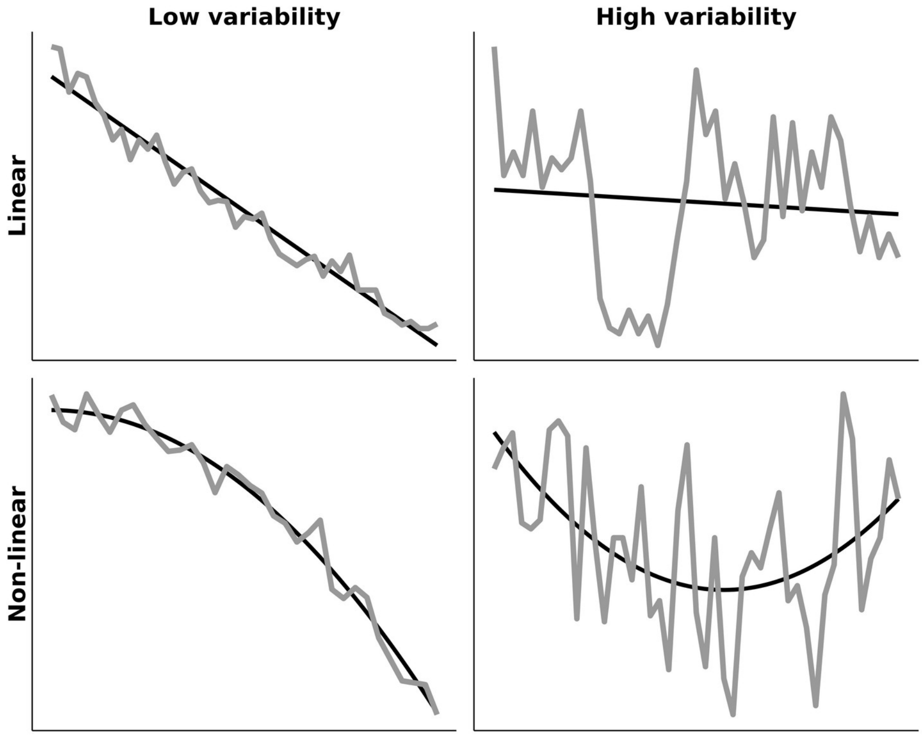

Figure 1. Illustrations of non-linearity and temporal variability in hypothetised population dynamics. Representation of different possible magnitude of temporal variability within population linear or non-linear trajectories. Black solid lines represent the trajectory of the time series, which might be a linear or non-linear fit. Solid grey lines represent hypothetical abundance time series. Variability in populations may occur even when the apparent trajectory is null or going upwards.

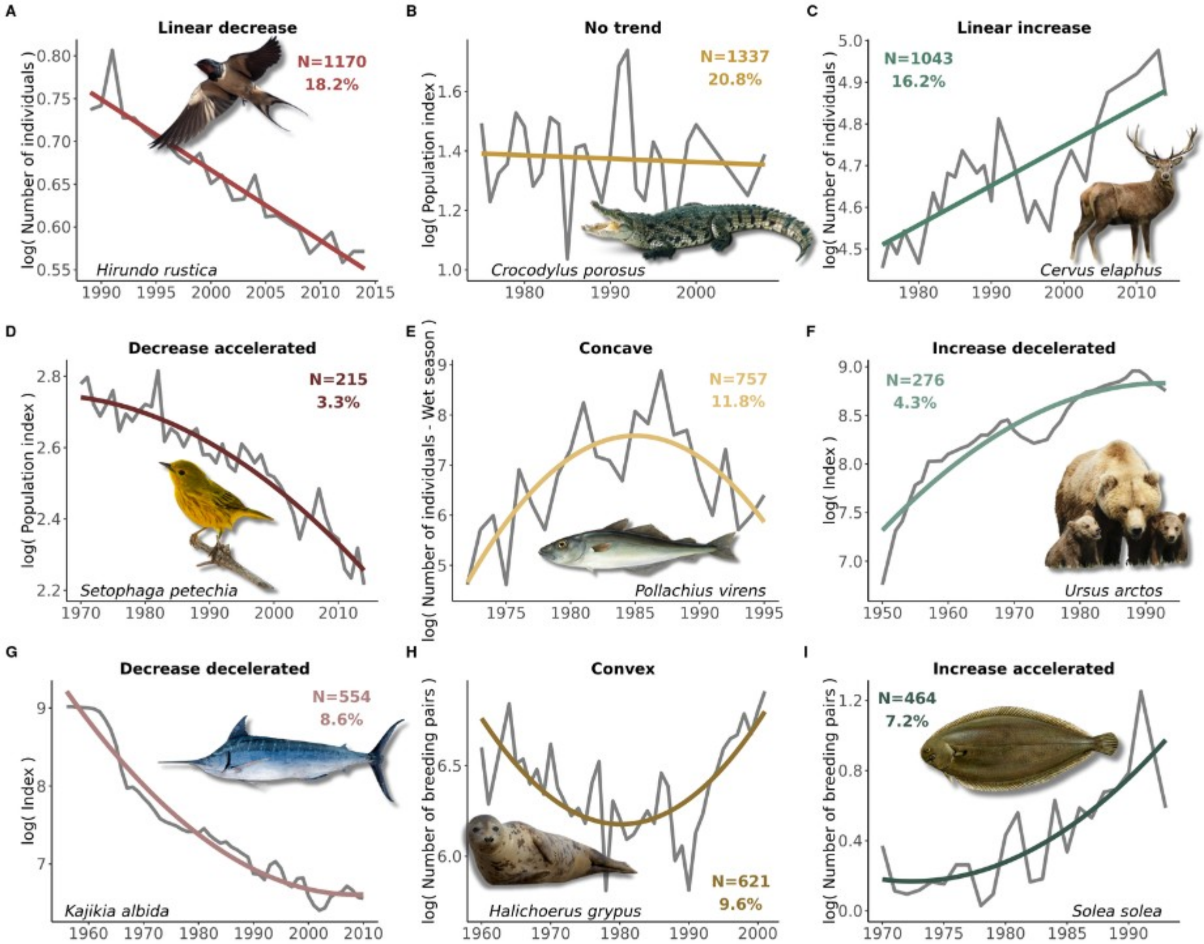

Figure 2. Non-linear trajectories account for almost 45% of the population trajectories studied. Classification of the 6,437 population trajectories (log transformed abundances) from 1950 to 2020 into nine possible shape categories. ‘N’ indicates the number of populations within each category. The percentages are relative to the total number of population (6,437). Log transformed abundances are shown for one population of each trajectory type by a gray line and best-fitted first or second order polynomials are shown by a bold coloured line.

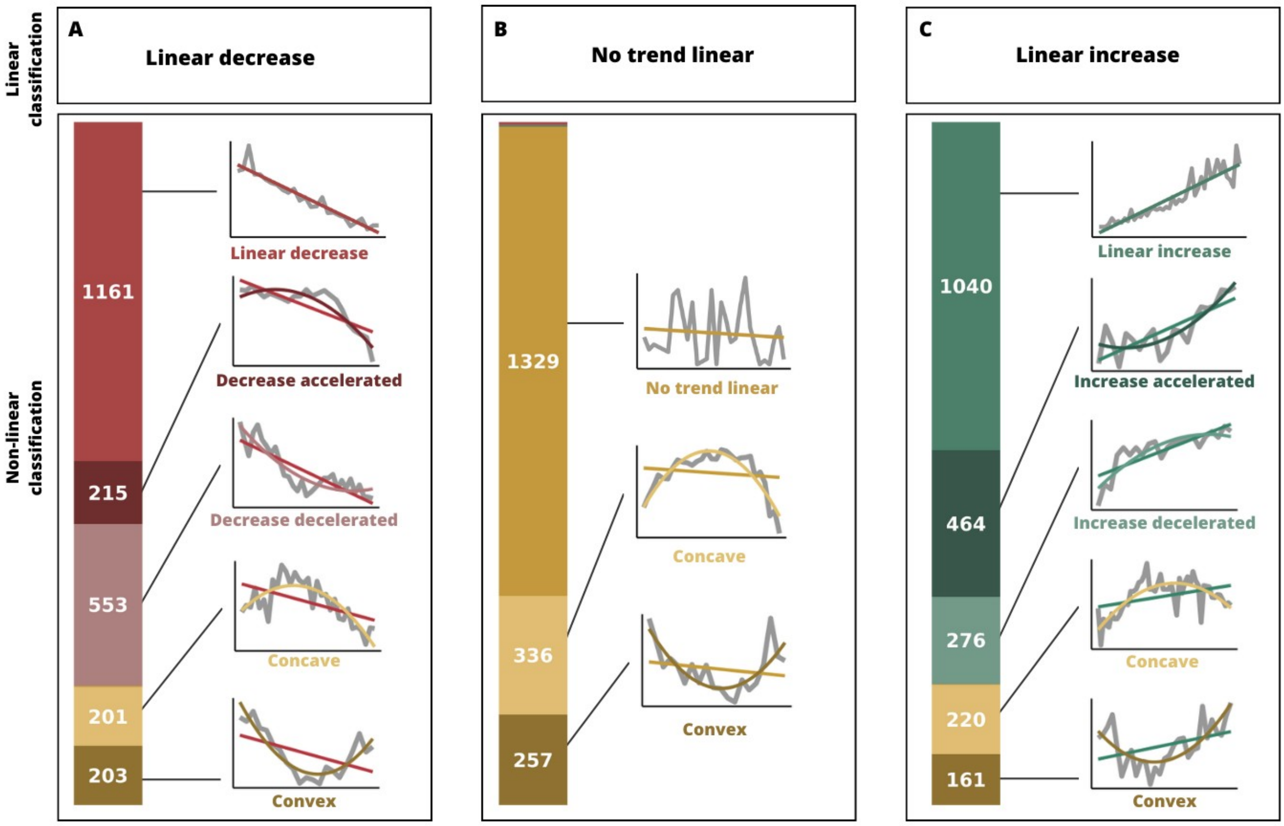

Figure 3. Cross-classification of population trajectories according to the use of linear or non-linear classifications reveals potential misinterpretations of population status. Cross-classification of the populations classified as **(A)** linear decrease, **(B)** no trend, and **(C)** linear increase according to the use of linear models. Within each column, the same populations are classified according to the non-linear models. For example (A), among the 2,338 populations classified as "decreasing" when fitting a linear regression, only 1,161 are still classified as “linear decrease” when fitting second order polynomials. 215 are classified as "decrease accelerated", 553 as "decrease decelerated", 201 as "concave" and 203 as "convex".

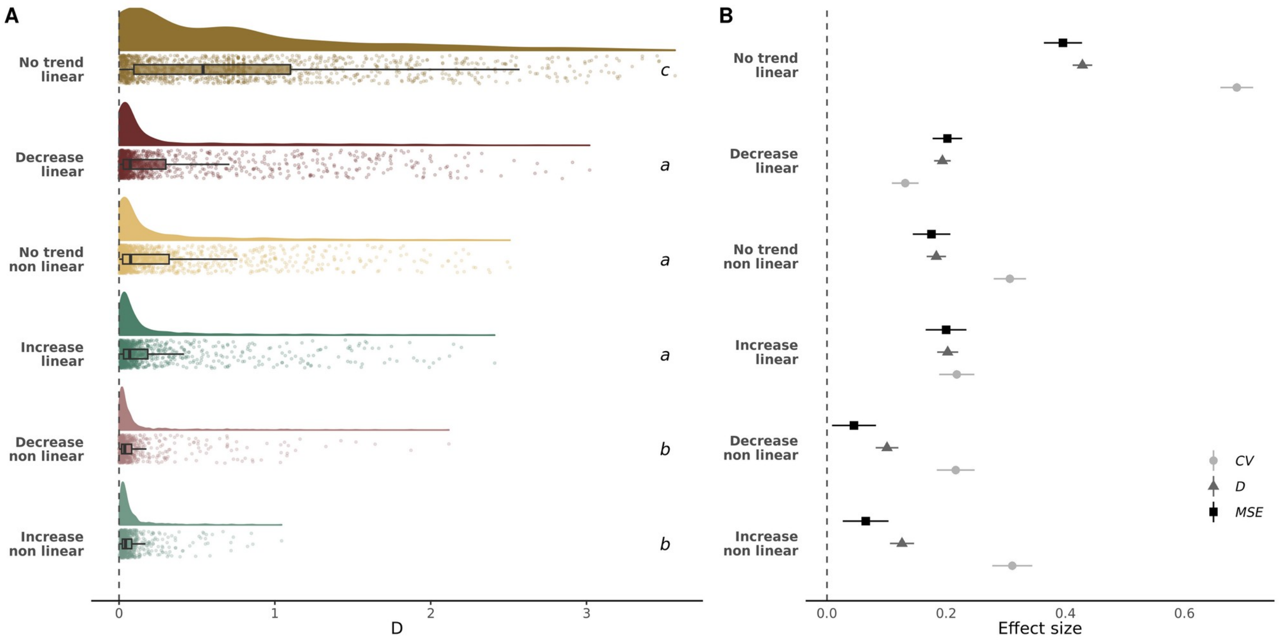

Figure 4. Temporal variability in population change differs according to trajectory types. (A) The consecutive disparity index (D) is used here as a proxy of temporal variability. Half violins represent the density distribution of temporal variability in populations for each trajectory type, points reprensent the raw values, boxplots are represented including the median, first and third quartiles. Letters indicate the significance of pairwise comparisons, calculated with post-hoc tests after running the linear mixed effect model. Results for CV and MSE can be found in SM4. **(B)** shows the different estimations of temporal variability depending on the metric used. The estimated effect sizes (represented at the centre of error bars) and intervals (standard errors) are the outputs from the linear mixed effects models for each metric. The detailed pairwise comparisons for each metric are presented in appendix SM4.

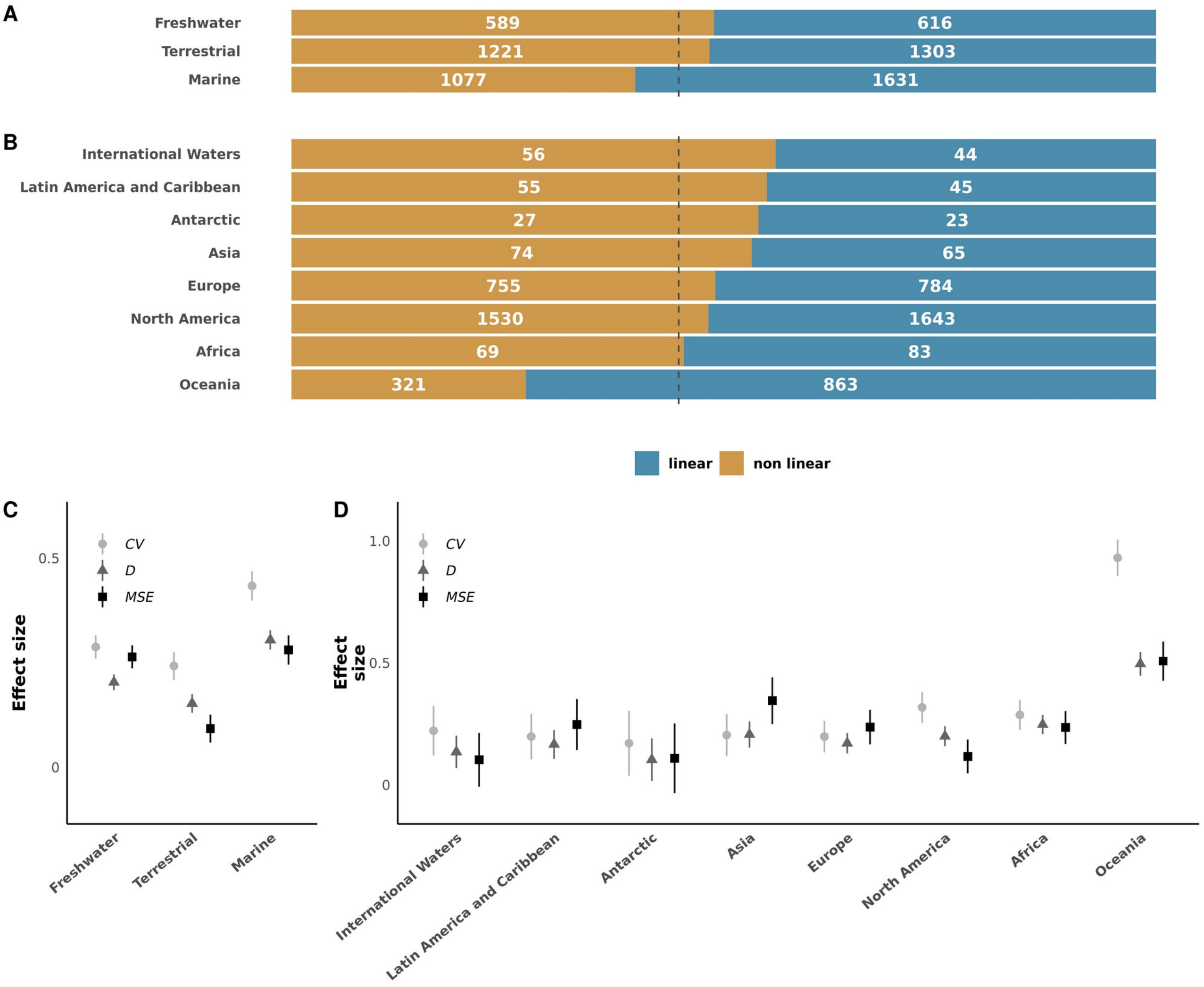

Figure 5. Non-linear trajectories and temporal variability in population dynamics are heterogeneous among habitat types and geographical regions. (A) and **(B)** show the proportion of non-linear trajectories in orange versus linear trajectories in blue among habitat types and geographical regions respectively. Exact numbers of populations are written in white. The vertical dashed line represents the mean proportion of non-linear trajectories among all the populations we classified within our study (44,8%, i.e. 2,887 populations out of the 6,437). **(C)** and **(D)** shows the different estimations of temporal variability depending on the metric used among habitat types and geographical regions respectively. The estimated effect sizes (represented at the centre of error bars) and intervals (standard errors) are the outputs from the linear mixed effects models for each metric. The detailed pairwise comparisons for each metric are presented in appendix SM4.

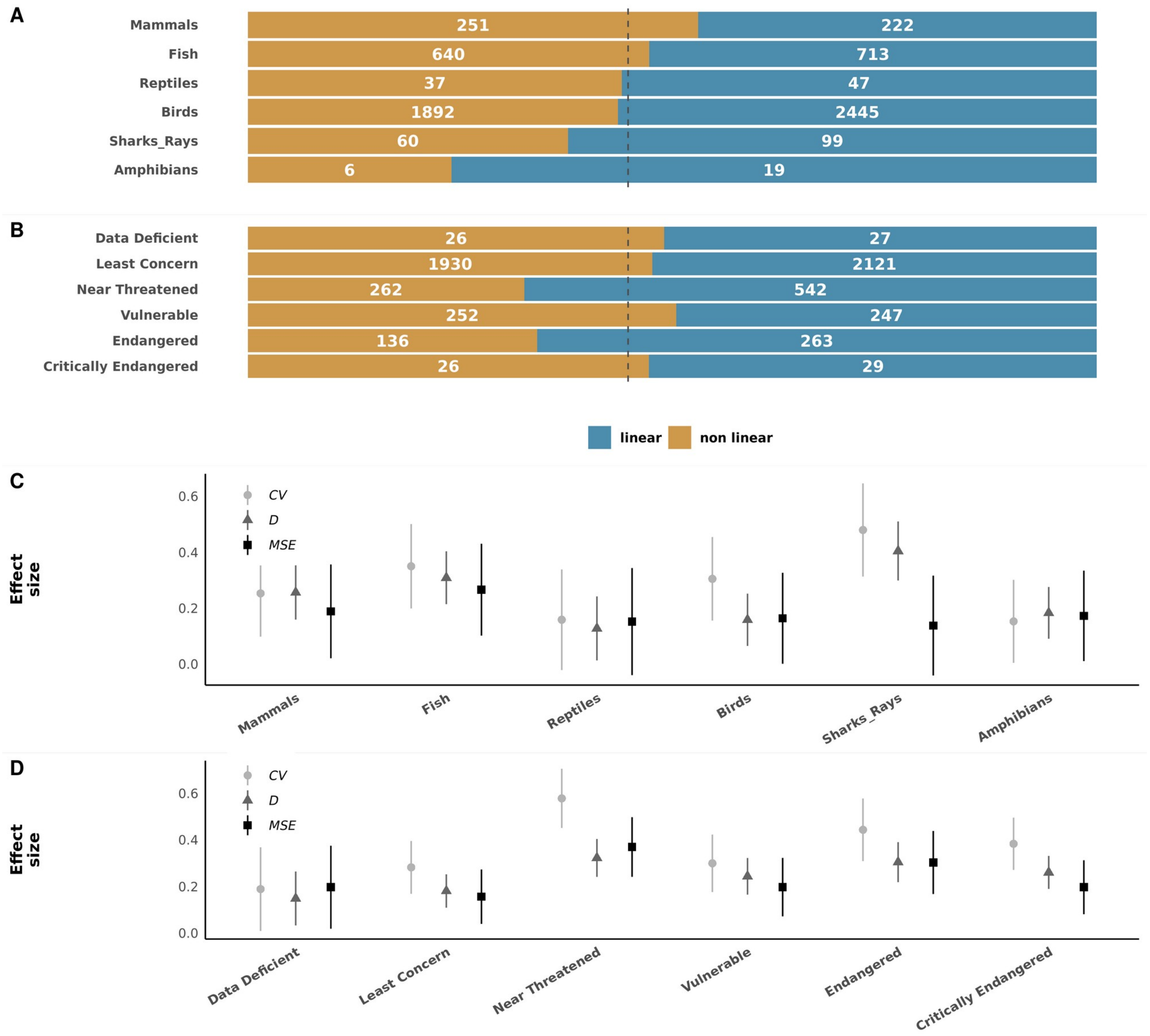

Figure 6. Non-linear trajectories and temporal variability in population dynamics vary more within taxonomic groups and IUCN Red List Categories than between them. (A) and **(B)** show the proportion of non-linear trajectories in orange versus linear trajectories in blue among taxonomic groups and IUCN Red List Categories respectively. Exact numbers of populations are written in white. The vertical dashed line represents the mean proportion of non-linear trajectories among all the populations that were classified within our study (44.8%, i.e. 2,887 populations out of the 6,437). **(C)** and **(D)** shows the different estimations of temporal variability depending on the metric used among taxonomic groups and IUCN Red List Categories respectively. The estimated effect sizes (represented at the centre of error bars) and intervals (standard errors) are the outputs from the linear mixed effects models for each metric. The detailed pairwise comparisons for each metric are presented in appendix SM4.