		N_{t-1}	N_t	N_t/N_{t-1}	d_t	LPI
a	Pop. A	100	200	2	0.30	
	Pop. B	100	50	0.5	−0.30	
	Average	100	125	1.25	0	1
	Change		+25%	+25%		0%
b	Pop. A	100	1,000	10	1	
	Pop. B	100	10	0.1	−1	
	Average	100	505	5.05	0	1
	Change		+405%	+405%		0%
c	Pop. A	100	150	1.5	0.18	
	Pop. B	100	50	0.5	−0.30	
	Average	100	100	1	−0.06	0.87
	Change		0%	0%		−13%
d	Pop. A	100	190	1.9	0.28	
	Pop. B	100	10	0.1	−1	
	Average	100	100	1	−0.36	0.44
	Change		0%	0%		−56%
e	Pop. A	100	136	1.36	0.13	
	Pop. B	100	70	0.7	−0.15	
	Average	100	103	1.03	−0.01	0.976
	Change		+3%	+3%		−2%
f	Pop. A	50	45	0.9	−0.05	
	Pop. B	25	5	0.2	−0.7	
	Pop. C	20	8	0.4	−0.4	
	Average	47.5	29	0.5	−0.38	0.42
	Change		−38%	−50%		−58%

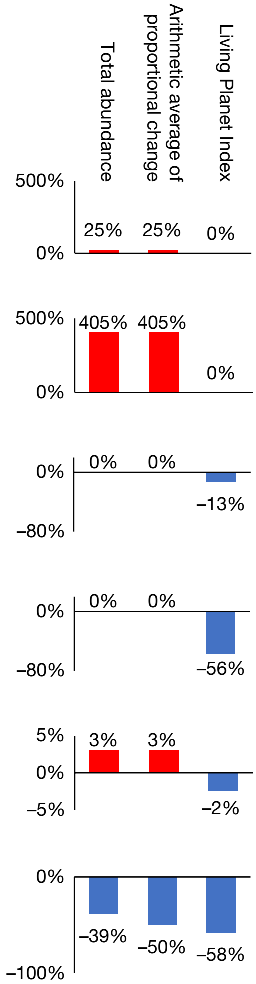

Fig. 1 | Numerical examples illustrating the relationship between population trends and percentage change in total abundance, arithmetic average of proportional change, and the LPI. See text for descriptions of examples.

drop of this magnitude comes about with a rather moderate constant yearly index value of 0.976 ($0.976^{45} = 0.32$). The example in Fig. 1e shows that an index value of 0.976 can arise as a result of moderate variation among population trends without a decrease in abundance (and actually even with increasing abundance). Indeed, the Living Planet Report[6] and other studies[7,8] have found that increasing and decreasing population trends are approximately equally common in larger datasets. It thus seems plausible that the discrepancy between the marked decline in the global LPI[1] and the other studies, which did not find strong evidence for global declines in vertebrate abundances[7,8], is likely to result from the geometric averaging in the LPI method causing bias when interpreted as abundance. We also point out that we do not intend to downplay the importance of extreme outliers in driving the decrease in the global LPI identified by Leung et al.[2], but rather to illustrate that the trouble with the LPI methodology is deeper than that, and cannot be resolved by removing extreme population trends from the analysis.

In the numerical examples above, we have made the simplifying assumption that all the initial populations are of the same size. Added complications arise if populations differ in absolute size and there is a correlation between population size and rate of change. This problem has been acknowledged in the Living Planet Report[6] (page 18), with a numerical example (replicated in Fig. 1f) showing how a negative correlation between population size and the rate of decline—with smaller populations declining faster than larger populations—results in a larger drop in the index value than in the proportion of individuals lost. However, this is a separate issue from the systematic downward bias caused by geometric averaging (when the LPI is interpreted as change in abundance), which arises even without a correlation between population size and rate of increase or decrease. Incidentally, in the Living Planet Report example[6], the 'percentage change' (standing in for the LPI) is reported to be −50%, but this is the arithmetic average of proportional changes in abundance, not the value obtained by the LPI methodology. As Fig. 1f shows, the LPI method yields a value of 0.42, corresponding to −58%; the additional eight-percentage-point reduction is caused by the geometric averaging in the LPI method. Furthermore, recent analysis of the data in the Living Planet Database suggests that absolute population size does not predict whether the population trend is increasing or decreasing[7], implying that correlations between population size and rate of increase or decrease are not likely to cause considerable bias in global estimates.

The decline in biodiversity is a real and serious phenomenon[9]. Thus, the technical issue identified here regarding the incorrect interpretation of the LPI must not be interpreted as a failure of conservation science in general, or as evidence that nature is not at risk. For example, the International Union for Conservation of Nature assessments of extinction risk, which are based on clearly defined criteria and do not use the LPI methodology, indicate that the extinction risk of mammals, birds, amphibians, reef-forming corals and cycads is increasing (https://www.iucnredlist.org/assessment/red-list-index, accessed 11 January 2021).

For a biodiversity index to be useful, it must not only have mathematically and statistically desirable properties, but also be easily understood[10]. The LPI clearly is not a good metric for abundance, and while the arithmetic average of proportional changes in abundance is easier to interpret with just two time points (Fig. 1), it does not serve well as a metric for abundance index either[3]. Finally, we urge scientists that have used the LPI methodology to scrutinize the conclusions of their work, and those negotiating future indicators for the UN CBD to critically review the interpretation of the LPI.

Data availability

All data generated or analysed during this study are included in this published article.

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Reply to: The Living Planet Index does not measure abundance

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Check for updates

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REPLYING TO M. Puurtinen et al. *Nature* https://doi.org/10.1038/s41586-021-03708-8 (2022)

In the accompanying Comment[1], Puurtinen et al. provide a clear example of why one must be careful when interpreting analyses using the Living Planet Database (LPD). We were pleased to read this Comment inspired by our recent paper[2]. It is an important continuation of the discussion about what can be learned from the rich data in the LPD. In brief, we concur that the Living Planet Index (LPI), and any summary analyses using the LPD (including ours), do not reflect changes in abundance. This is an important point that is often missed by the media, and it is exactly the type of nuance we wanted to promote with our paper.

Although the data in the LPD are based on estimates of population abundance, the database was never meant for comparisons of absolute abundance. The reason is that the metrics are standardized only within populations. The diversity of sampling methodologies and spatial scopes for each population makes it intractable to compare absolute abundance among species. What analyses of the LPD can provide, however, are comparable estimations of population trends. Population trends yield insight into whether populations are increasing or decreasing and the relative (rather than absolute) magnitudes of these changes. We believe that these are also important elements of changing biodiversity patterns.

More generally, we also want to recognize the difficulty in interpreting any conglomerate index, irrespective of whether it measures abundances or trends. The key difficulty, of course, is that the index is actually composed of non-interchangeable units (that is, different populations and species); a reduction in population 1 does not necessarily reflect any change in population 2, but the composite can make it appear as though it does. Thus, for indices based on geometric means, such as the LPI, extreme trends in a few populations can drive large declines in aggregate indices, which are easily misinterpreted as the entire system declining (as highlighted in our Article[2]). Alternatively, if one used an index based on absolute abundances, if species A doubled and species B went extinct, the index would suggest no change. Most conservationists would be likely to disagree that such a scenario reflects a stable system. Yet, simultaneously, owing to some set of underlying factors, systems can be broadly declining (or broadly improving), and it is important to identify such widespread trends.

A better approach would be to explicitly model the distribution of population trends. This is the basis of the Bayesian hierarchical mixture (BHM) model[2], which allows one to separate and consider both unexpectedly strong trends and more typical trends. A BHM approach thus provides a more accurate picture of how populations are doing, rather than being dominated by the extremes. Furthermore, the BHM model summarizes both general behaviour (primary clusters), and variation, and so can reveal the fraction of populations undergoing different levels of decline or growth (for example, in the ten taxonomic or geographic systems showing strong mean declines, 87% of those populations also showed strong mean declines). Finally, a BHM approach makes it difficult to conflate abundance with the distribution of trends. There are other advantages of a BHM model (for example, accounting for population fluctuations and differences in time series size), which we described in our paper[2].

In summary: (1) Puurtinen et al.[1] raise an excellent and correct point: both researchers and the media must guard against the unfortunately common mistake of interpretating the LPI as measuring abundance loss. (2) Analyses using the LPD necessarily refer to trends, given the type of data available. (3) Aggregate measures are inherently difficult to interpret, given the non-equivalence of species.

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