# Reply to: Capturing stochasticity properly is key to understanding the nuances of the Living Planet Index

Falko T. Buschke [1,*], James G. Hagan [2,3], Luca Santini [4,5] & Bernard W. T. Coetzee [5]

[1] Animal Ecology, Global Change and Sustainable Development, KU Leuven, Leuven, Belgium.

[2] Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden.

[3] Gothenburg Global Biodiversity Centre, Gothenburg, Sweden.

[4] Department of Biology and Biotechnologies "Charles Darwin", Sapienza University of Rome, Rome, Italy.

[5] Department of Zoology & Entomology, University of Pretoria, Hatfield, South Africa.

*Correspondence e-mail: falko.buschke@gmail.com

REPLYING TO E. J. Talis & H. J. Lynch Nature Ecology & Evolution https://doi.org/ 10.1038/s41559-023-0286-w (2023)

In their recent communication, Talis and Lynch [1] raise two issues about our study [2], which showed how random population fluctuations introduce biases when calculating the Living Planet Index (LPI). First, they maintain that because additive population fluctuations may be less prevalent in nature than multiplicative fluctuations, we overstated the effects of the former on the LPI. Second, they claim that the bias we identified in fluctuating populations that increase or decrease nonlinearly is not an inherent limitation of the LPI, but rather a shortcoming of the generalized additive models (GAMs) used to interpolate and smooth population time series. This can be remedied, they argue, by using state–space models instead of GAMs.

With regard to the first issue, Talis and Lynch conflate the prevalence of additive and multiplicative stochasticity in nature with their effects on the LPI. Our study did not claim that additive fluctuations play a dominant role in population time series, nor do our results depend on such claims. As explained in our original study, random population fluctuations can be caused by environmental stochasticity ($\varepsilon_{\text{env}}$), where randomness affects demographic rates, and demographic stochasticity ($\varepsilon_{\text{demo}}$, and its synonym ecological drift[3], the process through which randomness affects the number of individual births and deaths[4].

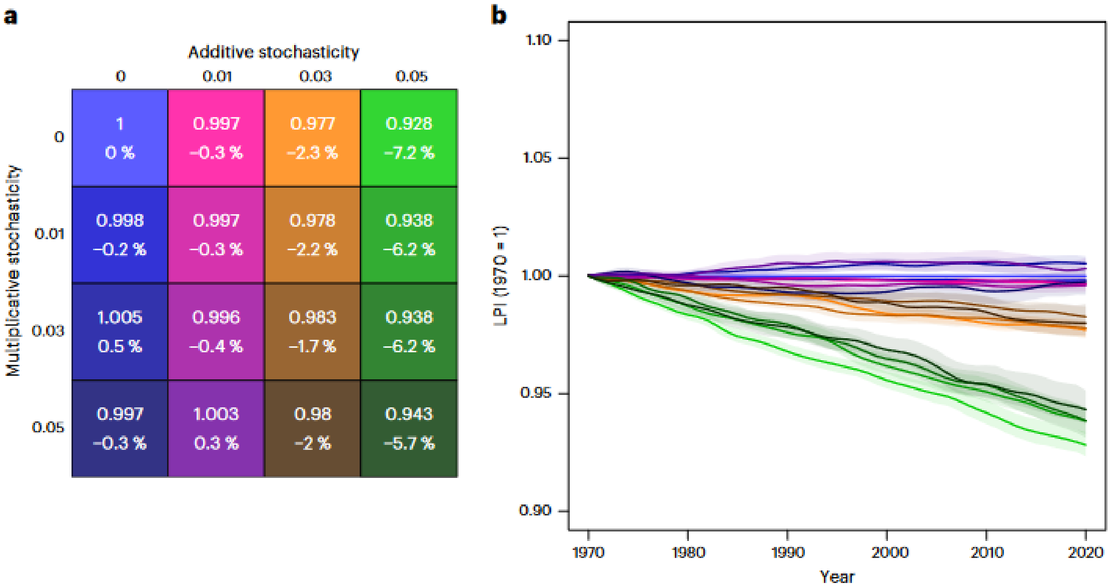
In the simplest case, both environmental and demographic stochasticity can affect population time series as follows:

$$N_{t+1} = N_t e^{(r+\varepsilon_{\text{env}})} + \varepsilon_{\text{demo}} \tag{1}$$

Here, $N_t$ is the population size at a defined time step $t$, and $r$ is the per capita growth rate. Environmental stochasticity is multiplicative, so positive and negative fluctuations are asymmetrical due to the exponent in the first term. By contrast, demographic stochasticity is additive, leading to symmetrical positive and negative fluctuations. For simplicity, we do not consider measurement error in this simplified example because previous research modelled measurement error using a Gaussian distribution[5], so its effect on the LPI could be comparable to that of demographic stochasticity because it also leads to additive individual-level fluctuations.

The LPI uses a log-transformation to calculate year-on-year population changes, $\lambda = \log_{10}\left(\frac{N_{t+1}}{N_t}\right)$, meaning that the asymmetrical positive and negative fluctuations caused by multiplicative environmental stochasticity can cancel each other out when calculating such changes[2,6]. By contrast, log-transformation means that the symmetrical positive and negative fluctuations due to demographic stochasticity cannot cancel out, leading to a gradual decline in the LPI[2,6]. The magnitude of this decline depends on the starting population and the magnitude of the fluctuations caused by demographic stochasticity. This effect is unequivocal, based on the mathematical formulation of the LP [2,7].

The relative prevalence of environmental and demographic stochasticity in natural time series is not what affects the LPI (Fig. 1). We show this by simulating 5,000 populations between 1970 and 2020, all starting with 100 individuals at equilibrium ($r = 0$). Population dynamics are simulated according to equation (1) incorporating environmental, $\epsilon_{env} \sim \mathcal{N}(0, \sigma_{\text{mult}})$ , and demographic stochasticity, $\epsilon_{demo} \sim N_t \times \mathcal{N}(0, \sigma_{\text{add}})$, according to a random normal distribution, $\mathcal{N}(\mu, \sigma)$, with a mean of $\mu = 0$ and a standard deviation of $\sigma_{\text{mult}}$ and $\sigma_{\text{add}}$ for multiplicative and additive stochasticity, respectively. We simulated every combination of $\sigma_{\text{mult}}$ and $\sigma_{\text{add}} = 0, 0.01, 0.03, 0.05$ to represent 0–5% fluctuations (Fig. 1a). Even in instances where multiplicative environmental stochasticity dominates natural time series, the primary effect of random fluctuations on the LPI was caused by additive demographic stochasticity (Fig. 1a: the LPI declines from left to right, not top to bottom). Declines in the LPI were largest when demographic stochasticity was high, irrespective of the magnitude of environmental stochasticity (Fig. 1b: all four green-shaded curves decline more than other curves).



| Multiplicative stochasticity \ Additive stochasticity | 0 | 0.01 | 0.03 | 0.05 |
|---|---|---|---|---|
| 0 | 1<br>0 % | 0.997<br>−0.3 % | 0.977<br>−2.3 % | 0.928<br>−7.2 % |
| 0.01 | 0.998<br>−0.2 % | 0.997<br>−0.3 % | 0.978<br>−2.2 % | 0.938<br>−6.2 % |
| 0.03 | 1.005<br>0.5 % | 0.996<br>−0.4 % | 0.983<br>−1.7 % | 0.938<br>−6.2 % |
| 0.05 | 0.997<br>−0.3 % | 1.003<br>0.3 % | 0.98<br>−2 % | 0.943<br>−5.7 % |

**Fig. 1. Additive stochasticity affects the LPI, whereas multiplicative stochasticity does not**. **a**, We simulated 16 combinations of four levels of multiplicative environmental stochasticity and additive demographic stochasticity, $\sigma = \langle 0, 0.01, 0.03, 0.05 \rangle$, for 5,000 populations at equilibrium (per capita growth rate $r = 0$) and starting populations of $N = 100$ in 1970. The LPI and the percentage decline for the year 2020 are shown for each combination. **b** The LPI (mean and shaded 95% confidence intervals) for each combination of multiplicative and additive stochasticity. The colours for each combination in a correspond with the lines in b.

While we fully support Talis and Lynch's recommendation for a comprehensive assessment of different sources of stochasticity in empirical time series, the potential effect on the LPI would be a poor motivation for this. Prior work has already identified normally distributed fluctuations in the Living Planet Database [5], which we used to inform our simulations because it is consistent with additive individual-level stochasticity. Even if these additive fluctuations are proved by subsequent research to comprise only a small proportion of total stochasticity, the findings of our original study remain unchanged because they depend on the magnitude of additive fluctuations and not their relative prevalence.

The second issue raised by Talis and Lynch is that the bias introduced in increasing or decreasing population fluctuations lies with the use of GAMs and not with the mathematical formulation of the LPI. They argue that state–space models would be a better solution to this bias than the reshuffling null model that we proposed in our study. To be clear, Talis and Lynch do not contest our diagnosis of the GAM as a source of bias in the LPI, but instead offer a different way to handle this bias.

We believe that Talis and Lynch's proposal hinges on whether the GAM is considered an integral part of the LPI, or a preparatory step that can be replaced by state–space models. Their perspective that the GAM is a substitutable step has merit because early versions of the LPI in 2005 were based on linear interpolation between individual data points in time series (that is, the chain method) or least-squares linear modelling across time series[8]. GAMs were only introduced four years later in 2009 [9], so there is a precedent of updating the method used to model imperfect empirical time-series data. Indeed, state–space models have already been used in this context for oceanic sharks and rays, for example [10]. So, we do not oppose Talis and Lynch's proposal in principle, nor do we find it necessary here to debate the relative statistical strengths of GAMs or state–space models.

However, we believe there are two main motivations for accommodating the GAM in the LPI (as we did using our reshuffling null model) rather than using alternative modelling approaches. First, GAMs are not biased fundamentally, but have known shortcomings when population fluctuations are high and time-series trajectories are strongly nonlinear (Fig. 3 in our original study [2]). There may be a risk in discarding a proven statistical approach that works in many cases, instead of trying to accommodate its known limitations. For example, the LPI values for the Nearctic and Palaearctic biogeographical realms were mostly unaffected by the GAM's shortcomings, and the LPI values for the Indo-Pacific and Afrotropical were well within the null-model expectations (Fig. 4 in our original study[2]). Second, although the LPI methodology has been updated before, the GAM has existed in its current form for 14 years [9], entrenching itself as an invaluable tool for communication, advocacy, policy and research[11]. This includes seven editions of the *Living Planet Report* and its use as an indicator for the Convention on Biological Diversity, the Sustainable Development Goals and other multilateral environmental agreements (summarized by ref. 11). Any effort to upgrade the LPI must, therefore, be sensitive to preserving this legacy and documenting the consequences of any changes because the value of the LPI is determined by the collective buy-in from a diverse range of stakeholders (which accrues over many years) and not just its statistical properties.

No single indicator encapsulates biodiversity perfectly. As a community, we should strive to understand the strengths and weakness of various indicators, not only in terms of statistical correctness but also in terms of the perceived legitimacy by stakeholders. Talis and Lynch's comments are valuable for interrogating the robustness of the LPI, but they do not invalidate any of the conclusions from our study.

## Reporting summary

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

## Data availability

This manuscript contains no empirical data. Simulated data can be generated using the accompanying R scripts, available at https://doi.org/10.5281/zenodo.7841252.

## Code availability

The code used to generate Fig. 1 is available at https://doi.org/10.5281/zenodo.7841252.

## Author contributions

F.T.B. developed the simulation and wrote the first draft, J.G.H., L.S. and B.W.T.C. revised and approved the final manuscript.

## Competing interests

The authors declare no competing interests.

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