

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

Received: 24 February 2023

Emma J. Talis ^{1,2} & Heather J. Lynch ^{2,3} 

Accepted: 30 April 2023

Published online: 05 June 2023

 Check for updates

ARISING FROM F. T. Buschke et al. *Nature Ecology & Evolution*
<https://doi.org/10.1038/s41559-021-01494-0> (2021)

In a recent study, Buschke et al.¹ found that small additive population fluctuations led to a declining Living Planet Index (LPI), despite average population sizes remaining steady, and argue that, rather than a constant baseline at 1, the null expectation of the LPI should be one of decline. Buschke et al.¹ do not invalidate the LPI as an effective tool for measuring biodiversity, but instead encourage the use of randomized null models as a baseline for assessing LPI trends. As the framework of the LPI is gaining momentum and is increasingly being used to quantify population changes in specific taxa^{2,3}, habitats⁴ and countries^{5,6}, having an accurate and robust null expectation for index values is critical.

We appreciate the authors' focus on this issue, as understanding how the LPI is affected by random population fluctuations is crucial to the interpretation of trends in the index. We disagree, however, with the authors' focus on additive population fluctuations, which we are concerned may represent a distracting straw man for evaluating the LPI's performance. Buschke et al.¹ argue that ecological drift, demographic stochasticity and observation error are all additive processes, and model them with constant annual fluctuations equal to a percentage of the initial population count. However, under the assumption of a closed population, demographic processes do not result in a constant number of births or deaths irrespective of the current population count⁷. Thus we argue that demographic stochasticity, similarly to environmental stochasticity and all other processes except for immigration, should not be modelled additively. Instead, ecologists overwhelmingly model growth, death and survival as multiplicative processes, resulting in abundances that fluctuate log-normally^{8–10}. For these reasons, the LPI was designed to consider populations undergoing exponential dynamics. When population fluctuations are assumed to be multiplicative, the resulting null model for the LPI (population growth rates symmetric about zero) shows no bias (the null expectation of the LPI is a constant line at 1). While the prevalence of additive demographic stochasticity was addressed by Buschke et al.¹ in the review of their original manuscript, there has been no evidence to suggest that additive fluctuations

play a dominant role for a meaningful number of time series. While the original paper points to previous work¹¹, this study did not directly compare additive and multiplicative models for observed time series and, as such, presents no direct evidence to support the idea of additive demographic stochasticity. Given its importance to the LPI, such a comprehensive assessment of stochasticity in empirical time series is urgently needed.

Buschke et al.¹ also show that the use of a generalized additive model (GAM) to interpolate and smooth empirical time series leads to biased LPI estimates when populations are increasing or decreasing nonlinearly. We could not agree more that the use of the GAM to interpolate time series in this context is problematic; in fact, given the title of the original manuscript, readers of the original paper may not fully appreciate that the issue lies with the GAM and not with the mathematical framework of the LPI. Here, we highlight that it is the use of the GAM to interpolate missing data that biases the LPI (as is clear from Buschke et al.'s analysis¹). The GAM has two additional downstream impacts on the LPI that were not emphasized in the original study. First, the GAM is highly sensitive to the density of the empirical data and even minor changes in the data (particularly at the beginning and end points of the time series) can have drastic impacts on the final estimated GAM and the resulting LPI. Second, the GAM not only interpolates missing data, but also smooths the time series where data were observed. This smoothing of the data leads to a drastic reduction in interannual variation that has a substantive impact on the resulting index. As abundance time series of some species display considerable interannual fluctuations^{12–14}, preserving this variability is critical to understanding their population dynamics and producing an accurate index of change through time. It is precisely for this reason that we are concerned about the authors' suggestion to combat this issue using a randomized reshuffling null model. As noted by Buschke et al.¹, this approach cannot be used to estimate the trend of the LPI across the whole time series, requiring instead a narrow focus on the value of

¹Department of Applied Mathematics and Statistics, Stony Brook University, Stony Brook, NY, USA. ²Institute for Advanced Computational Science, Stony Brook University, Stony Brook, NY, USA. ³Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY, USA.

✉ e-mail: emma.talis@stonybrook.edu; heather.lynch@stonybrook.edu

the final-year LPI at the expense of how changes in populations might accrue through time. Calculating the full trajectory of the LPI can yield clear epochs of population change that may link to ecological or anthropogenic drivers. These nuances are lost when reshuffling fluctuations between the beginning and ending abundances. We argue that a better approach would be to simply replace the GAM with a more mechanistic framework for data interpolation. The use of a state–space model^{3,12,15} addresses all of the above concerns with the GAM without requiring any ad hoc post-processing and preserves the capacity to look at change within the time series rather than simply at the two end points. State–space models also allow for a much more informed modelling approach to improve interpolation of missing data than is provided by a GAM, and easily facilitate the incorporation of covariates, spatial autocorrelation or even age structure. As the LPI grows in popularity as a biodiversity index for use by policy-makers, addressing these key statistical issues becomes increasingly important.

Data availability

Data sharing is not applicable to this article as no datasets were generated or analysed during the current study.

References

- Buschke, F. T., Hagan, J. G., Santini, L. & Coetzee, B. W. T. Random population fluctuations bias the Living Planet Index. *Nat. Ecol. Evol.* **5**, 1145–1152 (2021).
- Saha, A. et al. Tracking global population trends: population time-series data and a Living Planet Index for reptiles. *J. Herpetol.* **52**, 259–268 (2018).
- Pacoureau, N. et al. Half a century of global decline in oceanic sharks and rays. *Nature* **589**, 567–571 (2021).
- McRae, L., Böhm, M., Deinet, S., Gill, M. & Collen, B. The Arctic Species Trend Index: using vertebrate population trends to monitor the health of a rapidly changing ecosystem. *Biodiversity* **13**, 144–156 (2012).
- van Strien, A. J. et al. Modest recovery of biodiversity in a western European country: the Living Planet Index for the Netherlands. *Biol. Conserv.* **200**, 44–50 (2016).
- Currie, J. et al. Assessing the representation of species included within the Canadian Living Planet Index. *FACETS* <https://doi.org/10.1139/facets-2022-0063> (2022).
- Turchin, P. Does population ecology have general laws? *Oikos* **94**, 17–26 (2001).
- Kot, M. *Elements of Mathematical Ecology* (Cambridge Univ. Press, 2001).
- Nisbet, R. M. & Gurney, W. *Modelling Fluctuating Populations* (John Wiley & Sons, 1982).
- Murray, D. L. & Sandercock, B. K. *Population Ecology in Practice* (John Wiley & Sons, 2020).
- 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).
- Che-Castaldo, C. et al. Pan-Antarctic analysis aggregating spatial estimates of Adélie penguin abundance reveals robust dynamics despite stochastic noise. *Nat. Commun.* **8**, 832 (2017).
- Anderson, S. C., Branch, T. A., Cooper, A. B. & Dulvy, N. K. Black-swan events in animal populations. *Proc. Natl Acad. Sci.* **114**, 3252–3257 (2017).
- Talis, E. J., Che-Castaldo, C., Şen, B., Krumhardt, K. & Lynch, H. J. Variability, skipped breeding and heavy-tailed dynamics in an Antarctic seabird. *J. Anim. Ecol.* **91**, 2437–2450 (2022).
- Kindsvater, H. K. et al. Overcoming the data crisis in biodiversity conservation. *Trends Ecol. Evol.* **33**, 676–688 (2018).

Author contributions

E.J.T. and H.J.L. proposed the idea together, E.J.T. wrote the first draft of the manuscript, and both E.J.T. and H.J.L. finalized the manuscript together.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to Emma J. Talis or Heather J. Lynch.

Peer review information *Nature Ecology & Evolution* thanks the anonymous reviewers for their contribution to the peer review of this work.

Reprints and permissions information is available at 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 2023