“Towards a deeper understanding of how and why vertebrate populations are changing globally and regionally.”

PhD by Published Work

School of Biological Sciences

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Contents

Abstract

Tackling the threats to biodiversity and reversing declines requires an understanding of how it is changing and what the key drivers of change are. One of the largest data sets used to assess these trends globally is that underlying the Living Planet Index (LPI), a biodiversity indicator based on vertebrate population trends. This data set contains just under 40,000 population trends from over 5,000 species collected at monitoring sites in terrestrial, freshwater and marine habitats around the world. However, gaps in the geographic and taxonomic representation of the data set risk incorporating bias into our current understanding of biodiversity change. Assessing and addressing any potential bias in the LPI, coupled with an insight into how common drivers of biodiversity decline relate to the observed trends, can help advance knowledge of how and why vertebrate populations are changing regionally and globally.

Using the database that populates the LPI, I first analysed trends in vertebrate populations in the Arctic and revealed an average increase in relative abundance across the region but varying trends among the High, Low and Sub Arctic. Critically, declines were recorded in sea-ice associated species, which are particularly vulnerable to impacts in this rapidly changing ecosystem. My second paper assessed the taxonomic and geographic bias in the global LPI. The lowest representation of known vertebrate species was found in tropical biogeographic realms and among herptiles and fish. A method for mitigating this bias was proposed which employs a proportional weighting for each taxa-realm combination informed by the estimated species richness within that subset. Applying this diversity-weighted approach to calculating the global LPI produced an index which suggests that trends in vertebrate populations are more negative than previously thought.

The second two papers examine two of the most common drivers of biodiversity decline: habitat loss and exploitation. Firstly, I explored trends in species which are wholly reliant on forests as their habitat and found that their populations are declining more on average than terrestrial species in general. Along with my co-author we also used two forest data sets to examine the relationship between tree cover change and population trends. There was no evidence of a relationship between these two variables, but we did find a significant association with whether the population was threatened with overexploitation. For the final paper, I used information on whether or not a population was utilised to explore global and regional trends in populations that support people's wellbeing or livelihoods. I found an average decline of 50% in utilised populations since 1970 and a more negative trend than populations which are not utilised. Crucially, a positive trend was associated with when a population was subject to targeted management. Both of these papers resulted in two new indicators which have been identified for use in monitoring progress towards global

biodiversity goals and targets of the Convention on Biological Diversity: the Forest Specialist Index and the LPI for utilised populations.

Together these four publications present a clearer picture of how vertebrate populations are fluctuating globally and regionally, and better evidence of how common drivers of change relate to these trends. Limitations remain as to how population time-series data are aggregated into a global indicator and how data bias and uncertainty is addressed. Whilst abundance data is a valuable and sensitive metric for measuring biodiversity change, advances in how the data are analysed to produce global assessments will be vital to ensure a better understanding of trends in vertebrate populations and how they are predicted to change under future environmental change scenarios.

Submitted publications and declaration of authorship

I am submitting four publications for this PhD by published work, listed below with external links and the full manuscripts included in the Published work section at the end of my thesis. These publications were published between 2012 and 2022 and include co-authors primarily from the Zoological Society of London, WWF and UNEP-WCMC. A brief statement for each paper is included along with author contributions which are listed in the table according to the relevant CRediT terms.

1. McRae, L., Deinet, S., & Freeman, R. (2017). The diversity-weighted Living Planet Index: controlling for taxonomic bias in a global biodiversity indicator. *PloS one*, *12*(1), e0169156. https://doi.org/10.1371/journal.pone.0169156

One of the key challenges in the development of the Living Planet Index is how to address bias in the underlying data. This paper presented a potential solution to mitigate the taxonomic and geographic bias and provide a better estimate of vertebrate population trends globally. I led the analysis for this publication and RF led the development of the R package "rlpi", which accompanied the paper. The diversity-weighted method has since been used to calculate the global Living Planet Index for policy reports and biennial Living Planet Reports.

CRediT term	*Authors*
Conceptualization	LM, RF
Methodology	LM, SD, RF
Software	LM, SD, RF
Validation	LM
Formal analysis	LM, SD
Investigation	LM
Data Curation	LM, SD
Writing - Original Draft	LM
Writing - Review & Editing	LM, SD, RF
Visualization	LM, RF

2. McRae, L., Böhm, M., Deinet, S., Gill, M., & Collen, B. (2012). The Arctic Species Trend Index: Using vertebrate population trends to monitor the health of a rapidly changing ecosystem. *Biodiversity*, *13*(3-4), 144-156 https://doi.org/10.1080/14888386.2012.705085

As part of a project funded by the Conservation of Arctic Flora and Fauna (CAFF), a regional application of the Living Planet Index was developed. This index used data from vertebrate populations located within the Arctic boundaries (according to two definitions) to present aggregated trends in abundance over time and provide a picture of how vertebrate species were faring in the Arctic ecosystem. The results were used by CAFF in three reports and in the suite of environmental indicators used for their annual report cards. The publication of the results in this paper was part of a special issue of the journal *Biodiversity* on ‘Circumpolar Biodiversity’.

CRediT term	*Authors*
Conceptualization	LM, BC
Methodology	LM, BC, MB
Validation	LM, BC, MG
Formal analysis	LM
Investigation	LM
Data Curation	LM, SD
Writing - Original Draft	LM
Writing - Review & Editing	All authors
Visualization	LM, MB
Supervision	BC
Funding acquisition	MG

3. Green, E. J., McRae, L., Freeman, R., Harfoot, M. B., Hill, S. L., Baldwin-Cantello, W., & Simonson, W. D. (2020). Below the canopy: global trends in forest vertebrate populations and their drivers. *Proceedings of the Royal Society B*, *287*(1928), 20200533. https://doi.org/10.1098/rspb.2020.0533

This paper accompanied a WWF report of the same title and sought to assess trends in forest specialist vertebrate populations and explore whether the trends in vertebrate populations in forests correlate with changes in tree cover. The work produced a new indicator, the Forest Specialist Index (FSI), which was used in the FAO’s State of the World’s Forests report. That tree cover and wildlife trends did not correlate provided support for including the FSI alongside indicators of forest cover and connectivity to ensure that trends in forest species are represented when measuring progress towards biodiversity targets. I led the analysis and development of the FSI and EJG led the correlational analysis between population trend and tree cover change.

CRediT term	*Authors*
Conceptualization	W B-C, WDS
Methodology	EJG, LM, RF, MBH, SLH
Validation	EJG, LM, W B-C, WDS
Formal analysis	EJG, LM
Investigation	EJG, LM
Data Curation	EJG, LM
Writing - Original Draft	EJG, LM
Writing - Review & Editing	All authors
Visualization	EJG, LM
Supervision	W B-C, WDS
Funding acquisition	W B-C

4. McRae, L., Freeman, R., Geldmann, J., Moss, G. B., Kjær-Hansen, L., & Burgess, N. D. (2022). A global indicator of utilized wildlife populations: Regional trends and the impact of management. *One Earth*, *5*(4), 422-433. https://doi.org/10.1016/j.oneear.2022.03.014

Here, I analysed the global and regional trends in populations that are utilised in order to assess the impact that this activity has on species that are important for people. I examined the relationship between whether a vertebrate population is utilised or not, the importance of body size and if the presence of conservation management can mitigate any negative impact on a population. Another objective of this work was to develop an indicator of utilised populations for use by the IPBES assessment of sustainable use of wild species. I wrote the manuscript, and I led the analysis with support from RF.

CRediT term	*Authors*
Conceptualization	All authors
Methodology	LM
Validation	LM
Formal analysis	LM, RF
Investigation	LM
Data Curation	LM
Writing - Original Draft	LM
Writing - Review & Editing	All authors
Visualization	LM, RF
Funding acquisition	NDB

Contextual chapter

Introduction

Globally, biodiversity is under pressure from five main anthropogenic drivers: habitat loss, invasive species and disease, overexploitation, pollution and climate change (Díaz *et al.*, 2019; IPBES, 2019). Few areas of the world are thought to remain unaffected by these drivers (Halpern *et al.*, 2008; Venter *et al.*, 2016) and many pressures are anticipated to continue at sustained or increasing levels (IPBES, 2019). Understanding the impact of this human activity on biodiversity is key in order to realise the scope and severity of the problem and implement strategies to mitigate it. Assessing biodiversity change at the global level is relevant as many underlying drivers are global in nature and scope and the response needed to address the issues is required at scale (Díaz *et al.*, 2019).

However, obtaining a single measure of global biodiversity is challenging given the complexity underlying the term and the heterogeneity with which biodiversity changes in space and time, and across different taxa and habitats (Valdez *et al.*, 2023). There are many measures for species alone, such as extinction risk (Rodrigues *et al.*, 2014), species richness (Dornelas *et al.*, 2014; Newbold *et al.*, 2015) and abundance (Newbold *et al.*, 2015; Daskalova, Myers-Smith and Godlee, 2020). Some of these global datasets have also been aggregated into biodiversity indicators to measure progress towards international policy targets (Butchart *et al.*, 2010; Tittensor *et al.*, 2014). These indicators produce a single value of change over time for the given metric and can be produced at global and regional scales: “Red List Index” (Butchart *et al.*, 2004; Szabo *et al.*, 2012); “Biodiversity Intactness Index” (Newbold *et al.*, 2016; De Palma *et al.*, 2021); “Living Planet Index” (Collen *et al.*, 2009; Marconi *et al.*, 2021).

In order for such indicators and underlying datasets to accurately report on changes in biodiversity, it is vital that they are representative of the component of biodiversity being measured and that drivers of change can be attributed to best explain the observed trends (Jones *et al.*, 2011; van Strien, Soldaat and Gregory, 2012). This can require describing and addressing bias within the data (Boyd *et al.*, 2022) and coupling biodiversity responses with data on anthropogenic pressures to uncover the most important factors behind the trends (Johnson *et al.*, 2023).

One of the main biodiversity indicators, the Living Planet Index, indicates trends in vertebrate populations globally. It has been used by WWF to communicate broad trends in biodiversity since 1998 (Ledger *et al.*, 2023) and was one of a suite of indicators selected to measure progress towards Convention on Biological Diversity targets (Butchart *et al.*, 2010; Tittensor *et al.*, 2014; Secretariat of the Convention on Biological Diversity, 2020). While the disparity in the geographic and taxonomic representation of the data has been well documented (Loh *et al.*, 2005; Collen *et al.*, 2009) the bias has never been quantified or mitigated. Furthermore, there has been little attempt to connect the trends shown by the LPI to direct drivers of change. Consequently, the current estimates shown by the LPI may not be representative of vertebrates globally. This body of work sets out to address these shortcomings and to develop techniques that will gain a deeper understanding of global vertebrate trends globally and regionally.

Aims and research questions

My key aims were to estimate global and regional trends in vertebrate populations and to understand how they relate to common drivers of biodiversity decline. I also sought to address the suitability of the current method for producing the Living Planet Index considering the variation in how poorly many regions and taxa are represented. I therefore assessed the taxonomic and geographic bias in the data and investigated options to mitigate this within the indicator calculation. To achieve these aims, I tackled the following research areas:

1. *Improving estimates of trends in vertebrate populations by addressing data biases.*
2. *Using vertebrate trend data to monitor the health of a rapidly changing ecosystem.*
3. *Exploring whether trends in forest vertebrate populations correlate with changes in forest habitat.*
4. *Using vertebrate trend data to help understand the impact of utilising wildlife populations and the benefits of management.*

I based my analysis on the data set that underpins the Living Planet Index, which is the largest database of vertebrate population time-series data available. The database and the index have been widely used in research and policy (Ledger *et al.*, 2023). As both the database and the method behind the calculation of the LPI form the basis of much of my work presented here, the following gives a brief introduction to these important components.

Living Planet Database (LPD: https://www.livingplanetindex.org/search)

The Living Planet Database is a resource containing vertebrate population time-series data. Data have been collated for the LPD on a near continual basis since the LPI was first developed in 1998. The data collation focusses on population-level abundance data as it can provide a sensitive measure of biodiversity change in response to environmental drivers. The decision was taken when the LPI was first developed to focus only on vertebrates, because data are more widely available than for invertebrates, plants and fungi. The primary use of the LPD is for populating the LPI but it has also been used for other research applications (Ledger *et al.*, 2023).

The LPD currently contains just under 40,000 population time-series from over 5,000 vertebrate species using monitoring data collected at specific sites in terrestrial, freshwater and marine habitats around the world. Since 2006 the data have been collected by the LPI team based at the Zoological Society of London using a combination of systematic and keyword searches. The systematic search involves regular scanning of a set of journals within the conservation biology, wildlife management and ecology disciplines, and the keyword searches encompass both academic and generic search engines. The data sources collected are primarily from peer-reviewed literature, but also from grey literature, online databases, and data holders. Data sources are identified if they meet the criteria for inclusion in the LPD: single vertebrate species abundance estimates from a multi-annual survey conducted since 1970, monitored using a consistent method and effort (Collen *et al.*, 2009). The time-series in the LPD vary in spatial and temporal extent. Time-series lengths range from 2 to over 50 years, and survey sites span spatial scales from forest plots to continents. Different metrics can be used to measure abundance and many of these are accepted into the LPD such as a total count of individuals, a population estimate, density or proxy such as number of nests (see https://www.livingplanetindex.org/about_index).

Data processing was also carried out by individuals from the LPI team and for any records entered by newly trained members, there was an additional check conducted by a more experienced member of the team. Details in the data sources, especially sections on limitations, were read to ensure that the abundance estimates were reliable and not an artifact, for example an increasing trend due to increased effort would not be included unless a correction factor was applied. Ancillary information on the survey location, ecology and human activity (conservation interventions, utilisation and threats) was collected from the data source alongside the time-series data.

Living Planet Index method

The LPI method was one of the main tools used within my publications to analyse the data from the LPD. It was developed specifically to measure trends in relative abundance using population time-series data of differing metrics, scale and length (Loh *et al.*, 2005; Collen *et al.*, 2009). The first stage of the method is the use of a generalised additive modelling (GAM) framework whereby time-series with six or more annual data points are modelled using a GAM and time-series with fewer than six annual data points are modelled using log linear interpolation (Collen *et al.*, 2009).

The method used to aggregate the time-series data in the index is the *geometric mean*, which is an approach used in other species abundance indicators, most notably the European bird indices (Gregory *et al.*, 2005). Geometric mean abundance has been assessed as a sensitive measure of biodiversity change which makes it suitable for use in indicators (van Strien, Soldaat and Gregory, 2012; Santini *et al.*, 2017). The geometric mean allows for the doubling of a population to equate with a halving and so it measures changes in relative abundance rather than absolute abundance (Buckland *et al.*, 2011). The use of the geometric mean also allows for different levels of aggregation within an index so in the case of the LPI, modelled abundance trends can be aggregated from populations to species and then to a single index (Figure 1). By averaging population trends within each species, rare and common species are given equal weight within an index.

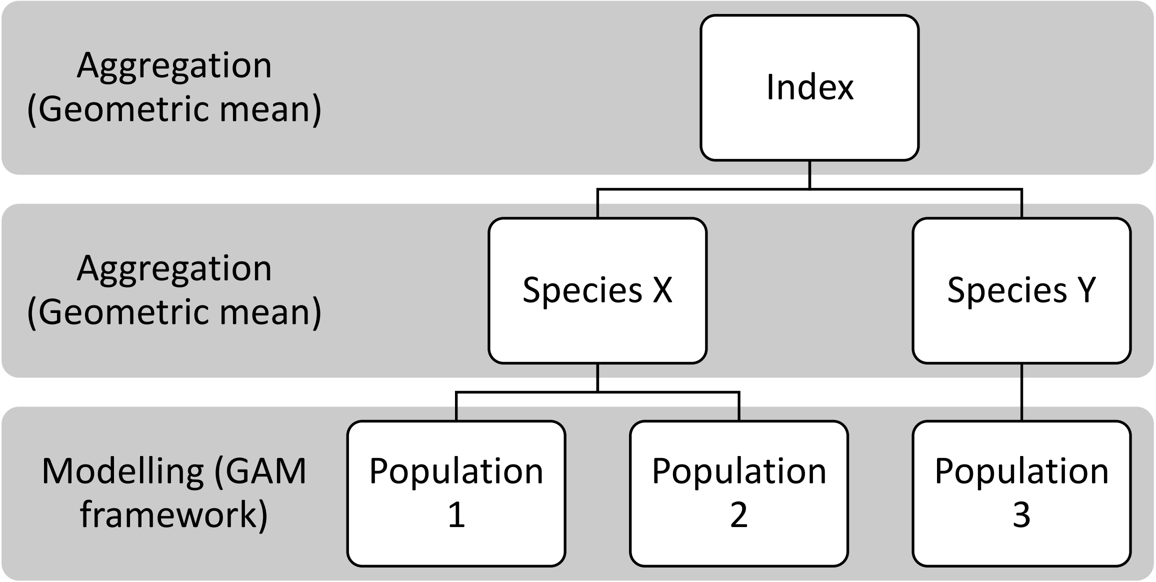

Figure 1: Schematic showing the basic aggregation of the Living Planet Index whereby modelled population trends are aggregated first to species level and then to a single index using a geometric mean (Collen *et al.*, 2009).

Further levels of aggregation can be implemented between species trends and the final index, and values can be attributed to each subset in the index so that they carry different weightings within the overall mean. This approach of assigning weights to different subsets of the data was introduced in my 2017 LPI paper in order to mitigate the taxonomic and geographic bias in the global LPI data (McRae, Deinet and Freeman, 2017). The subset of LPI data used and the method chosen for aggregating the index in each publication are summarised in Table 1 and detailed in each synthesis.

Confidence intervals for each index were calculated using bootstrap resampling of the species trends with replacement for 10,000 iterations (Collen *et al.*, 2009). With the exception of the 2012 Arctic Species Trend Index publication (McRae, Böhm, *et al.*, 2012), the LPI method was run using the R package “rlpi” (Freeman *et al.*, 2015).

Table 1: The subset from the Living Planet Database and the method of index aggregation used for the four papers in this thesis.

Publication	Data from the LPD used	Index aggregation
McRae *et al.* 2017	All vertebrate populations	Populations weighted equally within species; Species weighted equally within 57 taxa-realm subsets; Taxa-realm subsets weighted by estimated species richness within terrestrial, freshwater and marine systems; Terrestrial, freshwater and marine systems weighted equally in the global LPI.
McRae *et al*. 2012	Vertebrate populations located within the High, Low and Sub Arctic	Populations weighted equally within species; Species weighted equally within the Arctic Species Trend Index.
Green, McRae *et al.* 2020	Vertebrate populations for species which occur only in forests	Populations weighted equally within species; Species weighted equally within 14 terrestrial taxa-realm subsets; Taxa-realm subsets weighted by forest species richness within the Forest Specialist Index.
McRae *et al.* 2022	Vertebrate populations identified as a utilised population	Populations weighted equally within species; Species weighted equally within the LPI for utilised populations.

One of the outputs from the rlpi package is a matrix of lambda values (annual rates of change either at the population or species level). This is a product of the modelling framework and includes the model estimates of annual population, or annual species rates of change (the latter are the mean of annual population rates of change for that species). This output was used for the mixed-effects models in Green et al. (Green et al., 2020) and McRae et al. (McRae et al., 2022).

1. Improving estimates of trends in vertebrate populations by addressing data biases.

Synthesis

The Living Planet Index (LPI) has been used since 1998 as a global biodiversity indicator, based on a subset of vertebrate populations for which data are available (Ledger *et al.*, 2023). However, the taxonomic and geographic bias in the data has been well documented (Loh *et al.*, 2005; Collen *et al.*, 2009), and these assessments raise the question of how well the LPI represents vertebrate species globally, and what approaches could be taken in order to mitigate the effect of data bias on the resulting trends. Data bias does not necessarily lead to bias in trends (Boyd *et al.*, 2022), but through disaggregation of the LPI, the impact of data bias on trends became apparent when average trends calculated for a given region reflected the data-rich taxa but not others. One of the clearest examples of this was for the Palearctic, the biogeographic realm spanning Europe and the northern parts of Asia. The Palearctic LPI calculated using the current LPI method at that time (Collen *et al.*, 2009), showed a 38% increase in the index and when disaggregated by taxa, a similar increase was found in mammal and bird populations, whereas freshwater fish and herptile populations were found to be declining. This was because the number of bird and mammal species in the Palearctic outweighed the other taxa almost five-fold whereas their combined estimates represent less than 50% of known vertebrate species in the Palearctic (Table S6. (McRae, Deinet and Freeman, 2017)). Arguably an aggregated index should better reflect this heterogeneity in taxonomic trends.

To address this my co-authors and I explored a diversity-weighted approach to calculating the LPI. We first collated estimates of known species within each biogeographic realm. We then used these estimates to assign a weight to each of the 56 taxa-realm subsets of the LPI data based on the relative diversity (represented by species richness) that each subset represents (regardless of how many species had data available in the LPI). The existing LPI method incorporated an equal weighting for temperate and tropical regions as well as terrestrial, freshwater and marine systems. This new method retained the equal weighting for systems but now also included a proportional weighting for biogeographic realms and taxonomic groups. Species rich subsets of data such as Neotropical herptiles received a higher weighting than less species rich subsets such as Palearctic mammals. This new weighted approach for calculating the LPI (known as LPI-D) produced a new estimate of a 58% average decline in monitored vertebrate population abundance between 1970 and 2012 (Figure 5: Index value: 0.42, 95% CI: 0.34-0.52. (McRae, Deinet and Freeman, 2017)). The trend was more negative than using the previous LPI method (LPI-U), which produced an index with a decline of 20%, and we found this pattern globally and across terrestrial, freshwater, and marine systems (Figure 5-6. (McRae, Deinet and Freeman, 2017)).

As part of this analysis, we also assessed how many of the known species from each taxa-realm subset were currently represented in the LPI and found a broad range in representation from <1% of Afrotropical terrestrial and freshwater herptiles to 100% of Pacific north temperate marine reptiles. We also discovered that some of the groups that had the lowest representation were some of the most heavily weighted in our new LPI-D approach, and so conducted further analysis to test the implication of this on our results. We removed the subsets which represented <1% of known species - Afrotropical terrestrial and freshwater herptiles and Indo-Pacific freshwater fishes – but found that the removal of these low-representation groups did not significantly alter the global, terrestrial or freshwater trends (there were no marine subsets with representation <1%).

Biodiversity monitoring and global biodiversity databases are known to be taxonomically and geographically biased (Yesson *et al.*, 2007; Boakes *et al.*, 2010) but addressing this disparity in data would be resource intensive and could be challenging to implement quickly, with data possibly lacking for some groups. Whilst this new approach to aggregating vertebrate population trends globally is not without limitations (see below), it can provide a pragmatic approach to mitigating bias in lieu of a representative set of biodiversity data.

Impact and contribution to discipline

This publication provided an improved estimate of vertebrate population trends by mitigating the bias towards well-studied regions and taxa, an issue which had been previously highlighted as a shortcoming in the LPI and in global biodiversity monitoring and indicators in general (Loh *et al.*, 2005; Collen *et al.*, 2008, 2009; Proença *et al.*, 2017). To the best of my knowledge, this approach to calculating the LPI remains the most comprehensive indicator of global vertebrate population trends published to date. The primary output for new results of the LPI is the Living Planet Report, WWF's flagship publication on the global state of nature and of human pressures on the environment. This version of the LPI method was first used in the 2014 Living Planet Report (WWF, 2014) and has been used in all subsequent editions (WWF, 2016, 2018, 2020, 2022).

The LPI-D method was also used to produce a global indicator of vertebrate population trends for measuring progress towards international policy targets and was featured in the UN publications, Global Biodiversity Outlook 5 (Secretariat of the Convention on Biological Diversity, 2020) and Global Environment Outlook 6 (Stoett *et al.*, 2019). The diversity-weighted LPIs for terrestrial, freshwater and marine populations were also used to measure progress towards targets for wetlands as part of the Ramsar Convention reporting (Ramsar Convention on Wetlands, 2018).

Aside from the publication of the LPI-D method, the assessment of species representation in the LPI from this paper has been cited to highlight disparity in global biodiversity monitoring and to call for efforts to tackle data deficiency in under-represented taxa (Hochkirch *et al.*, 2021; Stephenson *et al.*, 2022; Samu *et al.*, 2023).

The R package “rlpi” that was the developed alongside this paper (Freeman *et al.*, 2015), has since been used in other publications to calculate trends for a range of species (Hardesty-Moore *et al.*, 2018; Spooner, Pearson and Freeman, 2018; He *et al.*, 2019) and to generate new indicators (Bayraktarov *et al.*, 2021; Marconi *et al.*, 2021; Millard *et al.*, 2021). The weighted approach to the LPI has been applied to derivatives of the LPI for reptiles (Saha *et al.*, 2018), forest specialists (Green *et al.*, 2020), Mediterranean vertebrates (Galewski *et al.*, 2021), and to produce a weighted version of the Wetland Extent Index (Darrah *et al.*, 2019).

Critique

Some of the limitations of the diversity-weighted LPI were noted at the time and others have arisen since, which I discuss below. One concern is that the placing of higher weight on trends from species-rich regions could produce unintended consequences. For example, tropical regions tend to have a higher species richness and a greater proportion of those that are threatened (Grenyer *et al.*, 2006), which may introduce a bias towards taxa at risk of extinction. These are also regions which tend to be less well monitored (Collen *et al.*, 2008), so the greater weight is placed on places with the least amount of data. A similar risk is faced when applying higher weights to the more species-rich taxa: fishes and herptiles. These groups have the lowest representation amongst vertebrates within the LPI and more broadly within species research and monitoring (Moussy *et al.*, 2022). Furthermore, it’s not known how well the species that have been monitored reflect trends in the taxonomic groups as a whole; this makes the placement of high weight alongside high uncertainty a potentially risky approach.

The weightings for the new approach to aggregating the LPI are based on current estimates of species richness within biogeographic realms. However, current species totals are likely to be underestimates so these values could change over time as new species are discovered, described or taxonomy evolves (Scheffers *et al.*, 2012). The extent of this discrepancy between known and actual species varies between taxonomic groups and regions (Scheffers *et al.*, 2012; Moura and Jetz, 2021); it has been suggested that, amongst terrestrial vertebrates, new species to be documented are more likely to be amphibians and reptiles and in high biodiverse regions (Moura and Jetz, 2021). These expected changes have consequences for the diversity-weighted method of calculating the LPI as the weights applied to taxa and regions will need to be reviewed regularly according to future revisions of species richness estimates. What is less clear is whether these amendments will have a significant bearing on the resulting global trend. It seems plausible that the groups currently weighted highly in the LPI - reptiles, amphibians, fishes - would remain so given that more newly described species are anticipated for these taxa than for birds and mammals (Scheffers *et al.*, 2012). However, as species estimates and associated weighting for reptiles, amphibians and fishes are revised upwards, one likely impact is an increased gap between the weighting for these taxa and for birds and mammals, particularly in tropical regions. The increased weighting for fishes and herptiles could be compounded by the prevalent declining trends in these groups and lead to a more negative global vertebrate trend.

Another limitation was proposed by Buckland and Johnston (Buckland and Johnston, 2017) who state that in order to represent biodiversity change in a given region, sampling locations should be representative of the region of interest. They raise concern that the LPI-D method attributes arbitrary weighting to a realm within which sampling is distributed unevenly and that this may bias estimates of trends (Buckland and Johnston, 2017). The LPI-D method was developed at a broad geographic scale, so whilst relative species-richness between biogeographic realms is accounted for, heterogeneity within realms is not. For example, the data from the Palearctic realm is largely from Western Europe and eastern and southern Africa are better represented that other areas of the Afrotropics (McRae, Deinet and Freeman, 2017).

Whilst the global LPI results suggest an average decline in vertebrate abundance globally, subsequent analyses have found contrasting results and imply that broadly there is no net change in population abundance over time at the global scale (Daskalova, Myers-Smith and Godlee, 2020; Leung *et al.*, 2020). However, both studies found evidence of declines either for particular taxa (Daskalova, Myers-Smith and Godlee, 2020), or for certain taxa-realm subsets of the data (Leung *et al.*, 2020). Two possible reasons as to why those publications did not find a global signal in the data are the use of state space models to analyse population trends, and that no weighting of the data was used even to species level. Although a comparison between linear models and state-space models in their estimation of average rates of population decline was conducted (Daskalova, Myers-Smith and Godlee, 2020), there has been no thorough analysis of the LPI data illustrating the difference between state-space models and generalised additive models, the latter of which is use in the current LPI method. In addition, as an index, the LPI measures cumulative change, and this is not something which is captured by state-space models or linear models which measure trend and slope respectively.

This contradiction in findings has echoes of a long-standing debate over whether local species richness is in decline globally (Dornelas *et al.*, 2014; Cardinale *et al.*, 2018). Whilst that debate centred on a different metric of biodiversity change – that of alpha diversity - the nature of some of the disputes may well apply to global analyses of data in the LPI. For example, some of the arguments state that no decline in local species richness is observed because the spatial bias and lack of long time-series renders the data unsuitable to draw conclusions at the global scale (Gonzalez *et al.*, 2016; Valdez *et al.*, 2023).

A direct criticism of the use of the geometric mean to aggregate trends in the LPI claimed that the global average is driven by a small number of populations in extreme decline and that if they are removed, the global LPI shows a positive trend (Leung *et al.*, 2020). Two responses to this publication highlighted shortcomings of the analysis: that the effect of extreme increases on the global average were not considered and that the declines were arbitrarily selected and unusually extreme (Loreau *et al.*, 2022; Murali *et al.*, 2022).

A subsequent publication has also raised concerns over the way the LPI is calculated. The sensitivity of the geometric mean to outliers was highlighted and caution was raised over the application of proportional weightings as it can place a lot of weight on poorly studied taxa or regions (Buschke *et al.*, 2021). An additional limitation raised by this analysis demonstrates that random fluctuations caused by ecological drift, stochasticity or observation error are not currently accounted for and may bias the LPI negatively by 9.6% (Buschke *et al.*, 2021). The production of a null model is recommended in order to visualise this uncertainty in the overall percentage change when an LPI is calculated.

Whilst some of the recent challenges have been rebutted in the literature, there are still some pertinent questions such as the impact of random fluctuations and the potential use of state-space models that have yet to be fully understood and warrant more investigation if we are to further improve estimates of vertebrate populations trends globally.

2. Using vertebrate trend data to monitor the health of a rapidly changing ecosystem.

Synthesis

This publication arose from an invitation to contribute to a special issue on ‘Circumpolar biodiversity’ for the journal Biodiversity. I had recently developed the Arctic Species Trend Index (ASTI) for the Conservation of Arctic Flora and Fauna (CAFF), the biodiversity working group of the Arctic Council (McRae *et al.*, 2010; Eamer, Russell, L. McRae, *et al.*, 2012), and this work was a continuation of that area of research.

The ASTI had already been used as part of CAFF’s suite of biodiversity indicators for the Arctic but the application of the LPI method to the Arctic region had not yet been peer-reviewed, nor a detailed analysis conducted on the underlying data to understand how species were responding to rapid environmental change in this region. The ASTI was produced using the LPI method applied to the Arctic, as defined by the floristic boundaries of the High, Low and Sub-Arctic regions (AMAP, 1998). The pan-Arctic index which consisted of 323 vertebrate species and 809 population trends showed a 19% increase between 1970 and 2007 (Figure 1: 2007 index value 1.19; 95% CI 1.03-1.39 (McRae, Böhm, *et al.*, 2012)). The disaggregation by region showed an overall increase in the Low Arctic index (Figure 3b: 2007 index value 1.67; 95% CI 1.30–2.36 (McRae, Böhm, *et al.*, 2012)) and stability in the Sub Arctic index (Figure 3c: 2007 index value 0.97; 95% CI 0.82–1.15 (McRae, Böhm, *et al.*, 2012)), both with a decline in the most recent years. The High Arctic index declined overall (Figure 3a: 2007 index value 0.96; 95% CI 0.69-1.53 (McRae, Böhm, *et al.*, 2012)) but there had been a recent stabilisation followed by an increase in trends in recent years. A focus on sea-ice associated species, found that six out of the nine species analysed had populations in decline (Box 1.(McRae, Böhm, *et al.*, 2012)).

An in-depth look at the taxonomic, spatial and temporal features of the data set was conducted in order to examine data bias and quality issues in the indicator. Whilst the taxonomic coverage of 37% of Arctic vertebrates was considered good, there was a bias towards bird species and much variation in the geographic representation of the data. The monitoring data available varied spatially as well as temporally, with data gaps apparent in Scandinavia, Alaska and Iceland in the most recent decade of the index (Figure 8. (McRae, Böhm, *et al.*, 2012)). Not all of the 890 populations in the ASTI had a full time-series of between 1970 and 2007: the matrix of potential data points if each population time-series had the full complement of annual data points was 51% complete (Figure 7. (McRae, Böhm, *et al.*, 2012)). These findings are discussed below in the critique.

Potential drivers behind the trends were identified. For example, the increase in the primarily marine Low Arctic could have been driven by both recoveries in depleted cetacean populations and increases in the abundance of some marine fish in response to favourable environmental conditions (higher sea surface temperature and increased primary production) in regions such as the Bering Sea. Different factors were thought to be behind the trends in the other Arctic regions. The overall decline in the High Arctic may be attributable in part to rapidly changing environmental conditions driven by higher temperatures and more variable extent of sea-ice, whereas the Sub Arctic is closer to areas of higher human density and are likely to be more impacted by human activity directly.

This paper presented trends for a globally important and rapidly changing region and highlighted how environmental change can manifest either positive or negative impacts for Arctic species. Gaps were evident in the data set and recommendations such as more multi-species monitoring sites and more frequent monitoring were suggested which could help remedy the issues identified.

Impact and contribution to discipline

This paper was the first peer-reviewed study to show pan-Arctic trends in vertebrate species. The results highlighted the pressure on sea-ice dependent species in particular, but also the gaps in monitoring both taxonomically and temporally. The analysis also expanded on earlier explorations into indicator quality and data representation (Collen *et al.*, 2009) to show how temporal trends and data availability varied across decades and spatially. This was an important addition to the set of diagnostics used to interpret indices produced using the LPI method.

The ASTI was used to monitor progress towards the Aichi targets as part of the Convention on Biological Diversity 2011-2020 strategic plan for biodiversity (UNEP (United Nations Environment Programme)., 2010), and specifically to monitor changes in Arctic species. The results from this paper were also published in two later reports as part of the CAFF assessment series which synthesised trends in Arctic ecosystems and wildlife (Eamer, Russell, McRae, *et al.*, 2012; L. McRae *et al.*, 2012). The results were included in the 2013 Arctic Biodiversity Assessment (CAFF, 2013) and associated Arctic Biodiversity Congress in 2014 where a session was convened on the ASTI.

The data set behind the ASTI was later used for two new indicators. An index of trends in utilised species which occur in the Arctic was developed and published alongside the ASTI to see if species in use were faring differently, on average, compared to the overall regional trend (Tierney *et al.*, 2014). As the use of species is important for people's livelihoods and levels of exploitation in the Arctic are high, this region provided a useful case study for this new indicator (Tierney *et al.*, 2014). The index for Arctic utilised species was found to be increasing at a higher rate that Arctic species overall. This was thought to be due to a combination of species recovering from historically depleted populations, and that exploitation has become increasingly sustainable since 1970 according to the harvest index which was also presented in the paper (Tierney *et al.*, 2014).

The Arctic is an incredibly important region for migratory birds, especially shorebirds and geese (Zöckler, 1998) due to a short but intensively productive summer suitable for breeding conditions. Based on the ASTI data set, an indicator of trends in birds which migrate to the Arctic was published in a subsequent report (Deinet *et al.*, 2015). The ASTI data set was filtered to a set of 129 Arctic migratory bird species and then population trend data from regions outside of the Arctic were added in order to obtain a broad picture of trends for this group. On average, abundance trends in Artic migratory birds increased by 40% between 1970 and 2011; however, this varied between flyway regions and among taxonomic groups with declines observed in East and Central Asia, and for shorebirds (Deinet *et al.*, 2015).

The ASTI data set that was compiled for this publication has been added to the Global Biodiversity Information Facility (www.gbif.org). This has increased the visibility of the underlying data and, according to the download statistics, the data sets have been accessed and used multiple times. The combined use of the terrestrial, freshwater and marine versions of the ASTI data has so far reached over 40,000 download events and 257 citations (Barry, 2019c, 2019a, 2019b).

Critique

The limitations of using a non-stratified set of monitoring data were discussed in the paper (McRae *et al.*, 2012). Similar constraints to the global LPI were found, such as a taxonomic bias towards birds and a reduction in data availability for the most recent time points in the index (Collen *et al.*, 2009). The turnover in the availability of data was illustrated by showing locations with data for each decade between 1970 and 2007, and highlighting those locations where data was present in earlier decades but not for more recent decades (Figure 8.(McRae *et al.*, 2012)). Notably in the final decade there were more data gaps than locations with data (Figure 8.(McRae *et al.*, 2012)). The time lag between data being collected and published could account for the drop off in data but it is also possible that some surveys were discontinued due to cessation of a project or funding cycle. The impact of this turnover in data was not explored but would be important to analyse to gain a fuller interpretation of the index.

There are some caveats to consider when it comes to interpreting the ASTI. Although not a feature limited to the Arctic, one of the caveats of aggregating multiple species trends into an index is that certain species exhibit cyclical populations in their demography such as lemmings (*Dicrostonyx* spp. and *Lemmus* spp.) and caribou (*Rangifer tarandus*). If the time-series used has stopped at a certain point in the cycle, this could incorrectly attribute the direction of the long-term trend. This may have been a limitation in the use of trend data for caribou as the average length of time-series in the ASTI for this species (24 years) was shorter than the shortest population cycle known for this species (40 years).

Another consideration is that the baseline of 1970 is not always an appropriate starting point to measure trends from when considering the length of time that some species have been impacted by human activity for (Mehrabi and Naidoo, 2022). For example, commercial whaling impacted species from the early 1800s and so using the trends in a species such as the Grey whale (*Eschrichtius robustus)* from 1970 shows an increasing trend in abundance but would not reflect the historical decline due to whaling and that the increase recorded was not a recovery to historical abundance (Alter, Rynes and Palumbi, 2007).

Given the rapid environmental changes and predicted impacts on species and ecosystems in the Arctic since this analysis was published (Lannuzel *et al.*, 2020), it would be worth revisiting and producing an update of the ASTI. A focus on sea-ice associated species and improvements to attributing spatial variables to population trend data should be prioritised in order to capture important changes in the vulnerable ecosystems within the Arctic.

3. Exploring whether trends in forest vertebrate populations correlate with changes in forest habitat.

Synthesis

This paper was one of the outputs from a project focussed on understanding the status and trends in forest specialist vertebrates, species which are entirely reliant on forests as their habitat. The primary aim of the research was to develop an indicator for forest specialists using the Living Planet Index approach. This would fill a gap in the set of available indicators for forest ecosystems, which are predominantly based on forest area and tree cover and don't directly incorporate trends in biodiversity below the canopy. The second objective was to explore whether there is a relationship between changes in forest cover and vertebrate population trends. Given that habitat degradation and loss is one of the key threats to species, we predicted that changes in forests would correlate with responses in wildlife populations.

We identified "forest specialists" using the habitat coding from IUCN Red List assessments (IUCN, 2022) and selected those species which had only forest recorded as a habitat. The underlying assumption here is that if a species has only forest listed as a habitat, it relies entirely on forests and therefore is specialised for these ecosystems. This definition of specialist is quite narrow as the 'Forest' category from the IUCN Red List refers to natural habitat and does not include artificial habitats such as plantations. We also coded "forest generalists" as those species with forest identified as a habitat alongside other habitat categories. We used existing population time-series from the Living Planet Database but augmented this with data gathered from the scientific literature using keyword searches and by contacting organisations involved in collating monitoring data, for example the IUCN SSC Ape Populations, Environments and Surveys (A.P.E.S.) database (http://apesportal.eva.mpg.de) for primate data. The final data set consisted of 455 populations of forest specialists and 1,668 populations of forest generalists.

Using the diversity-weighted LPI method, we calculated average trends in forest specialist populations to produce the Forest Specialist Index (FSI). This index showed a decline of 53% between 1970 and 2014 which equates to an average 1.7% decline per year (Figure 1a: index value: 0.47; range 0.30–0.73. (Green *et al.*, 2020)). The average trend was more negative for herptiles, followed by mammals and was slightly positive on average for birds (Figure 2.(Green *et al.*, 2020)). More negative trends were found in tropical realms and biomes compared to their temperate counterparts (Figure 2.(Green *et al.*, 2020)), which may be related to more rapid rates of forest loss in tropical regions over that period (FAO, 2016), although the subsequent analysis suggests that factors other than deforestation, such as overexploitation, may be important.

To assess the relationship between tree cover and population trend, we used two forest data sets and two population data sets in a mixed effects model. Two forest data sets were used in the analysis as one had a more precise spatial resolution but shorter temporal span (Hansen *et al.*, 2013), and the other had a longer temporal data span but coarser spatial resolution (Song *et al.*, 2018). We also chose to analyse the forest specialist and forest generalist populations separately to see if the relationship differed between these two subsets. The results were somewhat unexpected as we found no evidence of a relationship between tree cover and trends in either forest specialists or forest generalists. This was true for both forest data sets used. Given the importance of natural habitat to specialist species this was a surprise, but we discuss some possible explanations behind this finding, which relate to both the mechanisms behind population change, and also the data sets that we were using for this research.

Overall, this paper suggests that a satellite-derived assessment of forest cover change alone may be inadequate as an indicator of trends in forest biodiversity, and that additional data on forest type or quality, and incorporating other drivers of change would be important to consider. However, the development of a Forest Specialist Index provides a solution to this by incorporating a direct measure of wildlife population trends within forests.

Impact and contribution to discipline

One of the key outputs from this paper was the development of the Forest Specialist Index. The results were included as part of a section on policy targets relating to forest species in FAO's State of World's Forests 2020 (FAO and UNEP, 2020) and in a report by WWF advocating for the use of the index to track changes in forest ecosystem health when the post-2020 global biodiversity framework was under discussion (Green *et al.*, 2019). The FSI was also adopted into the suite of indicators under the Biodiversity Indicators Partnership (https://www.bipindicators.net/indicators/living-planet-index/living-planet-index-forest-specialists) and included in provisional lists of indicators for the CBD post-2020 Global Biodiversity Framework (UNEP (United Nations Environment Programme), 2021). The addition of this indicator provided a vertebrate population trend metric for forests within global biodiversity frameworks, where measures of forest area and extent currently dominate.

The lack of a relationship found between tree cover change and population change was an important finding which, although unexpected, could be explained by the notion of below canopy defaunation whereby other threats, such as hunting, impact species within an intact forest e.g., (Benítez-López *et al.*, 2019). Our study provided evidence of this at a global scale and for a broader set of taxa, suggesting that while conversion of forest for agriculture is the most commonly cited threat (Maxwell *et al.*, 2016), we only found a negative relationship between the threat of overexploitation and population trends. The impact of hunting especially in the tropics has been implicated in the population decline of tropical bird and mammal species (Benítez-López *et al.*, 2017), and hunting was listed as a primary threat for 301 threatened terrestrial mammals (Ripple *et al.*, 2016); utilisation of populations is something I explored further in my final publication (McRae *et al.*, 2022).

Defaunation not only threatens forest species persistence, but also wider ecosystem function and forest regeneration (Gardner *et al.*, 2019). The role of forest species in maintaining carbon stores has been described as one of the key roles that is under threat from declines in taxa such as primates and birds (Gardner *et al.*, 2019). This is one of the topics that warrants further study in order to analyse trends in different functional groups of forest species, such as frugivores, to understand whether a decline in forest specialists may have a knock-on effect on processes such as seed dispersal and pollination in the future.

Critique

Whilst the lack of a clear relationship between tree cover change and trends in forest vertebrate populations may be explained by the impact of other threats such as overexploitation, there are limitations to the analysis and the data sets used that are important to consider. The use of data from the Living Planet Database confers the advantage of having site level abundance trend data alongside information on specific threats to that population. However, the forest specialist data set suffers from the same taxonomic and geographic bias as the global data set (McRae, Deinet and Freeman, 2017). Indeed, the data set lacked populations from some of the largest and most biodiverse forest regions such as the Amazon and the Congo basin, so findings are limited in how broadly they can be applied.

Finding a suitable data set to use for trends in forest cover was challenging due to the need to balance a data set with a suitable frequency and time frame and with the appropriate spatial resolution for modelling the population data. We opted to use two datasets, one which had a longer and compatible timeframe for the population data but coarser resolution, and the second which had a higher resolution but a shorter time series which meant we could include fewer populations. In short, neither of these data sets optimised both timeframe and granularity, which may explain why we were not able to pick up a signal in the data. The second limitation is that nether data set distinguishes between natural, semi-natural and non-natural forests, which may have added confounding effects when comparing tree cover change and population change. For example, an increase in tree cover would expect to benefit species in natural forests but not necessarily if that tree cover increase occurred within a plantation.

Using global data sets to capture relationships between anthropogenic drivers and biodiversity change can present a series of challenges, such as data gaps and differences in the research methods applied to collate data (Joppa *et al.*, 2016; Davison, Rahbek and Morueta-Holme, 2021). One of the key limitations can arise from joining two independent data sets which were not compiled for the same purpose. This variation in how, when and at what scale the data are collected creates challenges for interpreting any relationships measured between them. For example, the tree cover data sets and the population data from the LPD do not exactly match in scale. The spatial resolution of the tree cover data is defined according to a grid cell size, but the corresponding information is not explicitly captured for each population monitored within the LPD; instead, the centroid of the survey area for each population is recorded as a point location. The approach taken with this paper to extract tree cover data was to use a 5km buffer around the geographic coordinate recorded for each population; however, this range may not be suitable for all vertebrate taxa. This could limit any inference drawn from attributing spatial variables to a population trend as scale matters in understanding patterns of biodiversity change (Chase *et al.*, 2018).

Using a single explanatory data set to interpret patterns in wildlife trends might oversimplify what is often a complex relationship between drivers of change and biodiversity responses. Populations can be exposed to multiple threats simultaneously, so if other environmental factors are not considered, this may undermine the conclusions derived from studying the impact of a single driver. In this study we focussed primarily on habitat change but did consider other threats in the model, including the presence of overexploitation and proxies for human pressure, such as road density. However, these variables don’t capture all drivers and the proxies only offer indirect measures of potential threats, so it is plausible that key explanatory factors were omitted from this analysis. Another consideration is that the impact of multiple threats on populations is complex, but is crucial to measure (Côté, Darling and Brown, 2016). Despite this, our analysis did not consider threat interactions even though the number of threats has since been identified as a significant driver of resilience decline in vertebrate populations (Capdevila *et al.*, 2022b). Given that multiple threats frequently affect vertebrates at the local scale (Capdevila *et al.*, 2022a), capturing the impact of interactions, rather than individual threats, could provide a more accurate picture of the factors influencing trends in forest populations.

Finally, our approach to modelling in this paper could have been improved by testing the use of different time lags between tree cover change and population responses, as biodiversity does not respond immediately to environmental changes (Essl *et al.*, 2015). These ecological lags vary depending on the nature of the environmental change, for example lags may be shorter for habitat loss than for habitat degradation, and time lags can also vary according to different types of drivers (Essl *et al.*, 2015; Jackson, Pawar and Woodward, 2021). A recent study recorded delayed impacts of environmental change on vertebrate populations of up to nine years and recommended that time lags are considered when exploring the relationship between land-use change and population trends (Cornford *et al.*, 2023). In this paper, we used a one-year time lag between annual tree cover change and population response; however, a large-scale analysis including some of the same data, and published later the same year, found that lags of up to 50 years were important in analysing the effect of forest loss on populations (Daskalova *et al.*, 2020). Our paper concluded that there was greater complexity behind forest population trends than can be explained by tree cover data alone; indeed, the analysis of multiple interacting drivers, whilst incorporating ecological lags, would be required to gain a full picture of change in forest ecosystems globally.

4. Using vertebrate trend data to help understand the impact of utilising wildlife populations and the benefits of management.

Synthesis

For this research paper, I conducted another global analysis but this time on a subset of vertebrate populations that are utilised by people. The use of wildlife supports many people for their food, medicine, and livelihoods. Ensuring that this use is sustainable is a central goal in conservation to ensure the persistence of species alongside continued utilisation by people. There were two key aims in this paper: one to illustrate trends in populations according to their utilisation status by developing an indicator of utilised and non-utilised populations and the other to explore the impact of management on mitigating any observed declines in population trends of utilised species.

Utilisation is a broad term, but for this paper we referred to consumptive use whereby individuals or parts of individuals are removed from the wild. This is opposed to non-consumptive uses such as wildlife tourism. The Living Planet Database was used as the main source of data, and alongside the population time-series data, we used two fields containing information about the utilisation and management of each population. This information had been taken solely from the data source for the population time-series, if available, and recorded whether a population was systematically utilised (whether sustainably or unsustainably). There was also information on whether the population was targeted by management which is described as activity usually in place to promote recovery in population size but can also be a means to limit the abundance of a population through culling.

Using the LPI method, global indicators for utilised and non-utilised vertebrate populations were produced from a data set of 11,123 population time-series from 2,944 species. Between 1970 and 2016, the utilised index showed a decline of 50% (Figure 4A: Index value: 0.50, 95%CI: 0.41–0.62. (McRae *et al.*, 2022)), a steeper negative decline than the non-utilised index which declined by just 3% (Figure 4A: Index value: 0.97, 95%CI: 0.80-1.18. (McRae *et al.*, 2022)). We found that this difference in average trend between utilised and non-utilised populations held when we restricted the comparison to a matched set of species in each group (Figure 5. (McRae *et al.*, 2022)). Regionally, the indices for terrestrial and freshwater utilised populations from Africa and the Americas revealed faster declines than other regions and the global terrestrial and freshwater average; utilised marine populations from Africa and Asia-Pacific were assessed as having more negative trends on average than other regions and the global marine average (Figure 3. (McRae *et al.*, 2022)).

From the mixed effects model analysis, we found that utilisation was a useful predictor of total population abundance change and was associated with declines across all taxonomic groups (Figure 4B. (McRae *et al.*, 2022)). Including body size as a fixed effect improved the models and trends were found to be more positive in larger-bodied birds, less negative in larger-bodied mammals and more negative in larger-bodied fish (Figure 4C. (McRae *et al.*, 2022)). When we included management as an explanatory variable we found that for those populations that are managed, the trends are more likely to be positive regardless of whether they are utilised or not (Figure 6. (McRae *et al.*, 2022)).

This research captures one of the challenges of balancing conservation with human needs. Whilst the overall result from this paper is one which implies that the use of species by people is at unsustainable levels and may threaten the very resource that people rely on, there is a positive message in the finding that management interventions can provide the necessary mitigation to stem population declines in utilised populations.

Impact/contribution to discipline

This work provided a broader geographic and taxonomic analysis of trends in populations in use than had previously been assessed and has broadly corroborated other findings of the impacts of utilisation on mammals and birds (Ripple *et al.*, 2016; Benítez-López *et al.*, 2017), and on fishes (FAO and UNEP, 2020; Palomares *et al.*, 2020). Exploring whether targeted management could mitigate declines was an important component in this analysis which otherwise painted quite a bleak picture of recent trends in utilised populations. This result adds to the growing evidence that conservation action (which is a subset of management as defined in this paper) can work and has prevented extinctions (Hoffmann *et al.*, 2010; Bolam *et al.*, 2021), and more recently has been suggested to promote population increases (Jellesmark *et al.*, 2022).

The lack of a species indicator for tracking the impact of utilisation had been identified by the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES) as a priority gap to fill (IPBES, 2018) and this had also been recognised as a need in the Convention on Biological Diversity (CBD) monitoring framework. Whilst species-level assessments for sustainable use have been developed (Marsh *et al.*, 2021), temporal trends and global-scale evidence based on site-level data were still lacking. The global and regional indices ("LPI for utilised populations") from this publication were selected for use as indicators in the status and trends chapter of the IPBES Thematic Assessment Report on the Sustainable Use of Wild Species, and the result of the positive impact of management was also highlighted in a section on sustainable use (Barron *et al.*, 2022). Since the agreement of the Kunming-Montreal Global Biodiversity Framework in 2022, the LPI for utilised populations has been listed as a component indicator to measure progress towards Goal B, Target 5 and Target 9 in the accompanying monitoring framework of the CBD (UNEP (United Nations Environment Programme)., 2022).

The analysis presented here may also contribute to the body of evidence on the status of “ecosystem services” or “nature’s contributions to people” by illustrating trends in species that are used by people. An assessment of global trends in nature’s contribution to people found declines in many of the contributions assessed since 1970 (Brauman *et al.*, 2020), mirroring the results we found. Such an assessment could include the LPI for utilised populations in future iterations. The data that underpin the LPI for utilised populations could also be used within the framework of Essential Ecosystem Service Variables (Balvanera *et al.*, 2022). The trends for individual utilised populations represent the ‘Ecological supply’ class of variables, in other words they can measure how the supply of a particular natural resource used by people is increasing or declining over time.

Critique

One of the possible shortcomings of this analysis is the extent to which the results can be interpreted. For example, we cannot infer causation from this analysis as there are other factors producing either negative or positive impacts which were not accounted for. Populations that were identified as utilised were not necessarily threatened by that use and so there are limits to how much we can attribute utilisation as the driver of the declines observed. Threats to populations were coded where information was available, and we found that utilised populations had a higher proportion of threats coded as overexploitation compared to non-utilised populations (Figure S2. (McRae *et al.*, 2022)); however, habitat loss, invasive species, pollution and climate change were also coded as threats and so there are likely to be drivers other than utilisation behind the trends in some populations. The same caveat applies to the positive association between management and population trends.

One complication was in how utilisation and management were defined. These terms had been coded in a way that was intended to be mutually exclusive but in fact there can be cases where the distinction is less clear. Some populations are utilised as a management tool, the Saltwater crocodile (*Crocodylus porosus*) from the Northern Territory of Australia being one example of this in practice whereby the controlled harvest of crocodile eggs is encouraged as a means of incentivising the conservation of this species.

Whilst my analysis here shows that average trends in utilised populations are in decline on average and it has been used in a global assessment on sustainable use, the indicator was not designed to measure sustainable use explicitly. A decline in population may imply unsustainable practices, but other components of sustainable use were not captured, for example what the level of offtake was for a population and whether any demographic changes were occurring other than a reduction in the number of individuals. This means that the LPI for utilised populations can measure one facet of sustainable use but should not be assumed to capture the entire concept.

Other than exploring dimensions of sustainable use in more detail, there are extensions to this work that could draw out other aspects relating to the pressure of utilisation which were not assessed in this analysis. For example, the type and scale of consumptive use may impact populations differentially. It would therefore be valuable to compare populations used for food versus sport or the pet trade, and the influence of subsistence versus commercial use from the local to the international scale. The value of doing this could be twofold: firstly, the relative impact of each type of pressure could be measured, and secondly, the consequences of that impact could be seen in terms of importance for local people’s wellbeing or the risk to a large business relying on a global trade in particular product.

Conclusion

Together these four publications provide better estimates of how and why vertebrate populations are changing globally, the results of which have contributed to many assessments of the progress (or lack of) towards international biodiversity targets. They illustrate how people are impacting species from the Arctic to tropical forests in varied ways and that if negative trends continue, this poses a concerning future for ecosystems and for people. The analysis synthesised here also highlights some of the limitations of biodiversity indicators and global datasets especially with respect to data representation. Despite efforts to improve data collection from priority regions and taxa, data gaps remain and often for some of the most highly biodiverse regions of the world. Furthermore, vertebrates comprise a small proportion of known biodiversity and so the absence of data in the LPI for invertebrates, plants and fungi ultimately limits our knowledge of broader trends in nature globally. However, this work does highlight the value in mobilising local-scale monitoring data whether from scientific literature or directly from field surveys. If we are to fully understand and address the decline in global biodiversity, it is essential to maintain primary data such as this at the heart of global assessments, indicators and decision making.

Future work

These publications and the data set they are built on provide the foundations of the future development of the Living Planet Index. One of the key priorities for the LPI should be to improve the taxonomic and geographic coverage of the data so that high biodiverse regions and taxa are better represented. Whilst enduring gaps in past and current species monitoring schemes may be a barrier to achieving this, some approaches could be taken to mobilise available data not yet captured through current data collection methods. For example, conducting data searches in languages other than English enables access to over a third of biodiversity literature which is published in non-English languages (Amano, González-Varo and Sutherland, 2016). Tackling the bias towards English is one way in which the representation of species in the most biodiverse regions could be improved, as a large proportion of scientific documents are published in languages native to megadiverse countries: Spanish, Portuguese and Mandarin (Amano, González-Varo and Sutherland, 2016).

Expanding the LPI beyond the coverage of vertebrate species is a potential adaptation to make future versions of the indicator more representative of biodiversity. Vertebrates represent fewer than 5% of all known animal species and so the current LPI arguably falls short of a model biodiversity indicator, even for the animal kingdom. However, if the unequal representation of invertebrates, plants and fungi in global databases such as GBIF (Troudet *et al.*, 2017) is indicative of the availability of abundance data for these taxa, then including them in the LPI could prove challenging. This development may also exacerbate the existing geographic bias in the data and introduce new taxonomic bias. To mitigate this, it may be feasible to develop a weighted method for calculating the index, as introduced in my first paper, although this approach has limitations such as the uncertainty around species richness estimates and the high weights which are often placed on small data sets. However, other methods of weighting can be explored that account for these shortcomings, for example aggregating and weighting trends within biomes or functional groupings. This could provide an important community or ecosystem lens within which to assess biodiversity trends rather than placing species as the main unit of measure; it might also be a suitable development to explore for weighting the current vertebrate LPI.

Another priority for the LPI is to improve the understanding of how environmental factors influence spatial and temporal patterns in vertebrate population trends. My paper on the relationship between population trends and tree cover change highlighted some of the challenges of this type of modelling, including how investigating a single driver does not sufficiently capture the complexity of biodiversity change (Williams *et al.*, 2022; Cornford *et al.*, 2023). Incorporating information on a broad range of environmental drivers and the interaction between them, alongside lagged population responses, would generate a more powerful explanatory model. In addition, global threat data sets can be poor predictors of population trends, so incorporating local threat information is important to improve the performance of correlative models linking drivers and trends (Daskalova, Myers-Smith and Godlee, 2020). Population-level threats have been coded for the time-series in the LPI and together have been used to demonstrate how the number of threats is a key predictor of resilience decline in vertebrate populations (Capdevila *et al.*, 2022b). Utilising this local scale data to explore the interactions between threats and the impact on populations in the LPI would be a valuable next step.

The next generation of methods for calculating the LPI should pioneer the work on extrapolating and predicting trends in vertebrate populations. This is reliant on developing better models linking drivers and trends as just outlined, so that environmental variables and scenarios of land-use and climate change can be used to estimate LPI values. Modelling extrapolations of the LPI at the national scale could serve as a valuable tool for measuring a country's progress towards biodiversity targets. The development of national LPIs is largely hindered by a lack of data so a spatially-extrapolated LPI would be a pragmatic application for policy, especially when attaining a comprehensive set of species population data for all countries remains challenging (Ledger *et al.*, 2023). Biodiversity indicators are also evolving from describing changes that have occurred, to predicting how nature would respond under different land-use and climate scenarios (Visconti *et al.*, 2016; Mace *et al.*, 2018). For the

LPI to remain effective as an indicator for policy it is vital that it can estimate how biodiversity might respond under different portfolios of environmental policy and management. Future work should build on the predictive LPIs that have already been developed for terrestrial species (Visconti *et al.*, 2016; Leclère *et al.*, 2020).

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References

Alter, S.E., Rynes, E. and Palumbi, S.R. (2007) ‘DNA evidence for historic population size and past ecosystem impacts of gray whales’, *Proceedings of the National Academy of Sciences*, 104(38), pp. 15162–15167. Available at: https://doi.org/10.1073/pnas.0706056104.

Amano, T., González-Varo, J.P. and Sutherland, W.J. (2016) ‘Languages Are Still a Major Barrier to Global Science’, *PLOS Biology*, 14(12), p. e2000933. Available at: https://doi.org/10.1371/journal.pbio.2000933.

AMAP (1998) *AMAP assessment report: Arctic pollution issues.* Oslo, Norway: Arctic Monitoring and Assessment Programme (AMAP).

Balvanera, P. *et al.* (2022) ‘Essential ecosystem service variables for monitoring progress towards sustainability’, *Current Opinion in Environmental Sustainability*, 54, p. 101152. Available at: https://doi.org/10.1016/j.cosust.2022.101152.

Barron, E.S. *et al.* (2022) *IPBES Sustainable Use of Wild Species Assessment - Chapter 3. Status of and trends in the use of wild species and its implications for wild species, the environment and people*. Zenodo. Available at: https://doi.org/10.5281/ZENODO.6451322.

Barry, T. (2019a) ‘Arctic Species Trend Index (ASTI) : Freshwater’. Conservation of Arctic Flora and Fauna. Available at: https://doi.org/10.15468/DTFELD.

Barry, T. (2019b) ‘Arctic Species Trend Index (ASTI) : Marine’. Conservation of Arctic Flora and Fauna. Available at: https://doi.org/10.15468/IL2VR5.

Barry, T. (2019c) ‘Arctic Species Trend Index (ASTI) : Terrestrial’. Conservation of Arctic Flora and Fauna. Available at: https://doi.org/10.15468/GD0XMY.

Bayraktarov, E. *et al.* (2021) ‘A threatened species index for Australian birds’, *Conservation Science and Practice*, 3(2). Available at: https://doi.org/10.1111/csp2.322.

Benítez-López, A. *et al.* (2017) ‘The impact of hunting on tropical mammal and bird populations’, *Science*, 356(6334), pp. 180–183. Available at: https://doi.org/10.1126/science.aaj1891.

Benítez-López, A. *et al.* (2019) ‘Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics’, *PLOS Biology*. Edited by A.P. Dobson, 17(5), p. e3000247. Available at: https://doi.org/10.1371/journal.pbio.3000247.

Boakes, E.H. *et al.* (2010) ‘Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data’, *PLoS Biol*, 8(6), p. e1000385. Available at: https://doi.org/10.1371/journal.pbio.1000385.

Bolam, F.C. *et al.* (2021) ‘How many bird and mammal extinctions has recent conservation action prevented?’, *Conservation Letters*, 14(1). Available at: https://doi.org/10.1111/conl.12762.

Boyd, R.J. *et al.* (2022) ‘ROBITT : A tool for assessing the risk-of-bias in studies of temporal trends in ecology’, *Methods in Ecology and Evolution*, 13(7), pp. 1497–1507. Available at: https://doi.org/10.1111/2041-210X.13857.

Brauman, K.A. *et al.* (2020) 'Global trends in nature's contributions to people', *Proceedings of the National Academy of Sciences*, 117(51), pp. 32799–32805. Available at: https://doi.org/10.1073/pnas.2010473117.

Buckland, S.T. *et al.* (2011) 'The geometric mean of relative abundance indices: a biodiversity measure with a difference', *Ecosphere*, 2(9), pp. 1–15. Available at: https://doi.org/10.1890/es11-00186.1.

Buckland, S.T. and Johnston, A. (2017) 'Monitoring the biodiversity of regions: Key principles and possible pitfalls', *Biological Conservation*, 214, pp. 23–34. Available at: https://doi.org/10.1016/j.biocon.2017.07.034.

Buschke, F.T. *et al.* (2021) 'Random population fluctuations bias the Living Planet Index', *Nature Ecology & Evolution*, 5(8), pp. 1145–1152.

Butchart, S.H. *et al.* (2010) 'Global biodiversity: indicators of recent declines', *Science*, 328(5982), pp. 1164–1168.

Butchart, S.H.M. *et al.* (2004) 'Measuring Global Trends in the Status of Biodiversity: Red List Indices for Birds', *PLoS Biology*. Edited by Walt V. Reid, 2(12), p. e383. Available at: https://doi.org/10.1371/journal.pbio.0020383.

CAFF (2013) *Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity.* Conservation of Arctic Flora and Fauna, Akureyri.

Capdevila, P. *et al.* (2022a) 'Body mass and latitude as global predictors of vertebrate populations exposure to multiple threats', *Ecography*, 2022(12), p. e06309. Available at: https://doi.org/10.1111/ecog.06309.

Capdevila, P. *et al.* (2022b) 'Global patterns of resilience decline in vertebrate populations', *Ecology Letters*. Edited by J. Chase, 25(1), pp. 240–251. Available at: https://doi.org/10.1111/ele.13927.

Cardinale, B.J. *et al.* (2018) 'Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends', *Biological Conservation*, 219, pp. 175–183. Available at: https://doi.org/10.1016/j.biocon.2017.12.021.

Chase, J.M. *et al.* (2018) 'Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities', *Ecology Letters*. Edited by F. Adler, 21(11), pp. 1737–1751. Available at: https://doi.org/10.1111/ele.13151.

Collen, B. *et al.* (2008) 'The tropical biodiversity data gap: addressing disparity in global monitoring', *Tropical Conservation Science*, 1(2), pp. 75–88.

Collen, B. *et al.* (2009) 'Monitoring Change in Vertebrate Abundance: the Living Planet Index', *Conservation Biology*, 23(2), pp. 317–327. Available at: https://doi.org/10.1111/j.1523-1739.2008.01117.x.

Cornford, R. *et al.* (2023) 'Ongoing over-exploitation and delayed responses to environmental change highlight the urgency for action to promote vertebrate recoveries by 2030', *Proceedings of the Royal Society B: Biological Sciences*, 290(1997), p. 20230464. Available at: https://doi.org/10.1098/rspb.2023.0464.

Côté, I.M., Darling, E.S. and Brown, C.J. (2016) 'Interactions among ecosystem stressors and their importance in conservation', *Proceedings of the Royal Society B: Biological Sciences*, 283(1824), p. 20152592. Available at: https://doi.org/10.1098/rspb.2015.2592.

Darrah, S.E. *et al.* (2019) 'Improvements to the Wetland Extent Trends (WET) index as a tool for monitoring natural and human-made wetlands', *Ecological Indicators*, 99, pp. 294–298. Available at: https://doi.org/10.1016/j.ecolind.2018.12.032.

Daskalova, G.N. *et al.* (2020) 'Landscape-scale forest loss as a catalyst of population and biodiversity change', *Science*, 368(6497), pp. 1341–1347. Available at: https://doi.org/10.1126/science.aba1289.

Daskalova, G.N., Myers-Smith, I.H. and Godlee, J.L. (2020) 'Rare and common vertebrates span a wide spectrum of population trends', *Nature Communications*, 11(1), p. 4394. Available at: https://doi.org/10.1038/s41467-020-17779-0.

Davison, C.W., Rahbek, C. and Morueta-Holme, N. (2021) 'Land-use change and biodiversity: Challenges for assembling evidence on the greatest threat to nature', *Global Change Biology*, 27(21), pp. 5414–5429. Available at: https://doi.org/10.1111/gcb.15846.

De Palma, A. *et al.* (2021) 'Annual changes in the Biodiversity Intactness Index in tropical and subtropical forest biomes, 2001–2012', *Scientific Reports*, 11(1), p. 20249. Available at: https://doi.org/10.1038/s41598-021-98811-1.

Deinet, S. *et al.* (2015) *The Arctic Species Trend Index: Migratory Birds Index*. Conservation of Arctic Flora and Fauna, Akureyri, Iceland.

Díaz, S. *et al.* (2019) 'Pervasive human-driven decline of life on Earth points to the need for transformative change', *Science*, 366(6471), p. eaax3100. Available at: https://doi.org/10.1126/science.aax3100.

Dornelas, M. *et al.* (2014) 'Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss', *Science*, 344(6181), pp. 296–299. Available at: https://doi.org/10.1126/science.1248484.

Eamer, J., Russell, D., McRae, Louise, *et al.* (2012) *CAFF Assessment Series No. 9. The Arctic Species Trend Index 2011: Key findings from an in-depth look at marine species and development of spatial analysis techniques*.

Eamer, J., Russell, D., McRae, L., *et al.* (2012) *The Arctic Species Trend Index 2011: Update of the ASTI, an in-depth look at marine species and development of spatial analysis techniques*. Conservation of Arctic Flora and Fauna, Iceland.

Essl, F. *et al.* (2015) 'Delayed biodiversity change: no time to waste', *Trends in Ecology & Evolution*, 30(7), pp. 375–378. Available at: https://doi.org/10.1016/j.tree.2015.05.002.

FAO (2016) *The State of the World's Forests 2016: Forests and agriculture: land-use challenges and opportunities*. FAO, Rome. Italy.

FAO and UNEP (2020) *The State of the World's Forests 2020*. FAO and UNEP. Available at: https://doi.org/10.4060/ca8642en.

Freeman, R. *et al.* (2015) 'rlpi: Tools for calculating indices using the Living Planet Index method'. R package version 0.1.0. Available at: https://github.com/Zoological-Society-of-London/living_planet_index.

Galewski, T. *et al.* (2021) *Living Mediterranean Report – Monitoring species trends to secure one of the major biodiversity hotspots.* Tour du Valat, France.

Gardner, C.J. *et al.* (2019) ‘Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis’, *Nature Communications*, 10(1), p. 4590. Available at: https://doi.org/10.1038/s41467-019-12539-1.

Gonzalez, A. *et al.* (2016) ‘Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity’, *Ecology*, 97(8), pp. 1949–1960. Available at: https://doi.org/10.1890/15-1759.1.

Green, E.J. *et al.* (2019) *Below the canopy: plotting global trends in forest wildlife populations*. WWF-UK, Woking, UK.

Green, E.J. *et al.* (2020) ‘Below the canopy: global trends in forest vertebrate populations and their drivers’, *Proceedings of the Royal Society B: Biological Sciences*, 287(1928), p. 20200533. Available at: https://doi.org/10.1098/rspb.2020.0533.

Gregory, R.D. *et al.* (2005) ‘Developing indicators for European birds’, *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 360(1454), pp. 269–288. Available at: https://doi.org/10.1098/rstb.2004.1602.

Grenyer, R. *et al.* (2006) ‘Global distribution and conservation of rare and threatened vertebrates’, *Nature*, 444(7115), pp. 93–96. Available at: https://doi.org/10.1038/nature05237.

Halpern, B.S. *et al.* (2008) ‘A Global Map of Human Impact on Marine Ecosystems’, *Science*, 319(5865), pp. 948–952. Available at: https://doi.org/10.1126/science.1149345.

Hansen, M.C. *et al.* (2013) ‘High-Resolution Global Maps of 21st-Century Forest Cover Change’, *Science*, 342(6160), pp. 850–853. Available at: https://doi.org/10.1126/science.1244693.

Hardesty-Moore, M. *et al.* (2018) ‘Migration in the Anthropocene: how collective navigation, environmental system and taxonomy shape the vulnerability of migratory species’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1746), p. 20170017. Available at: https://doi.org/10.1098/rstb.2017.0017.

He, F. *et al.* (2019) ‘The global decline of freshwater megafauna’, *Global Change Biology*, 25(11), pp. 3883–3892. Available at: https://doi.org/10.1111/gcb.14753.

Hochkirch, A. *et al.* (2021) ‘A strategy for the next decade to address data deficiency in neglected biodiversity’, *Conservation Biology*, 35(2), pp. 502–509. Available at: https://doi.org/10.1111/cobi.13589.

Hoffmann, M. *et al.* (2010) ‘The Impact of Conservation on the Status of the World’s Vertebrates’, *Science*, 330(6010), pp. 1503–1509. Available at: https://doi.org/10.1126/science.1194442.

IPBES (2018) *Report of the Plenary of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on the work of its sixth session*. Sixth session, Medellin, Colombia.

IPBES (2019) *Summary for policymakers of the global assessment report on biodiversity and ecosystem services*. Zenodo. Available at: https://doi.org/10.5281/ZENODO.3553579.

IUCN (2022) *The IUCN Red List of Threatened Species. Version 2022-2*. https://www.iucnredlist.org.

Jackson, M.C., Pawar, S. and Woodward, G. (2021) 'The Temporal Dynamics of Multiple Stressor Effects: From Individuals to Ecosystems', *Trends in Ecology & Evolution*, 36(5), pp. 402–410. Available at: https://doi.org/10.1016/j.tree.2021.01.005.

Jellesmark, S. *et al.* (2022) *Assessing the global impact of targeted conservation actions on species abundance*. preprint. Available at: https://doi.org/10.1101/2022.01.14.476374.

Johnson, T.F. *et al.* (2023) 'Socioeconomic factors predict population changes of large carnivores better than climate change or habitat loss', *Nature Communications*, 14(1), p. 74. Available at: https://doi.org/10.1038/s41467-022-35665-9.

Jones, J.P.G. *et al.* (2011) 'The Why, What, and How of Global Biodiversity Indicators Beyond the 2010 Target', *Conservation Biology*, 25(3), pp. 450–457. Available at: https://doi.org/10.1111/j.1523-1739.2010.01605.x.

Joppa, L.N. *et al.* (2016) 'Filling in biodiversity threat gaps', *Science*, 352(6284), pp. 416–418. Available at: https://doi.org/10.1126/science.aaf3565.

Lannuzel, D. *et al.* (2020) 'The future of Arctic sea-ice biogeochemistry and ice-associated ecosystems', *Nature Climate Change*, 10(11), pp. 983–992. Available at: https://doi.org/10.1038/s41558-020-00940-4.

Leclère, D. *et al.* (2020) 'Bending the curve of terrestrial biodiversity needs an integrated strategy', *Nature*, 585(7826), pp. 551–556. Available at: https://doi.org/10.1038/s41586-020-2705-y.

Ledger, S.E.H. *et al.* (2023) 'Past, present, and future of the Living Planet Index', *npj Biodiversity*, 2(1), p. 12. Available at: https://doi.org/10.1038/s44185-023-00017-3.

Leung, B. *et al.* (2020) 'Clustered versus catastrophic global vertebrate declines', *Nature*, 588(7837), pp. 267–271.

Loh, J. *et al.* (2005) 'The Living Planet Index: using species population time series to track trends in biodiversity', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1454), pp. 289–295. Available at: https://doi.org/10.1098/rstb.2004.1584.

Loreau, M. *et al.* (2022) 'Do not downplay biodiversity loss', *Nature*, 601(7894), pp. E27–E28. Available at: https://doi.org/10.1038/s41586-021-04179-7.

Mace, G.M. *et al.* (2018) 'Aiming higher to bend the curve of biodiversity loss', *Nature Sustainability*, 1(9), pp. 448–451. Available at: https://doi.org/10.1038/s41893-018-0130-0.

Marconi, V. *et al.* (2021) 'Population declines among Canadian vertebrates: But data of different quality show diverging trends', *Ecological Indicators*, 130, p. 108022. Available at: https://doi.org/10.1016/j.ecolind.2021.108022.

Marsh, S.M.E. *et al.* (2021) 'Prevalence of sustainable and unsustainable use of wild species inferred from the IUCN Red List of Threatened Species', *Conservation Biology*, n/a(n/a). Available at: https://doi.org/10.1111/cobi.13844.

Maxwell, S.L. *et al.* (2016) 'Biodiversity: The ravages of guns, nets and bulldozers', *Nature*, 536(7615), pp. 143–145. Available at: https://doi.org/10.1038/536143a.

McRae, L. *et al.* (2010) *Arctic Species Trend Index 2010: Tracking trends in Arctic wildlife*. Conservation of Arctic Flora and Fauna, Akureyri, Iceland.

McRae, L., Böhm, M., *et al.* (2012) 'The Arctic Species Trend Index: using vertebrate population trends to monitor the health of a rapidly changing ecosystem', *Biodiversity*, 13(3–4), pp. 144–156. Available at: https://doi.org/10.1080/14888386.2012.705085.

McRae, L., Deinet, S., *et al.* (2012) *Tracking Trends in Arctic marine populations*. CAFF Assessment Series No. 7.

McRae, L. *et al.* (2022) 'A global indicator of utilized wildlife populations: Regional trends and the impact of management', *One Earth*, 5(4), pp. 422–433. Available at: https://doi.org/10.1016/j.oneear.2022.03.014.

McRae, L., Deinet, S. and Freeman, R. (2017) 'The Diversity-Weighted Living Planet Index: Controlling for Taxonomic Bias in a Global Biodiversity Indicator', *PLOS ONE*, 12(1), p. e0169156. Available at: https://doi.org/10.1371/journal.pone.0169156.

Mehrabi, Z. and Naidoo, R. (2022) 'Shifting baselines and biodiversity success stories', *Nature*, 601(7894), pp. E17–E18. Available at: https://doi.org/10.1038/s41586-021-03750-6.

Millard, J.W. *et al.* (2021) 'The species awareness index as a conservation culturomics metric for public biodiversity awareness', *Conservation Biology*, 35(2), pp. 472–482. Available at: https://doi.org/10.1111/cobi.13701.

Moura, M.R. and Jetz, W. (2021) 'Shortfalls and opportunities in terrestrial vertebrate species discovery', *Nature Ecology & Evolution*, 5(5), pp. 631–639. Available at: https://doi.org/10.1038/s41559-021-01411-5.

Moussy, C. *et al.* (2022) 'A quantitative global review of species population monitoring', *Conservation Biology*, 36(1). Available at: https://doi.org/10.1111/cobi.13721.

Murali, G. *et al.* (2022) 'Emphasizing declining populations in the Living Planet Report', *Nature*, 601(7894), pp. E20–E24. Available at: https://doi.org/10.1038/s41586-021-04165-z.

Newbold, T. *et al.* (2015) 'Global effects of land use on local terrestrial biodiversity', *Nature*, 520(7545), pp. 45–50. Available at: https://doi.org/10.1038/nature14324.

Newbold, T. *et al.* (2016) 'Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment', *Science*, 353(6296), pp. 288–291. Available at: https://doi.org/10.1126/science.aaf2201.

Palomares, M.L.D. *et al.* (2020) 'Fishery biomass trends of exploited fish populations in marine ecoregions, climatic zones and ocean basins', *Estuarine, Coastal and Shelf Science*, 243, p. 106896. Available at: https://doi.org/10.1016/j.ecss.2020.106896.

Proença, V. *et al.* (2017) 'Global biodiversity monitoring: From data sources to Essential Biodiversity Variables', *Biological Conservation*, 213, pp. 256–263. Available at: https://doi.org/10.1016/j.biocon.2016.07.014.

Ramsar Convention on Wetlands (2018) *Global wetland outlook: State of the world's wetlands and their services to people*. Ramsar Convention Secretariat, Gland, Switzerland.

Ripple, W.J. *et al.* (2016) ‘Bushmeat hunting and extinction risk to the world’s mammals’, *Royal Society Open Science*, 3(10), p. 160498. Available at: https://doi.org/10.1098/rsos.160498.

Rodrigues, A.S.L. *et al.* (2014) ‘Spatially Explicit Trends in the Global Conservation Status of Vertebrates’, *PLoS ONE*. Edited by F. Moreira, 9(11), p. e113934. Available at: https://doi.org/10.1371/journal.pone.0113934.

Saha, A. *et al.* (2018) ‘Tracking Global Population Trends: Population Time-Series Data and a Living Planet Index for Reptiles’, *Journal of Herpetology*, 52(3), p. 259. Available at: https://doi.org/10.1670/17-076.

Samu, F. *et al.* (2023) ‘Agricultural spider decline: long-term trends under constant management conditions’, *Scientific Reports*, 13(1), p. 2305. Available at: https://doi.org/10.1038/s41598-023-29003-2.

Santini, L. *et al.* (2017) ‘Assessing the suitability of diversity metrics to detect biodiversity change’, *Biological Conservation*, 213, pp. 341–350. Available at: https://doi.org/10.1016/j.biocon.2016.08.024.

Scheffers, B.R. *et al.* (2012) ‘What we know and don’t know about Earth’s missing biodiversity’, *Trends in Ecology & Evolution*, 27(9), pp. 501–510. Available at: https://doi.org/10.1016/j.tree.2012.05.008.

Secretariat of the Convention on Biological Diversity (2020) *Global Biodiversity Outlook 5*. Montreal.

Song, X.-P. *et al.* (2018) ‘Global land change from 1982 to 2016’, *Nature*, 560(7720), pp. 639–643. Available at: https://doi.org/10.1038/s41586-018-0411-9.

Spooner, F.E.B., Pearson, R.G. and Freeman, R. (2018) ‘Rapid warming is associated with population decline among terrestrial birds and mammals globally’, *Global Change Biology*, 24(10), pp. 4521–4531. Available at: https://doi.org/10.1111/gcb.14361.

Stephenson, P.J. *et al.* (2022) ‘Measuring the Impact of Conservation: The Growing Importance of Monitoring Fauna, Flora and Funga’, *Diversity*, 14(10), p. 824. Available at: https://doi.org/10.3390/d14100824.

Stoett, P. *et al.* (2019) ‘Biodiversity-Global Environment Outlook (GEO-6): Healthy Planet, Healthy People Chapter 6’, *Global Environment Outlook (GEO-6): Healthy Planet, Healthy People* [Preprint].

van Strien, A.J., Soldaat, L.L. and Gregory, R.D. (2012) ‘Desirable mathematical properties of indicators for biodiversity change’, *Ecological Indicators*, 14(1), pp. 202–208. Available at: https://doi.org/10.1016/j.ecolind.2011.07.007.

Szabo, J.K. *et al.* (2012) ‘Adapting global biodiversity indicators to the national scale: A Red List Index for Australian birds’, *Biological Conservation*, 148(1), pp. 61–68. Available at: https://doi.org/10.1016/j.biocon.2012.01.062.

Tierney, M. *et al.* (2014) ‘Use it or lose it: measuring trends in wild species subject to substantial use’, *Oryx*. 2014/03/13 edn, 48(3), pp. 420–429. Available at: https://doi.org/10.1017/s0030605313000653.

Tittensor, D.P. *et al.* (2014) ‘A mid-term analysis of progress toward international biodiversity targets’, *Science*, 346(6206), pp. 241–244.

Troudet, J. *et al.* (2017) ‘Taxonomic bias in biodiversity data and societal preferences’, *Scientific Reports*, 7(1), p. 9132. Available at: https://doi.org/10.1038/s41598-017-09084-6.

UNEP (United Nations Environment Programme). (2010) *Decision X/2: The strategic plan for biodiversity 2011–2020 and the Aichi Biodiversity Targets.* Adopted at the 10th Conference Of The Parties (COP) to the Convention On Biological Diversity (CBD). UNEP, Montreal, Canada.

UNEP (United Nations Environment Programme) (2021) *Indicators for the post-2020 Global Biodiversity Framework*. Convention on Biological Diversity (CBD), Montreal, Canada.

UNEP (United Nations Environment Programme). (2022) *Monitoring framework for the Kunming-Montreal Global Biodiversity Framework. Decision adopted by the Conference of the Parties to the Convention on Biological Diversity.* Convention on Biological Diversity (CBD), Montreal, Canada.

Valdez, J.W. *et al.* (2023) ‘The undetectability of global biodiversity trends using local species richness’, *Ecography*, 2023(3). Available at: https://doi.org/10.1111/ecog.06604.

Venter, O. *et al.* (2016) ‘Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation’, *Nature Communications*, 7(1), p. 12558. Available at: https://doi.org/10.1038/ncomms12558.

Visconti, P. *et al.* (2016) ‘Projecting Global Biodiversity Indicators under Future Development Scenarios: Projecting biodiversity indicators’, *Conservation Letters*, 9(1), pp. 5–13. Available at: https://doi.org/10.1111/conl.12159.

Williams, J.J. *et al.* (2022) ‘Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change’, *Global Change Biology*, 28(3), pp. 797–815. Available at: https://doi.org/10.1111/gcb.15978.

WWF (2014) *Living Planet Report 2014: Species and spaces, people and places*. Gland, Switzerland: WWF.

WWF (2016) *Living Planet Report 2016: Risk and resilience in a new era*. WWF International, Gland, Switzerland.

WWF (2018) *Living Planet Report 2018: Aiming higher*. Gland, Switzerland: WWF.

WWF (2020) *Living Planet Report 2020: Bending the curve of biodiversity loss*. Gland, Switzerland: WWF.

WWF (2022) *Living Planet Report 2022: Building a nature-positive society*. Gland, Switzerland: WWF.

Yesson, C. *et al.* (2007) ‘How Global Is the Global Biodiversity Information Facility?’, *PLoS ONE*, 2(11), p. e1124. Available at: https://doi.org/10.1371/journal.pone.0001124.

Zöckler, C. (1998) *Patterns in biodiversity in Arctic birds*. WCMC Biodiversity Bulletin 3.

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McRae et al 2017. Additional permission and statement not required. Please note that during the course of writing my thesis, I became aware of the following typographical errors in this published work. These do not affect the results or conclusions of the work, but a correction has been submitted and will be published for this article.

- Abstract – the sign on one of the reported percentages is incorrect: (compared to trends of -46%, +12% and -15% respectively) not (compared to trends of -46%, +12% and +15% respectively)
- Equation 4: the equation is incorrect and part of it should be removed. This is an error in how it was written and does not affect the calculation (need to remove 1/NT from the equation)
- Figure 4: Caption describes the colours incorrectly. It should say 'Orange shows the unweighted index (LPI-U), green shows the diversity weighted index (LPI-D)'
- Figure 5: Caption describes the colours incorrectly. It should say 'Orange shows the unweighted index (Global LPI-U), green shows the diversity weighted index (Global LPI-D)'
- Figure 6: Caption describes the colours incorrectly. It should say 'In each case, orange shows the unweighted index (LPI-U), green shows the diversity weighted index (LPI-D)'
- Figure 6: The legend labels in the figure are incorrect and each refer to the wrong colour.

McRae et al. 2012. “This is an Accepted Manuscript of an article published by Taylor & Francis in Journal of Biodiversity on 07 Nov 2012, available online: *http://wwww.tandfonline.com/10.1080/14888386.2012.705085*”

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RESEARCH ARTICLE

The Diversity-Weighted Living Planet Index: Controlling for Taxonomic Bias in a Global Biodiversity Indicator

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Abstract

As threats to species continue to increase, precise and unbiased measures of the impact these pressures are having on global biodiversity are urgently needed. Some existing indicators of the status and trends of biodiversity largely rely on publicly available data from the scientific and grey literature, and are therefore prone to biases introduced through over-representation of well-studied groups and regions in monitoring schemes. This can give misleading estimates of biodiversity trends. Here, we report on an approach to tackle taxonomic and geographic bias in one such indicator (Living Planet Index) by accounting for the estimated number of species within biogeographical realms, and the relative diversity of species within them. Based on a proportionally weighted index, we estimate a global population decline in vertebrate species between 1970 and 2012 of 58% rather than 20% from an index with no proportional weighting. From this data set, comprising 14,152 populations of 3,706 species from 3,095 data sources, we also find that freshwater populations have declined by 81%, marine populations by 36%, and terrestrial populations by 38% when using proportional weighting (compared to trends of -46%, +12% and +15% respectively). These results not only show starker declines than previously estimated, but suggests that those species for which there is poorer data coverage may be declining more rapidly.

Introduction

Accurately quantifying trends in global biodiversity is crucial in order to understand the impacts of threats on the species and ecosystems on which humans rely [1]. The need for such metrics is pressing as threats and pressures upon the natural world continue largely unabated [2,3] and recent estimates of species extinction rates suggest they are significantly higher than background rates, having risen dramatically over the last 200 years [4,5]. Strategic Goal C of the Aichi Biodiversity Targets [6] aims 'to improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity'. In particular, Aichi Target 12 focusses on preventing the extinction of threatened species and improving and sustaining their conservation status. The mechanism required to assess progress towards this target relies on the development of robust and quantitative measures of the status of and trends in biodiversity and in this case, a focus on species [3].

The Living Planet Index (LPI) [7–9], one in the suite of global species indicators used to track progress towards Aichi Target 12, focusses on monitoring the population trends of vertebrate species. The LPI includes available published data, primarily in the scientific and grey literature (e.g. government/NGO reports) taken from the Living Planet Database (LPD) and records trends in 14,152 populations of 3,706 species. However, its reliance on available data means there is bias in the LPD resulting from the taxonomic and geographical distribution of the data used [8]. These types of bias are a common feature of other global biodiversity databases [10,11], usually with a noticeable gap in data from tropical regions [12]. The disparity in spatial coverage particularly reiterates that, in a time of persistent biodiversity decline, there are many gaps in our knowledge of the exact patterns and extent of this global problem [13]. Furthermore, the performance of biodiversity indicators such as the LPI can be compromised by the presence of bias in the data and limited in effectiveness as tools in measuring progress towards specific policy targets [1,14].

Other indicators based on species abundance (e.g. [15,16]) are developed for a selected group of species using a systematic monitoring protocol to collect the data used, so the indicator is spatially and taxonomically representative of the region and taxa in question. However, no indicator of this kind yet exists which has a global extent and covers taxonomic groups beyond birds and butterflies [15,16]. There is a tradeoff to be made between the time and resources required to develop a representative global monitoring scheme and the need to measure and report on biodiversity change [1]. In light of this, it can be prudent and cost-effective in the near term to build on existing indicators provided there is an understanding of any effects from the bias that they contain [17].

The database behind the Living Planet Index has been continually augmented since its inception in 1998 [18] and data are still being added (S1 Fig). In light of the applicability of the Living Planet Index as a global biodiversity indicator [3] and given the ongoing need for reporting tools for current and new targets for biodiversity, such as the Aichi Targets [6] and Sustainable Development Goals [19], we aim to continue the development of the LPI by both filling data gaps and by addressing the existing bias in the indicator. Here, we describe an approach which tackles the latter. We collated estimates of the known number of species across biogeographical realms and assessed the representativeness of the Living Planet Index database for species groups within these. We then developed the diversity weighted Living Planet Index which attempts to make the estimated index more representative of vertebrate biodiversity by accounting for the estimated diversity of species.

Materials and Methods

Data collection for the LPI

All data used in constructing the LPI are time series of either population size, density, abundance or a proxy of abundance. The species population data used to calculate the index are gathered from a variety of sources. Time series information for vertebrate species is collated from published scientific literature, online databases and grey literature (government/NGO reports), totaling 3,095 individual data sources. Data are only included if a measure of population size is available for at least two years, and information available on how the data were collected, what the units of measurement were, and the geographic location of the population. The data must be collected using the same method on the same population throughout the time series and the data source referenced and traceable (see [8] for further details).

The period covered by the index is from 1970 to 2012. The year 2012 is chosen as the cut-off point for the index because at present there are insufficient data to calculate a robust index after this point due to publication time-lag. Data sets are continually being added to the database. In addition to the population data, each time series is assigned to a system–terrestrial, freshwater and marine–based on both the location of the monitored population and the habitat the species mostly relies on. The geographic coordinates of the location are used to assign each population time series to a land-based or marine biogeographic realm (S2 Fig).

We examined the pattern of geographic bias in a data set which relies on using published data, in two ways. The first was to create a display of the broad spatial pattern of the LPD by mapping the location of each population time series onto a map depicting global vertebrate species richness (reproduced from [20]). Secondly, we followed the approach taken by Martin, et al [21] to analyse the geographic bias among terrestrial ecological study sites. Using the unique locations in the terrestrial component of the LPD we calculated the proportion of sites that are protected, the proportion in different woodland biomes and the proportion that occur in wealthy countries (S1 Appendix). We then compared this to the findings from Martin et al.

Assessing species representation

Numbers of species in the LPI database were compared with estimates of the number of known species in each of the following subcategories: system (terrestrial, freshwater, marine); taxonomic group (birds, mammals, reptiles, amphibians, fishes); land-based biogeographic realm for terrestrial and freshwater species (Afrotropical, Australasia, Indo-Malaya, Nearctic, Neotropical, Oceania, Palearctic); marine realm for marine species (Arctic, Atlantic north temperate, Atlantic tropical and subtropical, Pacific north temperate, Tropical and subtropical Indo-Pacific, Southern temperate and Antarctic).

Terrestrial and freshwater bird, mammal, reptile and amphibian species numbers were obtained from the WWF Wildfinder database [22]. This database lists extant species within each ecoregion. From this database, we extracted species lists and totals for the terrestrial and freshwater biogeographic realms. Freshwater fish species numbers were extracted from the Freshwater Ecoregions of the World data set [23] which also had ecoregion level species lists which we amalgamated into biogeographic realm lists.

Bird, mammal, reptiles and amphibian species numbers were further split into terrestrial and freshwater groups according to the habitat information on their species account on the IUCN Red List 2016.2 [24]. Species which were categorized as exclusively terrestrial or freshwater were placed in the relevant list. Species which were listed as both terrestrial and freshwater were placed in both, so these system lists are not mutually exclusive which mirrors the LPI database where species can be assigned to both terrestrial and freshwater systems.

In some cases, taxonomic discrepancies meant that it was not clear whether a species should be categorized as freshwater or terrestrial. To minimize this, we conducted synonym searches in the Red List taxonomic fields to increase matches and identify unique orders, families or genera that should be classified as exclusively terrestrial or freshwater. Any remaining species that were not matched were kept in both terrestrial and freshwater lists. For reptile species not assessed by the IUCN Red List, we based the decision on the system assigned to other species of the same genera or family level. Alternatively we searched for habitat preferences for the species on the Reptile Database [25].

Marine fish, bird and reptile species totals were obtained by searching for ‘Pisces’, ‘Aves’, and ‘Reptilia’ respectively within a polygon drawn for each marine realm from the Ocean Biogeographic Information System [26]. Species totals for marine mammals were obtained through advanced searches on the IUCN Red List to identify total numbers of marine mammals occurring in each FAO marine area [24]. The FAO marine areas were then assigned to the appropriate marine realm in order to estimate total species number for each realm.

For each realm, we then compared the estimated proportion of species from each taxonomic group within each realm with the proportions of species found in the LPI for that realm. We did this for terrestrial, freshwater and marine species separately. Binomial tests were used to assess significant over or under-representation. We assessed the impact of removing low representation (less than 1%) on the resulting indices. We also investigated whether the proportion of species in the LPI database assessed as threatened on the IUCN Red List [24] differed significantly from the actual proportions of threatened species within five of the extinction risk categories (Least Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered) and for each taxonomic group on the IUCN Red List. We did not compare proportions in the Data Deficient, Extinct or Extinct in the Wild categories as we would not anticipate having population trends data for such species in the LPD. For reptiles and fishes which have not been comprehensively assessed, we used estimates of proportion threatened from those species that have been assessed. As an extension of this analysis, we replicated the comparison removing any threatened species that had not been assessed under Criterion A, which is based on a reduction in population size. Species assessed under other criteria might not necessarily show population declines, so this approach aims to test for a bias towards threatened species that do have declining populations.

Calculating the LPI

To facilitate easy replication of the results presented here, an r package, *rlpi*, for calculating the Living Planet Index using either approach outlined below is provided with tutorial documentation, example data sets and the publically available records from the Living Planet Database [27] at https://github.com/Zoological-Society-of-London/rlpi. The Living Planet Database contains a number of abundance records that have been provided in confidence. These are used to calculate the presented trends and statistics, but cannot be made publically available. We calculated the geometric mean of trends for each species within a Generalised Additive Modelling (GAM) framework, following [8], whereby each population time series with six or more data points was modelled using a GAM. Population time series with fewer than six data points or that resulted in poor GAM fit were modelled using the chain method [9]. Where we had more than one population time series for a species, the modelled annual trends d_t for each population were averaged to provide a single set of annual trends for each species:

$$\bar{d}_t = \frac{1}{n_t}\sum_{i=1}^{n_t} d_{it} \tag{1}$$

where n_t is the number of populations, d_t is the annual rate of change for a population in a given year, given by

$$d_t = \log_{10}\left(\frac{N_t}{N_{t-1}}\right) \tag{2}$$

where N is the population measure and t is the year.

Having constructed species, group, regional or global trends, these can be converted back to index values by:

$$I_t = I_{t-1} * 10^{\bar{d}_t}, \qquad I_0 = 1 \tag{3}$$

Throughout the following processes, we refer to 'averaging' trends–in all cases, we refer to averaging lambda values, prior to converting them to index values–generating the geometric mean abundance. This final step only occurs after all other steps have taken place.

We used two approaches for calculating a global scale index. The first, unweighted method (LPI-U), follows the process outlined in [8] whereby the data are divided into six subsets based on region (tropical or temperate) and the three systems (terrestrial, freshwater & marine) within each region. Indices for each system (tropical terrestrial, temperate freshwater, etc.) are calculated by averaging species trends within them. Separate tropical and temperate indices are then calculated by averaging the trends for each system. The tropical and temperate indices are finally averaged to produce a global scale LPI. This process of hierarchical averaging addresses some of the geographical disparity in the data set by equally weighting tropical and temperate regions but does not address taxonomic disparity or apply any proportional weighting.

The second approach, the diversity weighted LPI (LPI-D), incorporates a proportionally weighted system based on the species richness estimates described above (building upon suggestions in [8,9]). Because the reptile and amphibian data sets are small, these were combined into one herpetological group ('herps'), leaving four species groups ('Birds', 'Mammals', 'Fish' and 'Herps'). For the same reason, we joined the biogeographic realms Australasia, Oceania and Indo-Malaya into one combined realm ('Indo-Pacific'). The final data set comprised 57 subsets which incorporated each system, realm and taxonomic group combination (Fig 1).

Within each system and realm combination, the average species trend for each taxonomic group was then given a proportional weight according to estimated species richness (S10 Table, S11 Table). For example, birds represent 43.3% of terrestrial vertebrate species in the Palearctic so this value is used in the weighted average to construct the Palearctic realm trend for terrestrial species. This method of a weighted average was used to produce 16 trends for each system/realm combination. Summary pseudocode for this process is presented in Box 1. For example, in calculating the trends for freshwater Afro-tropical species, we weight taxonomic groups using their calculated proportions:

$$\bar{\boldsymbol{d}}_{t,\ FW\_AT} = \frac{1}{N_T}\sum_{j=1}^{N_T}\bar{d}_{jt}.w_j \tag{4}$$

where N_T is the number of taxonomic groups within the realm in question, W_j is the estimated proportion of species that that group represents (S10 Table, S11 Table), and d_{jt} is the calculated average trend in abundance for that taxonomic group at time t.

The next stage was to produce three system-level trends (terrestrial, freshwater and marine). Each realm trend for that system was given a weighted value according to the proportion of species that the realm represents derived from the estimated number of known species. For example Palearctic species account for 10.6% of known terrestrial vertebrate species, so this value is used to weight the terrestrial Palearctic trend within the terrestrial index. This method of weighting was used to produce three indices for terrestrial, freshwater and marine which are then averaged to produce a single global trend as in [8]. This trend is indexed with the baseline of 1970 set to a value of 1.

As a smaller scale illustrative example, we calculated an index for the Palearctic realm using the two approaches described above. For the LPI-U approach, an average was taken of all terrestrial and freshwater species trends to produce the realm index. For the LPI-D approach, the index was calculated using a weighted average based on the combined proportion of terrestrial and freshwater species estimated for the Palearctic (see S10 Table, Palearctic column).

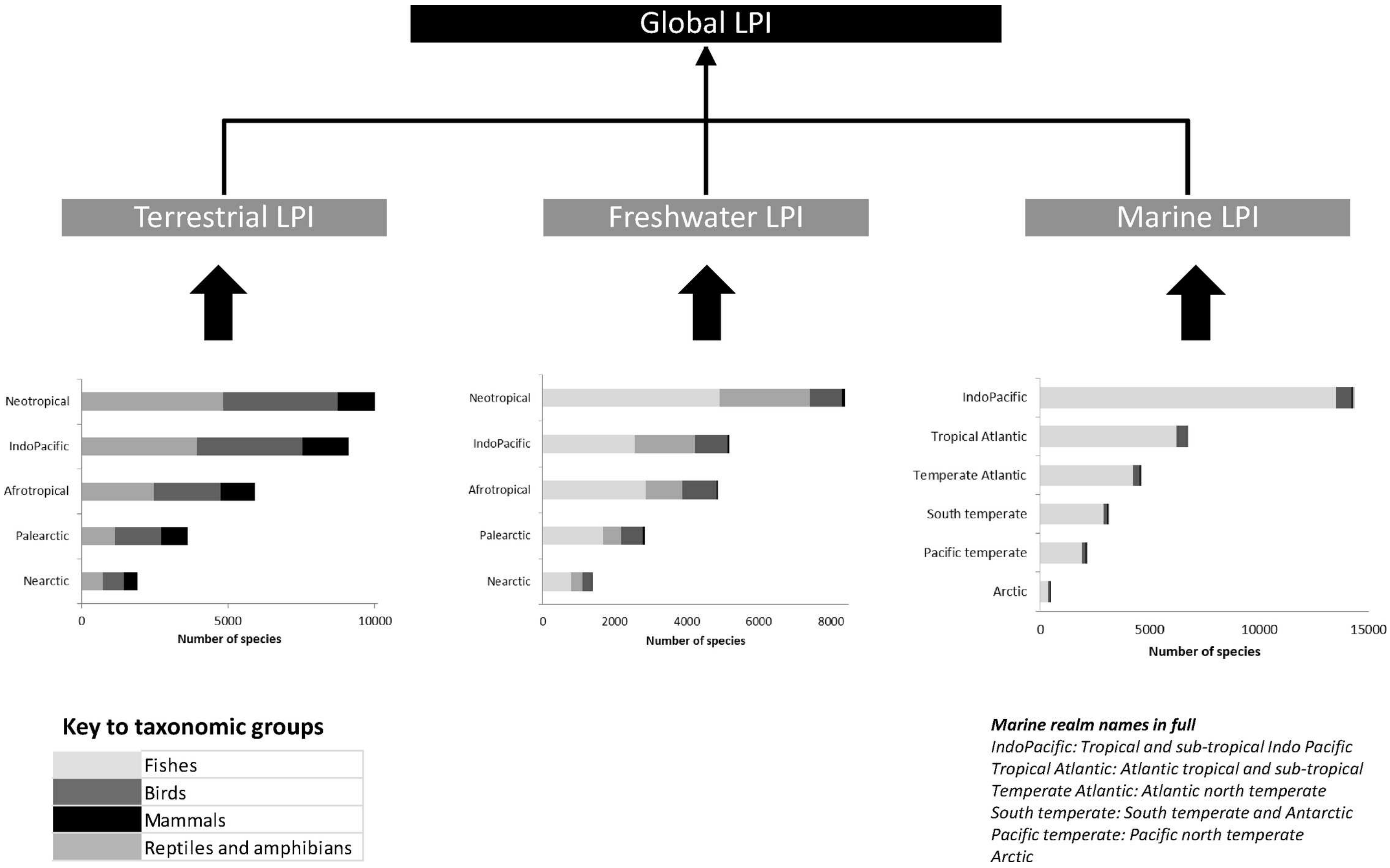

Fig 1. Schematic of the weighting process. Systems (Terrestrial/Freshwater/Marine) are weighted equally. Within each system, the proportion of species found across the realms that compose that system (the length of the bars above) is used to proportionally weight each realm's index. Within each realm, the diversity of species is used to weight taxonomic indices (the size of the grey-scale sections of the bars above).

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Box 1. Pseudocode outlining the algorithm for constructing the global Living Planet Index.

```
For each species, estimate rates of change:
  For each population,
    Estimate population lambdas (rates of change):
  Average population lambdas for each species to obtain species trend
For each System (terrestrial, freshwater, marine):
  For each biogeographical realm (Palearctic, Indo-Pacific, etc):
    For each taxonomic group (birds, mammals, fish, herps):
      Average species trends within group
    Average taxonomic trends, using taxonomic weightings, obtaining realm trend
  Average biogeographical realm trends, using realm weightings, obtaining system trend
Average system trends equally.
Convert average system rates of change to index values
```

For each index, we generated 95% confidence intervals using a bootstrap resampling technique for 10,000 iterations (as [8]). These confidence intervals demonstrate the uncertainty in the index values inherited from the baseline in 1970 and propagated through the time series.

Results

Geographic representation within the living planet index

Global vertebrate richness overlaid with locations of populations currently recorded within the Living Planet Index shows biases towards temperate regions, which the Living Planet Index over-represents, and under-representation of tropical regions (Fig 2). Our comparison to a study on geographic bias in terrestrial ecological sites revealed that 63% of the terrestrial sites in the LPD occur in a protected area which is the same proportion as found in Martin et al. ($\chi^2 = 0.004$, $df = 1$, $p = 0.95$), and more than the expected 13% ($\chi^2 = 883.83$, $df = 1$, $p = 0.00$). For all woodland biomes, the LPI differs significantly to Martin et al.'s observed values except for Tundra (S2 Table). Compared to the expected number of sites across biomes, the LPI over-represents Tropical deciduous woodland and under-represents Tropical evergreen woodland (S3 Table). For values derived from an equal distribution of sites by global area, all other biomes except Tundra are over-represented while results are less clear by an assumed equal distribution among biomes (S3 Table). The pattern of representation in wealthy countries was similar to Martin et al. but overall results were mixed with over- und under-representation of high and low income countries compared to the number of sites expected (S4 Table). While comprising significantly more terrestrial sites from High income countries and significantly fewer sites from Upper middle income countries, representation is even when combining categories into higher (High and Upper middle) and lower (Lower middle and Low) groupings (S5 Table).

Taxonomic representation and bias within the living planet index

Fig 3 shows the geographic and taxonomic representation of species in the LPI. This representation is varied with 12 subsets representing between 1 and 10% and 7 subsets representing

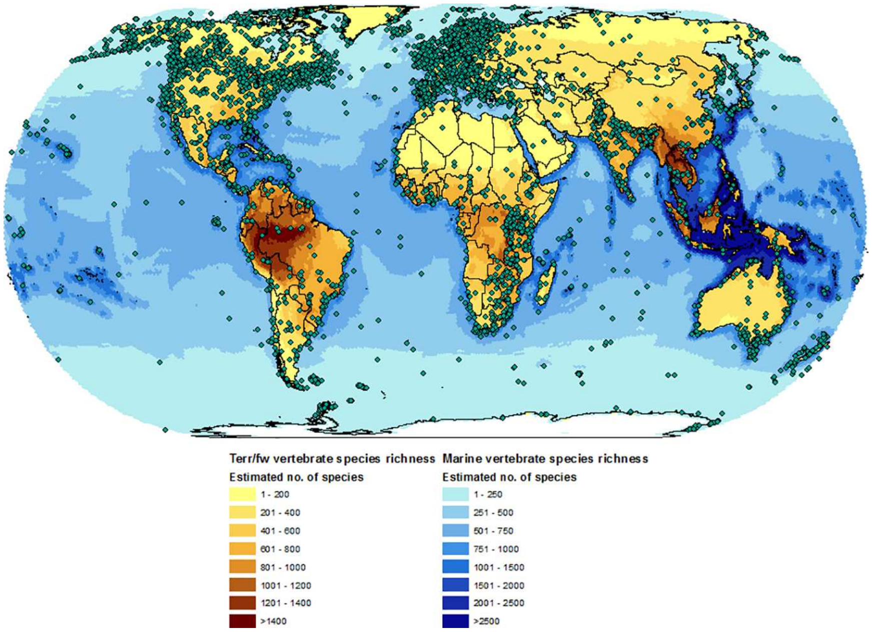

Fig 2. Global vertebrate richness map overlaid with populations recorded in the Living Planet Database. Species richness map reproduced from [20]

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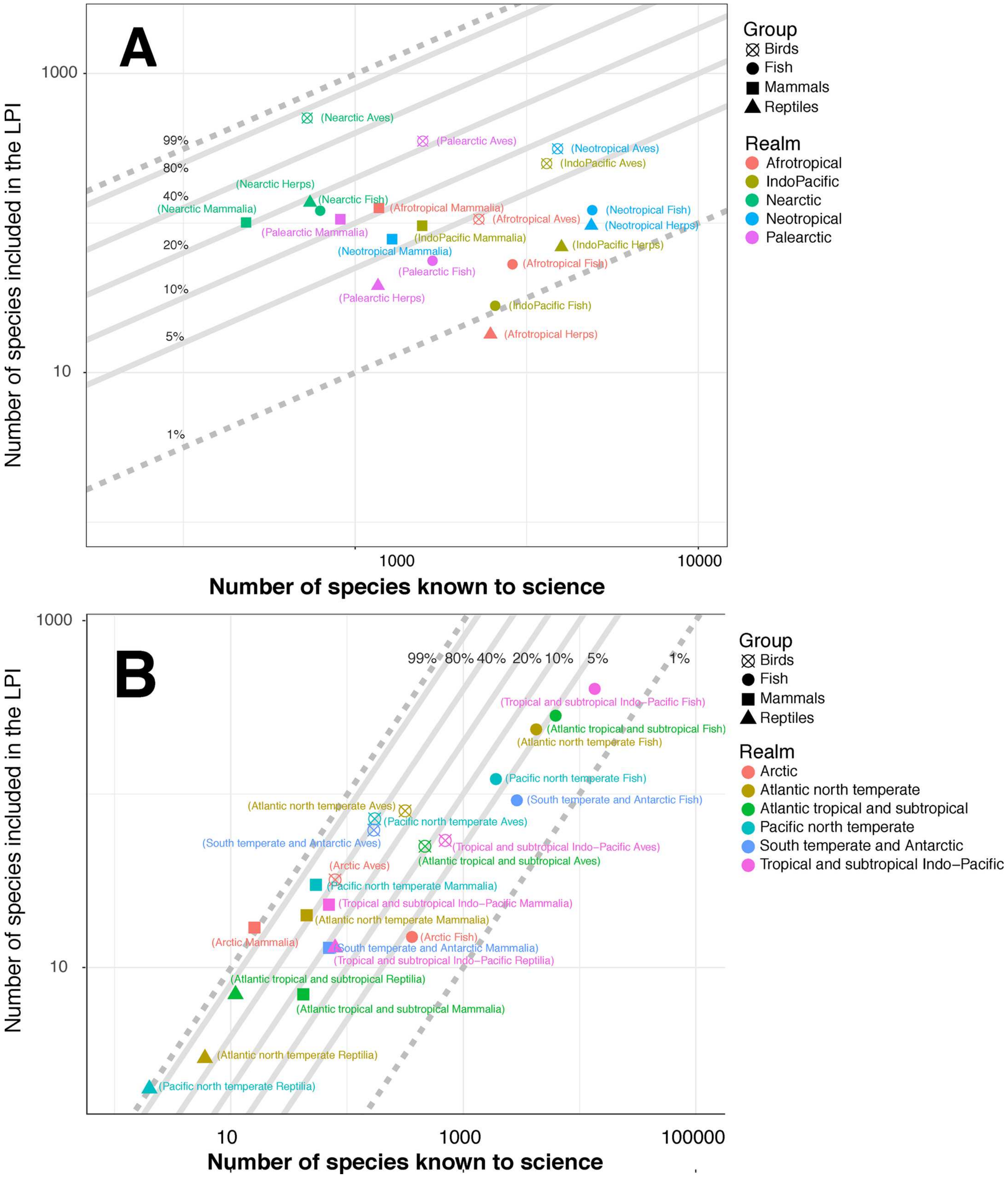
A
Number of species included in the LPI
1000
10
Number of species known to science
1000
10000
99%
80%
40%
20%
10%
5%
1%
(Nearctic Aves)
(Palearctic Aves)
(Neotropical Aves)
(IndoPacific Aves)
(Nearctic Herps)
(Nearctic Fish)
(Afrotropical Mammalia)
(Nearctic Mammalia)
(Afrotropical Aves)
(Neotropical Fish)
(Neotropical Herps)
(Palearctic Mammalia)
(IndoPacific Mammalia)
(Neotropical Mammalia)
(IndoPacific Herps)
(Afrotropical Fish)
(Palearctic Fish)
(Palearctic Herps)
(IndoPacific Fish)
(Afrotropical Herps)
Group
Birds
Fish
Mammals
Reptiles
Realm
Afrotropical
IndoPacific
Nearctic
Neotropical
Palearctic
B
Number of species included in the LPI
1000
10
Number of species known to science
10
1000
100000
99%
80%
40%
20%
10%
5%
1%
(Tropical and subtropical Indo–Pacific Fish)
(Atlantic tropical and subtropical Fish)
(Atlantic north temperate Fish)
(Pacific north temperate Fish)
(South temperate and Antarctic Fish)
(Atlantic north temperate Aves)
(Pacific north temperate Aves)
(South temperate and Antarctic Aves)
(Tropical and subtropical Indo–Pacific Aves)
(Atlantic tropical and subtropical Aves)
(Arctic Aves)
(Pacific north temperate Mammalia)
(Tropical and subtropical Indo–Pacific Mammalia)
(Atlantic north temperate Mammalia)
(Arctic Fish)
(Arctic Mammalia)
(South temperate and Antarctic Mammalia)
(Tropical and subtropical Indo–Pacific Reptilia)
(Atlantic tropical and subtropical Reptilia)
(Atlantic tropical and subtropical Mammalia)
(Atlantic north temperate Reptilia)
(Pacific north temperate Reptilia)
Group
Birds
Fish
Mammals
Reptiles
Realm
Arctic
Atlantic north temperate
Atlantic tropical and subtropical
Pacific north temperate
South temperate and Antarctic
Tropical and subtropical Indo–Pacific

Fig 3. Comparison of number of known species and number of species recorded within the Living Planet Database. Colours represent different biogeographic realms, shapes indicate species groups and overlaid lines show 1 and 99% representation (dotted) and increments in between (solid). A–terrestrial and freshwater species and realms; B–marine species and realms

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over 10% of known species in the terrestrial and freshwater systems (S6A Table). For the marine system, 6 subsets represent between 1 and 10% and 16 subsets represent 10% or more of known species (S6B Table). Afrotropical amphibians and reptiles ('Afrotropical Herps') represent less than 1% of known species and South temperate and Antarctic reptiles are currently not represented at all in the LPI database (0%, of a possible 3 species; not shown in figure). In the marine system, the highest representation of species is for Pacific north temperate reptiles (100%, 2 species). The highest terrestrial and freshwater representation is for Nearctic birds (68%, 492 species out of a possible 725 species) and the lowest is for Afrotropical reptiles and amphibians (0.7%, 18 species of a possible 2,480 species).

When compared to the expected diversity of species across realms, the significant results for birds and mammals show over-representation within terrestrial and freshwater realms with the exception of Afrotropical birds which are under-represented (Binomial test of proportions, see S7 Table). The taxonomic groups that are significantly under-represented in each terrestrial and freshwater realm are amphibians and reptiles, as well as fishes, the exception being Nearctic species which are all over-represented. For marine realms, the significant results for birds, mammals and reptiles show they are over-represented in all realms with the exception of South temperate and Antarctic reptiles where there is no representation of the three species (S8 Table). Fishes are a significantly under-represented group in the tropical and south temperate marine realms but are significantly over-represented in the Pacific north temperate.

Impact of diversity weighting at the level of a realm: the palearctic

Using the unweighted method (LPI-U) the index for the Palearctic realm shows an overall significant increase of 38.4% (95% CI: 12.7–66.2) over the period 1970–2012 (Fig 4). Using the diversity weighted method (LPI-D), the index for the Palearctic realm shows an overall significant decline of 30.3% (95% CI: -1.4 –-50.2). The LPI-D index for the Palearctic realm shows wider confidence intervals than the LPI-U index as well as a more undulating trend. When an unweighted average is used to calculate the Palearctic index, the group which contains the most species in the LPI database carries the most weight (S6A Table). The effect of using proportional weighting means that the influence of the over-represented groups such as birds and mammals has been reduced by over half and almost a fifth respectively, whereas the influence of fishes has been increased by over three-fold and amphibians/reptiles by over two-fold. This is compared to how much weight they would carry using the LPI-U approach where no taxonomic weighting is used.

Applying the LPI-D approach to the global living planet index

The global index produced using the LPI-D approach shows a decline of 58% (95% CI: -48.3 –-66.0) between 1970 and 2012 (Fig 5) which equates to an average annual decline of 2% per year. This result shows a greater rate of decline than the index calculated using the LPI-U approach which has an average annual decline of 0.52% per year and an overall decline of 19.7% (95% CI: -6.6 –-30.9), over the 42-year period. The confidence intervals around the LPI-U index are slightly wider than the LPI-D index illustrating greater uncertainty in the trend since 1970.

System trends: terrestrial, freshwater and marine

The results of the LPI-D approach on the three system indices reveal that each show a greater decline than the LPI-U approach (Fig 6). The terrestrial index shows a 37.9% decline (95% CI: -20.4 –-51.5) from 1970 to 2012, averaging at a 1.13% decline per year. The marine index shows a similar decline of 35.6% (95% CI: -19.5 –-48.8) over the same period, with an average annual decline of 1.04% per year. The freshwater index shows a decline of greater magnitude, 81.5% (95% CI: -68.5 –-89.3) over the 42-year period and an average annual decline of 3.94% per year. Table 1 compares the weighted and unweighted indices for each system.

The impact of low-representation groups

To gauge the impact of less represented species groups on the indices, we explored the effect of removing them. If there was little impact, we would expect the average trend for the other groups that remain in the index to look similar after removal. Fig 7 compares the impact of

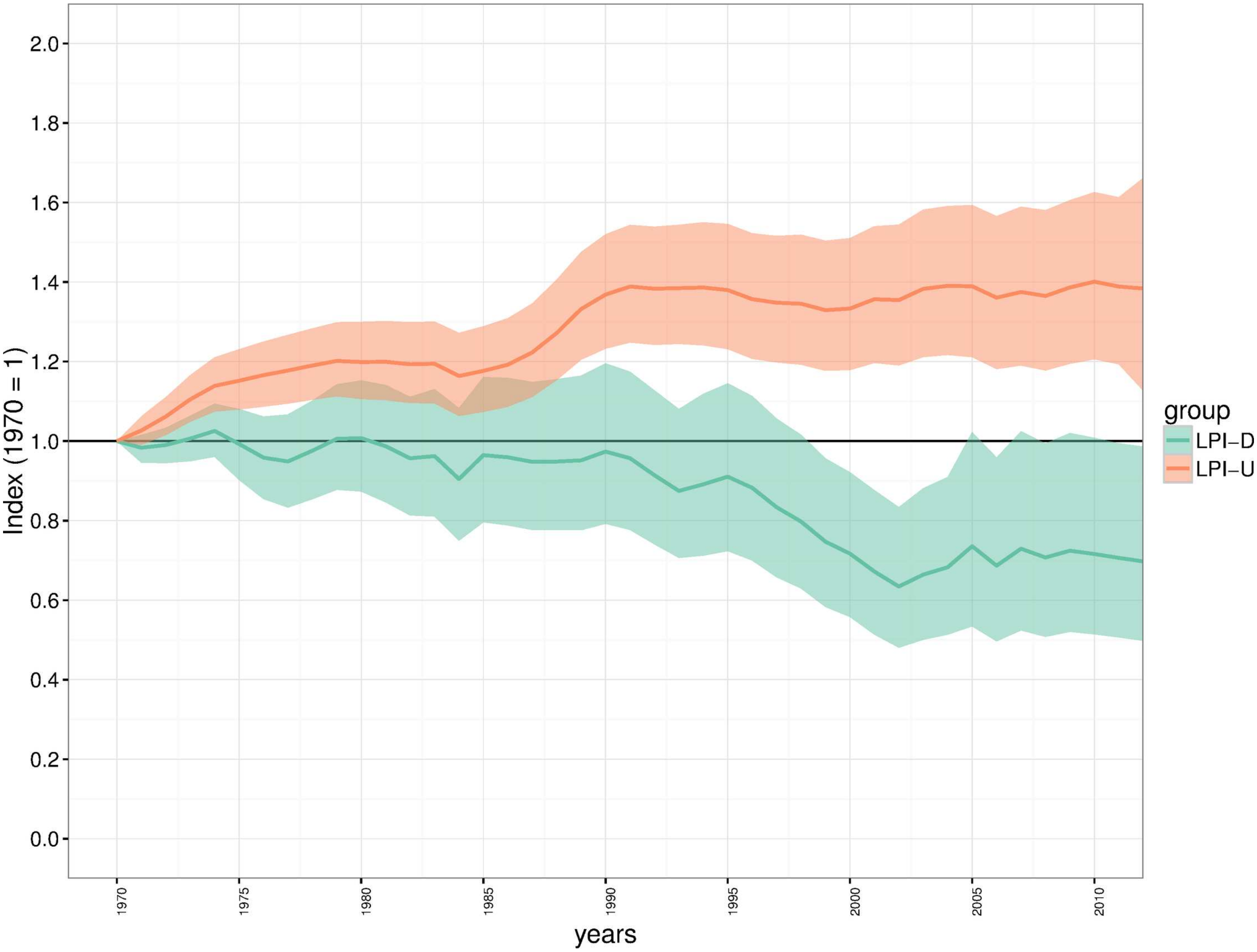

Fig 4. Comparison of the unweighted and diversity weighted Living Planet Index for the Palearctic realm. Green shows the unweighted index (LPI-U), orange shows the diversity weighted index (LPI-D). Solid coloured lines show the average trend and shaded regions show the 95% confidence interval of that trend.

doi:10.1371/journal.pone.0169156.g004

removing these groups on global and system level trends using both the weighted and unweighted method. As no groups within the marine realm have < 1% representation, we only present the differences in global, freshwater and terrestrial indices. In general, the diversity weighted approach does not have a significant impact on the effect of removing these groups. In both weighted and unweighted cases for each index, no significant difference is seen when groups with less than 1% representation are removed. Each index shows a greater decline when these groups are removed, which is most noticeable in the Terrestrial LPI-D index but it is not significantly different. The exception is the Freshwater LPI-U index where there is a very marginal increase in the trend.

Representation of threatened species

Comparing the proportion of species from each IUCN Red List category in the Living Planet Database with all assessed species on the IUCN Red List revealed some significant results for

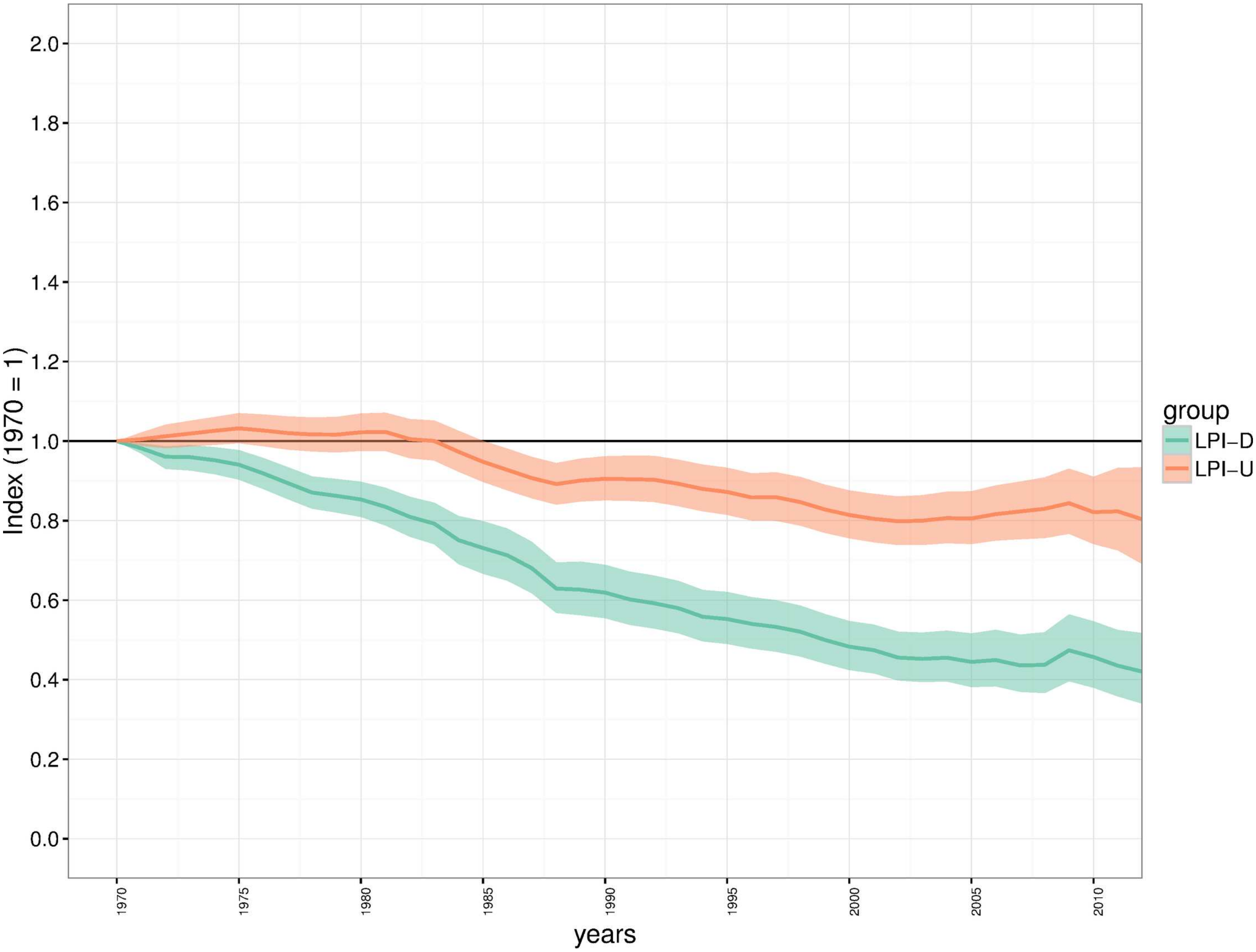

Fig 5. Comparison of the unweighted and diversity-weighted Living Planet Index for the global data set. Green shows the unweighted index (Global LPI-U), orange shows the diversity weighted index (Global LPI-D). Solid coloured lines show the average trend and shaded regions show the 95% confidence interval of that trend.

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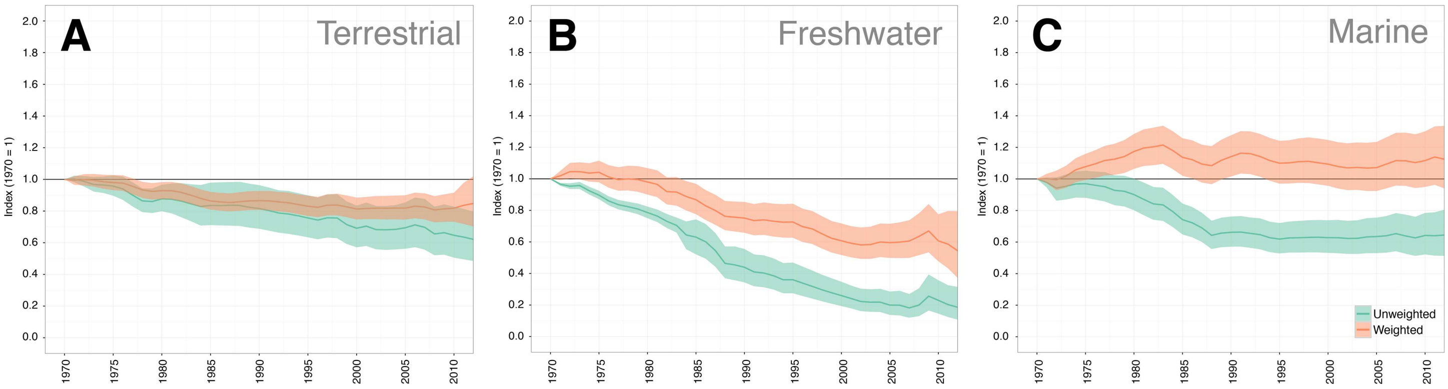

Fig 6. Comparison of the unweighted and diversity weighted Living Planet Index for each System (A -Terrestrial, B -Freshwater and C -Marine). In each case, green shows the unweighted index (LPI-U), orange shows the diversity weighted index (LPI-D). Solid coloured lines show the average trend and shaded regions show the 95% confidence interval of that trend.

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both threatened (CR, EN, VU) and non-threatened (NT/LR, LC) categories (Table 2). We find that Critically Endangered reptiles are significantly over-represented, along with Least Concern birds and amphibians, and Near Threatened/Lower Risk reptiles and fishes. The significantly under-represented groups are Near Threatened/Lower Risk birds, Least Concern reptiles and fishes, Endangered amphibians and fishes, and Vulnerable birds and amphibians. None of the categories for mammals showed significant over- or under- representation.

When we subsetted the threatened species to include only those that have been assessed under Criterion A (a reduction in population size), we found more significance in the results between the proportions in the LPI and the IUCN Red List (S9 Table). All three threat categories are significantly over-represented for mammals, reptiles and fishes. Critically endangered and Endangered birds are significantly over-represented whereas Vulnerable birds are significantly under-represented. There were no significant results for amphibians.

Discussion

Trends in abundance of species populations are a crucial indicator of biodiversity [28,29] and can provide early warnings of declines prior to species qualifying for high levels of extinction risk [30]. Consequently, this metric has been recommended as an Essential Biodiversity Variable [31], and, its use in geometric mean abundance indicators such as the Living Planet Index (LPI), is part of the mechanism to monitor biodiversity and assess progress towards the Aichi Targets.

The Living Planet Database (LPD), which underpins the LPI, relies on the collation of data from available sources such as government reports, scientific articles and research programmes which represents a cost effective method to develop a global biodiversity indicator. However, it necessarily suffers from a variety of publication biases arising for reasons such as lack of resources or infrastructure for monitoring, logistical difficulties in accessing sites or

Table 1. Comparing the results of the weighted (LPI-D) and unweighted (LPI-U) indices in 2012. Confidence intervals are calculated from 10,000 bootstraps.

	LPI-D index value in 2012	95% Confidence interval	LPI-U index value in 2012	95% Confidence interval
Terrestrial	0.621	0.485–0.796	0.848	0.702–1.02
Freshwater	0.185	0.107–0.315	0.544	0.371–0.795
Marine	0.644	0.513–0.805	1.125	0.940–1.336

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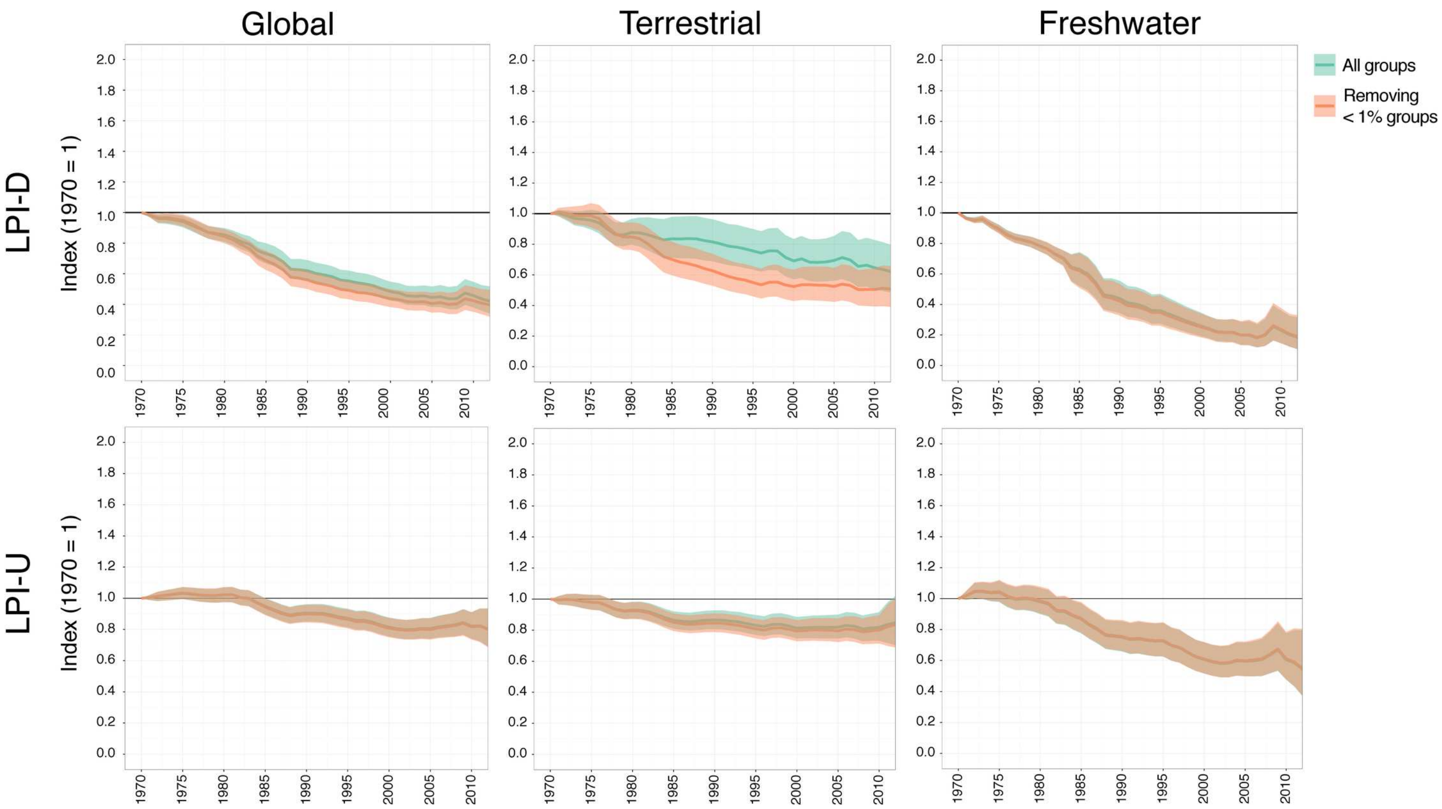

Fig 7. The impact of removing species groups for which the Living Planet Database has < 1% representation. Green trends show the Living Planet Index for all groups, orange trends show trends without less represented groups. Upper row shows trends calculated using the weighted (LPI-D) method, lower rows show the unweighted (LPI-U) method. Solid lines show the average trend, shaded regions show 95% confidence intervals. Stars (*) indicate when the final 2012 index values are significantly different.

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barriers to the dissemination of data into the public realm [12]. This is exacerbated by a tendency for monitoring to occur in areas where scientists live and work [21,32]. Across many of the species groups that are surveyed within the LPD, we see both significant over- and under-representation in comparison to the estimated number of species (S7 Table, S8 Table, Fig 3). The data tend to be over-represented for temperate bird and mammal species, and under-represented for most species groups in tropical realms and for marine fishes. We also find a geographic bias in the terrestrial data portion of the LPD towards protected areas, tropical deciduous woodland and some wealthy countries, at the same time as under-representation of tropical evergreen woodland biomes.

While the geographic and taxonomic bias we demonstrate in the LPI is consistent with other studies [8,33] and comparable data sets [21], the spatial mismatch between the known diversity of vertebrate species and the available data (Fig 2) could lead to inaccurate estimates of status and trends in biodiversity. More specifically, trends that equally weight these species groups (as in the 'traditional' Living Planet Index) will be significantly biased by the disproportionate representation of these groups, skewing the calculation of trends in global wildlife abundance. Given the need for developed indicators of biodiversity and the overriding challenges of obtaining globally comprehensive biodiversity data [12], we have outlined an approach to deal with bias as an interim solution in lieu of attaining more representative monitoring data. This weighted approach (LPI-D) suggests that, on average, species populations within the Palearctic may have declined by 30.3% as opposed to increasing in abundance by 38.4% (Fig 4) in the

Table 2. Comparing the proportion of species within the Living Planet Database (LPI) and the IUCN Red List of Threatened Species (IUCN) for each Red List category (LC–Least Concern, NT/LR–Near Threatened/Lower Risk, VU—Vulnerable, EN–Endangered, CR–Critically Endangered).

Taxon	Category	LPI	IUCN	X^2	Representation
Mammalia	CR	0.05	0.04	0.26	over
	EN	0.12	0.10	1.34	over
	VU	0.11	0.11	0.11	under
	NT/LR	0.07	0.07	0.19	under
	LC	0.64	0.66	0.44	under
	Total # sp.	*531*	*4753*		
Aves	CR	0.02	0.02	0.21	over
	EN	0.04	0.04	0.17	under
	VU	**0.05**	**0.07**	**10.34****	**under**
	NT/LR	**0.06**	**0.09**	**12.75*****	**under**
	LC	**0.82**	**0.76**	**27.31*****	**over**
	Total # sp.	*1415*	*10363*		
Reptilia	**CR**	**0.12**	**0.05**	**15.72*****	**over**
	EN	0.11	0.09	0.34	over
	VU	0.13	0.10	1.87	over
	NT/LR	**0.13**	**0.08**	**4.04***	**over**
	LC	**0.49**	**0.68**	**21.96*****	**under**
	Total # sp.	*149*	*4244*		
Amphibia	CR	0.07	0.11	2.79	under
	EN	**0.06**	**0.17**	**15.48*****	**under**
	VU	**0.04**	**0.14**	**12.96*****	**under**
	NT/LR	0.08	0.08	0.00	under
	LC	**0.72**	**0.50**	**35.12*****	**over**
	Total # sp.	*178*	*4958*		
Fishes	CR	0.03	0.04	0.20	under
	EN	**0.03**	**0.05**	**4.22***	**under**
	VU	0.09	0.10	0.96	under
	NT/LR	**0.07**	**0.05**	**5.65***	**over**
	LC	**0.63**	**0.75**	**45.45*****	**under**
	Total # sp.	*602*	*12093*		

Chi-squared values are given for the binomial test of proportions, with significance levels indicated.

*p < 0.05.

**p < 0.01.

***p < 0.001.

presentation indicates whether the given group is 'over' or 'under' represented. Mammals, birds and amphibians have been comprehensively assessed by the IUCN.

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unweighted index (LPI-U). The difference is also notable at the global level where the LPI-U suggests a decline of 19.7%, compared to a significantly larger declines of 58% in the LPI-D.

Declines appear to be masked in the LPI-U as a result of a high proportion of well monitored, increasing populations in temperate regions in the data set. Weighting by species diversity in the LPI-D thus distributes the responsibility for the index across regions and taxa according to species richness. However, tropical regions tend to have higher richness and a greater proportion of threatened species [34], so this method may introduce another bias by placing a high proportion of weight on groups that may be less well monitored, under-represented, or more likely to be categorized as threatened. Comparing the proportion of threatened species within the LPI database to the IUCN Red List, we find that Critically Endangered reptiles are the only threatened group which is over-represented, while Endangered and Vulnerable amphibians are under-represented (Table 2). Conversely, we see significant results for nearly all groups when we examine only those threatened species from the analysis that have been assessed using Criterion A (S9 Table).

The implication of this is complex to interpret. As threatened species assessed under Criterion A are significantly over-represented in all groups except for amphibians, we can infer that the LPI has a bias towards negative population trends. However the impact may be partially tempered by the proportional weighting at taxonomic group level. For example, amphibians, which are not significantly over-represented by threatened species, along with reptiles, are given the highest weighting among the terrestrial species and the second highest weighting among freshwater species. Furthermore, species threatened under other criteria may be experiencing population declines but sufficient data are just not available to contribute to the Red Listing assessment. What is also important to note is that the majority of fish species (745 out of 1,369 species) have not yet been assessed by the IUCN Red List and a further 40 species are assessed as Data Deficient so these species were not included in this analysis.

Accounting for the diversity of species using the LPI-D method allows the LPI to be calculated in a more taxonomically representative way. However, it would clearly be more beneficial to continue to improve species representation within the LPD. The rate with which new data are incorporated is relatively constant (S1 Fig), as a wealth of data remains available in the literature. Manual entry of these data is a critical limitation in growing biodiversity databases such as the LPD, so tools for automating this process would be of value, e.g. working relationships and support with scientific journals to identify useful research papers and the data they contain [35]. New technologies such as remote sensing may also provide ways to improve the spatial coverage of data [36], and incorporating other data types such as occurrence or opportunistic data (e.g. from citizen science [37]) may help expand taxonomic coverage as abundance data is rare for non-vertebrates. Encouragingly, improvements will happen as existing biodiversity databases continue to be augmented and techniques to harness the power of citizen science projects improve [38]. In addition, initiatives to harmonise and standardise existing biodiversity databases are underway to enhance the current resource base for monitoring global biodiversity [39]. The demand for measures to report on biodiversity change however remains a challenge [40] and one where improving our resource base will not provide answers fast enough.

As well as addressing taxonomic disparity in the data set, the LPI-D approach accounts for the broad scale geographic bias present in the LPD by placing more weight on the largely tropical, more species-rich realms. However, issues of coverage still remain at smaller spatial scales which this approach does not tackle. For example, the data from the Palearctic realm is largely from Europe and there is much less coverage in Asia (Fig 2). Likewise in the Afrotropics, eastern and southern Africa are better represented than western and central Africa. For the marine system, data tend to be clustered near the coasts which is where most known impact from human activity occurs [41] but also the areas of higher species richness [42]. Understanding whether and how these patterns bias the trends in the LPI will be an important continuation of this work and one which is hard to untangle given the inferred impact of different types of bias. For example, the bias towards data from protected areas might suggest the LPI would show a greater decline if counterfactuals from unprotected sites were equally monitored, on the assumption that protection has a positive effect on population trends. Improving the coverage of Data Deficient species, as categorised by the IUCN Red List, might introduce negative trends if these species are likely to be threatened, as has been predicted for terrestrial mammals [43]. Alternatively, declines may be exacerbated by a prevalence of coastal marine data; areas of high human impact and where many heavily exploited commercial fish stocks are monitored.

We note that weighting by species diversity is only one of a number of potential weightings that could be applied to make the trends more 'representative'. Other approaches have been used, for example, to account for the differing proportion of a species' total population across different countries [15]. Depending on the question of interest, other methods of weighting could also be explored such as weighting by genetic diversity, functional diversity, biomes or other metrics. As well as the use we have outlined for the global scale, the application of weighting by species diversity could be applied when developing a national biodiversity indicator when species lists are readily available for the country in question. As the Convention on Biological Diversity requires Parties to report on their biodiversity trends, having a method that can be adapted at smaller scales is essential.

A limitation of our current approach is that it is reliant on reasonable species lists, which are known to change over time and may be of lower quality for less studied groups and regions. Estimates for the number of as yet unidentified birds and mammals are small (e.g. ~10–15 species), but the number of unidentified amphibians, reptiles and fish are much larger with respective estimates of 57%, 13% and 22% undescribed [44]. These latter groups would therefore be given even greater weight, suggesting that vertebrate populations may be declining, on average, even more rapidly that we currently estimate. As estimates of the known number of species improve, the relative weighting of species groups can be updated to better estimate overall trends.

Our analysis suggests that prior estimates of the trends in global wildlife populations may have underestimated their global decline. This appears to be due to those well monitored groups for which we have disproportionate amounts of data (predominantly in the Nearctic and Palearctic) declining less than those species in more speciose regions for which we have proportionally less data. We might expect that as the weighted index places more weight on less monitored groups in more species-rich regions, we would be exaggerating the declines in abundance–as we might expect these groups to be declining more. For example we know that tropical vertebrate populations are in worse decline than those in temperate regions [45] and that amphibians are threatened with a greater risk of extinction than mammals or birds [46]. However, we note that when we remove those species groups for which we have very little data ($< 1\%$ species), the overall trends decline more (Fig 7), potentially suggesting that overall declines may be worse than we currently present. We urgently need more data for these groups to better determine their trends.

Supporting Information

S1 Appendix. Assessing geographic bias in the LPD.
(DOCX)

S1 Fig. The cumulative number of population time series in the global LPI from 2006 to 2016.
(DOCX)

S2 Fig. The boundaries for land and marine realms used for the geographical divisions of the LPI database. Terrestrial realm data from Olson et al., (2001) and marine realms were drawn in ArcGIS 10.2.2 for Desktop.
(DOCX)

S1 Table. Mapping of terrestrial biomes in the LPD to those in Martin *et al.* Asterisks denote significant differences in Martin *et al.*
(DOCX)

S2 Table. Test of proportions for unique locations in the LPI compared to observed values in Martin *et al* (2012) with significance levels indicated ($^{*}p < 0.05$, $**p < 0.01$, $***p < 0.001$).
(DOCX)

S3 Table. Test of proportions for unique locations in the LPI compared to expected values by area and distribution in Martin *et al* (2012) with significance levels indicated ($^{*}p < 0.05$, $**p < 0.01$, $***p < 0.001$). Asterisks denote significant differences in Martin *et al*.
(DOCX)

S4 Table. Test of proportions for unique locations by country in the LPI compared to expected values in Martin *et al* (2012) with significance levels indicated ($^{*}p < 0.05$, $**p < 0.01$, $***p < 0.001$). Asterisks denote significant differences in Martin *et al*.
(DOCX)

S5 Table. Test of proportions for unique locations by income category in the LPI compared to expected values in Martin *et al* (2012) with significance levels indicated ($^{*}p < 0.05$, $**p < 0.01$, $***p < 0.001$).
(DOCX)

S6 Table. Known vertebrate species ('Global estimate') for A. terrestrial and freshwater system and B. marine system, compared to species recorded within the LPI database, and the proportion that this represents of the global estimate.
(DOCX)

S7 Table. Comparing the proportion of terrestrial and freshwater species within the Living Planet Database (LPI) and the estimated known number of species (Known species) for each biogeographic realm and class. Chi-squared values are given for the binomial test of proportions, with significance levels indicated ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$). 'Representation' indicates whether the given group is 'over' or 'under' represented.
(DOCX)

S8 Table. Comparing the proportion marine species within the Living Planet Database (LPI) and the estimated known number of species (Known species) for each biogeographic realm and class. Chi-squared values are given for the binomial test of proportions, with significance levels indicated ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$). 'Representation' indicates whether the given group is 'over' or 'under' represented.
(DOCX)

S9 Table. Comparing the proportion of species within the Living Planet Database (LPI) and the IUCN Red List of Threatened Species (IUCN) for each Red List category (LC–Least Concern, NT/LR–Near Threatened/Lower Risk, VU—Vulnerable, EN–Endangered, CR–Critically Endangered). Only threatened species listed under Criterion A were included. Chi-squared values are given for the binomial test of proportions, with significance levels indicated ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$). Representation indicates whether the given group is 'over' or 'under' represented. Mammals, birds and amphibians have been comprehensively assessed by the IUCN.
(DOCX)

S10 Table. Terrestrial and freshwater weightings applied to taxa/realm subsets within the global LPI. The values also represent the weighting applied to the data when calculating the

system LPIs.
(DOCX)

S11 Table. Marine weightings applied to taxa/realm subsets within the global LPI. The values also represent the weighting applied to the data for when calculating the system LPIs.
(DOCX)

S12 Table. Terrestrial and freshwater realm weightings applied to data.
(DOCX)

S13 Table. Marine realm weightings applied to data.
(DOCX)

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Data curation: LM SD RF.

Formal analysis: LM SD RF.

Investigation: LM SD RF.

Methodology: LM SD RF.

Resources: LM SD RF.

Software: LM SD RF.

Validation: LM SD RF.

Visualization: LM SD RF.

Writing – original draft: LM SD RF.

Writing – review & editing: LM SD RF.

References

1. Collen B, Nicholson E (2014) Taking the measure of change. Science 346: 166–167. doi: 10.1126/science.1255772 PMID: 25278506
2. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, et al. (2014) Defaunation in the Anthropocene. Science 345: 401–406. doi: 10.1126/science.1251817 PMID: 25061202
3. Tittensor DP, Walpole M, Hill SLL, Boyce DG, Britten GL, et al. (2014) A mid-term analysis of progress toward international biodiversity targets. Science 346: 241–244. doi: 10.1126/science.1257484 PMID: 25278504
4. De Vos JM, Joppa LN, Gittleman JL, Stephens PR, Pimm SL (2015) Estimating the normal background rate of species extinction. Conservation Biology 29: 452–462. doi: 10.1111/cobi.12380 PMID: 25159086
5. Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, et al. (2015) Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances 1.

6. SCBD (2010) COP-10 Decision X/2. In: Secretariat of the convention on biological diversity, editor.
7. WWF (2016) Living Planet Report 2016: Risk and resilience in a new era WWF International, Gland, Switzerland.
8. Collen B, Loh J, Whitmee S, McRae L, Amin R, et al. (2009) Monitoring Change in Vertebrate Abundance: the Living Planet Index. Conservation Biology 23: 317–327. doi: 10.1111/j.1523-1739.2008.01117.x PMID: 19040654
9. Loh J, Green RE, Ricketts T, Lamoreux J, Jenkins M, et al. (2005) The Living Planet Index: using species population time series to track trends in biodiversity. Philosophical Transactions of the Royal Society of London B: Biological Sciences 360: 289–295. doi: 10.1098/rstb.2004.1584 PMID: 15814346
10. Boakes EH, McGowan PJK, Fuller RA, Chang-qing D, Clark NE, et al. (2010) Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. PLoS Biol 8: e1000385. doi: 10.1371/journal.pbio.1000385 PMID: 20532234
11. Yesson C, Brewer PW, Sutton T, Caithness N, Pahwa JS, et al. (2007) How Global Is the Global Biodiversity Information Facility? PLoS ONE 2: e1124. doi: 10.1371/journal.pone.0001124 PMID: 17987112
12. Collen B, Ram M, Zamin T, McRae L (2008) The tropical biodiversity data gap: addressing disparity in global monitoring. Tropical Conservation Science 1: 75–88.
13. Pereira HM, Navarro LM, Martins IS (2012) Global Biodiversity Change: The Bad, the Good, and the Unknown. Annual Review of Environment and Resources 37: 25–50.
14. Nicholson E, Collen B, Barausse A, Blanchard JL, Costelloe BT, et al. (2012) Making Robust Policy Decisions Using Global Biodiversity Indicators. PLoS ONE 7: e41128. doi: 10.1371/journal.pone.0041128 PMID: 22815938
15. Gregory RD, van Strien A, Vorisek P, Gmelig Meyling AW, Noble DG, et al. (2005) Developing indicators for European birds. Philosophical Transactions of the Royal Society of London B: Biological Sciences 360: 269–288. doi: 10.1098/rstb.2004.1602 PMID: 15814345
16. van Swaay CAM, Nowicki P, Settele J, van Strien AJ (2008) Butterfly monitoring in Europe: methods, applications and perspectives. Biodiversity and Conservation 17: 3455–3469.
17. Jones JPG, Collen B, Atkinson G, Baxter PWJ, Bubb P, et al. (2011) The Why, What, and How of Global Biodiversity Indicators Beyond the 2010 Target. Conservation Biology 25: 450–457. doi: 10.1111/j.1523-1739.2010.01605.x PMID: 21083762
18. Loh J, Randers J, MacGillivray A, Kapos V, Groombridge B, et al. (1998) Living Planet Report 1998. WWF, Gland, Switzerland.
19. UN (2015) Transforming our world: the 2030 Agenda for Sustainable Development. A/RES/70/1. https://sustainabledevelopment.un.org/post2015/transformingourworld.
20. Baillie J, Griffiths J, Turvey S, Loh J, Collen B (2010) Evolution Lost: status & trends of the world's vertebrates. Zoological Society of London, United Kingdom.
21. Martin LJ, Blossey B, Ellis E (2012) Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. Frontiers in Ecology and the Environment 10: 195–201.
22. World Wildlife Fund (2006) WildFinder: Online database of species distributions, ver. Jan-06. www.worldwildlife.org/WildFinder.
23. Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, et al. (2008) Freshwater Ecoregions of the World: A New Map of Biogeographic Units for Freshwater Biodiversity Conservation. BioScience 58: 403–414.
24. IUCN (2016) The IUCN Red List of Threatened Species. Version 2016–2. http://www.iucnredlist.org/. Downloaded on 22nd November 2016.
25. Uetz PJHe (2014) The Reptile Database, http://www.reptile-database.org, accessed April 15, 2014.
26. OBIS (2014) Distribution records of marine vertebrate species (numerous data sets). Ocean Biogeographic Information System Intergovernmental Oceanographic Commission of UNESCO. http://www.iobis.org. Accessed: 2014-10-31.
27. McRae L, Deinet S, Freeman R (2016) Data from: The diversity-weighted Living Planet Index: controlling for taxonomic bias in a global biodiversity indicator. Dryad Digital Repository.
28. Santini L, Belmaker J, Costello MJ, Pereira HM, Rossberg AG, et al. Assessing the suitability of diversity metrics to detect biodiversity change. Biological Conservation.
29. Buckland ST, Studeny AC, Magurran AE, Illian JB, Newson SE (2011) The geometric mean of relative abundance indices: a biodiversity measure with a difference. Ecosphere 2: 1–15.
30. Collen B, McRae L, Deinet S, De Palma A, Carranza T, et al. (2011) Predicting how populations decline to extinction. Philosophical Transactions of the Royal Society B: Biological Sciences 366: 2577–2586.
31. Pereira HM, Ferrier S, Walters M, Geller GN, Jongman RHG, et al. (2013) Essential Biodiversity Variables. Science 339: 277–278. doi: 10.1126/science.1229931 PMID: 23329036

32. Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, et al. Geographical and taxonomic biases in invasion ecology. Trends in Ecology & Evolution 23: 237–244.
33. Proença V, Martin LJ, Pereira HM, Fernandez M, McRae L, et al. Global biodiversity monitoring: From data sources to Essential Biodiversity Variables. Biological Conservation.
34. Grenyer R, Orme CDL, Jackson SF, Thomas GH, Davies RG, et al. (2006) Global distribution and conservation of rare and threatened vertebrates. Nature 444: 93–96. doi: 10.1038/nature05237 PMID: 17080090
35. Huang X, Qiao G (2011) Biodiversity databases should gain support from journals. Trends in Ecology & Evolution 26: 377–378.
36. Pettorelli N, Wegmann M, Skidmore A, Mücher S, Dawson TP, et al. (2016) Framing the concept of satellite remote sensing essential biodiversity variables: challenges and future directions. Remote Sensing in Ecology and Conservation: n/a-n/a.
37. Isaac NJB, van Strien AJ, August TA, de Zeeuw MP, Roy DB (2014) Statistics for citizen science: extracting signals of change from noisy ecological data. Methods in Ecology and Evolution 5: 1052–1060.
38. Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, et al. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. Science 344.
39. Kissling WD, Hardisty A, García EA, Santamaria M, De Leo F, et al. (2015) Towards global interoperability for supporting biodiversity research on essential biodiversity variables (EBVs). Biodiversity 16: 99–107.
40. Walpole M, Almond REA, Besançon C, Butchart SHM, Campbell-Lendrum D, et al. (2009) Tracking Progress Toward the 2010 Biodiversity Target and Beyond. Science 325: 1503–1504. doi: 10.1126/science.1175466 PMID: 19762630
41. Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, et al. (2008) A Global Map of Human Impact on Marine Ecosystems. Science 319: 948–952. doi: 10.1126/science.1149345 PMID: 18276889
42. Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, et al. (2010) Global patterns and predictors of marine biodiversity across taxa. Nature 466: 1098–1101. doi: 10.1038/nature09329 PMID: 20668450
43. Bland LM, Collen B, Orme CDL, Bielby J (2015) Predicting the conservation status of data-deficient species. Conservation Biology 29: 250–259. doi: 10.1111/cobi.12372 PMID: 25124400
44. Scheffers BR, Joppa LN, Pimm SL, Laurance WF (2012) What we know and don't know about Earth's missing biodiversity. Trends in Ecology & Evolution 27: 501–510.
45. McRae L, Freeman R, Deinet S (2014) 'The Living Planet Index' in: Living Planet Report 2014: species and spaces, people and places WWF, Gland, Switzerland.
46. Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, et al. (2004) Status and Trends of Amphibian Declines and Extinctions Worldwide. Science 306: 1783–1786. doi: 10.1126/science.1103538 PMID: 15486254

S1 Appendix. Assessing geographic bias in the LPD

Method

We compared our data with Martin *et al.* (2012) who describe several geographic biases including the overrepresentation of PAs, temperate woodlands and wealthy countries in study sites from recent publications. To use a comparable data set, we selected only terrestrial populations from the LPD and unique sites. We also only included those sites that have a specific location recorded – this avoids the use of sites which are a mid-point of a large survey area.

Protected areas – the populations in the LPD are already coded as to whether they occur in a protected area. We looked at the proportion of sites that are in protected areas as denoted in the LPD assessed using World Database on Protected Areas (IUCN and UNEP-WCMC, 2016).

Biomes – Martin *et al*. used Ramankutty & Foley's Potential Natural Vegetation Cover (Ramankutty and Foley, 1999) to categorise biomes. In the LPD, the biomes have been categorised using WWF Ecoregions (Olson et al, 2001). We matched up the categories (Table S1) focussing only on woodland biomes as these were the ones highlighted in Martin *et al*. We compared the proportion of sites in each biome to the observed and expected proportions in Martin *et al*.

Wealthy countries – we used the categorisation from Martin *et al.* to look at the proportion of sites in wealthy and other countries, and combined for different country income categories as defined by the World Bank (World Bank, 2012).

References

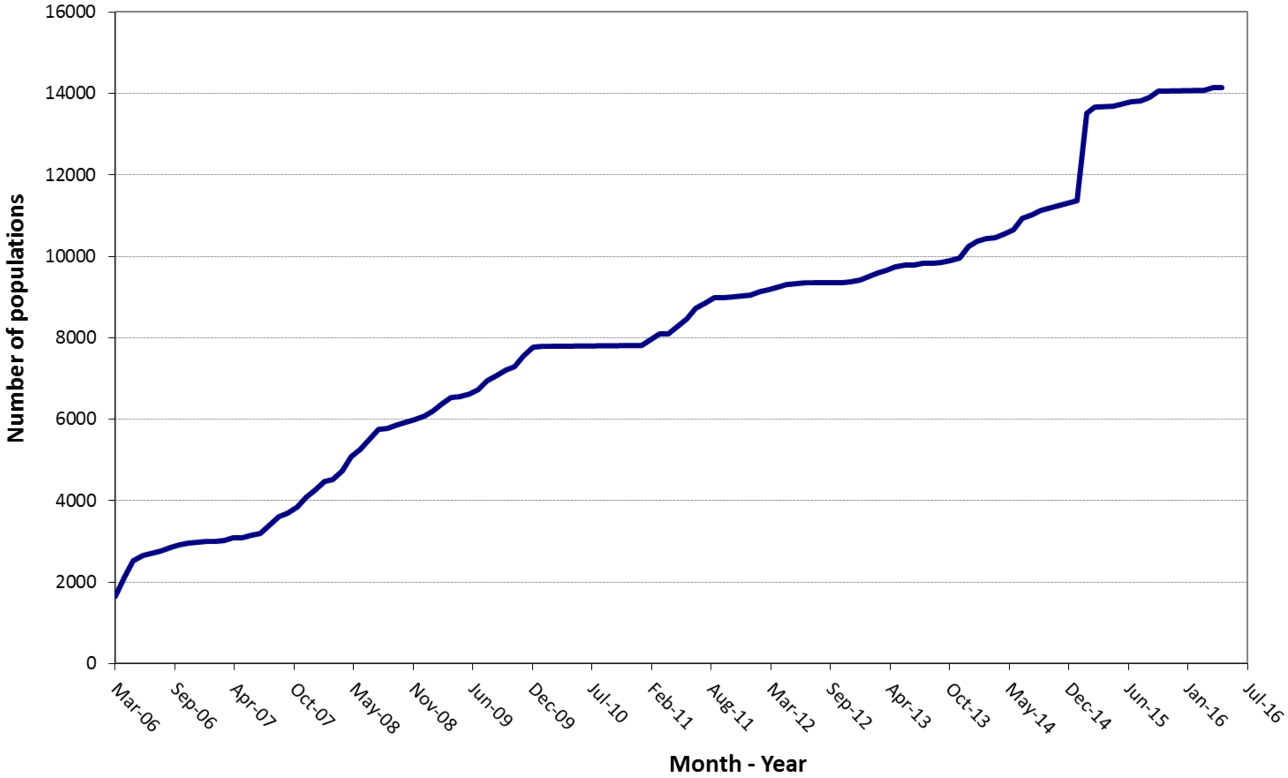
Martin LJ, Blossey B, Ellis E. (2012) Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. Frontiers in Ecology and the Environment 10(4):195-201.

IUCN and UNEP-WCMC (2016), The World Database on Protected Areas (WDPA) [On-line], June 2016, Cambridge, UK: UNEP-WCMC. Available at: www.protectedplanet.net.

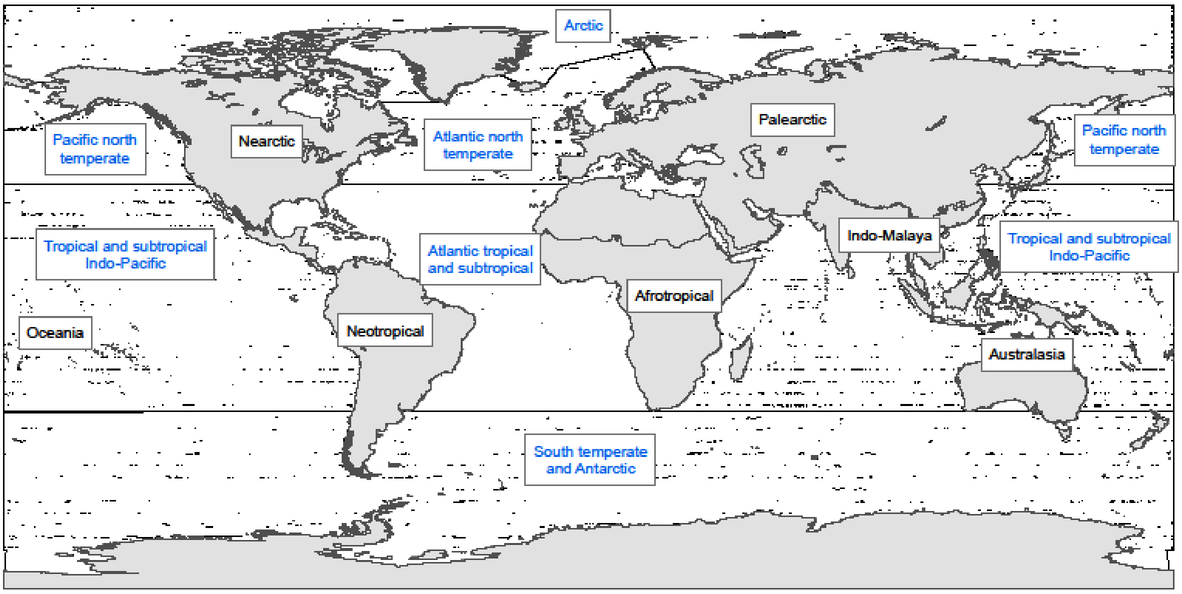
Ramankutty, N., and J.A. Foley (1999). Estimating historical changes in global land cover: Crop lands from 1700 to 1992. Global Biogeochemical Cycles 13(4), 997-1027.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, et al. (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience 51(11):933-8.

World Bank (2012) World Bank list of economies (July 2012).



S1 Fig. The cumulative number of population time series in the global LPI from 2006 to 2016.



S2 Fig. The boundaries for land and marine realms used for the geographical divisions of the LPI database. Terrestrial realm data from Olson et al., (2001) and marine realms were drawn in ArcGIS 10.2.2 for Desktop.

S1 Table

Biome (Martin)	Biome (LPI)
Tropical evergreen woodland*	Tropical & subtropical coniferous forests
Tropical deciduous woodland*	Tropical dry broadleaf forests / Tropical moist broadleaf forests
Temperate evergreen woodland*	Temperate coniferous forests
Temperate deciduous woodland* / Mixed woodland*	Temperate broadleaf and mixed forests
Boreal woodland	Boreal forests & taiga
Tundra*	Tundra

S2 Table

Biome (Martin)	Representation (Martin)	Proportion (LPI)	Proportion (Martin, observed)	χ2	
Tropical evergreen woodland	over	0.01	0.14	129.36	***
Tropical deciduous woodland	under	0.18	0.02	204.55	***
Temperate evergreen woodland	over	0.07	0.11	8.53	**
Temperate deciduous woodland / Mixed woodland	over	0.20	0.31	30.42	***
Boreal woodland	NS	0.09	0.08	0.20	NS
Tundra	under	0.07	0.03	15.17	***

S3 Table

		By area (Martin, expected)				By equal distribution (Martin, expected)			
Biome (Martin)	Proportion (LPI)	Proportion	χ2		Representation	Proportion	χ2		Representation
Tropical evergreen woodland*	0.01	0.13	114.81	***	under	0.08	63.60	***	under
Tropical deciduous woodland*	0.18	0.05	116.86	***	over	0.08	49.76	***	over
Temperate evergreen woodland*	0.07	0.04	13.93	***	over	0.08	1.04	NS	NS
Temperate deciduous woodland / Mixed woodland*	0.20	0.15	11.32	***	over	0.17	5.59	NS	NS
Boreal woodland	0.09	0.06	4.81	*	over	0.08	0.04	NS	NS
Tundra*	0.07	0.05	1.84	NS	NS	0.08	1.46	NS	NS

S4 Table

Country	Income	Proportion (LPI)	Proportion (Martin, expected)	χ2	Sig	Representation
Afghanistan	Low	0.00	0.00	3.16	NS	NS
Albania	Lower middle	0.00	0.00	0.00	NS	NS
Algeria	Upper middle	0.00	0.02	15.56	***	under
American Samoa	Upper middle	0.00	0.00	NA	NA	NA
Andorra	High	0.00	0.00	NA	NA	NA
Angola	Upper middle	0.00	0.01	5.50	*	under
Antigua & Barbuda	Upper middle	0.00	0.00	3.87	*	over
Argentina	Upper middle	0.02	0.02	0.64	NS	NS
Armenia	Lower middle	0.00	0.00	0.00	NS	NS
Aruba	High	0.00	0.00	NA	NA	NA
Australia	High	0.03	0.06	12.31	***	under
Austria	High	0.00	0.00	0.00	NS	NS
Azerbaijan	Upper middle	0.00	0.00	0.00	NS	NS
Bahrain	High	0.00	0.00	0.00	NS	NS
Bangladesh	Low	0.00	0.00	0.03	NS	NS
Barbados	High	0.00	0.00	NA	NA	NA
Belarus	Upper middle	0.00	0.00	0.00	NS	NS
Belgium	High	0.00	0.00	0.00	NS	NS
Belize	Lower middle	0.00	0.00	0.00	NS	NS
Benin	Low	0.00	0.00	0.00	NS	NS
Bhutan	Lower middle	0.00	0.00	0.00	NS	NS
Bolivia	Lower middle	0.00	0.01	6.41	*	under
Bosnia & Herzegovina	Upper middle	0.00	0.00	0.00	NS	NS
Botswana	Upper middle	0.00	0.00	2.76	NS	NS
Brazil	Upper middle	0.02	0.07	29.33	***	under
Brunei Darussalam	High	0.00	0.00	0.00	NS	NS
Bulgaria	Upper middle	0.00	0.00	0.00	NS	NS
Burkina Faso	Low	0.00	0.00	0.70	NS	NS
Burundi	Low	0.00	0.00	0.00	NS	NS
Cambodia	Low	0.00	0.00	0.00	NS	NS
Cameroon	Lower middle	0.00	0.00	0.00	NS	NS
Canada	High	0.16	0.07	49.59	***	over
Central African Republic	Low	0.01	0.00	0.05	NS	NS
Chad	Low	0.00	0.01	3.98	*	under
Chile	Upper middle	0.01	0.01	0.41	NS	NS
China	Upper middle	0.01	0.07	52.53	***	under
Colombia	Upper middle	0.00	0.01	6.80	**	under
Comoros	Low	0.00	0.00	0.04	NS	NS
Congo	Lower middle	0.00	0.00	1.13	NS	NS
Congo, DRC	Low	0.01	0.02	6.12	*	under
Costa Rica*	Upper middle	0.00	0.00	1.40	NS	NS
Côte d'Ivoire	Lower middle	0.01	0.00	0.60	NS	NS
Croatia	High	0.00	0.00	0.35	NS	NS
Cuba	Upper middle	0.00	0.00	0.00	NS	NS
Cyprus	High	0.00	0.00	0.00	NS	NS
Czech Republic	High	0.00	0.00	0.19	NS	NS
Denmark	High	0.00	0.00	2.83	NS	NS
Djibouti	Lower middle	0.00	0.00	0.00	NS	NS
Dominica	Upper middle	0.00	0.00	0.04	NS	NS
Dominican Republic	Upper middle	0.00	0.00	0.00	NS	NS
Ecuador	Upper middle	0.00	0.00	0.03	NS	NS
Egypt	Lower middle	0.00	0.01	5.77	*	under
El Salvador	Lower middle	0.00	0.00	0.00	NS	NS
Equatorial Guinea	High	0.00	0.00	0.00	NS	NS
Eritrea	Low	0.00	0.00	0.00	NS	NS
Estonia	High	0.00	0.00	0.00	NS	NS
Ethiopia	Low	0.01	0.01	0.00	NS	NS
Falkland Islands	Not listed	0.00	0.00	0.00	NS	NS
Fiji	Lower middle	0.00	0.00	0.00	NS	NS
Finland	High	0.02	0.00	17.69	***	over
France	High	0.02	0.00	13.69	***	over
French Guiana	Not listed	0.00	0.00	0.00	NS	NS
Gabon	Upper middle	0.00	0.00	0.61	NS	NS
Georgia	Lower middle	0.00	0.00	0.00	NS	NS
Germany*	High	0.02	0.00	12.28	***	over

Ghana	Lower middle	0.01	0.00	4.33	*	over
Greece	High	0.00	0.00	0.00	NS	NS
Greenland*	High	0.00	0.00	1.06	NS	NS
Grenada	Upper middle	0.00	0.00	NA	NA	NA
Guadeloupe	Not listed	0.00	0.00	0.00	NS	NS
Guatemala	Lower middle	0.00	0.00	0.00	NS	NS
Guinea	Low	0.00	0.00	0.00	NS	NS
Guinea-Bissau	Low	0.00	0.00	0.00	NS	NS
Guyana	Lower middle	0.00	0.00	0.33	NS	NS
Haiti	Low	0.00	0.00	0.00	NS	NS
Honduras	Lower middle	0.00	0.00	0.00	NS	NS
Hungary	High	0.00	0.00	0.00	NS	NS
Iceland	High	0.00	0.00	0.00	NS	NS
India	Lower middle	0.05	0.02	12.09	***	over
Indonesia	Lower middle	0.01	0.01	3.83	Near	(under)
Iran	Upper middle	0.00	0.01	3.45	NS	NS
Iraq	Lower middle	0.00	0.00	1.72	NS	NS
Ireland	High	0.00	0.00	2.27	NS	NS
Isle of Man	High	0.00	0.00	0.00	NS	NS
Israel*	High	0.00	0.00	0.00	NS	NS
Italy	High	0.01	0.00	9.49	**	over
Jamaica	Upper middle	0.00	0.00	0.00	NS	NS
Japan	High	0.00	0.00	0.00	NS	NS
Jersey	Not listed	0.00	0.00	NA	NA	NA
Jordan	Upper middle	0.00	0.00	0.00	NS	NS
Kazakhstan	Upper middle	0.00	0.02	17.97	***	under
Kenya	Low	0.02	0.00	13.22	***	over
Kuwait	High	0.00	0.00	0.00	NS	NS
Kyrgyzstan	Low	0.00	0.00	0.25	NS	NS
Laos	Lower middle	0.00	0.00	0.45	NS	NS
Latvia	Upper middle	0.00	0.00	0.00	NS	NS
Lebanon	Upper middle	0.00	0.00	0.00	NS	NS
Lesotho	Lower middle	0.00	0.00	0.00	NS	NS
Liberia	Low	0.00	0.00	0.00	NS	NS
Libya	Upper middle	0.00	0.01	10.38	**	under
Liechtenstein	High	0.00	0.00	NA	NA	NA
Lithuania	Upper middle	0.00	0.00	0.00	NS	NS
Luxembourg	High	0.00	0.00	0.00	NS	NS
Macedonia	Upper middle	0.00	0.00	0.00	NS	NS
Madagascar	Low	0.01	0.00	0.38	NS	NS
Malawi	Low	0.00	0.00	0.81	NS	NS
Malaysia	Upper middle	0.00	0.00	0.11	NS	NS
Mali	Low	0.00	0.01	5.55	*	under
Malta	High	0.00	0.00	0.05	NS	NS
Martinique	Not listed	0.00	0.00	0.00	NS	NS
Mauritania	Low	0.00	0.01	4.06	*	under
Mauritius	Upper middle	0.00	0.00	1.06	NS	NS
Mayotte	Not listed	0.00	0.00	NA	NA	NA
Mexico	Upper middle	0.01	0.02	0.00	NS	NS
Moldova	Lower middle	0.00	0.00	0.00	NS	NS
Mongolia	Lower middle	0.00	0.01	3.03	NS	NS
Montenegro	Upper middle	0.00	0.00	0.01	NS	NS
Montserrat	Not listed	0.00	0.00	NA	NA	NA
Morocco	Lower middle	0.01	0.00	0.24	NS	NS
Mozambique	Low	0.01	0.01	0.00	NS	NS
Myanmar	Low	0.00	0.01	3.37	NS	NS
Namibia	Upper middle	0.00	0.01	1.40	NS	NS
Nepal	Low	0.01	0.00	11.56	***	over
Netherlands	High	0.00	0.00	0.00	NS	NS
Netherlands Antilles	Not listed	0.00	0.00	NA	NA	NA
New Caledonia	High	0.00	0.00	0.00	NS	NS
New Zealand	High	0.01	0.00	7.47	**	over
Nicaragua	Lower middle	0.00	0.00	0.00	NS	NS
Niger	Low	0.00	0.01	7.13	**	under
Nigeria	Lower middle	0.00	0.01	0.93	NS	NS
North Korea	Low	0.00	0.00	0.01	NS	NS
Norway	High	0.02	0.00	13.40	***	over
Oman	High	0.00	0.00	0.00	NS	NS

Pakistan	Lower middle	0.05	0.01	42.84	***	over
Panama*	Upper middle	0.01	0.00	6.26	*	over
Papua New Guinea	Lower middle	0.00	0.00	1.97	NS	NS
Paraguay	Lower middle	0.00	0.00	1.50	NS	NS
Peru	Upper middle	0.00	0.01	4.08	*	under
Philippines	Lower middle	0.00	0.00	0.83	NS	NS
Poland	High	0.01	0.00	2.25	NS	NS
Portugal	High	0.00	0.00	0.89	NS	NS
Puerto Rico*	High	0.01	0.00	14.20	***	over
Qatar	High	0.00	0.00	0.00	NS	NS
Reunion	Not listed	0.00	0.00	0.00	NS	NS
Romania	Upper middle	0.00	0.00	0.05	NS	NS
Russian Federation	Upper middle	0.03	0.13	59.31	***	under
Rwanda	Low	0.00	0.00	0.67	NS	NS
Samoa	Lower middle	0.00	0.00	0.00	NS	NS
San Marino	High	0.00	0.00	NA	NA	NA
São Tomé & Principe	Lower middle	0.00	0.00	0.00	NS	NS
Saudi Arabia	High	0.00	0.01	8.31	**	under
Senegal	Lower middle	0.00	0.00	0.16	NS	NS
Serbia	Upper middle	0.00	0.00	0.00	NS	NS
Sierra Leone	Low	0.00	0.00	0.00	NS	NS
Singapore	High	0.00	0.00	0.00	NS	NS
Slovakia	High	0.00	0.00	1.44	NS	NS
Slovenia	High	0.00	0.00	0.00	NS	NS
Solomon Islands	Lower middle	0.00	0.00	0.00	NS	NS
Somalia	Low	0.00	0.00	3.18	NS	NS
South Africa	Upper middle	0.05	0.01	31.99	***	over
South Korea	High	0.00	0.00	1.74	NS	NS
Spain	High	0.03	0.00	26.95	***	over
Sri Lanka	Lower middle	0.00	0.00	0.00	NS	NS
St Kitts & Nevis	High	0.00	0.00	0.05	NS	NS
St Lucia	Upper middle	0.00	0.00	0.04	NS	NS
St Pierre & Miquelon	Not listed	0.00	0.00	NA	NA	NA
St Vincent & the Grenadines	Upper middle	0.00	0.00	NA	NA	NA
Sudan	Lower middle	0.00	0.02	16.84	***	under
Suriname	Upper middle	0.00	0.00	0.05	NS	NS
Swaziland	Lower middle	0.00	0.00	0.77	NS	NS
Sweden*	High	0.02	0.00	11.11	***	over
Switzerland*	High	0.01	0.00	11.64	***	over
Syria	Lower middle	0.00	0.00	0.22	NS	NS
Tajikistan	Low	0.00	0.00	0.03	NS	NS
Tanzania	Low	0.03	0.01	24.04	***	over
Thailand	Upper middle	0.00	0.00	0.00	NS	NS
The Bahamas	High	0.00	0.00	0.02	NS	NS
The Gambia	Low	0.00	0.00	0.00	NS	NS
Timor-Leste	Lower middle	0.00	0.00	0.00	NS	NS
Togo	Low	0.00	0.00	0.00	NS	NS
Tonga	Lower middle	0.00	0.00	NA	NA	NA
Trinidad & Tobago	High	0.00	0.00	0.00	NS	NS
Tunisia	Upper middle	0.00	0.00	0.09	NS	NS
Turkey	Upper middle	0.00	0.01	4.14	*	under
Turkmenistan	Upper middle	0.00	0.00	1.97	NS	NS
Turks & Caicos Islands	High	0.00	0.00	NA	NA	NA
Uganda	Low	0.02	0.00	24.60	***	over
Ukraine	Lower middle	0.00	0.00	2.79	NS	NS
United Arab Emirates	High	0.00	0.00	0.00	NS	NS
United Kingdom*	High	0.02	0.00	20.66	***	over
United States*	High	0.06	0.07	0.40	NS	NS
Uruguay	Upper middle	0.00	0.00	0.17	NS	NS
Uzbekistan	Lower middle	0.00	0.00	0.01	NS	NS
Vanuatu	Lower middle	0.00	0.00	0.00	NS	NS
Venezuela	Upper middle	0.00	0.01	1.85	NS	NS
Vietnam	Lower middle	0.01	0.00	0.57	NS	NS
Virgin Islands (U.S.)	High	0.00	0.00	NA	NA	NA
Western Sahara	Not listed	0.00	0.00	0.65	NS	NS
Yemen	Lower middle	0.00	0.00	1.89	NS	NS
Zambia	Lower middle	0.02	0.01	6.06	*	over
Zimbabwe	Low	0.01	0.00	5.40	*	over

S5 Table

Income category	**No. of countries**	**Proportion (Martin, expected)**	**Proportion (LPI)**	**χ2**	**Sig**	**Representation**
High	57	0.25	0.49	137.21	***	over
Low	36	0.13	0.15	2.42	NS	NS
Lower middle	47	0.16	0.17	0.37	NS	NS
Not listed	11	0.00	0.00	0.19	NS	NS
Upper middle	50	0.46	0.19	175.39	***	under
Higher (High + Upper middle)	*107*	*0.71*	*0.68*	*2.58*	*NS*	*NS*
Lower (Low + Lower middle)	*83*	*0.28*	*0.32*	*2.89*	*NS*	*NS*

A

Species numbers

		Global estimate	LPI database	Proportion
Amphibia and Reptilia	Afrotropical	2480	18	0.01
	IndoPacific	3994	69	0.02
	Nearctic	739	137	0.19
	Neotropical	4879	96	0.02
	Palearctic	1166	42	0.04
Aves	Afrotropical	2294	106	0.05
	IndoPacific	3616	249	0.07
	Nearctic	725	492	0.68
	Neotropical	3890	312	0.08
	Palearctic	1575	353	0.22
Mammalia	Afrotropical	1173	126	0.11
	IndoPacific	1568	96	0.06
	Nearctic	481	101	0.21
	Neotropical	1282	78	0.06
	Palearctic	906	117	0.13
*FW Fishes**	Afrotropical	-	51	0.02
	IndoPacific	-	28	0.01
	Nearctic	-	121	0.15
	Neotropical	-	122	0.02
	Palearctic	-	56	0.03

B **Species numbers**

		Global estimate	LPI database	Proportion
Reptilia	Arctic	0	0	N/A
	Atlantic north temperate	6	3	0.50
	Atlantic tropical and subtropical	11	7	0.64
	Pacific north temperate	2	2	1.00
	South temperate and Antarctic	3	0	0.00
	Tropical and subtropical Indo-Pacific	79	13	0.16
Aves	Arctic	79	29	0.37
	Atlantic north temperate	316	81	0.26
	Atlantic tropical and subtropical	467	50	0.11
	Pacific north temperate	172	61	0.35
	South temperate and Antarctic	167	62	0.37
	Tropical and subtropical Indo-Pacific	694	53	0.08
Mammalia	Arctic	16	16	1.00
	Atlantic north temperate	45	20	0.44
	Atlantic tropical and subtropical	42	6	0.14
	Pacific north temperate	54	29	0.54
	South temperate and Antarctic	70	13	0.19
	Tropical and subtropical Indo-Pacific	70	20	0.29
Fishes	Arctic	291	15	0.05
	Atlantic north temperate	1826	237	0.13
	Atlantic tropical and subtropical	4454	280	0.06
	Pacific north temperate	1681	121	0.07
	South temperate and Antarctic	2721	91	0.03
	Tropical and subtropical Indo-Pacific	11627	404	0.03

S6 Table. Known vertebrate species (‘Global estimate’) for A. terrestrial and freshwater systems and B. marine system, compared to species recorded within the LPI database, and the proportion that this represents of the global estimate. *The exact estimates for freshwater fishes based on Abell et al (2008) are not publicly available.

Realm	**Taxon**	**LPI**	**Known species**	**X-squared**	**Significant?**	**Representation**
Afrotropical	Amphibia and Reptilia	0.01	0.06	130.93	***	under
Afrotropical	Aves	0.04	0.05	11.54	***	under
Afrotropical	Fishes	0.02	0.07	101.09	***	under
Afrotropical	Mammalia	0.05	0.03	30.75	***	over
IndoPacific	Amphibia and Reptilia	0.02	0.09	147.55	***	under
IndoPacific	Aves	0.09	0.08	1.09		over
IndoPacific	Fishes	0.01	0.06	118.02	***	under
IndoPacific	Mammalia	0.04	0.04	2.32		over
Nearctic	Amphibia and Reptilia	0.05	0.02	142.94	***	over
Nearctic	Aves	0.18	0.02	2595.10	***	over
Nearctic	Fishes	0.04	0.02	84.12	***	over
Nearctic	Mammalia	0.04	0.01	130.66	***	over
Neotropical	Amphibia and Reptilia	0.03	0.11	165.70	***	under
Neotropical	Aves	0.11	0.09	15.21	***	over
Neotropical	Fishes	0.04	0.11	129.77	***	under
Neotropical	Mammalia	0.03	0.03	0.19		under
Palearctic	Amphibia and Reptilia	0.02	0.03	13.96	***	under
Palearctic	Aves	0.13	0.04	530.49	***	over
Palearctic	Fishes	0.02	0.04	24.81	***	under
Palearctic	Mammalia	0.04	0.02	52.55	***	over

S7 Table. Comparing the proportion of terrestrial and freshwater species within the Living Planet Database (LPI) and the estimated known number of species (Known species) for each biogeographic realm and class. Chi-squared values are given for the binomial test of proportions, with significance levels indicated (*p < 0.05, **p < 0.01, ***p < 0.001). 'Representation' indicates whether the given group is 'over' or 'under' represented.

Realm	Taxon	LPI	Known species	X-squared	Significant?	Representation
Arctic	Aves	0.02	0.00	107.94	***	over
Arctic	Fishes	0.01	0.01	0.49		under
Arctic	Mammalia	0.01	0.00	130.87	***	over
Atlantic North Temperate	Aves	0.05	0.01	205.11	***	over
Atlantic North Temperate	Fishes	0.15	0.13	1.82		over
Atlantic North Temperate	Mammalia	0.01	0.00	88.50	***	over
Atlantic North Temperate	Reptilia	0.00	0.00	10.16	**	over
Atlantic Tropical and Sub-tropical	Aves	0.03	0.01	24.76	***	over
Atlantic Tropical and Sub-tropical	Fishes	0.17	0.20	5.69	*	under
Atlantic Tropical and Sub-tropical	Mammalia	0.00	0.00	4.48	*	over
Atlantic Tropical and Sub-tropical	Reptilia	0.00	0.00	37.83	***	over
Pacific North Temperate	Aves	0.04	0.01	223.25	***	over
Pacific North Temperate	Fishes	0.08	0.06	5.18	*	over
Pacific North Temperate	Mammalia	0.02	0.00	155.48	***	over
Pacific North Temperate	Reptilia	0.00	0.00	9.17	**	over
S.Temperate and Antarctic	Aves	0.04	0.01	235.35	***	over
S.Temperate and Antarctic	Fishes	0.06	0.09	23.18	***	under
S.Temperate and Antarctic	Mammalia	0.01	0.00	18.57	***	over
S.Temperate and Antarctic	Reptilia	0.00	0.00	0.00		under
Tropical and Sub-tropical Indo-Pacific	Aves	0.03	0.02	7.31	**	over
Tropical and Sub-tropical Indo-Pacific	Fishes	0.25	0.43	201.20	***	under
Tropical and Sub-tropical Indo-Pacific	Mammalia	0.01	0.00	54.76	***	over
Tropical and Sub-tropical Indo-Pacific	Reptilia	0.01	0.00	15.06	***	over

S8 Table. Comparing the proportion of marine species within the Living Planet Database (LPI) and the estimated known number of species (Known species) for each biogeographic realm and class. Chi-squared values are given for the binomial test of proportions, with significance levels indicated (*p < 0.05, **p < 0.01, ***p < 0.001). 'Representation' indicates whether the given group is 'over' or 'under' represented.

Taxon	Category	LPI	IUCN	X^2	Representation
Mammalia	**CR**	**0.04**	**0.02**	**4.26***	**over**
	EN	**0.08**	**0.03**	**26.71*****	**over**
	VU	**0.08**	**0.06**	**4.55***	**over**
	Total # sp.	*485*	*3985*		
Aves	**CR**	**0.01**	**0.01**	**13.45*****	**over**
	EN	**0.02**	**0.01**	**11.84*****	**over**
	VU	**0.03**	**0.03**	**4.69E-29*****	**under**
	Total # sp.	*1352*	*9438*		
Reptilia	**CR**	**0.12**	**0.02**	**58.44*****	**over**
	EN	**0.08**	**0.01**	**36.11*****	**over**
	VU	**0.08**	**0.03**	**11.31*****	**over**
	Total # sp.	*133*	*3458*		
Amphibia	CR	0.07	0.06	0.09	over
	EN	0.03	0.02	0.97	over
	VU	0.02	0.01	0.63	over
	Total # sp.	*170*	*3186*		
Fishes	**CR**	**0.03**	**0.01**	**6.23***	**over**
	EN	**0.03**	**0.01**	**7.90****	**over**
	VU	**0.08**	**0.03**	**38.90*****	**over**
	Total # sp.	*590*	*10381*		

S9 Table. Comparing the proportion of species within the Living Planet Database (LPI) and the IUCN Red List of Threatened Species (IUCN) for each Red List category (LC – Least Concern, NT/LR – Near Threatened/Lower Risk, VU - Vulnerable, EN – Endangered, CR – Critically Endangered). Only threatened species listed under Criterion A were included. Chi-squared values are given for the binomial test of proportions, with significance levels indicated (*p < 0.05, **p < 0.01, ***p < 0.001). Representation indicates whether the given group is 'over' or 'under' represented. Mammals, birds and amphibians have been comprehensively assessed by the IUCN.

		Afrotropical	Nearctic	Neotropical	Palearctic	Indo-Pacific
Terrestrial groups	Birds	0.387	0.376	0.387	0.433	0.396
	Mammals	0.197	0.249	0.127	0.249	0.172
	Reptiles and amphibians	0.414	0.373	0.484	0.316	0.431
Freshwater groups	Fishes	0.590	0.565	0.584	0.592	0.493
	Birds	0.192	0.203	0.107	0.211	0.176
	Mammals	0.009	0.013	0.010	0.015	0.008
	Reptiles and amphibians	0.207	0.217	0.298	0.179	0.321

S10 Table. Terrestrial and freshwater weightings applied to taxa/realm subsets within the global LPI. The values also represent the weighting applied to the data when calculating the system LPIs.

	Arctic	Atlantic North Temperate	Atlantic Tropical and Sub-tropical	Pacific North Temperate	Tropical and Sub-tropical Indo-Pacific	South Temperate and Antarctic
Reptiles	0	0.001303	0.001630	0.000935	0.005505	0.000957
Birds	0.172867	0.068635	0.069353	0.080916	0.048714	0.054261
Mammals	0.035011	0.009774	0.006224	0.025257	0.004878	0.022342
Fishes	0.792123	0.920286	0.922791	0.892890	0.940901	0.922438

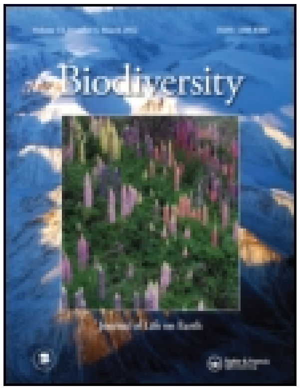
S11 Table. Marine weightings applied to taxa/realm subsets within the global LPI. The values also represent the weighting applied to the data for when calculating the system LPIs.

	Afrotropical	Nearctic	Neotropical	Palearctic	Indo-Pacific
Terrestrial LPI	0.189738	0.061683	0.321132	0.116431	0.292168
Freshwater LPI	0.211701	0.060853	0.365550	0.123314	0.225576

S12 Table. Terrestrial and freshwater realm weightings applied to data.

	Arctic	Atlantic North Temperate	Atlantic Tropical and Sub-tropical	Pacific North Temperate	Tropical and Sub-tropical Indo Pacific	South Temperate and Antarctic
Marine LPI	0.014541	0.146489	0.214706	0.068026	0.456553	0.099685

S13 Table. Marine realm weightings applied to data.



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The Arctic Species Trend Index: using vertebrate population trends to monitor the health of a rapidly changing ecosystem

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The Arctic Species Trend Index: using vertebrate population trends to monitor the health of a rapidly changing ecosystem

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The task of measuring the change of Arctic biodiversity and instituting changes to halt and reverse any downturn has been taken up in response to the rapid changes observed in the region. It is an undertaking made more difficult by the rate at which environmental change is occurring and the difficulty in monitoring species in remote and challenging habitats. We explored techniques to aggregate population trends among vertebrate species. We compiled almost 900 time series data sets tracking trends in Arctic vertebrate populations over the past four decades representing 37% of all known Arctic vertebrate species. Our results showed strengths in the breadth of populations and species monitored and the disaggregation of the data to uncover regional trends. Limitations of the data set were still apparent, due to the lack of any stratified monitoring scheme. Specifically, there were more bird species data than any other vertebrate class. To measure progress towards global targets for the environment, such as the Aichi biodiversity targets for the Convention on Biological Diversity (CBD), indicators like the one we have developed must be strengthened and adapted. Never has it been more important to understand how Arctic ecosystems and the living resources they support are responding to environmental change; tracking how they respond to growing and cumulative pressures will enable pre-emptive action to safeguard their future.

Keywords: Arctic; biodiversity indicator; climate change; generalised additive modelling; monitoring; population trend; vertebrate species

Introduction

The Arctic region contributes significantly to global biodiversity by supporting globally important populations of vertebrates. For example, 80% of the global goose population (Zöckler 2008) and over 50% of the world's breeding shorebirds (Zöckler, Delany, and Hagemeijer 2003) reside in the Arctic during the breeding season. However, the Arctic is a region experiencing the most rapid visible and measurable changes in its climate and environment in the world (ACIA 2005; Stroeve et al. 2007) and this is predicted to lead to dramatic changes in ecosystems (Post et al. 2009). It is therefore vital that accurate, scaled and integrated wildlife monitoring systems are in place, the output of which we can use to investigate how species in the Arctic are responding, both spatially and temporally, to cumulative factors.

Documenting biodiversity change at the global, regional and national level has been a challenge for the conservation community since the Convention on Biological Diversity (CBD) set its 2010 target in 2002 (UNEP 2002). Since the 2010 target was not met globally (Butchart et al. 2010; Secretariat of the Convention on Biological Diversity 2010), new targets, such as the Aichi biodiversity targets, have been set, (Convention on Biological Diversity 2012). Two of these targets are immediately relevant for Arctic species conservation: firstly, the need to measure species trends at the national, regional and the global level (Target 12: By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained) and secondly, to monitor pressure on areas vulnerable to climate change (Target 10: By 2015, the multiple anthropogenic pressures on coral reefs, and other vulnerable ecosystems impacted by climate change or ocean acidification are minimized, so as to maintain their integrity and functioning). Tracking progress towards both of these targets requires long-term monitoring of wildlife in the Arctic.

One approach to uncovering broad-scale patterns of biodiversity change is to evaluate species population trends. Change in population size is critical to understanding changes in biodiversity primarily because the loss of populations, which are sensitive to short-term

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changes caused by anthropogenic pressures (Balmford, Green, and Jenkins 2003), is a prelude to species extinction. Therefore measuring population change may be a better indicator of biodiversity loss (Ceballos and Ehrlich 2002). Also, because species abundance is integral to maintaining the variability of biodiversity (Mace 2005) and hence the provisioning and regulating services it provides, it is a fundamental variable to measure when tracking biodiversity trends over time. A method developed to track change in abundance using vertebrate population time series data – the Living Planet Index (LPI) - has been used extensively as a global biodiversity indicator (Loh et al. 2005; Collen et al. 2009; Butchart et al. 2010). It has been applied to biogeographic realms (Collen et al. 2009), at regional scales to look at trends in Mediterranean wetland species (Galewski et al. 2011), at national scales for Norway (WWF Norway 2005) and Canada (McRae et al. 2007) and to look at conservation management by measuring trends of species in protected areas across Africa (Craigie et al. 2010). Using population time series data in this way provides a direct measure of changes in population size which can be more location- and time-sensitive than measurements at the species level or using changes in habitat as a proxy (Pereira and Cooper 2006; Collen et al. 2009; Mace et al. 2010).

The same approach has also been adapted to develop the Arctic Species Trend Index (ASTI) to explore trends across different Arctic regions, habitats and taxa (McRae et al. 2010; Eamer et al. 2012) and the ASTI has been a complement to the suite of indicators being compiled to monitor different components of Arctic biodiversity (CAFF 2010). This biodiversity indicator is based on a database of population time series data and associated attributes which is continually updated to include the most recent data available and to fill data gaps. As a result, the underlying database does not only allow the compilation of an overall Arctic vertebrate biodiversity indicator, but also forms a central repository which can feed into other, smaller scale analyses. Here we used this database of 890 vertebrate population time series to explore the nature of trend data available to describe temporal and spatial trends across the Arctic region. We assessed the data collected for quality and representation and looked at the scope of applying the method at this scale. Finally we concluded how the data can be used to identify gaps in current monitoring schemes, and suggested priorities for expanding the current vertebrate monitoring network, with the aim of achieving a measure of Aichi biodiversity targets 10 and 12 for the CBD and the continued development of the database for use in Arctic research.

Method

Data collection

Population time series trends for Arctic species were collected by the Conservation of Arctic Flora and Fauna (CAFF) and from the Living Planet Database (Loh et al. 2005; Collen et al. 2009; WWF/ZSL 2012). These data were collated from published scientific literature, online databases, Arctic researchers and institutions, and from grey literature. The data were not selected according to species, region or conservation status but by a set of criteria on location and data quality. Following Collen et al. (2009) data were only included if:

1. a measure or proxy measure of population size – e.g. full population count, biomass, catch per unit effort, density – was available for at least two years;
2. information was available on how the data were collected and what the units of measurement were;
3. the geographic location of the population was provided and lay within the defined Arctic boundaries;
4. the data were collected using the same method on the same population throughout the time series; and
5. the data source was referenced and traceable.

Ancillary information to the time series data was also added to the database at both the species and population level encompassing data on taxonomic, geographic and ecological factors, such as sea-ice association (see Appendix). Each time series was georeferenced using the mid-point of the study area. In order to gauge how motivations behind the data collected may have changed over time, the primary aim of each monitoring scheme was recorded (see Appendix). The Arctic region was also divided up according to floristic boundaries (AMAP 1998) so that trends could be compared between High, Low and Sub Arctic populations. This additional information collected produced a database containing both population data and several variables that could be used to disaggregate the abundance data for detailed descriptive and statistical analysis. The limits of the time series collected was from 1950 to 2010 and yielded a data set of 890 populations from 323 species. The length of each time series varied according to the data available for each population so this meant that the composition of the data set changed annually as time series started and ended. Data for all species and all populations was therefore not available for every year from 1950 to 2010.

Analysis

We evaluated long term trends in Arctic fauna by producing a series of abundance trend indices according to the method below. We used the entire dataset to produce a pan-Arctic trend index and then disaggregated the data set to look at trends in each Arctic region, and among terrestrial and marine habitats. Furthermore, we briefly examined population trends among sea-ice associated species, since changes in sea ice are perceived to be one of the key drivers of change in the Arctic (Stroeve et al. 2007).

All trend indices were calculated using a Generalised Additive Modelling (GAM) framework to obtain population trends, followed by a geometric aggregation method to produce an index of change following Collen et al. (2009) and were carried out in R version 2.12.0 (R Development Core Team 2010). The baseline was set to 1970 for all indices as that was the year that the substantial number of monitoring projects started. Even though we collected data up until 2010, the end year of each index was set to either 2007 or 2005 (depending on the data set) as the amount of available data starts to decline thereafter. This is often due to a publication time lag effect which can delay the availability of data for a few years after it has been collected. As it is important to ensure as full a data set as possible is used, recent years with much fewer data points were not included in the index calculation. A bootstrap re-sampling technique developed by Loh (Loh et al. 2005) was used to generate confidence limits around annual index values and to calculate significant positive and negative change points in the index, i.e. points in time at which the second derivative of the index differed significantly from zero (Collen et al. 2009).

Based on the outputs of the GAM framework, and following Collen et al. (2009), an individual population trend value was calculated for each time series by using the total annual rate of change for the period 1970 to 2007. With each time series georeferenced, this allowed the population trends to be mapped using ArcGIS v9.3.1. In addition, we used the trend value to assign a categorical value of ‘declining’ (a negative value) or ‘stable/increasing’ (a positive or zero value) to each population. Firstly we used this information to examine how numbers in each category have changed over time and secondly to examine the status of populations of sea-ice associated species.

A systematic monitoring scheme for vertebrates would provide accurate trend information for species, but might be prohibitively costly. Our collection of data from existing monitoring schemes can fill this gap, but results are at the influence of the biases afforded by non-random data collection (e.g. monitoring schemes may be biased towards certain taxa, or focus on declining species). In order to examine the impact of this non-systematic data collection on indices produced, we evaluated availability and bias by assessing:

(1) Taxonomic representation of species by class using actual species numbers in the Arctic.
(2) Geographic representation of the data using number of species and populations by country and mapping each location for a visual assessment of the spatial distribution.
(3) The fullness of the data set by looking at gaps in the time series from 1970 to 2007 for all

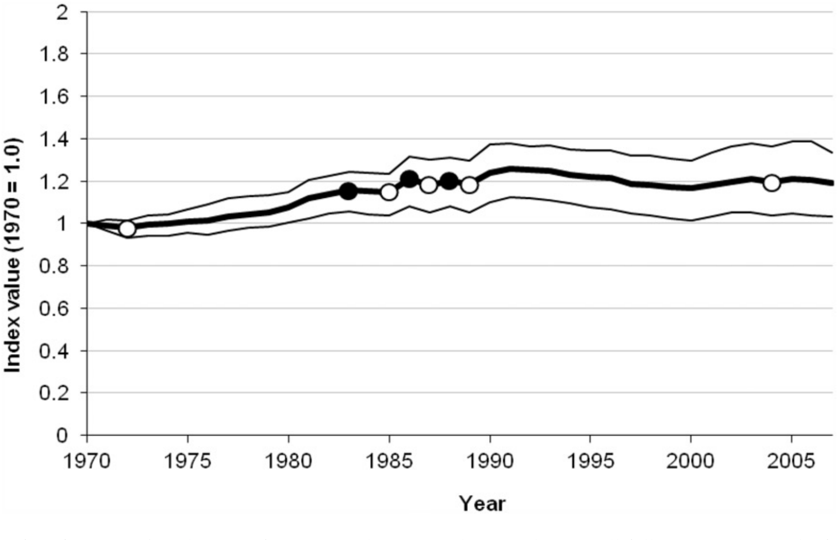

Figure 1. Abundance index for 323 Arctic vertebrate species (890 time series). Solid line represents index values; thin lines are 95% confidence intervals; white circles are positive change points and black circles are negative change points.

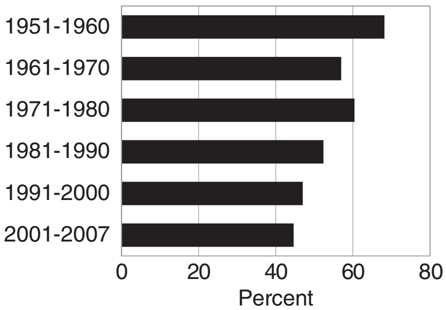

Figure 2. Percentage of time series showing a stable or increasing trend during each decade from 1950 to 2010.

populations and the number of time series data available for each year.

(4) Monitoring bias by looking at the motivation behind the monitoring scheme which yielded the population data to see if this changed over time and/or was dominated by any particular bias.

Results

Temporal and spatial trends

The average trend in abundance for the 323 species was a 19% increase in population size which occurred from 1970 to 2007 (Figure 1: 2007 index value 1.192; 95% CI 1.025-1.386). The increase largely occurred during the first half of the 37 year time period to a peak in 1991 (Figure 1: 1991 index value 1.258; 95% CI 1.117–1.423) after which the index levelled and slowly declined until 2007. This pattern was mirrored in the percentage of time series that show a stable or an increasing trend during each decade (Figure 2). There was consistently a lower proportion of stable or increasing time series during each subsequent decade from 1970 (Figure 2). In the latest seven years, from 2001 to 2007, a greater proportion of populations were declining than were stable or increasing. There were eight significant change points in the index; the latest was a significant increase in the index in 2004.

The division of the data set into broad ecological zones revealed different population trends across the Arctic region (Figure 3a–c). High Arctic populations declined from 1970 to the mid-1990s and then remained fairly stable with an apparent slight recovery observed in recent years after a significant increase in the index in 2004 (Figure 3a). The Low Arctic index suggests that populations increased to a peak index value in 1994 (Figure 3b: 1994 index value 1.951; 95% CI 1.601–2.514) after which the trend fluctuated until a significant decline in trend from 2003 to 2007 (Figure 3b). Sub Arctic population size increased by 15% from 1970 to 1986 (Figure 3c: 1986 index value 1.155; 95% CI 1.056–1.328) and then declined at a steady rate until 2007 (Figure 3c).

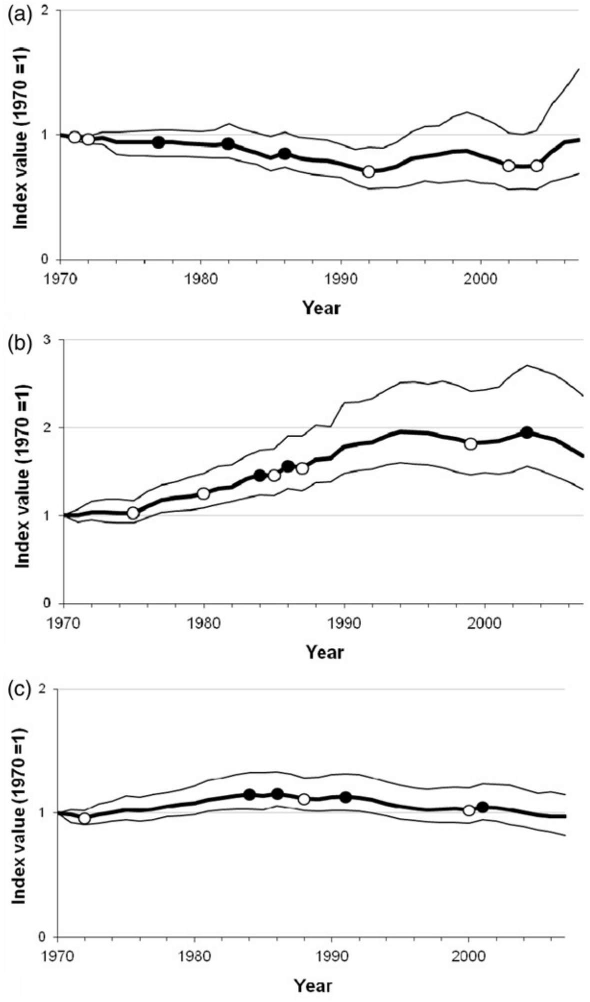

Figure 3. Abundance indices for (a) High, (b) Low and (c) Sub Arctic vertebrate species. Solid line represents index values; thin lines are 95% confidence intervals; white circles are positive change points and black circles are negative change points.

An Arctic-wide map of the spatial extent of population trends showed clusters of population growth and decline (Figure 4). For example, locations both in the Labrador Sea (with data mainly for Atlantic cod *Gadus morhua*, American plaice *Hippoglossoides platessoides*, Ocean perch *Sebastes marinus*, and Arctic char *Salvelinus alpinus*) and on the Queen Elizabeth Islands in the Canadian Arctic archipelago (with data mainly for caribou *Rangifer tarandus*, lemmings *Cricetidae* spp, and shorebirds

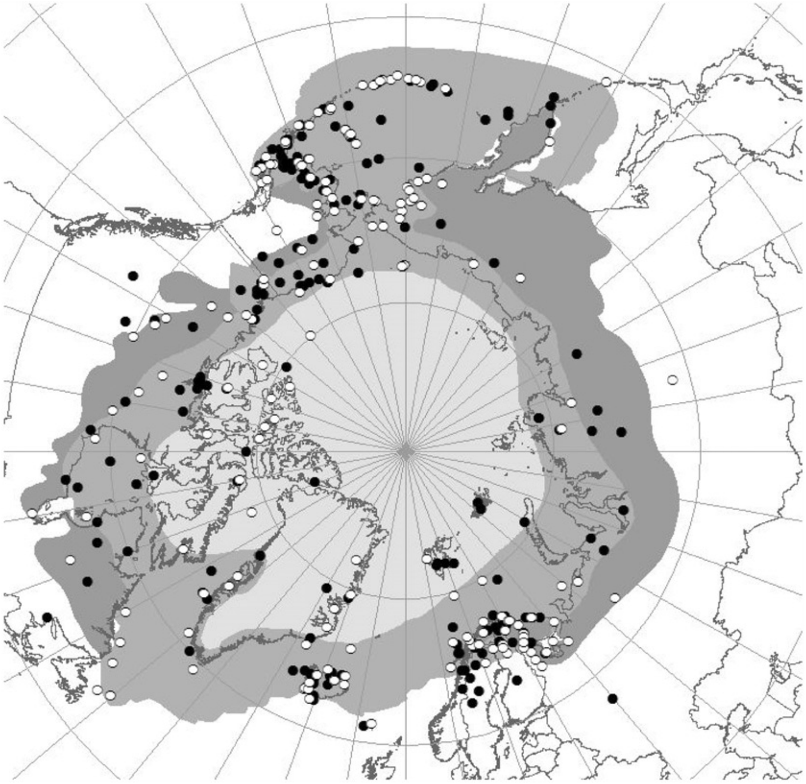

Figure 4. Vertebrate population trends in the Arctic with a projection from the North Pole. Dots denote the mid point of the monitored population; white dots show a decline (log-transformed rate of change <0) and black dots show an increase (log-transformed rate of change >0). Shaded areas show the High Arctic (light grey), Low Arctic (medium grey) and Sub Arctic (dark grey) regions.

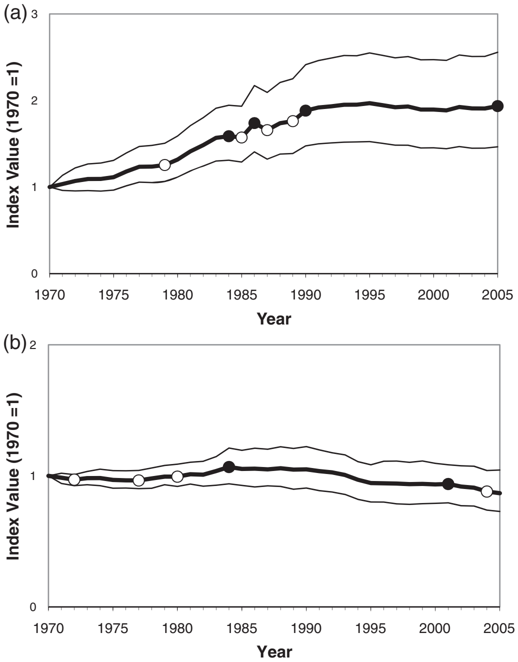

Figure 5. Abundance indices for (a) marine and (b) terrestrial vertebrate species. Solid line represents index values; thin lines are 95% confidence intervals; white circles are positive change points and black circles are negative change points.

Charadriiformes spp) showed multiple populations undergoing marked declines (Figure 4). Clusters of population growth were found on the coast of North West Canada and Alaska and also in Iceland. These were largely bird species and predominantly ducks and geese *Anatidae* spp.

The division of the Arctic data set into marine and terrestrial populations showed a significant contrast in trend as shown by the difference in the indices and confidence intervals which do not overlap (Figure 5a–b). The marine index increased almost constantly until a peak in 1995 (Figure 5a: 1995 index value 1.969; 95% CI 1.526–2.550) after which the trend remained largely stable for the rest of the time series. In contrast, the terrestrial index remained close to a value of 1 until 1994 (Figure 5b: 1994 index value 0.971; 95% CI 0.821–1.108) after which the trend declined to indicate an overall 13% decline by 2005 (Figure 5b: 2005 index value 0.867; 95% CI 0.729–1.044). There was a higher degree of variation in trends in marine populations than terrestrial, expressed by the width of the confidence intervals.

Box 1. Sea-ice association – focus on a key driver of change.

Data were available for two bird, six mammal and one fish species of ice-associated vertebrates (identified as sea-ice associated according to the Arctic sea-ice ecosystems indicator (CAFF 2010)). We found declining populations for six of the nine ice-associated species (Figure 6). Over the full period of monitoring for each species, three – Ringed Seal *Pusa hispida*, Beluga Whale *Delphinapterus leucas* and Thick-billed Guillemot *Uria lomvia* – showed overall declines in abundance where the magnitude of population declines outweighed increases in population size.

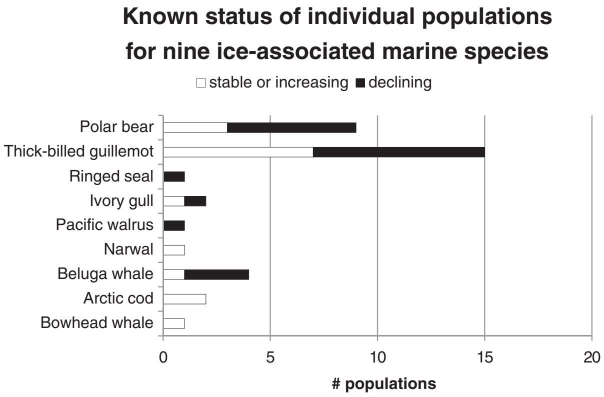

Figure 6. Number of population time series that are stable or increasing and that are declining for nine sea ice-associated species between 1970 and 2007. Year range varies for each time series and species.

Data availability and representation

The data set consisted of 890 population time series with available trend data from 1970 to 2007. The time period and time series length varied in the dataset to the extent that the trend data available increased steadily from 224 population time series in 1970 and reached peak availability in the late 1990s where the number of time series exceeded 600 (Figure 7a). If the 890 time series in our data set had population values for each of the 38 years from 1970 to 2007 then the number of data points available would be 24,920. In actuality we had 12,722 data points in total which equates to 51% of this potential matrix. This is shown visually in Figure 7b which depicts the start year and length of each population time series in the data set ordered by start year.

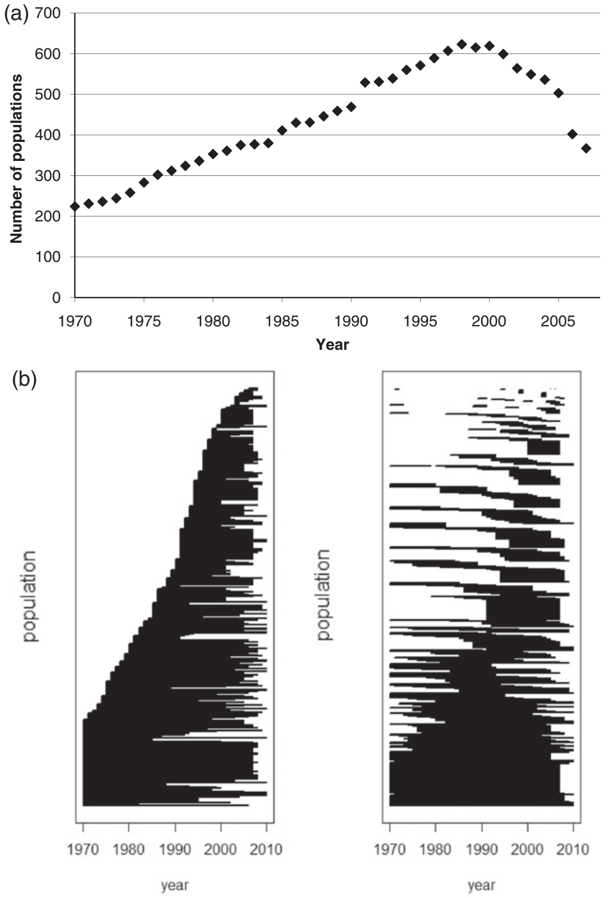

Figure 7. (a). Number of population time series with annual data points from 1970 to 2007. (b) Visualisation of data showing length of time series ordered according to start year from 1970 to 2007 (left) and ordered by time series length (right).

Table 1. Number and proportion of species by class that occur in the Arctic and that are contained in the ASTI data set.

	Species in ASTI	Species in Arctic	Proportion of total in ASTI	Proportion of total in Arctic	Percentage of Arctic species in ASTI
Birds	201	280	0.62	0.33	72
Mammals	53	130	0.16	0.15	41
Fishes	69	450	0.21	0.52	15
Total	**323**	**860**	**1.00**	**1.00**	**37**

Population trend data were available for 323 vertebrate species of which 201 were birds, 69 were fishes and 53 were mammals. The number of time series from each species varied (from one time series for 176 of the species to 39 time series for Caribou *Rangifer tarandus*) and covered different proportions of each species' Arctic range. Overall, the total species number represented 37% of known Arctic vertebrate species. The estimated proportions of species coverage for Arctic birds, mammals and fishes (Table 1) showed the best coverage for birds (72%) and worst for fishes (15%).

Looking at the representation of Arctic trend data by country, data availability varied widely. Data from Canada provided the most number of species, and data

Table 2. Number of species and populations per country in the ASTI data set.

Country	Species	Populations
Canada	130	179
United States	116	244
Russian Federation	97	253
Norway	50	68
Iceland	36	52
Greenland	32	49
Finland	19	22
Sweden	13	14
Svalbard and Jan Mayen Islands	7	7
Faroe Islands	2	2
Total	**323 (unique species)**	**890**

from the Russian Federation and the United States provided the most population time series (Table 2).

Data availability varied temporally as well as spatially. Figures 8a–d show how trend data reached a peak in availability between 1991 and 2000 (Figure 8c). Gaps in data coverage started to appear in the 1980s (Figure 8b) and by 2001–2007 the number of data gaps exceeded the number of time series available (Figure 8d). During this decade, clusters of gaps in available data occurred largely in Scandinavia, Iceland and Alaska.

Discussion

Overview of temporal and spatial trends

A large degree of both spatial and temporal variation was observed in the population trends of Arctic vertebrate species. Our results showed that the average population trend among Arctic vertebrates increased approximately 19% between 1970 to 2007; however, there was a large difference in trend between marine and terrestrial vertebrates, and a particularly striking difference between declining ice dependent species and increasing Low Arctic species (an area which largely covers the Bering Sea, Arctic Ocean and Atlantic Ocean). In the Low Arctic and marine data sets there were a large number of time series from the Bering Sea and Aleutian Islands and as the majority of these showed increasing trends, predominantly in fish populations, this was largely reflected in both the marine and Low Arctic index. The increase in marine species from 1970 to the mid-1980s is likely to have been influenced by strong increases in populations of some fishes (NPFMC 2008) and marine mammals (Reeves et al. 2003). A broad scale study of fish abundance in the Eastern Bering Shelf found increases in fish biomass in the 1970s and 1980s (Hoff 2005) which coincides with the pattern of increase we observed in this study and suggests favourable environmental conditions such as elevated sea surface temperature, reduced sea-ice extent and high primary production levels, were behind the abundant populations.

Declining trends were observed in the latter half of the time series for the Sub Arctic and terrestrial index and throughout the 38 year period of the High Arctic index. In addition, the proportion of stable and increasing populations in the entire Arctic data set declined over 60 years so that, in the decade from 2001–2010, the majority of populations were declining.

However, interpretation is challenging when looking at broad scale patterns, partly because of the unknown effects of not having comprehensive data coverage. The ideal data set for this kind of analysis would consist of full temporal and geographical coverage of population time series from all vertebrate species that occur in the Arctic, or, at least, continuous temporal coverage of a representative geographic and trophic assemblage of species. Unfortunately, Arctic species are not systematically monitored to this extent, so it is worthwhile examining certain qualities of our data set to assess how far it departs from the ideal monitoring system. One approach is to look at taxonomic and spatial coverage; another is to investigate whether observed changes are caused by a genuine decline in the number of increasing or stable populations, or by a shift in the focus of monitoring schemes towards declining species or species of perceived conservation concern. Interestingly, looking at the motivation behind each data source in the year it was published showed a lot of variation over time and no trend towards an increase in monitoring declining species or species of perceived conservation concern (see Appendix, Figure A1), which intimates that there was no obvious change in why data were collected over the study period. In turn this suggests there was no large artificial effect from monitoring bias (e.g. an increasing focus on threatened or declining species towards the present could result in a declining index) affecting the changes we found in population trend.

Both the Sub and High Arctic regions showed population decline but there are likely to have been different drivers behind the trends. Sub Arctic populations are potentially the most susceptible to direct human influence as they are found in the most densely populated area of the Arctic. The High Arctic, although remote, is undergoing the most visible change in the environment with recent dramatic declines in sea ice extent (Stroeve et al. 2007) and corresponding changes in Arctic tundra biomass and structure (Frey, Arrigo, and Gradinger 2011; Walker et al. 2011) which could directly impact species reliant on this habitat or act in synergy with other threats such as hunting.

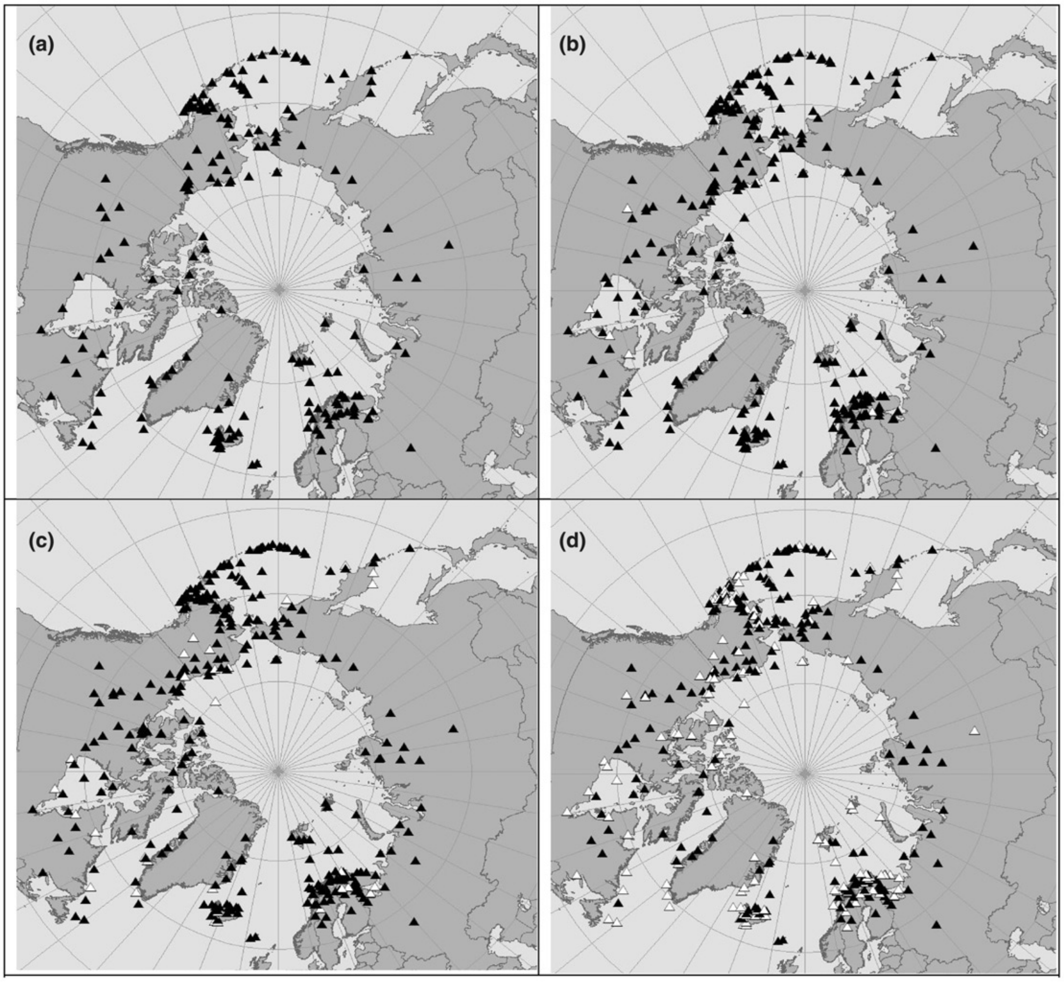

Figure 8. Data availability over time summarised by decade, 1971 to 2010. (a) 1971–1980 (b) 1981–1990 (c) 1991–2000 (d) 2001–2010. Data available (black triangle) represents a time series in the data set for that decade. Data not available (white triangle) denotes that there were no further data points for that specific location and period in our data set, but data were available in previous decades. This does not necessarily mean that monitoring has ceased in that location.

Climate change impacts on the Sub Arctic are likely to be acting on a different set of species such as herbivores, as the observed environmental changes here have affected the extent and type of vegetation available (Wahren, Walker, and Bret-Harte 2005). A more detailed analysis on the nature of the threats facing populations from these different regions would be required to interpret the trends further.

Natural cycles in species abundance must also be factored into trends across all regions of the Arctic. Lemming species (*Dicrostonyx* spp. and *Lemmus* spp.) and caribou (*Rangifer tarandus*) are the dominant species with cyclical populations. Looking at the average length of each time series for these species in the database – which is 10 and 24 years, respectively – we have the equivalent of about two or three abundance cycles for lemmings (cycle period of 3–5 years; Krebs 2011), and no full cycles for caribou (cycle period of 40 to 70 years; Gunn 2003). This means that trends are much harder to ascertain when a population is cyclical (Vors and Boyce 2009), highlighting the importance for long-term continuous monitoring and frequent updates of this indicator to elucidate the long term trends in abundance from short term fluctuations.

Recent changes in sea-ice extent in the Arctic have been well documented (Stroeve et al. 2007; Polyak et al. 2010) and there is evidence emerging of adverse effects on biodiversity (Gleason and Rode 2009; Heide-Jørgensen et al. 2010; Kovacs et al. 2010). The nature of a species' association with sea ice is important and varies from the availability of ice algae as the basis of the food chain to the provision of suitable habitat for breeding and for use as a hunting platform (Marz 2010). As a crude look at assessing the trends in such species, the number of populations declining and those stable or increasing were counted. In light of the paucity of available data, the fact that just over half of the 36 populations in total showed declines (six out of the nine sea ice-associated species showed declining populations) and that rapid changes in sea ice are predicted (Holland, Bitz, and Tremblay 2006; Weslawski, Kwasniewski, and Stempniewicz 2009), these species are a priority for monitoring if we want to uncover the effects of a changing climate.

A baseline for biodiversity monitoring

The concept of the baseline against which recent change in population size is measured is critical to interpreting relative changes in abundance over time. For example, current trends in marine ecosystems need to be interpreted against a solid understanding of the magnitude and drivers of past changes (Lotze and Worm 2009; Lotze et al. 2011). The same is undoubtedly true of those species in terrestrial and freshwater ecosystems. Due to the lack of widespread abundance data pre-1970, the approach taken here is to set the baseline to unity in the year 1970 (Loh et al. 2005), an approach taken with nearly all the major indicators of biodiversity change (e.g. Butchart et al. 2010). For certain populations that have increased in abundance since 1970, it can be meaningful to put the positive trend of the ASTI into an historical context. Anthropogenic threats such as exploitation may have had an impact on population size before this time and hence the recovery, although positive, may not be equivalent to the decline that occurred previously. Several techniques are being developed to try to reconstruct historical baselines, specifically for marine species (Baker and Clapham 2004; Lotze and Worm 2009; Lotze et al. 2011), in order to obtain a more accurate picture of a species' current conservation status and as guidelines for future ecosystem restoration and management.

This concept is particularly pertinent to the marine mammals of the Arctic as there has been a long established practice of subsistence and commercial hunting of many species and severe population reductions of some species from historical, unsustainable commercial whaling. Some marine mammal populations have increased dramatically of late - positive news when comparing trends against a 1970 baseline year. However, many populations are unlikely to have increased back to historical highs (Baker and Clapham 2004; Alter, Rynes, and Palumbi 2007; Lotze and Worm 2009; Lotze et al. 2011; Wade et al. 2011). For example, research on Grey Whale (*Eschrichtius robustus*) from the eastern Pacific suggested that, while abundance has increased substantially, the whales have, at best, recovered to between 28–56% of their original abundance levels (Alter, Rynes, and Palumbi 2007). Similar findings have been documented for populations of Greenland Walrus (*Odobenus rosmarus*) (Witting and Born 2005), the Western Arctic population of Bowhead Whale (*Balaena mysticetus*) (George *et al.* 2004), and for the heavily fished Atlantic Cod (*Gadus morhua*) (Rosenberg et al. 2005). The implications of setting a baseline therefore imply that the next steps for the ASTI would be to investigate how to quantify pre-1970 abundance levels and incorporate these into the interpretation of the recent population trends that we produce from the ASTI.

Data coverage, quality and availability

Data availability varied across the time series which meant that a different number of populations and hence locations contributed to each annual index point. The recent decline in available data after 2000 may reflect the fact that data collected over recent years are not yet published, or it may reflect reductions in biodiversity monitoring efforts, or a combination. The change in available data spatially suggested that there were certain areas where population trends were no longer contributing to the latter years of the Arctic index. It will be important to develop techniques to decipher if changes in geographic and taxonomic representation in the data are influencing the trends.

Using a data set consisting of only vertebrate species focuses on a small component of biodiversity, and the relation between this group and other components is still largely unknown. Given that vertebrate abundance data are more widely available, it seems prudent to use the data that are available, given the limited time and resources constraining conservation efforts. However, it is important to assess how well the dataset represented the total number of vertebrate species for this region. Although the collection of population data for 37% of known Arctic vertebrate species provided a substantial amount of data, the dataset was affected by a monitoring bias towards birds, similar to the one reported for the global Living Planet Index (Collen et al. 2009). In addition it is hard to gauge how representative the populations available are for each species are and also how representative they are geographically (spatial extent of a population monitoring scheme is rarely reported). The number of vertebrate species per country ranged from two to 130 which could be proportional to the differences in species assemblages found between the Arctic countries or, what is more likely, could be that the numbers were strongly influenced by monitoring effort in that country, funding for monitoring schemes, research focus, and the extent to which population data have been made globally and publicly available.

Developing the data set

One of the principal weaknesses of relying on a non-stratified monitoring network, which must be overcome to provide a comprehensive and representative data set, is the dominance of particular data due to the imbalance in monitoring focus and the non-random distribution of monitoring sites. In order to address this, improvement in the taxonomic and spatial coverage of the data set is needed, which would increase the utility of monitoring results in the following ways:

(1) Establishing more multi-species monitoring programs in areas with mainly single species monitoring could help with identifying whether observed population trends are congruent among species occupying the same area.
(2) More frequent monitoring in areas with few data points in time series, especially where abundance may be declining or populations are potentially at risk, could be used to pinpoint inflection points in the time series and distinguish between naturally occurring fluctuations and actual population reductions in a timelier manner.

Spatial analysis has been primarily used in fields like epidemiology (Dogan, Cetin, and Egri 2010) and ecology (e.g. for modelling habitat characteristics at broad scales (Bellier et al. 2010; Kleisner et al. 2010), but has not been widely applied for spatially assessing population declines at regional scales. Due to the wealth of the ASTI data set in terms of the number of time series as well as species and area coverage, there is the potential to use spatial variables that have been mapped for testing hypotheses of drivers of decline in spatial context, which can improve the focussing of conservation efforts for Arctic populations. Potential drivers of vertebrate population change include variables such as measures of the impacts of climate change on habitat e.g. changes in sea-ice conditions, and the level of human activity, e.g. the degree to which populations are harvested. Preliminary attempts to predict spatial patterns of Arctic population trends now need to incorporate a fuller set of key variables to advance our current knowledge of spatial trends in abundance (Böhm et al. 2012).

A wealth of research into environmental patterns over recent years has brought to light changes, both cyclical and long-term, and also interactions among species that occur in the Arctic region, clearly showing that drivers of biodiversity change and interactions amongst them are manifold and complex. Recent research shows, for example, impacts on biodiversity of declines in sea-ice extent (Heide-Jørgensen et al. 2010; Kovacs et al. 2010); warming sea surface temperatures in areas such as the Bering Sea and possible effects on species (Coyle et al. 2007; Stabeno, Bond, and Salo 2007; Irons et al. 2008); trophic interactions and cascades that can occur as a result of environmental changes in the marine habitat (Stempniewicz, Blachowiak-Samolyk, and Weslawski 2007; Anthony et al. 2008); and the effect of climate change on ecological dynamics (Post et al. 2009). In light of previous research and the results shown in this study, the importance of obtaining a clear picture and improving understanding of biodiversity trends in the Arctic environment, both as a communication tool for policy makers and as a resource for researchers and practitioners to look at regional or local patterns, cannot be overstated. This can be done by continually adding to the ASTI database and improving the coverage of species with additional information on threats which can provide broad overviews of Arctic trends and can lend itself to more detailed analysis for specific species and regions. The expansion of the network of current data providers will aid this process and in turn make a greater pool of data available to important future research in the Arctic.

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References

ACIA 2005. *Arctic climate impact assessment*. Cambridge: Cambridge University Press.

Alter, S.E., E. Rynes, and S.R. Palumbi. 2007. DNA evidence for historic population size and past ecosystem impacts of gray whales. *Proceedings of the National Academy of Sciences of the United States of America* 104: 15162–7.

AMAP 1998. *AMAP assessment report: Arctic pollution issues*. Oslo, Norway: Arctic Monitoring and Assessment Programme (AMAP).

Anthony, R.G., J.A. Estes, M.A. Ricca, A.K. Miles, and E.D. Forsman. 2008. Bald eagles and sea otters in the Aleutian Archipelago: indirect effects of trophic cascades. *Ecology* 89: 2725–35.

Baker, C.S., and P.J. Clapham. 2004. Modelling the past and future of whales and whaling. *Trends in Ecology and Evolution* 19: 365–71.

Balmford, A., R.E. Green, and M. Jenkins. 2003. Measuring the changing state of nature. *Trends in Ecology and Evolution* 18: 326–30.

Bellier, E., G. Certain, B. Planque, P. Monestiez, and V. Bretagnolle. 2010. Modelling habitat selection at multiple scales with multivariate geostatistics: an application to seabirds in open sea. *Oikos* 119: 988–99.

Böhm, M., L. McRae, S. Deinet, M.J. Gill, and B. Collen. 2012. *Tracking trends in Arctic vertebrate populations though space and time*, CAFF Assessment Series No.8. Akureyri, Iceland: Conservation of Arctic Flora and Fauna (CAFF).

Butchart, S.H.M., M. Walpole, B. Collen, A. van Strien, J.P.W. Scharleman, R.E.A. Almond, and J.E.M. Baillie. 2010. Global biodiversity decline continues. *Science* 328: 1164–8.

CAFF 2010. *Arctic biodiversity trends 2010 – selected indicators of change*. Akureyri, Iceland: CAFF International Secretariat.

Ceballos, G., and P.R. Ehrlich. 2002. Mammal population losses and the extinction crisis. *Science* 296: 904–7.

Collen, B., J. Loh, S. Whitmee, L. McRae, R. Amin, and J.E.M. Baillie. 2009. Monitoring change in vertebrate abundance: the Living Planet Index. *Conservation Biology* 23: 317–27.

Collen, B., L. McRae, S. Deinet, A. De Palma, T. Carranza, N. Cooper, J. Loh, and J.E.M. Baillie. 2011. Predicting how populations decline to extinction. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2577–86.

Convention on Biological Diversity. (2012). Aichi Biodiversity Targets. http://www.cbd.int/sp/targets/

Coyle, K.O., B. Bluhm, B. Konar, A., and R.C. Highsmith. 2007. Amphipod prey of gray whales in the northern Bering Sea: comparison of biomass and distribution between the 1980s and 2002–2003. *Deep Sea Research Part II: Topical Studies in Oceanography* 54: 2906–18.

Craigie, I.D., J.E.M. Baillie, A. Balmford, C. Carbone, B. Collen, R.E. Green, and J.M. Hutton. 2010. Large mammal population declines in Africa's protected areas. *Biological Conservation* 143: 2221–8.

Dogan, H.M., I. Cetin, and M. Egri. 2010. Spatiotemporal change and ecological modelling of malaria in Turkey by means of geographic information systems. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 104: 726–32.

Eamer, J., D.E. Russell, L. McRae, M. Böhm, S. Deinet, B. Collen, and M.J. Gill. 2012. *The Arctic Species Trend Index 2011: update of the ASTI, an in-depth look at marine species and development of spatial analysis techniques*, CAFF Assessment Series No.9. Akureyri, Iceland: Conservation of Arctic Flora and Fauna (CAFF).

Frey, K.E., K.R. Arrigo, and R.R. Gradinger. 2011. Arctic Ocean Primary Productivity [in Arctic Report Card 2011]. http://www.arctic.noaa.gov/reportcard

Galewski, T., B. Collen, L. McRae, J. Loh, P. Grillas, M. Gauthier-Clerc, and V. Devictor. 2011. Long-term trends in the abundance of Mediterranean wetland vertebrates: from global recovery to localized declines. *Biological Conservation* 144: 1392–9.

George, J.C.C., J. Zeh, R. Suydam, and C. Clark. 2004. Abundance and population trend (1978-2001) of western arctic Bowhead whales surveyed near Barrow, Alaska. *Marine Mammal Science* 20: 755–73.

Gleason, J.S., and K.D. Rode. 2009. Polar bear distribution and habitat association reflect long-term changes in fall sea ice conditions in the Alaskan Beaufort Sea. *Arctic* 62: 405–17.

Gunn, A. 2003. Voles, lemmings and caribou – population cycles revisited? *Rangifer* 14: 105–11.

Heide-Jørgensen, M.P., K.L. Laidre, D. Borchers, T.A. Marques, H. Stern, and M. Simon. 2010. The effect of sea-ice loss on beluga whales (*Delphinapterus leucas*) in West Greenland. *Polar Research* 29: 198–208.

Hoff, G.R. 2005. Biodiversity as an index of regime shift in the eastern Bering Sea. *Fishery Bulletin* 104: 226–37.

Holland, M.M., C.M. Bitz, and B. Tremblay. 2006. Future abrupt reductions in the summer Arctic sea ice. *Geophysical Research Letters* 33: L23503.

Irons, D.B., T. Anker-Nilssen, A.J. Gaston, G.V. Byrd, K. Falk, G. Gilchrist, M. Hario, et al. 2008. Fluctuations in circumpolar seabird populations linked to climate oscillations. *Global Change Biology* 14: 1455–63.

Kleisner, K.M., J.F. Walter III, S.L. Diamond-Tissue, and D.J. Die. 2010. Modeling the spatial autocorrelation of pelagic fish abundance. *Marine Ecology – Progress Series* 411: 203–213.

Kovacs, K., C. Lydersen, J. Overland, and S. Moore. 2010. Impacts of changing sea-ice conditions on Arctic marine mammals. *Marine Biodiversity* 41: 1–14.

Krebs, C.J 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. *Proceedings of the Royal Society B: Biological Sciences* 278: 481–9.

Loh, J., R.E. Green, T. Ricketts, J.F. Lamoreux, M. Jenkins, V. Kapos, and J. Randers. 2005. The Living Planet Index: using species population time series to track trends in biodiversity. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 360: 289–95.

Lotze, H.K., M. Coll, A.M. Magera, C. Ward-Paige, and L. Airoldi. 2011. Recovery of marine animal populations and ecosystems. *Trends in Ecology and Evolution* 26: 595–605.

Lotze, H.K., and B. Worm. 2009. Historical baselines for large marine animals. *Trends in Ecology and Evolution* 24: 254–62.

Mace, G.M. 2005. Biodiversity: an index of intactness. *Nature* 434: 32–3.

Mace, G.M., B. Collen, R.A. Fuller, and E.H. Boakes. 2010. Population and geographic range dynamics: implications for conservation planning. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3743–51.

Marz, S 2010. *Arctic sea ice ecosystem: a summary of species that depend on and associate with sea ice and projected impacts from sea ice changes*. Akureyri, Iceland: Conservation of Arctic Flora and Fauna (CAFF).

McRae, L., J. Loh, B. Collen, S. Holbrook, R. Amin, J. Latham, S. Tranquilli, and J.E.M. Baillie. 2007. Living Planet Index. In *Canadian Living Planet Report 2007*, eds. S. Mitchell and A. Peller, Canada: WWF.

McRae, L., C. Zöckler, M. Gill, J. Loh, J. Latham, N. Harrison, J. Martin, and B. Collen. 2010. *Arctic Species Trend Index 2010: tracking trends in Arctic wildlife*. , CAFF CBMP Report no. 20. Akureyri, Iceland: CAFF International Secretariat.

NPFMC 2008. *North Pacific Fishery Management Council ecosystem considerations for 2009*. 77–80, Seattle, WA: Joint Institute for the Study of the Atmosphere and Ocean (JISAO) and the School of Aquatic and Fishery.

Pereira, H.M., and H.D. Cooper. 2006. Towards the global monitoring of biodiversity change. *Trends in Ecology and Evolution* 21: 123–9.

Polyak, L., R.B. Alley, J.T. Andrews, J. Brigham-Grette, T.M. Cronin, D.A. Darby, A.S. Dyke, et al. 2010. History of sea ice in the Arctic. *Quaternary Science Reviews* 29: 1757–78.

Post, E., M.C. Forchhammer, M.S. Bret-Harte, T.V. Callaghan, T.R. Christensen, B. Elberling, and A.D. Fox. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325: 1355–8.

R Development Core Team 2010. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reeves, R.R., B.D. Smith, E.A. Crespo, and G. Notarbartolo di Sciara. 2003. *Dolphins, whales and porpoises: 2002–2010 conservation action plan for the world's cetaceans*. Gland, Switzerland, Cambridge, UK: ISCS Group, IUCN.

Rosenberg, A.A., W.J. Bolster, K.E. Alexander, W.B. Leavenworth, A.B. Cooper, and M.G. McKenzie. 2005. The history of ocean resources: modeling cod biomass using historical records. *Frontiers in Ecology and the Environment* 3, no. 2: 84–90.

Secretariat of the Convention on Biological Diversity 2010. *Global biodiversity outlook 3*. Vol. 94, Montreal: United Nations Environment Programme.

Stabeno, P.J., N.A. Bond, and S.A. Salo. 2007. On the recent warming of the southeastern Bering Sea shelf. *Deep Sea Research Part II: Topical Studies in Oceanography* 542: 599–618.

Stempniewicz, L., K. Blachowiak-Samolyk, and J.M. Weslawski. 2007. Impact of climate change on zooplankton communities, seabird populations and arctic terrestrial ecosystem – a scenario. *Deep Sea Research Part II: Topical Studies in Oceanography* 54: 2934–45.

Stroeve, J., M.M. Holland, W. Meier, T. Scambos, and M. Serreze. 2007. Arctic sea ice decline: faster than forecast. *Geophysical Research Letters* 34: L09501.

UNEP. 2002. Report on the sixth meeting of the Conference of the Parties to the Convention on Biological Diversity (UNEP/CBD/COP/20/Part 2) Strategic Plan Decision VI/26. Montreal: CBD, United Nations Environment Programme.

Vors, L.S., and M.S. Boyce. 2009. Global declines of caribou and reindeer. *Global Change Biology* 15: 2626–33.

Wade, P.R., A. Kennedy, R. LeDuc, J. Barlow, J. Carretta, K. Shelden, W. Perryman, et al. 2011. The world's smallest whale population? *Biology Letters. 1* 7: 83–5.

Wahren, C.-H.A., M.D. Walker, and M.S. Bret-Harte. 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* 11: 537–52.

Walker, D.A., U.S. Bhatt, T.V. Callaghan, J.C. Comiso, H.E. Epstein, B.C. Forbes, M. Gill, et al. 2011. Vegetation. [in Arctic Report Card 2011]. http://www.arctic.noaa.gov/reportcard

Weslawski, J.M., S. Kwasniewski, and L. Stempniewicz. 2009. Warming in the arctic may result in the negative effects of increased biodiversity. *Polarforschung* 78, no. 3: 105–108.

Witting, L., and E.W. Born. 2005. An assessment of Greenland walrus populations. *ICES Journal of Marine Science* 62: 266–84.

WWF/ZSL. 2012. The Living Planet Database. www.livingplanetindex.org (accessed 15th February 2011).

WWF Norway 2005. *Naturindeks for Norge 2005 – Utfor bake med norsk nature*. Norway: WWF.

Zöckler, C. 2008. The role of the Goose Specialist Group in the Circumpolar Biodiversity Monitoring Programme (CBMP). *Vogelwelt* 129: 127–30.

Zöckler, C., S. Delany, and W. Hagemeijer. 2003. Wader populations are declining – how will we elucidate the reasons? *Wader Study Group Bulletin* 100: 202–11.

Appendix

Table A1. Ancillary data coded for the Arctic data set for each population time series. Information was recorded at either the species or the population level.

	System	Terrestrial; Freshwater; Marine
Population based	Arctic region	High Arctic; Low Arctic; Sub Arctic (based on floristic boundaries (AMAP 1998))
	Marine ocean	Atlantic; Pacific; Arctic
	Country	Canada; Faroe Islands; Finland; Greenland; Iceland; Norway; Russian Federation; Svalbard and Jan Mayen Islands; Sweden
	Georeference	Latitude and longitude denoting the midpoint of the study area where population was monitored
	Motivation for study (based on aims from data source)	Baseline monitoring; Conservation management; Natural resource management; Population dynamics; Tracking declining species; Unspecified
Species based	Taxonomic class	Birds; mammals; fish (as there are only 3 Elasmobranch species in the data set, we grouped these with Actinopterygii to create one fish class)
	Sea ice association	Yes; No (identified as sea-ice associated according to the Arctic sea-ice ecosystems indicator (CAFF 2010))

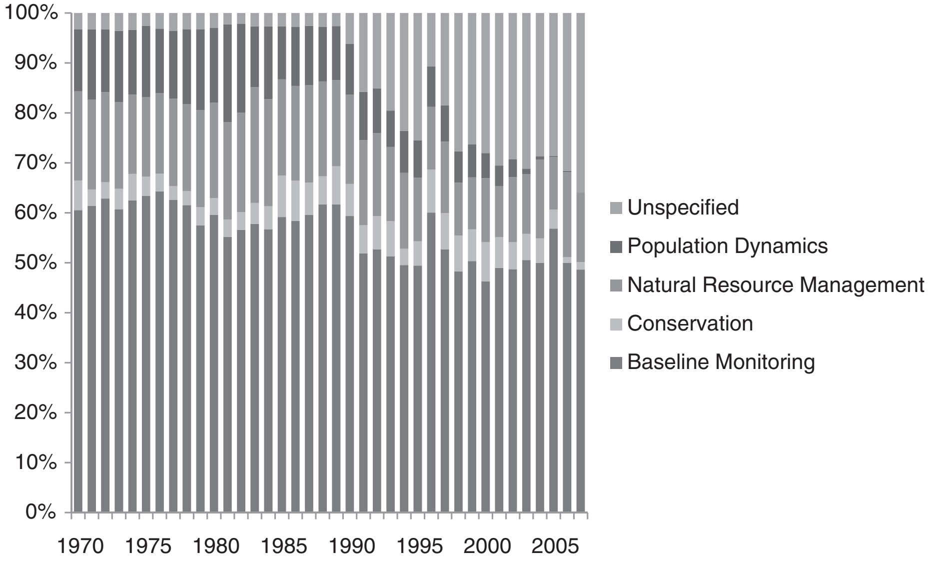

Figure A1. Aims for monitoring by year. Bars show the relative proportion of time series that were assigned to each motivation category each year. The conservation category combined conservation management and tracking declining species categories.

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Below the canopy: global trends in forest vertebrate populations and their drivers

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Global forest assessments use forest area as an indicator of biodiversity status, which may mask below-canopy pressures driving forest biodiversity loss and 'empty forest' syndrome. The status of forest biodiversity is important not only for species conservation but also because species loss can have consequences for forest health and carbon storage. We aimed to develop a global indicator of forest specialist vertebrate populations to improve assessments of forest biodiversity status. Using the Living Planet Index methodology, we developed a weighted composite Forest Specialist Index for the period 1970–2014. We then investigated potential correlates of forest vertebrate population change. We analysed the relationship between the average rate of change of forest vertebrate populations and satellite-derived tree cover trends, as well as other pressures. On average, forest vertebrate populations declined by 53% between 1970 and 2014. We found little evidence of a consistent global effect of tree cover change on forest vertebrate populations, but a significant negative effect of exploitation threat on forest specialists. In conclusion, we found that the forest area is a poor indicator of forest biodiversity status. For forest biodiversity to recover, conservation management needs to be informed by monitoring all threats to vertebrates, including those below the canopy.

1. Introduction

As we arrive at the 2020 expiration of the Aichi Biodiversity Targets under the Convention on Biological Diversity (CBD), the continuing loss of biodiversity remains a seemingly intractable environmental challenge [1] with grave implications for human wellbeing and the supply of valuable ecosystem services [2]. Some 322 vertebrates have become extinct since 1500, and more than 27% of all assessed extant species are threatened with extinction [2,3]. At a global scale, the average abundance of monitored vertebrate populations declined by 60% between 1970 and 2014 [4]. With the average rate of vertebrate species loss over the last century being up to 100 times the background rate, there is little doubt that we have entered an era representing the sixth mass extinction [1].

Deforestation has been a significant driver of this worldwide biodiversity crisis. Over a century ago, most clearance was of temperate forests [5], leading to observed species extinctions [6], while in the last decades, the main deforestation frontiers and risks to biodiversity have been in the tropics [7,8]. Tropical forests are some of the most biodiverse ecosystems on Earth, harbouring over half the world's terrestrial species [9]. Yet, deforestation of tropical forests, reducing their land coverage from 12% to less than 5% [10], along with their degradation and fragmentation, have resulted from large-scale industrial and local subsistence agriculture [11] as well as logging, fires and road building

[12]. This represents a loss of important resources and habitat for humanity (between 1.2 and 1.5 billion people are directly dependent on ecosystem services provided by tropical forests [13]) as well as biodiversity, with far-reaching implications for the climate system [14] and global carbon cycle [15,16].

Land-use change is predicted to continue as a major driver of terrestrial biodiversity loss for the rest of this century [17]. In order to assess the impacts of land conversion pressures, it is crucial to develop national-to-global scale biodiversity measurements [18]. Owing to the importance of forests as habitat for many species, forest area is often employed as an indicator in global agreements and processes aimed at slowing and reversing the decline of biodiversity. Under the Strategic Plan for Biodiversity 2011–2020, for example, Aichi Target 5 focuses on halving the rate of loss of forests and other natural habitats by 2020 [19]. The suite of indicators for Sustainable Development Goal (SDG) 15 (Life on land) of the 2030 Agenda on Sustainable Development includes forest area as a proportion of total land area, and the proportion of forest and other ecosystems covered by protected areas [20]. Similarly, indicators used to monitor biodiversity conservation in the Forest Resources Assessment of the Food and Agricultural Organization (FAO) comprise area of primary forest, forest area designated for the conservation of biodiversity and forest area in legally established protected areas [21]. However, the pertinence of forest area as a relevant indicator of forest biodiversity has never been tested at a global scale. While habitat loss is the major driver of forest biodiversity loss, a focus on forest area alone risks masking other pressures on forest vertebrates that can operate below the canopy in conjunction with or independently of forest cover change. Consequently, areas with stable or increasing forest cover might be experiencing undetected declines in forest vertebrates, leading to the so-called empty forests that appear intact but have lost many of their large animals [22].

Understanding the status of forest biodiversity is important not only for species conservation but also because biodiversity loss can have consequences for forest health [12,23] and carbon stocks [24,25]. The status of the world's forests is a critical factor in the avoidance of dangerous climate change, with afforestation or reforestation being critical to many of the scenarios consistent with meeting the 1.5°C target [26]. Concurrently, the conservation of biodiversity in forests can have direct carbon benefits. Forest vertebrates, particularly large birds and primates, play an important role in forest regeneration and long-term carbon storage [27]. A loss or reduction in forest vertebrates from regions with a high proportion of large-seeded animal-dispersed tree species, such as Africa, Asia and the Neotropics, can lead to carbon losses in forests [24,25,28]. Defaunation therefore threatens the role that forests play as essential carbon stores and sinks, risking the investments made by governments and non-state actors in forests as carbon 'banks'.

Using the Living Planet Index (LPI) methodology [29,30], we aimed to develop the first global indicator of forest vertebrate specialist populations to improve assessments of forest biodiversity status. Given the decline in area of natural forest over time [31] and the link between habitat loss and biodiversity loss [32], we expected to find that forest vertebrates were in decline. We then assessed whether trends in forest vertebrate populations were related to changes in tree cover, derived from satellite-derived tree cover datasets that matched the forest vertebrate data in space and time. If tree cover were a good indicator of forest biodiversity, we would expect to find a positive relationship between forest vertebrate population change and tree cover change. We therefore tested two hypotheses:

1. Forest vertebrates are in decline worldwide.
2. Forest vertebrate population change is positively correlated to tree cover change.

2. Methods

(a) Development of a Forest Specialists Index

The Living Planet Database (LPD) contains time-series abundance data for over 22 000 vertebrate populations including more than 4200 species across the globe, with the earliest records dating back to the 1950s (www.livingplanetindex.org). The data are collated from a range of sources, including peer-reviewed literature, grey literature, online databases and data holders. Metadata associated with each population, such as taxa, region, biome or habitat association, are also entered into the database.

The decision to develop an indicator for forest specialists as opposed to all forest species follows the approach, but not the same method of selection, of the indicators developed for European birds [33]. Given that specialists depend entirely on forests, their use in this indicator would provide a better representation of ecosystem health. We defined forest specialists using the habitat coding from the IUCN Red List [3]. Those with 'Forest' listed as one of multiple major habitats for that species were considered forest generalists, while those with only 'Forest' listed as the major habitat were considered forest specialists. This definition of specialist is narrow as the 'Forest' category from the IUCN Red List refers to natural habitat and does not include artificial habitats such as plantations. However, as the category applies to the major habitats a species occurs in, it is still possible that all or part of a population may be located in or adjacent to a plantation. The forest specialists dataset comprised 268 forest specialist species (455 populations): 135 birds, 89 mammals, 19 reptiles and 25 amphibians. See electronic supplementary material, S1 for a breakdown by realm and taxonomic class.

We followed the approach of the diversity-weighted LPI [30] to create a weighted index proportional to the species richness of each biogeographic realm and taxa in the dataset, and also to enable results to be compared with the global terrestrial LPI. In order to calculate weightings for each taxon and realm, the total number of vertebrate species from each taxonomic class and biogeographic realm that have 'Forest' listed as a habitat was taken from the IUCN Red List. Unlike for birds, mammals and amphibians, the coverage of reptile assessments in the IUCN Red List is not comprehensive so we did not have a full list of forest reptile species globally. However, the number of forest reptiles by realm was considered usable, given that the proportion of reptile species in each realm was similar to amphibians and also because spatial patterns of species richness tend to be similar among other vertebrate groups [34].

To create the subsets for the indicator, we disaggregated the data according to three taxonomic groups (mammals, birds, herptiles) by five realms (Nearctic, Palaearctic, Neotropical, Afrotropical, Indo-Pacific). Combining amphibians and reptiles into a herptile group, and Indo-Malaya, Australasia and Oceania into a single Indo-Pacific realm was a response to low data availability for these subsets. The final combinations yielded a total of 14 subsets as there were no time-series data available for Palaearctic herptiles.

The Forest Specialist Index was calculated using the R package rlpi (https://github.com/Zoological-Society-of-London/rlpi) following the approach in McRae *et al.* [30]. The weightings calculated above for forest species were applied to each of the 14 subsets. In order to examine trends within these subsets of the data and by forest biome, we compared the mean and standard error of the species trends within each of the subsets. The individual species trends were available as one of the outputs of the rlpi package.

(b) Correlates of forest vertebrate population change

(i) Forest populations and tree cover change

While the Forest Specialist Index reflects population changes in forest specialists to more accurately reflect ecosystem health, changes in tree cover may also affect populations of forest generalists. We, therefore, selected all forest specialists and generalists that were surveyed at a specific location (defined as a discrete area such as a national park or sample area of a forest; a non-specific location comprises a larger survey area such as a province or country). For each population, the period encompassing the first and last year of survey data is subsequently referred to as the study period. Many population records do not have data available for every year of the study period. We determined annual predicted abundance values per population by fitting generalized additive models (GAMs) to the time-series population data where survey data were available for at least 6 years, and linear regressions where data were available for between 2 and 5 years, following Spooner *et al.* [35].

In order to assess the relationship between tree cover change and forest vertebrate populations, we required a continuous measure of tree cover spanning multiple years and at a resolution that is sensitive to the local changes that are likely to be relevant to populations. Various global datasets exist that provide continuous tree cover values for multiple years and vary in tree cover definition, spatial resolution, temporal coverage and frequency (electronic supplementary material, S2). Currently, the highest resolution global datasets (e.g. approx. 30 m) are available for a shorter temporal coverage than some datasets with a coarser resolution. Higher resolution datasets allow more fine-scale detection of changes in vegetation cover, while longer-term datasets increase the likelihood of detecting a relationship between tree cover change and population change by increasing the number of populations and years that can be analysed. We opted to run our analyses twice, once using the shorter-term (2000–2017) 30 m Landsat Global Forest Change dataset (hereafter referred to as the Hansen dataset; [36]) and once using the longer-term (1982–2016) 5.6 km MEASURES VCF5KYR dataset, which includes annual fractional tree cover and bare ground cover values (hereafter referred to as the Song dataset; [8]). In addition to fractional tree cover in 2000 and 2010 (2010 layer accessed from [37]), the Hansen dataset provides annual tree cover loss as a binary presence/absence value for 2000–2017, defined as complete stand replacement or a change from a forest to a non-forest state within a pixel. This information allows the estimation of deforestation rates, but may mask fine-scale changes within pixels such as a reduction (but not complete loss) in tree cover and assigns gradual losses that occur over multiple years to a single year.

It is important to note that, while the 30 m dataset used in these analyses comes from the Global Forest Change dataset, neither this nor the Song dataset differentiate between natural, semi-natural or non-natural forests (such as plantations). Thus, while losses (or gains) in tree cover might reflect deforestation (or regeneration) in natural forests, in plantations, this might reflect harvest (or growth) of products grown specifically for human extraction that may provide lower quality habitat for forest vertebrate populations. Systematically collected global data on tree plantations are lacking. The Global Forest Watch (GFW) Tree Plantations layer records tree plantations in a single year (2013/2014) for only seven countries [38] and is, therefore, unsuitable for our analyses. A recently released near-global dataset on plantations by GFW [14] is also unsuitable, as the reference year is 2015. In the absence of suitable global information distinguishing natural and planted forests, we, therefore, refer to tree cover rather than forest cover whenever discussing values derived from the spatial tree cover datasets used in this analysis.

We fitted a 5 km radius around each population, based on the mean range size across all forest populations (electronic supplementary material, S3), and extracted annual tree cover area and bare ground area for 1982–2016 using the Song dataset and tree cover area in 2000 and 2010 using the Hansen dataset. We additionally extracted annual loss values for 2001–2017 from the Hansen dataset, using per-pixel tree cover in 2000 to estimate how much tree cover was lost per buffer per year. All data extraction was carried out in Google Earth Engine [39]. We plotted annual tree cover values from the Song dataset against year to visually assess temporal changes in tree cover per location. We identified substantial inter-annual fluctuations in tree cover at some locations that were unlikely to reflect true changes. To smooth these fluctuations in the Song dataset, GAMs were fitted to the annual tree cover values within each buffer to obtain annual fitted tree cover values.

We reduced the annual fitted population data to only include years that fell within 1982–2016 when analysing the effects of tree cover change with the Song dataset and 2000–2015 when analysing with the Hansen tree cover dataset. In both cases, we removed populations that no longer had greater than or equal to 2 years of data spread over at least a 5-year period (electronic supplementary material, S4 and S5). Using the annual logged values from the GAM and linear regression performed earlier, we calculated an average rate of change value per each remaining population as our response variable, following Spooner *et al.* [35]. Using the Song dataset, we reduced the annual fitted tree cover values to match the study period of each population, with a 1-year lag (i.e. tree cover in year t matched to population data in year $t+1$). We then calculated three predictor variables from the fitted tree cover values: mean tree cover during the study period; mean bare ground cover during the study period; and the tree cover trend over the study period, taken as the year coefficient from an ordinary least-squares regression of annual fitted tree cover on year. We also calculated three predictor variables from the Hansen dataset: tree cover in 2000; the area of tree cover lost over the study period (based on loss data only); and the proportional change in tree cover between 2000 and 2010 (as these are the two years with percentage tree cover per pixel available). We removed populations with zero tree cover in all years from the analyses, leaving 1668 generalist and 175 specialist populations in the analyses using the Song dataset compared with 685 generalist and 74 specialist populations in the analyses with the Hansen dataset (see electronic supplementary material, S3 and S4 for a breakdown by realm and taxonomic class, respectively). Fewer populations were included in the analyses with the Hansen dataset because the shorter temporal period covered by the Hansen dataset (2000–2015) meant fewer populations had data overlapping that period, compared with the longer-term Song dataset (1982–2016).

In order to examine the agreement between the two tree cover datasets, we calculated tree cover change per population from 2000 to 2010 using values derived from the Song dataset and from the Hansen dataset. We then assessed the correlation between the two sets of tree cover change values for the 685 populations included in the Hansen analyses. The correlation between the two datasets was highly significant but had a low correlation coefficient (Pearson correlation coefficient = 0.171; $p < 0.001$). This is in agreement with other studies that have found discrepancies between tree cover datasets when assessing tree cover change or area [40,41].

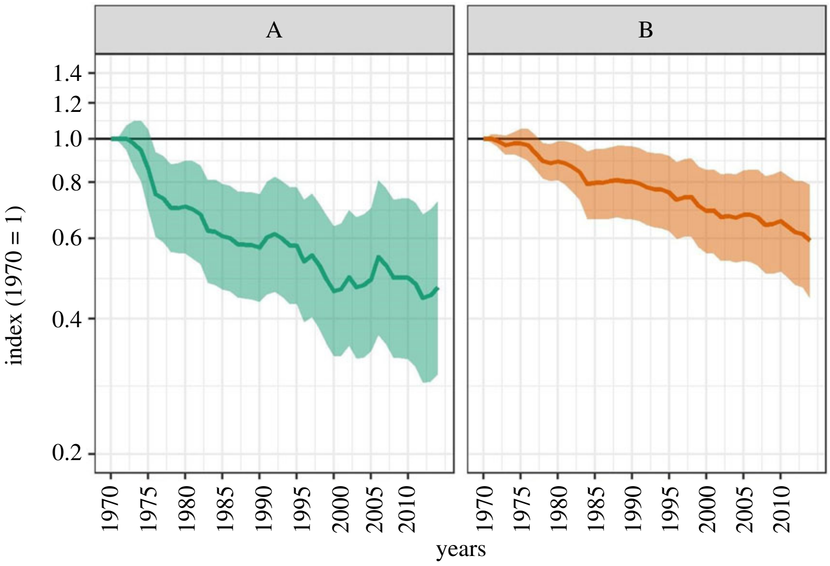

Figure 1. Weighted index of population change from 1970 to 2014 for (*a*) 268 forest specialist species and (*b*) 1853 terrestrial species (includes the forest specialist species). Solid line shows the weighted index values and shaded region shows the 95% confidence for the index. (Online version in colour.)

(ii) Additional drivers of forest population change

Forest vertebrates are affected by many drivers that may occur independently of, or in conjunction with, tree cover change. We selected correlates for our analyses through a literature review and information stored in the LPD, which includes any threats specified by the source of the population data. Exploitation, including the hunting, persecution, indirect killing or collection of wild individuals for trade, is likely to be a key driver of some forest vertebrate populations [42]. We, therefore, included in our analyses a binary variable specifying whether the primary threat to the population was or was not exploitation. It is possible that body size may impact species' sensitivity to forest change [43]. To investigate this effect, we took adult body mass values per species from the Amniote [44], AmphiBIO [45] and Elton-Traits 1.0 [46] databases. Where species-level body mass information was not available, we assigned the species the mean body mass of its genus, family or order (higher taxonomic ranks used where data were unavailable for lower ranks). The body mass values were log-transformed (base 10) to normalize them. We calculated the density of roads within the study area, defined as the total length of roads within each population's 5 km buffer, using the gROADS v. 1 dataset [47]. We used the UN-Adjusted Gridded Population of the World V. 4 dataset [48] to calculate the mean human population density (HPD) within each buffer in the year 2000. Finally, we calculated the mean travel time to the nearest city or densely populated area for each buffer from the Accessibility to Cities 2015 dataset [49].

(iii) Model structure

At some locations, multiple populations were monitored over the same period, so we chose to fit a model to the data that would take into account their non-independence. For each predictor variable, we fitted mixed effects models using the 'lme4' package [50] with the average rate of change of each population as the dependent variable, location as a random effect and the predictor as a fixed effect. We fitted separate models for each predictor variable to identify any relationships between these variables and population change, with the aim of fitting multivariate models where evidence of a relationship was found for more than one predictor variable. To determine whether a predictor variable was a significant driver of population change, we calculated Akaike's information criterion (AIC) for all models and compared them with the AIC of the null model including only a random effect of location. We considered a predictor variable to have significantly improved the model fit if inclusion of the variable lowered the AIC by at least 2 compared with the null model (a more negative AIC indicates a better model fit; [51]).

We fitted these models to all forest populations (generalists and specialists) and additionally to forest specialist populations only. All analyses were carried out in the statistical software R v. 3.5.1 [52].

(iv) Influential genera

We investigated whether any groups of species were having a significant influence on the models. In the absence of any groups of influential species, models iteratively excluding one group at a time would not produce substantially different model estimates. We used the 'influence.ME' package [53] to produce estimates from models that iteratively excluded the influence of each genus, where each predictor variable was fitted in a univariate mixed effects model with genus as a random effect. We used the 'sigtest' function to test whether excluding any genus changed the statistical significance of any of the predictor variables in our models. We then examined the influential genus to determine the cause and, if the genus was known to be responding to a driver other than those included in our analyses (e.g. disease, poisoning), we repeated our analyses with the genus omitted.

3. Results

(a) Forest Specialist Index

The Forest Specialist Index declined by 53% between 1970 and 2014 (figure 1*a*; index value: 0.47; range 0.30–0.73). This indicates an average decline in 455 monitored populations of forest specialists at an annual rate of 1.7% per year. By comparison, the terrestrial LPI declined by 41% between 1970 and 2014 (figure 1*b*; index value: 0.59; range 0.44–0.79), representing an average decline for 5175 monitored terrestrial populations with an annual rate of 1.2% per year. The decline in the Forest Specialist Index was steepest between 1970 and 1976. The percentage of all species that had an annual declining trend was consistently between 50 and 65% during the time period except for the late 1980s, early 2000s and 2013–2014, when the proportion dropped below half (electronic supplementary material, S6). These

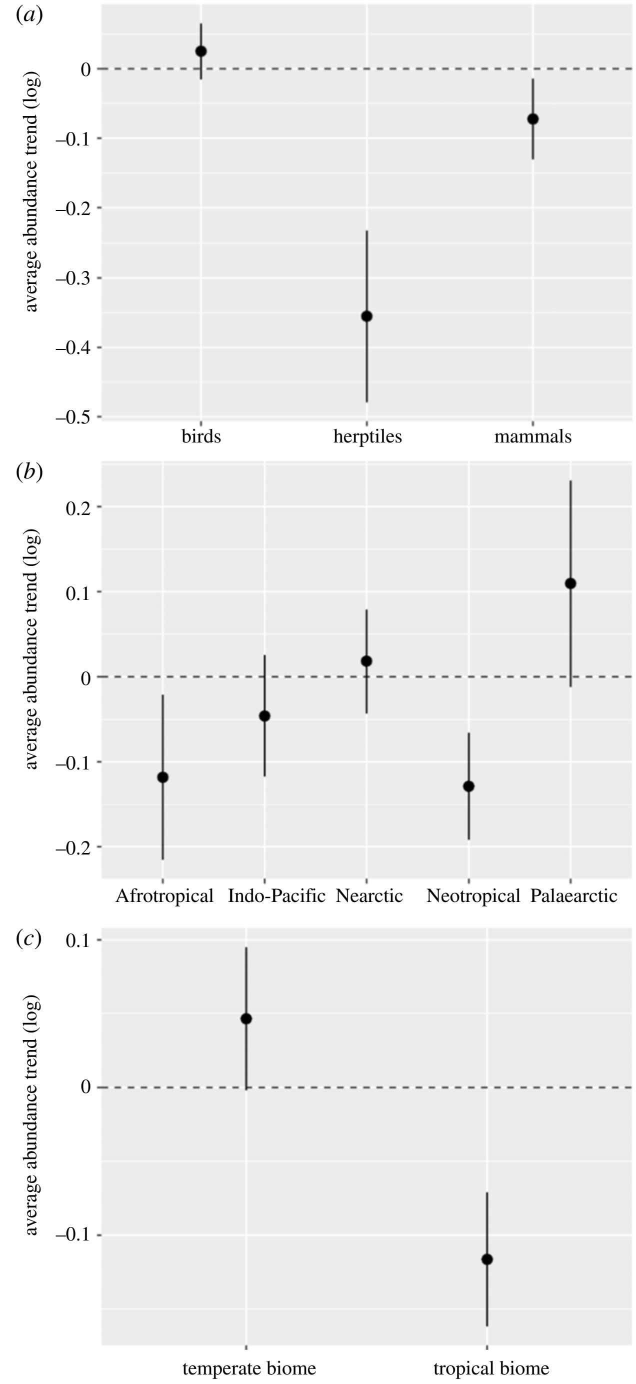

Figure 2. Total rate of change in forest specialist populations averaged by species, with standard error. Comparison by class (*a*), realm (*b*) and biome group (*c*). (Online version in colour.)

time periods are illustrated by corresponding changes in the index to a slower decline. There is an increase in the percentage of increasing annual trends in 2013 and 2014 and the percentage in 2014 is the highest out of all 44 years; this pattern is notable across all taxa (electronic supplementary material, S7). The average rate of change per species was negative for herptiles and mammals and slightly positive for birds (figure 2), with no overlap between the error bars of each group. This result was echoed when comparing declining and increasing years. There were more declining years than increasing among species trends for mammals (53% of all annual data points) and herptiles (63% of all annual data points); the reverse was true for birds, where there were more increasing years (52% of all annual data points). For all taxa, the percentage of increasing and declining annual trends varied across the time series (electronic supplementary material, S7). The average rate of change per species was negative for tropical realms and tropical biomes and positive for temperate realms and biomes (figure 2), with no overlap between the error bars for the two biome groups. Similarly, the number of declining species trends from tropical realms and tropical forest biomes was greater than increasing (electronic supplementary material, S8), while the reverse was true of temperate realms and temperate forest biomes (electronic supplementary material, S8).

(b) Correlates of forest vertebrate population change

We identified one genus (*Gyps*) that had a large influence on the model estimates. *Gyps* vultures are a group of generalist species that have declined severely since the 1990s because of accidental poisoning from the veterinary drug diclofenac [54], and are, therefore, a very specific case that does not reflect responses of forest populations to any of the widespread pressures we have investigated. We, therefore, excluded *Gyps* vultures from our analyses.

Mixed effects models including specialist and generalist forest populations and using the long-term Song tree cover dataset showed no evidence of a relationship between forest population change and tree cover trend (figure 3), mean tree cover, mean bare ground, exploitation, HPD, mean travel time or road density (electronic supplementary material, S9).

We found a significant negative effect of exploitation on forest specialist population change, although this was based on exploitation being the primary threat to just 12 out of 175 forest specialist populations. We found no evidence of a relationship between forest specialist population change and any other predictor variable (electronic supplementary material, S10).

Mixed effects models including forest specialists and generalists and using the Hansen tree cover dataset found no evidence of any relationships between population change and any predictor variables (electronic supplementary material, S11). We found no significant relationships between any predictors and population change when repeating the analyses using only forest specialist data (electronic supplementary material, S12).

4. Discussion

Our results indicate that the global abundance of forest specialists more than halved, on average, from 1970 to 2014. In context, populations of terrestrial species declined globally by an average of 41% over the same time period, which suggests that vertebrates in other terrestrial habitats have fared less badly. However, the population trends among forest specialists remain better than for species living in freshwater habitats, which exhibit more negative population trends [4,55] and a greater risk of extinction [56] than terrestrial counterparts. The result for the forest specialist index was consistent among mammals and herptiles but less so among birds, especially from temperate forests. Differences in average trends between taxonomic groups were significant and, while the effect of threats has not been quantified, the available evidence suggests the negative trend in mammals could be the result of targeted hunting, especially in the tropics [57]. The fungal disease chytridiomycosis, sometimes exacerbated by climate change, could explain

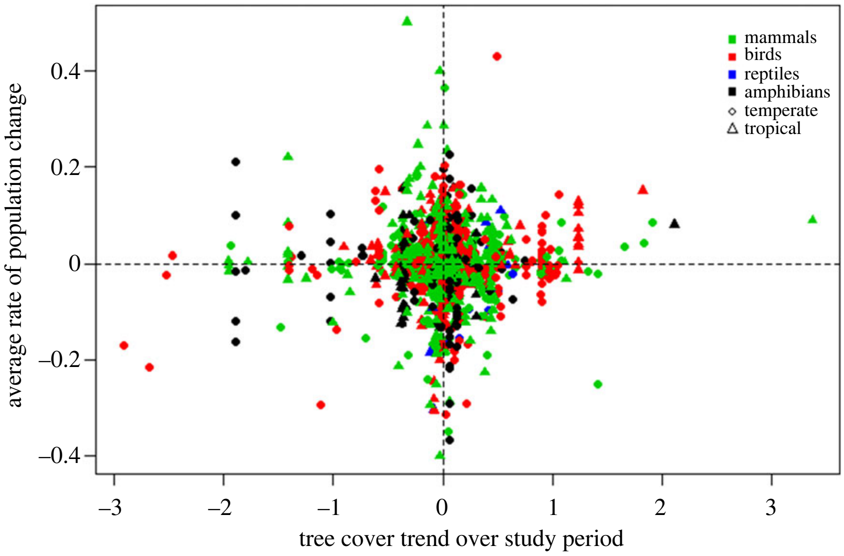

Figure 3. Average rate of change of forest vertebrate populations (specialists and generalists) with abundance data covering at least a 5-year range between 1982 and 2016 from the LPD, and tree cover trend within a 5 km radius of each population's study location calculated over the same period as the population data from remotely sensed tree cover data [8]. Green, mammals; red, birds; blue, reptiles; black, amphibians. Circles, temperate biomes; triangles, tropical biomes. $N=1668$. (Online version in colour.)

the stronger negative result for herptiles (e.g. [58,59]). Abundance trends are worse in the tropics, as might be expected, given the more rapid rates of forest loss in tropical regions [21] over that period. The final years of the index, 2013 and 2014, showed an increasing trend as a result of a greater proportion of increasing annual trends among species than in previous years, across all taxa. As there have been other increasing trend years in the index throughout the time series followed by a decline (1991–1992, 2001–2002, 2004–2006), it is not possible to say at this stage whether the latest upturn in the Forest Specialist Index is a sign of a significant, longer-term increase in the abundance of forest specialists.

In understanding the overall reduction in the rate of decline of the index after 2000, we need to consider three factors that are pertinent to interpreting trends in composite indices: species with increasing trends entering the dataset, species with declining trends leaving the dataset and improvement in species trends from declining to increasing or stable during this time period. The first two factors result from turnover in the species data that contributes to the index as data are not available for all 44 years for all species. This turnover in data is observed in our dataset: for example, between 2000 and 2002, data for 12 declining and four increasing species ended at the same time as data for 10 increasing and four declining species entered the dataset. This type of change in the dataset suggests that the reduced rate of decline may not entirely reflect overall improving status for species in the dataset, rather a change in the underlying data coupled with some species recoveries. This highlights a limitation of composite indices such as this where the temporal representation of species data is not comprehensive across the time series [60] and illustrates the need for diagnostics to accompany interpretation as well as additional data to strengthen the index. In addressing the third factor, and in order to eliminate any effect of data turnover, we looked at species with data present in all decades. These are predominantly bird species from the Nearctic, which are well monitored over the long term. After an initial decline, the average trend for this set of species does show an improvement to stability from the mid-2000s, but this trend is not yet increasing (electronic supplementary material, S13). The stabilization of trends in forest bird species in the Nearctic is consistent with other findings [61]. It is worth noting that species biodiversity data are currently skewed away from where species richness is greatest [62], limiting our ability to identify and address threats in some of the most biodiverse areas on the planet. The lack of population time series in the LPD from forest hotspots in Africa, Asia and the Amazon highlights this issue. To develop a more representative picture of the status of forest biodiversity and drivers of population change, these data gaps need to be filled. This will require greater investment in systematic, long-term, on-the-ground monitoring of forest vertebrates and improved data sharing within the research community.

While remote sensing allows quantitative monitoring of forest cover change, limitations are to be expected in its use for monitoring forest populations: processes of defaunation are more cryptic and difficult to track [2], even occurring in large protected habitats [63]. The use of remote sensing to inform assessments of extinction risk for forest-dependent species has been demonstrated [64]. However, the relationship between habitat change and population change is not necessarily linear and the influence of threats other than habitat loss could also be important, which means that a species-specific approach may need to be taken when using habitat or land cover change to inform the status of a species [64,65]. Our results provide evidence that a satellite-derived assessment of forest cover change alone is inadequate as an indicator of trends in forest biodiversity. We did not find significant evidence of a consistent relationship between forest vertebrate populations and tree cover change in the surrounding area. Further, discrepancies between satellite-derived tree cover datasets in estimates of tree cover change or area indicate the uncertainties associated with tree cover assessments [40,41]. Analyses such as these would benefit from a global, systematically developed dataset categorizing forest areas into natural or planted forests, with temporal information detailing when each plantation was established. This would allow tree cover losses or gains within plantations to be identified, allowing for more rigorous checks of the relationship between populations of forest-dwelling species and natural forest cover change.

Our finding of exploitation as a key driver of forest specialist population decline supports evidence presented elsewhere. An analysis of threat information for 8688 species on the IUCN Red List of Threatened Species identified overexploitation alongside agriculture (principally crop and livestock farming) as the main drivers of biodiversity loss [42]. The intensification of climate and other global environmental changes is predicted to interact with overexploitation and other pressures to lead to severe future degradation of tropical forests unless alternative, non-destructive development pathways are followed [12]. With most drivers of change interacting in space, time and organizational level [66], an explicitly linked set of forest biodiversity indicators may be more useful than reliance on any individual indicator to understand and communicate forest biodiversity trends and guide policy [67].

The Forest Specialist Index should be among such a set of indicators. This indicator has now been put forward through the Biodiversity Indicators Partnership to measure progress towards Aichi Targets 5, 7 and 12 (https://www.bipindicators.net/indicators/living-planet-index/living-planet-index-forest-specialists) and would complement existing indicators in monitoring progress towards SDG 15, the post-2020 framework under the CBD and in the delivery of the Paris Agreement. As such, it would also be a valuable inclusion in the Global Core Set of forest-related indicators as being coordinated by the FAO.

The findings presented here also demonstrate the importance of complementing satellite-derived datasets with repeated on-the-ground species surveys and site-specific threat information when assessing the status and drivers of forest biodiversity, as advocated for elsewhere [68–70]. While remote sensing data have undoubtedly improved our ability to independently monitor and assess changes in forest cover, there are many additional drivers of forest population change that can only be identified by looking below the canopy. A focus on forest cover change alone risks masking below-canopy processes, such as defaunation, with grave consequences not only for forest biodiversity but also long-term forest health and carbon storage [24,27,28]. Therefore, we must not lose sight of the crucial role that site-level species monitoring plays in understanding trends and drivers of forest biodiversity change.

Data accessibility. The vertebrate population data were taken from the Living Planet Database which is hosted online at www.livingplanetindex.org. The data used for the analysis are available in the electronic supplementary material. Part of the dataset includes confidential data which have been shared under an agreement and are not publicly available. The species details, location and reference have been anonymized and the raw population data replaced with modelled population lambda values. The Forest Specialists Index was calculated using the R package rlpi available at https://github.com/Zoological-Society-of-London/rlpi.

Authors' contributions. E.J.G. and L.M. carried out the statistical analyses with guidance from R.F., M.B.J.H. and S.L.L.H. W.B.-C. and W.D.S. conceived and coordinated the study. All authors contributed to the drafting of the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed herein.

Competing interests. We declare we have no competing interests.

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References

1. Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015 Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci. Adv.* **1**, e1400253. (doi:10.1126/sciadv.1400253)
2. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. 2014 Defaunation in the Anthropocene. *Science* **345**, 401–406. (doi:10.1126/science.1251817)
3. IUCN. 2019 The IUCN Red List of Threatened Species. Version 2019-1. See http://www.iucnredlist.org (accessed 11 April 2019).
4. WWF. 2018 *Living planet report—2018: aiming higher* (eds M Grooten, REA Almond). Gland, Switzerland: WWF.
5. Brooks TM, Pimm SL, Oyugi JO. 1999 Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* **13**, 1140–1150. (doi:10.1046/j.1523-1739.1999.98341.x)
6. Pimm SL, Askins RA. 1995 Forest losses predict bird extinctions in eastern North America. *Proc. Natl Acad. Sci. USA* **92**, 9343–9347. (doi:10.1073/pnas.92.20.9343)
7. Myers N. 1993 Tropical forests: the main deforestation fronts. *Environ. Conserv.* **20**, 9–16. (doi:10.1017/S0376892900037176)
8. Song X-P, Hansen MC, Stehman SV, Potapov PV, Tyukavina A, Vermote EF, Townshend JR. 2018 Global land change from 1982 to 2016. *Nature* **560**, 639–643. (doi:10.1038/s41586-018-0411-9)
9. Groombridge B, Jenkins MD. 2003 *World atlas of biodiversity: Earth's living resources in the 21st century*. Berkeley, CA: University of California Press.
10. Brandon K. 2014 Ecosystem services from tropical forests: review of current science. *CGD Working Pap.* **380**, 2622749. (doi:10.2139/ssrn.2622749)
11. Hosonuma N, Herold M, Sy VD, Fries RSD, Brockhaus M, Verchot L, Angelsen A, Romijn E. 2012 An assessment of deforestation and forest degradation drivers in developing countries. *Environ. Res. Lett.* **7**, 044009. (doi:10.1088/1748-9326/7/4/044009)
12. Lewis SL, Edwards DP, Galbraith D. 2016 Increasing human dominance of tropical forests. *Science* **349**, 827–832. (doi:10.1126/science.aaa9932)
13. Vira B *et al.* 2015 Forests, trees and landscapes for food security and nutrition. A global assessment report. In *Forests and food: addressing hunger and nutrition across sustainable landscapes* (eds B Vira, C Wildburger, S Mansourian), p. 172. Cambridge, UK: Open Book Publishers. (doi:10.11647/OBP.0085.01)
14. Harris N, Goldman ED, Gibbes S. 2019 *Spatial database on planted trees (SDPT version 1.0)*. Washington, DC: World Resources Institute.
15. McNicol IM, Ryan CM, Mitchard ETA. 2018 Carbon losses from deforestation and widespread degradation offset by extensive growth in African woodlands. *Nat. Commun.* **9**, 3045. (doi:10.1038/s41467-018-05386-z)
16. Sullivan MJP *et al.* 2017 Diversity and carbon storage across the tropical forest biome. *Scient. Rep.* **7**, 39102. (doi:10.1038/srep39102)

17. Sala OE *et al.* 2000 Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774. (doi:10.1126/science.287.5459.1770)
18. Scholes RJ, Mace GM, Turner W, Geller GN, Jürgens N, Larigauderie A, Muchoney D, Walther BA, Mooney HA. 2008 Toward a global biodiversity observing system. *Science* **321**, 1044–1045. (doi:10.1126/science.116205)
19. Convention on Biological Diversity. 2010 *The strategic plan for biodiversity 2011–2020 and the Aichi Biodiversity Targets. COP 10 Decision X/2*. See https://www.cbd.int/decision/cop/?id=12268.
20. UN DESA. 2017 *The sustainable development goals report*. New York, NY: United Nations. (doi:10.18356/4d038e1e-en)
21. Food and Agriculture Organization of the United Nations. 2016 *Global forest resources assessment 2015: how are the world's forests changing?*, 2nd edn. Rome, Italy: FAO.
22. Redford KH. 1992 The empty forest. *BioScience* **42**, 412–422. (doi:10.2307/1311860)
23. Trumbore S, Brando P, Hartmann H. 2015 Forest health and global change. *Science* **349**, 814–818. (doi:10.1126/science.aac6759)
24. Bello C, Galetti M, Pizo MA, Magnago LFS, Rocha MF, Lima RAF, Peres CA, Ovaskainen O, Jordano P. 2015 Defaunation affects carbon storage in tropical forests. *Sci. Adv.* **1**, e1501105. (doi:10.1126/sciadv.1501105)
25. Osuri AM, Ratnam J, Varma V, Alvarez-Loayza P, Hurtado Astaiza J, Bradford M, Sankaran M. 2016 Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nat. Commun.* **7**, 11351. (doi:10.1038/ncomms11351)
26. Harper AB *et al.* 2018 Land-use emissions play a critical role in land-based mitigation for Paris climate targets. *Nat. Commun.* **9**, 2938. (doi:10.1038/s41467-018-05340-z)
27. Gardner CJ, Bicknell JE, Baldwin-Cantello W, Struebig MJ, Davies ZG. 2019 Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. *Nat. Commun.* **10**, 4590. (doi:10.1038/s41467-019-12539-1)
28. Poulsen JR, Clark CJ, Palmer TM. 2013 Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. *Biol. Conserv.* **163**, 122–130. (doi:10.1016/j.biocon.2013.03.021)
29. Collen B, Loh J, Whitmee S, McRae L, Amin R, Baillie JEM. 2009 Monitoring change in vertebrate abundance: the living planet index. *Conserv. Biol.* **23**, 317–327. (doi:10.1111/j.1523-1739.2008.01117.x)
30. McRae L, Deinet S, Freeman R. 2017 The diversity-weighted living planet index: controlling for taxonomic bias in a global biodiversity indicator. *PLoS ONE* **12**, e0169156. (doi:10.1371/journal.pone.0169156)
31. Keenan RJ, Reams GA, Achard F, de Freitas JV, Grainger A, Lindquist E. 2015 Dynamics of global forest area: results from the FAO Global Forest Resources Assessment 2015. *For. Ecol. Manage.* **352**, 9–20. (doi:10.1016/j.foreco.2015.06.014)
32. Brooks TM *et al.* 2002 Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* **16**, 909–923. (doi:10.1046/j.1523-1739.2002.00530.x)
33. Gregory RD, van Strien A, Vorisek P, Gmelig Meyling AW, Noble DG, Foppen RP, Gibbons DW. 2005 Developing indicators for European birds. *Phil. Trans. R. Soc. B* **360**, 269–288.
34. Grenyer R *et al.* 2006 Global distribution and conservation of rare and threatened vertebrates. *Nature* **444**, 93. (doi:10.1038/nature05237)
35. Spooner FEB, Pearson RG, Freeman R. 2018 Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Glob. Change Biol.* **24**, 4521–4531. (doi:10.1111/gcb.14361)
36. Hansen MC *et al.* 2013 High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853. (doi:10.1126/science.1244693)
37. USGS Land Cover Institute. 2017 *Tree cover for 2010*. See https://archive.usgs.gov/archive/sites/landcover.usgs.gov/globallandcover.html.
38. Petersen R *et al.* 2016 *Mapping tree plantations with multispectral imagery: preliminary results for seven tropical countries.* Washington, DC: World Resources Institute.
39. Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. 2017 Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* **202**, 18–27. (doi:10.1016/j.rse.2017.06.03)
40. Sexton JO *et al.* 2016 Conservation policy and the measurement of forests. *Nat. Clim. Change* **6**, 192–196. (doi:10.1038/nclimate2816)
41. Gross D, Achard F, Dubois G, Brink A, Prins HH. 2018 Uncertainties in tree cover maps of sub-Saharan Africa and their implications for measuring progress towards CBD Aichi Targets. *Remote Sens. Ecol. Conserv.* **4**, 94–112. (doi:10.1002/rse2.52)
42. Maxwell SL, Fuller RA, Brooks TM, Watson JEM. 2016 Biodiversity: the ravages of guns, nets and bulldozers. *Nat. News* **536**, 143. (doi:10.1038/536143a)
43. Henle K, Davies KF, Kleyer M, Margules C, Settele J. 2004 Predictors of species sensitivity to fragmentation. *Biodivers. Conserv.* **13**, 207–251. (doi:10.1023/B:BIOC.0000004319.91643.9e)
44. Myhrvold NP, Baldridge E, Chan B, Sivam D, Freeman DL, Ernest SKM. 2015 An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* **96**, 3109. (doi:10.1890/15-0846R.1)
45. Oliveira BF, São-Pedro VA, Santos-Barrera G, Penone C, Costa GC. 2017 AmphiBIO, a global database for amphibian ecological traits. *Scient. Data* **4**, 170123. (doi:0.1038/sdata.2017.123)
46. Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W. 2014 EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027. (doi:10.1890/13-1917.1)
47. CIESIN, ITOS. 2013 *Global roads open access data set, version 1 (gROADSv1)*. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). (doi:10.7927/H4VD6WCT)
48. CIESIN. 2016 *Gridded population of the world, version 4 (GPWv4): population density*. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). (doi:10.7927/H4NP22DQ)
49. Weiss DJ *et al.* 2018 A global map of travel time to cities to assess inequalities in accessibility in 2015. *Nature* **553**, 333–336. (doi:10.1038/nature2518)
50. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
51. Burnham KP, Anderson DR. 2004 Multimodel inference: understanding AIC and BIC in model selection. *Soc. Methods Res.* **33**, 261–304. (doi:10.1177/0049124104268644)
52. R Core Team. 2018 *R: a language and environment for statistical computing*. Venna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org/.
53. Nieuwenhuis R, Grotenhuis MT, Pelzer B. 2012 influence.ME: tools for detecting influential data in mixed effects models. *R J.* **4**, 38–47. (doi:10.32614/RJ-2012-011)
54. Oaks JL *et al.* 2004 Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature* **427**, 630–633. (doi:10.1038/nature02317)
55. He F, Zarfl C, Bremerich V, David JN, Hogan Z, Kalinkat G, Tockner K, Jähnig SC. 2019 The global decline of freshwater megafauna. *Glob. Change Biol.* **25**, 3883–3892. (doi:10.1111/gcb.14753)
56. Collen B *et al.* 2014 Global patterns of freshwater species diversity, threat and endemism. *Global Ecol. Biogeogr.* **23**, 40–51. (doi:10.1111/geb.12096)
57. Benitez-Lopez A, Santini L, Schipper AM, Busana M, Huijbregts MA. 2019 Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLoS Biol.* **17**, 5. (doi:10.1371/journal.pbio.3000247)
58. Bell BD, Carver S, Mitchell NJ, Pledger S. 2004 The recent decline of a New Zealand endemic: how and why did populations of Archey's frog *Leiopelma archeyi* crash over 1996–2001? *Biol. Conserv.* **120**, 189–199. (doi:10.1016/j.biocon.2004.02.011)
59. Burrowes PA, Joglar RL, Green DE. 2004 Potential causes for amphibian declines in Puerto Rico. *Herpetologica* **60**, 141–154. (doi:10.1655/03-50)
60. Buckland ST, Johnston A. 2017 Monitoring the biodiversity of regions: key principles and possible pitfalls. *Biol. Conserv.* **214**, 23–34. (doi:10.1016/j.biocon.2017.07.034)
61. BirdLife International. 2018 *State of the world's birds: taking the pulse of the planet*. Cambridge, UK: BirdLife International. See http://edepot.wur.nl/448977.
62. Collen B, Ram M, Zamin T, McRae L. 2008 The tropical biodiversity data gap: addressing disparity in global monitoring. *Trop. Conserv. Sci.* **1**, 75–88. (doi:10.1177/194008290800100202)
63. Peres CA, Palacios E. 2007 Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated

seed dispersal. *Biotropica* **39**, 304–315. (doi:10.1111/j.1744-7429.2007.00272.x)

64. Tracewski Ł, Butchart SH, Di Marco M, Ficetola GF, Rondinini C, Symes A, Wheatley H, Beresford AE, Buchanan GM. 2016 Toward quantification of the impact of 21st-century deforestation on the extinction risk of terrestrial vertebrates. *Conserv. Biol.* **30**, 1070–1079. (doi:10.1111/cobi.12715)
65. Santini L, Butchart SH, Rondinini C, Benítez-López A, Hilbers JP, Schipper AM, Cengic M, Tobias JA, Huijbregts MA. 2019 Applying habitat and population-density models to land-cover time series to inform IUCN Red List assessments. *Conserv. Biol.* **33**, 1084–1093. (doi:10.1111/cobi.13279)
66. Liu J *et al.* 2015 Systems integration for global sustainability. *Science* **347**, 1258832. (doi:10.1126/science.1258832)
67. Butchart SHM *et al.* 2010 Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168. (doi:10.1126/science.1187512)
68. Nagendra H, Lucas R, Honrado JP, Jongman RH, Tarantino C, Adamo M, Mairota P. 2013 Remote sensing for conservation monitoring: assessing protected areas, habitat extent, habitat condition, species diversity, and threats. *Ecol. Indic.* **33**, 45–59. (doi:10.1016/j.ecolind.2012.09.014)
69. Kuenzer C, Ottinger M, Wegmann M, Guo H, Wang C, Zhang J, Dech S, Wikelski M. 2014 Earth observation satellite sensors for biodiversity monitoring: potentials and bottlenecks. *Int. J. Remote Sens.* **35**, 6599–6647. (doi:10.1080/01431161.2014.964349)
70. Pettorelli N, Safi K, Turner W. 2014 Satellite remote sensing, biodiversity research and conservation of the future. *Phil. Trans. R. Soc. B* **369**, 20130190. (doi:10.1098/rspb.2013.0190)

Below the canopy: global trends in forest vertebrate populations and their drivers.

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Supplementary Material

S1. Number of species and populations in the forest specialist index by realm and taxonomic class

	Afrotropical		Indopacific		Nearctic		Neotropical		Palearctic	
	Species	Populations	Species	Populations	Species	Populations	Species	Populations	Species	Populations
Birds	1	1	27	44	45	47	60	75	8	42
Mammals	27	49	19	32	6	32	31	54	6	14
Reptiles and amphibians	5	5	7	11	4	11	27	37	0	0

S2. Specifications of some global tree cover datasets with continuous vegetation fields

Dataset name	**Definition of tree cover**	**Spatial resolution**	**Temporal coverage/ cadence**	**Reference**
Landsat Global Forest Change	Canopy closure for all vegetation taller than 5 meters in height.	30 m	Fractional tree cover available for 2000 and 2010 only; tree cover loss available for 2001-2017	Hansen et al (2013)
Landsat VCF (GLCF)	The percentage of horizontal ground in each 30-m pixel covered by woody vegetation greater than 5 meters in height	30 m	2000, 2005, 2010	(Sexton et al., 2013)
MEASURES VCF5KYR	The proportion of the ground covered by the vertical projection of tree crowns. Trees are defined as all vegetation taller than 5 meters in height.	0.05 degree (5600 m)	1982-2016, annual	Song et al (2018)
MODIS VCF	Percent of the pixel covered by tree canopy equal to or greater than 5 m in height.	250 m	2000-2015, annual	(DiMiceli et al., 2015)

S3. Calculation of 5-km radius

Range size estimates were not known for every species, but body mass estimates were available (see *Additional drivers of forest population change* in main text). We calculated the correlation between body mass and range size (both log-10 transformed) for the species with both estimates available, and found a strong positive relationship (Pearson correlation coefficient = 0.87, $p < 0.001$). We therefore used body mass to predict range size for all populations using the ‘predict.lm’ function in the ‘stats’ package (R Core Team, 2018) and calculated the mean range size across all populations as 58.5 km^2, equivalent to a circle with a radius of 4.32 km. We rounded this up and fitted buffers with a 5-km radius around the central coordinates of each forest population.

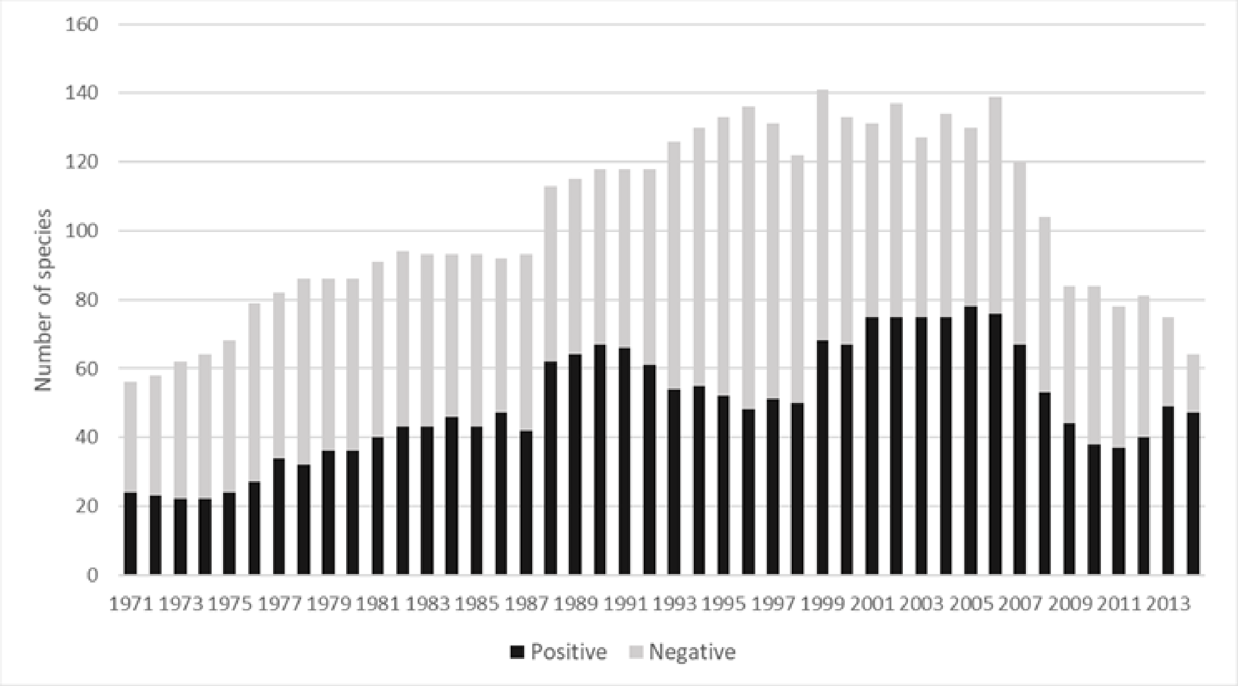
S4. Number of forest populations (generalists and specialists) and forest specialist populations per realm included in analyses using long-term and short-term tree cover datasets.

Analysis	Realm	All forest populations	Forest specialist populations
Long-term (Song)	Afrotropical	365	36
	Australasia	64	3
	Indo-Malayan	98	20
	Nearctic	321	14
	Neotropical	315	76
	Oceania	30	12
	Palearctic	475	14
Short-term (Hansen)	Afrotropical	172	12
	Australasia	42	3
	Indo-Malayan	52	10
	Nearctic	96	2
	Neotropical	127	43
	Oceania	0	0
	Palearctic	196	4

S5. Number of forest populations (generalists and specialists) and forest specialist populations per taxonomic class included in analyses using long-term and short-term tree cover datasets.

Analysis	Taxa	All forest populations	Forest specialist populations
Long-term (Song)	Amphibians	154	19
	Birds	701	73
	Mammals	767	78
	Reptiles	46	5
Short-term (Hansen)	Amphibians	52	2
	Birds	251	33
	Mammals	348	34
	Reptiles	34	5

S6. Number of species trends in the FSI annually, with proportions of positive and negative annual trends



S7. Percentage of annual species trends which are positive or negative for birds (A), mammals (B) and herptiles (C)

S8. Number of average declining, increasing and stable (less than 5% change in abundance) species trends in tropical and temperate realms (A) and biomes (B). Nine species were not located in a forest biome (where forest is the dominant habitat type), so were not included in B.

A Realm		**Decline**	**Increase**	**Stable**
Temperate realms	Nearctic	22	28	4
	Palearctic	3	7	3
	Total	***25***	***35***	***7***
Tropical realms	Afrotropical	18	13	2
	Neotropical	53	48	13
	Indo-Pacific	28	22	4
	Total	***99***	***83***	***19***
B Biome		**Decline**	**Increase**	**Stable**
Temperate forest biomes	Boreal forests / taiga	2	10	
	Mediterranean forests, woodlands and scrub	1	1	
	Temperate broadleaf and mixed forests	21	24	7
	Temperate coniferous forests	5	4	
	Total	***29***	***39***	***7***
Tropical forest biomes	Mangroves	1	2	
	Tropical and subtropical coniferous forests	2	1	
	Tropical and subtropical dry broadleaf forests	9	1	5
	Tropical and subtropical moist broadleaf forests	77	72	14
	Total	***89***	***76***	***19***

S9. Average rate of forest population change regressed on fixed predictor effects with a random effect of location: mixed effects model results for forest vertebrate populations (generalists and specialists). Populations had at least 2 years of data covering at least a 5 year period from 1982-2016. Tree cover variables calculated using the Song et al (2018) dataset. N = 1668.

Fixed effect	**Estimate**	**CI**	**AIC**	**ΔAIC to null model**
NULL	*NA*	*NA*	-4113.666	0
Tree cover trend	1.09 x 10-2	8.43 x 10^{-4}– 2.09 x 10^{-2}	-4107.464	+6.202
Body mass	3.92 x 10-3	1.44 x 10^{-3}– 6.40 x 10^{-3}	-4109.732	+3.934
Mean tree cover	-1.91 x 10-3	-7.45 x 10^{-3}– 3.65 x 10^{-3}	-4102.222	+11.444
Mean bare ground	8.79 x 10-4	-8.66 x 10^{-3}– 1.04 x 10^{-2}	-4102.885	+10.781
Exploitation (Y)	1.87 x 10-3	-1.26 x 10^{-2}– 1.64 x 10^{-2}	-4103.753	+9.913
HPD	3.69 x 10-3	-1.25 x 10^{-3}– 8.63 x 10^{-3}	-4103.674	+9.992
Road density	-2.30 x 10-5	-3.85 x 10^{-4}– 3.39 x 10^{-4}	-4096.325	+17.341
Mean travel time	-1.22 x 10-3	-7.58 x 10^{-3}– 5.14 x 10^{-3}	-4102.185	+11.481

S10. Average rate of forest population change regressed on fixed predictor effects with a random effect of location: mixed effects model results for forest vertebrate populations (specialists only). Populations had at least 2 years of data covering at least a 5 year period from 1982-2016. Tree cover variables calculated using the Song et al. (2018) dataset. N = 175.

Fixed effect	**Estimate**	**CI**	**AIC**	**ΔAIC to null model**
NULL	*NA*	*NA*	-461.632	0
Tree cover trend	1.86×10^{-2}	-5.19×10^{-3}– 4.25×10^{-2}	-454.989	+6.643
Body mass	-4.03×10^{-3}	-1.17×10^{-2}– 3.69×10^{-3}	-451.438	+10.194
Mean tree cover	-1.82×10^{-2}	-6.40×10^{-2}– 2.76×10^{-2}	-454.560	+7.072
Mean bare ground	2.37×10^{-2}	-1.99×10^{-2}– 6.72×10^{-2}	-454.991	+6.641
Exploitation (Y)	-8.79×10^{-2}	-1.38×10^{-1}– -3.74×10^{-2}	-465.041	-3.409
HPD	-6.68×10^{-3}	-2.48×10^{-2}– 1.15×10^{-2}	-452.625	+9.007
Road density	-1.08×10^{-3}	-3.18×10^{-3}– 1.00×10^{-3}	-448.816	+12.816
Mean travel time	1.34×10^{-2}	-9.01×10^{-3}– 3.58×10^{-2}	-453.894	+7.738

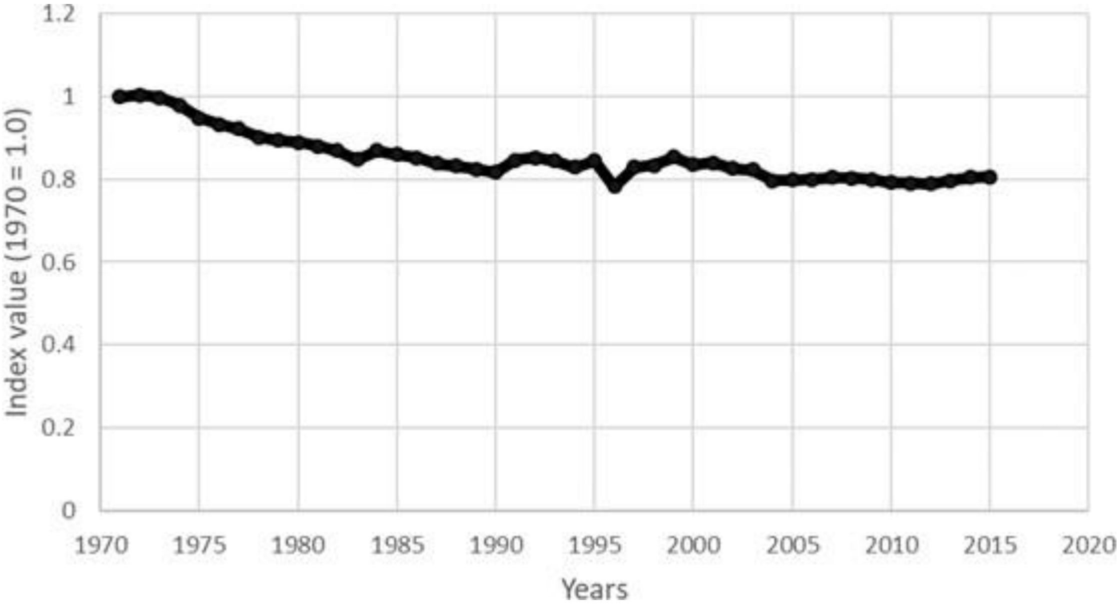
S11. Model results from mixed effects models of average rate of population change of forest generalists and specialists regressed on fixed predictor effects with a random effect of location. Populations had at least 2 years of data covering at least a 5 year period from 2000-2015. Tree cover variables calculated using the Hansen dataset. N = 685.

Fixed effect	**Estimate**	**CI**	**AIC**
NULL	*NA*	*NA*	-1479.421
Tree cover 2000	-1.50×10^{-3}	-1.15×10^{-2} – 8.54×10^{-3}	-1468.794
Total tree loss	8.60×10^{-4}	-4.13×10^{-3} – 5.85×10^{-3}	-1467.425
Tree cover change 2000-2010	-2.77×10^{-3}	-2.70×10^{-2} – 2.15×10^{-2}	-1470.524
Body mass	4.82×10^{-3}	7.34×10^{-4} – 8.90×10^{-3}	-1472.199
Exploitation (Y)	1.59×10^{-2}	-1.09×10^{-2} – 4.27×10^{-2}	-1472.025
HPD	9.34×10^{-3}	1.31×10^{-3} – 1.75×10^{-2}	-1473.445
Road density	1.87×10^{-4}	-5.26×10^{-4} – 9.03×10^{-4}	-1463.679
Mean travel time	-6.97×10^{-3}	-1.85×10^{-2} – 4.49×10^{-3}	-1470.392

S12. Model results from mixed effects models of average rate of population change of forest specialists regressed on fixed predictor effects with a random effect of location. Populations had at least 2 years of data covering at least a 5 year period from 2000-2015. Tree cover variables calculated using the Hansen dataset. N = 74.

Fixed effect	**Estimate**	**CI**	**AIC**
NULL	*NA*	*NA*	-158.048
Tree cover 2000	-1.90×10^{-2}	-6.88×10^{-2} – 2.97×10^{-2}	-151.075
Total tree loss	2.58×10^{-3}	-1.36×10^{-2} – 1.75×10^{-2}	-148.242
Tree cover change 2000-2010	6.14×10^{-2}	-2.73×10^{-1} – 3.96×10^{-1}	-154.474
Body mass	-1.27×10^{-3}	-1.30×10^{-2} – 1.07×10^{-2}	-147.690
Exploitation (Y)	-5.43×10^{-2}	-1.17×10^{-2} – 8.55×10^{-3}	-153.850
HPD	-2.14×10^{-4}	-1.75×10^{-2} – 1.98×10^{-2}	-148.417
Road density	-1.07×10^{-3}	-3.43×10^{-3} – 1.29×10^{-3}	-145.234
Mean travel time	1.37×10^{-3}	-2.90×10^{-2} – 2.97×10^{-2}	-149.413

S13. Abundance index for 74 species from the FSI with data present throughout all decades from 1970 to 2014 (these are primarily birds from the Nearctic)



REFERENCES (excluding those cited in the main text)

DiMiceli, C., Carroll, M., Sohlberg, R., Kim, D. H., Kelly, M., & Townshend, J. R. G. (2015). *MOD44B MODIS/Terra Vegetation Continuous Fields Yearly L3 Global 250m SIN Grid V006 [Data set]*. Retrieved from https://doi.org/10.5067/MODIS/MOD44B.006

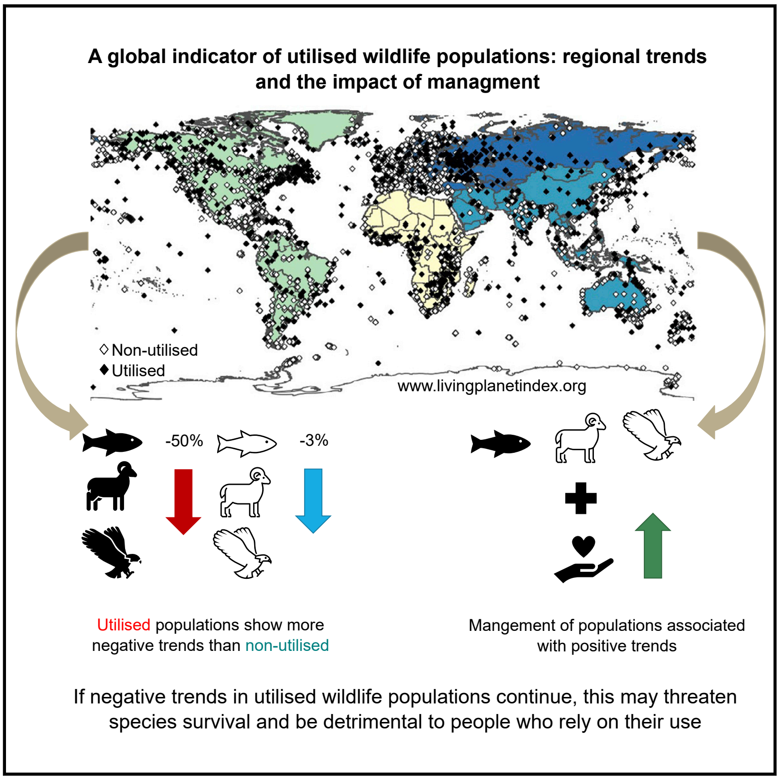
Sexton, J. O., Song, X.-P., Feng, M., Noojipady, P., Anand, A., Huang, C., … Townshend, J. R. (2013). Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS vegetation continuous fields with lidar-based estimates of error. *International Journal of Digital Earth*, *6*(5), 427–448. https://doi.org/10.1080/17538947.2013.786146

Article

One Earth

A global indicator of utilized wildlife populations: Regional trends and the impact of management

Graphical abstract



Highlights

- Utilized vertebrate populations declined by 50% on average from 1970 to 2016
- Body size is an important predictor of trends in utilized populations
- Importantly, populations that are managed are more likely to be increasing
- Reversal of decline in utilized populations is crucial for biodiversity and people

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In brief

Sustainable use of natural resources is central to biodiversity conservation. Using more than 11,000 vertebrate population time series, we developed a global indicator of utilized populations and propose its use in the Post-2020 Global Biodiversity Framework. We found that trends in utilized bird, mammal, and fish populations were more negative than non-utilized ones and that body size was an important predictor of trends. Crucially, we found that populations where management was in place were more likely to show positive trends.

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One Earth

Article

A global indicator of utilized wildlife populations: Regional trends and the impact of management

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SCIENCE FOR SOCIETY The use of wildlife supports many people for their food, medicine, and livelihoods. Ensuring that this use is sustainable is central to conservation to ensure the persistence of species alongside continued utilization by people. Using more than 11,000 wildlife population trends, we conducted a global analysis of local-scale data to better understand how populations respond to utilization. We found that utilized populations declined on average by 50% between 1970 and 2016 and showed steeper negative trends than populations that were not utilized (−3%). If these trends continue, then this may threaten species survival and be detrimental to people who rely on their use.

We also highlight how these trends might be reversed. Encouragingly, populations under targeted management, whether utilized or not, fared better than those that are not managed. This evidence can be used to track progress toward international and national targets on the sustainable use of species.

SUMMARY

Sustainable use of wildlife is a core aspiration of biodiversity conservation but is the subject of intense debate in the scientific literature, including the extent to which use is impacting species and whether management can mitigate any impact. Although positive and negative outcomes of sustainable use are known for specific taxa or local communities, a global and regional picture of trends in wildlife populations in use is lacking. We use a global dataset of more than 11,000 time series to derive indices of "utilized" and "not utilized" wildlife populations. Our results show that population trends globally are negative on average but that utilized populations tend to decline more rapidly, especially in Africa and the Americas. Crucially, where populations are managed, they are more likely to be increasing. This evidence can inform global biodiversity assessments and provide an operational indicator to track progress toward the Post-2020 Global Biodiversity Framework.

INTRODUCTION

Direct use of wild species is one of the ways in which biodiversity is fundamental to the subsistence and livelihoods of people.[1–6] Consequently, any unsustainable impact of anthropogenic activity on species, particularly those that are important for peoples' livelihoods or wellbeing, presents a threat to those species and ecosystems as well as to human health and development.[7–9] Moreover, any prohibition of species use can have serious consequences for people, particularly risks to food security,[10] so striving for sustainable use is key. The importance of sustainable use of resources has been recognized as central to biodiversity conservation and is embedded in international bodies and conventions for nature.[11–15] However, progress toward achieving the sustainable use of resources globally remains a challenge. As part of the Convention on Biological Diversity's Strategic Plan for Biodiversity 2011–20, Aichi target 4.2 was set to keep the impacts of use of natural resources well within safe ecological limits by 2020. Progress toward this target was assessed as "poor" in the final decadal review of the Aichi targets,[16] and an assessment of the research and management behind the use of wild meat found limited progress toward sustainability.[9]

Overexploitation is a highly prevalent threat to biodiversity,[9,17] with evidence showing that harvesting, logging, fishing, and hunting often occur at unsustainable levels.[3] Together with activities such as logging and agriculture, hunting and trapping have a higher average probability of impacting species compared with other threats, with hotspots of this threat largely concentrated in the tropics.[18] Combined pressures of land use change and hunting have reduced the distribution of terrestrial tropical mammals, with large-bodied species the most impacted.[19] The effect of hunting, especially for commercial use, has been implicated in the population decline of 97 tropical bird and 254 tropical mammal species,[20] and a global assessments of 301 terrestrial mammals threatened with extinction lists hunting as a primary threat.[21] In the marine realm, the percentage of commercial fish stocks that are within biologically sustainable levels decreased from 90% to 65.8% between 1974 and 2017,[22] although recent trends suggest that stocks that are scientifically assessed are now increasing on average, and intensively managed stocks are faring better.[23]

The role of wildlife management is also evident in some notable examples on land. The rise of community-based natural resource management over 30 years ago, which may include managing the use of species in place of more centralized wildlife management policies, has yielded examples of economic and ecological benefits in many countries.[6,24,25] Similarly, even in regions where utilized species have been heavily impacted over centuries,[26,27] examples of recoveries have been recorded often as a result of efforts to stem unsustainable use.[28,29]

To understand how species in use (hereafter called "utilized species" or "utilized populations"; see "definitions" in experimental procedures) are faring at the global scale, existing indicators have largely focused on the species level; e.g., the Red List Index for internationally traded species or those used for food and medicine and the Living Planet Index for utilized species.[30,31] These indices cannot integrate any potential heterogeneity of impacts of use because of factors influencing individual populations within the same species differently, as identified for commercial harvesting.[32] In the marine environment, indicators have measured fishing pressure and the proportion of fish stocks that are unsustainable.[22] At a smaller scale, harvest models are used to assess sustainability and the status of a utilized population, which can provide detailed information on how a population and ecosystem are impacted by use and inform local management.[33]

We propose that global and large regional views are needed and present a population-based approach with information on utilization at the site-level aggregated to the global scale. This approach can provide important insights that are not available at the level of species assessments through incorporating population-level information on use, threats, and management into the analysis. To follow this approach, we develop an indicator of utilized vertebrate populations following the method used to calculate the Living Planet Index (LPI),[34–36] a multi-species indicator of relative abundance based on population trends of vertebrates used to monitor progress toward international and national biodiversity targets.[37–39] We explore differences in these trends with respect to taxonomic groups and Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) regions and test the sensitivity of the indicator to data quality. The Living Planet Database, which underpins the index, collates data collected locally from around the world, which can be divided in different ways to deliver a suite of indices of species population change; the data are also suitable for within-species comparisons and identification of correlates predicting trends using mixed-effect models.[40,41] We then use this to contrast trends in utilized populations with those that are not used for the complete set of species in the dataset and only for species with data for utilized and non-utilized populations ("matched"). Finally, using mixed-effect models, we explore the role of targeted management (see "definitions" in experimental procedures) in predicting populations trends in utilized populations. Our results can help to measure progress toward policy targets and identify trends in resources that are important for people. Our results, thus, feed directly into global processes such as the IPBES thematic assessment of sustainable use of wild species[15] and development of indicators for the Post-2020 Global Biodiversity Framework.

RESULTS

Geographic, taxonomic, and threat data summary

Our final dataset comprised 11,123 population time series from 2,944 species, of which 5,811 populations from 1,348 species were coded as utilized, and 5,312 populations from 1,996 species were coded as not utilized (Table S1). For utilized populations, most data were available for fish (n = 3,233), followed by mammals (n = 2,098), birds (n = 331), reptiles (n = 142), and amphibians (n = 7). Fish and mammals had more utilized populations than not, whereas the reverse was true for birds, reptiles, and amphibians (Table S1). Compared with the expected distribution of body mass values for all species, the utilized dataset showed a skewed distribution toward larger-bodied species for birds and mammals but a distribution of body masses to all fish species (Figure S1). Geographically, our sample contained data from all IPBES regions and from 146 countries (Figure 1; Table S2). Utilized and not-utilized populations were found in all regions, but there were noticeable clusters of more utilized populations in parts of Africa, Central Asia, and Canada. The largest regional dataset was for the Americas. Results for Africa are based on the smallest dataset of the regions; data availability throughout the time series dropped after 2012, so the indices were shorter than for the other regions, finishing in 2015 and 2013 for terrestrial/freshwater and marine, respectively.

Threat information was available for 3,195 populations—1,694 utilized and 1,501 not utilized (Table S3). There was a difference in the distribution of threats coded between utilized and not utilized populations, with a greater proportion of threats listed as overexploitation for utilized populations (Figure S2). Nearly three-quarters of the overexploitation threats coded for utilized populations were a result of hunting, fishing, and collecting (Figure S3). Of the utilized populations, 46% had information available on targeted management, and 23% were unmanaged (the remainder had no information; Table S4).

Global indices for utilized populations show decline

The index for utilized populations shows a decrease of 69% for terrestrial and freshwater populations (Figure 2; index value in 2016, 0.31; range, 0.21–0.44) and a decrease of 34% for marine populations (Figure 2; index value in 2016, 0.66; range, 0.52–0.85) between 1970 and 2016. Although the overall trend for utilized populations showed a steep decline, there was considerable heterogeneity at the level of individual populations,

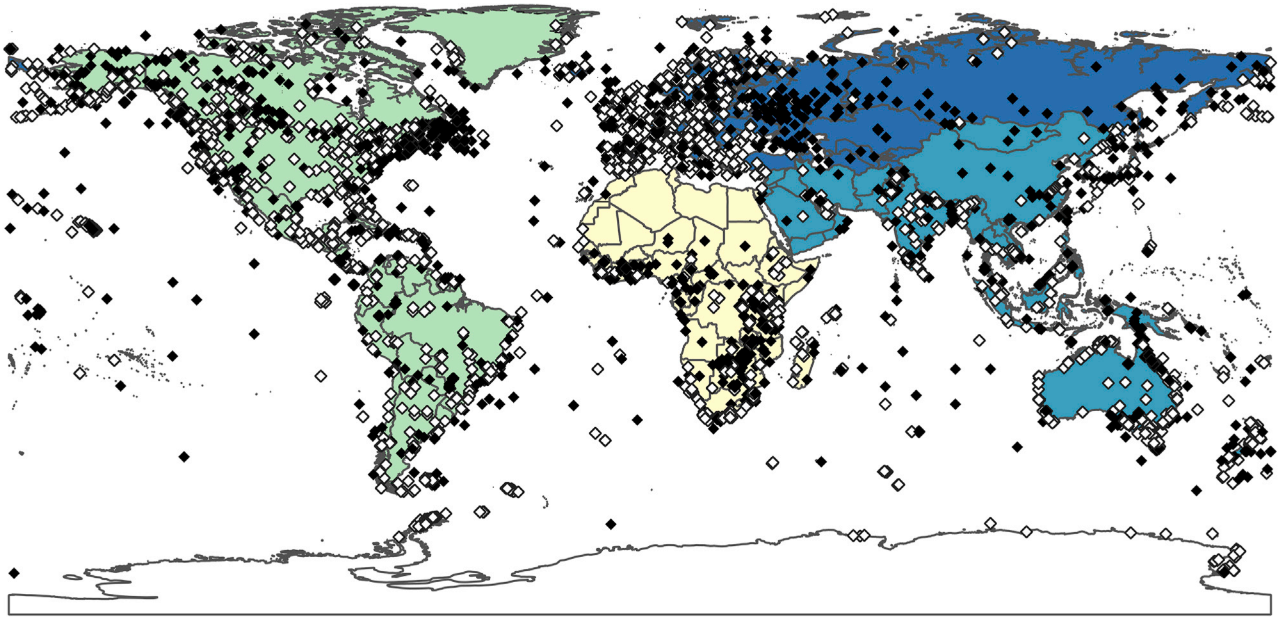

Figure 1. Locations of populations used in the analysis overlaid onto IPBES regions

The point location is shown for the utilized (black diamonds) and non-utilized (white diamonds) populations used in the analysis (Table S2). IPBES regions shown are Americas (green), Africa (yellow), Europe and Central Asia (blue), and Asia-Pacific (light blue). IPBES regions were sourced from the IPBES Technical Support Unit on Knowledge and Data.[42]

with 46.3% showing an overall increase, 48.9% showing an overall decrease, and 4.8% were stable in the terrestrial and freshwater index. In the marine index, 53.2% of utilized populations showed an overall decline, 42.6% an overall increase, and 4.2% were stable.

We tested the robustness of the indices to time series length. This is important to check when using population trends that vary in sample duration,[43] particularly the effect of short time series that may exhibit more extreme or fluctuating trends and bias in the index.[44,45] We observed whether similar trends were seen when restricting the dataset to different thresholds for the minimum time series length in numbers of years. When a more stringent minimum threshold for time series length was applied, similar trajectories of decline were observed for indices with a minimum of 5 years, and shallower decline was reported for indices with a minimum of 10 years (Figure S4).

Regional indices show steeper decline in the tropics

The indices for utilized populations trends since 1970 grouped by IPBES regions show disparate trends, with largely tropical regions faring worse than the global indices of utilized populations (Figure 2) and compared with more temperate regions (Figure 3). Africa showed the greatest decline since 1970 in the terrestrial/freshwater and marine subsets; both indices show steeper decline than the global average for utilized species (Figure 3; terrestrial/freshwater index value in 2015, 0.07; range, 0.03–0.16; marine index value in 2013, 0.08; range, 0.04–0.17). The Asia-Pacific index shows a near-continuous decline in the marine index from 1970 to 2016 and an 83% overall decline, which is worse than the global marine index (Figure 3; index value in 2016, 0.17; range, 0.09–0.31); the terrestrial and freshwater index fluctuates from a positive to a negative trend, with high variation in the underlying species trends, and ends at a baseline value similar to 1970, above the global average (Figure 3; index value in 2016, 1.07; range, 0.31–3.76). The terrestrial/freshwater index for the Americas showed a trajectory of decline very similar to the global terrestrial and freshwater index of 67% between 1970 and 2016 (Figure 3; index value in 2016, 0.33; range, 0.19–0.58), whereas the marine index fluctuated throughout the time series and ended at a baseline value similar to 1970, with no significant overall change and a more positive trend than the global marine index (Figure 3; index value in 2016, 1.07; range, 0.78–1.45). The marine indices for Europe and Central Asia showed a slow increase for most of the time series after an initial decline, ending in an overall increase of 41% between 1970 and 2016 (Figure 3; index value in 2016, 1.41; range, 0.95–2.13). The terrestrial/freshwater index had a fluctuating trend for most of the time period but ended with a recent decline (Figure 3; index value in 2016, 0.76; range, 0.43–1.30). Both of these regional indices had trends that were better than the respective global indices.

The utilized index declines more than the non-utilized index

To explore the effect of utilization, we compared trends between utilized and non-utilized populations. For this analysis, we removed all reptile and amphibian data because these two taxa contained low numbers of species and populations in general but particularly those that are in the utilized category, resulting in a large proportional difference when comparing utilized with non-utilized populations. This is likely to make unbalanced comparisons, especially when dividing the dataset into systems (Table S1). This is not to suggest that these two taxa are not important to consider in the context of utilization; indeed, chelonians are one group particularly at risk from use.[46] Comparing

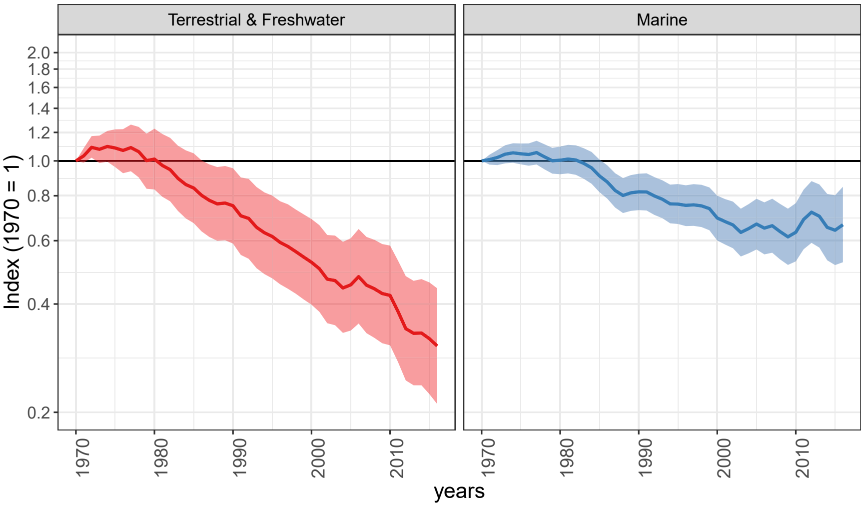

Figure 2. Index of utilized populations globally from 1970 to 2016

Shown are terrestrial and freshwater indices with 95% confidence intervals (CIs) (−69%; Number of species (nspp) = 607, number of populations (npop) = 3,123) and the marine index (−34%; nspp = 761, npop = 2,688).
See Table S5 for CIs.

the trend for mammals, birds, and fish, populations that are not utilized show a more stable trend, with index values above the 1970 baseline throughout the period, except for a recent decline, resulting in an overall decrease of 3% over the time period (Figure 4A; index value in 2016, 0.97; range, 0.80–1.18). In comparison, the index for utilized populations for the same taxa showed an overall decline of 50% (Figure 4A; index value in 2016, 0.50; range, 0.41–0.62). After 1985, there is no overlap in the confidence intervals of each index, which means they are significantly different.

Utilization is a predictor of population trends

We used mixed-effects models to explore the relationship between utilization, taxonomic class, body size, and time series length with overall population trends as the response variable. Utilization was consistently a useful predictor of overall population trends, with utilized populations more likely to be declining than non-utilized ones (Tables S6–S9). Removing utilization from our models produced significantly worse predictions of population trends ($\Delta AIC = -10$, $\chi^2 = 11.835$, $p < 0.01$). In general, our models did not suggest an interaction between utilization and taxonomic group, highlighting that all taxonomic groups are impacted by utilization. Using our most comprehensive dataset (mammals, birds, and fish in terrestrial, freshwater, and marine systems), body size interacting with class was in our top model, and the coefficients suggest that bird population trends are slightly positive, more so for larger birds; however, the confidence intervals span zero, so these are non-significant (Figures 4B and 4C). Fish trends were significantly positive but with larger species in decline, whereas mammal populations are in decline, but larger species show positive population changes (Figures 4B and 4C). The length of a population time series has no clear positive or negative effect on overall population trends. In the full model, which was very close in AIC value to the top model, there is a suggestion that the observed relationship with body size for fish (with smaller species generally doing better than larger species in utilized and non-utilized populations) may be reversed, but only for non-utilized fish populations (Table S6; Figure S5).

We explored two modifications to this dataset. The first removed marine populations, most of which comprise marine fish, which may represent groups of species that have been under long-term utilization pressure that is heavily managed. However, after removing marine populations, our results showed the same pattern, with utilized populations in more significant decline and larger species showing positive trends, but here the interaction between body size and taxonomic class was no longer supported (Figure S6B).

Because our classification of utilization is at the population level, this may result in our models comparing groups of different species (e.g., all utilized populations may be different species than those that are not utilized). We therefore also explored a second refinement of the data, only including bird, mammal, and fish species for which we had both utilized and non-utilized populations (4,255 populations of 339 species; Figure 5). The comparison of trends between utilized and not utilized indices shown in Figure 4A largely holds when the trends for "matched" species are compared, although there is considerable overlap in confidence intervals until the final 10 years of the time series (Figure 5A). Our models suggest that even in these matched species populations, utilized population trends are negative compared with positive trends in the non-utilized populations (Figure 5B). Body size and interactions are not in the best model here (Table S8).

Populations that are managed show less negative trends

For species where we also record whether the populations are under some form of management, we find that populations within our "matched" dataset show a positive trend when management actions are in place (Figure 6). This is mirrored by looking at the number of increasing and declining trends among utilized populations, where unmanaged populations show a greater proportion of declining trends than those that are managed; this applied across all three taxa (Figure S8). Our models suggest that, within our limited data, managed utilized populations may be stable, but unmanaged utilized populations tend to show steeper declining trends. However, many populations with unknown management status were removed, so this dataset is smaller than other sections of our analysis.

DISCUSSION

Global and regional trends in utilized populations

Here, we present a global indicator of trends in utilized vertebrate populations that show that, on average, monitored

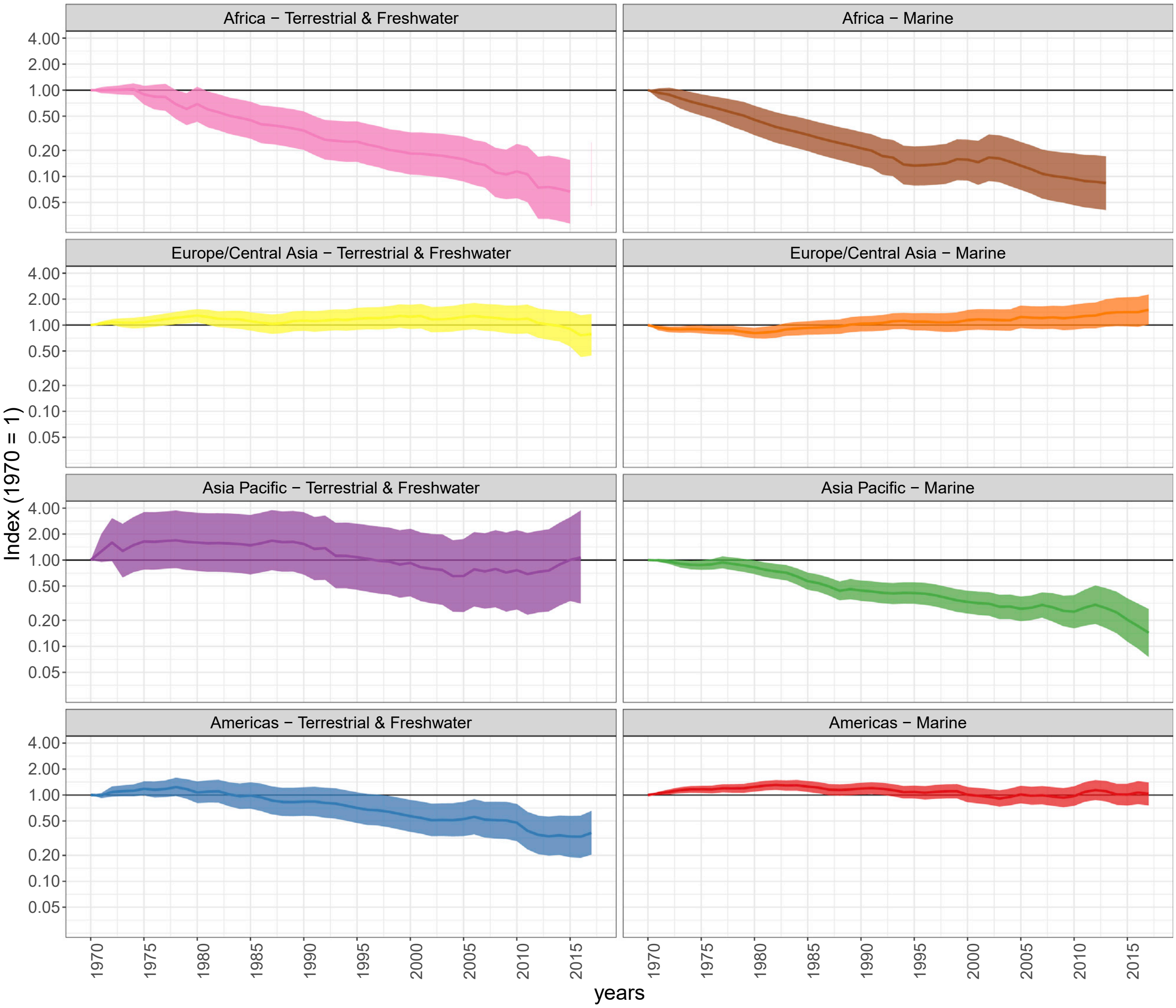

Figure 3. Index of utilized populations for IPBES regions from 1970 to 2016

Shown are terrestrial and freshwater indices with 95% CIs (left panels): Africa (−93%; nspp = 110, npop = 314), Europe and Central Asia (−24%; nspp = 124, npop = 1886), Asia-Pacific (+7%; nspp = 166, npop = 286), and Americas (−67%; nspp = 239, npop = 637) and marine indices (right panels): Africa (−92%; nspp = 77, npop = 132), Europe and Central Asia (+21%; nspp = 100, npop = 252), Asia-Pacific (−83%; nspp = 204, npop = 349), and Americas (+7%; nspp = 465, npop = 1,852).

See Table S5 for CIs.

utilized populations declined, and more so than non-utilized ones, between 1970 and 2016. This trend was even starker among terrestrial and freshwater populations compared with marine ones. Although populations that are not utilized may be affected by threat processes such as habitat loss, it appears that the impact of utilization in addition to the presence of other threats is significant, as suggested in other studies.[19,20] However, the global average masks some interesting variation because just under half of the utilized populations had a stable or increasing trend over the time period. This implies that, for some populations, the use may be sustainable (according to population trend only) and that uncovering explanatory factors behind what drives population trends is crucial.

Our results also uncovered regional differences in trends in utilized populations with overall positive trends in the Americas, Europe, and Central Asia among marine populations; the Asia Pacific index was the only terrestrial and freshwater region with a positive trend. It is important to note that comparisons between regions should be interpreted with care because of the vastly different environmental conditions around the world at the onset of our data in 1970; assessments can skew the state or trends in biodiversity without considering shifting baselines.[47] The baseline year chosen can be important for assessing long-term trends,[48] particularly in regions where high human impact has been prevalent over centuries. In the case of North America and Western Europe, the baseline of 1970 hides a historical decline in species abundance that occurred as land use was

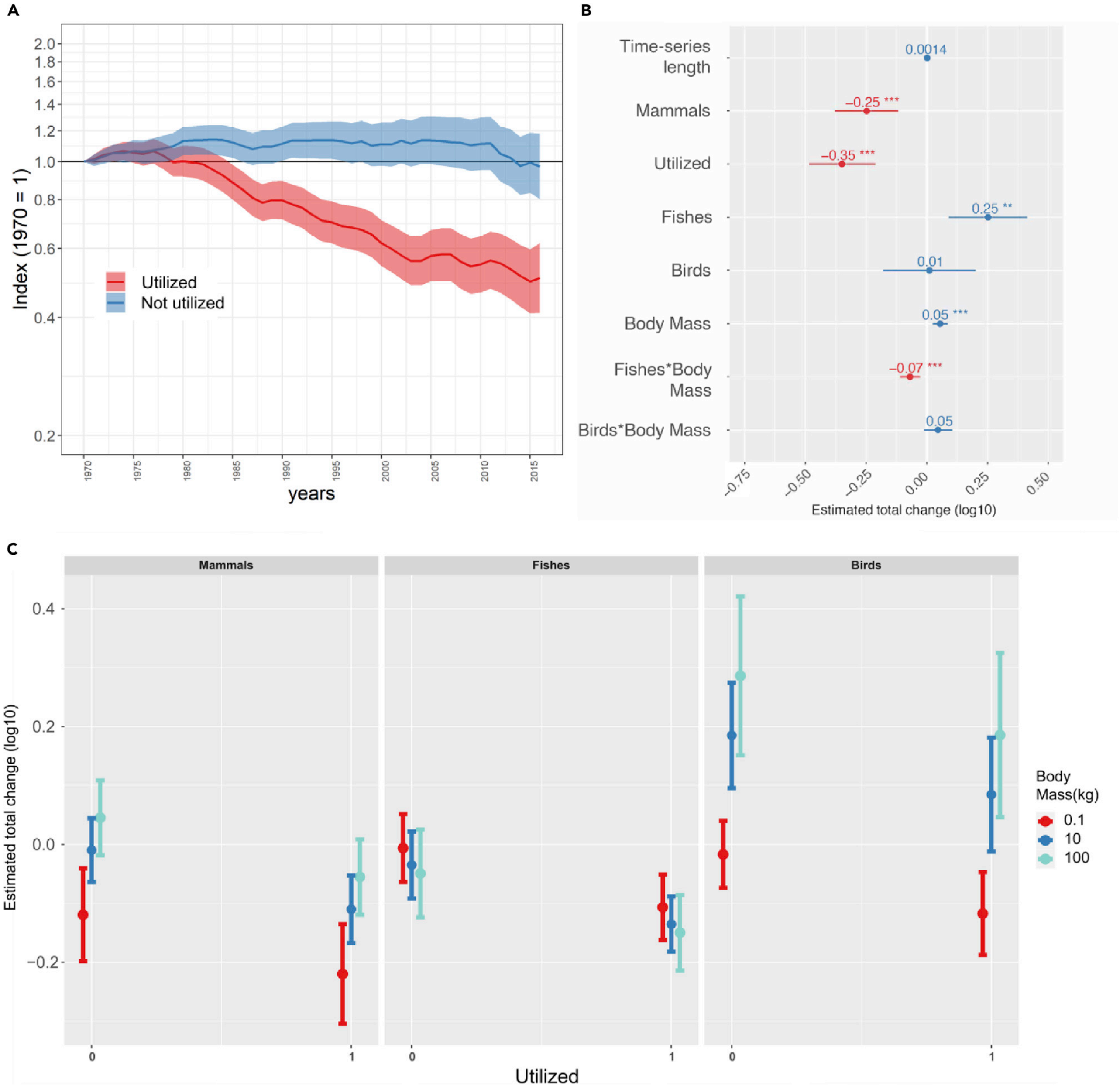

Figure 4. Comparison of trends in utilized and non-utilized populations from 1970 to 2016

The dataset included 2,163 species and 9,284 populations.

(A) Index with 95% CIs of utilized and non-utilized populations for species of birds, mammals, and fish. Between 1970 and 2016, on average, utilized populations had declined by 50% (0.41–0.62), and non-utilized populations had declined by 3% (0.80–1.18).

(B) Estimated overall total change from the best linear mixed-effect model including family, binomial, and location as random effects. Coefficients show the estimated overall change (log10) in each group with 95% CIs. We found no significant interaction between taxonomic group and utilization, with utilized populations of any taxa (Utilized) significantly more likely to be in decline. Larger species tended to be less likely to be in decline, except in fish. where the opposite trend was seen.

(C) Estimated overall population change from the best linear mixed-effect model including family, binomial, and location as random effects. Coefficients show the estimated overall change (log10) for the body mass values 0.1, 10, and 100 kg with 95% CIs, highlighting the impact of the interactions on the estimated response for different body mass values.

See also Tables S5 and S6; Figures S5 and S6.

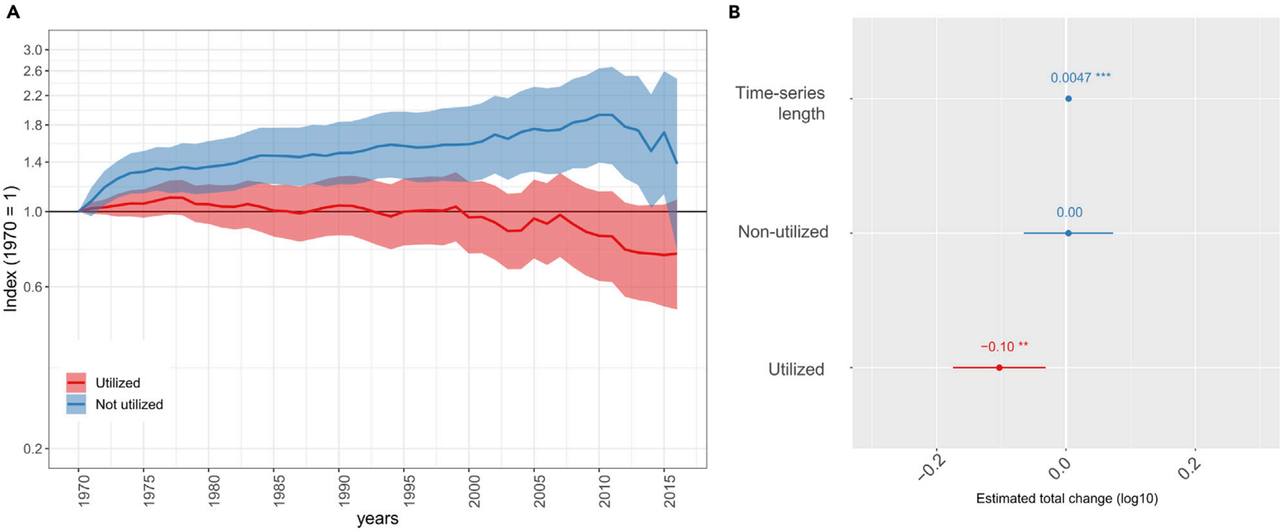

Figure 5. Index of utilized and non-utilized populations for matched species of terrestrial, freshwater, and marine birds, mammals, and fish. (i.e., species that have both utilized and non-utilized populations: 339 species and 4,255 populations)

(A) Index with 95% CIs of utilized and non-utilized populations for matched species of bird, mammals, and fish. Between 1970 and 2016, on average, utilized populations had declined by 25% (0.51–1.09), and non-utilized populations had increased by 138% (0.77–2.46). See also Table S5.

(B) Estimated overall total change from the best linear mixed-effect model including family, binomial, and location as random effects. Coefficients show the estimated overall change (log10) in each group with 95% CIs. Utilized species were more likely to be declining, but the effects of class, body mass, and any interaction were no longer important for explaining trends.

See also Table S8.

transformed after the industrial revolution;[49] after 1970, trends may therefore show less decline as populations stabilize, but at lower numbers.

Data availability was a limitation when assessing trends for Asia Pacific and Africa; for the latter, it was mainly an issue in the later years of the time series. With the analysis conducted at a regional scale, the results may mask the relative differences between countries and even communities.[24] For example, successful examples of conservation and development have been identified in many African countries, particularly those managed by local communities.[25,50] These regional indices therefore have the advantage of providing a large-scale indicator as an overview, but the results do not necessarily represent trends at smaller scales and can hide many local examples of "best-practice." However, the data and method described here are applicable at national and regional levels[51–53] and could be tailored to assess trends in utilized species at difference scales, provided sufficient data are available.

Results in the context of sustainable use and management

Our results show a long-term decline, on average, among utilized populations globally, suggesting that use, overall, is likely unsustainable. This aligns with broad-scale findings of the threat and impacts of utilization on mammals and birds[20,21] and of trends in utilized fish.[22,54] Sustainable use as a tool is harder to analyze explicitly with this dataset because implementation of this as a tool was not recorded; for example, we did not measure whether any initial population decline plateaued when levels of use remained constant. However, utilized populations where use was incentivized for conservation are likely to also be categorized as "managed" because of regulations or guidance to manage the use; for example, populations of the saltwater crocodile (*Crocodylus porosus*) from the Northern Territory of Australia, where controlled harvesting of eggs has been an incentive for its conservation,[55] are coded as utilized and managed in our dataset. Other populations are utilized as a consequence of management through culling; e.g. red deer (*Cervus elaphus*) in Europe. These examples illustrate how the terms "utilized" and "managed" are closely linked, and more work to categorize these terms into types of use and management would aid further interpretation.

Incorporation of management into this analysis introduces important nuance, suggesting that more positive trends are likely when management of utilized species is pursued. Management can take many forms, and utilization itself can be a tool for conservation and human development, providing incentives for habitat and species conservation to support provision of resources for people into the future.[55,56] Establishment of communal conservancies in Namibia has been found to provide dual benefits to the local community from tourism and hunting, especially when these activities occurred in parallel.[57]

Sustainable management has arguably had more focus in the marine realm, which could offer an explanation for the more positive trends seen in the marine indices for Europe, Central Asia, and the Americas. In response to concerns about overfishing, and in light of well-documented cases of fish stock collapse, such as Newfoundland cod[58] and Northeast Atlantic herring,[59] efforts to manage fisheries at national and international levels began to develop in the 1970s and 1980s.[60] Although commercial stocks are often reported as being in decline globally,[54] there are studies that highlight positive trends in stocks, particularly

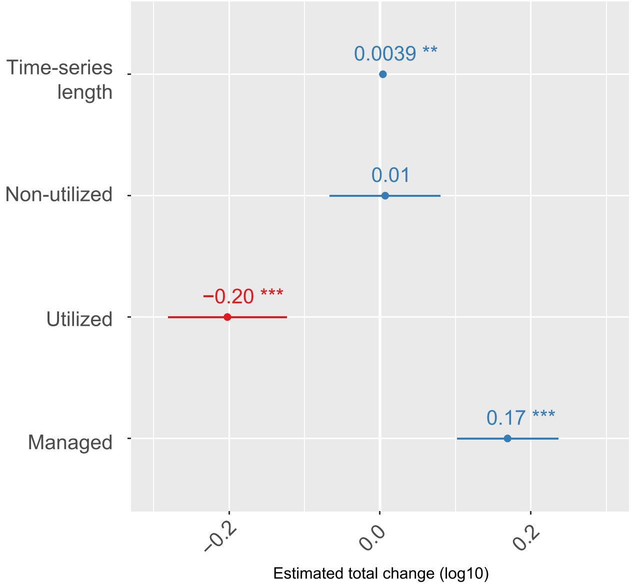

Figure 6. Role of utilization and management together for the matched dataset

For a limited number of species (316 species and 2,867 populations) for which we had information on populations that were managed and unmanaged, we estimated overall total change from the best linear mixed-effect model including family, binomial, and location as random effects. Coefficients show the estimated overall change (log10) in each group with 95% CIs. Utilized populations were more likely to be declining, and populations that were managed were more likely to be increasing.
See also Table S9 and Figure S8.

those that have been intensively managed to avoid overfishing.[23] Our regional results for marine populations reflect some of this disparity because we found average population decline only in Africa and Asia-Pacific, regions where stocks in poor status were found.[23] The Americas, Europe, and Central Asia, which largely include data from the temperate Atlantic and Pacific, fared better, as broadly found in these studies.[23,54] The nature of the global fishing industry means that global management is required for many fish stocks, in particular those outside of national waters. However, for fisheries nearer to coastal communities, management at smaller scales, specifically community co-management, is advocated as a viable and realistic long-term solution for sustainable fishing.[61]

Potential use as an indicator of utilized populations

A key element of the Post-2020 Global Biodiversity Framework (Target 5: ensure that the harvesting, trade and use of wild species is sustainable, legal, and safe for human health[62]) and the Sustainable Development Goals is balancing the sustainable use of Earth's resources with halting the loss of biodiversity. The lack of appropriate indicators on how wildlife is being used has been identified as a critical gap. Our approach presents an advance of our understanding of the role of use in the trend of wildlife. We see three factors that could suggest that our approach could be used as one indicator for sustainable use. First, our index builds on data and methods that are already established in research and policy.[16,35,36,38] Second, using population trend data allows integration of site-level information on the type of utilization and management. Third, abundance trends allow incorporation of sensitivity, meaning that the index can respond quickly to changes in populations.[63] Thus, we believe that the index we present in this paper, based on locally collected data but analyzed using freely available methods that can be applied at national, regional, and global scales, can provide a valuable addition to the indicator dataset available for use in the Post-2020 Global Biodiversity Framework.

A primary shortcoming of this approach concerns the shortage of comprehensive information for all vertebrate groups and the lack of plant or invertebrate data. The dataset behind the index suffers much of the same biases as found in other datasets and indicators,[36,64] with data available for well-studied taxa such as birds and mammals and those of commercial importance, such as fish. Geographic gaps in the data also remain, particularly in South America and Southeast Asia, regions that are hotspots of wildlife trade[65] and of mammals threatened by hunting.[21] Extreme trends and random fluctuations in primary population data can bias the LPI;[44,45] these effects are often associated with temporal gaps in the dataset but can be mitigated by testing the robustness of an index to time series length, as shown in our results. It remains prudent to develop indicators in lieu of comprehensive data, providing that the gaps in data are clear and biases are addressed when feasible.[36,66]

Although population trend is one measure of sustainability, there are other factors that are not considered here and might not be appropriate to aggregate into a global indicator, such as changes in population structure or behavior.[67,68] We also note that we may not be able to attribute the use directly to the trend measured because other drivers could be contributing to any declines and that the non-consumptive component of utilization is not incorporated in this indicator at present. Finally, this index is not able to demonstrate the level of sustainable use and how far beyond this limit current levels of pressure are; i.e., how much would the current use need to be reduced to reverse the decline observed. The human dimension of sustainable use, relating to the needs and benefits of peoples' use of wildlife, is not factored into this analysis but is a fundamental aspect of how sustainably species are used.[1]

Conclusion

Alignment of conservation and human development goals is a challenge, particularly when it comes to sustainable use of resources.[1] Using a large global dataset comprised of site-level data, we added important detail to current knowledge on the status of species in use. The results presented here reveal that globally utilized populations are in decline on average, which presents a risk to the conservation of these species and to people who directly benefit from their use. We found that management of populations has a positive impact, which suggests that this decline can be mitigated with appropriate actions in place to achieve sustainability. With sustainable use, a core component of the Post-2020 Global Biodiversity Framework and the Sustainable Development Goals, indicators are required to monitor progress toward the associated targets; the index presented here can address this need.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, L.M. (louise.mcrae@ioz.ac.uk).

Materials availability

This study did not generate new unique materials.

Data and code availability

The population data used in this paper are stored in the online database at www.livingplanetindex.org. The utilization and management data are not in the public database yet because they are being used in another manuscript. We provided a list of species from each category on our Figshare site (https://doi.org/10.6084/m9.figshare.17085998.v1). Part of the dataset includes confidential data that have been shared under an agreement and are not publicly available. In this case, the species details were anonymized, but the remaining metadata are available. The R package used for LPI analysis is available at https://github.com/Zoological-Society-of-London/rlpi.

Definitions

Three terms used in this paper often have multiple interpretations. These are defined here for clarity.

1. Sustainable use. We refer to the definition from the Convention on Biological Diversity: "the use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining its potential to meet the needs and aspirations of present and future generations".[11]
2. Utilized population. This is the definition used for coding data in the Living Planet Database: a population that is intentionally regularly or systematically utilized, either individuals or eggs. This may be sustainable or unsustainable, and the population does not necessarily have to be threatened by use or overexploited. This refers to consumptive use, where individuals or parts of individuals are removed from the wild. The use may also be a secondary purpose when management, through culling, is the primary aim; e.g., culling to control populations of red deer (*C. elaphus*) in some European countries.
3. Management. This is the definition used for coding data in the Living Planet Database: a population that receives targeted management (e.g., supplementary feeding, reintroduction, sustainable use). This is usually to promote recovery in a population or can incentivize its use for conservation. It can include measures to stem "unsustainable" population growth, so these management activities are not always for the purpose of conservation.

Collection and coding of dataset

Vertebrate population time series data were extracted from the Living Planet Database (LPD),[69] a global repository of annual abundance estimates collated primarily from the scientific literature and online databases.[35,36] The annual abundance measures were collected using a consistent monitoring method in a given and consistent location. The time series vary from 2 to 46 years in terms of length of time frame and in the number of raw annual data points. Units of abundance were population size estimates, densities, or proxies of abundance, such as nests or breeding pairs (see McRae et al.[36] for more details). Alongside the abundance data for each population, several ancillary data fields were extracted to use for summaries, disaggregation, and modeling of the data (Table S10).

The use of species can be consumptive (hunting, fishing, harvesting) or non-consumptive (tourism, cultural experiences, catch-and-release fishing) and for commercial, subsistence, or recreational purposes.[70] The definition of "utilized" in the LPD refers only to consumptive use and does not include non-consumptive use (Table S10). The definition of "management" in the LPD refers to a targeted form of management for a population that may or may not be utilized. We acknowledge that utilization can be deployed as a form of management, and these terms may not be seen as distinct; however, this does not impact the analysis we conduct here because the two categories still allow us to differentiate between populations that are utilized and under management and those that are utilized and unmanaged. If a population is utilized as a form of management, then it will be tagged as "utilized" and "managed" because both terms apply. Not all populations that are "managed" are also "utilized." For example, some populations are managed for some other purpose; e.g., provision of nest boxes for a species whose nesting habitat has been degraded.

We also incorporated species body size into the analysis because it can be an important factor in predicting species trends,[71] especially when related to use.[19] We used body mass data collated from sources listed in Table S12, according to the method detailed in Noviello et al.[72] Body mass values were log10 transformed and used as a continuous predictor variable in the mixed models.

Index calculation

Using the R package rlpi (https://github.com/Zoological-Society-of-London/rlpi) and following the Generalized Additive Modeling framework in Collen et al.,[35] we calculated global and regional indices of abundance for populations that were utilized and populations that were not. For the global and regional indices of utilized populations, we divided the dataset into terrestrial, freshwater, and marine populations. This was to show a marine- and land-based comparison because many freshwater species, with the exception of fish, are not freshwater obligates, and combining them with terrestrial species was more appropriate. We explored the influence of marine populations on the trends later in the analysis. IPBES regions were chosen to divide the datasets to allow the information to be used in the IPBES sustainable use assessment and future thematic assessments. Because marine areas beyond national jurisdiction and Antarctica lie outside IPBES regions, 248 populations from the dataset from these areas were not included in the regional analysis. The indices were calculated for different subsets of the data (Table S11). The subset of species in the dataset with data for both utilized and non-utilized populations are referred to as "matched" species (Figure S7).

The finer-scale subregional analysis was conducted for three subregions: Southern Africa, Central and Western Europe, and North America. Wildlife management in these subregions has arguably been more widespread, so a comparison with the wider regional trends is of interest.

The baseline year set for the index was 1970, and it was run until 2016 because data availability decreases beyond this year as a result of the publication time lag. Each population trend carried equal weight within each species, and each species trend carried equal weight within each index. We did not incorporate any diversity weighting by taxa and regional species richness, as done for the global LPI,[36] because the species richness for utilized species only is not known, and we assume that the numbers may not necessarily be proportional to overall species richness across regions and terrestrial, freshwater, and marine habitats This means that indices produced here are not directly comparable with the global LPI because of the difference in weightings used. The confidence intervals were calculated using bootstrap resampling of 10,000 iterations to indicate variability in the underlying species trends.[35]

Mixed models

We considered how total population abundance change (T_lambda, cumulative year-on-year population change at the end of the time series) varied in response to utilization (Utilized) and body mass (Body Mass) for different taxonomic groups (Class: Mammalia, Aves, Fish). Time-series length, the number of years between the first and last population measure, was included to understand whether longer population trends tended to reflect more positive or negative overall change. Taxonomic and site effects were accounted for by including a random intercept for family, binomial (genus and species) and population location. T_lambda values were taken from the rlpi package, which generates a matrix of annual rates of change for each population. The annual rates were summed to give a logged value of total change in abundance for each population. The most complex/maximal model we considered therefore included Utilization, Class, and Body Mass all interacting. We compared this with a null model and with simpler models using Akaike information criterion (AIC). See Tables S6–S9 for a full model selection table comparing AIC values for each model. Here we reported models with the lowest AIC. Other models may have similar (e.g. <2 AIC) scores, in which case we report the simplest model (which, in our results, were also the top models). To manipulate data, construct models, compare their performance, and visualize their coefficients, we used the following packages: plyr,[73] dplyr,[74] lme4,[75] performance,[76] and sjPlot.[77]

We also explored how including marine populations affected our results (Table S7). Finally, for a subset of these populations, we also have information on whether they are subject to some form of management. We therefore assess a second series of models including Management as an additional explanatory factor (Table S9).

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2022.03.014.

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AUTHOR CONTRIBUTIONS

Conceptualization, all authors; data curation, L.M. and R.F.; formal analysis, L.M. and R.F.; funding acquisition, N.D.B; writing – original draft, L.M.; writing – review & editing, all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

1. Hutton, J.M., and Leader-Williams, N. (2003). Sustainable use and incentive-driven conservation: realigning human and conservation interests. Oryx *37*, 215–226. https://doi.org/10.1017/s0030605303000395.
2. Díaz, S., Demissew, S., Carabias, J., Joly, C., Lonsdale, M., Ash, N., Larigauderie, A., Adhikari, J.R., Arico, S., Báldi, A., et al. (2015). The IPBES Conceptual Framework — connecting nature and people. Curr. Opin. Environ. Sustain. *14*, 1–16. https://doi.org/10.1016/j.cosust.2014.11.002.
3. Bongaarts, J. (2019). IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Popul. Dev. Rev. *45*, 680–681. https://doi.org/10.1111/padr.12283.
4. Alves, R.R.N., and Albuquerque, U.P. (2018). Chapter 1 - introduction: animals in our lives. In Ethnozoology, R.R. Nóbrega Alves and U.P. Albuquerque, eds. (Academic Press), pp. 1–7. https://doi.org/10.1016/B978-0-12-809913-1.00001-6.
5. Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Brauman, K.A., et al. (2018). Assessing nature's contributions to people. Science *359*, 270–272. https://doi.org/10.1126/science.aap8826.
6. Cooney, R., Roe, D., Dublin, H., and Booker, F. (2018). Wild Life, Wild Livelihoods: Involving Communities in Sustainable Wildlife Management and Combatting the Illegal Wildlife Trade (United Nations Environment Programme). http://wedocs.unep.org/bitstream/handle/20.500.11822/22864/WLWL_Report_web.pdf.
7. Pascual, U., Balvanera, P., Díaz, S., Pataki, G., Roth, E., Stenseke, M., Watson, R.T., Başak Dessane, E., Islar, M., Kelemen, E., et al. (2017). Valuing nature's contributions to people: the IPBES approach. Curr. Opin. Environ. Sustain. *26-27*, 7–16. https://doi.org/10.1016/j.cosust.2016.12.006.
8. Golden, C.D., Allison, E.H., Cheung, W.W.L., Dey, M.M., Halpern, B.S., McCauley, D.J., Smith, M., Vaitla, B., Zeller, D., and Myers, S.S. (2016). Nutrition: fall in fish catch threatens human health. Nature *534*, 317–320. https://doi.org/10.1038/534317a.
9. Ingram, D.J., Coad, L., Milner-Gulland, E.J., Parry, L., Wilkie, D., Bakarr, M.I., Benítez-López, A., Bennett, E.L., Bodmer, R., Cowlishaw, G., et al. (2021). Wild meat is still on the menu: progress in wild meat research, policy, and practice from 2002 to 2020. Annu. Rev. Environ. Resour. *46*, 221–254. https://doi.org/10.1146/annurev-environ-041020-063132.
10. Booth, H., Clark, M., Milner-Gulland, E.J., Amponsah-Mensah, K., Antunes, A.P., Brittain, S., Castilho, L.C., Campos-Silva, J.V., Constantino, P.d.A.L., Li, Y., et al. (2021). Investigating the risks of removing wild meat from global food systems. Curr. Biol. *31*, 1788–1797.e1783. https://doi.org/10.1016/j.cub.2021.01.079.
11. United Nations (1992). Convention on Biological Diversity (United Nations).
12. Hickey, M.J. (1998). Acceptance of sustainable use within the CITES community. Vt. Law Rev. *23*, 861.
13. IUCN (2000). The IUCN Policy Statement on Sustainable Use of Wild Living Resources (IUCN).
14. United Nations General Assembly (2015). Transforming Our World: The 2030 Agenda for Sustainable Development (United Nations General Assembly).
15. IPBES (2018). Report of the Plenary of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on the Work of its Sixth Session (IPBES).
16. (2020). Secretariat of the convention on biological diversity. Glob. Biodivers. Outlook *5*.
17. Marsh, S.M.E., Hoffmann, M., Burgess, N.D., Brooks, T.M., Challender, D.W.S., Cremona, P.J., Hilton-Taylor, C., de Micheaux, F.L., Lichtenstein, G., Roe, D., and Böhm, M. (2021). Prevalence of sustainable and unsustainable use of wild species inferred from the IUCN Red List of Threatened Species. Conserv. Biol. https://doi.org/10.1111/cobi.13844.
18. Harfoot, M.B.J., Johnston, A., Balmford, A., Burgess, N.D., Butchart, S.H.M., Dias, M.P., Hazin, C., Hilton-Taylor, C., Hoffmann, M., Isaac, N.J.B., et al. (2021). Using the IUCN Red List to map threats to terrestrial vertebrates at global scale. Nat. Ecol. Evol. *5*, 1510–1519. https://doi.org/10.1038/s41559-021-01542-9.
19. Gallego-Zamorano, J., Benítez-López, A., Santini, L., Hilbers, J.P., Huijbregts, M.A.J., and Schipper, A.M. (2020). Combined effects of land use and hunting on distributions of tropical mammals. Conserv. Biol. *34*, 1271–1280. https://doi.org/10.1111/cobi.13459.
20. Benítez-López, A., Alkemade, R., Schipper, A.M., Ingram, D.J., Verweij, P.A., Eikelboom, J.A.J., and Huijbregts, M.A.J. (2017). The impact of hunting on tropical mammal and bird populations. Science *356*, 180–183. https://doi.org/10.1126/science.aaj1891.
21. Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P.A., Macdonald, D.W., Machovina, B., et al. (2016). Bushmeat hunting and extinction risk to the world's mammals. R. Soc. Open Sci. *3*, 160498. https://doi.org/10.1098/rsos.160498.
22. FAO (2020). The State of World Fisheries and Aquaculture 2020. Sustainability in Action (FAO).
23. Hilborn, R., Amoroso, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., de Moor, C.L., Faraj, A., Hively, D., Jensen, O.P., et al. (2020). Effective fisheries management instrumental in improving fish stock status. Proc. Natl. Acad. Sci. U S A *117*, 2218–2224. https://doi.org/10.1073/pnas.1909726116.
24. Anderson, J., and Mehta, S.. Global assessment of community based natural resource management: addressing the critical challenges of the rural

sector. https://rmportal.net/library/content/global-assessment-cbnrm-challenges-rural-sector/at_download/file.

25. Roe, D., Nelson, F., and Sandbrook, C. (2009). Community Management of Natural Resources in Africa: Impacts, Experiences and Future Directions (International Institute for Environment and Development).
26. Ceballos, G., and Ehrlich, P.R. (2002). Mammal population losses and the extinction crisis. Science *296*, 904–907. https://doi.org/10.1126/science.1069349.
27. Laliberte, A.S., and Ripple, W.J. (2004). Range contractions of North American carnivores and ungulates. Bioscience *54*, 123–138. https://doi.org/10.1641/0006-3568(2004)054[0123:rconac]2.0.co;2.
28. Deinet, S., Ieronymidou, C., McRae, L., Burfield, I.J., Foppen, R.P., Collen, B., et al. (2013). Wildlife Comeback in Europe: The Recovery of Selected Mammal and Bird Species (London, UK: Zoological Society of London).
29. Sanderson, E.W., Redford, K.H., Weber, B., Aune, K., Baldes, D., Berger, J., Carter, D., Curtin, C., Derr, J., Dobrott, S., et al. (2008). The ecological future of the North American Bison: conceiving long-term, large-scale conservation of wildlife. Conserv. Biol. *22*, 252–266. https://doi.org/10.1111/j.1523-1739.2008.00899.x.
30. Butchart, S.H.M. (2008). Red list indices to measure the sustainability of species use and impacts of invasive alien species. Bird Conserv. Int. *18*, S245–S262. https://doi.org/10.1017/s095927090800035x.
31. Tierney, M., Almond, R., Stanwell-Smith, D., McRae, L., Zöckler, C., Collen, B., Walpole, M., Hutton, J., and de Bie, S. (2014). Use it or lose it: measuring trends in wild species subject to substantial use. Oryx *48*, 420–429. https://doi.org/10.1017/s0030605313000653.
32. Di Minin, E., Brooks, T.M., Toivonen, T., Butchart, S.H.M., Heikinheimo, V., Watson, J.E.M., Burgess, N.D., Challender, D.W.S., Goettsch, B., Jenkins, R., and Moilanen, A. (2019). Identifying global centers of unsustainable commercial harvesting of species. Sci. Adv. *5*, eaau2879. https://doi.org/10.1126/sciadv.aau2879.
33. Salo, M., Sirén, A., and Kalliola, R. (2013). Diagnosing Wild Species Harvest: Resource Use and Conservation (Academic Press).
34. Loh, J., Green, R.E., Ricketts, T., Lamoreux, J., Jenkins, M., Kapos, V., and Randers, J. (2005). The Living Planet Index: using species population time series to track trends in biodiversity. Philos. Trans. R. Soc. B: Biol. Sci. *360*, 289–295. https://doi.org/10.1098/rstb.2004.1584.
35. Collen, B., Loh, J., Whitmee, S., Mcrae, L., Amin, R., and Baillie, J.E.M. (2009). Monitoring change in vertebrate abundance: the living Planet index. Conserv. Biol. *23*, 317–327. https://doi.org/10.1111/j.1523-1739.2008.01117.x.
36. McRae, L., Deinet, S., and Freeman, R. (2017). The diversity-weighted living Planet index: controlling for taxonomic bias in a global biodiversity indicator. PLoS One *12*, e0169156. https://doi.org/10.1371/journal.pone.0169156.
37. Butchart, S.H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J.P., Almond, R.E., Baillie, J.E., Bomhard, B., Brown, C., and Bruno, J. (2010). Global biodiversity: indicators of recent declines. Science *328*, 1164–1168.
38. Tittensor, D.P., Walpole, M., Hill, S.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H., Leadley, P.W., Regan, E.C., and Alkemade, R. (2014). A mid-term analysis of progress toward international biodiversity targets. Science *346*, 241–244.
39. Green, E.J., McRae, L., Freeman, R., Harfoot, M.B.J., Hill, S.L.L., Baldwin-Cantello, W., and Simonson, W.D. (2020). Below the canopy: global trends in forest vertebrate populations and their drivers. Proc. R. Soc. B Biol. Sci. *287*, 20200533. https://doi.org/10.1098/rspb.2020.0533.
40. Collen, B., McRae, L., Deinet, S., Palma, A.D., Carranza, T., Cooper, N., Loh, J., and Baillie, J.E.M. (2011). Predicting how populations decline to extinction. Philos. Trans. R. Soc. B Biol. Sci. *366*, 2577–2586. https://doi.org/10.1098/rstb.2011.0015.
41. Hardesty-Moore, M., Deinet, S., Freeman, R., Titcomb, G.C., Dillon, E.M., Stears, K., Klope, M., Bui, A., Orr, D., Young, H.S., et al. (2018). Migration in the Anthropocene: how collective navigation, environmental system and taxonomy shape the vulnerability of migratory species. Philos. Trans. R. Soc. B Biol. Sci. *373*, 20170017. https://doi.org/10.1098/rstb.2017.0017.
42. IPBES Technical Support Unit on Knowledge and Data (2020). IPBES regions and sub-regions (1.1). Zenodo https://doi.org/10.5281/zenodo.3928281
43. Wauchope, H.S., Amano, T., Sutherland, W.J., and Johnston, A. (2019). When can we trust population trends? A method for quantifying the effects of sampling interval and duration. Methods Ecol. Evol. *10*, 2067–2078. https://doi.org/10.1111/2041-210x.13302.
44. Leung, B., Hargreaves, A.L., Greenberg, D.A., McGill, B., Dornelas, M., and Freeman, R. (2020). Clustered versus catastrophic global vertebrate declines. Nature *588*, 267–271.
45. Buschke, F.T., Hagan, J.G., Santini, L., and Coetzee, B.W. (2021). Random population fluctuations bias the living Planet index. Nat. Ecol. Evol. *5*, 1145–1152.
46. Stanford, C.B., Iverson, J.B., Rhodin, A.G.J., Paul van Dijk, P., Mittermeier, R.A., Kuchling, G., Berry, K.H., Bertolero, A., Bjorndal, K.A., Blanck, T.E.G., et al. (2020). Turtles and tortoises are in trouble. Curr. Biol. *30*, R721–R735. https://doi.org/10.1016/j.cub.2020.04.088.
47. Papworth, S.K., Rist, J., Coad, L., and Milner-Gulland, E.J. (2009). Evidence for shifting baseline syndrome in conservation. Conserv. Lett. *2*, 93–100.
48. Collins, A.C., Böhm, M., and Collen, B. (2020). Choice of baseline affects historical population trends in hunted mammals of North America. Biol. Conserv. *242*, 108421. https://doi.org/10.1016/j.biocon.2020.108421.
49. Ellis, E.C., Klein Goldewijk, K., Siebert, S., Lightman, D., and Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. Glob. Ecol. Biogeogr. *19*, 589–606. https://doi.org/10.1111/j.1466-8238.2010.00540.x.
50. Hughes, O., Roe, D., Thomas, D.H., Kabihogo, B., Kuria, D.K., Ligare, J.I., Nyiratuza, M., and Amooti, T.J. (2014). Getting it Together. How Some Local Organisations in East Africa Have Succeeded in Linking Conservation and Development (JSTOR).
51. McRae, L., Böhm, M., Deinet, S., Gill, M., and Collen, B. (2012). The Arctic Species Trend Index: using vertebrate population trends to monitor the health of a rapidly changing ecosystem. Biodiversity *13*, 144–156. https://doi.org/10.1080/14888386.2012.705085.
52. WWF-Canada (2020). Living Planet Report Canada: Wildlife at Risk (World Wildlife Fund Canada).
53. Marconi, V., McRae, L., Müller, H., Currie, J., Whitmee, S., Gadallah, F., and Freeman, R. (2021). Population declines among Canadian vertebrates: but data of different quality show diverging trends. Ecol. Indicat. *130*, 108022. https://doi.org/10.1016/j.ecolind.2021.108022.
54. Palomares, M.L.D., Froese, R., Derrick, B., Meeuwig, J.J., Nöel, S.L., Tsui, G., Woroniak, J., Zeller, D., and Pauly, D. (2020). Fishery biomass trends of exploited fish populations in marine ecoregions, climatic zones and ocean basins. Estuarine. Coastal Shelf Sci. *243*, 106896. https://doi.org/10.1016/j.ecss.2020.106896.
55. Fukuda, Y., Webb, G., Manolis, C., Delaney, R., Letnic, M., Lindner, G., and Whitehead, P. (2011). Recovery of saltwater crocodiles following unregulated hunting in tidal rivers of the Northern Territory, Australia. J. Wildl. Manag. *75*, 1253–1266. https://doi.org/10.1002/jwmg.191.
56. Lichtenstein, G. (2009). Vicuña conservation and poverty alleviation? Andean communities and international fibre markets. Int. J. Commons *4*, 100–121. https://doi.org/10.18352/ijc.139.
57. Naidoo, R., Weaver, L.C., Diggle, R.W., Matongo, G., Stuart-Hill, G., and Thouless, C. (2016). Complementary benefits of tourism and hunting to communal conservancies in Namibia. Conserv. Biol. *30*, 628–638. https://doi.org/10.1111/cobi.12643.
58. Hutchings, J.A., and Myers, R.A. (1994). What can be learned from the collapse of a renewable resource? Atlantic cod, Gadus morhua, of Newfoundland and labrador. Can. J. Fish. Aquat. Sci. *51*, 2126–2146. https://doi.org/10.1139/f94-214.

59. Dickey-Collas, M., Nash, R.D.M., Brunel, T., van Damme, C.J.G., Marshall, C.T., Payne, M.R., Corten, A., Geffen, A.J., Peck, M.A., Hatfield, E.M.C., et al. (2010). Lessons learned from stock collapse and recovery of North Sea herring: a review. ICES J. Mar. Sci. *67*, 1875–1886. https://doi.org/10.1093/icesjms/fsq033.

60. Sissenwine, M.M., Mace, P.M., and Lassen, H.J. (2014). Preventing overfishing: evolving approaches and emerging challenges. ICES J. Mar. Sci. *71*, 153–156. https://doi.org/10.1093/icesjms/fst236.

61. Gutiérrez, N.L., Hilborn, R., and Defeo, O. (2011). Leadership, social capital and incentives promote successful fisheries. Nature *470*, 386–389. https://doi.org/10.1038/nature09689.

62. CBD (2021). First draft of the post-2020 global biodiversity framework (CBD), CBD/WG2020/3/3, issued 5 July 2021.

63. Santini, L., Belmaker, J., Costello, M.J., Pereira, H.M., Rossberg, A.G., Schipper, A.M., Ceaușu, S., Dornelas, M., Hilbers, J.P., Hortal, J., et al. (2017). Assessing the suitability of diversity metrics to detect biodiversity change. Biol. Conserv. *213*, 341–350. https://doi.org/10.1016/j.biocon.2016.08.024.

64. Proença, V., Martin, L.J., Pereira, H.M., Fernandez, M., McRae, L., Belnap, J., Böhm, M., Brummitt, N., García-Moreno, J., Gregory, R.D., et al. (2017). Global biodiversity monitoring: from data sources to essential biodiversity variables. Biol. Conserv. *213*, 256–263. https://doi.org/10.1016/j.biocon.2016.07.014.

65. Scheffers, B.R., Oliveira, B.F., Lamb, I., and Edwards, D.P. (2019). Global wildlife trade across the tree of life. Science *366*, 71–76. https://doi.org/10.1126/science.aav5327.

66. Jones, J.P., Collen, B., Atkinson, G., Baxter, P.W., Bubb, P., Illian, J.B., Katzner, T.E., Keane, A., Loh, J., and Mcdonald-Madden, E. (2011). The why, what, and how of global biodiversity indicators beyond the 2010 target. Conserv. Biol. *25*, 450–457.

67. Garel, M., Cugnasse, J.-M., Maillard, D., Gaillard, J.-M., Hewison, A.M., and Dubray, D. (2007). Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. Ecol. Appl. *17*, 1607–1618.

68. Ciuti, S., Muhly, T.B., Paton, D.G., McDevitt, A.D., Musiani, M., and Boyce, M.S. (2012). Human selection of elk behavioural traits in a landscape of fear. Proc. R. Soc. B Biol. Sci. *279*, 4407–4416.

69. WWF/ZSL (2020). Living Planet Database (WWF/ZSL).

70. Sustainable Use and Livelihoods Specialist Group (2020). Sustainable Use of Wild Species. A Critical Element of Conservation and Rural LivelihoodsIUCN & SULIhttps://iucnsuli.org/wp-content/uploads/2020/03/webSULIbrochure.pdf

71. Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., and Collen, B. (2014). Defaunation in the anthropocene. Science *345*, 401–406. https://doi.org/10.1126/science.1251817.

72. Noviello, N., McRae, L., Freeman, R., and Clements, C. (2020). Body mass and latitude predict the presence of multiple stressors in global vertebrate populations. Preprint at bioRxiv. https://doi.org/10.1101/2020.12.17.423192.

73. Wickham, H. (2011). The split-apply-combine strategy for data analysis. J. Stat. Softw. *40*, 1–29.

74. Wickham, H., François, R., Henry, L., and Müller, K. (2020). Dplyr: A Grammar of Data Manipulation. The Comprehensive R Archive Network https://CRAN.R-project.org/package=dplyr.

75. Bates, D., Mächler, M., Bolker, B., and Walker, S. (2014). Fitting linear mixed-effects models using lme4. Preprint at arXiv. 1406.5823. https://doi.org/10.48550/arXiv.1406.5823.

76. Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., and Makowski, D. (2021). Performance: an R package for assessment, comparison and testing of statistical models. J. Open Source Softw. *6*, 3139.

77. Lüdecke, D. (2021). sjPlot: Data Visualization for Statistics in Social Science. The Comprehensive R Archive Network https://CRAN.R-project.org/package=sjPlot.

One Earth, Volume *5*

Supplemental information

A global indicator of utilized wildlife populations: Regional trends and the impact of management

Louise McRae, Robin Freeman, Jonas Geldmann, Grace B. Moss, Louise Kjær-Hansen, and Neil D. Burgess

Table S1 Number of species and populations in the LPD by Class, system and utilized status

		Species		Populations	
		Utilized	Not utilized	Utilized	Not utilized
Birds	**Freshwater**	69	154	80	310
	Marine	15	189	39	707
	Terrestrial	60	442	212	849
	total	**144**	**785**	**331**	**1866**
Mammals	**Freshwater**	11	15	129	49
	Marine	27	55	76	211
	Terrestrial	164	356	1893	802
	total	**202**	**426**	**2098**	**1062**
Reptiles	**Freshwater**	25	31	66	59
	Marine	6	14	68	80
	Terrestrial	4	144	8	212
	total	**35**	**189**	**142**	**351**
Amphibians	**Freshwater**	3	81	4	154
	Terrestrial	2	93	3	149
	total	**5**	**174**	**7**	**303**
Fish	**Freshwater**	276	113	728	233
	Marine	713	404	2505	1497
	total	**989**	**517**	**3233**	**1730**

Table S2 Number of populations in each IPBES region

IPBES region	**Utilized**	**Not utilized**
Africa	446	396
Americas	2489	2729
Asia-Pacific	635	949
Europe-Central Asia	2138	1093

Table S3 Number of populations with population-level threat information

Population threat status	**Utilized**	**Not utilized**
No threats	390	1065
Threatened	1694	1501
Unknown (large data set)	1475	1386
Unknown (no information)	2252	1360

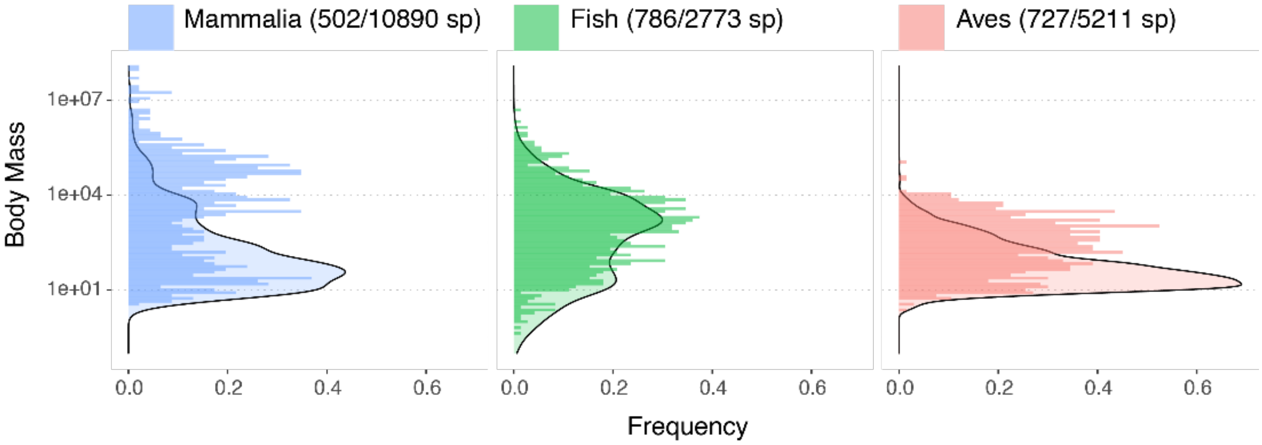

Figure S1. Mass of study species vs. species for which mass data was available. Bar plots show distribution of mass for study species, while density plot (black outline with shaded fill) shows distribution for all species. Species mass data from Noviello et al. (see Table S12). Titles for taxonomic groups show number of species in study vs. number of species for which mass data was available.

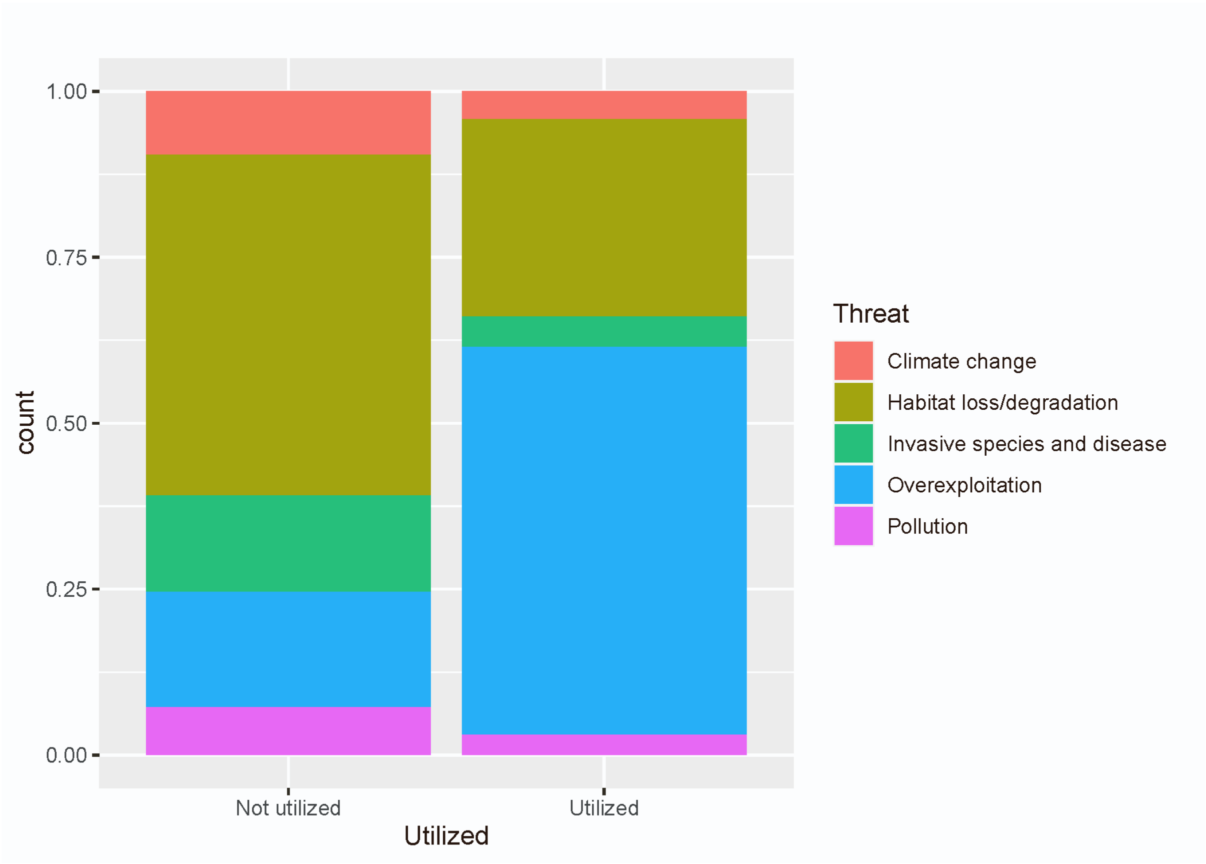

Figure S2. Recorded threats to populations. Utilized populations that face a threat can be threatened by pressures other than use as shown here; however, the most recorded threat for utilized populations was Overexploitation. Populations that are not utilized faced habitat loss and degradation as the most recorded threat and they can still be threatened by exploitation e.g. indirect killing, persecuted as a pest

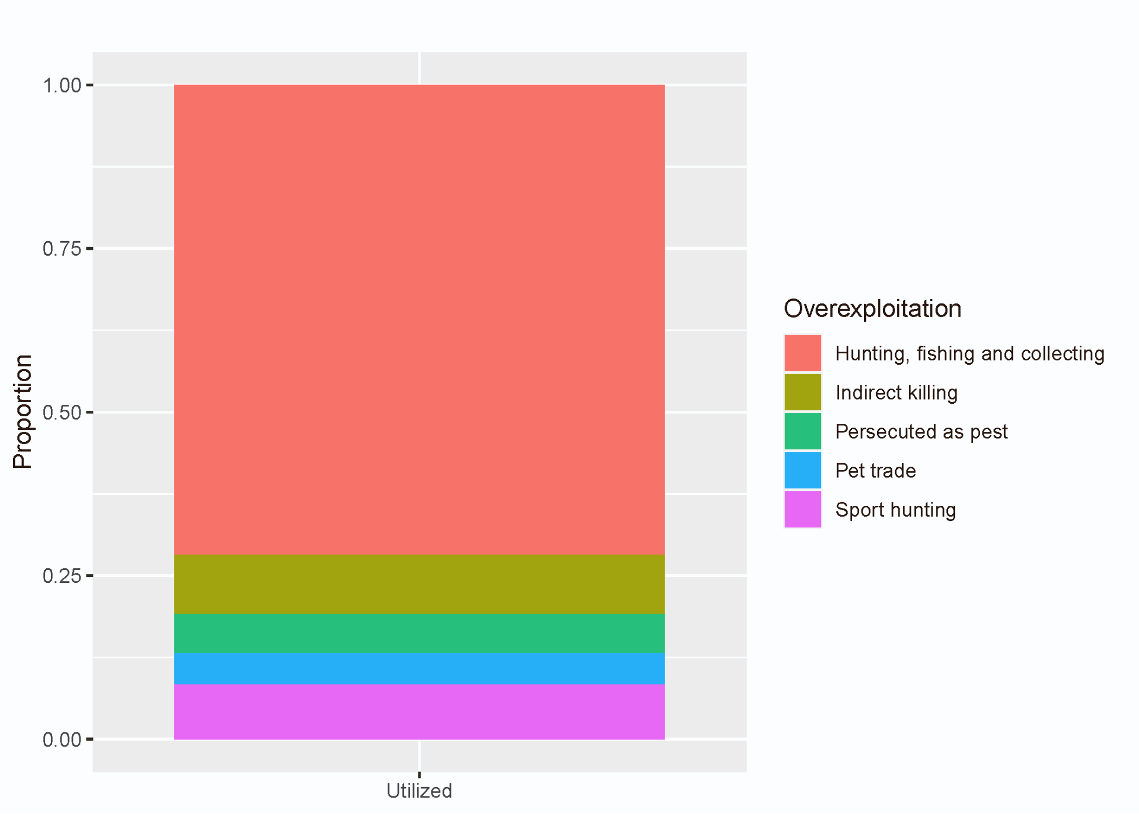

Figure S3 Recorded categories for populations threatened by Overexploitation

Table S4 Number of populations with management information

Managed population	**Utilized**	**Not utilized**
No	1329	2902
Yes	2671	704
Unknown	1811	1706

Table S5 – Final Index values for Indices presented in main text, Related to Figure 2, 3, 4 and 5. For each trend the final index value (2016) is shown with the calculated lower and upper 95% bounds of that value from bootstrapping.

Name	Final Value (2016)	Lower	Upper
Global Utilized (TFW)	0.31	0.21	0.44
Global Utilized (Marine)	0.66	0.52	0.85
Africa (TFW)	0.07†	0.03	0.16
Africa (Marine)	0.08††	0.04	0.17
Europe and Central Asia (TFW)	0.76	0.43	1.30
Europe and Central Asia (Marine)	1.41	0.95	2.13
Asia Pacific (TFW)	1.07	0.31	3.76
Asia Pacific (Marine)	0.17	0.09	0.31
Americas (TFW)	0.33	0.19	0.58
Americas (Marine)	1.07	0.78	1.45
Utilized Populations (Birds, Mammals, Fish)	0.50	0.41	0.62
Non-utilized populations (Birds, Mammals, Fish)	0.97	0.80	1.18
Utilized Populations (TFW) > 5 years	0.31	0.22	0.45
Utilized Populations (Marine) > 5 years	0.71	0.56	0.90
Utilized Populations (TFW) > 10 years	0.46	0.34	0.62
Utilized Populations (Marine) > 10 years	0.83	0.66	1.05
Utilized Populations (Birds, Mammals, Fish; TFW)	0.33	0.22	0.50
Non-utilized populations (Birds, Mammals, Fish; TFW)	0.81	0.65	1.01
Utilized Populations (Birds, Mammals, Fish; Matched Species)	0.75	0.51	1.09
Non-utilized populations (Birds, Mammals, Fish; Matched Species)	1.38	0.77	2.46

† 2015 value due to lack of later data; †† 2013 value due to lack of later data

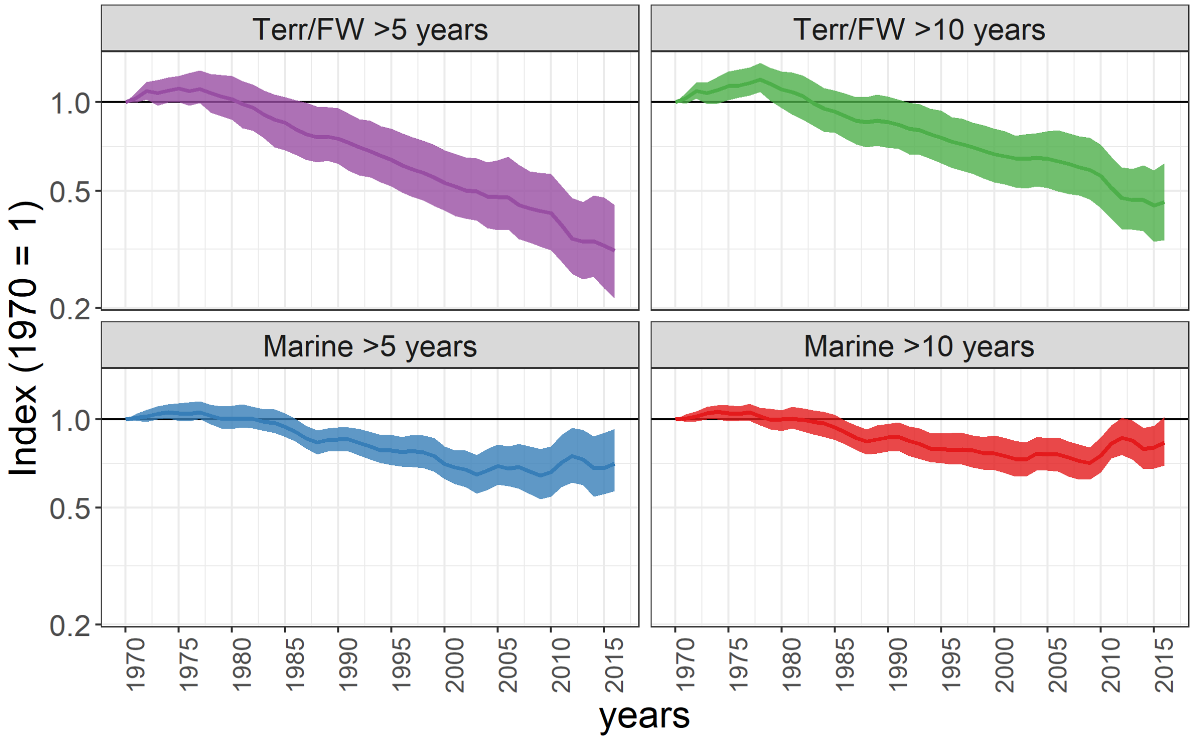

Figure S4 Effect of time-series length on index of utilized populations, related to Figure 2. Indices with 95% confidence intervals of utilized populations of terrestrial/freshwater (Terr/FW, upper) or marine (lower) for different subsets of data which only include time series that span more than 5 years (>5) or more than 10 years (>10). Terr/FW >5 years (nspp = 496, npop = 2,599), Terr/FW >10 years (nspp = 366, npop = 2,131), Marine >5 years (nspp = 707, npop = 2,338), Marine >10 years (nspp = 639, npop = 1,999). See Table S5 for final values and confidence intervals.

Table S6. AIC values and model details for models including marine populations. Related to Figure 4B

9284 Populations of 2163 Species in 421 Families across 3144 locations

Name	Fixed effects	Random Effects	AIC	ΔAIC	AIC weights	R2 (cond.)	R2 (marg.)
m1_sum_nointer_bm_inter	TS_length + Utilized + Class * log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	18475.848	0	0.748	0.271	0.017
m1_sum_full	TS_length + Utilized * Class * log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	18478.041	2.193	0.25	0.271	0.019
m1_sum_utilized_inter_bm	TS_length + Class + Utilized * log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	18488.543	12.695	0.001	0.273	0.012
m1_sum_additive_bm	TS_length + Utilized + Class + log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	18491.273	15.425	< 0.001	0.274	0.011
m1_sum_noclass_bm	TS_length + Utilized + log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	18493.596	17.748	< 0.001	0.272	0.007
m1_sum_bm	TS_length + Utilized * Class + log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	18493.673	17.825	< 0.001	0.274	0.011
m1_sum_noclass	TS_length + Utilized	(1 | Family/Binomial) + (1 | pop_loc)	18496.814	20.966	< 0.001	0.273	0.006
m1_sum_additive	TS_length + Utilized + Class	(1 | Family/Binomial) + (1 | pop_loc)	18497.316	21.468	< 0.001	0.274	0.009
m1_sum_inter	TS_length + Utilized * Class	(1 | Family/Binomial) + (1 | pop_loc)	18499.485	23.637	< 0.001	0.273	0.009
m1_sum_noutil_bm	TS_length + Class + log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	18510.148	34.3	< 0.001	0.274	0.007
m1_sum_noutil	TS_length + Class	(1 | Family/Binomial) + (1 | pop_loc)	18512.434	36.586	< 0.001	0.274	0.005
m1_sum_null	TS_length	(1 | Family/Binomial) + (1 | pop_loc)	18532.587	56.739	< 0.001	0.274	5.85E-05

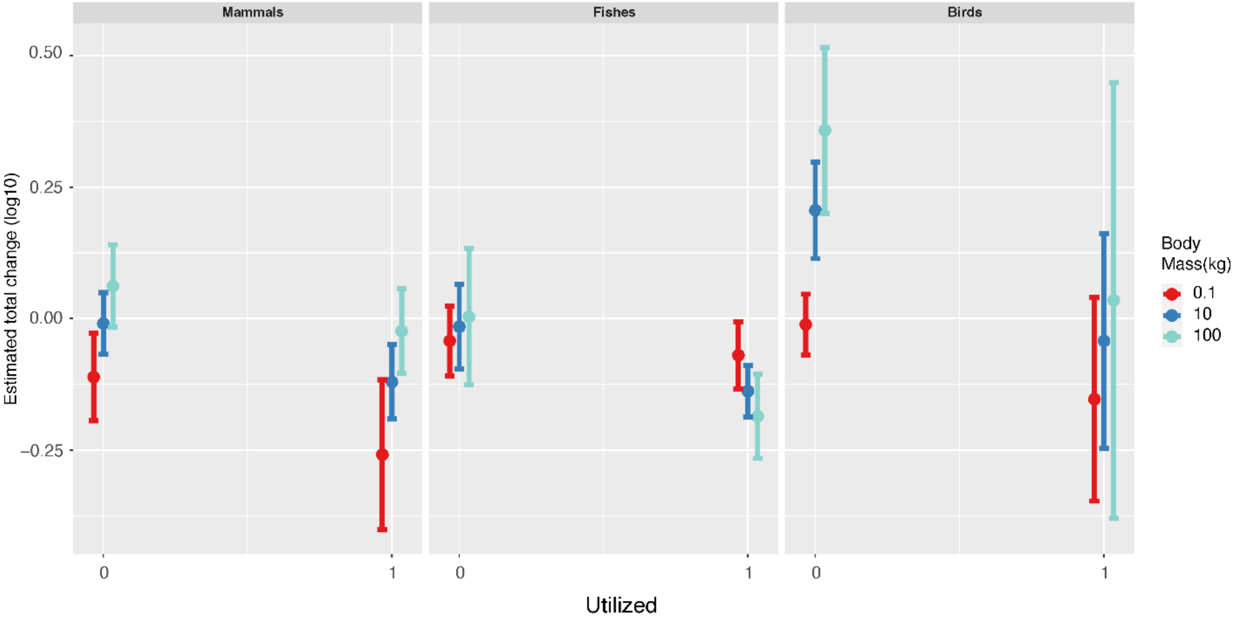

Figure S5 Predicted overall population change (log10) with 95% confidence intervals for the full model. The relationship with body size is reversed for non-utilized fish populations compared to the top model. Relationships with other taxa remain the same. Related to Figure 4B, Figure 4C and Table S6

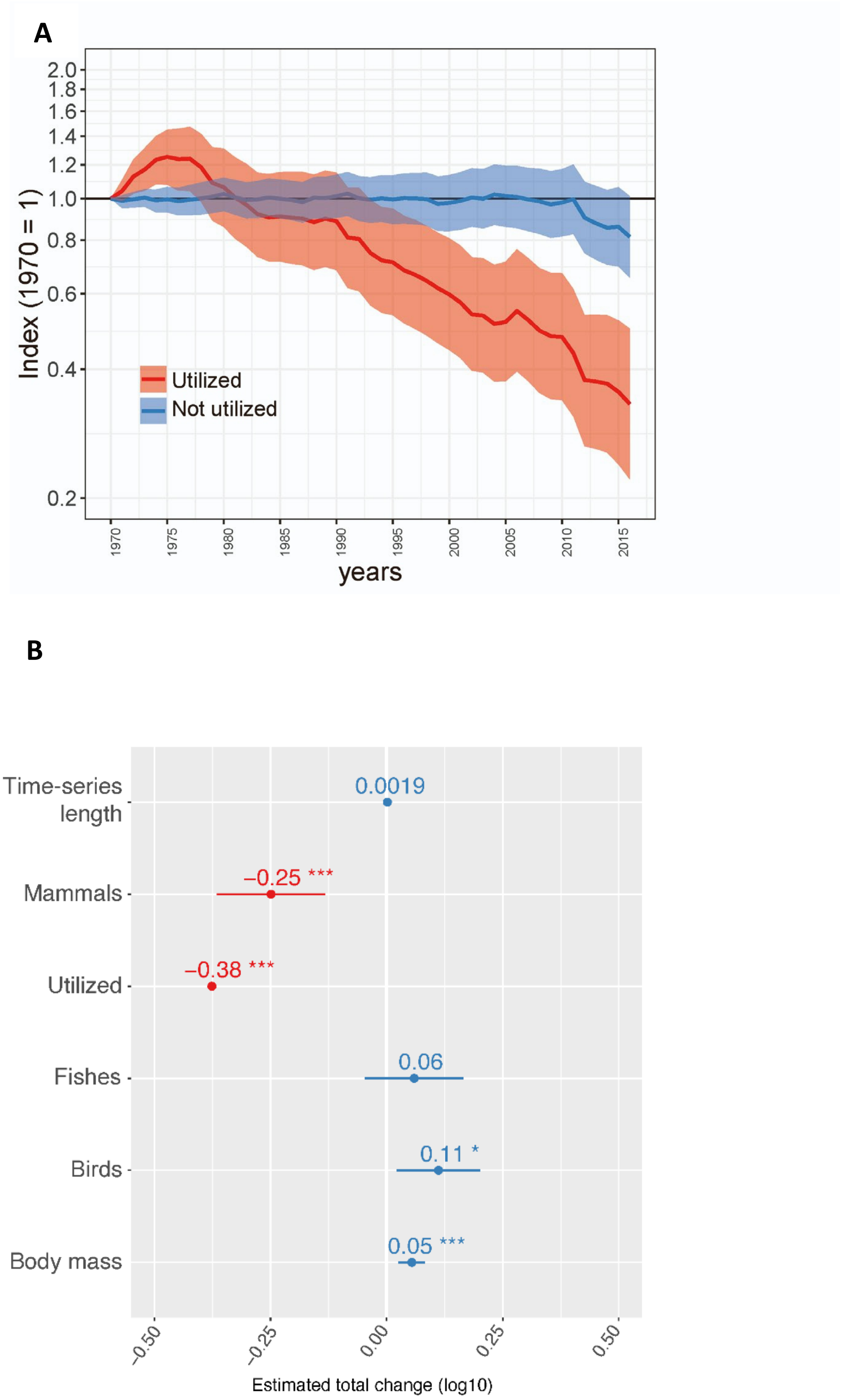

Figure S6 Index of utilized and non-utilized populations for species of terrestrial and freshwater birds, mammals and fish; Related to Figure 4. Data set included 1,297 species and 5,031 populations. **(A)** Index with 95% confidence intervals of utilized and non-utilized populations for terrestrial and freshwater species of bird, mammal and fish. Between 1970 and 2016, on average, utilized populations had declined by 67% (0.22 - 0.50) and non-utilized populations had declined by 19% (0.65 - 1.01). **(B)** Estimated overall total change from the best linear mixed-effect model including Family, Binomial and location as random effects. Coefficients show the estimated overall change (log10) in each group with 95% confidence intervals. We found no significant interaction between taxonomic group and utilisation, with utilized populations of any taxa (*Utilized*) significantly more significantly more likely to be in decline and larger species more likely to have a positive trend.

Table S7. AIC values and model details for models excluding marine populations. Related to Figure S6B

5031 Populations of 1297 Species in 274 Families across 1796 locations

Name	Fixed effects	Random Effects	AIC	ΔAIC	AIC weights	R2 (cond.)	R2 (marg.)
m1_sum_B_nointer_bm_inter	TS_length + Utilized + Class * log10(BodyMass)	(1 | Family/Binomial) + (1 | pop_loc)	9550.955	0	0.456	0.393	0.019
m1_sum_B_additive_bm	**TS_length + Utilized + Class + log10(BodyMass)**	**(1 | Family/Binomial) + (1 | pop_loc)**	**9552.842**	**1.887**	**0.177**	**0.397**	**0.016**
m1_sum_B_full	TS_length + Utilized * Class * log10(BodyMass)	(1 | Family/Binomial) + (1 | pop_loc)	9553.324	2.369	0.139	0.395	0.023
m1_sum_B_noclass_bm	TS_length + Utilized + log10(BodyMass)	(1 | Family/Binomial) + (1 | pop_loc)	9554.327	3.372	0.084	0.396	0.011
m1_sum_B_utilized_inter_bm	TS_length + Class + Utilized * log10(BodyMass)	(1 | Family/Binomial) + (1 | pop_loc)	9554.714	3.759	0.07	0.397	0.017
m1_sum_B_bm	TS_length + Utilized * Class + log10(BodyMass)	(1 | Family/Binomial) + (1 | pop_loc)	9554.774	3.819	0.068	0.397	0.017
m1_sum_B_noclass	TS_length + Utilized	(1 | Family/Binomial) + (1 | pop_loc)	9560.378	9.423	0.004	0.399	0.007
m1_sum_B_additive	TS_length + Utilized + Class	(1 | Family/Binomial) + (1 | pop_loc)	9563.292	12.337	< 0.001	0.399	0.01
m1_sum_B_inter	TS_length + Utilized * Class	(1 | Family/Binomial) + (1 | pop_loc)	9565.096	14.141	< 0.001	0.399	0.01
m1_sum_B_noutil_bm	TS_length + Class + log10(BodyMass)	(1 | Family/Binomial) + (1 | pop_loc)	9566.179	15.224	< 0.001	0.395	0.009
m1_sum_B_noutil	TS_length + Class	(1 | Family/Binomial) + (1 | pop_loc)	9572.374	21.419	< 0.001	0.397	0.004
m1_sum_B_null	TS_length	(1 | Family/Binomial) + (1 | pop_loc)	9580.341	29.386	< 0.001	0.398	9.73E-07

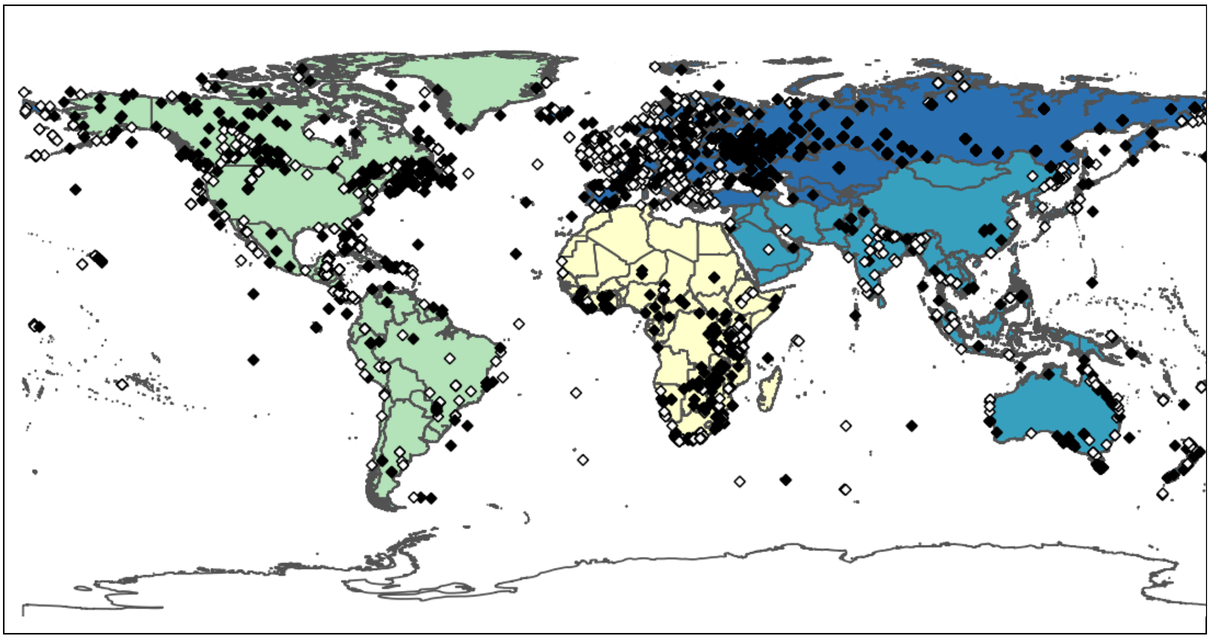

Figure S7. Locations of utilized (black diamonds) and non-utilized (white diamonds) matched populations for birds, mammals and fish. Related to Figure 5

Table S8. AIC values and model details for terrestrial, freshwater and marine populations where each species has at least one utilized and one non-utilized population. Related to Figure 5B

4255 Populations of 339 Species in 129 Families across 1439 locations

Name	Fixed effects	Random Effects	AIC	ΔAIC	AIC weights	R2 (cond.)	R2 (marg.)
matched_m1_sum_C_noclass	TS_length + Utilized	(1 | Family/Binomial) + (1 | pop_loc)	7788.977	0	0.232	0.271	0.009
matched_m1_sum_C_additive	TS_length + Utilized + Class	(1 | Family/Binomial) + (1 | pop_loc)	7789.003	0.026	0.229	0.271	0.014
matched_m1_sum_C_additive_bm	TS_length + Utilized + Class + log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	7789.666	0.689	0.164	0.271	0.014
matched_m1_sum_C_noclass_bm	TS_length + Utilized + log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	7789.865	0.888	0.149	0.272	0.01
matched_m1_sum_C_nointer_bm_inter	TS_length + Utilized + Class * log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	7791.135	2.158	0.079	0.27	0.015
matched_m1_sum_C_utilized_inter_bm	TS_length + Class + Utilized * log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	7791.515	2.538	0.065	0.271	0.014
matched_m1_sum_C_inter	TS_length + Utilized * Class	(1 | Family/Binomial) + (1 | pop_loc)	7792.234	3.257	0.045	0.27	0.014
matched_m1_sum_C_bm	TS_length + Utilized * Class + log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	7792.868	3.891	0.033	0.271	0.014
matched_m1_sum_C_full	TS_length + Utilized * Class * log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	7797.814	8.837	0.003	0.269	0.017
matched_m1_sum_C_noutil	TS_length + Class	(1 | Family/Binomial) + (1 | pop_loc)	7801.331	12.354	< 0.001	0.274	0.011
matched_m1_sum_C_noutil_bm	TS_length + Class + log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	7801.552	12.575	< 0.001	0.275	0.011
matched_m1_sum_C_null	TS_length	(1 | Family/Binomial) + (1 | pop_loc)	7804.399	15.422	< 0.001	0.274	0.002

Table S9. AIC values and model details for terrestrial, freshwater and marine populations where each species has at least one utilized and one non-utilized population and some populations are recorded as 'managed'. Related to Figure 6

2867 Populations of 316 Species in 124 Families across 1069 locations

Name	**Fixed effects**	**Random Effects**	**AIC**	**ΔAIC**	**AIC weights**	**R2 (cond.)**	**R2 (marg.)**
matman_m1_sum_B_noclass_man	TS_length + Utilized + Managed	(1 | Family/Binomial) + (1 | pop_loc)	4992.478	0	0.44	0.256	0.023
matman_m1_sum_B_nointer_bm_inter_man	TS_length + Utilized + Class * log10(Body.mass..g.) + Managed	(1 | Family/Binomial) + (1 | pop_loc)	4993.625	1.147	0.248	0.255	0.031
matman_m1_sum_B_noclass_x_man	TS_length + Utilized * Managed	(1 | Family/Binomial) + (1 | pop_loc)	4994.435	1.957	0.165	0.256	0.023
matman_m1_sum_B_additive_bm_man	TS_length + Utilized + Class + log10(Body.mass..g.) + Managed	(1 | Family/Binomial) + (1 | pop_loc)	4994.838	2.36	0.135	0.26	0.029
matman_m1_sum_B_full	TS_length + Utilized * Class * log10(Body.mass..g.) * Managed	(1 | Family/Binomial) + (1 | pop_loc)	4999.62	7.142	0.012	0.255	0.044
matman_m1_sum_B_noclass	TS_length + Utilized	(1 | Family/Binomial) + (1 | pop_loc)	5014.333	21.855	< 0.001	0.262	0.017
matman_m1_sum_B_nointer_bm_inter	TS_length + Utilized + Class * log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	5014.605	22.127	< 0.001	0.263	0.025
matman_m1_sum_B_additive_bm	TS_length + Utilized + Class + log10(Body.mass..g.) + Managed	(1 | Family/Binomial) + (1 | pop_loc)	5015.063	22.585	< 0.001	0.264	0.021
matman_m1_sum_B_full_noman	TS_length + Utilized * Class * log10(Body.mass..g.)	(1 | Family/Binomial) + (1 | pop_loc)	5016.773	24.295	< 0.001	0.26	0.028
matman_m1_sum_B_justman	TS_length + Managed	(1 | Family/Binomial) + (1 | pop_loc)	5029.298	36.82	< 0.001	0.272	0.011
matman_m1_sum_B_null	TS_length	(1 | Family/Binomial) + (1 | pop_loc)	5036.276	43.798	< 0.001	0.271	0.003
matman_m1_sum_B_noutil	TS_length + Class	(1 | Family/Binomial) + (1 | pop_loc)	5037.313	44.835	< 0.001	0.269	0.01

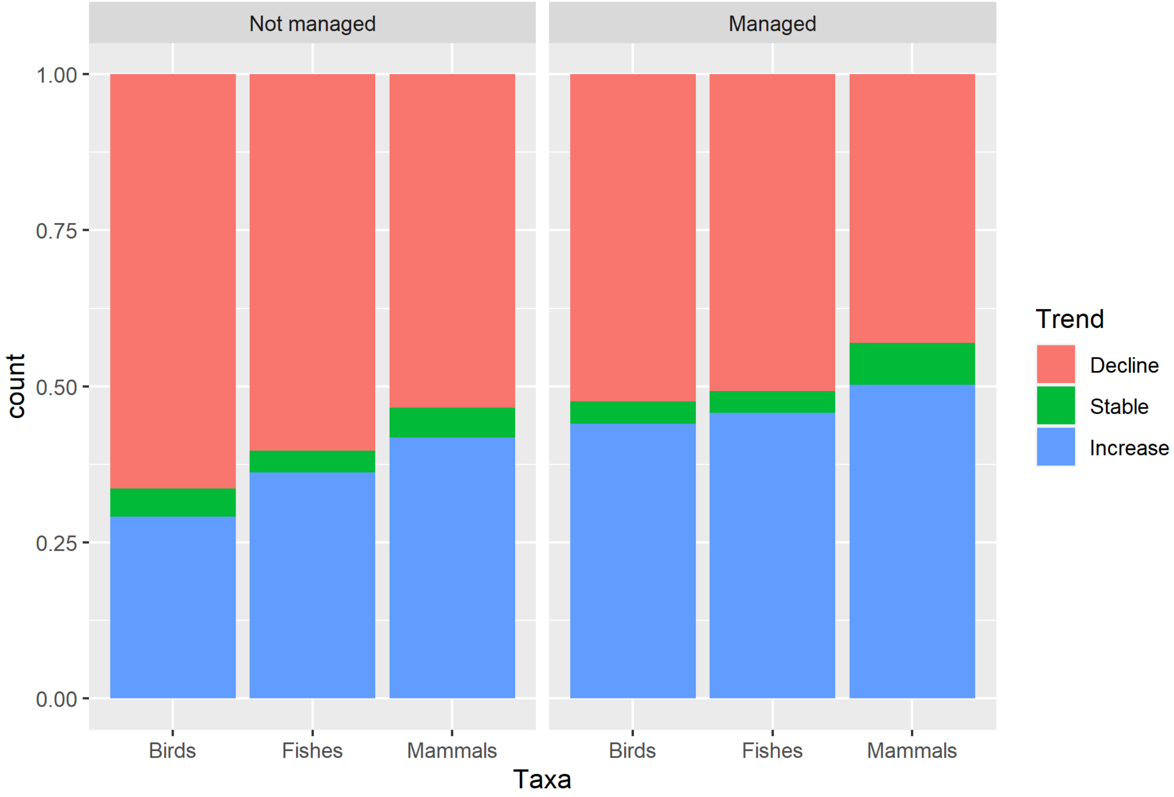

Figure S8. Trend category for utilized populations by management category. Related to Figure 6

Table S10. Ancillary data fields used for disaggregation and modelling

Database field	Definition, coding and source of data	Examples or categories
Utilized	*Definition*: A population that is intentionally regularly or systematically utilized, either individuals or eggs. This may be sustainable or unsustainable, and the population does not necessarily have to be threatened by use or overexploited. This refers to consumptive use whereby individuals or parts of individuals are removed from the wild. *Coding*: 'Yes', 'No', 'Unknown' *Source*: This information was taken from the source of the population data	What is included: Hunting (including subsistence, sport and trophy hunting) Collecting Fishing (consumptive including commercial, artisanal, sport, angling) What is not included: Wildlife tourism Capture and release fishing Education and research in situ Viewing or experiencing for cultural or spiritual reasons
Managed	*Definition*: A population that receives targeted management (some of which involves sustainable use). This is usually to promote recovery in a population or can incentivise it's use for conservation. It can include measures to stem 'unsustainable' population growth. *Coding*: 'Yes', 'No', 'Unknown' *Source*: This information was taken from the source of the population data	What is included: Supplementary feeding Reintroduction Captive breeding Legal protection Quotas for hunting Provision of nest materials Culling of predators of species being monitored Culling of species being monitored (e.g. if overpopulated) What is not included: Protected area (unless it is specifically for that species – e.g. a tiger reserve)
Threats	*Definition*: A current threat that has been identified for the population, according to expert opinion. *Coding*: Up to three threats coded per population *Source*: This information was taken from the source of the population data	Climate change Overexploitation (includes hunting, fishing and collecting, indirect killing, pet trade, sport hunting, persecuted as a pest) Habitat loss/degradation Invasive species and disease Pollution
System	*Definition*: The system that best represents the location and habitat the population (not species) occupies. This is based largely on where the population was monitored and its primary habitat. *Coding*: One system selected *Source*: The location information is taken from the source of the population data. The primary habitat information is taken from Birdlife (birds), IUCN Red List (mammals, amphibians, reptiles), Fishbase (fish)	Terrestrial Freshwater Marine
IPBES region	*Definition*: Socio-political region defined by IPBES (IPBES 2015). If a population spans more than one region, the region containing the greater proportion of the location is selected. *Coding*: One region selected *Source*: (IPBES 2015)	Africa Americas Europe and Central Asia Asia Pacific
IPBES subregion	*Definition:* Socio-political region defined by IPBES (IPBES 2015). If a population spans more than one subregion, the subregion containing the greater proportion of the location is selected. *Coding:* One region selected *Source:* (IPBES 2015)	Southern Africa Central and Western Europe North America
Geographical coordinates	*Definition*: The XY coordinates for the population – usually the centroid *Coding*: Degrees, minutes and seconds or Decimal degrees *Source*: This information was taken from the source of the population data or, if absent, an online geographical database	
Time-series length	*Definition*: The timeframe (number of years) from the first year the population was monitored to the final year. All intervening years were counted regardless of whether monitoring occurred in that year or not *Coding*: Number of years *Source*: This information was taken from the source of the population data	
Body Mass	*Definition*: Collation or estimation of body mass *Coding*: Mean body mass in g *Source*: Trait databases and individual sources (Table S12)	

Table S11. Indices of abundance calculated according to taxa, system and utilisation categories

	Utilized (All vertebrates)	**Utilized and non-utilized (Birds, fish and Mammals)**	**Utilized and non-utilized (Birds and Mammals)**
Terrestrial and freshwater	Global IPBES regions IPBES subregions	Global Global – matched species only	
Marine	Global IPBES regions IPBES subregions		
All systems		Global Global – matched species only	Global Global – matched species only

Table S12 Sources of body mass data used within the study with the measurements taken (sources and methods follow Noviello, N., L. McRae, et al. (2020). "Body mass and latitude predict the presence of multiple stressors in global vertebrate populations." bioRxiv: 2020.2012.2017.423192.)

Data	**Measurement**	**Reference**
Amniote	Body Mass	Nathan P. Myhrvold, Elita Baldridge, Benjamin Chan, Dhileep Sivam, Daniel L. Freeman, S. K. Morgan Ernest. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. Ecology 96: 3109
AmphiBIO	Body Mass	Oliveira, B., São-Pedro, V., Santos-Barrera, G. et al. AmphiBIO, a global database for amphibian ecological traits. Sci Data 4, 170123 (2017)
Atelopus longirostris	Body mass	Elicio Eladio Tapia, Luis Aurelio Coloma, Gustavo Pazmiño-Otamendi & Nicolás Peñafiel (2017) Rediscovery of the nearly extinct longnose harlequin frog Atelopus longirostris (Bufonidae) in Junín, Imbabura, Ecuador, Neotropical Biodiversity, 3: 1, 157-167, DOI: 10.1080/23766808.2017.1327000
Chalcorana (Rana) chalconota	SVL	Robert F. Inger, Bryan L. Stuart, Djoko T. Iskandar, Systematics of a widespread Southeast Asian frog, Rana chalconota (Amphibia: Anura: Ranidae), Zoological Journal of the Linnean Society, Volume 155, Issue 1, January 2009, Pages 123–147, https: //doi.org/10.1111/j.1096-3642.2008.00440.x
Elton Traits	Body Mass	Smith et al 2003, Dunning 2007 – see Elton traits metadata
Encyclopedia of Life	Body Mass	Parr, C. S., N. Wilson, P. Leary, K. S. Schulz, K. Lans, L. Walley, J. A. Hammock, A. Goddard, J. Rice, M. Studer, J. T. G. Holmes, and R. J. Corrigan, Jr. 2014. The Encyclopedia of Life v2: Providing Global Access to Knowledge About Life on Earth. Biodiversity Data Journal 2: e1079, doi:10.3897/BDJ.2.e1079
Fishbase	Length (TL / FL / SL)	Froese R. & Pauly D. (eds). (2020). FishBase (version Feb 2018). In: Species 2000 & ITIS Catalogue of Life, 2020-09-01 Beta (Roskov Y.; Ower G.; Orrell T.; Nicolson D.; Bailly N.; Kirk P.M.; Bourgoin T.; DeWalt R.E.; Decock W.; Nieukerken E. van; Penev L.; eds.). Digital resource at www.catalogueoflife.org/col. Species 2000: Naturalis, Leiden, the Netherlands. ISSN 2405-8858.
Handbook of the Birds of the World Alive	Body Mass	S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg (Editors) (2020). Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA. https://birdsoftheworld.org/bow/home
Leiopelma archeyi	Body mass	Stark, G, Meiri, S. Cold and dark captivity: Drivers of amphibian longevity. Global Ecol Biogeogr. 2018; 27: 1384– 1397. https: //doi.org/10.1111/geb.12804
Litoria australis* aka *Ranoidea australis, Litoria dahlia* aka *Ranoidea dahlii, Ranoidea genimaculata* aka *Litoria genimaculata	SVL	Vanderduys, E. (2019). Field Guide to the Frogs of Queensland. In Field Guide to the Frogs of Queensland. doi: 10.1071/9780643108790

Litoria nannotis* aka *Ranoidea nannotis	Body mass	Liem, D.S. (1974). A review of the Litoria nannotis species group and a description of a new species of Litoria from north-east Queensland, Australia. Memoirs of the Queensland Museum 17(1), 151-168. Cogger, H.G. (1994). Reptiles and Amphibians of Australia. Reed Books, Sydney. McDonald, K.R. & Alford, R.A. (1999). A Review of Declining Frogs in Northern Queensland. Pp 14-22 in A. Campbell (ed), Declines and Disappearances of Australian Frogs. Environment Australia, Canberra. 234 pp.
Myotis escalerai	Body mass	Quetglas, J. (2016). Murciélago ratonero ibérico – Myotis escalerai. En: Enciclopedia Virtual de los Vertebrados Españoles. Salvador, A., Barja, I. (Eds.). Museo Nacional de Ciencias Naturales, Madrid.
PanTHERIA	Body Mass	Kate E. Jones, Jon Bielby, Marcel Cardillo, Susanne A. Fritz, Justin O'Dell, C. David L. Orme, Kamran Safi, Wes Sechrest, Elizabeth H. Boakes, Chris Carbone, Christina Connolly, Michael J. Cutts, Janine K. Foster, Richard Grenyer, Michael Habib, Christopher A. Plaster, Samantha A. Price, Elizabeth A. Rigby, Janna Rist, Amber Teacher, Olaf R. P. Bininda-Emonds, John L. Gittleman, Georgina M. Mace, and Andy Purvis. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90: 2648.
Rana tavasensis	SVL	Düşen, S. (2012). First data on the helminth fauna of a locally distributed mountain frog, "Tavas frog" Rana tavasensis Baran & Atatür, 1986 (Anura: Ranidae), from the inner-west Anatolian region of Turkey. Turkish Journal of Zoology, 36, 496-502.
Trachycephalus venulosus	Body mass	Domingos J. Rodrigues, Masao Uetanabaro & Frederico S. Lopes (2005) Reproductive patterns of Trachycephalus venulosus (Laurenti, 1768) and Scinax fuscovarius (Lutz, 1925) from the Cerrado, Central Brazil, Journal of Natural History, 39: 35, 3217-3226, DOI: 10.1080/00222930500312244
Various amphibian	Body Mass	Santini L., Benítez-López A., Ficetola G.F., Huijbregts M.A.J. 2017. Length – Mass allometries in Amphibians. Integrative Zoology, 13: 36-45. doi:10.1111/1749-4877.12268
Various amphibian	Body mass	Stark, G, Pincheira-Donoso, D, Meiri, S. No evidence for the 'rate-of-living' theory across the tetrapod tree of life. Global Ecol Biogeogr. 2020; 00: 1– 28. https: //doi.org/10.1111/geb.13069
Various amphibian	SVL	AmphibiaWeb. 2020. <https://amphibiaweb.org> University of California, Berkeley, CA, USA.
Various amphibians	Body Mass	Trochet A, Moulherat S, Calvez O, Stevens V, Clobert J, Schmeller D (2014) A database of life-history traits of European amphibians. Biodiversity Data Journal 2: e4123.
Various avian	Body Mass	Terje Lislevand, Jordi Figuerola, and Tamás Székely. 2007. Avian body sizes in relation to fecundity, mating system, display behavior, and resource sharing. Ecology 88: 1605
Various avian	Body Mass	Renner, S.C.; Hoesel, W. Ecological and Functional Traits in 99 Bird Species over a Large-Scale Gradient in Germany. Data 2017, 2, 12.
Various mammals	Body Mass	Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H. and Haskell, J.P. (2003), Body mass of late quaternary mammals. Ecology, 84: 3403-3403.
Various primates	Body Mass	Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E. et al. Ecological traits of the world's primates. Sci Data 6, 55 (2019) doi: 10.1038/s41597-019-0059-9
Various vertebrates	Body Mass	Anthony I. Dell, Samraat Pawar, Van M. Savage. 2013. The thermal dependence of biological traits. Ecology 94: 1205.