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

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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 Figure). 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 Figure).

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 (see Supplementary materials for more details). 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[1] (27) at https://github.com/Zoological-Society-of-London/rlpi. 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:

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

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

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

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:

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

[1] 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.

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 (Figure 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:

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

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.

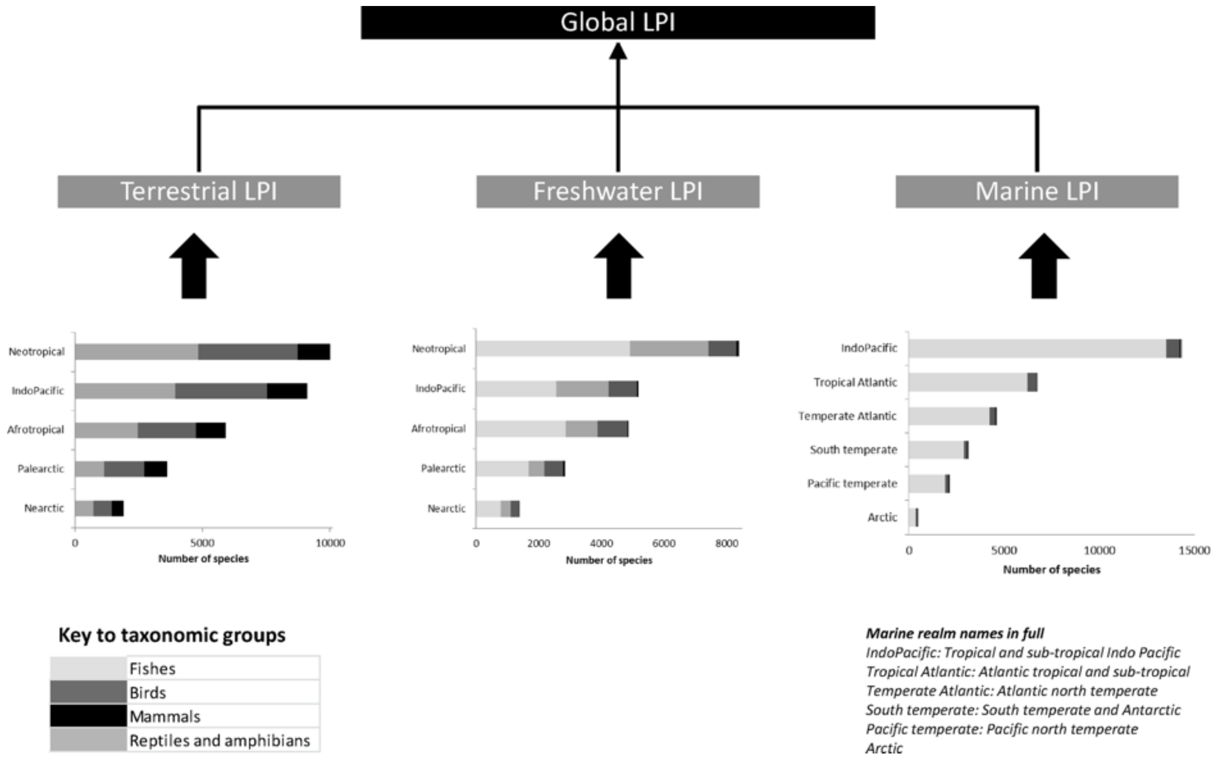

Figure 1 – Schematic of the weighting process. Systems (Terrestrial/Freshwater/Marine) are weighted equally. Within each system, the proportion of species found across the realms that compose that system (the length of the bars above) is used to proportionally weight each realm's index. Within each realm,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

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.

```
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
```

Box1: Pseudocode outlining the algorithm for constructing the global Living Planet Index

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).

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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 (Figure 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. (χ^2=0.004, *df*=1, *p*=0.95), and more than the expected 13% (χ^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 (Table S3). 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).

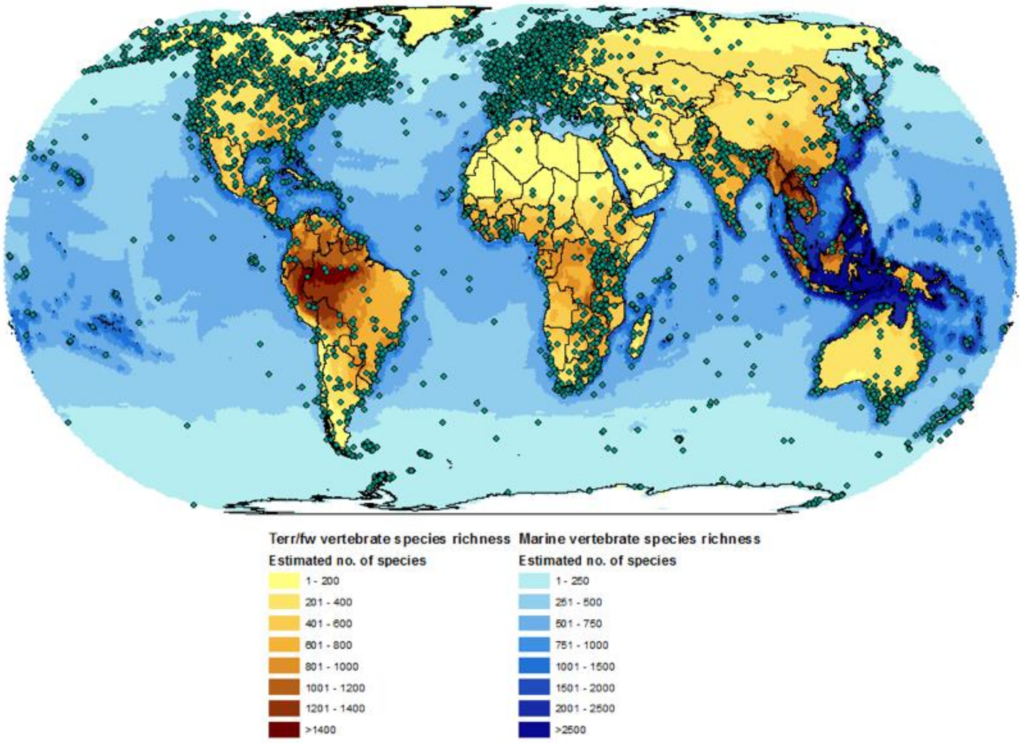

Figure 2: Global vertebrate richness map overlaid with populations recorded in the Living Planet Database. Species richness map reproduced from (20)

Taxonomic representation and bias within the Living Planet Index

Figure 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 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).

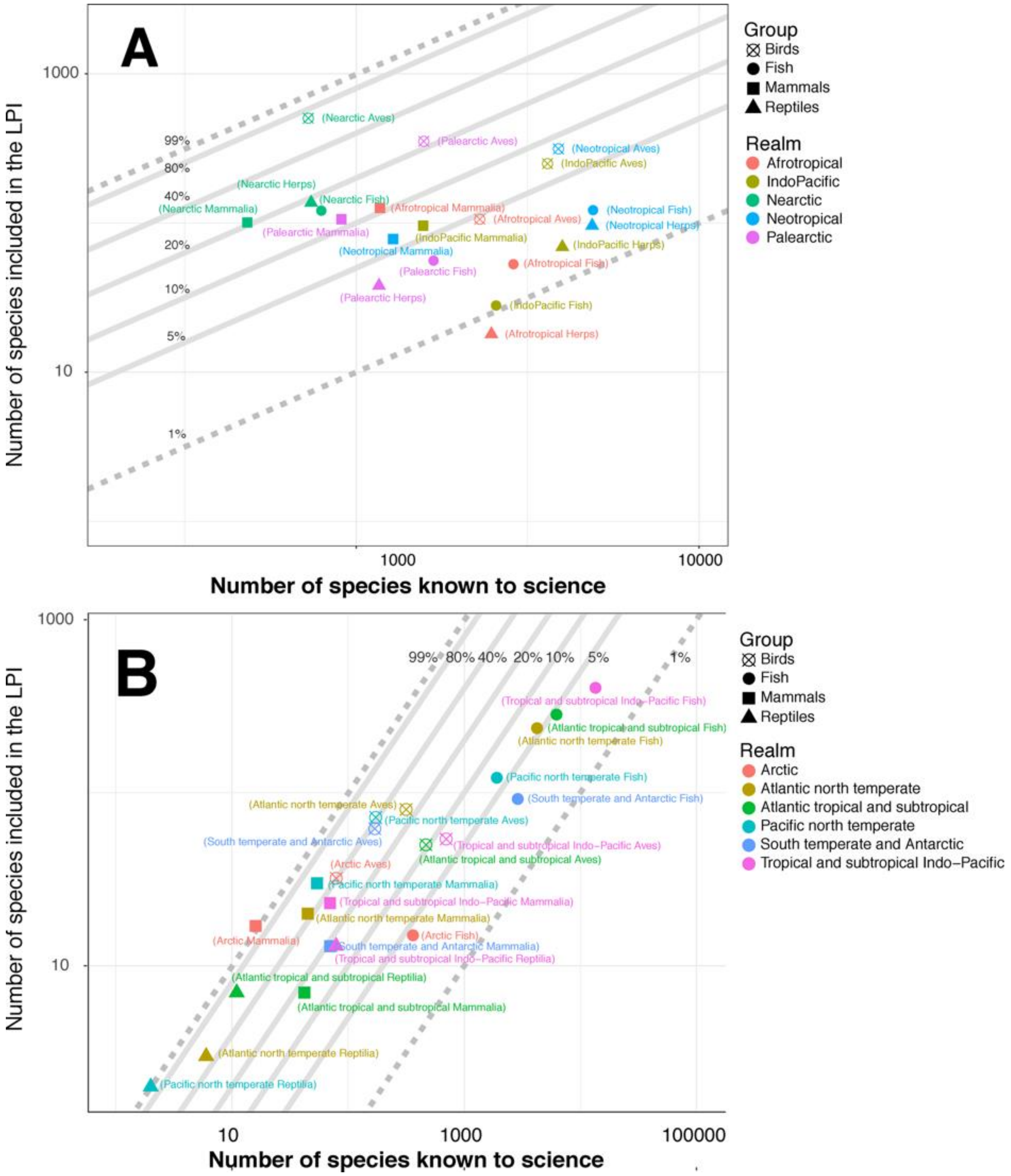

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Figure 3 – Comparison of number of known species and number of species recorded within the Living Planet Database. Colours represent different biogeographic realms, shapes indicate species groups and overlaid lines show 1 and 99% representation (dotted)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

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 (Figure 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 (S6ATable). 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.

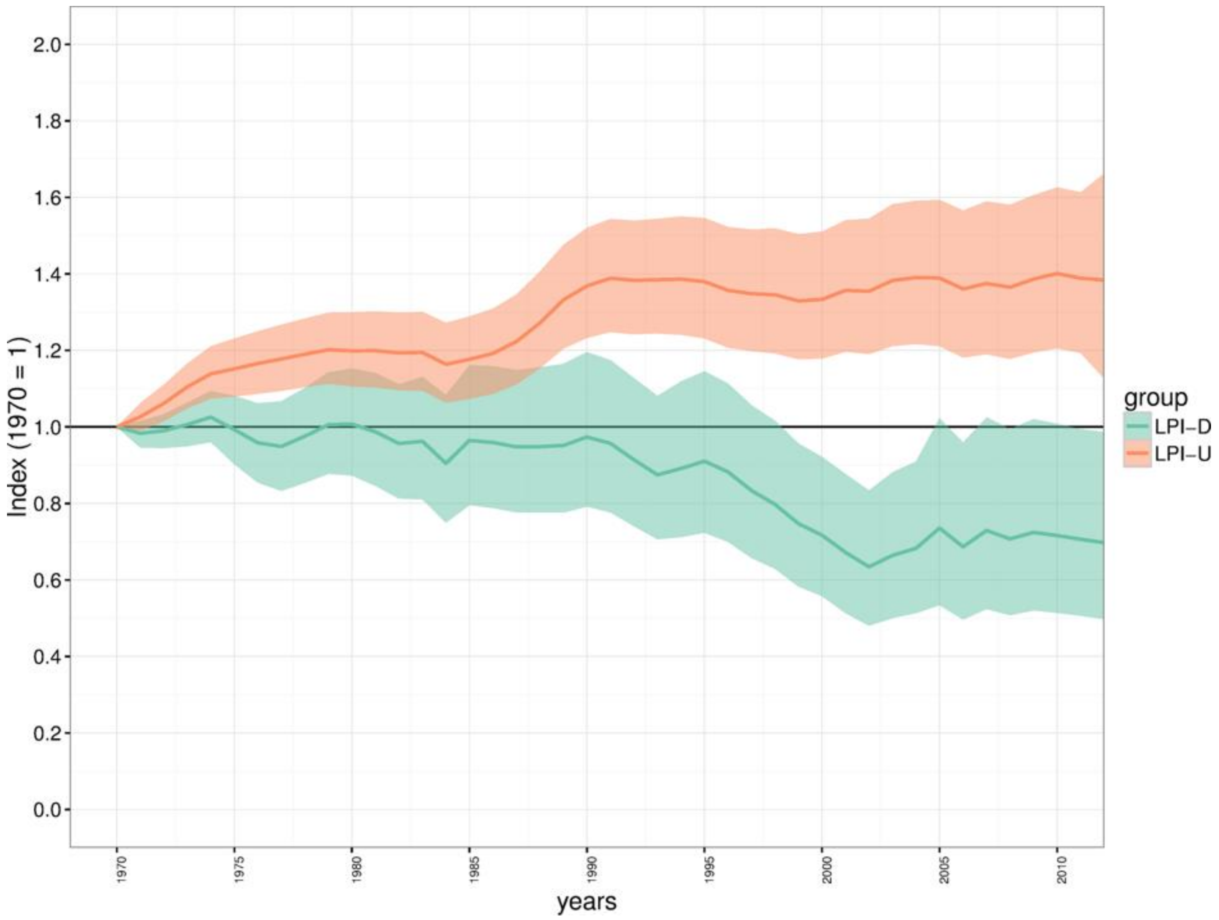

Figure 4 - Comparison of the unweighted and diversity weighted Living Planet Index for the Palearctic realm. Green shows the unweighted index (LPI-U), orange shows the diversity weighted index (LPI-D). Solid coloured lines show the average trend and shaded regions show the 95% confidence interval of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

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 (Figure 5) which equates to an average annual decline of 2% per year. This

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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.

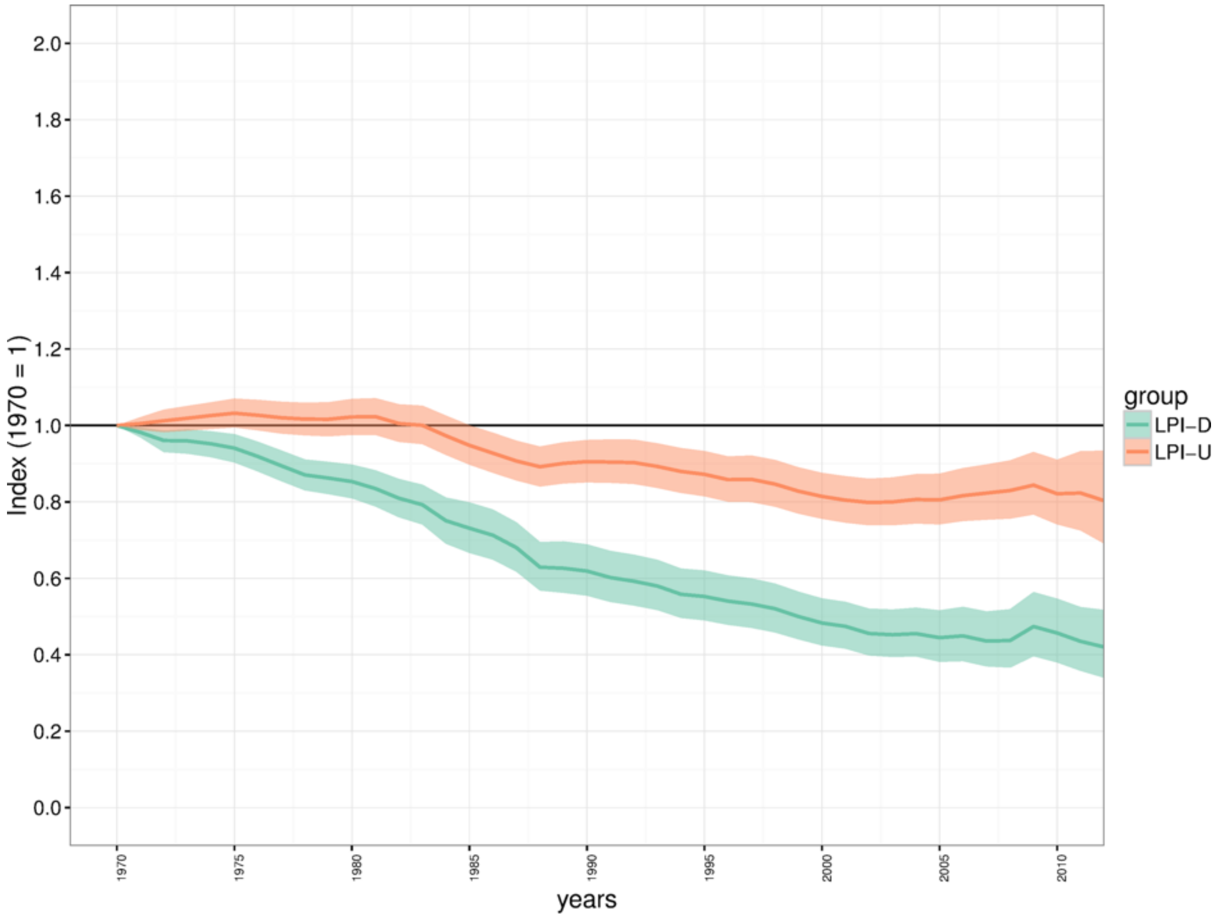

Figure 5 - Comparison of the unweighted and diversity-weighted Living Planet Index for the global data set. Green shows the unweighted index (Global LPI-U), orange shows the diversity weighted index (Global LPI-D). Solid coloured lines show the average trend and shaded regions show the 95% confidence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

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 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.

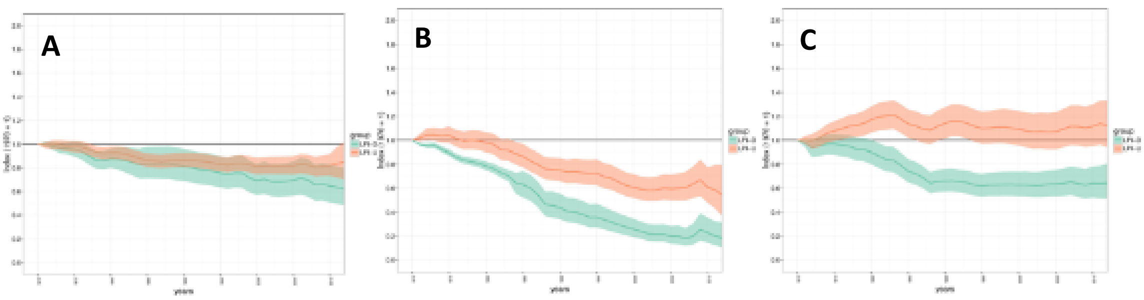

Figure 6 - Comparison of the unweighted and diversity weighted Living Planet Index for each System (A - Terrestrial, B -Freshwater and C -Marine). In each case, green shows the unweighted index (LPI-U), orange shows the diversity weighted index (LPI-D). Solid coloured lines show the average trend and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

	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

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.

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. Figure 7 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 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.

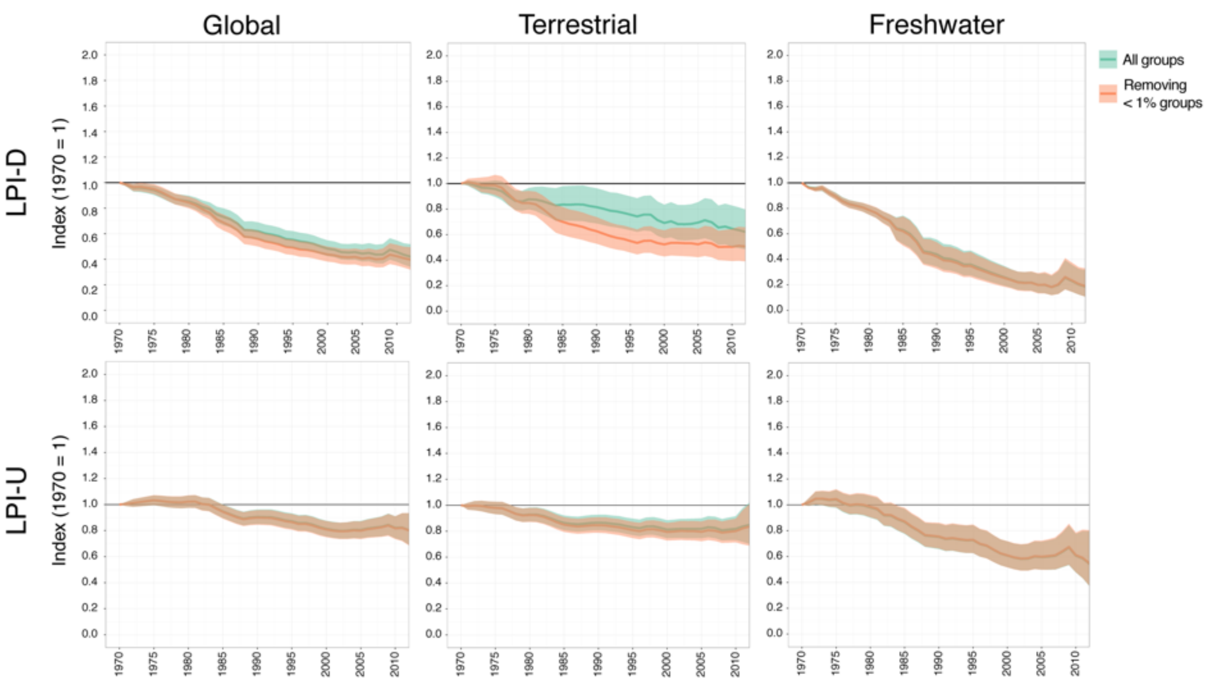

Figure 7 – The impact of removing species groups for which the Living Planet Database has < 1% representation. Green trends show the Living Planet Index for all groups, orange trends show trends without

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.

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 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.

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*		

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). 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.

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

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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 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, Figure 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 (Figure 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% (Figure 4) in the 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 Figure), 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 (Figure 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 (Figure 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.

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Supporting Information

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

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

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).

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*.

S4 Table. 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*.

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).

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.

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.

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.

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

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

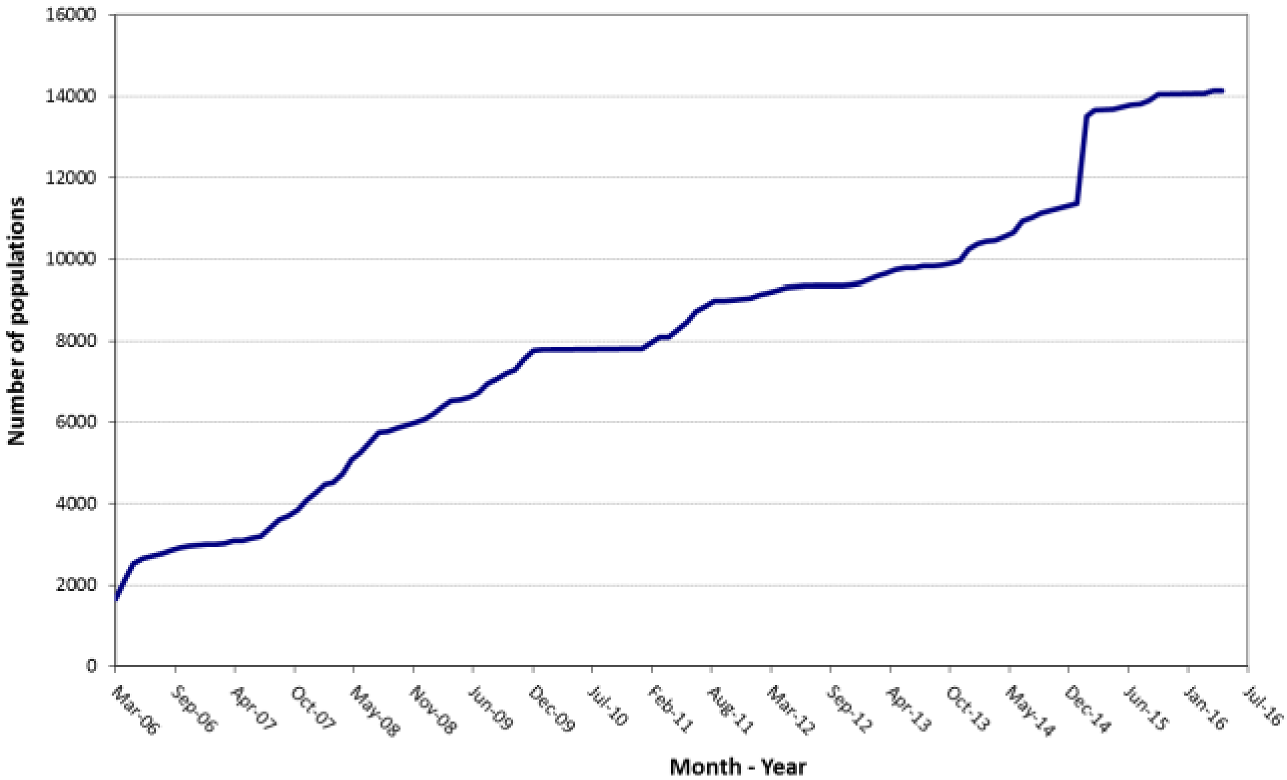
S10 Table. Terrestrial and freshwater weightings applied to taxa/realm subsets within the global LPI. The values also represent the weighting applied to the data when calculating the system LPIs.

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.

S12 Table. Terrestrial and freshwater realm weightings applied to data

S13 Table. Marine realm weightings applied to data

S2 Figure. 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 Figure. The cumulative number of population time series in the global LPI from 2006 to 2016.

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*.

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

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

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	***

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).

		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

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*.

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).

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

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*.

Income category	No. of countries	Proportion (Martin, expected)	Proportion (LPI)	χ2	df	p-value	Sig	Representation
High	57	0.25	0.49	137.21	1	0.00	***	over
Low	36	0.13	0.15	2.42	1	0.12	NS	NS
Lower middle	47	0.16	0.17	0.37	1	0.54	NS	NS
Not listed	11	0.00	0.00	0.19	1	0.66	NS	NS
Upper middle	50	0.46	0.19	175.39	1	0.00	***	under
Higher (High + Upper middle)	*107*	*0.71*	*0.68*	*2.58*	*1*	*0.11*	*NS*	*NS*
Lower (Low + Lower middle)	*83*	*0.28*	*0.32*	*2.89*	*1*	*0.09*	*NS*	*NS*

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).

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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.

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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.

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		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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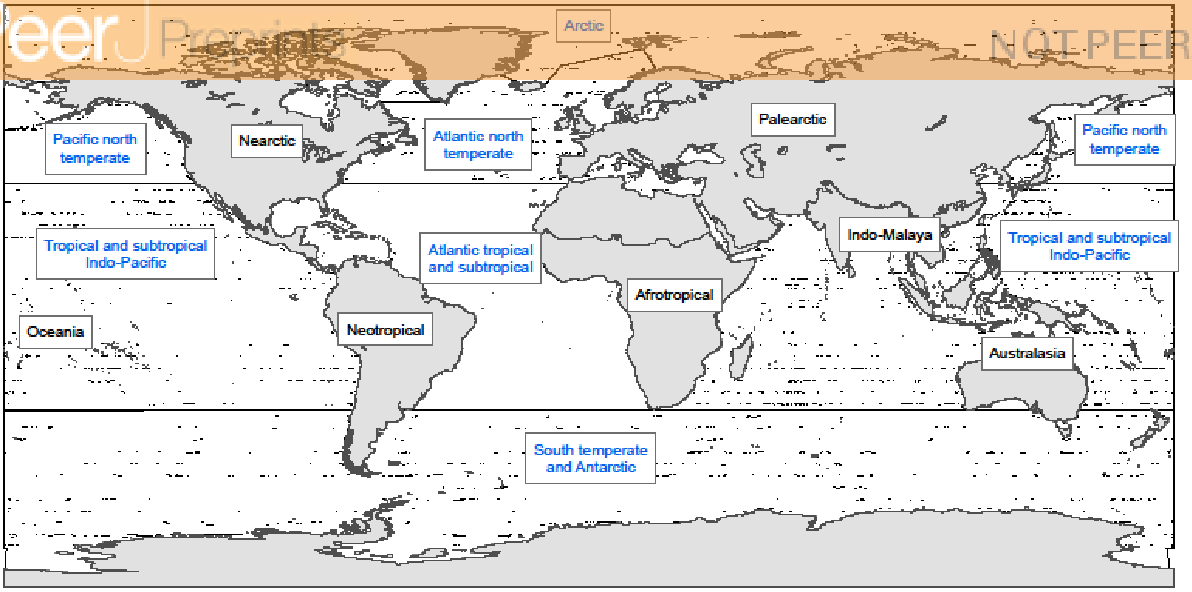

S2 Figure. The boundaries for land and marine realms used for the geographical divisions of the LPI database. Terrestrial realm data from Olson et al., (2001) and marine realms were drawn in ArcGIS 10.2.2 for Desktop.

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