Matters arising **Do not downplay biodiversity loss**

https://doi.org/10.1038/s41586-021-04179-7

Received: 12 January 2021

Michel Loreau^{1⊠}, Bradley J. Cardinale², Forest Isbell³, Tim Newbold⁴, Mary I. O'Connor⁵ & Claire de Mazancourt¹

Accepted: 7 October 2021

ARISING FROM B. Leung et al. Nature https://doi.org/10.1038/s41586-020-2920-6 (2020)

Published online: 26 January 2022

Check for updates

The Living Planet Index (LPI), which seeks to summarize population trends of wildlife, has been used as evidence for current biodiversity loss. Leung et al.¹, reanalysing the LPI data, found that 98.6% of vertebrate populations showed no overall trend, and concluded that "many systems ... appear to be generally stable or improving". Here we show that their methodological approach is ineffective as it would not detect trends in either global warming or continental bird abundance data. Detecting trends in biodiversity requires long-term data, appropriate methods and careful interpretation; otherwise, there is a very serious danger of downplaying biodiversity loss.

Summarizing complex datasets using aggregate indices can hide meaningful variation, and we commend the attempt by Leung et al.¹ to identify sources of temporal variations in the LPI. However, the methodology they devised has limitations that strongly restrict its ability to deliver biologically significant results and conclusions.

First, their methodology uses summary statistics of short-term population changes that are ineffective at detecting long-term trends. To understand why, consider an analogy with climate change. Scientists agree that global warming is taking place currently; indeed, the global annual mean temperature shows a clear historical trend (Fig. 1a). When these same data are plotted as a frequency distribution of annual temperature changes, however, they do not reveal any significant global warming signal (Fig. 1b) because long-term trends are then masked by short-term, year-to-year variability. Logically, analyses of the full time series are much more appropriate than analyses of the statistical properties of its many pieces to detect trends. Yet the methodology of Leung et al.¹ follows the approach shown in Fig. 1b. as it uses the mean and standard deviation of the distribution of year-to-year changes in population abundance as its building blocks (the only difference from the climate change data is that it uses a log-transformed ratio of population abundances, which is appropriate as demographic processes are typically multiplicative). We do not claim that this approach is completely incapable of detecting trends. Rather, we claim that splitting time series into many pieces is not an effective approach for detecting long-term trends, and that failing to detect trends using this approach cannot be held as evidence that no long-term trend exists.

Second, the previous limitation is compounded by the extreme heterogeneity of the LPI data, which is known to limit the reliability of the LPI². Data heterogeneity strongly reduces the ability to detect and interpret trends. Although the sheer number of population time series included in the LPI dataset contributes to enhancing the power of trend detection across populations, their heterogeneity has the opposite effect because it aggregates populations with qualitatively different trends. Data heterogeneity also increases the likelihood of either obtaining unrepresentative trends or misinterpreting them. As a hypothetical but plausible example, suppose that populations in protected areas were increasing in abundance because of effective conservation in these areas and were simultaneously overrepresented in the LPI dataset because they are censused more comprehensively than elsewhere. This would generate an artefactual increasing trend driven by overrepresentation of protected populations. Experts in meta-analyses have repeatedly warned about misinterpretations that can result when authors do not properly control for major sources of heterogeneity among studies³, in particular in datasets that were collected for differing purposes⁴.

Instead of addressing these fundamental issues directly, Leung et al.¹ used a Bayesian hierarchical model that split LPI data into two clusters: a small, homogeneous cluster that isolates strongly declining populations, and a large, heterogenous primary cluster that aggregates all the remaining populations. These two clusters did not result from an objective data analysis; rather, they were dictated by a subjective decision to look for two simplified alternatives, which they called the 'catastrophic declines' and 'clustered declines' hypotheses. Although considering these alternatives might serve as a first step in disaggregating LPI data, the resulting clusters are largely arbitrary and neither cluster provides particularly useful new information on population trends.

The small outlying clusters show a particularly extreme form of population decline, with an average decline of 98% per year. With such a precipitous decline, a large population of five million individuals would go extinct in only four years. We know that many populations go extinct because of factors such as wholesale habitat destruction, but it is unclear whether the small extreme clusters identified in the analysis are representative of such extinctions and how they can help to devise new conservation strategies.

Conversely, the large primary clusters are very heterogeneous, as they include populations that show diverse trends, including populations that increase steeply for a variety of reasons (for example, they might be recovering from previous declines because of successful conservation efforts or they might be invasive species). As steeply declining populations were removed from primary clusters while steeply increasing populations were kept-at least in the main analyses¹-it is unclear what can be learned from the absence of a trend in these clusters. When steeply increasing populations are also removed, the declining trend of the LPI reappears (see 'Clusters, extremes and biodiversity loss' in the 'Data' section of http://stats.livingplanetindex.org/). Most populations (about 94%) in the LPI database show either an increasing or a decreasing trend (see 'Mixture of trends' in the 'Data' section of http://stats.livingplanetindex.org/). Thus, the failure to detect an aggregate trend in primary clusters¹ does not allow any meaningful conclusion to be drawn. This failure clearly does not support the conclusion by Leung et al.1 that the vast majority of populations are not in decline and that biodiversity loss is therefore not as catastrophic as commonly thought.

This optimistic conclusion also stands in marked contrast to many studies that have accumulated evidence for population declines across

¹Theoretical and Experimental Ecology Station, CNRS, Moulis, France. ²Department of Ecosystem Science and Management, Penn State University, University Park, PA, USA. ³Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN, USA. ⁴Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, UK. ⁵Biodiversity Research Centre and Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada. ⁵²e-mail: michel.loreau@gmail.com

Matters arising



Fig. 1|**The methodology adopted by Leung et al.**¹**would not detect global climate change. a**, Changes in the global annual mean temperature anomaly from 1880 to 2019 (data from the Goddard Institute for Space Studies (https://data.giss.nasa.gov/gistemp/)) reveal an exceedingly strong global warming signal (Spearman's rank correlation coefficient between temperature

anomaly and year = 0.88, $P < 10^{-15}$). **b**, When plotted as a frequency distribution of annual changes in global mean temperature (as the LPI does for population abundance), the same data do not detect any global warming signal (mean annual increase of 0.0082 °C, which is not significantly different from zero by a *t*-test (P = 0.38)).

a wide range of taxonomic groups, ecosystems and geographic regions. Declines in vertebrate abundance are not restricted to a few systems in the Indo-Pacific realm, as suggested¹. They are widespread even in Europe and North America, two continents that are losing biodiversity at much lower rates, mostly because they already lost a large part of their native vertebrate fauna centuries or millennia ago. For instance, recent studies have estimated that Europe lost 20% of total bird abundance in 30 years from 1980⁵, while North America lost 29% of total bird abundance in 48 years from 1970⁶. These figures show massive declines of bird abundance on both continents despite the fact that they represent an average loss of only 0.7–0.8% per year. Such a small average loss would probably be swamped by yearly fluctuations in abundance if one were to use annual population change data, and would certainly be drowned in the primary clusters showing no aggregate trend¹. This again shows how deceptive short-term fluctuations in abundance can be.

While new data can certainly bring information to bear that contradicts and even overturns the conclusions of prior studies, it is incumbent on authors to resolve differences in their data, analyses and conclusions to prior work before suggesting that other scientists may have exaggerated the biodiversity crisis. The optimistic conclusion of Leung et al.¹ not only stands in conflict with more rigorously designed studies that have used data appropriate for measuring biodiversity change, but they run the risk of generating misinformation for conservation efforts.

We suggest that two important conclusions can be drawn here. First, population decline and biodiversity loss are long-term processes, which need to be assessed using appropriate methods. Detecting trends in biodiversity requires long-term data⁷, and thus a reliable and coordinated global biodiversity observation system⁸, which is still sorely missing. Data analyses need to account for known sources of heterogeneity and representativity biases. Current trends should be interpreted carefully and compared with baseline historical data whenever possible, as is common practice with climate change.

Second, Leung et al.¹ claimed that their results "provide a reason to hope that our actions can make a difference". Hope, however, will not come from downplaying biodiversity loss—hope will come only from new perspectives and approaches to resolve the current biodiversity crisis once the seriousness of this crisis has been fully acknowledged.

Reporting summary

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

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-021-04179-7.

Data availability

Data used to produce Fig. 1 are freely available from https://data.giss. nasa.gov/gistemp/.

- Leung, B. et al. Clustered versus catastrophic global vertebrate declines. Nature 588, 267–271 (2020).
- McRae, L., Deinet, S. & Freeman, R. The diversity-weighted Living Planet Index: controlling for taxonomic bias in a global biodiversity indicator. *PLoS ONE* 12, e0169156 (2017).
- Koricheva, J. & Gurevitch, J. Uses and misuses of meta-analysis in plant ecology. J. Ecol. 102, 828–844 (2014).
- Cardinale, B. J., Gonzalez, A., Allington, G. R. H. & Loreau, M. Is local biodiversity in decline or not? A summary of the debate over analysis of species richness time trends *Biol. Conserv.* 219, 175–183 (2018).
- Inger, R. et al. Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecol. Lett.* 18, 28–36 (2015).
- Rosenberg, K. V. et al. Decline of the North American avifauna. Science 366, 120–124 (2019).
- Gonzalez, A. et al. Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. *Ecology* 97, 1949–1960 (2016).
- Scholes, R. J. et al. Toward a global biodiversity observing system. Science 321, 1044–1045 (2008).

Acknowledgements M.L. and C.d.M. acknowledge support from the TULIP Laboratory of Excellence (ANR-10-LABX-41).

Author contributions M.L. designed the work and wrote the first draft of the manuscript. C.d.M. analysed the climate change data. All authors contributed to idea development and manuscript revisions.

Competing interests The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41586-021-04179-7.

Correspondence and requests for materials should be addressed to Michel Loreau. Reprints and permissions information is available at http://www.nature.com/reprints. Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s), under exclusive licence to Springer Nature Limited 2022

nature portfolio

Corresponding author(s): Michel Loreau

Last updated by author(s): Sep 16, 2021

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our <u>Editorial Policies</u> and the <u>Editorial Policy Checklist</u>.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.		
n/a	Cor	nfirmed
		The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
\boxtimes		A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
		The statistical test(s) used AND whether they are one- or two-sided Only common tests should be described solely by name; describe more complex techniques in the Methods section.
\boxtimes		A description of all covariates tested
\boxtimes		A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
\boxtimes		A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
		For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted Give P values as exact values whenever suitable.
\ge		For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
\boxtimes		For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
\boxtimes		Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
	1	Our web collection on <u>statistics for biologists</u> contains articles on many of the points above.

Software and code

Policy information about <u>availability of computer code</u>		
Data collection	(R 4.0.3	
Data analysis	R 4.0.3	

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

- All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:
 - Accession codes, unique identifiers, or web links for publicly available datasets
 - A description of any restrictions on data availability
 - For clinical datasets or third party data, please ensure that the statement adheres to our policy

Data used to produce Fig. 1 are freely available from https://data.giss.nasa.gov/gistemp/.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences Behavioural & social sciences K Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see <u>nature.com/documents/nr-reporting-summary-flat.pdf</u>

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Matters Arising from Leung et al. (2020), no new study, except the analysis of climate change data in Fig. 1.
Research sample	The only sample used is the climate change data used in Fig. 1, which are freely available.
Sampling strategy	No sampling strategy.
Data collection	No data collection.
Timing and spatial scale	N/A
Data exclusions	No data exclusions.
Reproducibility	N/A
Randomization	N/A
Billuaing	
Did the study involve field	d 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

Palaeontology and archaeology

Animals and other organisms

Human research participants

Dual use research of concern

Involved in the study

Eukaryotic cell lines

Clinical data

Antibodies

n/a

 \boxtimes

 \boxtimes

 \boxtimes

 \boxtimes

 \boxtimes

 \boxtimes

n/a	Invo
\boxtimes	
\boxtimes	

Methods

n/a	Involved in the study
\boxtimes	ChIP-seq
\boxtimes	Flow cytometry

\boxtimes	MRI-based	neuroimaging
-------------	-----------	--------------

Matters arising

Reply to: Do not downplay biodiversity loss

https://doi.org/10.1038/s41586-021-04180-0

Brian Leung^{1,2}[⊠], Anna L. Hargreaves¹, Dan A. Greenberg³, Brian McGill⁴, Maria Dornelas⁵ & Robin Freeman⁶

Published online: 26 January 2022

Check for updates

REPLYING TO M. Loreau et al. Nature https://doi.org/10.1038/s41586-021-04179-7 (2022)

In the accompanying Comment¹, Loreau et al. present two main criticisms of our article²: (1) that because annual population fluctuations are high and declines gradual, only 'long-term' time series can be trusted; and (2) that heterogeneity in the Living Planet Database (LPD) makes it more difficult to interpret aggregate trends. The first criticism is based on a simple statistical misunderstanding, and the second argument is a main point that is addressed in the original article² and –explicitly–by the Bayesian hierarchical mixture (BHM) model. Nonetheless, we agree these issues are worth discussing, and ultimately reinforce the use of BHM and the conclusions of our paper².

To illustrate the issue of long-term time series, Loreau et al.¹ compare estimating biodiversity changes to climate change. In their analogy, they show that a 150-year climate dataset shows a significant trend when temperature is regressed against year¹ ($P < 10^{-15}$; figure 1a of their Comment), whereas aggregating the 'annual changes' finds no signal of warming¹ (P = 0.38; figure 1b of their Comment). They use this analogy to argue that using annual changes² causes real temporal trends in abundance to be missed. This analogy is a false equivalence: the overwhelming scientific evidence for global climate warming is not derived from a simple linear regression of a single time series, and nor should our assessment of global biodiversity be.

Equally, the suggested approach¹ (figure 1a of their Comment) is incorrect and statistically flawed. It conflates temporal autocorrelation with the metric of interest—the population growth rate (r). In brief, the size of a population at time $t(X_t)$ is related to its size one year earlier (that is, $X_t = X_{t-1} \times e^{(r+\varepsilon)}$, in which ε denotes random fluctuations); such time series have a high probability of finding chance correlations (that is, a random walk). This is not just a minor detail. To illustrate this, we simulated a stable population with no systematic change (that is, r=0) across 50 years, and repeated the simulation 1,000 times. The described approach¹ resulted in a false positive rate of about 80%. Using the annual growth², the error rate was 5% (that is, the theoretical expectation, which is therefore preferable).

Further, the climate analogy conflates analysis of an aggregated global trend with a single population (the procedure generating figure 1b in the Comment¹ would be applied to a single population in our analyses). Comparable collections of short temperature time series across many sites do indeed detect warming³. In our analysis, with 14,700 populations, an average of 15 years of data per population (as in the LPD), and the observed within-population variation (average $\sigma = 0.53$), one would be able to detect a mean annual decline as small as 0.2% with 95% certainty if all populations are changing equally was a central message of our article².

Finally, if the argument of Loreau et al.¹ was correct, we would expect stronger evidence of declines in longer time series; however, the reverse is empirically true (Fig. 1). If smaller time series are excluded (such as those in refs. ^{4,5}), the global trend of primary clusters increases slightly (from an aggregate mean trend of -0.00035 to +0.0043). It is the small time series that drive patterns of loss and it is critical to understand them². In a BHM model any additional data are useful—including short-term trends—and improve our estimate of systemic patterns; data-poor time series contribute less, whereas longer time series contribute more, in a statistically coherent way.

Loreau et al. point out that populations may be overrepresented in some areas (for example, in protected areas), and highlight the heterogeneity among growth rates. These are two different issues and should not be conflated—one is about bias and the other about variation. Regarding potential biases in the data, we think this is a valid point, and is a well-known issue in ecology. Less biased sampling is a common goal, but we cannot ignore decades of biodiversity trends until improved data is available. Our article analyses the patterns found in the LPD, which has been interpreted previously as showing a 68% decline in vertebrate abundance (despite having the same biases).

Loreau et al. also criticize the LPD for containing heterogeneous growth rates. This, of course, is not limited to the LPD; any database of population trends will contain heterogeneity and any attempt at identifying broad patterns will need to contend with this. It would be a disservice to throw out the world's most comprehensive data on populations trends (the LPD) because of heterogeneity. A better option is to properly account for heterogeneity statistically, which is exactly what a BHM model does.

For clarity, we discuss explicitly the consequences of heterogeneity in relation to the BHM. First, heterogeneity increases variance. Unexplained variation is describable using distributions. This is basic statistics, and consistent with the BHM. Second, as heterogeneity increases, our ability to conclude that changes are significant decreases. This is not a flaw and is statistically appropriate-uncertainty should increase with variance. That said, despite the heterogeneity, ten systems showed significant changes (both declines and increases). Moreover, the presence of uncertainty does not preclude analysis. We identified seven systems with strong but uncertain mean declines, which could be the foci for new monitoring programs. These systems are more likely to be at risk than the 14 systems showing strong but uncertain increases. Third, increased heterogeneity changes the uncertainty, but not the mean trend. Thus, heterogeneity does not affect the global aggregated estimate, as argued¹. Fourth, a heterogeneous system could contain groups that are declining, as well as groups that are increasing. Using BHM, we do not lose this information-as variance increases, a greater fraction of the distribution will show strong declines (and increases).

Loreau et al. also raise a number of other criticisms¹. They argue that our BHM model is not "objective data analysis". We find their logic unclear. The use of statistics to estimate the mean and variance of a distribution based on the data is objective, as is using statistics to

¹Department of Biology, McGill University, Montreal, Quebec, Canada. ²Bieler School of Environment, McGill University, Montreal, Quebec, Canada. ³Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada. ⁴School of Biology and Ecology and Mitchell Center for Sustainability Solutions, University of Maine, Orono, ME, USA. ⁵Centre for Biological Diversity, University of St Andrews, St Andrews, UK. ⁶Indicators and Assessments Unit, Institute of Zoology, Zoological Society of London, London, UK. ⁵Centre for Biological Diversity, University of St Andrews, St Andrews, UK. ⁶Indicators and Assessments Unit, Institute of Zoology, Zoological Society of London, UK.

Matters arising



Fig. 1 | **Mean log annual growth rates as a function of the number of yearly abundance estimates in each time series.** Data are from the LPD (1970–2014) (www.livingplanetindex.org/). Each data point represents the average across all time series with a given number of annual estimates. Time series with only 2 or 3 abundance estimates showed substantially more negative growth than time series with more points.

estimate the fraction of populations and magnitude of growth rates in extreme clusters. The model does not arbitrarily 'split' the data into clusters as they implied¹, it objectively identifies whether extreme clusters exist on the basis of empirical evidence. Using this approach across 57 systems, we found strong evidence for 24 clusters of populations with extreme declines or increases that were statistically distinguishable from trends in the majority of populations.

Loreau et al. suggest¹ that the steeply declining populations making up the 'clusters of extreme decline' provide no information (note that ref.⁶ critiques our article on the basis of the opposite argument). These extreme trends were previously aggregated into the Living Planet Index (LPI) and largely drove the estimated 68% population decline in the LPI; thus if one accepts this argument it must logically be extended to disregard the massive global declines suggested by the LPI. However, we think that discarding extreme trends is the wrong approach. Whether or not the cause is known, the precautionary principle suggests that we should be concerned about any strong declines as potentially indicating risk. Further, these extreme trends can and should be separated statistically, so that they can be analysed without dominating the rest of the distribution; this is what our BHM model does.

Loreau et al. state¹ that in our model, "steeply declining populations were removed from primary clusters while steeply increasing populations were kept". This is incorrect—our main analysis, using the BHM model, identified and separated both positive and negative extreme clusters from the primary cluster. However, as a preliminary analysis, we had serially removed extreme populations from one side of the distribution at a time, and had shown the high sensitivity of the LPI². We agree that it is worth considering the effect of simultaneous removal of extremes from both sides on the LPI; this has now been explored in depth^{6,7}. Of note, the results from such analyses support the conclusion that the LPI's 68% decline is driven by small number of extreme populations⁷.

Finally, Loreau et al. argue that our conclusion "stands in marked contrast to many studies that have accumulated evidence for population declines across a wide range of taxonomic groups, ecosystems and geographic regions" (notably, the reverse has also often been shown: for example, in refs. ^{5,8}). Of course, if each study was evaluated on the basis of whether it supported previous conclusions, science would become exceedingly biased. We found systems showing improvements with high confidence (based on 95% credible intervals and clearly not a result of low power or being "swamped by yearly fluctuations" as argued), several of which had more than 70% of populations increasing. If these can still be argued to be in general decline, then data and evidence no longer matter, and conservation becomes more faith than science⁹. Further, the focus on our finding that 98.6% of vertebrate populations showed no global decline in aggregate misses the point of the paper. Both increases and decreases are occurring; importantly, increases in one region (for example, Europe) do not negate losses in others (for example, Asia). We found almost a fifth (10 out of 57) of Earth's systems and 15% of populations in the remaining systems showed evidence of serious decline. These findings should be sufficient to raise alarms, and not be characterized as 'downplaying biodiversity loss'.

Ultimately, we second the call¹ for a coordinated global biodiversity observation system. Yet, the criticisms raised¹ would negate such an effort-newly sampled populations would not allow inferences until sufficient time had passed (presumably more than 15 years, the average length of the LPD time series), nor would they be useful if the resulting data showed heterogeneity (presumably the rule rather than the exception). Fortunately, the BHM provides a coherent framework to include and appropriately analyse such data.

Reporting summary

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

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-021-04180-0.

Data availability

Data can be accessed from the Living Planet Index database (www. livingplanetindex.org/).

- Loreau, M. et al. Do not downplay biodiversity loss. Nature https://doi.org/10.1038/ s41586-021-04179-7 (2022).
- Leung, B. et al. Clustered versus catastrophic global vertebrate declines. Nature 588, 267–271 (2020).
- Antão, L. H. et al. Temperature-related biodiversity change across temperate marine and terrestrial systems. Nat. Ecol. Evol. 4, 927–933 (2020).
- Leung, B., Greenberg, D. A. & Green, D. M. Trends in mean growth and stability in temperate vertebrate populations. *Divers. Distrib.* 23, 1372–1380 (2017).
- Daskalova, G. N., Myers-Smith, I. H. & Godlee, J. L. Rare and common vertebrates span a wide spectrum of population trends. *Nat. Commun.* 11, 4394 (2020).
- Murali, G. et al. Emphasizing declining populations in the Living Planet Report. Nature https://doi.org/10.1038/s41586-021-04165-z (2022).
- Leung, B., et al. Reply to: Emphasizing declining populations in the Living Planet Report. Nature https://doi.org/10.1038/s41586-021-04166-y (2022).
- Dornelas, M., et al. A balance of winners and losers in the Anthropocene. Ecol. Lett. 22, 847–854 (2019).
- 9. Hilborn, R. Faith based fisheries. Fisheries 31, 554–555 (2006).

Acknowledgements This work was supported by a Natural Sciences and Engineering Research Council (NSERC) Discovery grant to B.L.

Author contributions B.L. wrote the response. A.L.H. and D.A.G. helped with writing, editing and discussing ideas. B.M. and M.D. discussed ideas and helped with editing. R.F. contributed discussions to the original manuscript².

Competing interests The authors declare no competing interests.

Additional information

 $\label{eq:superior} {\mbox{Supplementary information} The online version contains supplementary material available at https://doi.org/10.1038/s41586-021-04180-0.}$

Correspondence and requests for materials should be addressed to Brian Leung.

Reprints and permissions information is available at http://www.nature.com/reprints. Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

 \circledast The Author(s), under exclusive licence to Springer Nature Limited 2022

nature portfolio

Corresponding author(s): Brian Leung

Last updated by author(s): Sep 27, 2021

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our <u>Editorial Policies</u> and the <u>Editorial Policy Checklist</u>.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.		
n/a	Сог	nfirmed
\boxtimes		The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
\boxtimes		A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
\boxtimes		The statistical test(s) used AND whether they are one- or two-sided Only common tests should be described solely by name; describe more complex techniques in the Methods section.
\boxtimes		A description of all covariates tested
\boxtimes		A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
\boxtimes		A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
\boxtimes		For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted Give P values as exact values whenever suitable.
\ge		For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
\boxtimes		For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
\boxtimes		Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
		Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code		
Data collection	Data from the original ms was from the Living Planet Index database. <www.livingplanetindex.org></www.livingplanetindex.org> . (2016) was scraped in R 3.6.3.	
Data analysis	Bayesian analyses from the original ms were conducted using the STAN 2.14 language, and processed and analyzed in R 3.6.3. Custom code from this article can be obtained at: https://doi.org/10.5281/zenodo.3901586	

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

Data from the original ms can be obtained from the Living Planet Index database. <www.livingplanetindex.org/>. (2016), AmphiBIO database from <https:// figshare.com/articles/Oliveira_et_al_AmphiBIO_v1/4644424>, Fishbase database <www.fishbase.org>, and mammal, bird and reptile life history traits from <https://doi.org/10.6084/m9.figshare.c.3308127.v1>

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences Behavioural & social sciences X Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see <u>nature.com/documents/nr-reporting-summary-flat.pdf</u>

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study rebuts the "matters arising" by Loreau et al. based on logic, and a re-analysis of the relation between time series size and mean logged growth rate.	
Research sample	The data was obtained from the Living Planet Index database. <www.livingplanetindex.org></www.livingplanetindex.org> . (2016), and consisted of 15241 vertebrate populations. To avoid double counting, when a species contained both finer resolution estimates within a country (2593 entries) as well as a country-wide aggregate, we excluded the country-wide aggregate (537 entries). This resulted in 14700 populations remaining in our analysis. Each system was defined by a combination of habitat domain (terrestrial, freshwater and marine), biogeographic realm, and taxonomic grouping (Fish=Actinopterygii, Elasmobranchii, Holocephali, Myxini, Chondrichthyes, Sarcopterygii, Cephalaspidomorphi; Birds=Aves, Mammals=Mammalia, Herps = Amphibia, Reptilia). Terrestrial and freshwater habitat domains were separated into five realms (Afrotropical, Nearctic, Neotropical, Palearctic, and Indo-Pacific), whereas the marine domain was separated into six realms (Arctic, Atlantic north temperate, Atlantic tropical/sub-tropical, Pacific north temperate, Indo-Pacific tropical, and South-temperate/Antarctic).	
Sampling strategy	All population time-series data in the LPI dataset were used. To avoid double counting, when a species contained both finer resolution estimates within a country (2593 entries) as well as a country-wide aggregate, we excluded the country-wide aggregate (537 entries). This resulted in 14700 populations remaining in our analysis.	
Data collection	The data was obtained by Dan Greenberg, and downloaded from publicly available databases identified in the data availability statement	
Timing and spatial scale	Data were analyzed from 1970-2014, as these coincided with the analyses from the Living Planet Index. The spatial scale for the analysis was global. The data was comprised of 14700 populations across many studies, and thus was measured at many scales. Thus, relative changes per population was used.	
Data exclusions	To avoid double counting, when a species contained both finer resolution estimates within a country (2593 entries) as well as a country-wide aggregate, we excluded the country-wide aggregate (537 entries). This resulted in 14700 populations remaining in our analysis.	
Reproducibility	NA	
Randomization	NA	
Blinding	NA	
Did the study involve fiel	d work? Yes X 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	Involved in the study
\boxtimes	Antibodies
\boxtimes	Eukaryotic cell lines
\boxtimes	Palaeontology and archaeology
\boxtimes	Animals and other organisms
\boxtimes	Human research participants
\boxtimes	Clinical data
\boxtimes	Dual use research of concern

Methods



MRI-based neuroimaging