Random population fluctuations bias the Living Planet Index

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The Living Planet Index (LPI) is a standardised indicator for tracking population trends through time. Due to its ability to aggregate many time-series in a single metric, the LPI has been proposed as an indicator for the Convention on Biological Diversity's post-2020 Global Biodiversity Strategy. However, here we show that random population fluctuations introduce biases when calculating the LPI. By combining simulated and empirical data, we show how random fluctuations lead to a declining LPI even when overall population trends are stable, and imprecise estimates of the LPI when populations increase or decrease non-linearly. We applied randomisation null models that demonstrate how random fluctuations exaggerate declines in the global LPI by 9.6%. Our results confirm substantial declines in the LPI, but highlight sources of uncertainty in quantitative estimates. Randomisation null models are useful for presenting uncertainty around indicators of progress towards international biodiversity targets.

Nations of the world are in the process of negotiating the post-2020 Global Biodiversity Framework under the Convention on Biological Diversity. One of the ambitions of the post-2020 framework is "bending the curve of biodiversity loss" by first slowing down declines by 2030 and then improving the state of biodiversity by mid-century[1–3]. Reliable biodiversity indicators are essential for tracking progress towards global biodiversity targets[4]. A prominent indicator of species abundance over time is the Living Planet Index (LPI)[5–7]. The LPI aggregates population time-series for vertebrates from terrestrial, freshwater and marine systems into a relative index (where the baseline is

scaled according to population levels in 1970), which is reported biennially as part of the Living Planet Report[8].

In addition to being widely reported by the popular press, the LPI has developed a significant policy footprint. Global declines, as measured by the LPI, were reported in the *Global Assessment* of the *Intergovernmental Science-Policy Platform for Biodiversity and Ecosystem Services*[9], the most authoritative synthesis of policy-relevant biodiversity science. Similarly, the index was also used in the *Global Biodiversity Outlook Report 5*[10] to monitor progress toward Aichi Target 12 (Reducing Risk of Extinction) for the period 2010-2020. Recently, the LPI was a central feature in pioneering efforts to model adaptation and mitigation pathways for biodiversity in the upcoming century[2]. There is, therefore, considerable policy inertia behind the Living Planet Index.

Despite the LPI's broad influence, it has several known caveats[11,12]. First, since each time-series is standardised as a relative rate of change, declines in small populations are viewed as equivalent to similar proportional declines in large populations, even though the absolute declines are much larger in the latter[6,11]. Second, population trends are summarised using the geometric mean, which is always lower than the arithmetic mean, resulting in an index that is sensitive to a small minority of extremely declining populations[12]. Third, the LPI weighs time-series prior to averaging to account for imperfect regional and taxonomic sampling, essentially giving greater weight to time-series from poorly studied geographic areas or taxonomic groups.

Each of these caveats is the result of a deliberate trade-off in the design of the LPI. Standardisation is necessary because abundance is often estimated from indices of varying units (e.g. densities or breeding pairs) and because populations that may be naturally common or rare (although it has been shown that weighing sub-populations in

proportion to their contribution to the global population of a species does not affect the LPI qualitatively[6]). The geometric mean accommodates multiplicative population dynamics, where averages may be distorted by exponentially increasing populations[13]. Finally, weighting is necessary to account for misleading estimates caused by incomplete data coverage[7], because populations from certain taxa or regions are more likely to be represented in monitoring databases.

It seems impractical to redesign the LPI to address caveats that were introduced due to deliberative trade-offs, especially considering how the index is already embedded in global conservation monitoring frameworks. The usefulness of the LPI should be evaluated by distinguishing between inconvenient drawbacks that require more careful interpretation, and fundamental flaws that may render the index uninformative. Population time-series (the input data for the LPI) combine two components: deterministic increasing or decreasing tendencies, and the stochastic fluctuations around these tendencies[14,15]. The three known caveats of the LPI (standardisation, geometric mean, and weightings) affect estimates of the deterministic tendencies of the LPI. While this can be seen as an inconvenient drawback, it can be addressed by explaining carefully how to interpret the LPI. For example, the technical supplement to the latest Living Planet Report[16] describes clearly how the LPI should be interpreted as the average trend in population change, rather than the average loss in the absolute number of animals or species.

The other, previously ignored, point of concern is the potential effect of random population fluctuations on the LPI. If the LPI is disproportionately affected by random population fluctuations relative to deterministic tendencies, then any meaningful association between the index and underlying populations breaks down. If this is the

case, careful interpretation of the LPI will be insufficient. Random population fluctuations might be caused by ecological drift[17,18]; environmental or demographic stochasticity[19,20]; or random observational error[21,22]. Ecological drift, demographic stochasticity, and observational error tend to cause symmetrical positive or negative population fluctuations because randomness affects individual births, deaths, or detections (note: demographic stochasticity is often treated as a synonym for ecological drift[18]). By contrast, environmental stochasticity leads to asymmetrical positive and negative population fluctuations, because randomness causes variability in multiplicative birth or death rates[20]. The LPI is formulated to consider exponential population dynamics, so it should also accommodate asymmetrical environmental stochasticity. In their analysis of time-series in the Living Planet Database, Daskalova and colleagues[15] used state-space models to distinguish between population tendencies, process noise, and observational error. They used Gaussian distributions to model process noise and observational error additively and found that population fluctuations in time-series from the Living Planet Database are relatively small (approximately 2.2 % per year on average for terrestrial time-series and 2.8 % per year for freshwater and marine populations) but were greater in rare and threatened species[15]. The consequences of these symmetrical population fluctuations for the LPI have yet to be investigated.

Here we quantified the effect of random population fluctuations on the magnitude of the LPI by answering two questions. First, what is the effect of random population fluctuations on the LPI assuming that populations are stable on average (i.e. no deterministic directional tendencies)? Answering this question identifies a more accurate counterfactual for the LPI, which is currently assumed to be static in the absence of general positive or negative trends. Second, what is the effect of random

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population fluctuations on the LPI when populations do show increasing or decreasing tendencies? This identifies whether stochasticity over- or underestimates the LPI. To answer each of these two questions, we began by illustrating general principles using simple simulation models and then combined empirical data with null models to estimate the contribution of random population fluctuations to the LPI.

Results

The effect of random fluctuations on the LPI for stable populations

The formulation of the LPI means that the index can decline, even when populations are stable on average (Fig. 1). The LPI was designed for multiplicative population dynamics, so additive population fluctuations mean that random increases cannot compensate for random declines even when of equal magnitude. We demonstrated this effect by simulating sets of 500 populations that fluctuate along a random walk (Fig. 1a) and subsequently calculating the LPI for each of these sets (Fig. 1b). The LPI declined in these simulations by as much as 8 % over 50 years (Fig. 1b), even when the average population sizes remained unchanged. The LPI is based on annual changes in populations, $\lambda = log_{10}(N_{t+1}/N_t)$, where N is the time-dependent population size (see methods and Extended Data Fig. 1). The log_{10}-transformation used to calculate λ means that the relative effects of positive or negative fluctuations are asymmetrical (Fig. 1c) and this asymmetry is exaggerated in small starting populations due to smaller denominators (N_t) when calculating λ. We then investigated different starting population sizes and annual fluctuations and found that the LPI in otherwise stable populations was mostly unaffected when annual fluctuations were less than 1 % per year but declined by as much as 40 % once annual fluctuations exceeded 4 % (Fig. 1d).

We simulated how random population fluctuations might affect the empirical LPI by iterating three separate null models with starting populations identical to those in the Living Planet Database. For each null model, we simulated random positive or negative fluctuations of 1 %, 3 % and 5 % annually (see methods). This represented how the LPI would be affected by population fluctuations in otherwise stable populations. Empirical declines in the global LPI were much greater than could be attributed to random fluctuations in stable populations (Fig. 2a). Here, the LPI declined by 64 %, which differed from the 68 % reported in the Living Planet Report[8], but this is because we used the public dataset, which excludes several private time-series (see methods).

A null model with 1 % annual random fluctuations resulted in a global LPI decline by 2016 of only 0.2 % (sd = 0.3 %) (Fig. 2b). When fluctuations increased to 3 % in the null model, the LPI in an otherwise stable populations declined by 1.5 % (sd = 0.8%), while annual fluctuations of 5 % reduced the LPI by 4.9 % (sd = 1.7 %) (Fig. 2b). These patterns were consistent for LPIs calculated for terrestrial, freshwater and marine realms separately, as well as for different biogeographical regions (Extended Data Fig. 2). Although LPI declines attributable solely to population fluctuations are small, they do suggest that the null expectation of the LPI should be a declining counterfactual rather than a static baseline set at 1970. This is likely to become more important in upcoming years because the effects of random fluctuations are exacerbated in small populations (Fig. 1d) and the starting populations of newly added time-series in the Living Planet Database have declined exponentially between 1950 and 2015 (ln-transformed starting populations have declined by 6.4 % ± 0.2 % annually; Extended Data Fig. 3).

The effect of random fluctuations on the final LPI for increasing or decreasing populations

The extent of declines in the empirical LPI cannot be ascribed to random population fluctuations (Fig. 2), so we explored whether fluctuations affect the quantitative precision of LPI estimates for populations with increasing or decreasing tendencies. For this, we simulated sets of populations that declined along concave-up, linear, and concave-down trajectories[23] and showed how random annual population fluctuations can lead to biased estimates of the final LPI in declining populations (Fig. 3; comparable simulations for increasing populations are shown in Extended Data Fig. 4). Although the final LPI estimates at the end of the time interval are relatively robust for both linear and non-linear declines when population fluctuations are small (Fig. 3a,c), large fluctuations biased final LPI estimates by more than 10% for non-linear trajectories (Fig. 3b,d). This is likely an artefact introduced by the Generalised Additive Models (GAM) used to smooth population trends and interpolate missing data when calculating the LPI (see methods, Appendix 1, Extended Data Figs. 5 and 6). Random population fluctuations cause the GAM to underestimate the curvature of non-linear trajectories, which underestimates the magnitude of population losses for declining trajectories (Extended Data Fig. 5) and population gains for increasing populations (Extended Data Fig. 6).

We were able to correct for the effect of random fluctuations on the LPI using a null model that maintained the starting and ending populations in time-series, but which randomised the order of incremental changes to the population (see methods and Extended Data Fig. 7). By iterating this null model 100 times, we were able to generate a distribution of LPI estimates at the end of the time-series. Each estimate in the distribution represents a possible population trajectory to the same end-state and thus

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averages out any artefacts introduced when fitting the GAM to non-linear trajectories. Although this approach cannot be used to approximate the whole trajectory of the LPI across the entire time-series, it provides a more accurate estimate of the true final state in our simulated populations (Fig. 3 e,f and Fig S4 e,f) because it calculates the same cumulative population changes across 100 possible trajectories that are approximately linear on average (Extended Data Fig. 7).

We applied this null model to empirical population time-series in the Living Planet (Fig. 4) and found that random fluctuations exaggerated declines in the global LPI in 2016 (empirical LPI = 0.36; null model LPI = 0.46 ±0.03) (Fig. 4a). This demonstrates how declines in the LPI can differ by 9.6 % even when all the time-series start and end at exactly the same population sizes. Empirical declines in the LPIs were also overestimated by 23.2 % in terrestrial systems and by 8.1 % in freshwaters systems compared to the null model, but were underestimated by 19.6 % in marine systems (Fig. 4b). Similarly, declines in empirical LPI for biogeographical realms were overestimated in the Neotropics (by 14.2%), Paleartic (by 5.9%) and Indo-Pacific (by 6.9%) realms, but were slightly underestimated in the Nearctic (by 2.8%) and Afrotropical (by 11.6%) realms (Fig. 4c).

Discussion

Precise quantitative targets are essential for meeting international biodiversity commitments[24–26], and so are reliable indicators to track progress towards these targets[1,4]. The zero draft of the Convention on Biological Diversity's post-2020 Global Biodiversity Framework[3] lists as one of the milestones for 2030 (Goal A.2) that "*the abundance of species has increased on average by [X%]*". The LPI is proposed as an

indicator towards this goal, but our findings demonstrate that random population fluctuations can compromise the accuracy of the LPI for tracking progress towards international biodiversity commitments.

Our results do not detract from the main message of the LPI, which is one of dramatic declines in populations since 1970[8,9]. Even though random fluctuations caused declines in the LPI for otherwise stable populations, these effects were too small to explain empirical declines. Recent evidence suggests that the declining LPI may be caused by major declines in relatively few population time-series, rather than consistent decline across the majority of species[12]. This is supported by other studies that do not corroborate wholesale population declines[15,27]. These studies show that while many populations have declined, an equivalent number of populations have increased. Thus, on average, monitored populations seem to be quite stable. Such observations are consistent with the technical supplement to Living Planet Report, which also showed that the frequencies of increasing and decreasing populations were approximately equal[16].

This raises the question: why does the LPI show dramatic declines while other studies do not? We offer two reasons, neither of which invalidates the use of the LPI. First, the LPI assumes that population dynamics are exponential, so doubling a population is the positive equivalent of halving the same population even though the absolute change in the populations is twice as much. By contrast, other studies of global population change do not always assume exponential growth, favouring instead population data standardised between 0 and 1[15] or square-root transformed population data[27]. These transformation imply that population increases could more easily compensate for population declines mathematically.

The second reason for the disparity between declines in the LPI and related studies is that the LPI measures *cumulative* population changes since 1970 rather than *average* population changes (Extended Data Fig. 8). Declines tend to be greater when population sizes in the first year of monitoring are larger than the long-term average population[28], so selecting a fixed starting year standardizes this potential sampling artefact. More importantly, setting a fixed baseline has the important advantage of avoiding shifting-baseline syndromes[29,30]. This is illustrated using a hypothetical population that declined rapidly from 100 individuals in 1970 to 60 individuals in 1980 due to habitat loss and then approached a new equilibrium of 40 individuals by 2020 (Extended Data Fig. 9 a). In this example, the LPI approaches 0.4 as new data are collected (Fig S9 d), while the mean rate of decline becomes smaller as new survey data is added and the large initial declines are averaged out by subsequent smaller declines. Perversely, mean rates of decline in this hypothetical scenario tend to zero as the length of the time-series grows (Extended Data Fig. 9 b & c) because average declines become smaller as populations settle in alternative equilibria and newly collected data are added to time-series. Maintaining consistent baselines is essential when populations settle into alternative stable equilibria; something that is likely to become more prevalent in the upcoming decades[31]. Hence, the LPI is superior when the aim is quantifying cumulative population change over a time-period, rather than estimating mean annual rates of change.

Even though the LPI represents cumulative population change, we have shown that we must be cognisant of the effect of random fluctuations on the LPI (Figs. 1 & 2). We suggest that the LPI should be interpreted against declining counterfactuals, similar to the way economists interpret investments relative to inflation. The appropriate counterfactual for population fluctuations is still unclear because estimates from the Living Planet Database suggest that the median population fluctuations for vertebrate

species is likely around 2.2 - 2.8 %[15]. However, these estimates are strongly right-skewed across populations and may be higher for smaller populations and for threatened species[15]. Moreover, population fluctuations estimated retrospectively from empirical data do not necessarily reflect future fluctuations, so we should be cautious of using these to estimate the potential effect on the LPI by 2050 (the year of the Conventional on Biological Diversity's mid-century goals). Instead, we recommend using a range of fluctuations to simulate multiple scenarios of stable, but fluctuating, populations (e.g. Fig. 2), which can be used as alternative frames of reference against which real declines can be interpreted[32,33].

Alternative frames of reference will be particularly important if the LPI is calculated using data containing many small populations because the effect of fluctuations is particularly strong in smaller populations (Fig. 1d). Such effects of small populations could be exacerbated by (a) incrementally adding new time-series of rare populations to the Living Planet Database (Extended Data Fig. 3); (b) real population declines caused by human pressures; or (c) smaller population sizes used for national or sub-regional LPI calculations (e.g. ref. 34). This latter point will become increasingly important if countries must calculate national LPIs as part of their reporting on the Convention on Biological Diversity. Therefore, regional assessment could be improved by following standard criteria for including time-series when calculating the LPI, such as minimum sampling frequencies or time-series length[35,36].

Even with realistic frames of reference, it is still necessary that the LPI reported at any given point in time should not be an artefact of the population trajectories at preceding time points. Our results suggest that this is not the case because declines in a reshuffled LPI may be 9.6% less severe than the empirical LPI reported in the most recent Living

Planet Report[8], even though starting and ending population sizes were identical. This bias is introduced by the way the LPI smooths and interpolates time-series using GAM, which misidentifies starting and ending populations in noisy time-series (Figs. S5 & S6). Nevertheless, interpolation and smoothing are necessary features of the LPI because it allows messy data with sampling gaps to be aggregated in a uniform index. Therefore, rather than redesigning the LPI by changing the GAM, our results support efforts to account for biases using randomised null models (e.g. Fig. 4). These null models can be iterated to generate a distribution of final LPI values, which more accurately represent the uncertainty inherent in single composite metrics of biodiversity[11,12].

Efforts to bend the curve of biodiversity loss will require considerable transformation of all sectors of society[2]. Science should ensure that the indicators that guide these actions are as accurate as possible. Therefore, we need to explore and understand sources of bias and uncertainty in global biodiversity indicators such as the LPI. Our study confirms substantial population declines reported in global syntheses of policy-relevant biodiversity science[9,10,16], but highlights how random fluctuations affect quantitative estimates. Reshuffling null models can account for the mathematical artefacts introduced when calculating the LPI. These null models not only provide more accurate estimates of population declines but can also be iterated to assess uncertainty around these estimates. Therefore, we recommend using null models to improve the accuracy of and uncertainty around global biodiversity indicators when measuring progress towards international biodiversity targets.

Data availability

Empirical data of population time-series in the Living Planet database are available from the dedicated website maintained by the Zoological Society of London (ZSL) (http://stats.livingplanetindex.org/) and are subject to the Data Use Policy by the Indicators & Assessments Unit at the ZSL and WWF International. Simulated data to replicate the results are available from: http://doi.org/10.5281/zenodo.4744533.

Code availability

All simulation outputs and code (R-scripts) to reproduce the results in this manuscript are available from: http://doi.org/10.5281/zenodo.4744533.

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Author contributions

FTB led the simulation and analysis, with conceptual inputs from JGH, LS, and BWTC. FTB wrote the first draft, while JGH, LS and BWTC revised subsequent drafts for framing, clarity, and technical correctness.

Competing Interests Statement

The authors declare no competing interests.

FIGURE CAPTIONS

Fig. 1 | Fluctuating, but otherwise stable, populations lead to a declining Living Planet Index. a, Three sets of 500 populations each (fine lines) that fluctuate randomly by two individuals on average each year, but which are stable on average (thick lines). The sets are identical except for their starting populations (N = 50, 100, 150). **b**, The Living Planet Index declines for these sets of populations even when they are stable on average because **c,** fluctuations upwards or downwards cause asymmetrical estimates of λ, which are exaggerated in smaller populations. **d**, The effect of fluctuations on the Living Planet Index is greatest in small populations that experience large fluctuations (here, the diagonal lines represent the magnitude of the fluctuations as relative percentages of the starting population).

Fig. 2 | Larger random fluctuations in otherwise stable populations lead to greater declines in the empirical Living Planet Index. a The Global Living Planet Index (mean and 95% confidence intervals) between 1970 and 2016 compared against declining counterfactuals caused by random fluctuations (1 %, 3 %, 5 %) in otherwise stable populations. The shaded grey area in **a** shows the scaling of the following panel, **b**, which presents the LPI for fluctuating, but otherwise, stable populations (mean and interquartile range of 100 iterations of the randomisation null model).

Fig. 3 | Larger population fluctuations cause less precise estimates of the Living Planet Index (LPI) in non-linear population trajectories. a and **b**, Simulated sets of populations each with 500 species that decline from 100 to 40 individuals along concave-up, linear and concave-down trajectories with low (**a**) and high (**b**) population

fluctuations. **c** and **d**, The accompanying trends in LPI for declining populations with low (**c**) and high (**d**) fluctuations; the confidence intervals around the LPI are negligible because the starting (solid horizontal grey lines) and ending (dashed horizontal grey lines) populations are identical in all sets. **e** and **f**, The LPI in the final year of the simulation, 2020. Here, vertical coloured lines correspond to the LPI from the simulated data (**c** and **d**) and the dashed black line is the true value based on the actual final populations. The distribution is the density of LPI values from a null model that approximated linear declines by randomly reshuffling the order of population changes (100 times), while keeping the starting and end values constant.

Fig. 4 | Random population fluctuations cause the misestimation of the Living Planet Index (LPI) compared to a reshuffling null model. Violin plots show the distribution of final mean LPI values in 2016 from 100 iterations of a null model that randomises the order of incremental population changes between time-steps, while maintaining starting and ending population sizes. Data are grouped for the global LPI (**a**); terrestrial, freshwater and marine systems (**b**); and five biogeographical realms (**c**). Values show the magnitude by which the median LPI from the null model (white circles) is higher (blue) or lower (red) than the empirical LPI (white diamonds).

Methods

A brief overview to calculating the LPI

While others have explained the details of the LPI[5-7], it is necessary to give a short overview of the method to understand how random fluctuations could affect the LPI (Extended Data Fig. 1). For all subsequent calculations, we used the purpose-built `rlpi` (v 0.1.0) package in R version 3.6.2[37] to ensure that our methods were identical to those used to generate the LPI. We also used the public data released with the 2020 Living Planet Report[8]. This dataset includes 15,348 population time-series between 1950 and 2016, apart from 5,463 confidential time-series that are not publicly available.

Calculating the LPI requires nine steps (Extended Data Fig. 1). The first step is obtaining a time-series for each population. Not all the time-series in the dataset are integer counts of abundance, but also include measurements of density, biomass, or proxies of abundance (e.g. number of breeding pairs). These time-series also have different start- and end-dates, and irregular sampling frequencies. The second step is, therefore, fitting a Generalised Additive Model (GAM) to each log_{10}-transformed population time-series with at least six population measurements. This smooths the population time-series and interpolates missing data. Time-series with fewer than six measurements are interpolated using a chain rule, which assumes that populations changed linearly between each pair of subsequent measurements. The smoothed predictions from the GAM model are used to estimate sequential changes in population sizes over successive years (step 3), which is calculated as $\lambda = log_{10}(N_{t+1}/N_t)$ (step 4). The fifth step for calculating the LPI is standardising population trends by setting the value in 1970 to one, and calculating subsequent trends using the annual changes, λ, through time. Annual changes are summarised across all populations of the same species using the

geometric mean (step 6). These standardised species-level time-series are then aggregated across vertebrate classes (step 7) using a weighted mean relative to the total number of species in the taxonomic group and then aggregated into composite indices for terrestrial, freshwater and marine ecosystems (step 8) after weighting averages based on the total number of species of each vertebrate class per biogeographical realm[7]. These weighing processes account for geographic and taxonomic sampling biases in the population time-series. The final step is aggregating terrestrial, freshwater and marine indices into a global LPI, assigning equal weights to each system.

Mathematical asymmetries when calculating the LPI

A limitation inherent to the LPI is that a population declining by a fixed value, Δ, has an asymmetrical negative effect on λ, compared to an equivalent increase by Δ. When fluctuations are truly stochastic and additive (i.e. due to ecological drift[17,18], demographic stochasticity[19,20]; or random observational error[21,22]) then positive and negative changes by Δ should be equally probable. For fluctuations to have no effect on the LPI, it is necessary that an increase of Δ should have a positive λ, which is the same magnitude as the negative λ caused by a decrease in Δ:

$\lambda_{increase} = -\lambda_{decrease}$

$log_{10}\left[(N + \Delta)/N\right] = -log_{10}\left[(N - \Delta)/N\right]$

$(N + \Delta)/N = N/(N - \Delta)$

$(N + \Delta).(N - \Delta) = N^2$

$N^2 - \Delta^2 = N^2$

Clearly, this is only true when $\Delta = 0$, and false otherwise. The term $-\Delta^2$ also shows that the relationship between λ and the size of the fluctuation, Δ, is a quadratic concave-down function indicative of an asymmetrical effect of positive and negative fluctuations (Fig. 1c). Another truism of this equation is that the inequality is proportionally smaller when the size of the fluctuation, Δ, is small relative to the starting population size, N, which also scales quadratically. Thus, a population fluctuating randomly around equilibrium conditions can result in a declining LPI because random increases cannot compensate fully for equivalent random declines, but this effect is less prevalent in large populations.

The effect of random fluctuations on the LPI for stable populations

To illustrate how randomly fluctuating populations can result in a declining LPI, we simulated a set of 500 populations, which fluctuated randomly through time. Each population in the simulation was from a unique species and each had the same starting population, N. We allowed the populations to fluctuate for each year between 1970 and 2020, by randomly selecting the annual fluctuation, Δ, from a Poisson distribution and varying the sign of the fluctuation (i.e. positive or negative) with equal probability. After allowing all the populations to fluctuate for the duration of the simulation, we calculated the LPI for each set of populations. We simulated three sets of 500 populations for illustrative purposes ($N = 50, 100, 150$; mean $\Delta = 2$: Fig. 1 a-c), but then also iterated the entire process 25 times for combinations of N (between 50 and 300 in increments of 10) and mean Δ (between 0.5 and 5, in 0.1 increments) (Fig. 1d).

We then examined the potential effect of random fluctuations on the empirical data used in the LPI. To do this, we first identified the starting population size for each time-series.

We then allowed each population to fluctuate randomly in three separate simulations by 1%, 3% and 5% each year. This range of fluctuations includes the mean fluctuations for terrestrial (2.2 %), freshwater and marine (both 2.8 %) populations[15]. For each simulation, the annual direction of the fluctuation was selected randomly so that positive and negative fluctuations were equiprobable. We allowed the simulated populations to fluctuate annually for the whole period between the first measurement in the time-series (which differed among populations) and 2016 (the final year of the publicly available LPI data). The empirical data had gaps in the time-series, so we removed the simulated time-series measurement that coincided with the gaps in the empirical dataset to ensure that the simulated and empirical data had identical sample completeness. After allowing all 15,348 populations to fluctuate randomly, we calculated the LPI using the same weightings as the empirical data to account for geographic and taxonomic biases[7]. This entire stochastic process was iterated 100 times for each of the three levels of fluctuation (i.e. 1 %, 3 %, 5 %).

The effect of random fluctuations on the final LPI for increasing or decreasing populations

To be a reliable indicator of biodiversity trends, the LPI for any given year should reflect the state of populations at that specific point in time, rather than the population state at an earlier time. In other words, the LPI at time t should be independent of the population trajectories at preceding time points. This is not the case for the LPI when populations fluctuate randomly because fluctuations affect the accuracy of GAM models fitted to population time-series (Extended Data Figs. 5 and 6). We explored the consequences of imprecise GAM estimates by simulating sets of species that all declined from a starting population size of $N_0 = 100$ in the year 1970, to a final population of $N_F = $

40 in 2020 (a 60% decline, consistent with the findings of the global LPI). We simulated these populations along varying trajectories as:

$$N_t = N_F + (N_0 - N_F). \left[1 - \left(\frac{t - min(t)}{max(t) - min(t)}\right)^d\right]$$
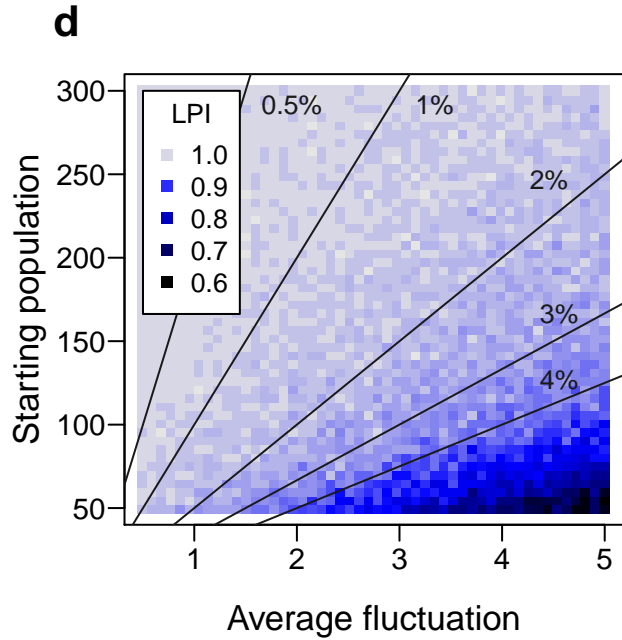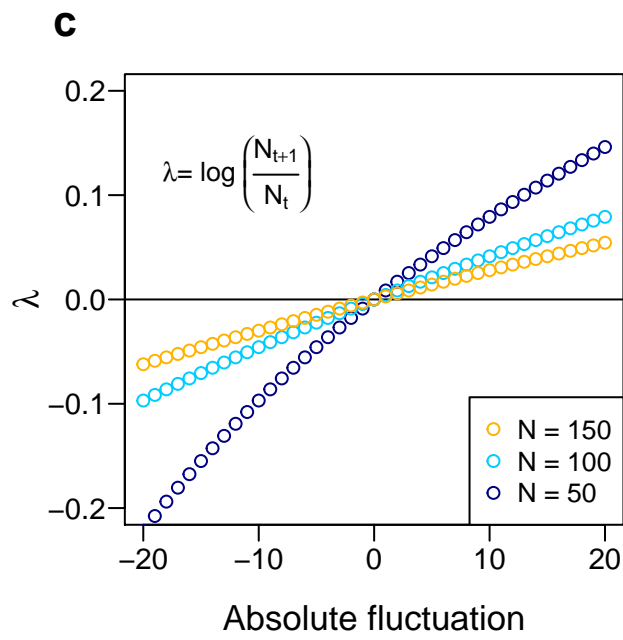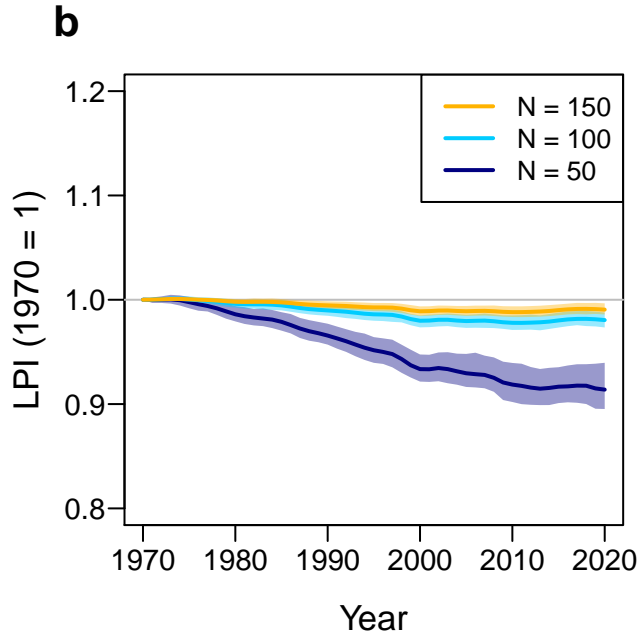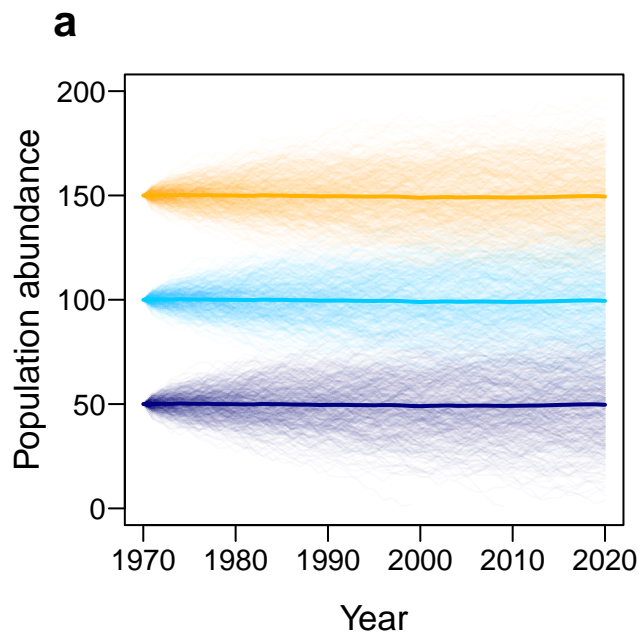
In this equation, time is standardised so that the first year in the times-series is 0 and the final year is 1; and parameter d controls the shape of the trajectory, which is concave-up for $d < 1$, linear for $d = 1$, and concave down for $d > 1$[38]. We simulated three general shapes by setting d to 0.2, 1 and 5 for concave-up, linear and concave-down trajectories respectively. We simulated 500 populations of unique species and added random noise to each annual population estimate, with the exceptions of the first and last values in the time-series to ensure that all time-series started and ended at the same population values. We simulated two fluctuation scenarios for each trajectory shape: a low fluctuation scenario, where error was randomly drawn from a normal distribution with a mean = 0 and a standard deviation = 1; and a high fluctuation scenario where the random normal variable was from a distribution with mean = 0 and standard deviation = 7. These standard deviation values represent the lowest (e.g. temperate grassland populations, where lower 95% confidence interval = 1 %) and highest (e.g. montane freshwater populations, where upper 95% confidence interval = 7.5 %) estimates of empirical fluctuations in the Living Planet Database[15]. We calculated the LPI for all six sets of 500 populations (three trajectory shapes and two levels of random noise), which all had identical starting and ending populations and should, therefore, have identical ending LPI. This entire process was also replicated for populations that increased from a starting population size of N_0 = 100 in the year 1970, to a final population of N_F = 160 in 2020 (results shown in Extended Data Fig. 4).
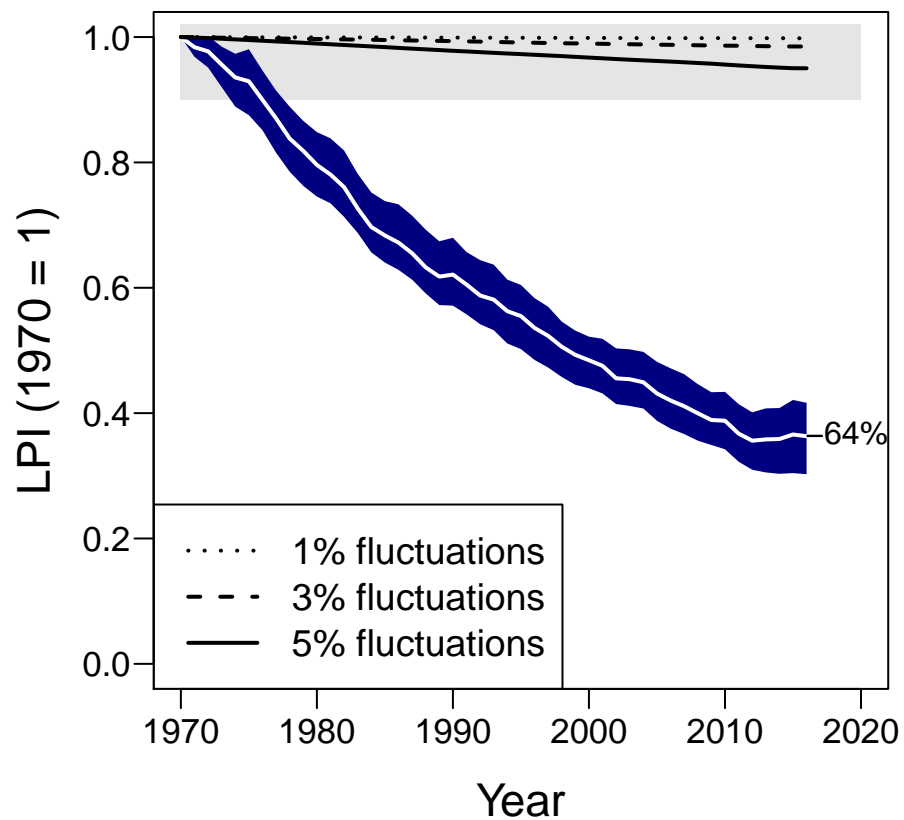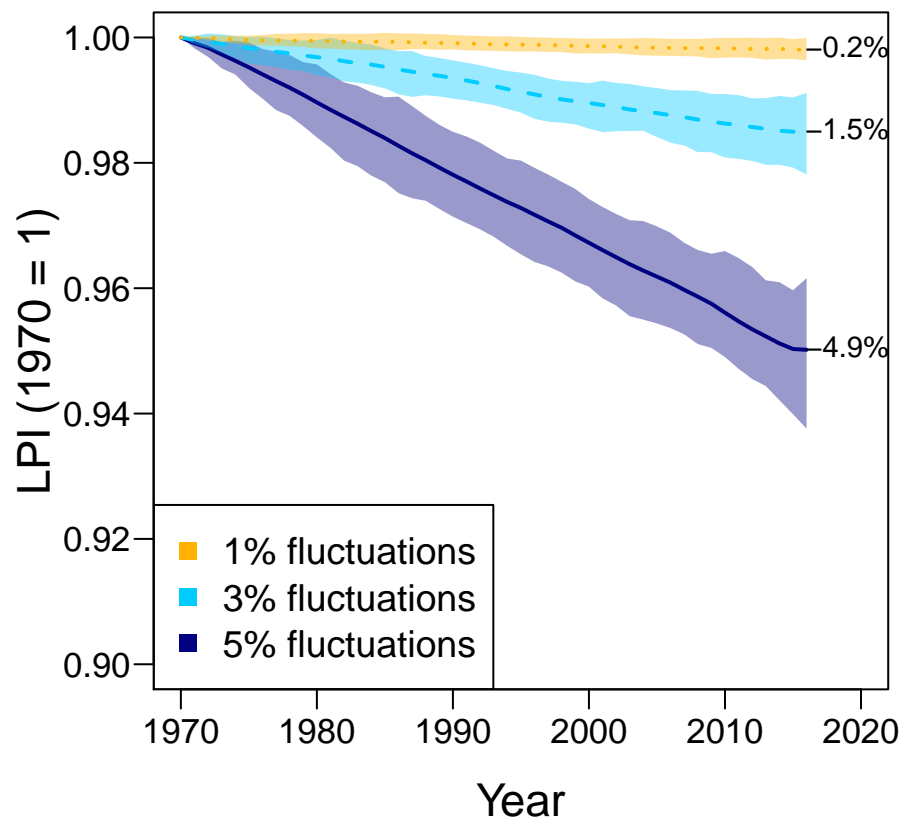
Reshuffling null model to account for the effects of random population fluctuations
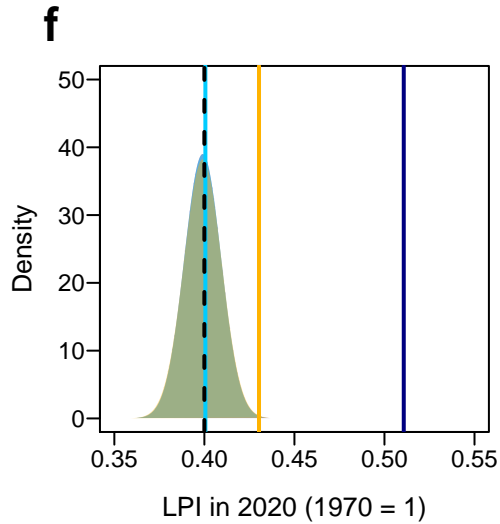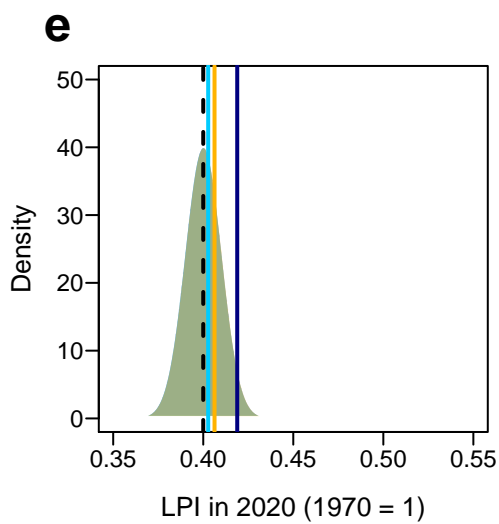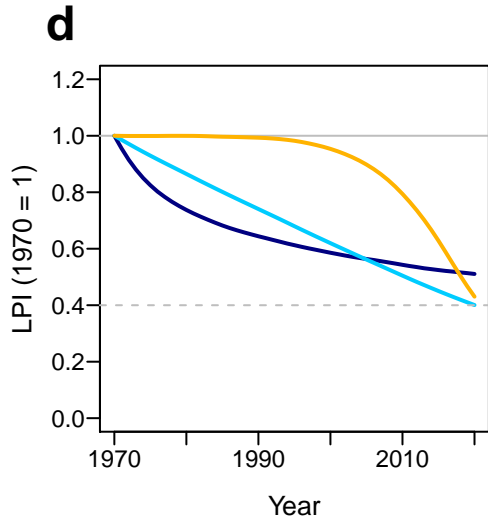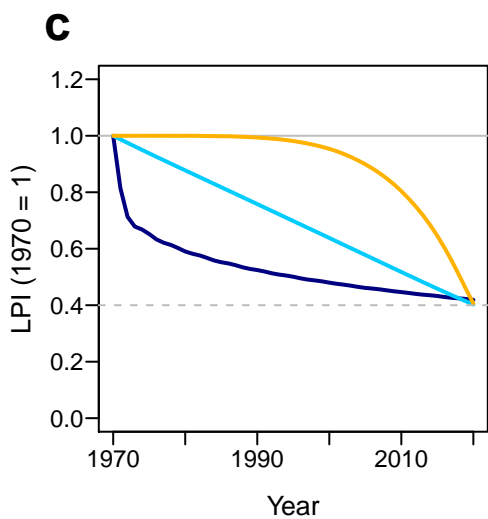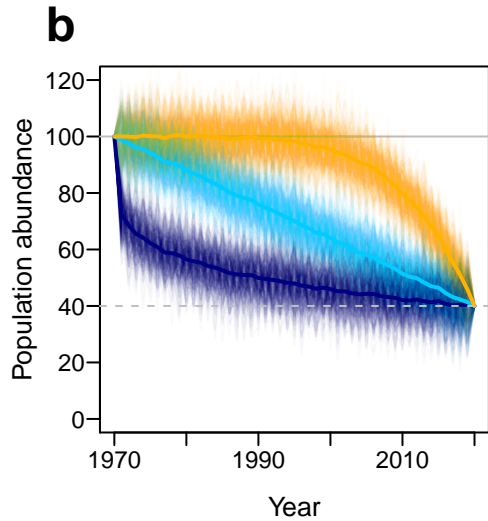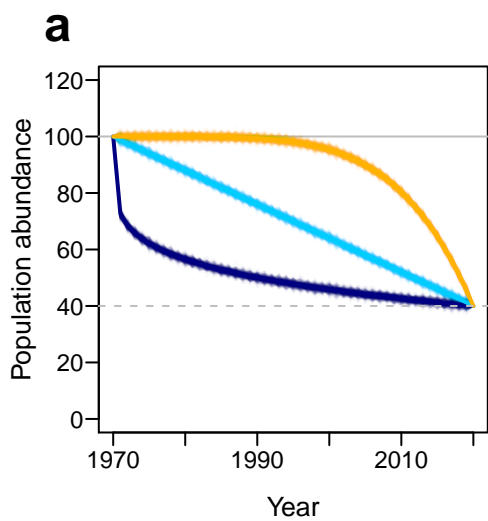
We developed a reshuffling null model to account for the effect of random fluctuations on declining populations (Extended Data Fig. 7). The rationale for this null model was that maintaining the starting- and ending-populations while rearranging the trajectories of population time-series would average out the effects of imprecise GAM estimates across multiple iterations. Moreover, reshuffling population time-series would result in declines that, on average, approximated linear trajectories (Extended Data Fig. 7d), which were less sensitive to the effects of random fluctuations (Extended Data Figs. 5 and 6).

In the null model we calculated the incremental differences between subsequent population measures (i.e. $\Delta_1 = N_2 - N_1; \Delta_2 = N_3 - N_2...$) (Extended Data Fig. 7a), which represented a distribution of incremental population changes (Extended Data Fig. 7b). We then randomly sampled this distribution of Δ, without replacement, to simulate a time-series with identical starting and ending-populations, but with a randomised trajectory (Extended Data Fig. 7c). For time-series with non-monotonic trajectories, reshuffling could lead to temporary negative population sizes (i.e. if the order of a large increase and subsequent decline was reversed in a small population). In these rare instances, we completed the simulation, after which we removed the years with negative populations because λ cannot be calculated for negative populations. We repeated this for each population and calculated the LPI in the final year. By iterating the process 100 times, we generated a distribution of final LPI values that were approximately linear (Extended Data Fig. 7d).
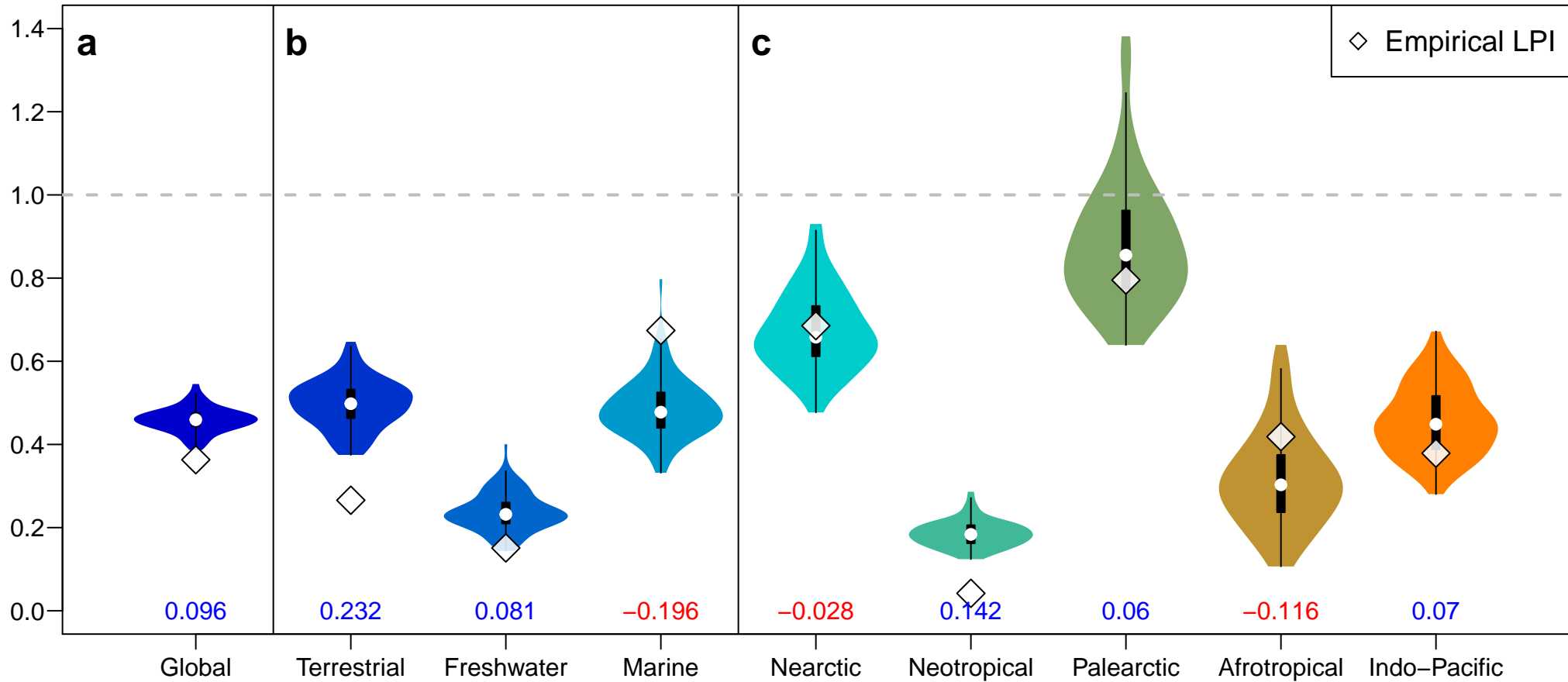
We first tested this reshuffling null model on the six sets of simulated population time-series (Fig. 3 e,f for six sets of decreasing populations & Extended Data Fig. 4 e,f for six sets of increasing populations), which confirmed that the null model produced more accurate estimates of the LPI for time-series that changed non-linearly with large annual population fluctuations. We then applied this null model to the empirical LPI by reshuffling the trajectories of all 15,348 time-series in the Living Planet Database and calculating the final LPI in 2016 for the global dataset, three planetary systems (terrestrial, freshwater and marine), as well as the five biogeographical realms for the terrestrial and freshwater systems (Nearctic, Neotropics, Palearctic, Afrotropics, Indo-Pacific). This entire process was iterated 100 times to produce a distribution of final LPI values, all of which had identical starting and ending population sizes as the empirical LPI, but population trajectories that approximated a linear decline over the 100 iterations.
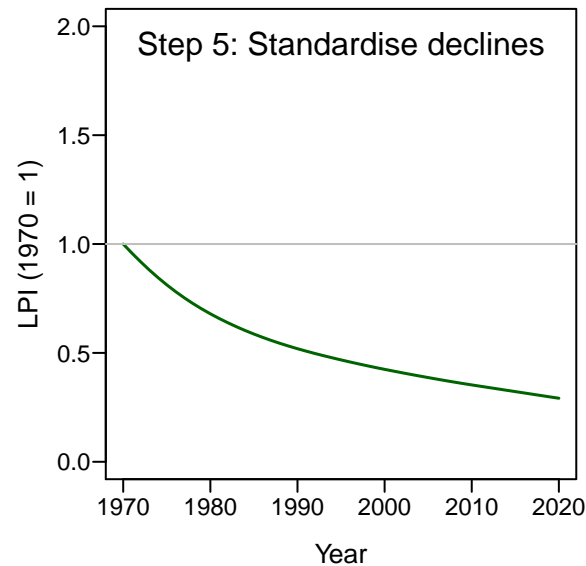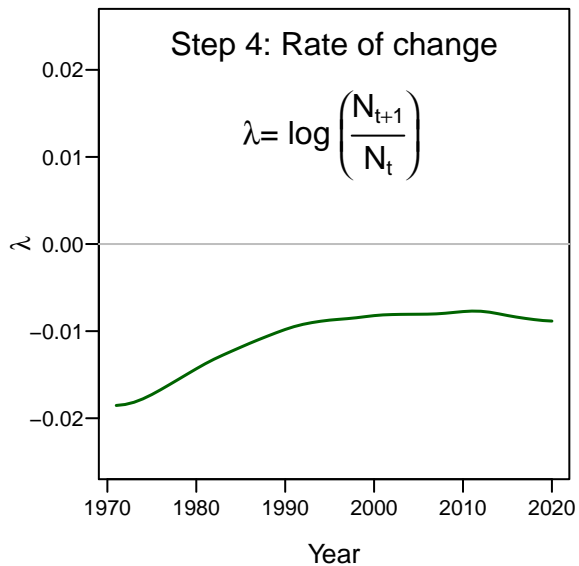
a

Population abundance

Year

b

LPI (1970 = 1)

Year

N = 150
N = 100
N = 50

c

$\lambda = \log\left(\dfrac{N_{t+1}}{N_t}\right)$

λ

Absolute fluctuation

N = 150
N = 100
N = 50

d

Starting population

Average fluctuation

LPI
1.0
0.9
0.8
0.7
0.6

0.5% 1% 2% 3% 4%

a

b

Step 1: Single population trend — Population abundance vs Year

Step 2: Model trend using GAM — log10(Population) vs Year

Step 3: Sequential change — Population vs Year

Step 4: Rate of change

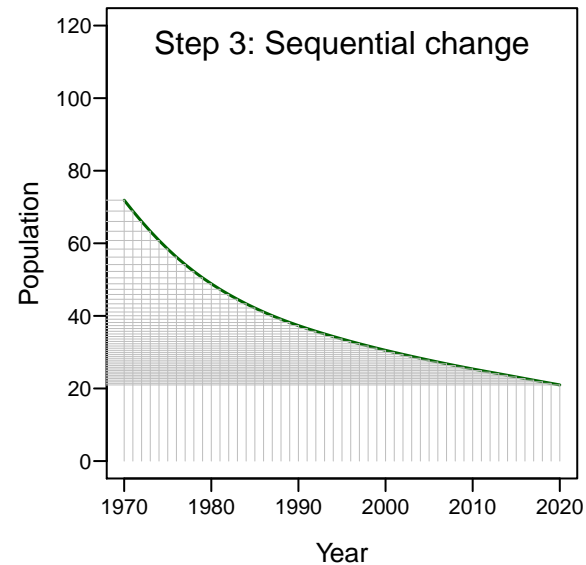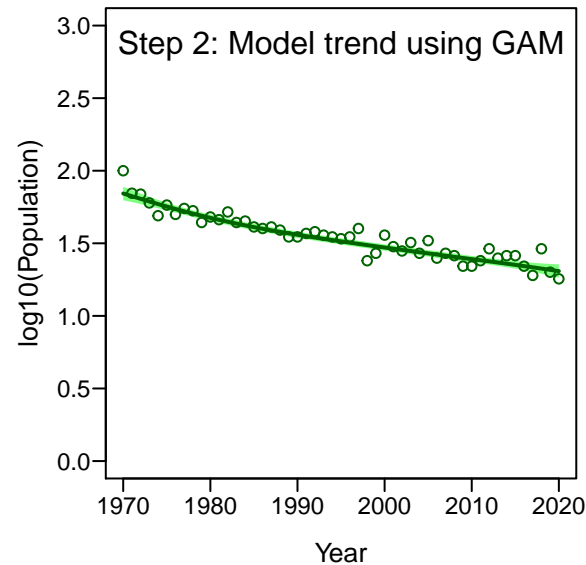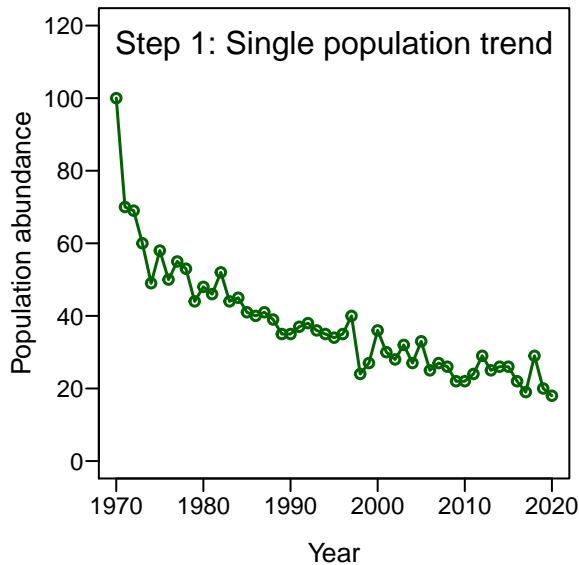$$\lambda = \log\left(\frac{N_{t+1}}{N_t}\right)$$

Step 5: Standardise declines — LPI (1970 = 1) vs Year

Steps 6–9: Aggregate data

Geometric mean across populations

Geometric mean across vetebrate classes (with weighting)

Geometric mean across biogeographical regions (with weighting)

Geometric mean across realms (equal weighting)

a Population trend

b

c Reshuffled trend

d Iterated 100 times

One iteration — — Mean trend

a Density vs Regression slope

b Density vs Mean λ, where $\lambda = \log\left(\frac{N_{t+1}}{N_t}\right)$

c Density vs Cumulative λ, where $\lambda = \log\left(\frac{N_{t+1}}{N_t}\right)$