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

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Main Text

Summary

Human-driven habitat loss is recognised as the greatest cause of the biodiversity crisis yet to date we lack

2 robust, spatially explicit metrics quantifying the impacts of anthropogenic changes in habitat extent on

species' extinctions. Existing metrics either fail to consider species identity or focus solely on recent habitat

losses. The persistence score approach developed by Durán et al. (1) 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 extinction. 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 29772 species of terrestrial vertebrates at 1 arc-minute resolution (3.4km² at the
- equator). These maps provide quantitative estimates, for the first time, of the marginal changes in the expected number of extinctions (both increases and decreases) 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 be used at

14 scales from 0.5-1000km², and offer unprecedented opportunities to estimate the impact on extinctions of

diverse actions that affect change land cover, from individual dietary choices through to global protected area

- development.
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1. Introduction

Biodiversity loss is one of the greatest environmental challenges of our age, with declines associated with

- significant negative impacts on human wellbeing (2). 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 (3,4). According
- to the IUCN Red List, agriculture and logging, the two main activities that drive land-use change, threaten

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- 70% and 46% of terrestrial vertebrate species, respectively (5). Moreover, land-use change looks set to remain
- the largest single threat for at least the next few decades (6–9) and is likely to interact with other threats to
- biodiversity such as climate change, underscoring the importance of biodiversity metrics that are linked
- directly with trends in land use (10).
- While biodiversity is complex and multifaceted, metrics used in conservation arguably represent two primary
- motivations, as reflected in the targets of the Global Biodiversity Framework (11): preventing species loss
- (12), and maintaining the integrity of ecosystems and their contributions to people (2). In broad terms such
- metrics typically comprise measures of spatial and temporal 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 biodiversity loss and reductions in ecosystem functions and associated ecosystem
- services.
- To track variation in extinction risk or ecosystem intactness in relation to targets, 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 (13)
- 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 (14).
- IUCN's Species Threat Abatement Restoration metric (STAR) (6) currently covers amphibians, birds and
- 23 mammals. However as STAR considers species of Least Concern to have zero extinction risk, it is currently
- unable to quantify the impact of land use changes on those species and instead focuses on threatened and near-
- threatened species. Some other metrics, such as the Biodiversity Intactness Index (BII) (15), are based on data
- which are more representative taxonomically and by threat 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, across 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 (3). Metrics that treat all pristine habitats as of equal
- value such as Mean Species Abundance (MSA) and the BII (15,16)- make it difficult to compare the impact
- of actions on habitats which differ markedly in the communities or ecosystem services they support.
- 37 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. Although IUCN's STAR metric identifies gains in
- biodiversity that could result from habitat restoration and threat abatement, it does not currently consider the
- impacts of continued habitat loss (6).
- 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. Further, biodiversity metrics play a key role
- in halting biodiversity loss through raising awareness with the public and policy makers. Given this, it is
- important that such metrics are easy to understand and interpret (17). Globally aggregated metrics are often
- difficult to understand or relate to, but disaggregation can allow stakeholders to understand policy targets
- relating to both national and international commitments. Many metrics, however such as Mean Species
- Abundance and SEED (16,18) 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? The importance of this is highlighted by the
- inclusion in the SMART targets paradigm of "Measurable", defined as "being able to assess progress towards
- 14 the target using data already available or feasible to mobilize" (19).
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2. Conceptual basis of the LIFE metric

- 17 In this paper we present a new global metric, which we term LIFE (Land-cover change Impacts on Future
- Extinctions), which attempts to map for the first time the numbers of extinctions resulting from marginal
- losses and gains in the extent of natural habitats. LIFE is a global-scale progression of Durán et al.'s (1)
- persistence score approach, and builds on a series of earlier foundational papers (20–24). It is based on five
- fundamental assumptions and assertions around mapping anthropogenic extinction risks:
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23 1. That it is useful to focus on quantifying likely human-caused extinctions. Extinctions of course arise

- 24 naturally, but given that current extinction rates are roughly 3 orders of magnitude above background (25),
- here we look at changes in risks of extinction relative to extinctions in the absence of people.
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- 2. That a species' change in extinction risk as a result of human action depends on its current or future population size relative to that in the absence of people (hereafter its 'original population'), as well as on its 29 absolute population size. Absolutely small populations are of course at greater risk of extinction due to chance
30 events (26), but we suggest that species which have had small population sizes through their evolutiona events (26), but we suggest that species which have had small population sizes through their evolutionary 31 history are likely to have been selected to be more resilient to extinction at that size than other species (27).
32 Hence reducing a species to half its original population size will have roughly the same effect on its Hence reducing a species to half its original population size will have roughly the same effect on its extinction risk regardless of whether it was naturally abundant or scarce. LIFE does not concern itself with species that are nowadays more abundant than in their evolutionary past.
- 3. That a species' risk of extinction scales non-linearly with its current relative to original population, with a given marginal decline having a small effect when a population is close to its long-run size but a much greater effect when a population has already been greatly reduced. The exact shape of this curve is not known and will presumably vary with a species' life history, demography and ecology. Importantly, non-linearity means that metrics which instead assume linearity will tend to underestimate the impacts of population declines in already severely-impacted species, and also that estimating contemporary impacts requires present-day population sizes to be expressed relative to original population sizes.
- 4. That in the first instance it is reasonable to focus on anthropogenic changes in habitat extent and quality,
- because these constitute the greatest current and future source of threat to terrestrial biodiversity (8,28,29) .
- Other threats, such as overexploitation (30) and invasive alien species (31), are also extremely important, and
- will determine how far a species is able to occupy an area of suitable habitat, but they are poorly mapped at
- global scale (32) so their incorporation into worldwide area-based metrics is problematic (but see Mair et al.
- 2021).

 5. That although species' occupation of suitable habitats will vary with their ecology, with habitat condition, fragmentation, connectivity and so on, until these effects can be estimated separately for very many species as a first step it is useful to estimate land cover-mediated changes in relative extinction risk using changes in species' Area of Habitat (AOH), again estimated relative to that in the absence of people. While AOH - defined conceptually as the habitat available to a species and in practice mapped as the intersection between a species' range and its environmental preferences (33) - is of course an imperfect surrogate it is for now the only measure of species' distributions that is available for tens of thousands of species.

3. Developing the LIFE metric

 LIFE takes as its starting point Durán et al.'s (1) persistence score. This uses species-specific distribution and habitat suitability information to estimate the consequences of marginal changes in land-cover for the modelled probability that species will persist (i.e. avoid extinction), relative to their probability of persisting in the absence of anthropogenic habitat change (see Conceptual basis). 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 the likely non-linear relationship between habitat loss and changes in species' probability of persistence, and considers the cumulative impact of habitat loss over the long term, rather than just recent changes. Both of these issues are overlooked in other metrics of extinction risk. Other approaches instead 19 typically assume extinction risk only depends on contemporary change in AOH: that a 100km² loss of habitat 20 for a species' currently occupying 1000km² has the same effect regardless of whether in the absence of people 21 it would occupy 1000 or 1 million km^2 (34–36). However, there is substantial evidence that the impacts of 22 habitat loss on species extinction risk are typically cumulative and non-linear, with the effect of losing a given 23 quantity of habitat increasing as the remaining habitat diminishes, and hence also dependent on habitat changes in the more distant past (37,38). Because different regions have been subject to anthropogenic pressures at different times (39), estimating the impact of contemporary changes in AOH thus necessitates information on each species' likely AOH in the hypothetical absence of people (hereafter its 'original' AOH)

(40).

The Durán et al. (1) method integrates original habitat extent and the non-linear impact of habitat loss on a

- species' probability of persistence assuming a power law relationship between species remaining area of
- habitat and probability of persistence (i.e. of avoiding extinction) (12). The probability of persistence is
- expressed as a function of the proportion of a species' AOH remaining relative to its original AOH, and so has
- a maximum value of 1 when a species occupies its original AOH (or indeed any larger area). Figure 1 illustrates the shape of this curve (assuming, for illustration, an exponent of 0.25) and the resultant change in
- probability of persistence of two hypothetical species when converting natural habitat in one cell. The shape of
- the curve means that if a species currently occupies a smaller fraction of its original AOH, the same absolute
- loss of AOH causes a greater reduction in persistence (Δ*P*; compare species A and B).
- The (1,40) method can be used to estimate the change in probability of persistence resulting from retaining or restoring natural habitat in any area for each species whose global range and ecological requirements are known, and then summed across all species whose original AOH overlaps the area. Initial analyses applied this method to 1368 amphibian, bird and mammal species as well as 641 plants in the Brazilian Cerrado (1,41). 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 these 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 (24).
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Figure 1. Illustrative example of calculating the change in probability of persistence and subsequently the LIFE score associated with a change in land cover of a single cell *(i)*. for the simple cases of two example LIFE score associated with a change in land cover of a single cell (*i*), for the simple cases of two example species (A and B). Species A currently still has all of its human-absent area of habitat (AOH), and loses 25% 5 upon conversion of cell *i*. Species B has already lost a large portion of its AOH, so the conversion of *i* has a greater impact on its probability of persistence than for A. The LIFE score for the conversion of the cell is the sum of the changes in the probabilities of extinction (which is equal and opposite to the changes in their probabilities of persistence), for all species present in the cell. LIFE can be calculated in the same way for any land use change including changes that result in increases in habitat such as restoration (Figure S1).

 In this paper we develop Durán's (6–8) method into the LIFE metric by bringing AOH data for >29K terrestrial vertebrates together with high performance computing to generate global, downloadable maps that summarise at 1 arc-minute resolution the impact on the expected number of extinctions (either increases or decreases) 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. To align with the broad policy and societal focus on extinctions, we express the metric in terms of changes in probability of extinction (rather than persistence), but of course a change in extinction probability of a species is simply equal and opposite to that in its probability of persistence. Conversion to arable land was chosen because food and farming are responsible for more biodiversity loss than any other sector (41) and so maps of where agricultural impacts will be most acute are useful in guiding conservation and other decisions. We focused on restoration because of its high profile in international policy (42), including within the [United Nation's Decade on Ecosystem Restoration,](https://www.decadeonrestoration.org/about-un-decade) 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 the LIFE metric explicitly assumes non-linear relationships between habitat loss and extinction risk we also examine its scalability - the extent to which scores derived for grid cells can be relied upon when actions are smaller or larger than those cells. 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-AOH curve), and how far our results differ across major taxonomic groups. We begin, though, by explaining in detail how LIFE scores are derived.

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) (5). We did not include species with missing data, 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. We also exclude species that are listed as 'marine', 'terrestrial+marine', 'freshwater', or 'freshwater+marine' in the IUCN 'systems' field (32,42,43), which removes just over 500 species - largely penguins, marine mammals, and sea snakes. This left us with 29772 species (6469 amphibians, 8228 reptiles, 9882 birds and 5193 mammals). Current and original AOHs were generated for each species following Brooks et al. (2019) (33,43,44) (see Coda). For current AOH we used a map of the estimated distribution of habitats (45) in 2016. For original AOH we used a map of Potential Natural Vegetation (PNV) (46) which estimates the distribution of habitat types in the absence of human impacts. The current layer maps IUCN level 1 and 2 habitats, but habitats in the PNV layer are mapped only at IUCN level 1, so to estimate species' proportion of original AOH now remaining we could only use 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 (47,48), and estimated AOH for each species' range as those parts of its range which are (or were) suitable based on its elevation and habitat preferences (from IUCN) (1). IUCN codes species' range polygons 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 22 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 indicates that 14.3 % of species have a larger estimated AOH currently

than in the absence of people, implying that human-mediated land use change has enabled these species to

 expand their potential distributions, sometimes very substantially. Across all species, the geometric mean proportion of AOH remaining is 0.80. However, this figure is strongly influenced by very marked AOH

expansions among some of those species that have apparently benefitted from human activity. Focusing

instead on the 85.7% of species with smaller AOHs now than those estimated in the absence of people, their

geometric mean proportion of AOH remaining is 0.62.

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

 Following Durán et al (2020), 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 all areas classified as arable or pasture were restored to their PNV (as mapped by ref. (46)). 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.

 Figure 2. Histogram of the proportion of original AOH remaining for terrestrial vertebrate species (n=29772). 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 and their distribution is depicted in the inset. The black line in the inset marks a value of 1. The geometric mean across all species and for those that have lost AOH as a result of human activity are depicted by blue and red lines respectively.

 Next, for each species we translated the scenario-driven change in its AOH into a cell-specific change in its global probability of persistence and subsequently extinction risk (following the approach summarised in Developing the LIFE metric, above, and in Fig. 1). The 'true' form of the persistence-habitat loss curve is of course not known and is likely to vary across taxa. To take a conservative approach and to avoid conjecture, we have based this iteration of LIFE on established literature, with a view to implementing improved persistence-AOH curves in future. We followed previous studies using this approach by assuming an exponential function with an exponent of 0.25 (1,20,24,41) but we also tested the sensitivity of our broad findings to this assumption by using several alternative curve shapes (see Sensitivity analyses below). Because we were not concerned with those species with greater current than original population sizes (see Conceptual basis, above), where the current or scenario estimate of a species' AOH exceeded its original AOH we capped its probability of persistence at 1 (20). Following maps made by the IUCN for threatened species we account for species occupying novel regions within the limits of their native range, but not the colonisation of areas beyond it, but note that new iterations of LIFE maps could be adjusted to include natural range expansions and assisted colonisations. For migratory species, probability of persistence in any scenario was derived separately

- for the species' breeding and non-breeding ranges, with the overall change in persistence extinction risk 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.(48); see section S4).
- In the last stage, we summed the change in probability of persistence for all the species found in the cell.
- Significantly, this summed value of change in probability of persistence across species in a grid cell is
- numerically equal to the expected number of extinctions caused or avoided by conversion or restoration of that
- grid cell (for proof, see section S3). To align with the broad policy focus on extinctions, we then multiply our
- persistence score values by -1 to convert them to changes in extinction risk. Finally, because the area
- undergoing change varies widely across cells, we divided the summed change in extinction risk scores by the
- 11 area (in km²) of the cell restored or converted under that scenario, to obtain an overall LIFE score describing
- 12 the likely impact on expected number of extinctions of converting or restoring 1km² of land. The scaling error
- associated with summing and then averaging 100m pixel changes in this way is explored under section 7
- (Scalability), below.

6. Global maps of the LIFE score

The LIFE score maps for our conversion and restoration scenarios (Fig. 3) prompt two overarching

17 observations. First, while the per-km² impacts on extinction of converting remaining habitats and pasture to

- arable land are very largely positive (indicating an increase in extinction risk) and those of restoring natural
- habitats very largely negative (indicating a decrease in extinction risk), the increases in extinction risk from
- conversion tend to be both greater and more widely distributed than the decreases in extinction risk resulting
- 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
- 26 and in many cases lower impacts of real-world habitat restoration compared with conversion (51,52): any
- 27 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.
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7. Dissecting spatial variation in LIFE scores

To check our understanding of 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 that
- absolute values would covary positively with species richness. Because a unit area of land-cover change
- should have a greater impact on the probability of extinction of species with smaller global ranges, we
- expected absolute 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 absolute LIFE scores and
- the average proportional loss of AOH to date of those species present.

 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 changes in extinction risk 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 extinction are derived assuming a power-law persistence-habitat loss curve with z=0.25. Break points divide the scores into octiles, except for the uppermost octile where we also show the top 2.5% of most impactful land use changes. Positive values indicate an increase in extinction risk, whilst negative values show a decrease in extinction risk. Negative values in the conversion map arise where species can inhabit arable farmed land but not the natural habitat that it replaces. Conversely, positive values occur in the restoration map where species can inhabit farmed land but not the natural habitat that replaces it. Where land use changes have the opposite 16 from the predominant effect they are shown in grey.

 To test these predictions, 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. S5). For the two scenarios (conversion and restoration) we focussed on LIFE values with the

predominant effect (i.e. positive LIFE scores associated with conversion and negative LIFE scores associated

- 23 with restoration). The absolute value was taken for restoration values. We then modelled our log_{10} -transformed
- LIFE scores in relation to these 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). Absolute values
- associated with conversion and restoration 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 across
- runs from 79.4 to 89.6% and 69.1 to 76.4% for conversion and restoration respectively.
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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 log10-transformed values of the response and predictor variables. Negative LIFE scores
- from restoration were multiplied by -1 prior to log transformation.

8. Scalability of LIFE scores

 A central conceptual premise of the LIFE framework is that the relationship between a species' remaining 18 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 entire grid cell which overlays it. However, running bespoke extinction risk 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 32 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

42 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

2 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 fact that species at lower latitudes have on average lost a greater proportion of their AOH already.

Intervention size (km²)

 $\begin{array}{c} 7 \\ 8 \end{array}$ 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.

 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 21 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.

 With these results in mind, we are confident that the LIFE surfaces presented in Fig. 3 can be used to evaluate 25 changes in the statistically expected number of extinctions driven by land-cover changes of up to $\sim 1000 \text{km}^2$.

-
- This does not preclude the use of LIFE as a means to assess larger changes, but doing so will incur a higher
- level of uncertainty or else bespoke calculations of LIFE, tailored to specific interventions (see Coda). Of
- course, LIFE metric values are representative of a snapshot of the current state of global land cover, which is
- subject to change. This is also true of all other biodiversity metrics that consider land-cover. Therefore, to
- minimize the risk of inaccuracies in the LIFE metric, it will be important to make use of the best and most-
- recent land-cover data as and when it becomes available, especially in regions undergoing large-scale, rapid
- land-cover change.

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 its loss of AOH, 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 and rates of reproduction and dispersal, evolutionary history, and vulnerability to other threats may each shape how species' populations respond to anthropogenic habitat loss (49). For our main analyses we followed other studies (1,20,24,41,50) 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 11 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 probability of persistence changes according to a modified Gompertz curve (which allows for the disproportionate impact of stochasticity on persistence at low AOH

values; see Fig. S2 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. S6). 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 20 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 (37) 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. We also conducted a simple variance analysis of the curve exponents and the Gompertz curve by comparing the 28 variance of the scores within each pixel when different curve shapes were used. Most cells (77%) had a 29 variance of less than 1% from the z=0.25 curve. There was a higher level of variance in areas with a greater number species, up to approximately 60% of the z=0.25 value. This variance did not strongly correlate with

- 31 the score itself $(r=0.0001)$.
- 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. S7): for each of our taxonomic groups the same regions would generally experience marked (and others, negligible) changes in species extinction risk following habitat conversion or restoration. However, there are some interesting differences when amphibians or reptiles are considered in isolation. Compared with all terrestrial vertebrates combined, for amphibians, land-cover changes in eastern North America and southern Europe are more 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. 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. Overview, limitations and applications

 By combining data on ranges and habitat preferences for 29772 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 note that statistical exploration of variation in biodiversity metrics is unusual, but suggest similar formal interrogation of spatial patterns would be helpful in interpreting other

global 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 extinction 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 22 can provide reasonably reliable estimates of impacts on extinction risk of land-cover changes ranging from 0.5 23 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 (53).

The LIFE framework has several other limitations. Here we discuss five, the first two of which are linked to its

underlying assumptions. 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. Clearly

- more work in needed to establish plausible curve shapes and explore how they are likely to vary across and
- within 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 (6,34,36,54) 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 differences in whether a habitat type is suitable or marginal for a species (because this
- information is currently only reported for 11% of species, and because we lack information on what this
- difference in suitability means for species in terms of occupancy). This simplification assumes that population
- density is equal across different habitats within the species' AOH, potentially overestimating the importance
- of marginal populations at range limits (and vice versa). Likewise, to date LIFE also ignores effects of habitat
- patch size, fragmentation, connectivity, degradation, and critically the impacts of other threatening processes
- (such as overexploitation or invasive species) that may limit a species' ability to make use of otherwise
- suitable habitat (55). 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 extinction risk scores take no account of differences in how that
- 4 land is managed and hence underestimate the benefit of restoring areas currently subject to particularly
- damaging practices. Conversely we take a conservative approach and, in line with the IUCN, do not allow
- species' to colonise newly suitable areas outside of their current ranges, potentially underestimating the value
- of restoration (55). 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 (56), 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 (57,58), and the natural habitat preferences for some species (including some nowadays exclusively associated with anthropogenic land uses) are entirely unknown. Estimates of
- species' distributions in the absence of people are poor for many taxa, and this means that where we
- underestimate them and hence species' habitat loss to date, LIFE scores will underestimate the effects both of
- further conversion and of 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 habitats, especially in regions of rapid conversion.
- 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 (6,52,59)); 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 (17). Although the concept of extinction risk is relatively easy to communicate, the LIFE scores presented here are numerically 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.

11. Conclusions

- These significant caveats notwithstanding we believe that the explicit consideration of the non-linear impacts
- of habitat loss and of long-term anthropogenic conversion, 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 (41). 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 (60). 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 and economic 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.

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Ethics

19 No human or animal trials were conducted.

Coda on data accessibility and pipeline transparency

- 22 The LIFE surface data are provided in GeoTIFF format [\(https://quantify.earth/life\)](https://quantify.earth/life) under the terms and
- conditions of the underlying species' elevation and habitat preference data and distribution polygons as laid
- 24 out by the IUCN Redlist [\(https://www.iucnredlist.org/\)](https://www.iucnredlist.org/). Digital elevation maps are available from the USGS
- [\(https://earthexplorer.usgs.gov\)](https://earthexplorer.usgs.gov/), and potential natural vegetation [\(https://zenodo.org/records/4038749\)](https://zenodo.org/records/4038749) and
- 26 present land cover maps [\(https://zenodo.org/records/4058819\)](https://zenodo.org/records/4058819) from their original sources. The LIFE pipeline
- 27 source code is available under an open-source license [\(https://github.com/quantifyearth/life\)](https://github.com/quantifyearth/life), allowing tailored
- 28 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 [\(https://gitlab.com/daniele.baisero/iucn-modlib\)](https://gitlab.com/daniele.baisero/iucn-modlib).

Competing Interests

- We have no competing interests.
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1 **Article II. S1. Illustrative example of calculating LIFE score**

2 **associated with restoration.**

$\frac{3}{4}$

4 S1 **.** Illustrative example of calculating the change in probability of persistence and subsequently the LIFE score associated with the restoration of a single cell (i), for the simple case of two example species (A and score associated with the restoration of a single cell (i), for the simple case of two example species (A and B).

6 Species A currently still has 80% of its human-absent area of habitat (AOH), and gains 20% upon restoration of

7 cell i. Species B has already lost a large portion of its AOH (>90%) , so the restoration of i has a greater impact

8 on its probability of persistence than for A. The LIFE score for the restoration of the cell is the sum of the

9 changes in the probabilities of extinction (which is equal and opposite to the changes in their probabilities of

10 persistence), for all species present in the cell.

-
- **Article III. S2. Sensitivity to specification of the persistence-habitat**

loss curve

Figure S2: Different relationships between the probability of a species' persistence and the

proportion of its AOH remaining.

1 **Article IV. S3. Equivalence with probable extinctions**

For a given number of species S, the expected number of extinctions in the current state (X_0) is the

3 sum of the expectation for the extinction of each species

4 (1)

5

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

- 6 However, 'extinction' is a binary random variable, only taking values of 0 (species persists) and 1
- 7 (species goes extinct) with associated probabilities $P_s(p)$ and $P_s(x)$. Thus the full expression for the
- 8 expectation value of a given species extinction simplifies to
- 9 (2)
- 10 E_s (extinction) = $P_s(x)$ Now consider some change in the area of the species' habitat caused by an
- 11 event K and a corresponding change in the species probability of extinction $\Delta P_{s,K}$. The updated
- 12 probability of the species' extinction in light of event K is
- 13 (3)

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

- 15 Combining (1), (2), and (3); the expected number of extinctions across S species following K 16 becomes
- 17 (4)
- 18

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

- 19 The change in expected number of extinctions caused by K is
- 20 (5)
- 21 $\Delta X(K) = X(K) X_0$
22 Which, by substituting for (4) and (1) can be written as:
- Which, by substituting for (4) and (1) can be written as:
- 23 (6) 24

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

25 (7)

26
$$
\Delta X(K) = \sum_{s \in S} [P_s(x) + \Delta P_{s,K}] - \sum_{s \in S} P_s(x)
$$

- 27 (8)
- $\Delta X(K) = \sum \Delta P_{s,K}$ s∈S 28

29 Therefore, it can be said that the event K causes a change in the expected number of extinctions equal 30 to the sum of ΔP values for affected species. In the case of LIFE values, the 'events' in question are

31 the conversion of grid-cells between habitat types. The number of species for which this is 32 considered is all species. Those whose ranges don't intersect with the changing cell, or whose habitat

- 33 preferences preclude them from losing any area-of-habitat due to the change will have a ΔP value of
- 34 zero for that cell and hence won't contribute to any change in the expected number of extinctions.
- 35 We therefore assert that LIFE values are equivalent to 'expected extinctions caused' by the
- 36 conversion of each grid-cell.

Article V. S4. Migratory species

Following the case set out in Durán et al. (2020) we treat the probability of a migratory species'

extinction as a multiplicative combination of the species' extinction 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 extinction
- scores are independent probabilities, when in actuality they are not independent, and instead are
- 9 temporally exclusive. Over the course of a migratory cycle (T, one year), each time $t \in T$ has an
- 10 independent probability of extinction P_t , and temporal weight ω_t such that
- (11)

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

 $t \in T$
13 Therefore the combined probability of extinction accounting for the amount of time a species spends exposed to its seasonal probabilities of extinction 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 extinction for a migratory species $(\Delta P_{\text{migrant}})$ it is therefore
- 24 necessary to calculate both P_{breeding} and $P_{\text{nonbreeding}}$ for all relevant scenarios.

Article VII.

- *Figure S5: Key components of land-cover change expected to increase global extinctions which were*
- *used as predictors of 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.*
-
- **Article VIII. S6. Sensitivity of LIFE scores to the persistence-habitat**
- **loss curve**

Article IX.

- *Figure S6: 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) of (c-d) 0.1, (e-f) 0.25, (g-h) 0.5, and (i-j) 1.0.*
- **Article X. S7. Variation in LIFE scores across taxonomic groups**
- **Article XI.**

- *Figure S7: 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.*
-