

LIFE: A metric for quantitatively mapping the impact of land-cover change on global extinctions

Alison Eyres^{1,2}, Thomas S. Ball^{1,2}, Michael Dales^{2,3}, Tom Swinfield^{1,2}, Andy Arnell⁴, Daniele Baisero⁵, América Paz Durán⁶, Jonathan M. H. Green⁷, Anil Madhavapeddy^{2,3}, Andrew Balmford^{1,2*†}.

¹ Department of Zoology, University of Cambridge, Cambridge, UK

² Conservation Research Institute, University of Cambridge, Cambridge, UK.

³ Department of Computer Science and Technology, University of Cambridge, Cambridge, UK

⁴ UN Environment Programme World Conservation Monitoring Centre, Cambridge, UK

⁵ Key Biodiversity Areas Secretariat, c/o BirdLife International, Cambridge, UK

⁶ Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile

⁷ Stockholm Environment Institute York, Department of Environment and Geography, University of York, York, UK

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Main Text

Summary

Tracking and preventing continued extinctions requires robust spatially explicit metrics quantifying the impacts of human activities on habitat extent. Existing metrics either fail to consider species identity or focus solely on recent habitat losses. The persistence score approach represented an important development by combining species ecologies and land-cover data whilst considering the cumulative and non-linear impact of past habitat loss on species' probability of persistence. However, it is computationally demanding, limiting its global use and application. Here we couple the persistence score approach with high-performance computing to generate global maps of what we term the LIFE (Land-cover change Impacts on Future Extinctions) metric for 29153 species of terrestrial vertebrates at 1 arc-minute resolution (3.4km² at the equator). These maps quantify, for the first time, the marginal changes in the expected number of extinctions caused by (1) converting remaining natural vegetation to agriculture, and (2) restoring farmland to natural habitat. We demonstrate statistically that this approach integrates information on species richness, endemism, and past habitat loss. Our resulting maps can reliably be used at scales from 0.5-1000km², and offer unprecedented opportunities to estimate the impact on extinctions of diverse actions, from dietary choices right through to global protected area development.

1. Introduction

Biodiversity loss is one of the greatest environmental challenges of our age, with declines associated with significant negative impacts on human wellbeing (1). Tracking and mitigating these losses requires robust, spatially explicit biodiversity metrics for monitoring overall trends, identifying where conservation actions might be most effective, and measuring progress towards local-to-global biodiversity targets (2,3). As land use change is and will for a considerable period remain the largest single threat to species (4–6) it is particularly important that biodiversity metrics are capable of directly linking trends in land use with changes in biodiversity.

*Author for correspondence (a.balmford@zoo.cam.ac.uk).

†Present address: Department of Zoology, University of Cambridge, Cambridge, UK

While biodiversity is complex and multifaceted, metrics used in conservation arguably represent two primary motivations: preventing species loss (7), and maintaining the integrity of ecosystems and their contributions to people (1). In broad terms such metrics typically comprise measures of spatial variation in extinction risk of species and intactness of ecosystems, respectively. Measures of extinction risk commonly incorporate features such as the number of species present in an area, their range sizes (and hence how important the area is for their persistence globally), and descriptions of how population sizes or ranges have changed or might do so. Intactness on the other hand describes anthropogenic impacts on biological communities, with declines in intactness taken to indicate reductions in ecosystem functions and associated ecosystem services. The agreed importance of both these motivations is evident in their inclusion in global biodiversity targets – with Target 2 of the 2030 Global Biodiversity Framework, for instance, calling for the enhancement of the integrity of degraded habitats, and Target 3 calling for the reduction of extinction risk and halting of extinctions.

To track variation in extinction risk or ecosystem intactness, and to identify the likely positive or negative impacts of anthropogenic actions in different places, we suggest that metrics should:

1. Strive to be representative - geographically, taxonomically and in terms of habitat types. Given marked differences in the availability of data for different regions, taxonomic groups, and habitat types, unrepresentativeness is a significant limitation of several metrics. For example the Living Planet Index (8) uses data only for vertebrates, much of it from Europe and North America, though in this case substantial efforts are made to adjust statistically for differences in the coverage of different classes and regions (9). IUCN's Species Threat Abatement Restoration metric STAR) (4) currently focuses exclusively on threatened species of amphibians, birds and mammals. Some other metrics, such as the Biodiversity Intactness Index (BII) (10), are based on data which are more representative taxonomically – in this case measures of relative abundance of nearly 60,000 non-threatened as well as threatened plant and animal species.
2. Be comparable across space and direction of biodiversity change (that is, when comparing gains and losses). Spatial comparability means that a given score for the metric in one location is equivalent in terms of the broad outcome of interest (extinction risk or ecosystem intactness) to the same value in any other location, and that an area with twice that value is twice as important. Spatial comparability is essential when comparing actions in different locations – and so is of particular relevance in setting spatial priorities, in assessing the impacts of actors (e.g. international NGOs or corporations) who operate in different countries, or understanding the contribution of national activities towards global targets (2). Directional comparability – where a score of x is equal and opposite to a score of $-x$ – is essential when there is interest in identifying opportunities to mitigate damaging operations through remedial actions elsewhere (although of course where those actions involve habitat restoration additional safeguards are necessary because of time lags and uncertainties in habitat recovery).
3. Be amenable to aggregation and disaggregation according to species, ecosystems and other factors. This can be useful where stakeholders are interested only in certain taxonomic groups, charismatic species or biomes, and can allow for analyses of the impacts of particular threatening processes, as well as the sensitivity of observed patterns to unrepresentativeness of the underlying data. Many metrics, however – such as Mean Species Abundance (11) – are not readily disaggregated, as species identity is not retained through computation.
4. Finally, to be useful in guiding real-world actions which vary in area it is important that biodiversity metrics provide information that is scalable without the need for extensive additional analysis. If an action is larger than the grid size at which the metric is presented can its impact be reliably estimated by using the scores for component grid cells – and likewise does the score for a grid cell reliably indicate the value of action smaller than one grid cell? To what degree can published maps of metric scores be used, without rerunning the underlying algorithms, to assess the biodiversity impact of restoration or conversion actions which are much larger or smaller than the grid cells used to derive the maps?

2. The persistence score

One relatively new metric which describes spatial variation in the importance of different areas for avoiding species extinctions while largely meeting these requirements is Durán et al.'s (2020) (12) persistence score. This uses species-specific distribution and habitat suitability information to estimate the consequences of changes in land-cover for the modelled probability that species will persist (i.e. avoid extinction), relative to their probability of persistence in the absence of anthropogenic habitat change (see Conceptual basis below). Changes can be gains or losses of suitable habitat, with negative scores equal and opposite to positive ones. Uniquely, the persistence score also accounts explicitly for two critically important issues which are overlooked in other metrics: the non-linear relationship between habitat loss and changes in species' probability of persistence; and the cumulative impact of habitat loss over the long term, rather than just recent changes.

In principle, the change in a species' probability of persistence of retaining or restoring natural habitat in any given location can be estimated for all species whose global range and ecological requirements are known. Initial analyses applied the method to 1368 amphibian, bird and mammal species as well as 641 plants in the Brazilian Cerrado (12,13). Because the metric is comparable across space, it was possible to estimate the changes in probability of persistence for all species as a consequence of sourcing soy from different parts of the Cerrado. Because results can be disaggregated, impacts on the probability of persistence of individual charismatic species (such as giant anteaters and jaguars) could also be derived. However, despite persistence scores having several desirable properties, their derivation for large numbers of species is computationally demanding, and so they have had limited uptake at global scale (14) and at the high resolution needed to accurately align species habitat and elevation requirements..

In this paper we develop the persistence score into a globally useful metric – hereafter called LIFE (for Land-cover change Impacts on Future Extinctions) - by generating global maps that summarise at 1 arc-minute resolution the impact on the expected number of extinctions of all mappable terrestrial vertebrate species of two archetypal land-cover changes: i) converting natural habitat and pasture to arable, and ii) restoration of current pasture and arable to its natural state. Conversion to arable land was chosen because food and farming are responsible for more biodiversity loss than any other sector (4–6) and so maps of where agricultural impacts will be most acute are useful in guiding conservation management and policy decisions. We focused on restoration because of its high profile in international policy (15), including within the [United Nation's decade on Ecosystem Restoration](#), and because mapping its potential impact provides information on where actions to reverse past habitat losses would be most effective. To better understand what the LIFE metric represents, for each of these mapped layers we investigate how our scores vary with an area's species richness, endemism and degree of habitat loss to date. Because persistence scores explicitly assume non-linear relationships between habitat loss and extinction risk we also examine their scalability - the extent to which aggregated scores can be relied upon when actions are smaller or larger than the size of the grid cells for which they are derived. Finally, we explore the sensitivity of our findings to different assumptions about how the probability of persistence responds to losses or gains of suitable habitat (i.e. to the shape of the persistence-habitat loss curve), and how far our results differ across major taxonomic groups. We begin, though, by explaining how persistence scores are derived.

3. Conceptual basis of persistence scores

The fundamental premise underpinning the derivation of the LIFE score is that as the total Area of Habitat (AOH) occupied by a species is reduced below that occupied prior to human actions, its probability of persistence relative to a pre-human background level decreases in a continuous and non-linear manner. Many approaches instead assume extinction risk only depends on contemporary change in AOH: that a 100km² loss of habitat for a species' currently occupying 1000km² has the same effect regardless of whether prior to people it occupied 1000 or 1 million km² (16–18). However, there is substantial evidence that the impacts of habitat loss on species persistence are typically cumulative and non-linear, with the effect of losing a given quantity of

habitat increasing as the remaining habitat diminishes, and hence also dependent on historic habitat changes (19,20). Because different regions have been subject to anthropogenic pressures at different points in the past (21), estimating the impact of contemporary changes in AOH thus necessitates information on each species' pre-human (hereafter "original") habitat area.

Figure 1 sets out how Durán et al. (2020) incorporated both original habitat extent and the non-linear impact of habitat loss on a species' probability of persistence (12) using, for illustration, a power-law persistence-habitat loss curve with an exponent of 0.25. The probability of persistence is expressed as a function of the proportion of AOH remaining relative to a species' original AOH, and so has a maximum value of 1 when a species occupies more than or equal to its original AOH. The curve describes how the probability of persistence p responds to changing AOH h , with a decrease from h_1 to h_2 causing p to decline by a value Δp , from p_1 to p_2 . The shape of the curve means that if a species currently occupies a smaller fraction of its original AOH ($h_3 < h_1$), the same absolute loss of AOH ($h_3 - h_4 = h_1 - h_2$) causes a greater reduction in persistence ($p_3 - p_4 = \Delta p' > p_1 - p_2 = \Delta p$).

If the range and habitat preferences of a given species are known, this method can then be used to estimate the impact on its global probability of persistence of changing land use within any area (such as a grid cell) from natural to human-dominated land cover, or the reverse. The LIFE score describing the marginal impact of that land-cover change is then the summed impact on all species whose original AOH overlaps the cell. These calculations obviously require estimates of each species' current and (critically) original AOH; and will vary with the assumed shape of the curve relating persistence to habitat loss. The following sections explore these two issues in detail.

4. Generating current and original Areas of Habitat

To derive global maps of the LIFE score for future land-cover changes we first calculated current and estimated original AOH for all terrestrial vertebrate groups (amphibians, reptiles, birds and mammals) (22). We did not include species with missing data, those which rely exclusively on marine habitats at any stage of their life cycle, those which inhabit caves or subterranean habitats, or those where mismatches between range maps, habitat maps and habitat preferences result in no measurable AOH either currently or in the past. This left us with 29153 species (6515 amphibians, 8240 reptiles, 9206 birds and 5192 mammals). Current and original AOHs were generated for each species following Brooks et al. (2019) (23–25) (see Coda). For current AOH we used a map of the estimated distribution of habitats (26) in 2016. For original AOH we used a map of Potential Natural Vegetation (PNV) (27) which reflects the distribution of habitat types in the absence of human impacts. The current layer maps IUCN level 1 and 2 habitats, whereas habitats in the PNV layer are mapped only at IUCN level 1, so for consistency we used natural habitats mapped at level 1 and artificial habitats at level 2. We overlaid these two habitat surfaces with species' range maps from IUCN and Birdlife International and a Digital Elevation Model (28,29), and estimated AOH for each species' range as those parts which are (or were) suitable based on its elevation and habitat preferences (from IUCN) (22). Species range polygons are coded based on species' presence, origin and seasonality. We included those parts of a species' range where its presence is 'extant' or 'possibly extinct', its origin is 'native', 'reintroduced' or 'uncertain' and the seasonal occurrence is 'resident', 'breeding', 'non-breeding' or 'unknown'. When generating original AOH maps we also included range polygons coded as 'extinct', acknowledging that these data are incomplete, particularly for amphibians. For species which exhibit seasonal habitat preferences AOH was calculated separately for the breeding and non-breeding season.

For each species, we then calculated the extant proportion of its original AOH as the ratio of its current to original AOH (Fig. 2). This analysis reveals that 14.3 % of species have a larger estimated AOH currently than prior to people, implying that human-mediated land use change has enabled these species to expand their distributions. Across all species, the geometric mean proportion of AOH remaining is 0.80. However, this figure is strongly influenced by substantial AOH expansions among some of those species that have

apparently benefitted from human activity. Focusing instead on the 86% of species that have instead declined, their geometric mean proportion of AOH remaining is 0.62.

5. Using current and original AOH to estimate marginal changes in probability of persistence

Following Durán et al (2020) (12), for each species we then used our estimates of its current and original AOH to estimate the marginal impact of two contrasting sets of land-cover changes: the conversion of remaining natural habitats and pasture to arable land (our ‘conversion scenario’), and the restoration of non-natural habitats (the ‘restoration scenario’). In the conversion scenario all habitats currently mapped as natural or pasture were converted to arable land. In the restoration scenario the current habitat map was modified by converting areas classified as arable or pasture to their potential natural habitat, as mapped by Jung et al. (2022) (27). In effect here we are treating pasture as a semi-natural habitat which, despite often being actively managed, can still harbour substantial levels of biodiversity and therefore sits between natural and arable land. In both scenarios, land currently classified as urban was left unmodified because it is highly unlikely that either farmland expansion or restoration will encroach into existing urban areas. We estimated the effect on each species’ AOH of any conversion or restoration occurring in its current range polygon, even if that fell outside its current AOH - so under conversion a species tolerant of arable could expand its AOH into previously unoccupied parts of its range, while under restoration a species intolerant of cropland could expand back into restored natural habitat.

Scenario-specific changes in AOH were calculated at the scale of 100m pixels and then aggregated into 1 arc-minute grid cells (approximately 1.86 x 1.86 km [3.4km² in area] at the equator) to facilitate downstream computation while still providing results at a fine enough scale to inform real-world decision-making. Next, for each species we then translated the scenario-driven change in its AOH into a cell-specific change in its global probability of persistence (following the approach summarised in Fig. 1). The “true” form of the persistence-habitat loss curve is of course not known and is likely to vary across taxa. Here we followed previous studies using the persistence score approach by assuming an exponential function with an exponent of 0.25 (12–14,30) but we also tested the sensitivity of our broad findings to this assumption by using several alternative curve shapes (see Sensitivity analyses below). Where the current or scenario estimate of a species’ AOH exceeded its original AOH we capped its probability of persistence at 1 (30). For migratory species, probability of persistence in any scenario was derived separately for the species’ breeding and non-breeding ranges, with the overall persistence score for a given set of habitat changes then calculated as the difference between the geometric means of their breeding and non-breeding probabilities of persistence before and after the changes (based on Equation 3 of Durán et al. 2020; see section S3).

In the last stage, we summed the persistence scores for all the species found in the cell. Significantly, this summed value of persistence scores across species in a grid cell is numerically equal to the expected number of extinctions caused by conversion or restoration of that grid cell (for proof, see section S2). Finally, because the area undergoing change varies widely across cells, we divided the summed persistence scores by the area (in km²) of the cell restored or converted under that scenario, to obtain an overall LIFE score describing the likely impact on expected number of extinctions of restoring or converting 1km² of land. The scaling error associated with summing and then averaging 100m pixel changes in this way is explored under Scalability, below.

6. Global maps of the LIFE score

The resulting LIFE score maps for our conversion and restoration scenarios (Fig. 3) prompt two overarching observations. First, while the summed per-km² impacts on extinction of converting remaining habitats and pasture to arable land are very largely negative and those of restoring natural habitats very largely positive, the losses from conversion tend to be both greater and more widely distributed than the gains from habitat restoration. The relatively lower and patchier gains from restoration arises because many grid cells currently

have relatively little area under farming, and because to date there has been no conversion (at 100m-resolution) in some 1 arc-minute grid cells of exceptional importance for vertebrate biodiversity. This overall comparison of the maps means that at global scale we have far more to gain through habitat retention than through restoration. The importance of retaining existing natural habitats is underscored by the delayed and in many cases uncertain impacts of habitat restoration compared with conversion (31,32): any benefits plotted in our restoration surface are less clearcut and would likely take far longer to materialise than the increases in extinction risk shown in our conversion map.

A second observation is that for both scenarios LIFE scores are highly skewed, with the majority of regions having relatively low values and a few regions scoring very highly. The conversion map highlights areas with high levels of vertebrate endemism including several species-rich regions – such as the Guiana Shield, Cameroon, New Guinea and northern Australia - where to date clearance for agriculture has been relatively limited. Under restoration, by contrast, the highest LIFE scores correspond to areas known to have large numbers of relatively narrowly-distributed vertebrates which have already undergone extensive conversion to agriculture – including much of Brazil’s Atlantic Forest, eastern Madagascar, the highlands of Ethiopia, and the Philippines. In the next section we set out a more formal exploration of these spatial patterns.

7. Dissecting spatial variation in LIFE scores

To explore what LIFE scores represent, we investigated how well their spatial variation is predicted by three key components of the importance of land-cover change for global extinctions: species richness, the degree of endemism of the species present, and the extent to which the species have already lost suitable habitat anywhere in their ranges. Because LIFE scores are summed across species, we anticipated they would covary positively with species richness. Because a unit area of land-cover change should have a greater impact on the probability of persistence of species with smaller global ranges, we expected LIFE scores should be higher in grid cells whose species are on average more narrowly endemic. And, because we consider that any given loss of AOH impacts more heavily those species which have lost more habitat already (Fig. 1), we expected positive associations between LIFE scores and the average proportional loss of AOH to date of those species present.

To test this, we calculated: richness as the number of species whose ranges overlapped a grid cell, endemism as the mean proportion of each species’ current total AOH made up by the cell, and habitat loss to date as the mean proportion across each of its species of their original AOH which is no longer suitable for them (Fig. S4). We then tested for correlations between log₁₀-transformed LIFE scores and the three predictor variables, including a spatial smoothing function for geographic location, by randomly sampling 170,000 cells (0.32% and 0.96% of the data for conversion and restoration respectively) without replacement and calculating mean standardized effect sizes across 200 independent runs. Conversion and restoration impacts were modelled separately, only considering losses and gains respectively in each.

These analyses confirmed our understanding of what is captured in LIFE scores (Table 1). Conversion and restoration scores were greater for grid cells with higher species richness of terrestrial vertebrates, cells whose species on average exhibit greater endemism, and cells whose species have already lost more of their original AOH. Standardized effect sizes were greatest for endemism, but all had relatively narrow confidence intervals across independent model runs. The modelled deviance explained ranged from 79.4 - 89.6% and 69.1 - 76.4% for conversion and restoration respectively.

8. Scalability of LIFE scores

A central conceptual premise of the LIFE framework is that the relationship between a species’ remaining AOH and its probability of persistence is non-linear. This means that the per km² impact on extinction risk of an action that is larger than the grid cell size at which an impact is computed is not exactly the same as the average across all affected grid cells, and that of a smaller action is not the same as that of the grid cell which

overlays it. However, running bespoke persistence calculations at the scale of any specific action would be impractical for most end-users, so instead we ran two sets of simulations to examine how far “true” LIFE scores derived at exactly the scale of an action deviate from those estimated simply from using our existing 1 arc-minute results. This deviation will depend on each species’ proportion of AOH remaining, the shape of the persistence-habitat loss curve, and the size of the action.

Spatially modelling hundreds of actions was computationally prohibitive, so to test the scalability of our maps we opted for a non-spatial statistical-modelling approach, focused on five regions: South America, sub-Saharan Africa, south-eastern Asia, western Europe, and northern Asia (Russia and Mongolia). For each region we calculated the proportion of AOH remaining for each species present. To examine the scalability of our mapped LIFE scores for actions larger than our grid cells we modelled 1000 actions across geometrically distributed sizes, ranging from the native resolution (3.4 km² at the equator) to 10 million km². For each action, the probability that a species was affected was governed by the portion of its AOH overlapping the region and the area of the action. The appropriate number of grid cells for the action size was then iteratively scattered across the region without replacement, with each having a chance to hit a given species. This procedure is essentially equivalent to assuming a homogenous random distribution of species within the region. Then, for each species we calculated the “true” impact of the simulated land-cover change and that derived from the grid cell values, expressed this deviation as a fraction of the “true” value, and summed these relative deviations across all species. We repeated the process for a total of 100 actions of each size.

These simulation exercises suggested that our mapped surfaces can be used to impute the approximate per-km² impact on extinctions of actions ranging up to 1000km² in size. Figure 4a shows how the summed relative deviation between the true and grid cell-derived values varies with action size. In western Europe and northern Asia the incurred error remains <10% for actions up to 30,000 km² and 40,000 km² respectively. SE Asia, South America and Sub-Saharan Africa reach 10% mean deviation at just under 1000km². These regional differences reflect the generally greater relative losses of species’ AOH at lower latitudes.

Adopting a similar modelling approach to test the validity of using mapped LIFE values for actions which are smaller than our mapped grid cells, we used the same sets of species and modelled 100 actions ranging in size from 0.05 to 1 arc-minute on the side (0.17 to 3.4km² at the equator). When calculating the “true” value of the simulated land-cover change, the area which the action alters within the grid cell is known and is added or removed from each species’ current AOH as appropriate. The fractional value on the other hand is calculated by multiplying the average LIFE score per unit area in the cell (which assumes land use changes across the entire cell) by the area of the action. Figure 4b shows the results of this process. The mean summed deviation between the “true” and grid cell-derived value remains low right down to 0.05 arc-minute actions (where it reaches ~7% in SE Asia and less elsewhere). However, here the uncertainty in this deviation is $\pm 25\%$, so we advise caution when using grid cell values for very small actions.

9. Sensitivity analyses

We tested the sensitivity of spatial variation in LIFE scores to: i) the assumed shape of the relationship between a species’ probability of persistence and loss of its habitat, and ii) what groups of species are included in the analysis.

Sensitivity to changing the persistence-habitat loss curve

The relationship between incremental losses of a species’ habitat and its risk of extinction is unknown, and likely to vary widely across species: modes of reproduction and dispersal, evolutionary history, and vulnerability to other threats may each shape how species’ populations respond to anthropogenic habitat loss (33). For our main analyses we followed other studies (12–14,30,34) in assuming all species exhibit an exponential persistence-habitat loss curve with an exponent of 0.25, but we also explored how our two LIFE

score surfaces differed using exponential curves with exponents set to 0.1, 0.5 and 1.0 (the latter indicating a linear response to habitat loss), and assuming persistence changes according to a modified Gompertz curve (see Fig. S1 for curve shapes).

The LIFE score maps generally pick out the same broad regions of the world as being important for conversion and restoration regardless of curve specification – typically species-rich parts of the tropics and subtropics (Fig. S5). However, comparison of the maps also shows, as might be expected, that assuming higher exponents tends to increase the homogeneity of LIFE scores: the impact of a unit area of habitat conversion (or restoration) becomes less sensitive to how much habitat conversion has already taken place. At the extreme, if persistence responds linearly to reductions in AOH (i.e. $z=1.0$), the loss of a given area of habitat has the same impact regardless of how much of a species' AOH has already cleared. If the assumption of a linear fit is biologically inappropriate (19) it thus risks underestimating the impact of losing (or restoring) the last remaining areas of habitat in highly converted regions, whilst overestimating the impact of changes elsewhere. Conversely maps generated with z set to 0.1 and especially those assuming a modified-Gompertz relationship show greater spatial variation in LIFE scores, and suggest the impacts of restoration or conversion would be relatively greater in regions which have already undergone extensive habitat clearance.

Variation across taxonomic groups

Disaggregating LIFE scores by major taxonomic group (amphibians, reptiles, birds, mammals) again suggested our metric is broadly robust at coarse scale (see Fig. S6): for each of our taxonomic groups the same regions would generally experience marked (and others, negligible) changes in species persistence following habitat conversion or restoration. However, there are some interesting differences when amphibians or reptiles are considered in isolation. For amphibians, land-cover changes in eastern North America and southern Europe seem disproportionately impactful, while for reptiles, changes in some arid regions (such as the Sahara and central Australia) appear more important and those in higher latitude regions less important than for vertebrates as a whole. These observations underscore the importance, in subsequent work, of expanding the LIFE metric to include additional taxa - most obviously any sizeable plant or invertebrate groups for which range maps and habitat preferences become available for a large proportion of the world's species.

10. Limitations and applications

By combining data on ranges and habitat preferences for 29153 species of terrestrial vertebrates together with maps of the current and estimated original extent of habitat types we generated two global, 1 arc-minute resolution LIFE surfaces describing the present-day impacts on probable number of extinctions of converting or restoring natural habitats worldwide. Assuming species' probability of persistence responds exponentially to changing Area of Habitat (with a z -value of 0.25; Fig. 1), habitat restoration would be particularly valuable per unit area in endemic-rich regions that have undergone extensive habitat clearance already (such as the Atlantic Forest, eastern Madagascar and the Ethiopian Highlands). Habitat retention, on the other hand, would have most impact in mitigating extinction in these regions too, but also in endemic- as well as species-rich regions where there has been less marked conversion to date (such as the Guyana Shield, SE Amazon Basin, Cameroon, eastern Congo, Greater Sundas and northern Australia). Statistical modelling of spatial variation in LIFE scores confirms these patterns, with impacts from conversion and restoration both co-varying positively with endemism, with the extent to which species have already lost AOH, and (especially for conversion scores) with species richness. We suggest similar formal interrogation of underlying predictors of spatial patterns would be helpful in interpreting other global biodiversity metrics as well.

In terms of the desirable characteristics of biodiversity metrics outlined above, LIFE scores have been devised to be directly comparable across space, such that a unit increase (or decrease) in summed probability of persistence reflects the same impact on expected number of extinctions regardless of where it occurs. Our investigation of the scalability of LIFE scores suggests in addition that, despite our premise that habitat loss impacts species' persistence in a non-linear way, the values presented in our 1 arc-minute resolution surface

can provide reasonably reliable estimates of impacts on extinction risk of land-cover changes ranging from 0.5 to 1000km². Our breakdown of findings by taxon illustrates that LIFE scores can be readily disaggregated according to the interests of the user. However, the resulting differences in LIFE score maps among major taxa make clear our vertebrate-only surface is not representative of terrestrial biodiversity as a whole, and so underline the importance of adding data on other groups as these become available. To be useable, such information needs to include the range and habitat preferences of all species in a taxon (or life-form, such as trees) – across the entire area of interest. In the absence of such data, LIFE scores should be treated cautiously, especially in regions (such as mediterranean biomes and the Cerrado) with higher relative richness and endemism among non-vertebrate groups.

The LIFE framework has several other limitations. Here we discuss five. First, as with any metric relating land-cover change to extinction risk, we lack a robust understanding of how species' probability of persistence decreases as their AOH is reduced, and how this varies across different groups of species. Reassuringly, we found broadly similar geographical variation in LIFE scores for exponential curves using z-values varying from 0.1 to 0.5, but a modified Gompertz curve resulted in markedly sharper geographical variation. The observation that a z-value of 1.0 produces somewhat more muted differences in apparent impacts suggests that assuming – as many metrics implicitly do – that extinction scales linearly with habitat loss (4,16,18,35) risks underestimating the potentially grave impacts of continued habitat conversion in already heavily-converted regions.

Second, at present the LIFE method treats all habitats listed as suitable by IUCN as being of equal value to a species – ignoring effects of habitat patch size, fragmentation, connectivity, degradation, and critically the impacts of other threatening processes (such as overexploitation or invasive species) (36). These oversimplifications mean our scores overestimate the relative impact of habitat loss or restoration for species and places that are particularly affected by such processes. Likewise for those species able to live in agricultural land our persistence scores take no account of differences in how that land is managed and hence underestimate the benefit of restoring areas currently subject to particularly damaging practices. We hope to address each of these simplifications in how LIFE deals with habitat suitability in future work.

Third, although our results on proportional losses of AOH (Fig. 2) align with a recent assessment that only around one-half of the area of ice-free biomes is still in areas of low human impact (37), our results are clearly only as reliable as the underlying data on species' ranges, habitat preferences and habitat maps. Information is poorer for certain taxa and regions (38,39), and the natural habitat preferences for some species (including some nowadays exclusively associated with anthropogenic land uses) are entirely unknown. Estimates of pre-human distributions are poor for many taxa and underestimating habitat loss to date will underestimate the effects of both conversion and restoration (because species are in reality further along the habitat loss trajectory than assumed). Work is in progress to ensure that the pipeline for calculating LIFE scores is readily updatable as new data on species and land cover distributions become available (see Coda). This is also important because the LIFE surfaces represent a snapshot of extinction risks today and should be updated periodically to reflect the changing availability of global habitats.

Fourth, we do not incorporate time lags between habitat change and biodiversity impact. In the case of conversion, we ignore extinction debts, and in the case of restoration we do not consider delays or indeed uncertainties in species' colonisation and recovery. Caution is thus needed when comparing LIFE scores between our two maps. Values for restoration should certainly not be viewed as equivalent to those for conversion, and efforts to make comparisons – for instance to inform offsetting activities for mitigating habitat damage – should employ explicit and conservative adjustment ratios to account for the much slower and less certain course of habitat restoration (see (4,32,40)); we suggest these ratios should be habitat- and region-specific.

Last, biodiversity metrics can be important in raising awareness of environmental change among the public and policy makers. Given this, it is important that metrics are easy to interpret (41). Although the concept of

extinction risk is relatively easy to communicate, the LIFE scores presented here are very small and not readily interpretable. Future developments should consider how to make these numbers more easily communicated – for example, by standardising values relative to a chosen ‘average’ or ‘outstanding’ place in the world.

These significant caveats notwithstanding we believe that the explicit consideration of the non-linear impacts of habitat loss and of habitat conversion to date, the transparent assumptions in the underlying method, and the use of best-available data on almost 30,000 species mean the LIFE score is among the most powerful tools to date for quantifying the likely impacts on extinction of spatially-explicit land-cover change. The LIFE layers are publicly available and can be easily combined with other data sources to assess the impact of land-cover changes across a broad range of actions, scales, and geographies. For example, in terms of damaging activities they can be linked in near-real time with remotely-derived imagery to estimate and potentially attribute the extinction impacts of clearance events or wildfires. Combined with consumption and trade data they can help assess the extinction footprint of specific products or businesses, the consequences of national trading decisions, and even the impacts of individuals’ diets (13). In terms of conservation actions the LIFE layers can be used to estimate the effects of retaining or restoring particular areas of habitat, and linked with cost data to help inform systematic conservation planning (42). And at very large scale they could be used to estimate the likely beneficial impacts of global-scale initiatives such as the recent international commitment to conserve 30% of land area by 2030 – as well (in combination with trade data) to explore the likely negative effects such actions will have through displacing commodity production to other parts of the world. We welcome any such applications, as well as advice on how to improve the LIFE metric to make it more useful, accurate and representative.

Acknowledgments

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Tables

Table 1. Mean standardized effect sizes and 95% confidence intervals for predictors of LIFE scores from our conversion and restoration scenarios. Effect sizes are from linear models fitted with a spatial smoother which used standardised \log_{10} -transformed values of the response and predictor variables.

Land-cover change	Predictor	Mean	2.5%	97.5%
Conversion	Endemism	1.106	0.809	1.287
	Habitat loss to date	0.188	0.078	0.302
	Species richness	0.705	0.548	0.845
Restoration	Endemism	0.603	0.453	0.763
	Habitat loss to date	0.448	0.346	0.554
	Species richness	0.113	0.033	0.264

Figures

All figures are original.

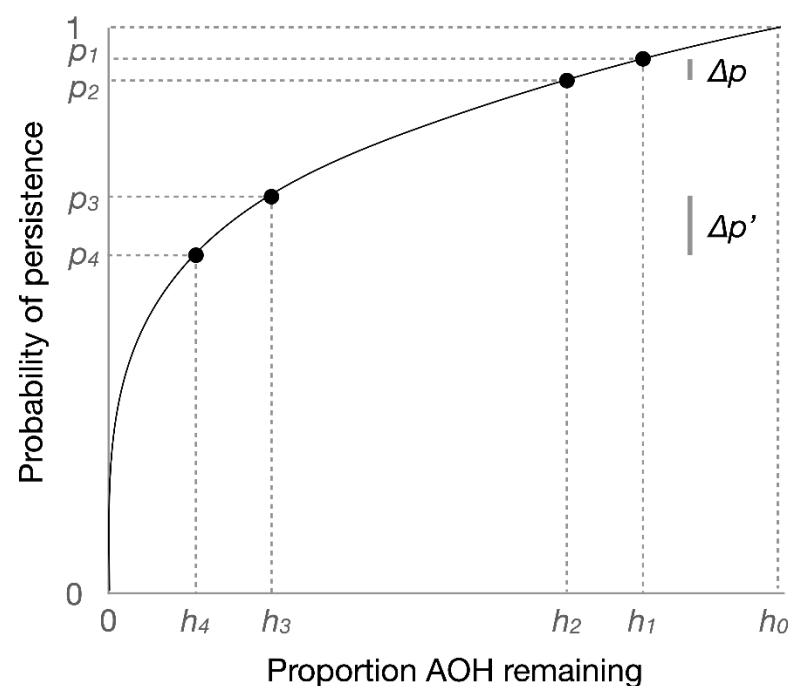


Figure 1. Illustration of how the LIFE score assumes a species' probability of persistence declines with the proportion of its pre-human Area of Habitat remaining. The curve shown is a power-law function with $z=0.25$. The LIFE score maps presented in this paper are based on changes in persistence that result from simulated habitat changes at 100m pixel-level (i.e. $h_2-h_1 = h_4-h_3 = -1\text{ha}$).

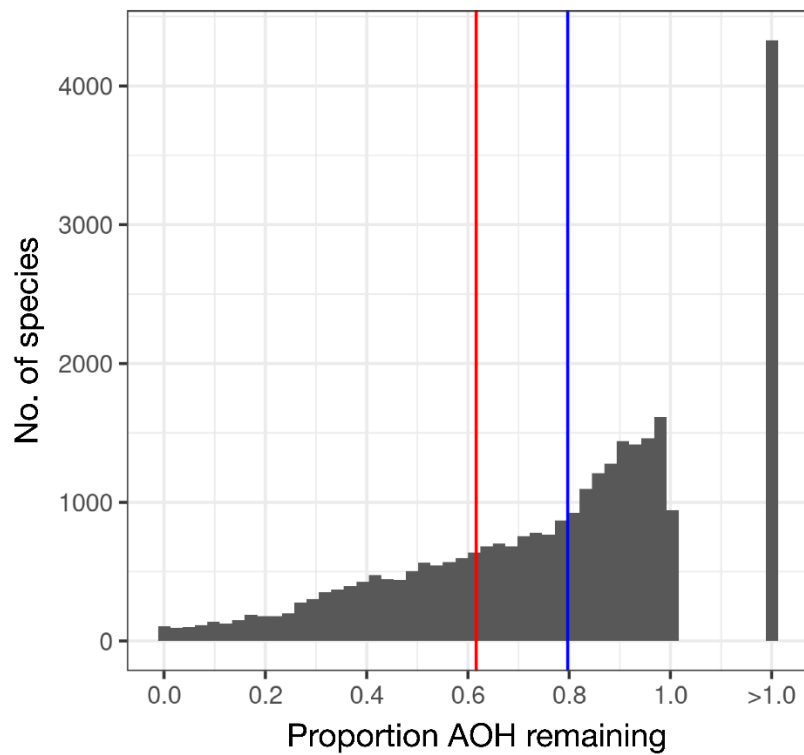


Figure 2. Histogram of the proportion of original AOH remaining for terrestrial vertebrate species (n=29153). For migratory species we plot data only for the season with the lower value. Species with increased AOHs as a result of human activity have values >1. The geometric mean across all species and for those have lost AOH as a result of human activity are depicted by blue and red dashed lines respectively.

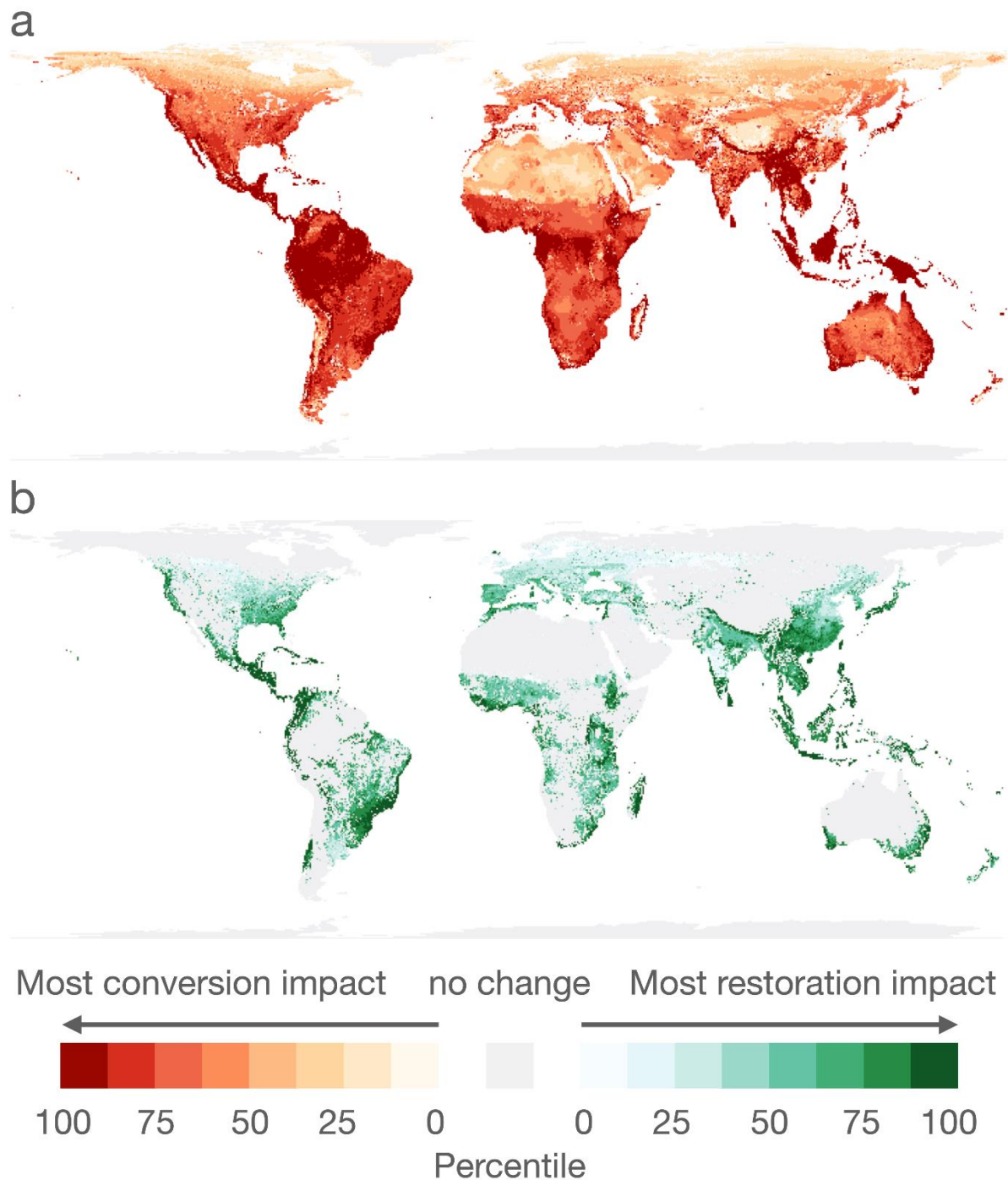


Figure 3. Global maps of LIFE scores associated with a) conversion of remaining natural habitats to arable land, and b) restoration of cropland and pasture to natural habitats. The maps show persistence scores summed across all study taxa (amphibians, reptiles, birds and mammals), aggregated to 1 arc-minute grid cells and expressed as the average impact per km² of conversion or restoration. Changes in probability of persistence are derived assuming a power-law persistence-habitat loss curve with $z=0.25$. Break points divide the scores into octiles. Positive values in the conversion map arise where species can inhabit arable farmed land but not the natural habitat that it replaces. Conversely, negative values occur in the restoration map where species can inhabit farmed land but not the natural habitat that replaces it.

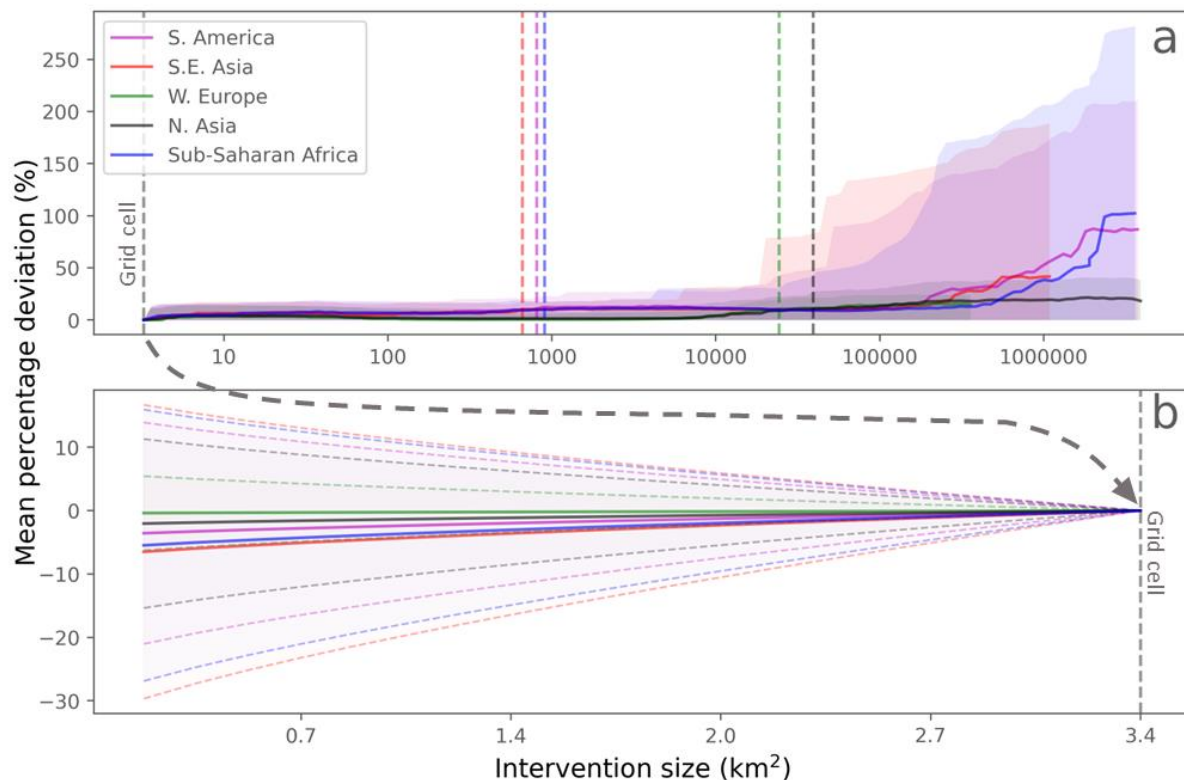


Figure 4. The modelled mean deviation (solid line) from the mapped LIFE scores for (a) actions that affect multiple pixels, with the 10% threshold marked by a dashed line, and (b) actions covering only a fraction of a pixel, with dashed lines marking the standard error ranges.

Supplementary material

An additional PDF is provided containing Supplementary Material.

Additional Information

Ethics

No human or animal trials were conducted.

Coda on data accessibility and pipeline transparency

The LIFE surface data are provided in GeoTIFF format (<https://quantify.earth/life>) under the terms and conditions of the underlying species' elevation and habitat preference data and distribution polygons as laid out by the IUCN Redlist (<https://www.iucnredlist.org/>). Digital elevation maps are available from the USGS (<https://earthexplorer.usgs.gov>), and potential natural vegetation (<https://zenodo.org/records/4038749>) and present land cover maps (<https://zenodo.org/records/4058819>) from their original sources. The LIFE pipeline source code is available under an open-source license (<https://github.com/quantifyearth/life>), allowing tailored impact analyses to be easily generated. Different land-cover maps and land-cover change scenarios may be examined, additional data may be used (such as better information on species occupancy), or users can focus on particular species sets of interest. The LIFE data can be easily regenerated as the underlying datasets are updated. We envisage our digital pipeline being regularly updated as upstream sources become available. All final statistical analyses for this manuscript were performed using the *mgcv* package (v1.9-0) in R (v4.3.2). IUCN data was processed using IUCN-modlib (<https://gitlab.com/daniele.baisero/iucn-modlib>).

Competing Interests

We have no competing interests.

Supplementary Information for

LIFE: A metric for quantitatively mapping the impact of land-cover change on global extinctions

Alison Eyres, Thomas S. Ball, Michael Dales, Tom Swinfield, Andy Arnell, Daniele Baisero, América Paz Durán, Jonathan M. H. Green, Anil Madhavapeddy, Andrew Balmford.

Correspondence to: a.balmford@zoo.cam.ac.uk

This document includes:

- S1. Sensitivity to specification of the probability of persistence-habitat loss curve
- S2. Equivalence with probable extinctions
- S3. Migratory species
- S4. Predictors of LIFE scores
- S5. Sensitivity of LIFE scores to the persistence-habitat loss curve
- S6. Variation in LIFE scores across taxonomic groups

S1. Sensitivity to specification of the probability of persistence-habitat loss curve

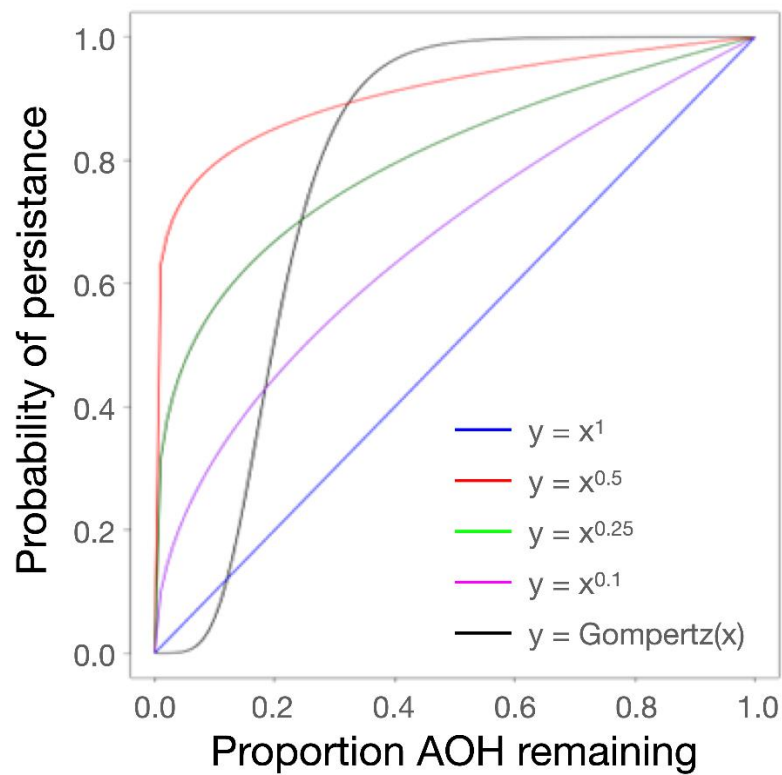


Figure S1: Assumed shapes of relationship between a species' probability of persistence and the proportion of its Area of Habitat remaining.

S2. Equivalence with expected extinctions

For an individual species s , with an associated probability of persistence $P_s(p)$, the corresponding probability of the species' extinction $P_s(x)$ is

(1)

$$P_s(x) = 1 - P_s(p)$$

For a given number of species S , the expected number of extinctions in the current state (X_0) is the sum of the expectation for the extinction of each species

(2)

$$X_0 = \sum_{s \in S} E_s(\text{extinction})$$

However, 'extinction' is a binary random variable, only taking values of 0 (species persists) and 1 (species goes extinct) with associated probabilities $P_s(p)$ and $P_s(x)$. Thus the full expression for the expectation value of a given species extinction simplifies to

(3)

$$E_s(\text{extinction}) = P_s(x) = 1 - P_s(p)$$

Now consider some change in the area of the species' habitat caused by an event K and a corresponding change in the species probability of persistence $\Delta P_{s,K}$. The updated probability of the species' extinction in light of event K is

(4)

$$P_s(x|K) = P_s(x) + \Delta P_{s,K}$$

Combining (2), (3), and (4); the expected number of extinctions across S species following K becomes

(5)

$$X(K) = \sum_{s \in S} P_s(x|K)$$

The change in expected number of extinctions caused by K is

(6)

$$\Delta X(K) = X(K) - X_0$$

Which, by substituting for (5) and (2) can be written as:

(7)

$$\Delta X(K) = \sum_{s \in S} P_s(x|K) - \sum_{s \in S} P_s(x)$$

(8)

$$\Delta X(K) = \sum_{s \in S} [P_s(x) + \Delta P_{s,K}] - \sum_{s \in S} P_s(x)$$

(9)

$$\Delta X(K) = \sum_{s \in S} \Delta P_{s,K}$$

Therefore, it can be said that the event K causes a change in the expected number of extinctions equal to the sum of ΔP values for affected species. In the case of LIFE values, the 'events' in question are the conversion of grid-cells between habitat types. The number of species for which this is considered is all species. Those whose ranges don't intersect with the changing cell, or whose habitat preferences preclude them from losing any area-of-habitat due to the change will have a ΔP value of zero for that cell and hence won't contribute to any change in the expected number of extinctions. We therefore assert that LIFE values are equivalent to 'expected extinctions caused' by the conversion of each grid-cell.

S3. Migratory species

Durán et al. (2020) makes the case for the probability of a migratory species' persistence being a multiplicative combination of the species persistence scores calculated from its breeding and non-breeding area of habitat:

(10)

$$P_{\text{migrant}} = P_{\text{breeding}} * P_{\text{nonbreeding}}$$

However, this formulation is based on the assumption that the breeding and non-breeding persistence scores are independent probabilities, when in actuality they are not independent, and instead are temporally exclusive. Over the course of a migratory cycle (T , one year), each time $t \in T$ has an independent probability of persistence P_t , and temporal weight ω_t such that

(11)

$$\sum_{t \in T} \omega_t = 1$$

Therefore the combined probability of persistence accounting for the amount of time a species spends exposed to its seasonal probabilities of persistence is

(12)

$$P_{\text{migrant}} = \prod_{t \in T} P_t^{\omega_t}$$

Our system has only two discrete time slices: {breeding, nonbreeding}, which we assume to both have equal temporal weight values of 0.5 (i.e. a species spends six months of the year in its breeding range, and six months in its nonbreeding range). This happens to be equivalent to the geometric mean of the probabilities, which for our two-state system becomes:

(13)

$$P_{\text{migrant}} = \sqrt{P_{\text{breeding}} * P_{\text{nonbreeding}}}$$

To calculate the change in probability of persistence for a migratory species ($\Delta P_{\text{migrant}}$) it is therefore necessary to calculate both P_{breeding} and $P_{\text{nonbreeding}}$ for all relevant scenarios.

S4. Predictors of LIFE scores

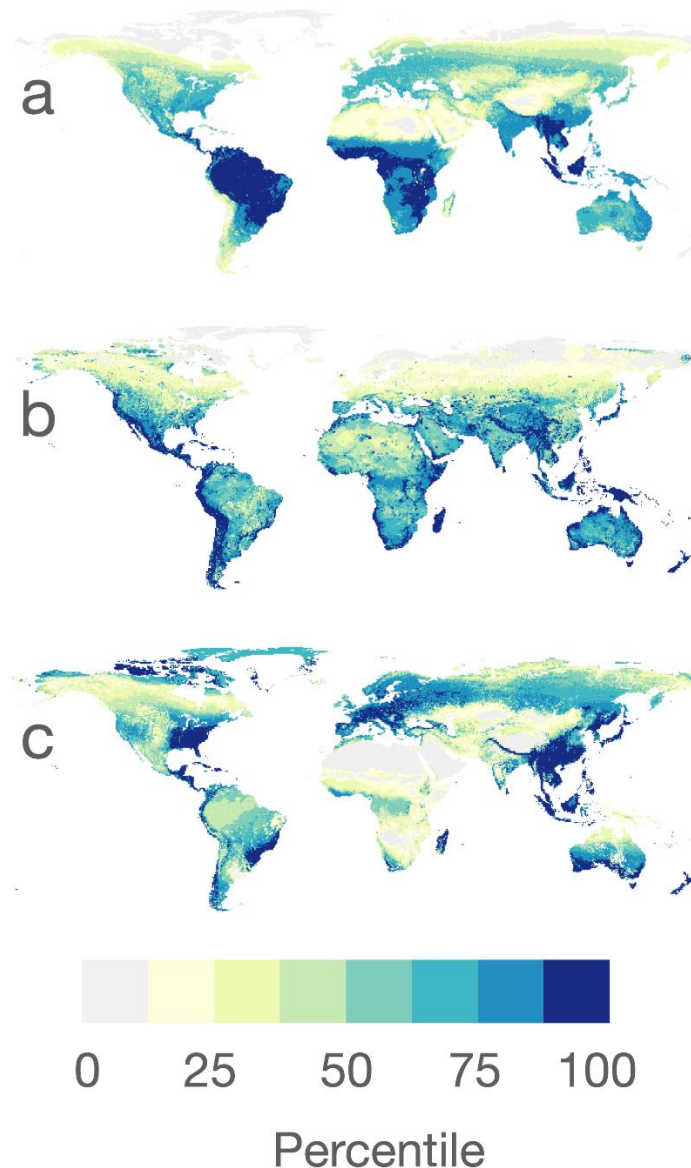


Figure S4: Variables which we anticipated would show spatial co-variation with LIFE scores: (a) species richness calculated as the number of species ranges overlapping the cell; (b) endemism calculated as the mean proportion of species' current total AOH contained within each cell; and (c) habitat loss to date calculated as the mean proportion of original AOH lost for each species occurring within the cell.

S5. Sensitivity of LIFE scores to changing the persistence-habitat loss curve

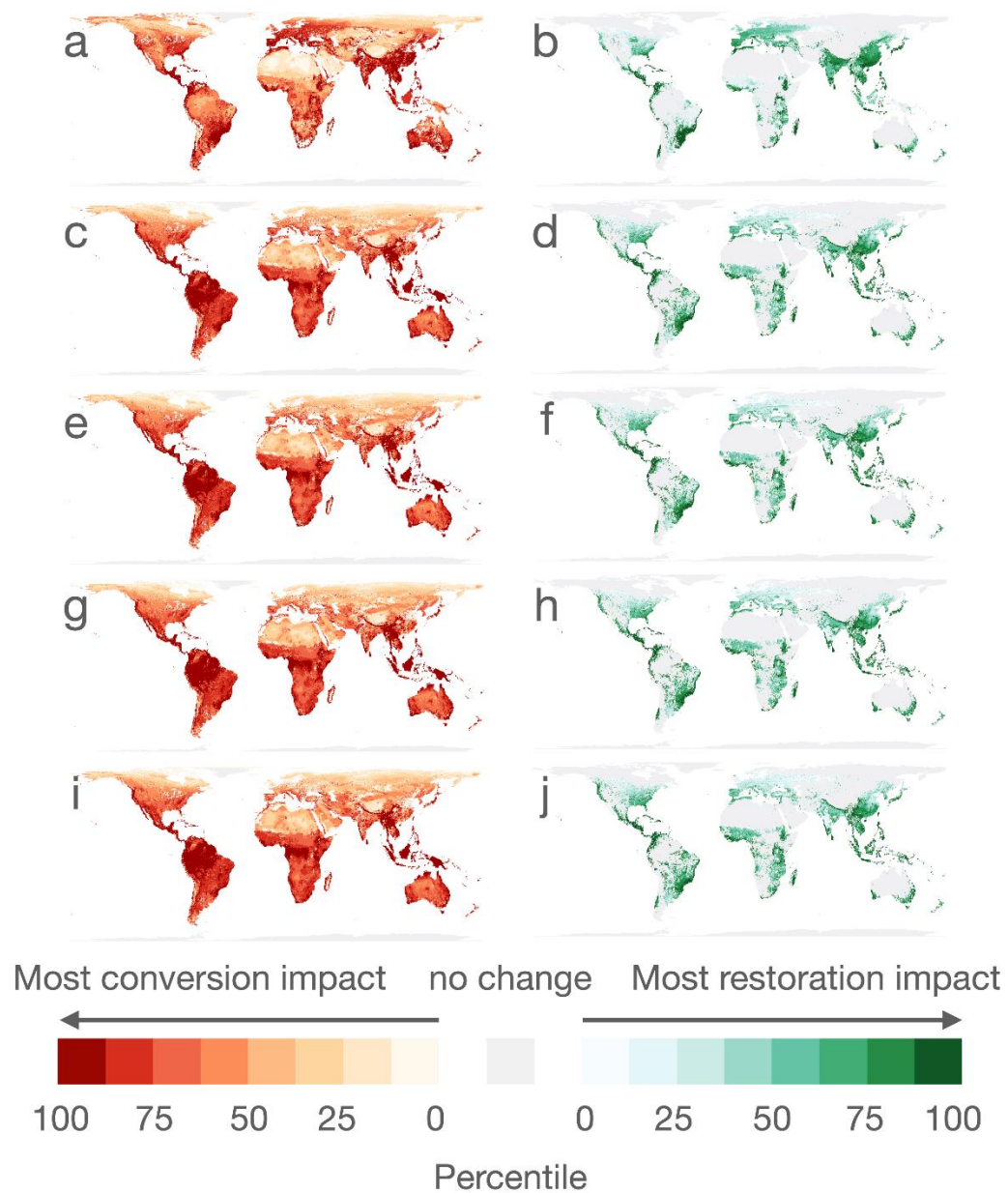


Figure S5: Sensitivity of LIFE scores to the shape of the persistence-habitat loss curve used. LIFE score surfaces are shown for (a-b) a modified Gompertz curve, and exponential curves with exponents (z -values) of (c-d) 0.1, (e-f) 0.25, (g-h) 0.5, and (i-j) 1.0.

S6. Variation in LIFE scores across taxonomic groups

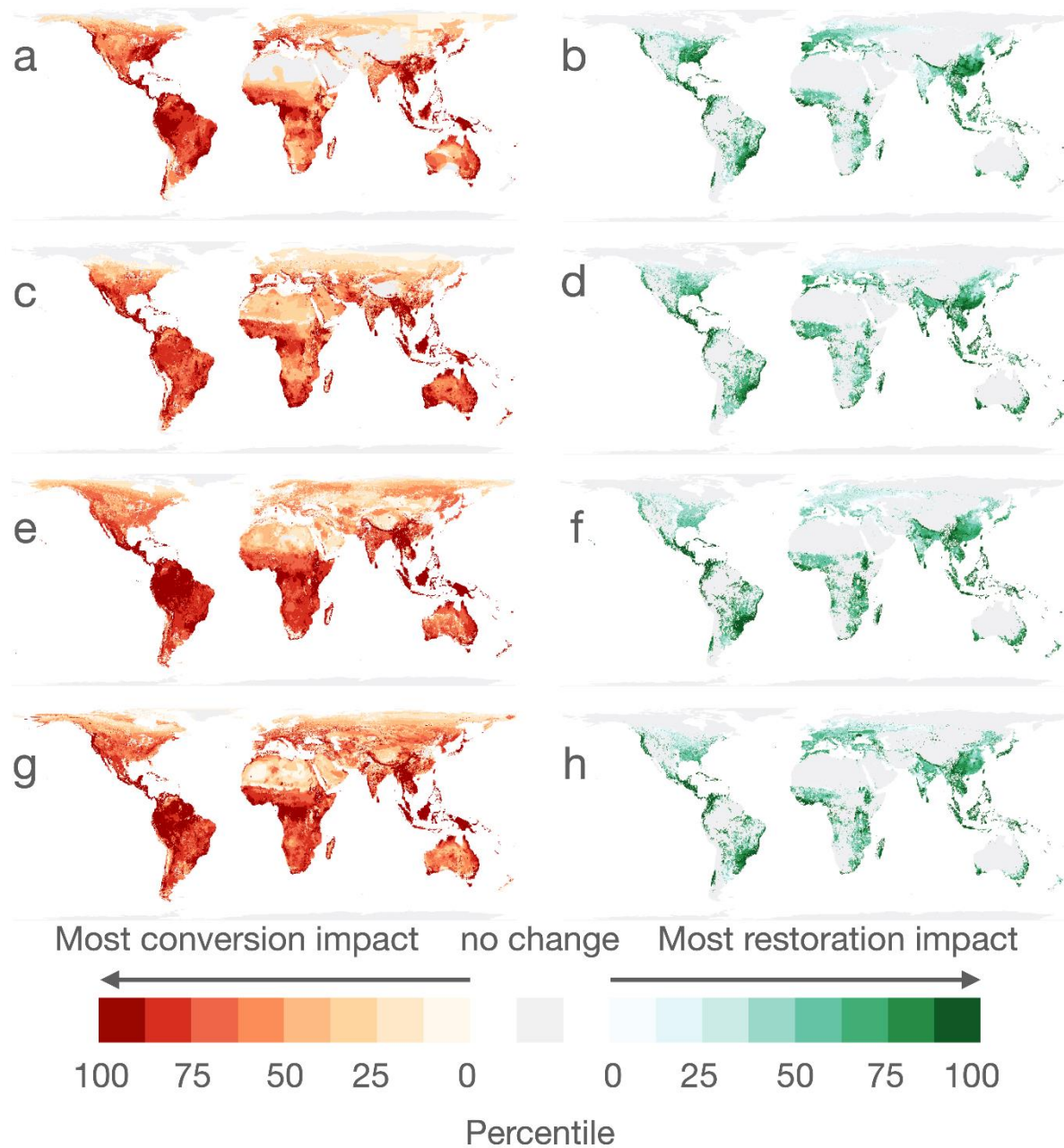


Figure S6: Variation in LIFE scores across different terrestrial vertebrate taxa. LIFE score surfaces are shown for (a-b) amphibians, (c-d) reptiles, (e-f) birds, and (g-h) mammals.