



Random population fluctuations bias the Living Planet Index

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The Living Planet Index (LPI) is a standardized 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 nonlinearly. We applied randomization 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. Randomization 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 targets⁴. 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 Report⁸.

In addition to being widely reported by the popular press, the LPI has developed a notable 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 Services⁹, the most authoritative synthesis of policy-relevant biodiversity science. Similarly, the index was also used in the Global Biodiversity Outlook Report 5 (ref. 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 century². There is, therefore, considerable policy inertia behind the LPI.

Despite the LPI's broad influence, it has several known caveats^{11,12}. First, since each time series is standardized 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 summarized 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 populations¹².

Third, the LPI weighs time series before 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. Standardization is necessary because abundance is often estimated from indices of varying units (for example, densities or breeding pairs) and because populations may be naturally common or rare (although it has been shown that weighing subpopulations in proportion to their contribution to the global population of a species does not affect the LPI qualitatively⁶). The geometric mean accommodates multiplicative population dynamics, where averages may be distorted by exponentially increasing populations¹³. Finally, weighting is necessary to account for misleading estimates caused by incomplete data coverage⁷ 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 (standardization, 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 Report¹⁶ 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.

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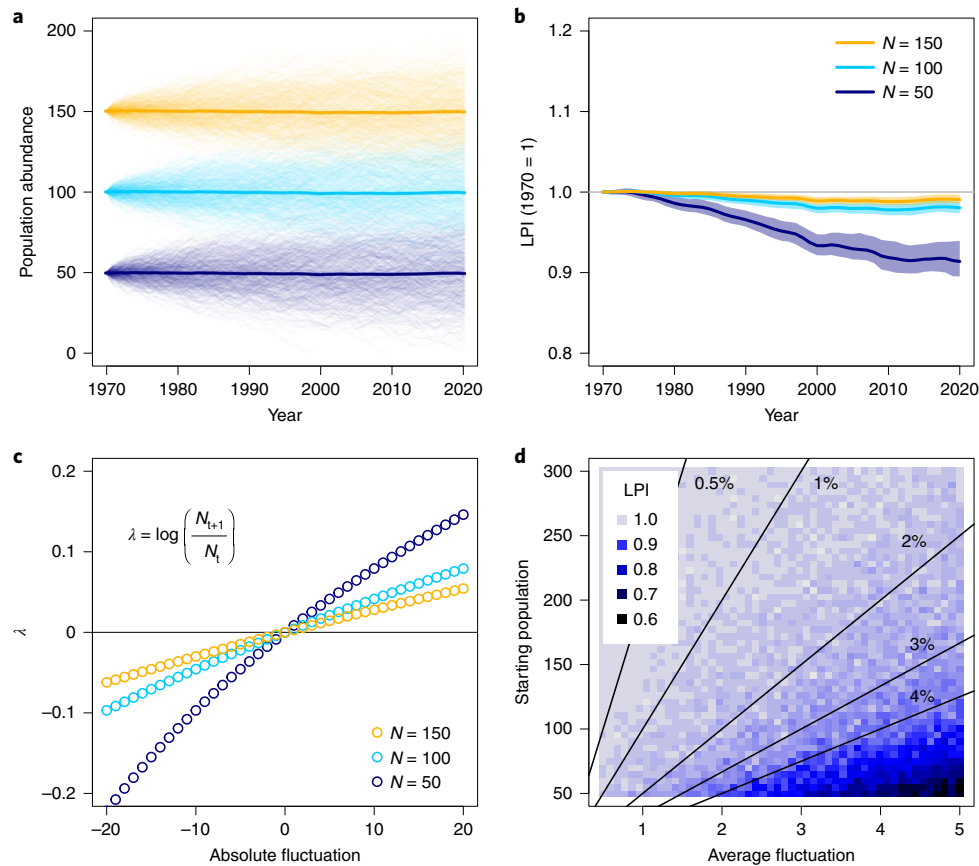


Fig. 1 | Fluctuating, but otherwise stable, populations lead to a declining LPI. **a**, Three sets of 500 populations each (fine lines) that fluctuate randomly by two individuals on average each year but which are stable on average (thick lines). The sets are identical except for their starting populations ($N=50$, 100, 150). **b,c**, The LPI declines for these sets of populations even when they are stable on average (**b**) because fluctuations upwards or downwards cause asymmetrical estimates of λ , which are exaggerated in smaller populations (**c**). **d**, The effect of fluctuations on the LPI 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).

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 that demographic stochasticity is often treated as a synonym for ecological drift¹⁸). By contrast, environmental stochasticity leads to asymmetrical positive and negative population fluctuations because randomness causes variability in multiplicative birth or death rates²⁰. 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 colleagues¹⁵ 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 (~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 species¹⁵. 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 (that is, 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 population fluctuations on the LPI when populations do show increasing or decreasing tendencies? This identifies whether stochasticity overestimates 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

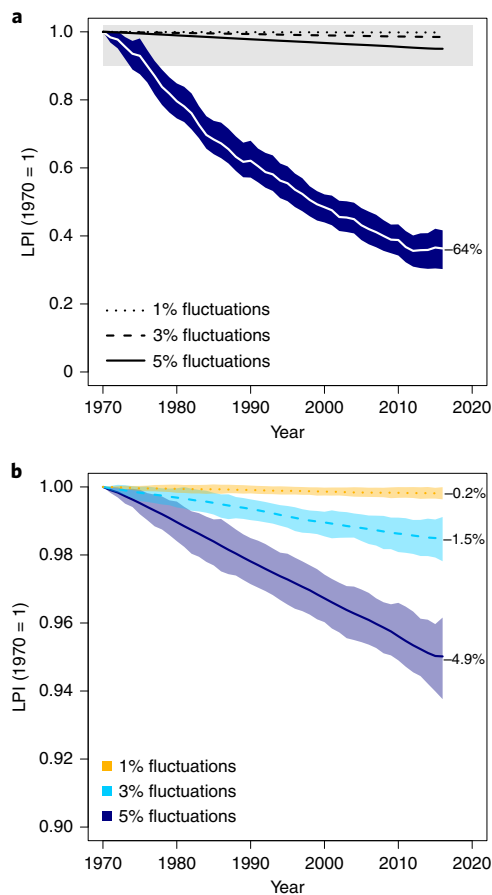


Fig. 2 | Larger random fluctuations in otherwise stable populations lead to greater declines in the empirical LPI. **a**, The Global LPI (mean and 95% confidence intervals) between 1970 and 2016 compared against declining counterfactuals caused by random fluctuations of 1, 3 and 5% in otherwise stable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

simulations by as much as 8% over 50 yr (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 (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 <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 (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 Report⁸ but this is because we

used the public dataset, which excludes several private time series (Methods).

A null model with 1% annual random fluctuations resulted in a global LPI decline by 2016 of only 0.2% (s.d. = 0.3%) (Fig. 2b). When fluctuations increased to 3% in the null model, the LPI in an otherwise stable populations declined by 1.5% (s.d. = 0.8%), while annual fluctuations of 5% reduced the LPI by 4.9% (s.d. = 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 $6.4 \pm 0.2\%$ 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 trajectories²³ 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 nonlinear trajectories (Fig. 3b,d). This is probably an artefact introduced by the Generalized Additive Models (GAM) used to smooth population trends and interpolate missing data when calculating the LPI (Methods, Supplementary Appendix and Extended Data Figs. 5 and 6). Random population fluctuations cause the GAM to underestimate the curvature of nonlinear 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 randomized the order of incremental changes to the population (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 averages out any artefacts introduced when fitting the GAM to nonlinear 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. 3e,f and Extended Data Fig. 4e,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

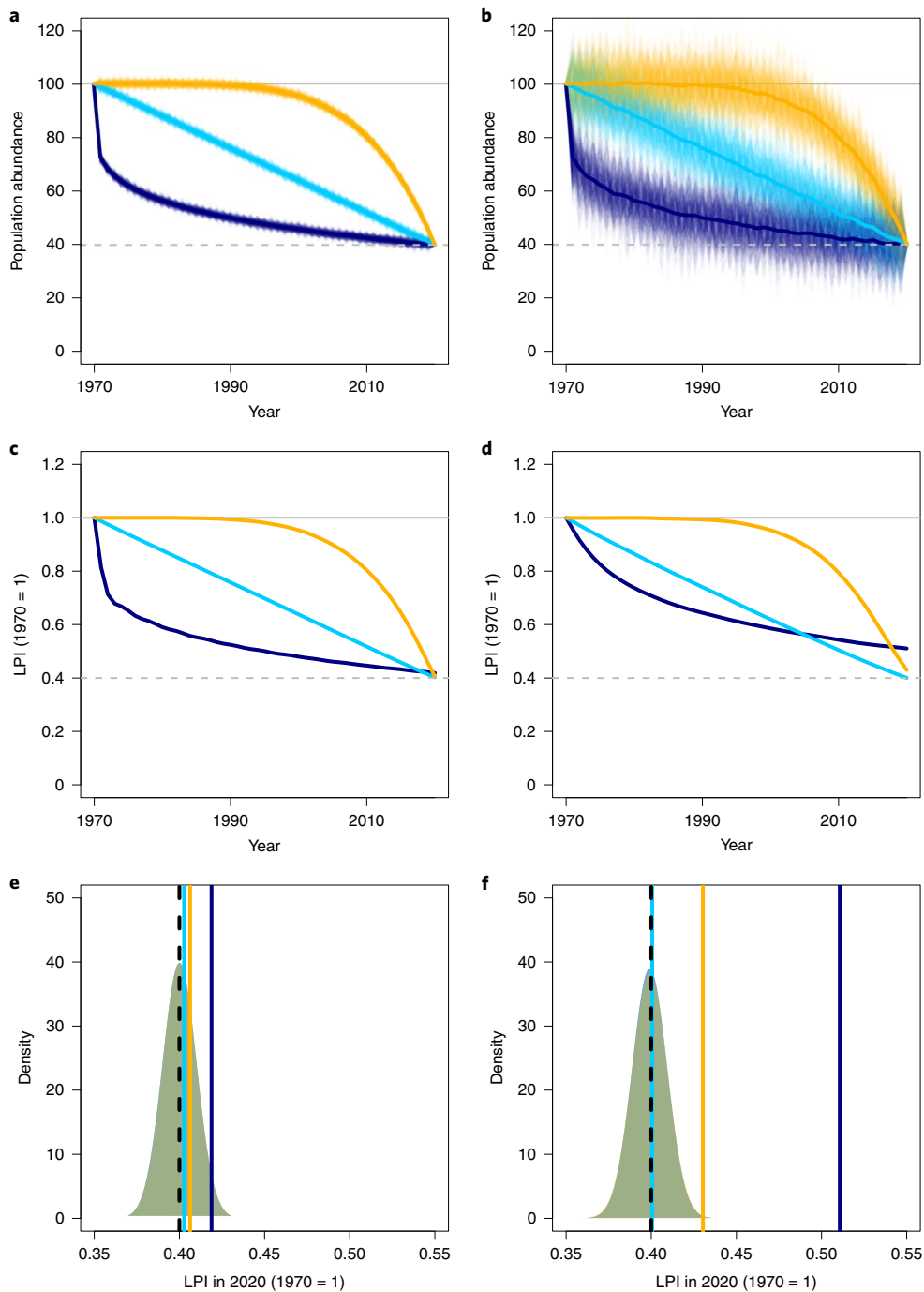


Fig. 3 | Larger population fluctuations cause less precise estimates of the LPI in nonlinear population trajectories. **a,b**, Simulated sets of populations each with 500 species that decline from 100 to 40 individuals along concave-up, linear and concave-down trajectories with low (**a**) and high (**b**) population fluctuations. **c,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,f**, The LPI in the final year of the simulation, 2020, for populations with low (**e**) and high (**f**) fluctuations. 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.

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%), Palaearctic (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 Framework³ lists as one of the milestones for 2030 (Goal A.2) that ‘the abundance

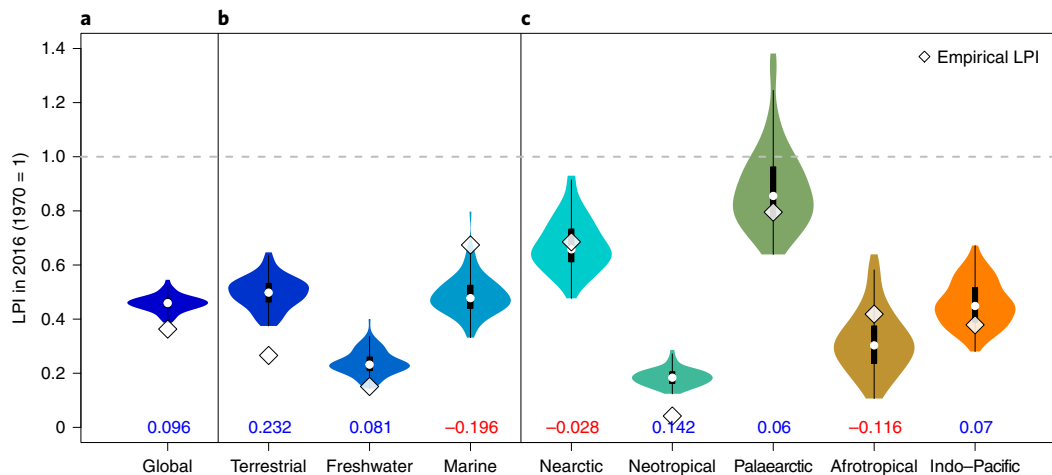


Fig. 4 | Random population fluctuations cause the misestimation of the LPI compared to a reshuffling null model. Violin plots show the distribution of final mean LPI values in 2016 from 100 iterations of a null model that randomizes the order of incremental population changes between time-steps, while maintaining starting and ending population sizes. **a–c**, 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).

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 most species¹². 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 equal¹⁶.

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 standardized between 0 and 1 (ref. ¹⁵) or square-root transformed population data (ref. ²⁷). These transformations 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 population²⁸, 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. 9a). In this example, the LPI approaches 0.4 as new data are collected (Extended Data Fig. 9d), while the mean rate of decline becomes smaller as new survey data are 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. 9b,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 decades³¹. 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 cognizant of the effect of random fluctuations on the LPI (Figs. 1 and 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 probably around 2.2–2.8% (ref. ¹⁵). However, these estimates are strongly right-skewed across populations and may be higher for smaller populations and for threatened species¹⁵. 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 Convention on Biological Diversity's mid-century goals). Instead, we recommend using a range of fluctuations to simulate multiple scenarios of stable, but fluctuating, populations (for example, 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 (1) incrementally adding new time series of rare populations to the Living Planet Database (Extended Data Fig. 3); (2) real population declines caused by human pressures; or (3) smaller population sizes used for national or subregional LPI

calculations (for example, ref. 34). This last 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 Report⁸, 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 (Extended Data Figs. 5 and 6). 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 randomized null models (for example, 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 society². 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.

Methods

A brief overview to calculating the LPI. While others have explained the details of the LPI⁷, 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 v.3.6.2 (ref. 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 Report⁸. 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 (for example, 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 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 standardizing population trends by setting the value in 1970 to one and calculating subsequent trends using the annual changes, λ , through time. Annual changes are summarized across all populations of the same species using the geometric mean (step 6). These standardized 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 on the basis of the total number of species of each vertebrate class per biogeographical realm⁷. 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 (that is, 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 :

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

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

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

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

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

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 (that is, 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 ($N = 50, 100$ and 150 ; mean $\Delta = 2$; Fig. 1a–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 increments of 0.1) (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%) populations¹⁵. 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 biases⁷. This entire stochastic process was iterated 100 times for each of the three levels of fluctuation (1, 3 and 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 $N_t = 40$ 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 standardized 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 $d > 1$ (ref. 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 s.d. = 1; and a high fluctuation scenario where the random normal variable was from a distribution with mean = 0 and s.d. = 7. These standard deviation values represent the lowest (for example, temperate grassland populations, where lower 95% confidence interval = 1%) and highest (for example, montane freshwater populations, where upper 95% confidence interval = 7.5%) estimates of empirical fluctuations in the Living Planet Database¹⁵. 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 (that is, $\Delta_1 = N_2 - N_1$; $\Delta_2 = N_3 - N_2$...) (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 randomized trajectory (Extended Data Fig. 7c). For time series with non-monotonic trajectories, reshuffling could lead to temporary negative population sizes (that is, 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. 3e,f for six sets of decreasing populations and Extended Data Fig. 4e,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 nonlinearly 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, Palaearctic, Afrotropics and 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.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

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 <https://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 <https://doi.org/10.5281/zenodo.4744533>.

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Author contributions

F.T.B. led the simulation and analysis, with conceptual inputs from J.G.H., L.S. and B.W.T.C. F.T.B. wrote the first draft, while J.G.H., L.S. and B.W.T.C. revised subsequent drafts for framing, clarity and technical correctness.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41559-021-01494-0>.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41559-021-01494-0>.

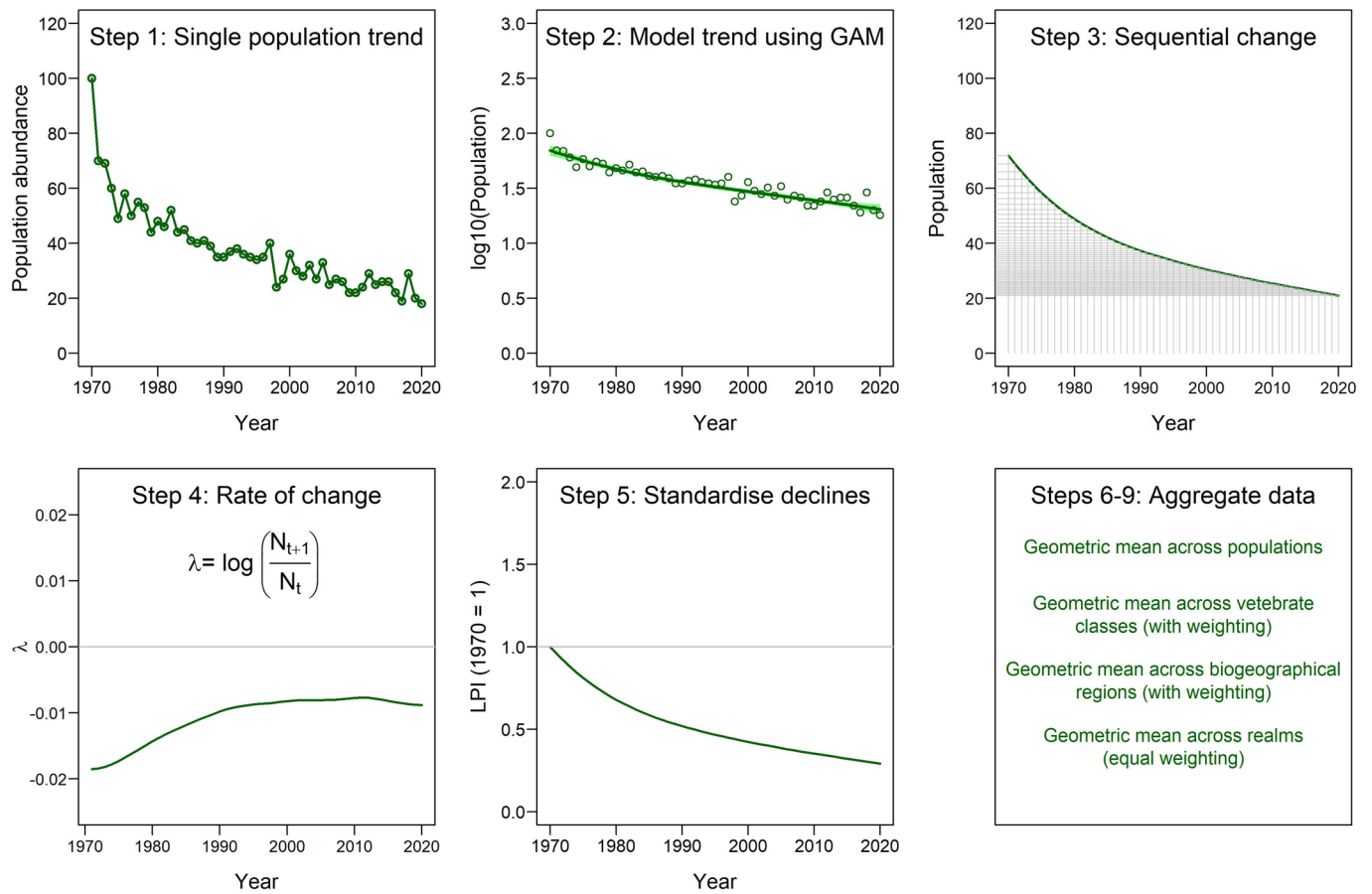
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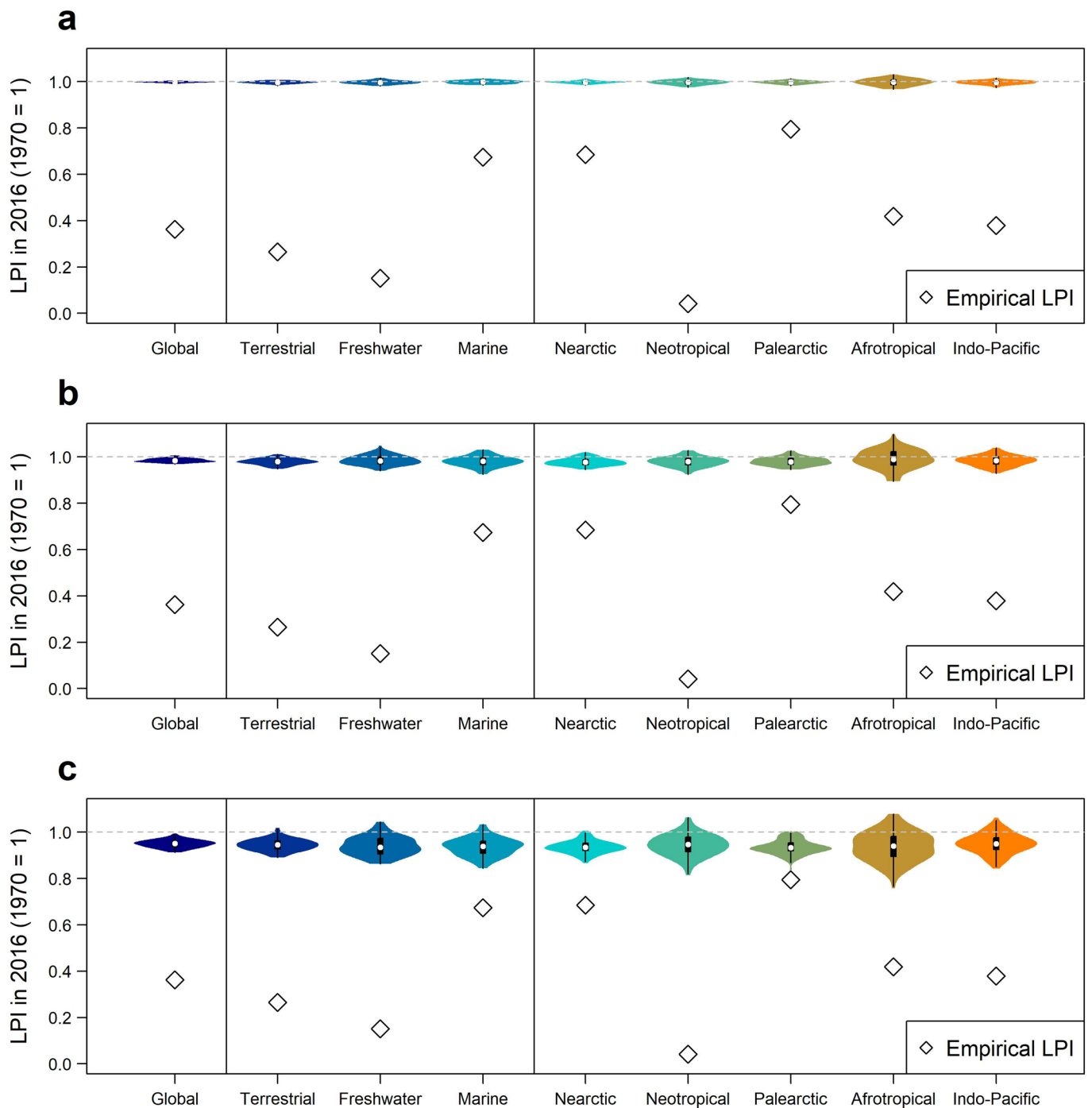
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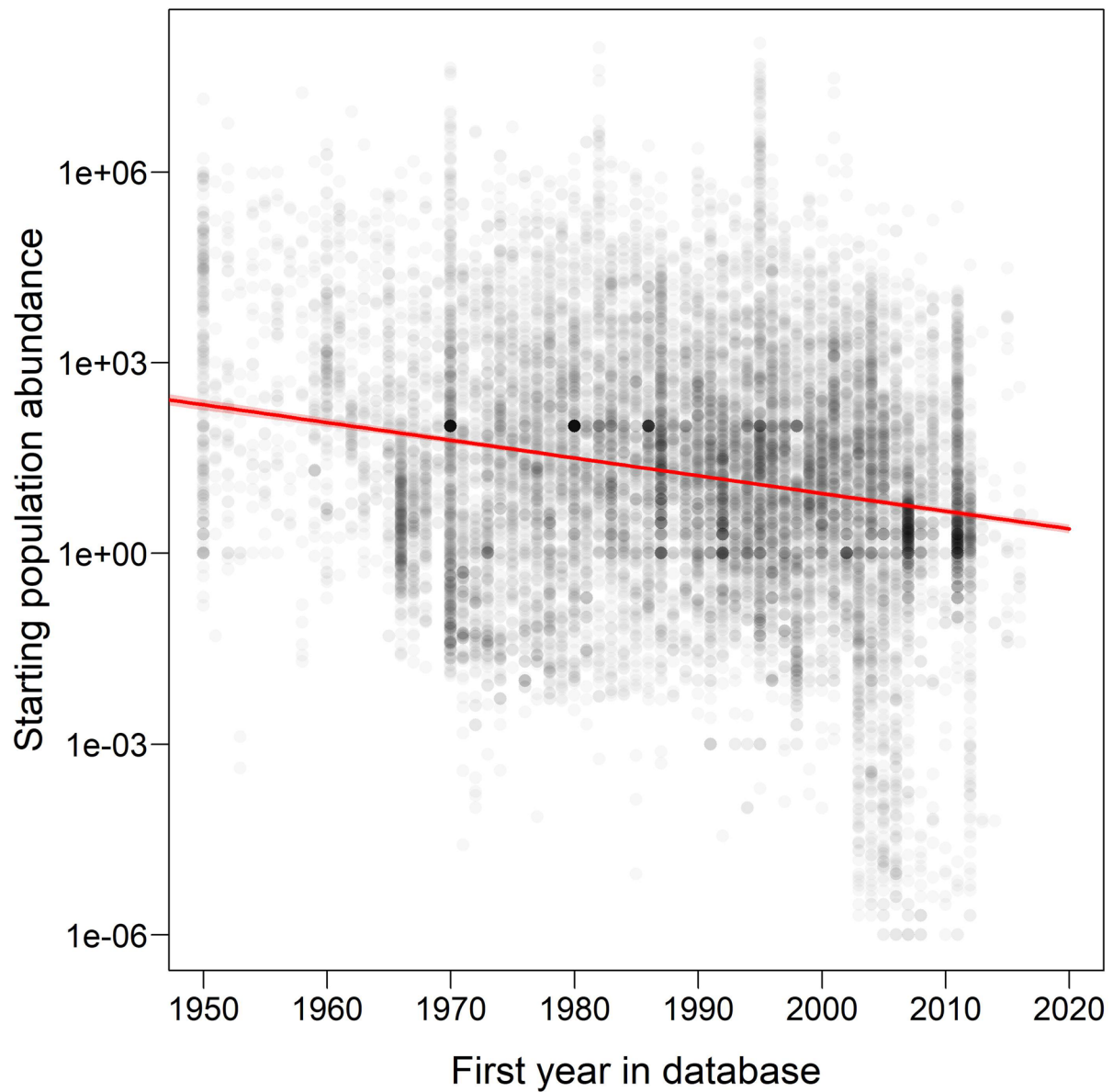
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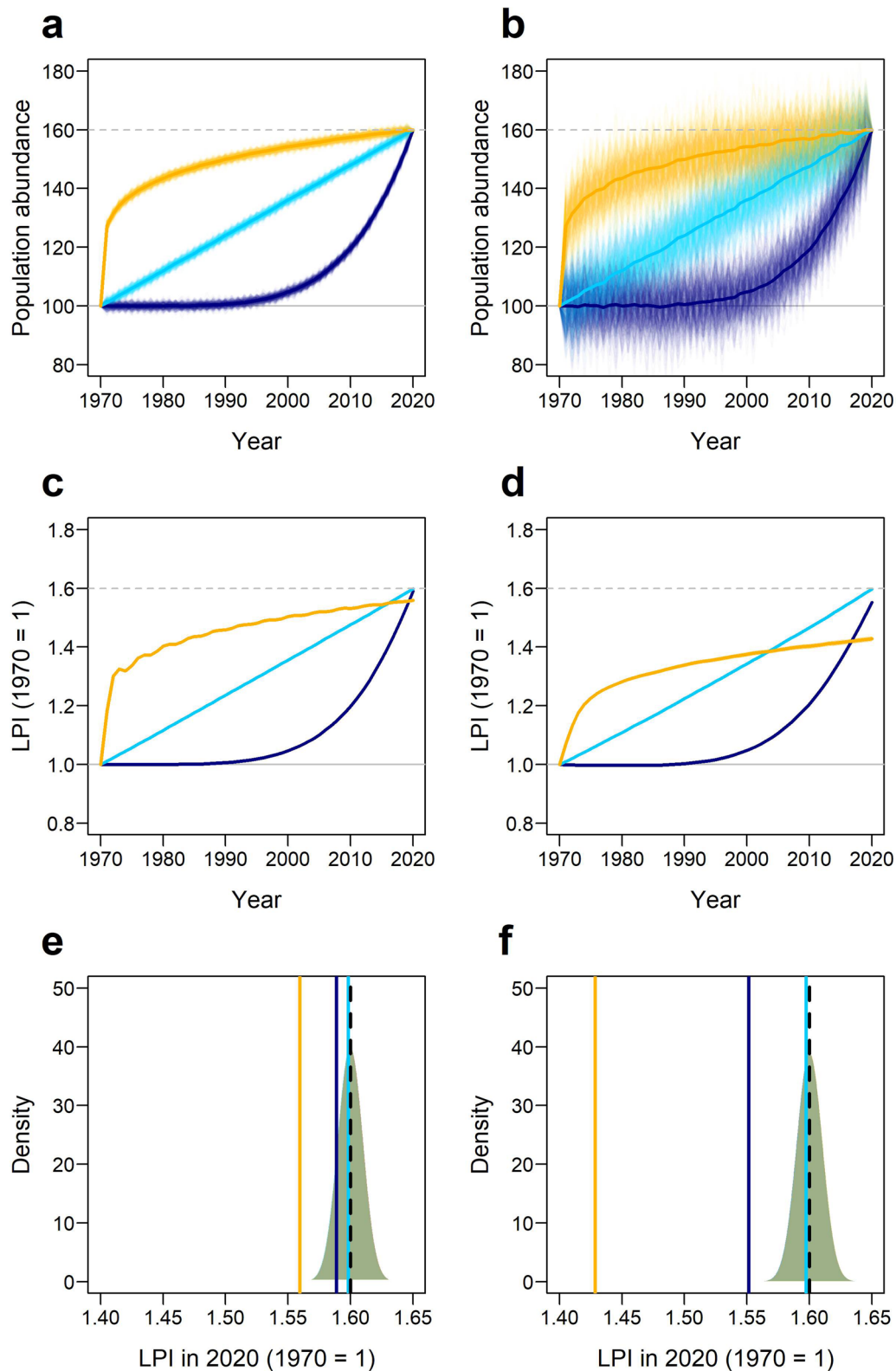
Extended Data Fig. 1 | The nine steps to calculating the Living Planet Index (LPI). Calculating the LPI begins with individual population time series (step 1), which are smoothed and interpolated using a Generalized Additive Model (GAM) on \log_{10} -transformed population measures (step 2). Annual changes are quantified from the GAM prediction (step 3) and summarized as λ , the \log_{10} -transformed ratio of population sizes in subsequent years (step 4). The population trends are standardized, by setting the population size in 1970 as 1 (step 5), and these standardized trends are averaged across populations of the same species using the geometric mean (step 6). Averaged species trends are aggregated across vertebrate classes (step 7) and biogeographical regions (step 8), using weightings that account for taxonomic and geographical differences in species richness⁷. Finally, the global LPI is the equal-weighted average of the LPIs from terrestrial, freshwater and marine systems (step 9).



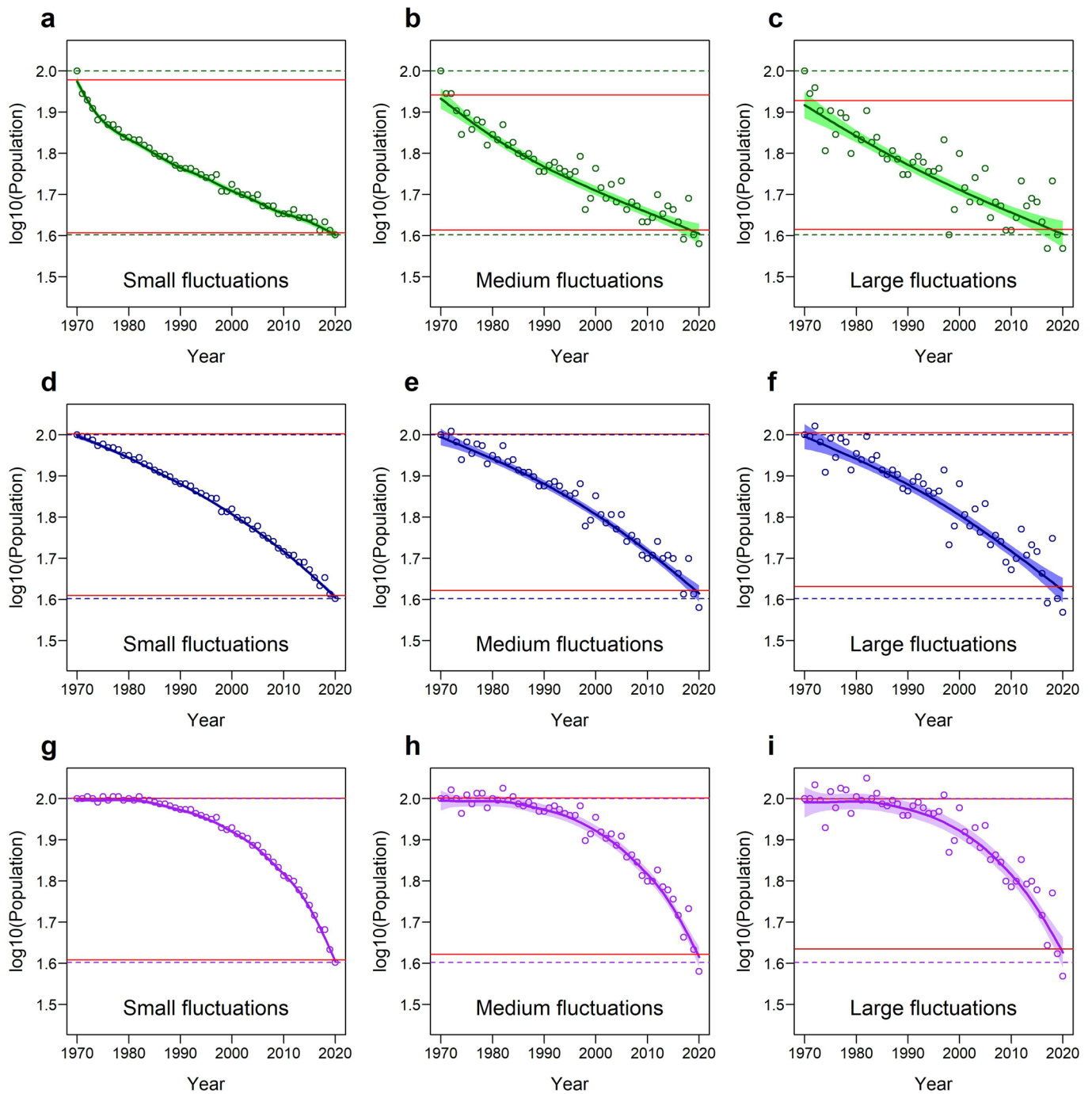
Extended Data Fig. 2 | The Living Planet Index (LPI) for randomly fluctuating populations that are stable on average. Empirical estimates of the LPI are consistently lower than stable time series with the same starting population, but which fluctuate by 1% (**a**), 3% (**b**) and 5% (**c**) each year. Violin plots show the distribution of LPI values from 100 iterations, with white circles representing mean LPI across all iterations of the null model and white diamonds showing the empirical LPI. Data are for the global, terrestrial, freshwater and marine LPI, as well as the LPI for each biogeographical realm.



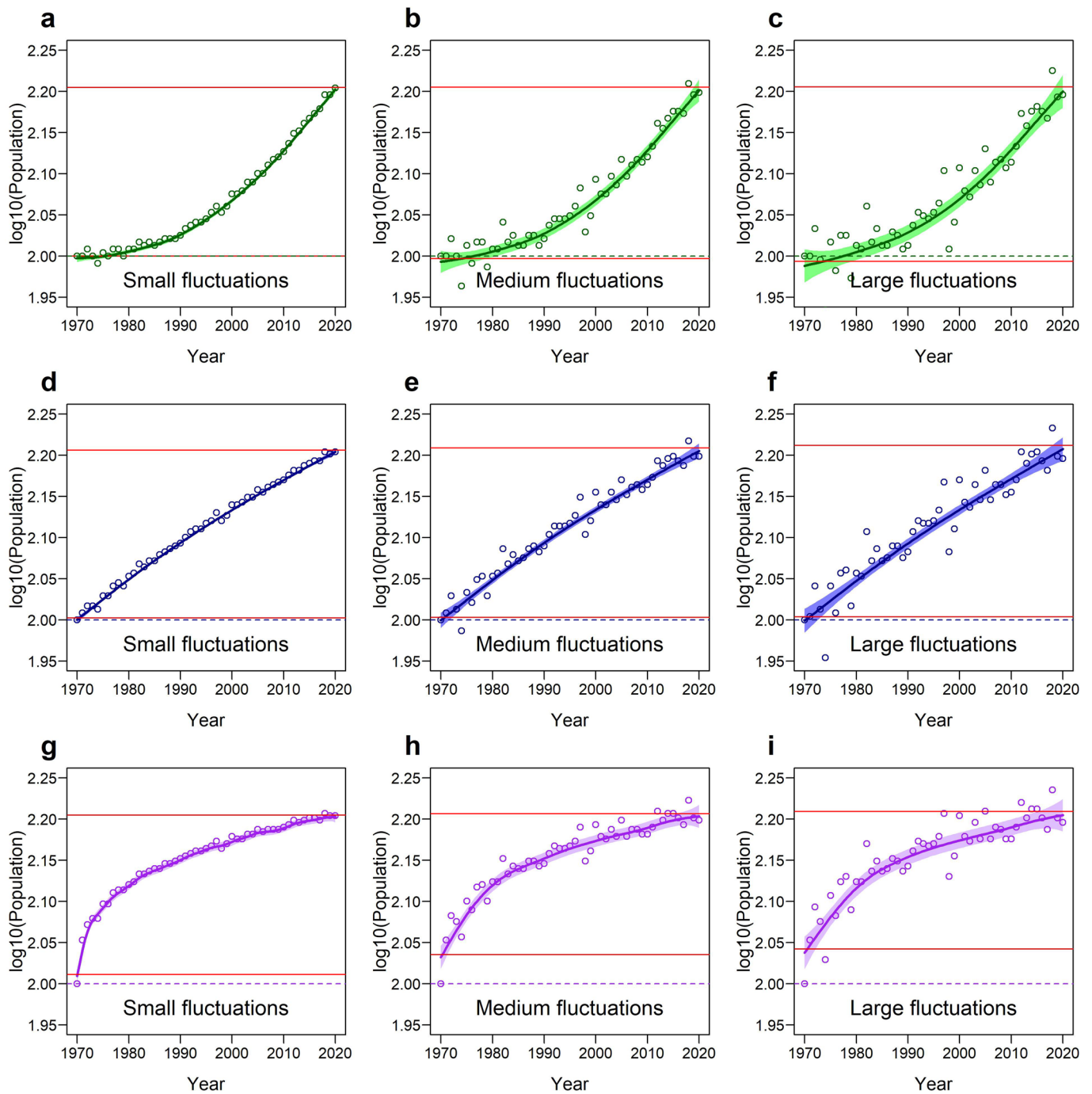
Extended Data Fig. 3 | Starting population sizes of time series added to the Living Planet Index have declined between 1950 and 2015. Each point is the initial population size of a time series for the first year in which it was monitored. The red line is the linear regression of the natural logarithm of population sizes through time. The vertical axis is ln-scaled.



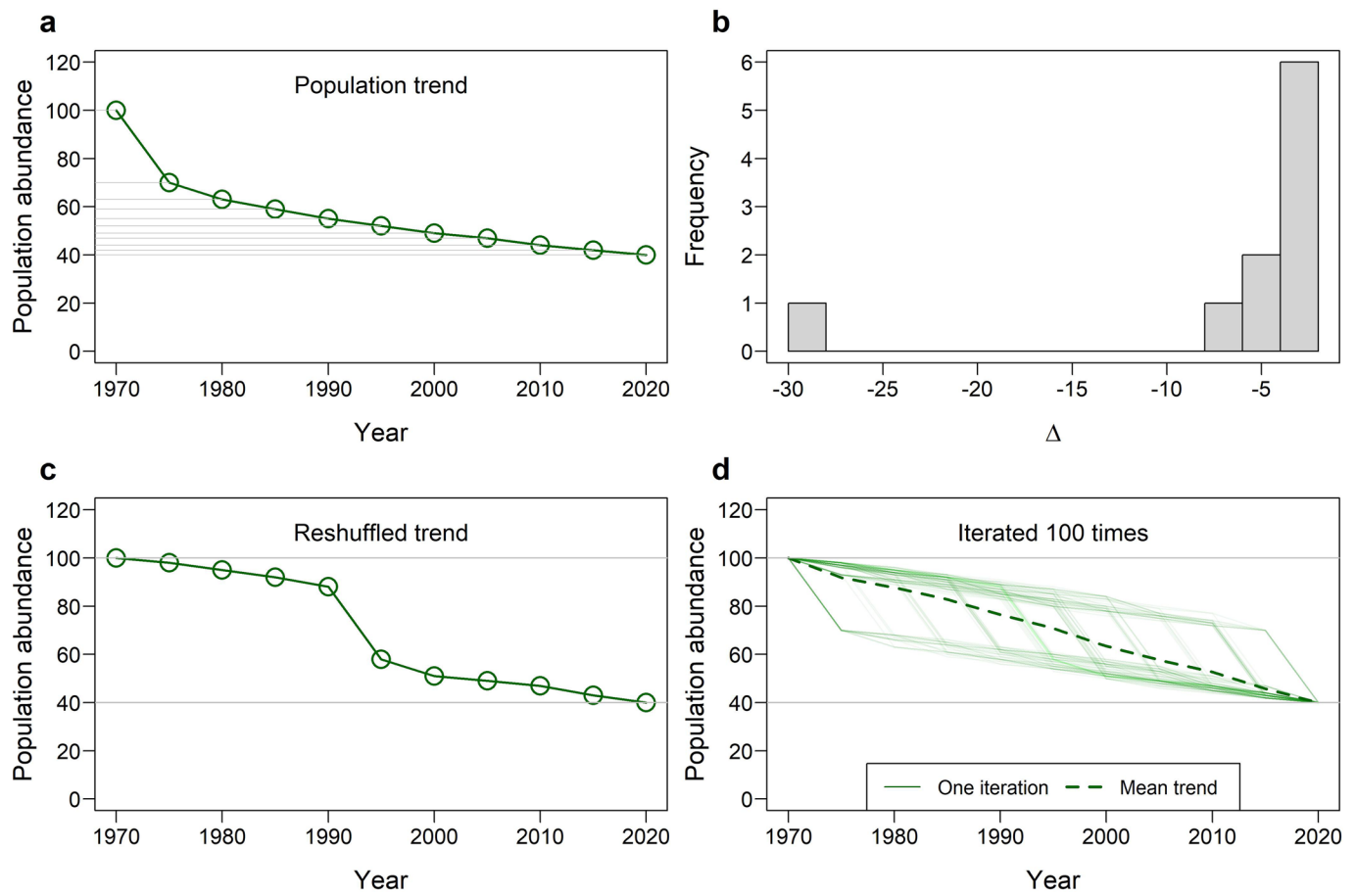
Extended Data Fig. 4 | Larger population fluctuations cause less precise estimates of the Living Planet Index (LPI) in nonlinear population trajectories. **a** and **b**, Simulated sets of populations each with 500 species that increase from 100 to 160 individuals along concave-up, linear and concave-down trajectories with low (**a**) and high (**b**) population fluctuations. **c** and **d**, The accompanying trends in LPI for increasing 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, coloured vertical 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.



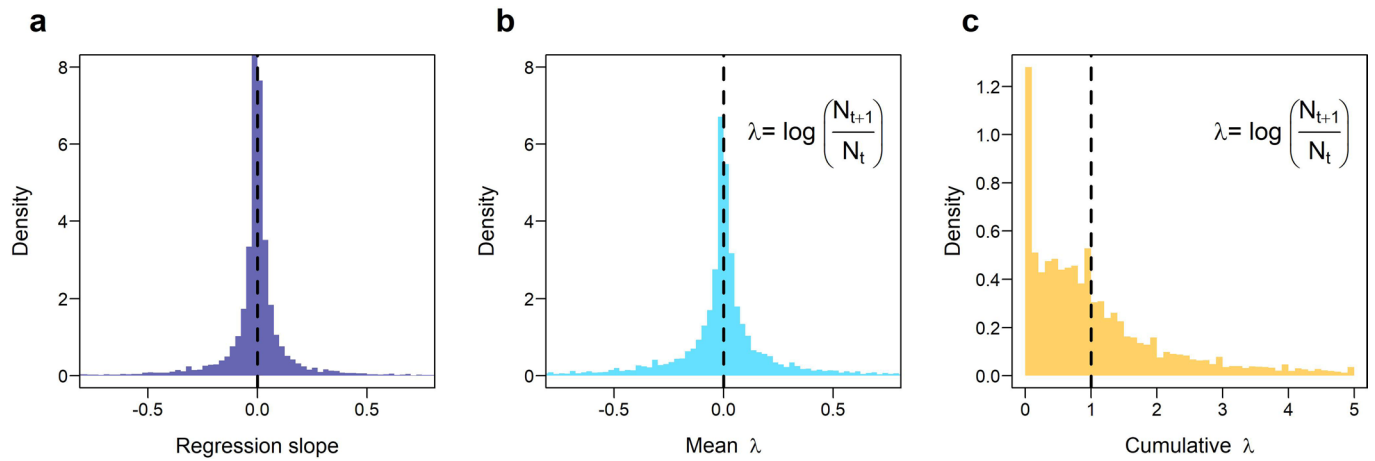
Extended Data Fig. 5 | Population fluctuations cause generalised additive models (GAM) to misestimate starting and ending populations when populations decrease from 100 to 40 individuals. GAM models fit to populations declining along concave-up (a–c), linear (d–f) and concave-down (g–i) trajectories and low ($sd = 1$: a, d, g), medium ($sd = 4$: b, e, h), and high ($sd = 7$: c, f, i) levels of population fluctuations. In all panels, the horizontal dashed lines show the actual starting and ending populations, while the solid red lines denote the starting and ending populations estimated from the GAM.



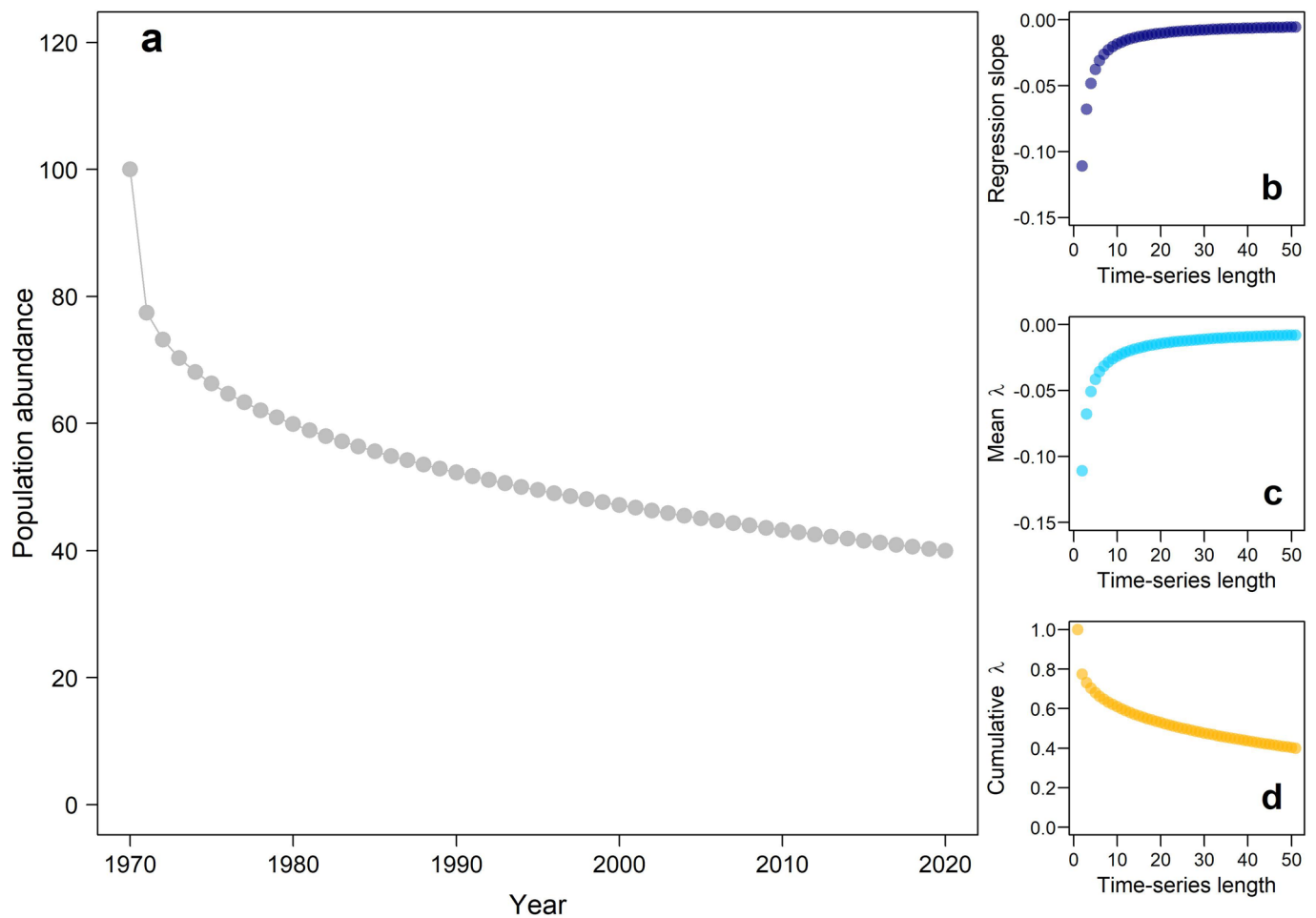
Extended Data Fig. 6 | Population fluctuations cause generalised additive models (GAM) to misestimate starting and ending populations when populations increase from 100 to 160 individuals. GAM models fit to populations declining along concave-up (a–c), linear (d–f) and concave-down (g–i) trajectories and low ($sd = 1$: a, d, g), medium ($sd = 4$: b, e, h), and high ($sd = 7$: c, f, i) levels of population fluctuations. In all panels, the horizontal dashed lines show the actual starting and ending populations, while the solid red lines denote the starting and ending populations estimated from the GAM.



Extended Data Fig. 7 | The reshuffling null model used to account for random population fluctuations. **a**, The incremental changes in an empirical time series (Δ) were used to identify, **b**, a distribution of Δ values. **c**, The reshuffled trajectory was simulated by sampling from the distribution of Δ , without replacement, to simulate a time series with identical starting and ending populations as the empirical time series (horizontal grey lines). **d**, Iterating this 100 times generated a series of trajectories (light green lines), which have a mean trajectory that approximates a linear decline (dashed green line).



Extended Data Fig. 8 | Cumulative population declines can occur in the Living Planet Index even when average population declines are zero. **a**, Fitting linear regressions to log₁₀-transformed population time series in the Living Planet Database produces a normal distribution of regression slopes centred on zero, where increases and decreases are equally likely across the 15,348 time series. **b**, Similarly, calculating population changes as the mean of year-on-year changes, $\lambda = \log_{10}\left(\frac{N_{t+1}}{N_t}\right)$, also produces a normal distribution centred on zero, with increases and decreases equally likely. **c**, However, calculating cumulative population changes as the sum of year-on-year changes, $\lambda = \log_{10}\left(\frac{N_{t+1}}{N_t}\right)$, produces a right-skewed distribution (here populations are scaled as in the Living Planet Index, so that starting values are 1). This is because the sum and mean of population changes do not scale proportionally when population trajectories are nonlinear (see discussion in main text).



Extended Data Fig. 9 | Cumulative population changes represent empirical trajectories more accurately than average changes as time series lengths increase. **a**, The trajectory of a hypothetical population that decreases nonlinearly from 100 individuals in 1970 to 60 individuals by 1980 and steadily settles to a new equilibrium of 40 individuals by 2020. **b**, If population changes were quantified as the slope of a linear regression on \log_{10} -transformed population data, declines are high when the time series is short, but tend to zero as new data is added to the time series. **c**, The same observation holds for mean year-on-year population changes, $\lambda = \log_{10}(N_{t+1}/N_t)$, where declines are dramatic at first and steadily tend to zero as the length of the time series increases. **d**, By contrast, cumulative year-on-year population changes, $\lambda = \log_{10}(N_{t+1}/N_t)$, accurately capture the hypothetical population trajectory because the population change in each subsequent year is added to the change from preceding years. Thus, measuring cumulative population change is more representative when population trajectories settle into alternative equilibria nonlinearly.

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Simulated data were generated using R version 3.6.2. Empirical population time-series data (in .csv format) were manually downloaded from the dedicated website maintained by the Zoological Society of London: <http://stats.livingplanetindex.org/>.

Empirical data were filtered into subsets for planetary systems (terrestrial, freshwater and marine), taxonomic classes, and biogeographical realm using R version 3.6.2. All R-scripts are open and freely available on a dedicated Zenodo repository: <http://doi.org/10.5281/zenodo.4744533>

The data in the public version of the Living Planet Database contains population information aggregated from 3,146 independent studies (cited in the database under the column titled 'Citation'). Data includes total population counts, abundance estimates, population densities, population indices, proxies of abundance (e.g. breeding pairs, tracks, nests, burrows), measures per unit effort, biomass. More information on the data collection is available from: <http://stats.livingplanetindex.org/>

Data analysis

All data analysis was carried out in R version 3.6.2 and all code is available from the dedicated Zenodo repository: <http://doi.org/10.5281/zenodo.4744533>

To calculate the Living Planet Index, we used the dedicated package 'rlpi' (v. 0.1.0), which was developed and maintained by the Zoological Society of London. This package is not available on the official CRAN repository, but can be accessed from the Github repository: <https://github.com/Zoological-Society-of-London/rlpi>

Other data analysis included linear regression ('lm' function in 'stats' package v. 4.0.4) and Generalized Additive Models, GAM ('gam' function in 'mgcv' package v 1.8.33). All code is fully annotated on the dedicated Zenodo repository (<http://doi.org/10.5281/zenodo.4744533>). Besides these, other analyses did not use inferential statistics, relying on descriptive statistics instead.

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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/>) as outlined by the Data Use Policy by the Indicators & Assessments Unit at the ZSL and WWF International.

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Study description

This study combines simulations, empirical population time-series, and null models to examine how random population fluctuations affect the calculation of the Living Planet Index.

QUESTION 1: EFFECT OF FLUCTUATIONS ON OTHERWISE STABLE POPULATIONS

For simulated data, we simulated the time-series of sets of 500 different species using R version 3.6.2. These simulations assumed that populations were stable on average but fluctuated along a random walk. In these simulations, populations fluctuated randomly between 0.5 and 5 individuals on average at intervals of 0.1 (magnitudes of fluctuations were based on previous published data, cited in the manuscript) and starting populations were arbitrarily selected from 50 to 300 individuals in intervals of 10 intervals. The Living Planet Index was calculated for each set of simulated time-series.

For empirical data, population time-series data were from the publicly available Living Planet Database (<http://stats.livingplanetindex.org/>). Starting population sizes and starting year of monitoring were extracted from the empirical data, but random fluctuations in these populations were randomly simulated across separate simulations where fluctuations were 1%, 3% or 5% per year (100 iterations each) using R version 3.6.2. The Living Planet Index was calculated for each set of simulated time-series.

QUESTION 2: EFFECT OF FLUCTUATIONS IN INCREASING OR DECREASING TIME-SERIES

For simulated data, we simulated the time-series of sets of 500 different species using R version 3.6.2. These simulations assumed that populations either increased from 100 to 160 individuals or decreased from 100 to 40 individuals. These time series were varied to change along concave-up, linear, or concave-down trajectories. Sets of simulations were replicated for two levels of fluctuations: either 1 individual per year on average (low fluctuation) or 7 individuals per year on average (high fluctuations). The Living Planet Index was calculated for each set of simulated time-series.

We simulated a null model that reshuffled the sequences of population changes in time-series. Thus, the cumulative change was unchanged, but the order of incremental changes was reshuffled. After iterating this reshuffling model 100 times, the time-series approximated linear trajectories. The Living Planet Index was calculated for each iteration of reshuffled time-series. For simulated data, the Living Planet Index from reshuffled null models quantified overall population changes more accurately than the simulated data with random fluctuations.

The same reshuffling null model was applied to empirical data on population time-series from the publicly available Living Planet

	Database (http://stats.livingplanetindex.org/).
Research sample	<p>The Living Planet Database includes 15,348 population time-series. The completeness of this sample, the inclusion criteria and the geographic and taxonomic bias of this database are described on the dedicated website maintained by the Zoological Society of London: http://stats.livingplanetindex.org/</p> <p>The data have taxonomic and geographic biases as outlined in: "WWF. Living Planet Report 2020. Bending the curve of biodiversity loss: a deep dive into the Living Planet Index. (World Wide Fund for Nature, 2020)".</p>
Sampling strategy	<p>We used all 15,348 time-series in the Living Planet Database from 4,182 different species.</p> <p>For parts of the manuscript, we calculated the Living Planet Index for separate subsets of the data. These subsets were for three planetary systems (Terrestrial, Freshwater, Marine) and five biogeographical realms (Nearctic, Neotropics, Palearctic, Afrotropics, Indo-Pacific). These samples were non-random, and were based on the characteristics of the sample time-series (i.e. system and geographic location).</p> <p>For planetary systems, we considered the following sub-samples:</p> <ul style="list-style-type: none"> - Terrestrial: 4,862 time-series from 1,953 species - Freshwater: 3,408 time-series from 918 species - Marine: 7,078 time-series from 1,531 species <p>For biogeographical realms (terrestrial and freshwater only), we considered the following sub-samples (values in parentheses are for terrestrial and freshwater systems, respectively):</p> <ul style="list-style-type: none"> - Nearctic: 2,119 (1,174 & 945) time-series from 815 (530 & 285) species - Neotropics: 1,223 (802 & 421) time-series from 804 (542 & 262) species - Palearctic: 2,691 (1,286 & 1,405) time-series from 656 (400 & 256) species - Afrotropical: 1,060 (825 & 235) time-series from 348 (227 & 127) species - Indo-Pacific: 1,174(772 & 402) time-series from 542(384 & 158) species
Data collection	<p>Simulated data were generated using the scripts available on a dedicated Zendo repository: http://doi.org/10.5281/zenodo.4744533</p> <p>Empirical population time-series were manually downloaded in .csv format from the dedicated website in accordance to the Terms of Use: http://stats.livingplanetindex.org/ Simulated data were generated using R version 3.6.2. Empirical population time-series data (in .csv format) were manually downloaded from the dedicated website maintained by the Zoological Society of London: http://stats.livingplanetindex.org/.</p> <p>The version of the Living Planet Database used in this study was downloaded from the dedicated website on 09 September 2021, after the global publication of the 2020 Living Planet Report.</p> <p>Empirical data were filtered into subsets for planetary systems (terrestrial, freshwater and marine), taxonomic classes, and biogeographical realm using R version 3.6.2. All R-scripts are open and freely available from the dedicated Zenodo repository http://doi.org/10.5281/zenodo.4744533</p> <p>The data in the public version of the Living Planet Database contains population information aggregated from 3,146 independent studies (cited in the database under the column titled 'Citation'). Data includes total population counts, abundance estimates, population densities, population indices, proxies of abundance (e.g. breeding pairs, tracks, nests, burrows), measures per unit effort, biomass. More information on the data collection is available from: http://stats.livingplanetindex.org/</p>
Timing and spatial scale	<p>The spatial scale of this study is global in scope, including terrestrial, freshwater and marine systems. Global coverage is, however, incomplete due to imperfect sampling. Spatial distribution of population time-series are described on the dedicated website: http://stats.livingplanetindex.org/</p> <p>Spatial biases in time-series can be examined by plotting the geographic localities of sample using the "Latitude" and "Longitude" coordinates in the Living Planet Database.</p> <p>The temporal scale of this study was between 1970-2020 for simulated data and 1970-2016 for empirical data, in accordance to the sample completeness in the Living Planet Database. Some empirical time-series started prior to 1970 (but all post-1950) as is shown in Figure S3.</p>
Data exclusions	<p>We excluded no data from the publicly available Living Planet Index. However, this public dataset excludes 5,463 confidential time-series, which cannot be openly shared (presumably due to the preference of the data owners, or due to the sensitivity of the data e.g. critically endangered or illegally traded species)</p> <p>For simulated data, negative population values were excluded because these are not realistic (can't have negative number of animals) and did not allow for the calculation of the Living Planet Index (because negative numbers cannot be log-transformed). These exclusions are described in the methods section of the manuscript.</p>
Reproducibility	<p>All these analyses are reproducible given that the same version of the Living Planet Database is used (this database is constantly upgraded by the Zoological Society of London as new data is available, so it is outside the control of the authors). All code for analyses are available on Zenodo (http://doi.org/10.5281/zenodo.4744533)</p> <p>The random seed for stochastic processes are stated explicitly, so even stochastic simulations should be reproducible if the same seed is used.</p>

Randomization

There was no randomization in this study besides the stochastic simulations. The empirical population time-series are as comprehensive as is possible given the logistical constraints of collecting long-term global data. Spatial and taxonomic biases are explained on the dedicated website (<http://stats.livingplanetindex.org/>) and these sampling biases are controlled for by weighing samples prior to calculating the Living Planet Index (as explained in the methods of the manuscript, especially Figure S1)

Blinding

Blinding was not relevant to our study as there were no observers and, therefore, no observational biases. We used all the publicly available population time-series in the Living Planet Database, which are open, transparent and published previously, so all authors were already aware of the characteristics of these data prior to this study.

Did the study involve field work? Yes No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

- | n/a | Involvement in the study |
|-------------------------------------|--|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Antibodies |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Eukaryotic cell lines |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Palaeontology and archaeology |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Animals and other organisms |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Human research participants |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clinical data |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Dual use research of concern |

Methods

- | n/a | Involvement in the study |
|-------------------------------------|---|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> ChIP-seq |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Flow cytometry |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> MRI-based neuroimaging |