

The diversity weighted Living Planet Index: controlling for taxonomic bias in a global biodiversity index.

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Abstract

As threats to species continue to increase, we urgently need precise and unbiased measures of the impact these pressures are having on global biodiversity. 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 overrepresentation 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 once 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 2010 of 55% rather than 22% from an index with no proportional weighting. From this dataset, comprising 10,380 populations of 3,038 species from 2,337 data sources, we also find that freshwater populations have declined by 76%, marine populations by 41%, and terrestrial populations by 39% when using proportional weighting (compared to declines of 45%, 2% and 30% respectively). This not only shows starker declines than previously estimated, but suggests that those species for which we have poorer data coverage may be declining more rapidly.

Introduction

Threats and pressures upon the natural world continue to increase (Dirzo et al., 2014; Tittensor et al., 2014), and species extinction rates are likely to rise to around 10,000 times the background rate (De Vos et al, 2014). Even today, the rate of extinctions is estimated to be 1000 times the background rate (De Vos et al, 2014). Strategic Goal C of the Aichi Biodiversity Targets (SCBD, 2010) 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. To this end, developing robust and quantitative measures of the status of and trends in biodiversity to measure progress towards this target is crucial (Tittensor et al., 2014).

The Living Planet Index (McRae et al, 2014; Collen et al, 2009; Loh et al, 2005), 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 database includes available published data, primarily in the scientific and grey literature (e.g. government/NGO reports) and records trends in 10,380 populations of 3,038 species. However, its reliance on available data means there may be bias in the LPI resulting from the taxonomic and geographical distribution of the data used.

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 (Figure 1). This mismatch between the known diversity of vertebrate species and the available data can lead to inaccurate estimates of overall status and trends in biodiversity.

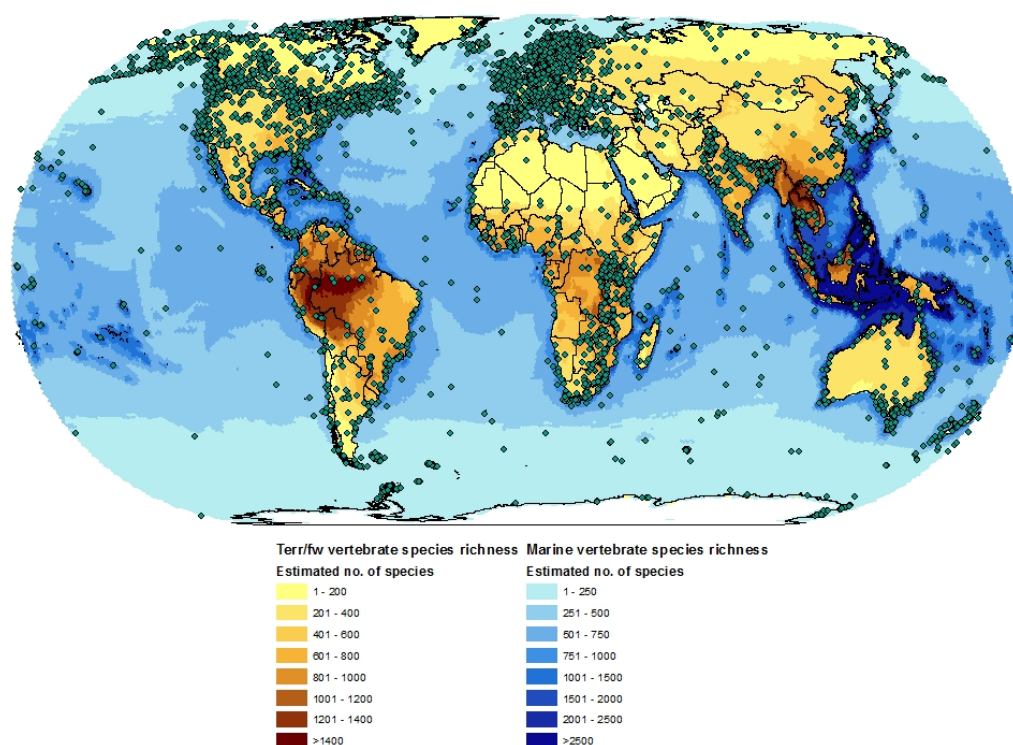


Figure 1: Global vertebrate richness map overlaid with populations recorded in the Living Planet Index database.

Other indicators based on species abundance (e.g. Gregory et al., 2005, van Swaay et al., 2008) 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 (Gregory et al., 2005, van Swaay et al., 2008). 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. In light of this, it can be prudent in the near term to build on existing indicators and address the bias that they contain (Jones et al., 2011)

The database behind the Living Planet Index has been continually augmented since its inception in 1998 (Loh et al., 1998) and data are still being added (Figure S1). In light of the applicability of the Living Planet Index as a global biodiversity indicator (Tittensor et al., 2014) and with current and new targets for biodiversity, such as the Aichi Targets (SCBD, 2010) and Sustainable Development Goals (UN, 2015), requiring a reporting tool, we aim to continue the development of the LPI by both addressing data gaps and by addressing the existing bias in the indicator. Here, we describe an approach which attempts to tackle the latter.

We collate estimates of the known number of species across biogeographical realms and assess the representativeness of the Living Planet Index database for species groups within these. We then develop and introduce 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.

Results

Taxonomic representation and bias within the Living Planet Index

Figure 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 over 10% of known species in the terrestrial and freshwater systems. For the marine system, 7 subsets represent between 1 and 10% and 15 subsets represent 10% or more of known species (Table S1). 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 (64%, 461 species out of a possible 725 species) and the lowest is for Afrotropical reptiles and amphibians (0.6%, 14 species of a possible 2,480 species).

When compared to the expected diversity of species across realms, birds and mammals are generally significantly over-represented within terrestrial and freshwater realms with the exception of Afrotropical birds which are under-represented (Binomial test of proportions, see Table S2). 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, birds, mammals and reptiles are significantly over-represented (Table S2). Fishes are a significantly under-represented group in three of the marine realms but are significantly over-represented in the Atlantic north temperate.

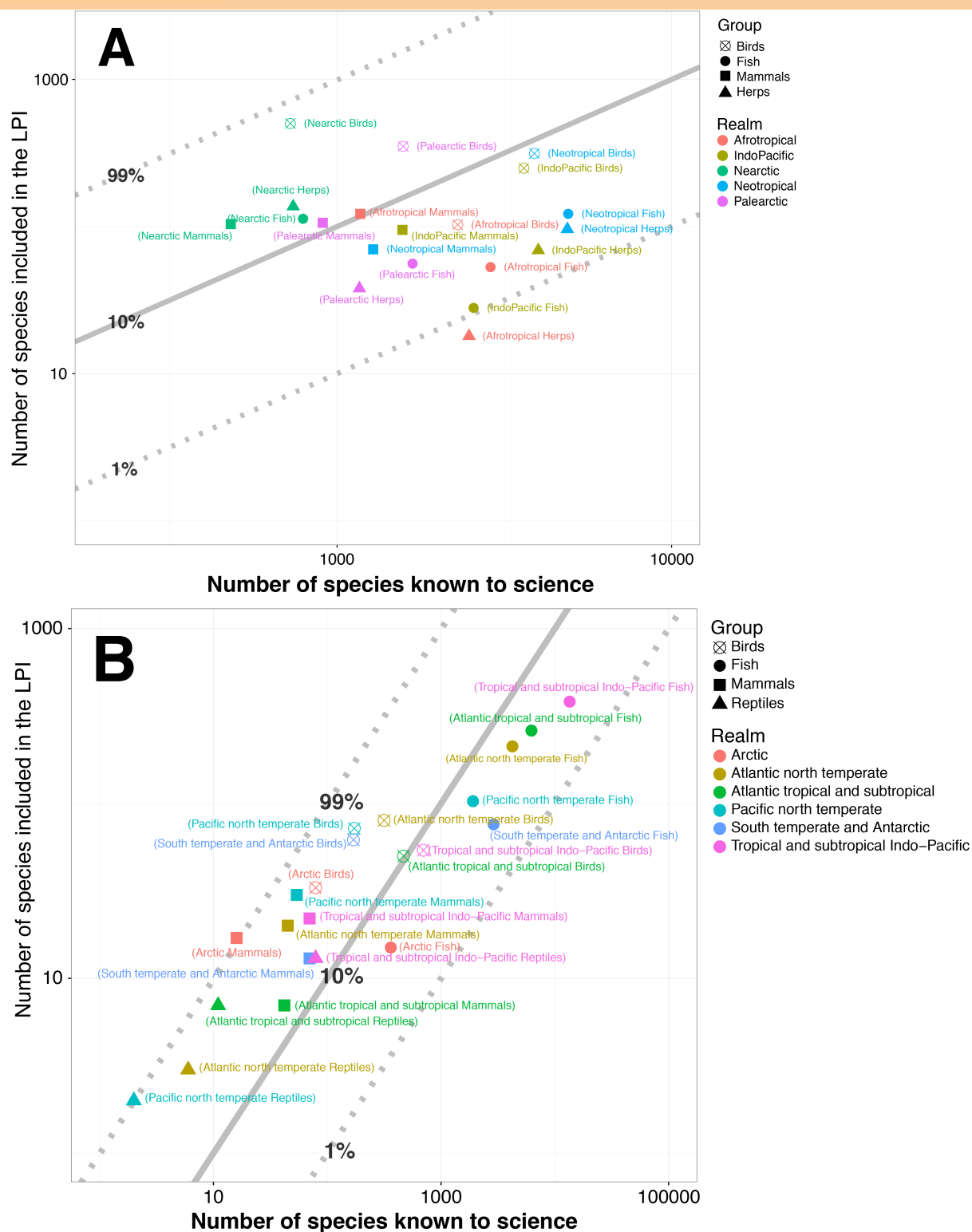


Figure 2 – Comparison of number of known species and number of species recorded within the Living Planet Database. Colours represent different biogeographic realms, shapes indicate species groups and overlaid lines show 1 and 99% representation (dotted) and 10% representation (solid) – i.e. 1 in 10 known species are recorded within the Living Planet Database. A – terrestrial and freshwater species and realms; B – marine species and realms

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 increase of 42% (22.8 – 70.1) over the period 1970-2010 (Figure 3). Using the diversity weighted method (LPI-D), the index for the Palearctic realm shows an overall decline of 27% (-0.01 – -45.5). The LPI-D index for the Palearctic realm shows wider confidence intervals than the LPI-U index as well as a more undulating trend. The LPI-D method shows a significant long-term decline, and the LPI-U shows a significant long-term increase.

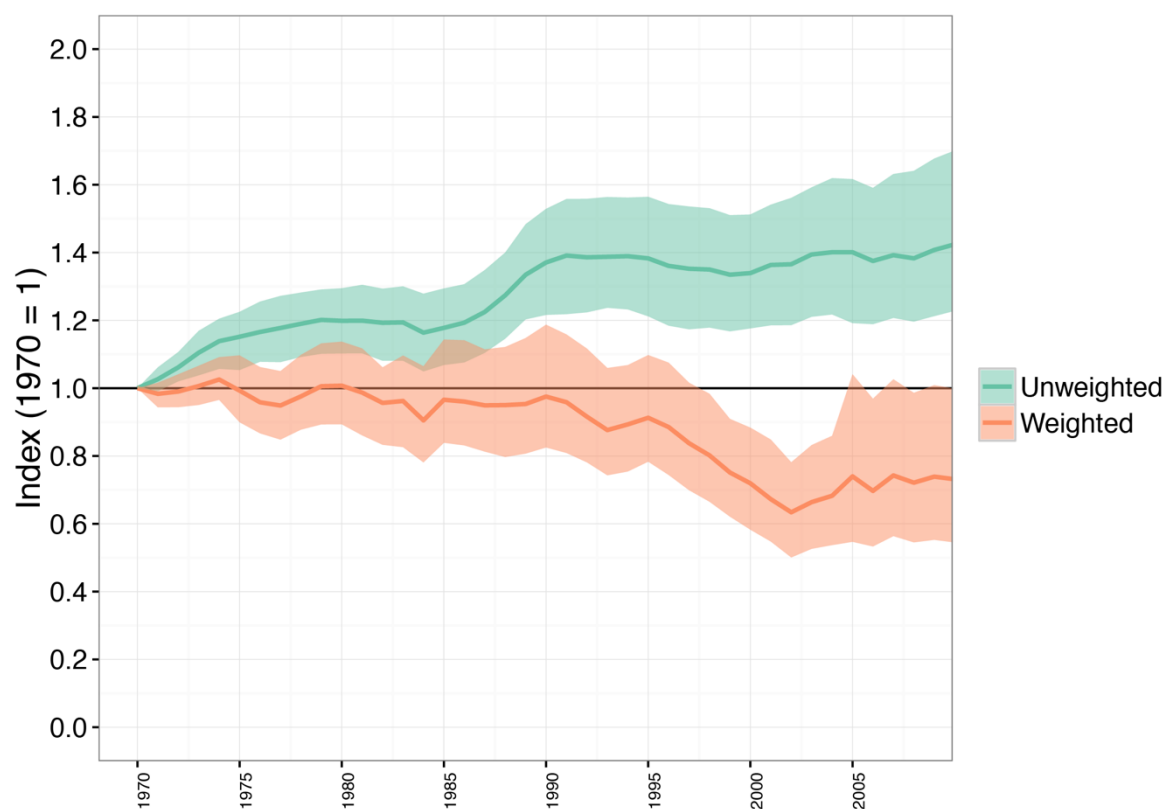


Figure 3 - Comparison of the unweighted and diversity weighted Living Planet Index for the Palearctic realm. Green shows the unweighted index (LPI-U), orange shows the diversity weighted index (LPI-D). Solid coloured lines show the average trend and shaded regions show the 95% confidence interval of that trend.

Applying the LPI-D approach to the global Living Planet Index

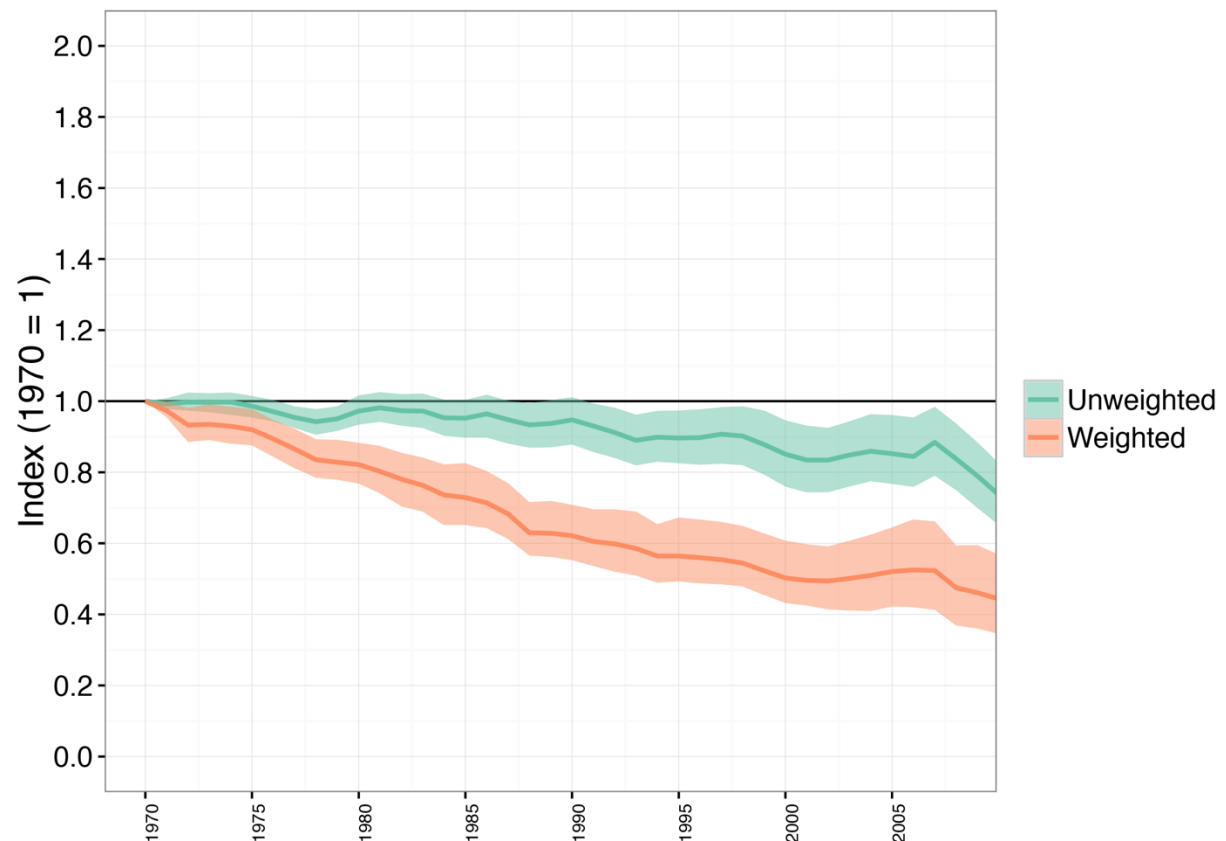


Figure 4 - Comparison of the unweighted and diversity-weighted Living Planet Index for the global dataset. Green shows the unweighted index (Global LPI-U), orange shows the diversity weighted index (Global LPI-D). Solid coloured lines show the average trend and shaded regions show the 95% confidence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

The global index produced using the LPI-D approach shows a decline of 55.4% (-46.7 – -63.1) between 1970 and 2010 (Figure 4) 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 0.63% per year and an overall decline of 22.2% (-14.5 – -28.9), over the 40 year period. The confidence intervals around the LPI-D index are slightly wider than the LPI-U 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 (Figure 5). The terrestrial index shows a 39% decline (95% CI: -22.5 – -52.4) from 1970 to 2010, averaging at a 1.23% decline per year. The marine index shows a similar decline of 41.4% (95% CI: -17.1 – -59.0) over the same period, with an average annual decline of 1.33% per year. The freshwater index shows a decline of greater magnitude, 75.6% (95% CI: -69.8 – -83.7) over the 40-year period and an average annual decline of 3.47% per year. Table 1 compares the weighted and unweighted indices for each system.

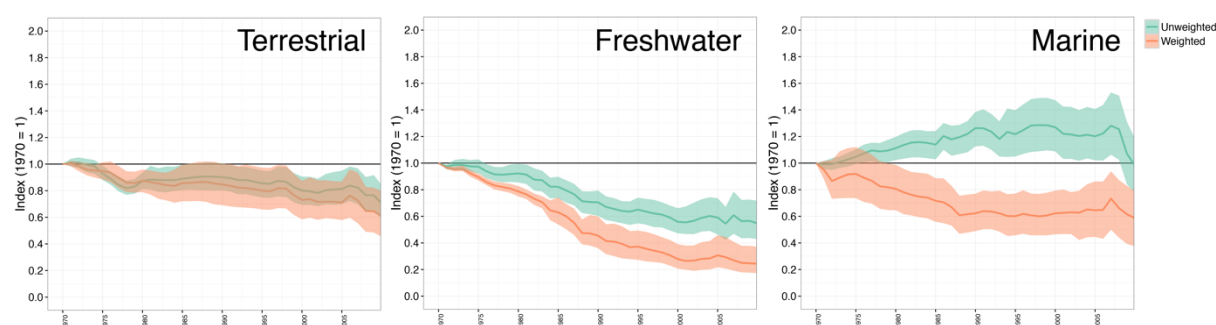


Figure 5 - Comparison of the unweighted and diversity weighted Living Planet Index for each System (Terrestrial, Freshwater and Marine). In each case, green shows the unweighted index (LPI-U), orange shows the diversity weighted index (LPI-D). Solid coloured lines show the average trend and shaded regions show the 95% confidence interval of that trend.

	LPI-D index value in 2010	95% Confidence interval	LPI-U index value in 2010	95% Confidence interval
Terrestrial	0.610	0.476 - 0.775	0.704	0.566 - 0.835
Freshwater	0.244	0.163 - 0.312	0.547	0.431 - 0.701
Marine	0.586	0.410 - 0.829	0.981	0.816 - 1.22

Table 1 – Comparing the results of the weighted (LPI-D) and unweighted (LPI-U) indices in 2010. Confidence intervals are calculated from 10,000 bootstraps.

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 the removal. Figure compares the impact of 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, when groups with less than 1% representation are removed, the terrestrial index shows *a greater decline* (LPI-D 58.2% vs 39.0%; LPI-U 43.4% vs 29.6%). This is significant in the weighted index (58.2% vs 39.0% (95% CI: -16.5 – -43.4), and marginal in the unweighted index (LPI-U 43.4% vs -29.6% (95% CI: -16.5 - -43.4)). In the freshwater and global index, no significant difference is seen when these groups are removed.

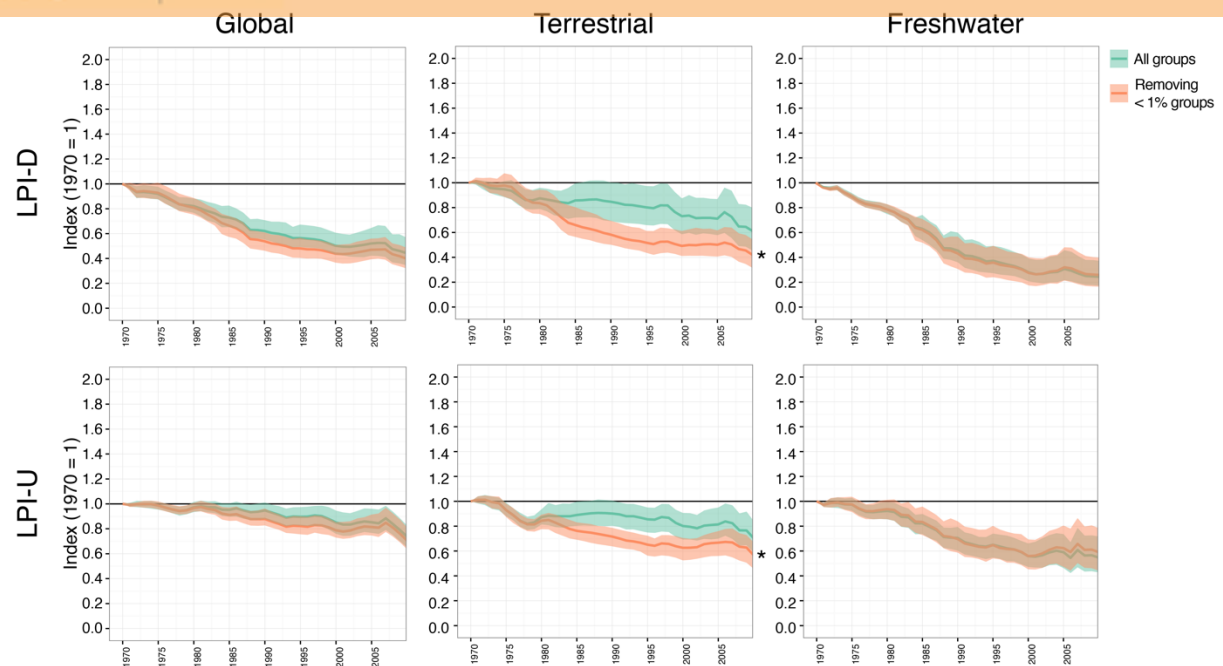


Figure 6 – The impact of removing species groups for which the Living Planet database has < 1% representation. Green trends show the Living Planet Index for all groups, orange trends show trends without less represented groups. Upper row shows trends calculated using the weighted (LPI-D) method, lower rows show the unweighted (LPI-U) method. Solid lines show the average trend, shaded regions show 95% confidence intervals. Stars (*) indicate when the final 2010 index values are significantly different.

Representation of threatened species

Altering the relative importance of different species groups within the index may cause some groups e.g. threatened species to have a disproportionate impact. Here we explore the relative proportions 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 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, and

Endangered and Vulnerable amphibians. None of the categories for mammals showed significant over or under representation.

TAXON	CATEGORY	LPI	IUCN	X ²	REPRESENTATION
MAMMALIA	CR	0.05	0.05	0.01	over
	EN	0.12	0.10	1.46	over
	VU	0.11	0.11	0.00	over
	NT/LR	0.07	0.07	0.01	over
	LC	0.65	0.66	0.17	under
	<i>Total # sp.</i>	<i>484</i>	<i>4714</i>		
AVES	CR	0.02	0.02	0.09	under
	EN	0.03	0.04	2.07	under
	VU	0.05	0.07	7.72	under
	NT/LR	0.05	0.09	24.93***	under
	LC	0.84	0.76	45.79***	over
	<i>Total # sp.</i>	<i>1376</i>	<i>10363</i>		
REPTILIA	CR	0.13	0.05	14.20***	over
	EN	0.11	0.10	0.00	over
	VU	0.16	0.11	2.08	over
	NT/LR	0.16	0.09	6.16*	over
	LC	0.45	0.65	18.97***	under
	<i>Total # sp.</i>	<i>114</i>	<i>3603</i>		
AMPHIBIA	CR	0.07	0.11	2.03	under
	EN	0.04	0.16	17.62***	under
	VU	0.04	0.14	11.90***	under
	NT/LR	0.08	0.08	0.00	under
	LC	0.75	0.50	38.52***	over
	<i>Total # sp.</i>	<i>170</i>	<i>4800</i>		
FISHES	CR	0.06	0.05	1.66	over
	EN	0.06	0.06	0.02	under
	VU	0.16	0.12	3.73	over
	NT/LR	0.12	0.05	22.74***	over
	LC	0.60	0.71	16.85***	under
	<i>Total # sp.</i>	<i>283</i>	<i>9737</i>		

Table 1 – 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 – Near Threatened, VU - Vulnerable, EN – Endangered, CR – Critically Endangered). 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.**

Discussion

Accurately quantifying trends in global biodiversity is crucial if we are to understand the impacts of threats on the species and ecosystems on which we rely. Recent estimates of species extinction rates suggest they are significantly higher than background rates and have increased dramatically over the last 200 years (De Vos et al., 2015; Ceballos et al., 2015). Trends in abundance are also a crucial indicator of the health of populations to gauge early warnings of declines prior to species qualifying for high levels of extinction risk. For this reason, trends in abundance of species populations have been suggested as an Essential Biodiversity Variable (Pereira et al., 2013), and, along with the Living Planet Index, are part of the mechanism to monitor biodiversity and assess progress towards the Aichi Targets. While the collation of data from available sources such as government reports, scientific articles and research programmes represents a cost effective method to develop a global biodiversity indicator, it necessarily suffers from a variety of biases from the processes and logistics of data collection and species selection.

These types of bias are a common feature of other global biodiversity databases (Boakes et al., 2010; Yesson et al., 2007), usually with a noticeable gap in data from tropical regions (Collen et al., 2008). 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 (Pereira et al., 2012). Encouragingly, improvements will happen as existing biodiversity databases continue to be augmented and techniques to harness the power of citizen science projects improves (Pimm et al., 2014). In addition, initiatives to harmonise and standardise existing biodiversity databases are underway to improve the current resource base for monitoring global biodiversity (Kissling et al., 2015). The demand for measures to report on biodiversity change however remains a challenge (Walpole et al., 2009) and one where improving our resource base will

not provide answers fast enough. We have outlined an approach to deal with bias as an interim solution in lieu of attaining more representative monitoring data.

Across many of the species groups that are monitored within the Living Planet database, we see significant over, or under, representation in comparison to the known number of species (Table S2, Figure 2). This trend, found in other large databases, is thought to occur for a number of reasons including lack of resources or infrastructure for monitoring, logistical difficulties in accessing sites or barriers to the dissemination of data into the public realm (Collen et al., 2008). 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, and will therefore be unrepresentative of the ‘true’ trends in global wildlife abundance.

As an example, in Figure 3, we compare overall trends for the Palearctic realm. While the unweighted index (LPI-U) would suggest that, on average, species populations within the Palearctic had increased in abundance by 42.4% (95% CI: +22.8 – +70.1), the weighted index (LPI-D) suggests that, on average, population abundance may have *declined* by 26.9% (95% CI: -0.01 – -45.5). 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 12% respectively, whereas the influence of fishes and amphibians/reptiles have each been increased 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. 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 (Table S1). This difference is also notable at the global level where the unweighted index suggests populations have declined by, on average, 22.2% (95% CI: -14.5 – -28.9), whereas the weighted index (LPI-D) suggests significantly larger declines of 55.4% (95% CI: -46.7 – -63.1).

Our method places additional weight on groups that may be less monitored or may be more likely to be categorized as threatened (tropical regions tend to have higher richness and a greater proportion of threatened species), and this may introduce a different form of bias to the trends. In part, we note that there is no perfect solution to address this – the unweighted index (LPI-U) appears to mask declines by placing additional weight on well monitored, increasing populations in temperate regions (these have other issues – declines may have occurred historically prior to the Living Planet Index baseline of 1970). Weighting by species diversity distributes the responsibility for the index more appropriately across regions and taxa. To explore the possible impact of this shift in relation to the distribution of threatened species we compared the proportion of threatened species within the LPI database to the proportions on the IUCN Red List (Table 1) and found that few threatened groups are significantly over or under-represented. Critically Endangered reptiles are the only threatened group which is over represented, while Endangered and Vulnerable amphibians are *under-represented* within the Living Planet database. This may account for why the shift seen when removing less-represented groups results in a worse decline than when they are included (Figure 6).

Accounting for the diversity of species using the LPI-D method allows the Living Planet Index to be calculated in a more taxonomically representative way. However, it would clearly be beneficial to continue to improve the representation of species within the Living Planet database. The rate with which new data is incorporated into the database remains relatively constant (Figure S1), as a wealth of data remains available in the literature. As manual entry of these data is a critical limitation in growing the Living Planet database, tools for automating this process would be of benefit. For example, biodiversity databases like the Living Planet database could benefit greatly from working relationships and support with journals to identify useful research papers and the data they contain (Huang, X. and Qiao, G. 2011). New technologies such as remote sensing may also provide useful ways to improve the spatial coverage of data (Pettorelli 2014; 2016), and incorporating other data

types such as occurrence or opportunistic data (e.g from citizen science, Isaac et al., 2014) may help expand taxonomic coverage as abundance data is rare for non-vertebrates.

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 (Gregory et al, 2005). Depending on the question of interest, other methods of weighting could also be explored such as weighting by genetic diversity, functional diversity or other metrics. One 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. As estimates of the known number of species improve, the relative weighting of species groups can be updated to better estimate overall trends. As well as the use we've 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.

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 speciose 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 (McRae et al., 2014) and that amphibians are threatened with a greater risk of extinction than mammals or birds (Stuart et al., 2004). However,

we note that when we remove those species groups for which we have very little data (< 1% species), the overall trends *decline more* (Figure), 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.

Finally, we note that not all vertebrates have yet been described. Estimates for the number of as yet unidentified birds and mammals are small (e.g. ~10-15 species), but estimates for the number of unidentified amphibians, reptiles and fish are much larger with around 57%, 13% and 22% undescribed (Scheffers et al, 2012). These latter groups would therefore be given even greater weight, suggesting that vertebrate populations may be declining, on average, even more rapidly than we currently estimate.

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 2,337 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 Collen, 2009 for further details).

The period covered by the index is from 1970 to 2010. The year 2010 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. Datasets 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 (see Figure S2).

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 (World Wildlife Fund, 2006). 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 (Abell, et al 2008) 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 2013.2 (IUCN, 2013). 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. This 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 (Uetz and Hošek, 2014).

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 (OBIS, 2014). 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 (IUCN, 2013). 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 database 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 differed significantly from the actual proportions of threatened species within each extinction risk category and for each taxonomic group on the IUCN Red List. For reptiles and fishes which have not been comprehensively assessed, we used estimates of proportion threatened from those species that have been assessed.

Calculating the LPI

We calculated average trends for each species within a Generalised Additive Modelling (GAM) framework, following Collen et al. (2009), 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 (Loh et al., 2005). Where we had more than one population time series for a species, the modelled annual trends for each population were averaged to provide a single set of annual trends for each species.

We used two approaches for calculating a global scale index. The first, unweighted method (LPI-U), follows the process outlined in Collen et al. (2009) 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 dataset 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 Loh et al., 2005; Collen et al. 2009). 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.

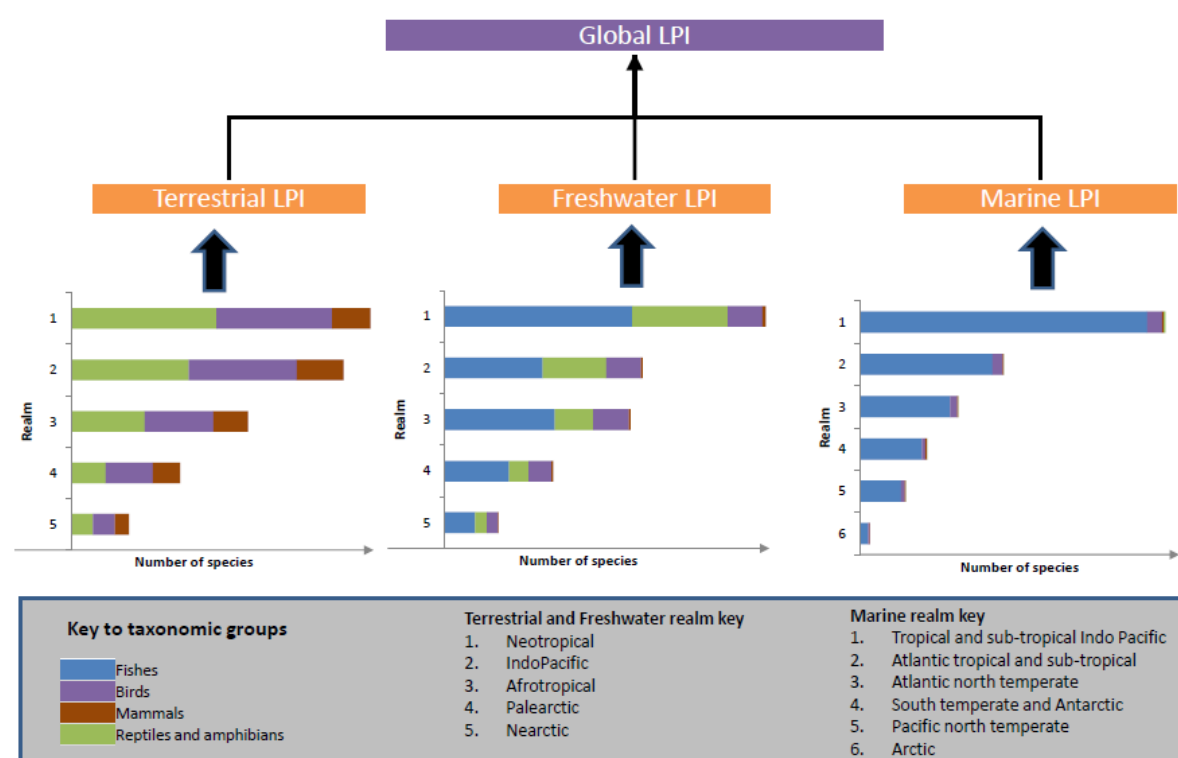


Figure 7 – Schematic of the weighting process. Systems (Terrestrial/Freshwater/Marine) are weighted equally. Within each system, the proportion of species found across the realms that compose that system (the length of the bars above) is used to proportionally weight each realm's index. Within each realm, the diversity of species is used to weight taxonomic indices (the size of the coloured sections of the bars above).

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 (Figure 7). 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.

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 Collen et al. (2009). 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 Table S4, Palearctic column).

For each index, we generated 95% confidence intervals using a bootstrap resampling technique for 10,000 iterations (as in Collen et al., 2009). These confidence intervals demonstrate the uncertainty in the index values inherited from the baseline in 1970 and propagated through the time series.

Acknowledgements

The authors would like to kindly acknowledge early conversations with Jonathan Loh and Raj Amin which helped frame this approach. We would also like to thank Monika Böhm, Jonathan Loh and

Valentina Marconi for providing some very useful feedback on a draft of this manuscript. We are grateful to Robin Abell and Michele Thieme who provided the data set behind the Freshwater Ecoregions of the World. LM was funded by WWF International.

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Supporting Information

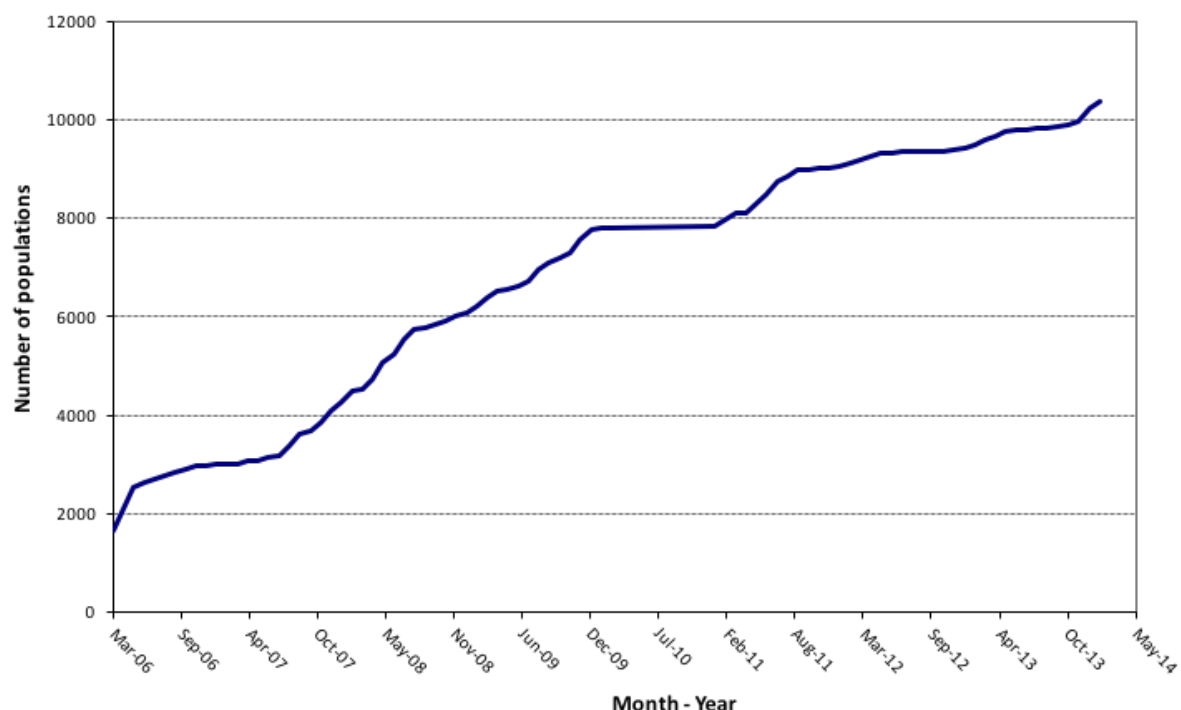


Figure S1: The cumulative number of population time series in the LPI database from 2006 to 2014.

A

Species numbers

		Global estimate	LPI database	Proportion
<i>Amphibia and Reptilia</i>	Afrotropical	2480	14	0.0056452
	IndoPacific	3994	50	0.0125188
	Nearctic	739	121	0.1637348
	Neotropical	4879	86	0.0176266
	Paleartic	1166	32	0.0274443
<i>Aves</i>	Afrotropical	2294	104	0.0453357
	IndoPacific	3616	249	0.0688606
	Nearctic	725	461	0.6358621
	Neotropical	3890	310	0.0796915
	Paleartic	1575	349	0.2215873
<i>Mammalia</i>	Afrotropical	1173	121	0.1031543
	IndoPacific	1568	95	0.0605867
	Nearctic	481	80	0.1663202
	Neotropical	1282	66	0.0514821
	Paleartic	906	104	0.1147903
<i>FW Fishes</i>	Afrotropical	2875	39	0.0135652
	IndoPacific	2559	29	0.0113326
	Nearctic	791	83	0.1049305
	Neotropical	4909	88	0.0179263
	Paleartic	1681	56	0.0333135

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B

Species numbers

		Global estimate	LPI database	Proportion
<i>Reptilia</i>	Arctic	0	0	N/A
	Atlantic north temperate	6	3	0.5
	Atlantic tropical and subtropical	11	13	1.181818182
	Pacific north temperate	2	2	1
	South temperate and Antarctic	3	0	0
	Tropical and subtropical Indo-Pacific	79	13	0.164556962
<i>Aves</i>	Arctic	79	28	0.35443038
	Atlantic north temperate	316	70	0.221518987
	Atlantic tropical and subtropical	467	58	0.124197002
	Pacific north temperate	172	61	0.354651163
	South temperate and Antarctic	167	55	0.329341317
	Tropical and subtropical Indo-Pacific	694	54	0.077809798
<i>Mammalia</i>	Arctic	16	15	0.9375
	Atlantic north temperate	45	20	0.444444444
	Atlantic tropical and subtropical	42	6	0.142857143
	Pacific north temperate	54	29	0.537037037
	South temperate and Antarctic	70	7	0.1
	Tropical and subtropical Indo-Pacific	70	19	0.271428571
<i>Fishes</i>	Arctic	291	15	0.051546392
	Atlantic north temperate	1826	153	0.083789704
	Atlantic tropical and subtropical	4454	132	0.029636282
	Pacific north temperate	1681	74	0.044021416
	South temperate and Antarctic	2721	44	0.016170526
	Tropical and subtropical Indo-Pacific	11627	248	0.021329664

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594 **S1 Table. Known vertebrate species ('Global estimate') for A. terrestrial and freshwater system and B.**
595 **marine system, compared to species recorded within the LPI database, and the proportion that this**
596 **represents of the global estimate.**

597

<i>Realm</i>	<i>Taxon</i>	<i>LPI</i>	<i>Known species</i>	<i>X-squared</i>	<i>Significant?</i>	<i>Representation</i>
<i>Afrotropical</i>	Amphibia and Reptilia	0.01	0.06	124.43	***	under
<i>Afrotropical</i>	Aves	0.04	0.05	6.9246	**	under
<i>Afrotropical</i>	Fishes	0.01	0.07	129.09	***	under
<i>Afrotropical</i>	Mammalia	0.05	0.03	35.812	***	over
<i>IndoPacific</i>	Amphibia and Reptilia	0.02	0.09	156.9	***	under
<i>IndoPacific</i>	Aves	0.10	0.08	6.142	*	over
<i>IndoPacific</i>	Fishes	0.01	0.06	101.97	***	under
<i>IndoPacific</i>	Mammalia	0.04	0.04	0.052703		over
<i>Nearctic</i>	Amphibia and Reptilia	0.05	0.02	119.44	***	over
<i>Nearctic</i>	Aves	0.18	0.02	2569	***	over
<i>Nearctic</i>	Fishes	0.03	0.02	25.611	***	over
<i>Nearctic</i>	Mammalia	0.03	0.01	80.342	***	over
<i>Neotropical</i>	Amphibia and Reptilia	0.03	0.11	154.45	***	under
<i>Neotropical</i>	Aves	0.12	0.09	28.984	***	over
<i>Neotropical</i>	Fishes	0.03	0.11	156.35	***	under
<i>Neotropical</i>	Mammalia	0.03	0.03	1.0265		under
<i>Palearctic</i>	Amphibia and Reptilia	0.01	0.03	18.953	***	under
<i>Palearctic</i>	Aves	0.14	0.04	603.68	***	over
<i>Palearctic</i>	Fishes	0.02	0.04	18.256	***	under
<i>Palearctic</i>	Mammalia	0.04	0.02	43.328	***	over

Table S2 – 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.**

<i>Realm</i>	<i>Taxon</i>	<i>LPI</i>	<i>Known species</i>	<i>X-squared</i>	<i>Significant?</i>	<i>Representation</i>
<i>Arctic</i>	Aves	0.03	0.00	119.51	***	over
<i>Arctic</i>	Fishes	0.01	0.01	0.14344		over
<i>Arctic</i>	Mammalia	0.01	0.00	136	***	over
<i>Arctic</i>	Reptilia					over
<i>Atlantic North Temperate</i>	Aves	0.06	0.01	178.72	***	over
<i>Atlantic North Temperate</i>	Fishes	0.14	0.07	60.29	***	over
<i>Atlantic North Temperate</i>	Mammalia	0.02	0.00	104.53	***	over
<i>Atlantic North Temperate</i>	Reptilia	0.00	0.00	12.053	***	over
<i>Atlantic Tropical and Sub-tropical</i>	Aves	0.05	0.02	57.566	***	over
<i>Atlantic Tropical and Sub-tropical</i>	Fishes	0.12	0.18	26.988	***	under
<i>Atlantic Tropical and Sub-tropical</i>	Mammalia	0.01	0.00	5.9825	*	over
<i>Atlantic Tropical and Sub-tropical</i>	Reptilia	0.01	0.00	133.22	***	over
<i>Pacific North Temperate</i>	Aves	0.05	0.01	268.02	***	over
<i>Pacific North Temperate</i>	Fishes	0.07	0.07	0.014773		under
<i>Pacific North Temperate</i>	Mammalia	0.03	0.00	182.46	***	over
<i>Pacific North Temperate</i>	Reptilia	0.00	0.00	10.71	**	over
<i>S.Temperate and Antarctic</i>	Aves	0.05	0.01	222.98	***	over
<i>S.Temperate and Antarctic</i>	Fishes	0.04	0.11	54.48	***	under
<i>S.Temperate and Antarctic</i>	Mammalia	0.01	0.00	3.2148		over
<i>S.Temperate and Antarctic</i>	Reptilia	0.00	0.00	1.60E-29		under
<i>Tropical and Sub-tropical Indo-Pacific</i>	Aves	0.05	0.03	15.201	***	over
<i>Tropical and Sub-tropical Indo-Pacific</i>	Fishes	0.22	0.47	259.04	***	under
<i>Tropical and Sub-tropical Indo-Pacific</i>	Mammalia	0.02	0.00	58.949	***	over
<i>Tropical and Sub-tropical Indo-Pacific</i>	Reptilia	0.01	0.00	19.335	***	over

Table S3 – 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.**

	Afrotropical	Nearctic	Neotropical	Palaearctic	Indo-Pacific
Fishes	0.32589	0.289108	0.328142	0.315503	0.218028
Birds	0.260032	0.264985	0.260027	0.295608	0.308086
Mammals	0.132963	0.175804	0.085695	0.170045	0.133595
Reptiles and amphibians	0.281115	0.270102	0.326136	0.218844	0.340291

S4 Table. Terrestrial and freshwater weightings applied to data. The values also represent the weighting applied to the data for each species group when calculating the realm and 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

S5 Table. Marine weightings applied to data. The values also represent the weighting applied to the data for each realm when calculating the system LPIs.

	Afrotropical	Nearctic	Neotropical	Palaearctic	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

S6 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

S7 Table. Marine realm weightings applied to data

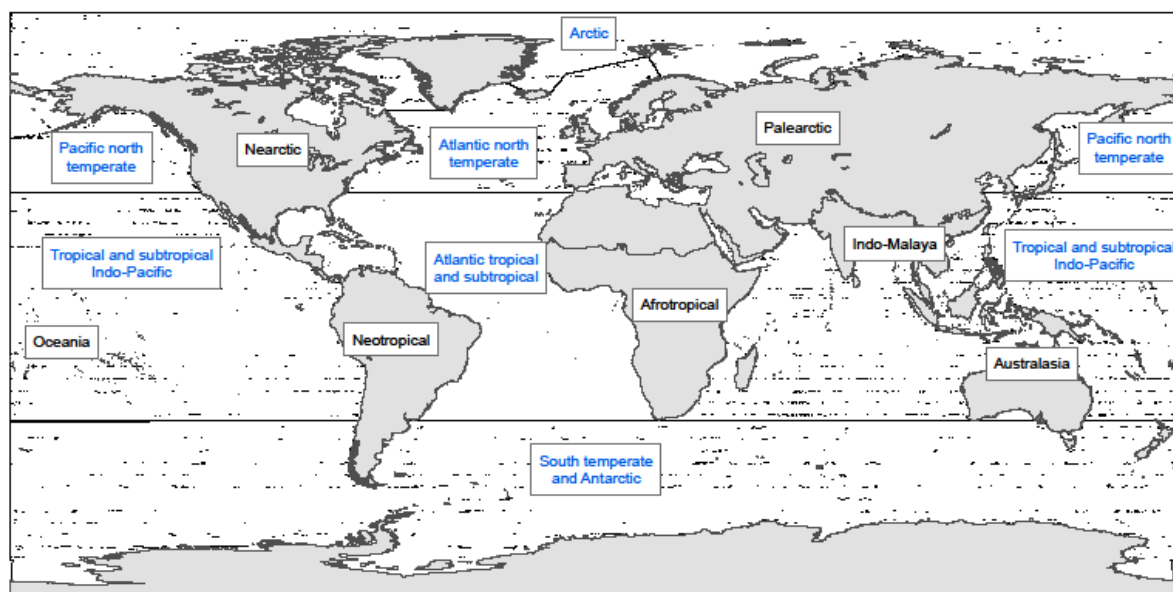


Figure S2: The boundaries for land and marine realms used for the geographical divisions of the LPI database