Matters arising

Emphasizing declining populations in the Living Planet Report

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Check for updates

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

The Living Planet Report[1], which has been published biannually since 1998, is key for understanding trends in wildlife populations and promoting sound conservation[1–4]. Leung et al.[5] recently disagreed with the conclusions of the Living Planet Report and found that the overall pattern of population declines stems from very few populations (extreme clusters), beyond which global vertebrate populations are not declining. However, when properly accounting also for the influence of the fastest-increasing populations, we find that the overall declines in the Living Planet Report are practically unchanged. Moreover, the Living Planet Database is heavily biased towards populations that receive more conservation attention, indicating that the true population trends are indeed dire and may actually be worse than depicted in the Living Planet Report.

The Living Planet Index (LPI) represents the weighted average change in the population of species over time across regions[6]. Leung et al.[5] suggested that the LPI is an oversimplification of regional trends and that it is an unreliable index for global declines. They removed the 2.4% most declining populations and found that this removal reverses "global vertebrate trends from a loss of more than 50% to a slightly positive growth"[5]. Using the updated Living Planet Database, we replicated their analyses and found that the removal of 3.1% of the most decreasing populations indeed reverses the overall declining trend (Fig. 1a). However, such a procedure misrepresents the true trends in these data. By removing only the most declining populations, the overall trend in the remaining data is heavily influenced by the fastest-increasing populations. To correct this, we simultaneously removed the 1.55% populations doing the best and the 1.55% populations doing the worst (that is, 3.1% of the populations from both extremes; Supplementary Information). The trend in the remaining data mimics the major declines reported in the Living Planet Report (65% decline for the remaining 96.9% of the data compared to a 67% decline for all 21,639 populations in the complete dataset). To achieve no net overall population declines, we needed to remove at least 43.3% of the extreme data (21.65% from each end) (Fig. 1a). Moreover, when removing 3.1% of populations from both extremes, the time series (from 1970 to 2014) mirrors the complete dataset very closely with pronounced declines in recent decades (Fig. 1b (orange and black lines)). Therefore, the analysis by Leung et al.[5] greatly exaggerates the effect of extreme-increasing populations and misrepresents the overall trends.

Moreover, Leung et al.[5] devised a method to identify extreme and primary clustered population growth trends (Bayesian hierarchical mixture model). They used this method to highlight the effects of either of these population types on overall trends. When they removed extreme clusters (populations with a growth rate of 1 s.d. away from the mean of the primary cluster), they found no mean global trend for the remaining 98.6% of the Living Planet Database populations[5]. This further emphasizes the effect of clustered populations on the LPI. However, it ignores the fact that this threshold delineates 147 decreasing populations but only 58 increasing populations (two-and-a-half times more decreasing populations). The LPI summarizes population trends to highlight global patterns[6]. The non-symmetric removal of extreme clustered declining populations is biased and negates the entire point of the LPI, and of conservation biology in general. As conservation biology focuses on declining and small populations[7], we should not ignore them in our global tallies of trends. Ultimately, there are many more extreme-decreasing populations than extreme-increasing ones. Failing to emphasize this point undercuts a central tenet of biodiversity conservation.

We further examined whether populations in the Living Planet Database received disproportionate conservation attention, which may bias conclusions drawn from their analysis. We assessed the location of populations sampled in the Living Planet Database relative to the global protected area network. We found that populations in the Living Planet Database are significantly more likely to be sampled inside protected areas than expected by chance (Fig. 2 and Supplementary Table 1). This trend is consistent across taxa (Extended Data Fig. 1) and most regions (Extended Data Fig. 2). Species and populations that are better covered by protected areas are usually less threatened than those that are less covered[8,9]. Thus, populations in the Living Planet Database are probably doing better than those that are not studied, and the true global population trends are probably worse than analyses based on the Living Planet Database suggest.

Although optimistic messages regarding conservation provide much-needed hope[5], we should strive to represent the accurate status of biodiversity. Biased or misinterpreted data can undermine conservation efforts[10]. Although the removal of only 3% of populations in the LPI reverses substantial declines, these results arise from not accounting for the effect of extremely increasing populations[5]. Moreover, the clustering methods of Leung et al.[5] find that there are 2.5 times more extreme-decreasing populations than extreme-increasing populations, a fact that they did not highlight. Thus, although extreme populations have much influence on the LPI, one should not ignore them in tallying the overall state of nature. The Living Planet Report is a commendable effort to summarize the status of global wildlife populations. It regularly reports major declines. Nevertheless, it is subject to biases such as the one that

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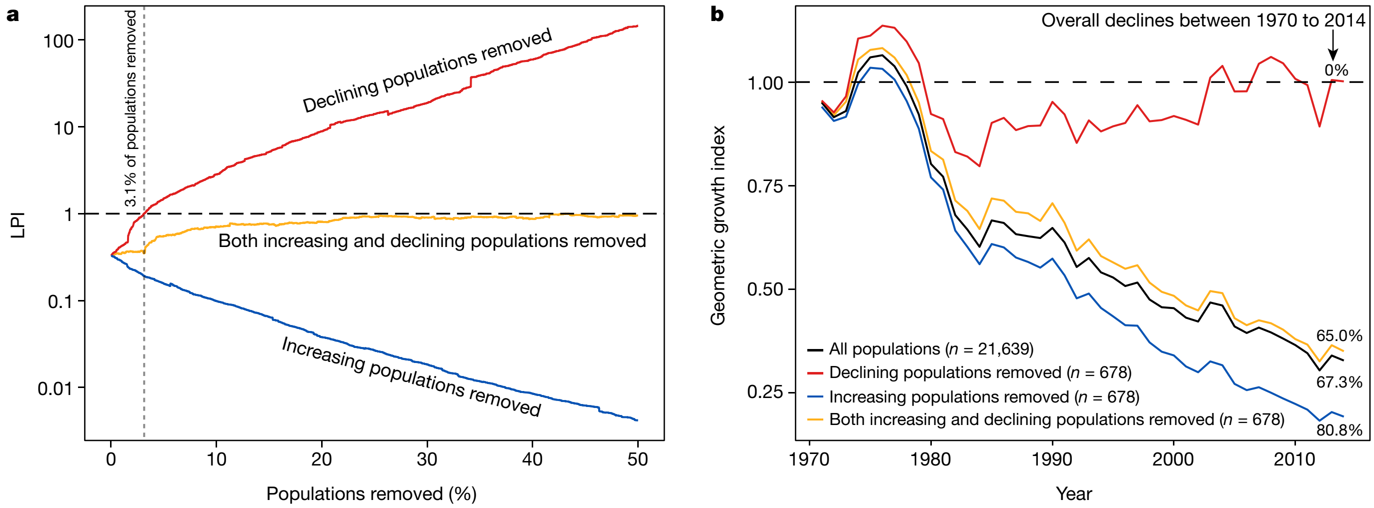

Fig. 1 | The effects of three different extreme population removal strategies to assess the sensitivity of overall growth rates. a, Changes in overall growth rates when removing populations under the three different strategies (up to 50% removal). The vertical dashed line represents the percentage of declining populations to be removed for the overall trend in LPI to be reversed from a decline to positive growth (3.1%; that is, 678 populations). **b**, Temporal variation in the overall global geometric growth rates (black line), and temporal variation after removing 3.1% of the populations under the three strategies. The horizontal dashed lines in **a** and **b** represent no population growth or decline.

we show for protected areas. As a consequence, the true status of nature is probably even worse than the Living Planet Report depicts. Addressing such biases and gaps is an important conservation task. Rather than discouraging efforts such as the Living Planet Report, we want to use this opportunity as a call to arms for greater monitoring of populations of diverse groups globally.

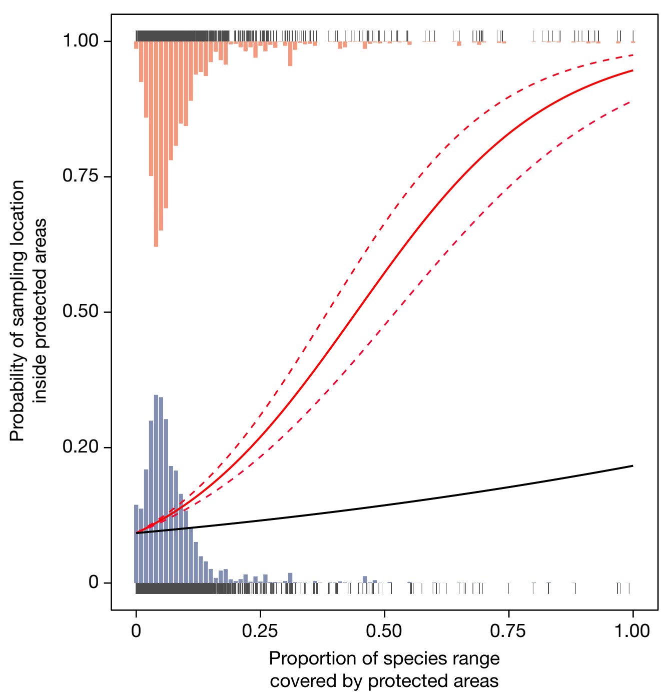

Fig. 2 | The probability of LPI populations' sampling location to be inside protected areas for given species range overlap with protected areas. The solid red line represents a generalized linear mixed model with a binomial fit, and the dashed lines represent the 95% confidence interval. The black line represents the expected slope of 1 if the populations were sampled at random in the species' range. The histograms represent the proportion of overlap of species ranges with protected areas. Red, LPI locations found within protected areas; blue, LPI location found outside protected areas.

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/s41586-021-04165-z.

Data availability

The Living Planet Database is available from the LPI website (https://livingplanetindex.org). The Protected Area maps are available at the World Database of Protected Area (https://www.protectedplanet.net). Species range size was obtained from the IUCN, BirdLife databases (https://www.iucnredlist.org; https://www.birdlife.org) and from Roll et al.[10] for reptiles.

Code availability

The R codes associated with the study are provided in the Supplementary Information.

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Author contributions All of the authors conceived the study. G.H.d.O.C. downloaded LPI data and conducted sensitivity analyses. G.H.d.O.C., G.B. and G.M. assembled and analysed the dataset. All of the authors drafted and substantially revised the manuscript.

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/s41586-021-04165-z.
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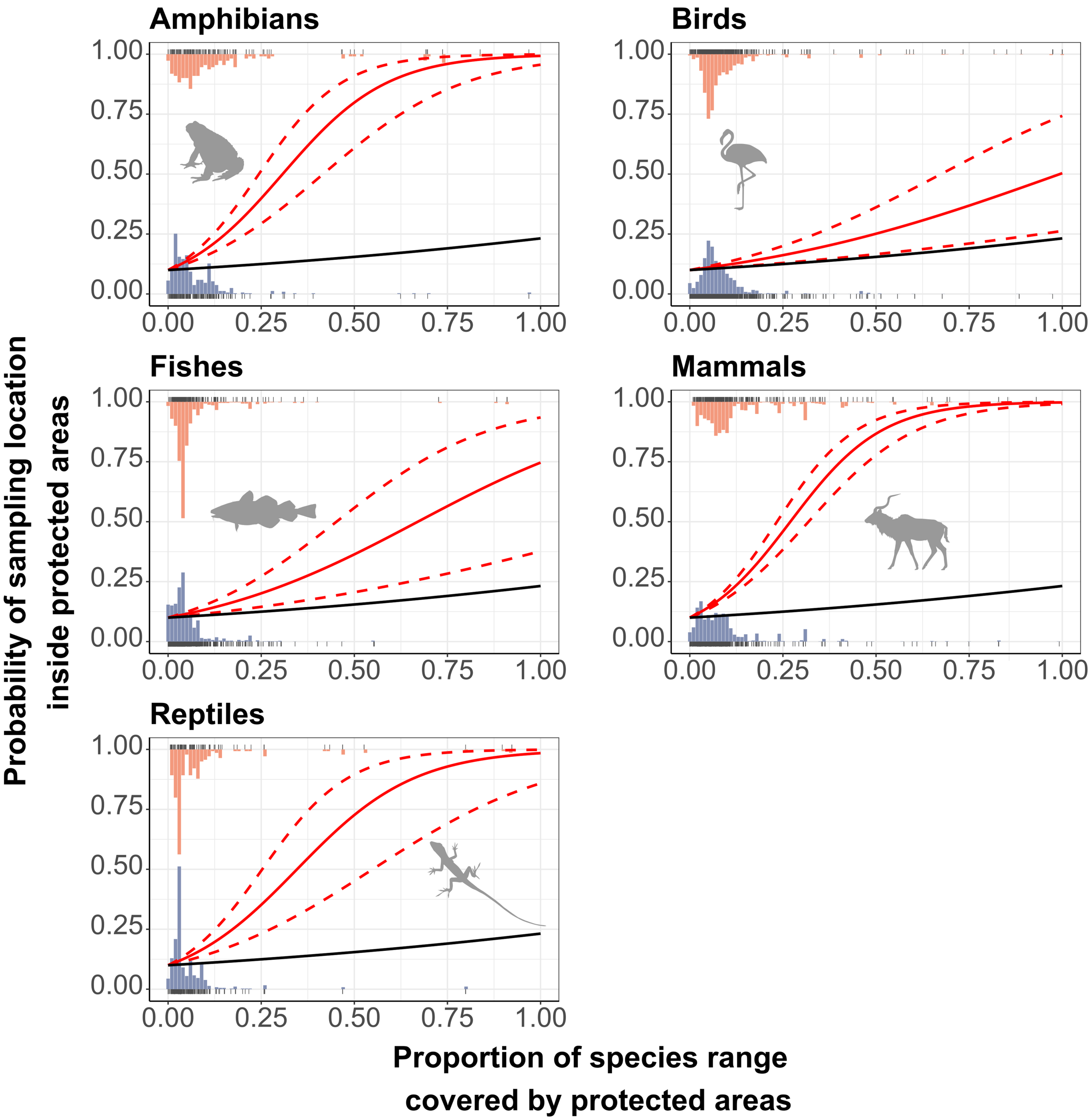
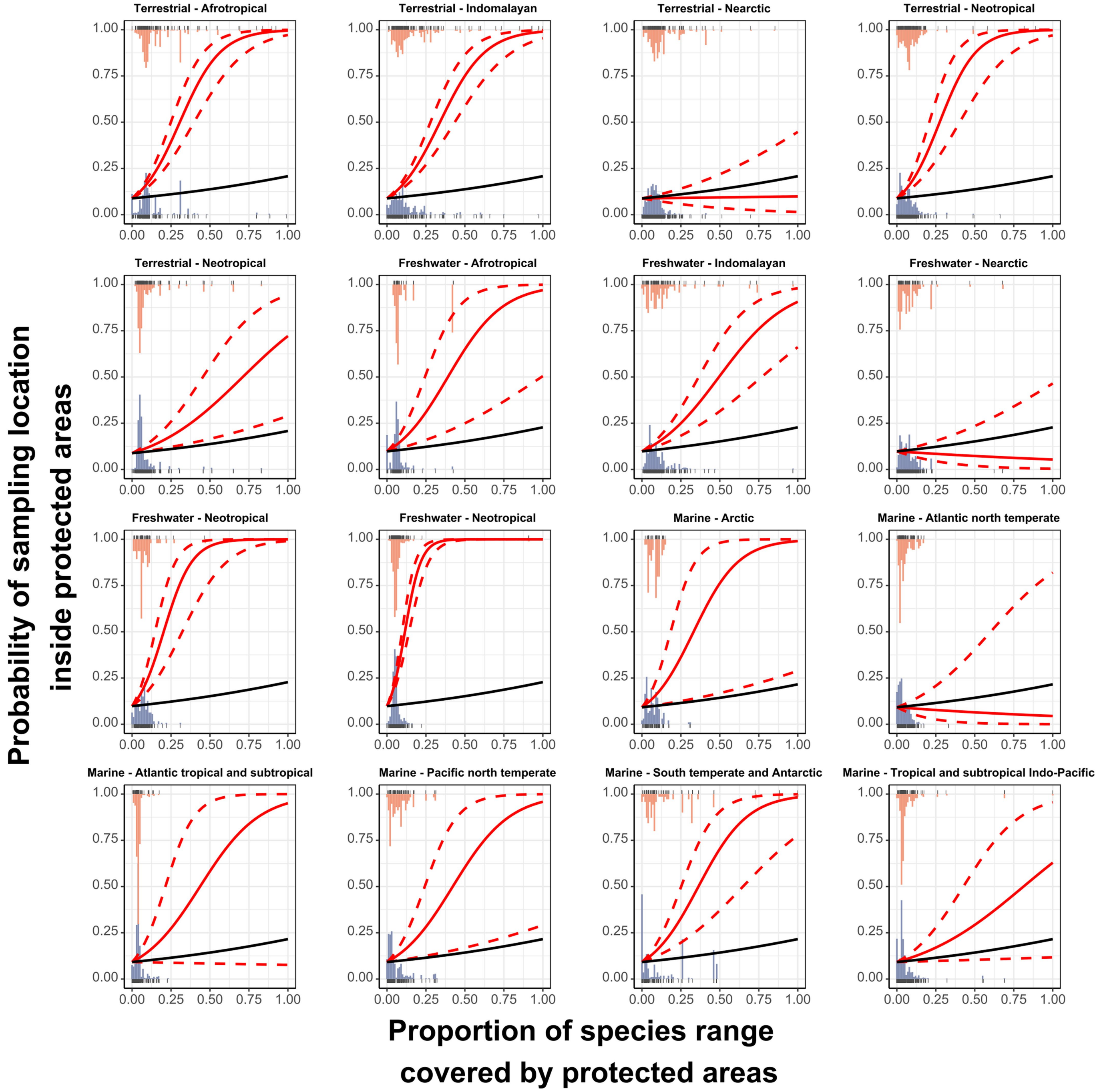


Extended Data Fig. 1 | The probability of LPI populations' sampling location to be inside protected areas for given species range overlap with protected areas (by taxon). Taxon was included as an interaction with the overlap area. The solid red line represents a generalized linear mixed model with the binomial fit and dashed lines 95% confidence interval. The black line represents the expected slope of 1 if populations were sampled at random in the species' range. The histograms represent the proportion of overlap of species ranges with protected areas. Red, LPI locations found within protected areas; blue, LPI location found outside protected areas.



Extended Data Fig. 2 | The probability of LPI populations' sampling location to be inside protected areas for given species range overlap with protected areas (by realm–domain combination). Realm-domain combination was included as interaction with overlap area. The solid red line represents a generalized linear mixed model with the binomial fit and dashed lines 95% confidence interval. The black line represents the expected slope of 1 if populations were sampled at random in the species' range. The histograms represent the proportion of overlap of species ranges with protected areas. Red, LPI locations found within protected areas; blue, LPI location found outside protected areas.

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Software and code

Policy information about availability of computer code

Data collection	We used a custom R code to download living planet index data and WCMC protected area data.
Data analysis	We used a custom R code to analyse living planet index data and WCMC protected area data.

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Living Planet Database is available from the LPI website (livingplanetindex.org). The Protected Area maps are available at the World Database of Protected Area (protectedplanet.net). Species range size was obtained from the IUCN, BirdLife databases (iucnredlist.org; birdlife.org) and from Roll et al. (2017) Nat E & E for reptiles.

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Ecological, evolutionary & environmental sciences study design

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

Study description	Exploring Living planet Index (LPI) trends across land vertebrates, and their underpinnings
Research sample	Not sampled - All LPI data for all land vertebrates
Sampling strategy	Not Sampled
Data collection	Downloaded from available sources
Timing and spatial scale	1970-2020, globally
Data exclusions	n/a
Reproducibility	All codes and data are available to enable reproducability
Randomization	n/a
Blinding	n/a

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Methods

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☒	☐	ChIP-seq
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☒	☐	MRI-based neuroimaging

Matters arising

Reply to: Emphasizing declining populations in the Living Planet Report

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Check for updates

Brian Leung[1,2]✉, Anna L. Hargreaves[1], Dan A. Greenberg[3], Brian McGill[4], Maria Dornelas[5] & Robin Freeman[6]

REPLYING TO G. Murali et al. *Nature* https://doi.org/10.1038/s41586-021-04165-z (2022)

We thank Murali et al.[1] for continuing the discussion on vertebrate trends from our original article[2]; Murali et al.[1] highlight two issues regarding the Living Planet Database (LPD) of vertebrate population trends, and the Living Planet Index (LPI) that aggregates these trends into one global statistic: (1) the LPI is insensitive to simultaneous removal of extreme population trends from both sides, and (2) biases in the LPD might mean that the LPI underestimates vertebrate declines. We note that the simultaneous removal approach of Murali et al.[1] relates to our preliminary analysis, wherein we illustrated that the LPI is highly sensitive to populations with extreme trends by serially removing extreme populations from one side of the distribution at a time[2]. Our main analysis used an alternative modelling framework, a Bayesian hierarchical mixture (BHM) model, which statistically detected and separated trends in extreme clusters on both sides simultaneously (both positive and negative), and also examined the main cluster containing the majority of populations[2]. Nonetheless, we show here that the 'simultaneous removals' analysis of Murali et al.[1] also supports our conclusions that the LPI pattern is driven by a small fraction of extremes.

Regarding index insensitivity, Murali et al.[1] showed that, whereas removing 3% of the most extremely declining populations from the (updated) LPD changes the LPI from declining to neutral, removing trends from both tails of the distribution (that is, the 1.5% most extreme increases and 1.5% most extreme declines) changes the LPI very little. Indeed, if removals are performed at both tails, the LPI does not switch from negative to positive until 43% of extreme populations are removed (21.5% declines, 21.5% increases).

It is important to understand what these results actually demonstrate. The simultaneous removal results of Murali et al.[1] might give the erroneous impression that the decline detected by the LPI is not driven by a small fraction of extreme populations, and that the declines are in fact the typical pattern (that is, a large fraction of extreme declines or the mean of the primary cluster being negative corresponding to our 'catastrophic' decline scenario[2]). This impression would be incorrect because even a small initial asymmetry (that is, slightly more negative extremes than positive extremes) will propagate as one removes populations from both sides of the distribution, such that the LPI should remain negative even as many extremes are removed. If the distribution was entirely symmetric, the LPI would not change at all, no matter how much data you removed.

To illustrate this effect, we built a simple simulation of 10,000 population trends, with a small initial asymmetry (5% extreme declines and 2.5% extreme increases; that is, only a 2.5% asymmetry favouring declines). We simulated the distribution of the remaining trends centred at zero (that is, most populations stable, so global declines are driven by a few extremes). We used parameter values that preserved the characteristics of the 2014 LPD (1970–2014), including yielding a LPI decline of 56.2% (real data yielded a comparable 54% decline; Fig. 1). We next applied the removal approach of Murali et al.[1] to both the simulated data and real data. We found the following patterns. Removing 3%, 10% and 20% of simulated extremes changed the simulated LPI to 54%, 29% and 20% declines, respectively (Fig. 1), and the LPI on the real data to 55%, 31% and 13% declines, respectively. Even after removing 45% of the data, the simulated decline still remained slightly negative (Fig. 1). In summary, a small asymmetry (2.5%) reproduced the observed empirical patterns, both for our 2014 data and the updated dataset of Murali et al.[1] (compare figure 1 in Murali et al.[1] with Fig. 1 below). More widespread declines would change less and would not reproduce the observed patterns. Thus, the results of Murali et al.[1] provide additional support for our original contention that the LPI global patterns are driven by a few extreme populations[2].

Murali et al.[1] further claim that our analysis "ignores the fact that this threshold delineates 147 decreasing populations but only 58 increasing populations", misrepresenting the overall effects of extreme clusters on global trends. They highlight that we found more declining than increasing extreme populations and that, by failing to emphasize this point, we are undercutting a "central tenet of biodiversity conservation". We did not "ignore" extreme-declining populations. We explicitly reported the difference in the fraction of extreme declines versus increases; specifically, our BHM model detected 2.5 times as many populations undergoing extreme declines (1% of total) versus extreme increases (0.4%)[2]. Nonetheless, we are happy to re-emphasize this asymmetry again. Far from ignoring them, our BHM model explicitly identifies and analyses extreme clusters (declines and increases) and the primary clusters that make up the remaining 98.6% of the data. Isolating and analysing both primary and extreme clusters is critical, as the global aggregated LPI estimate of 68% decline is too easily and persistently misunderstood. The LPI's 68% decline does not indicate that there are 68% fewer animals (as acknowledged in the Living Planet Report[3]), nor how many populations are declining (approximately half of the population trends are positive), but this is typically how the LPI is interpreted.

We agree with Murali et al.[1] on the importance of extreme declines[2]; however, we argue that it is of conservation interest to also assess where declines are widespread, and where populations are broadly improving. Although the primary clusters, which account for 98.6% of populations, showed no aggregate trend, our results showed that three primary clusters were declining with high certainty and another seven were declining with less certainty (red and orange distributions in figure 3

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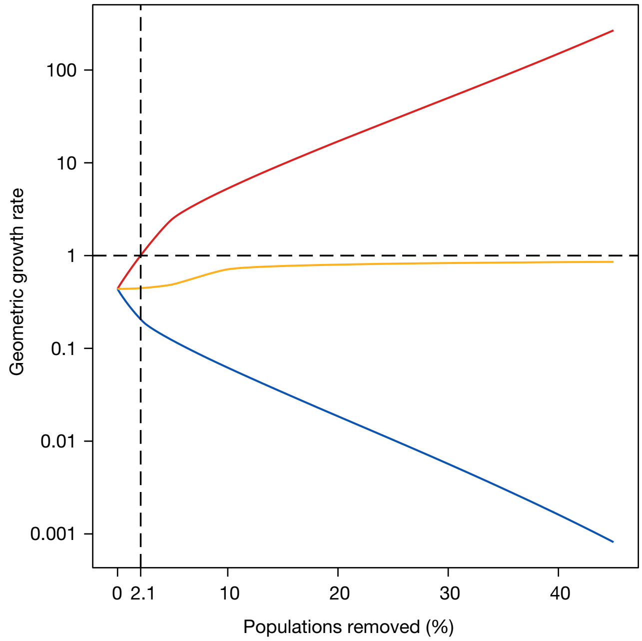

Fig. 1 | Simulation analysis showing effect of a small 2.5% asymmetry on LPI. We simulated 10,000 population trends, with a small initial asymmetry of 5% extreme declines and 2.5% extreme increases (that is, a 2.5% asymmetry favouring declines), and the remaining trends centred at zero. We used parameter values that approximated the characteristics of the LPD (1970 to 2014): a LPI = 56.2% mean decline, average within-population variation = 0.53, mean abundance estimates per population = 15. Abundance estimates were then distributed (randomly) across 45 years. The yellow line shows the simulated removal of extremes from both sides of the distribution (as performed in Murali et al.[1]), whereas the red line simulates the removal of only negative extremes and the blue line simulates the removal of only positive extremes (as performed in our original study[2]). The yellow line shows that a small initial asymmetry will yield the empirical observations, from simultaneous removal on both sides (that is, small initial change, followed by an inflection and persistent negative LPI values even with a high fraction of populations removed; compare with figure 1 of Murali et al.[1]).

of ref. [2], respectively); 87% of populations in these 10 systems showed strong declines (p. 270 of ref. [2]). We also reported systems that were increasing to provide a more accurate picture of biodiversity change. This message in no way obviates the need for conservation; increases in one region (such as Europe) or taxonomic group do not negate losses in others (such as Asia).

Finally, Murali et al.[1] argue that the LPD may be biased towards less threatened populations, for example, if they disproportionately sampled in protected areas. This is a good point, and we support additional analyses to more finely resolve where declines are occurring. As a note of caution, biased membership alone does not indicate biased decline estimates. For example, we might a priori predict that populations are more highly sampled from non-threatened species (easier to get permits) and species with larger ranges (sampling effect), and that these populations should be doing relatively well. Instead, population trends in the LPD are not predicted by whether or not a species is on the IUCN Red List[4] and, for temperate vertebrates, range size has little relation to population trends, except for mammals, in which wide-ranging species were (counterintuitively) more likely to be declining[5].

The goal of our paper was not to discourage efforts such as the Living Planet Report[3] as Murali et al.[1] suggest. Indeed, we believe that the Living Planet Report provides an impressive suite of analyses across many dimensions, and that the LPD is an excellent resource for conservation (despite potential biases that Murali et al.[1] highlight). Our goal is to promote more nuance in interpreting trends in the LPD, which in no way minimizes its value. Moreover, we want to re-emphasize that our analyses revealed numerous conservation concerns, even beyond the extreme clusters, including evidence of widespread decline in almost a fifth of vertebrate systems worldwide and in 15% of populations in remaining systems. Thus, we second the call of Murali et al.[1] for greater monitoring that addresses data gaps. To this end, our paper identified seven regions with high uncertainty but potentially serious widespread declines as potential foci for monitoring. It is very possible that we are not so far apart from Murali et al.[1] in our goals, despite disagreement on what the LPD data show.

Reporting Summary

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

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1. Murali, G. et al. Emphasizing declining populations in the Living Planet Report. *Nature* https://doi.org/10.1038/s41586-021-04165-z (2022).
2. Leung, B. et al. Clustered versus catastrophic global vertebrate declines. *Nature* **588**, 267–271 (2020)
3. Almond, R. E. A., Grooten, M. & Peterson, T. *Living Planet Report 2020—Bending the Curve of Biodiversity Loss* (World Wildlife Fund, 2020)
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5. Leung, B., Greenberg, D. A. & Green, D. M. Trends in mean growth and stability in temperate vertebrate populations. *Divers. Distrib.* **23**, 1372–1380 (2017).

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Author contributions B.L. wrote the response. A.C.H. and D.A.G. helped with writing, editing and discussing ideas. B.M. and M.D. discussed ideas with some editing. R.F. contributed discussions to the original manuscript[2].

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/s41586-021-04166-y.
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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/>. (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

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- 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 ☒ Ecological, evolutionary & environmental sciences

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

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/>. (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/sub-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 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	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging