On the decline of biodiversity due to area loss

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Predictions of how different facets of biodiversity decline with habitat loss are broadly needed, yet challenging. Here we provide theory and a global empirical evaluation to address this challenge. We show that extinction estimates based on endemics-area and backward species-area relationships are complementary, and the crucial difference comprises the geometry of area loss. Across three taxa on four continents, the relative loss of species, and of phylogenetic and functional diversity, is highest when habitable area disappears inward from the edge of a region, lower when it disappears from the centre outwards, and lowest when area is lost at random. In inward destruction, species loss is almost proportional to area loss, although the decline in phylogenetic and functional diversity is less severe. These trends are explained by the geometry of species ranges and the shape of phylogenetic and functional trees, which may allow baseline predictions of biodiversity decline for underexplored taxa.
Habitat loss due to accelerated climate change and direct human impact has been causing a decline of biodiversity and associated ecosystem services1–3. Direct estimates of biodiversity loss are challenging because of highly incomplete global species’ distribution knowledge4 and the difficulties of ascertaining actual extinctions5–7. Instead, estimates of diversity loss have relied on indirect methods, such as the relationship between area and the number of species in that area, the species–area relationship (SAR)8–11, or the relationship between an area that is lost and the number of species confined to it, the endemics–area relationship (EAR)12,13.

Recently, He and Hubbell12 initiated discussion over the reliability of the indirect methods, claiming that the SAR-based method (also known as backward estimation) overestimates extinctions when compared with the EAR-based method (forward estimation). This debate has generated several valuable insights, such as recognition that EAR and SAR are linked by the complementarity of area that is lost and the area that remains14, recognition of point reflection symmetry of the two curves13, or identification of critical role of aggregation of individuals15 and ecological context16,17 at small-scale plots. However, this debate has not yet been settled, and there are still critical unresolved issues, as well as opportunities for synthesis.

Specifically, it has been suggested that different spatial arrangements of habitat loss lead to different extinction estimates18–21, which follows implicitly from comparing estimates of the forward and backward methods8,12,16. The emerging pattern has been that, given the same amount of lost habitable area, inward area loss starting on the edges of a region leads to higher average proportional loss of species richness than when area is lost outward from within the centre of the region. Yet, it is unclear if such pattern is inevitable, that is, if there is a theoretical possibility that, contrary to He and Hubbell’s claim12, SARs (the backward method) can also actually underestimate extinction rates. Further, apart from the anecdotal case of US birds12, this discrepancy has been demonstrated, and explained by aggregation of individuals15 and ecological context16,17 at small-scale plots. However, this debate has not yet been settled, and there are still critical unresolved issues, as well as opportunities for synthesis.

Results

Geometry of area loss and its links to SAR and EAR. We begin by showing the complementary nature of different ways to calculate the decline of species richness under area loss (Fig. 1), independent of any specific SAR model (for example, power-law as in refs 12,18): Imagine a region of total area $A_{\text{tot}}$ that hosts $S_{\text{tot}}$ species, with a contiguous plot of area $A_{\text{in}}$ ($A_{\text{tot}} < A_{\text{tot}}$) somewhere within the region, with area outside the plot $A_{\text{out}} = A_{\text{tot}} - A_{\text{in}}$. The number of species that live exclusively within (are endemic to) the plot ($E_{\text{in}}$) is then given by $E_{\text{in}} = S_{\text{in}} - S_{\text{out}}$, where $S_{\text{out}}$ is the total number of species (both endemic and non-endemic) that live in $A_{\text{out}}$. With $S_{\text{in}}$ defined as all species occurring in $A_{\text{in}}$, it follows that $E_{\text{out}} = S_{\text{out}} - S_{\text{in}}$. When habitats in $A_{\text{in}}$ are destroyed, we speak about outward loss (Fig. 1a, left), whereas inward loss happens when habitats in $A_{\text{in}}$ are destroyed (Fig. 1a, right). The $E_{\text{in}}$ and $E_{\text{out}}$ scale with area according to their respective EAR$_{\text{in}}$ and EAR$_{\text{out}}$ relationships, whereas the $S_{\text{in}}$ and $S_{\text{out}}$ do so according to the SAR$_{\text{in}}$ and SAR$_{\text{out}}$ relationships (Fig. 1b).

Figure 1 | Schematic of inward and outward area loss and the corresponding endemics–area (EAR) and species–area (SAR) curves. The squares in (a) represent a hypothetical region with part of its habitable area lost. (b) Empirical curves for birds that inhabit 2,200 × 2,200 km$^2$ placed in South America (region SA2) as an example. In both panels, $A$, $S$ and $E$ are area, number of species and number of extinct species in the inner (in) and outer (out) area, respectively, all expressed as proportions of total (tot) area and diversity.
EAR_{in} thus follows a point reflection symmetry with SAR_{out} and analogically EAR_{out} is symmetrical to SAR_{in} (ref. 13).

Assuming immediate extinction (that is, no extinction debt), relevant for extinction estimates are always the EAR curves, which we also call extinction curves. The number of extinct species can be calculated directly from the EAR for the lost area, or indirectly by rotating the SAR for the remaining area on its axis about a central point (Fig. 1b); the latter being analogous to the backward method of estimating extinctions. The backward approach was considered incorrect by He and Hubbell (12), but recognized as valid by others (14,27), with differences from the forward (that is, direct or EAR-based) method arising from differing geometries of area loss. Specifically, in the case of contiguous area loss, the forward (EAR-based) method represents area loss that goes outward from within, whereas the backward (SAR-based) method corresponds to inward loss starting from the edges of a region (14).

Theoretical predictions. How severely diversity declines with area loss is reflected by steepness of EAR extinction curves, which in turn is determined by both the spatial arrangement of individual species ranges and of area loss. Using four distinct models of range placement (see Methods and Fig. 2 for details) and three scenarios of area loss in both analytical and simulation settings (Fig. 2), we make the following predictions:

Assuming random placement of discontinuous scattered ranges (Model 1; Fig. 2a), the inward and outward extinction curves should overlap; this coincidence of forward and backward curves for the randomly placed non-contiguous ranges stems from the same causes as the coincidence of complementary SAR, nested SAR and non-nested SAR for the random spatial distribution of individuals described by refs 12,15.

Assuming non-random concentration of contiguous ranges in one part of the region (Model 2; Fig. 2b), trivial and predictable differences should emerge between the inward and outward EARS—when ranges are packed by the edges of the region (Fig. 2b) they will obviously be removed first by the inward area loss, and the opposite holds for ranges concentrated in the middle of the region. However, differences between EAR_{in} and EAR_{out} also emerge from models of random range placement (see below), so the difference is not just an issue of range concentration in particular regions.

Assuming random placement of contiguous ranges (Models 3 and 4, Fig. 2c,d and Supplementary Fig. 4), that is, when ranges within a region are distributed randomly and are convex and contiguous geometrical shapes, non-trivial differences between EAR_{in} and EAR_{out} emerge because of the different ways the randomness is modelled. For analytical arguments, we use circular ranges in a circular region (Fig. 2e–g; here we were inspired by ref. 28), whereas for simulation purposes (Fig. 2a–d) we use rectangular ranges on a rectangular grid.

Let us have a circular region of area A_{tot} with radius r_{tot} divided into an outer domain of area A_{out} and an inner domain of area A_{in} with radius r_{in} (Fig. 2e). Imagine that either A_{in} or A_{out} are completely destroyed, causing the loss of E_{in} or E_{out}. Let us set A_{in} = A_{out} = A_{tot}/2, and hence r_{in} = r_{tot}/\sqrt{2}; in such case we are in the middle of the extinction curve (Fig. 1b), and any difference between E_{in} and E_{out} is due to reasons other than A_{in} \neq A_{out}. Now when we try to place a circular range of radius r_{i} (Fig. 2e) at a random location within the region, we realize that there are actually several ways to model such random placement (26). Here we consider two most distinct ones, and call them Models 3 and 4:

In Model 3 the whole range is placed randomly, so that its entire body must fall within the region boundary, which causes the well-known mid-domain effect (29) (Fig. 2c and Supplementary Fig. 4a). Of key interest is the probability P_{out} that the range falls exclusively (entirely) within the outer domain, contributing to E_{out}, and probability P_{in} that the range will fall exclusively within the inner domain, contributing to E_{in}. These probabilities are (see Supplementary Note 2 for further details):

\[ P_{out} = \begin{cases} 1, & \text{if } r_{in} = 0 \\ 0, & \text{if } r_{i} \geq \frac{r_{tot} - r_{in}}{2} \\ X_{out}, & \text{if } r_{i} < \frac{r_{tot} - r_{in}}{2}, \end{cases} \]

where \[ X_{out} = \frac{(r_{tot} - r_{in})^2 - (r_{in} + r_{i})^2}{(r_{tot} - r_{in})^2} \]

and

\[ P_{in} = \begin{cases} 0, & \text{if } r_{i} \geq r_{in} \\ X_{in}, & \text{if } r_{i} < r_{in}, \end{cases} \]

where \[ X_{in} = \frac{(r_{in} - r_{i})^2}{(r_{tot} - r_{in})^2} \]

In Model 4, the range is allowed to overlap the region’s outer boundary, and hence its area after the placement can be ‘cropped’ by the boundary, effectively eliminating the mid-domain effect (26) (Fig. 2d, Supplementary Figs 4a and 5). In this case, the probabilities are (see Supplementary Note 2 for further details):

\[ P_{out} = \begin{cases} 1, & \text{if } r_{in} = 0 \\ X_{out}, & \text{if } r_{i} > 0, \end{cases} \]

where \[ X_{out} = \frac{(r_{tot} + r_{i})^2 - (r_{tot} + r_{i})^2}{(r_{tot} + r_{i})^2} \]

and

\[ P_{in} = \begin{cases} 1, & \text{if } r_{i} = r_{tot} \\ X_{in}, & \text{if } r_{i} < r_{in} \end{cases} \]

where \[ X_{in} = \frac{(r_{in} - r_{i})^2}{(r_{tot} + r_{i})^2} \]

Here r_{i} is the radius of the potential circular range before its truncation by the region’s boundary.

In Models 3 and 4, the probability that the range will overlap the boundary between the inner and outer domain is:

\[ P_{overlap} = 1 - P_{out} - P_{in} \]
be equally or more severe than loss of the inner area (Fig. 2d, g). Hence, different models of random range placement (that is, different null models) should lead to different relative positions of the EAR curves and consequently different extinction estimates. These analytical considerations are supported by our simulations (Fig. 2a–d).

**Figure 2** | Expected differences between the inward and outward area loss based on theory and simulations. (a–d) Simulated extinction curves from four models of range placement and three scenarios of area loss. The insets show spatial patterns of species richness in a 20 × 20 cell domain, with lighter shades representing higher richness. The blue and red extinction curves are for inward and outward loss, respectively, the grey curves represent the scattered random loss scenario. (e–g) Theoretical demonstration of the probability that a randomly placed range falls exclusively within the inner ($P_{\text{in}}$) or outer domain ($P_{\text{out}}$), respectively, as a function of geographic range radius ($r_r$). (e) Illustration of the terms used in the theoretical predictions: a contiguous circular range of radius $r_r$ is placed into a circular region of radius $r_{\text{tot}}$, the region of area $A_{\text{tot}}$ is divided into the inner domain (with area $A_{\text{in}}$ and radius $r_{\text{in}}$) and outer domain of area $A_{\text{out}}$. Grey areas refer to regions where it is impossible to locate centres of the range with radius $r_r$ so that the range does not cross the boundary of some of the domains (that is, species cannot be endemic in one of the domains). Two models of random placement of contiguous ranges (Model 3 with mid-domain effect in c; Model 4 without mid-domain effect in d) give inverse relative positions of EAR$_{\text{in}}$ and EAR$_{\text{out}}$. The vertical axes in f–g refer to the probability that a range with given radius falls into the inner (red line) and outer (blue line) domain, or that it overlaps both domains (black line).

**Declines of PD and FD.** Compared with taxonomic richness, the loss of PD or FD (PDX or FDX, following the PDXAR and FDXAR curves; Fig. 3, Supplementary Fig. 2) is additionally affected by the structure of species’ functional and evolutionary similarity with one another. In contrast to the loss of species richness, relative PDX or FDX, calculated as the total branch length that is lost from a dendrogram$^{24,30}$, can only be calculated backwards by rotating the PD-area (PDAR) and FD-area (FDAR) curves of the non-destroyed area (Fig. 3 and Supplementary Fig. 2). Hence, the PDX cannot be calculated using the PD of endemic species alone, but requires information on the PD of the remaining species. Therefore, we need to know the complete phylogeny of all species in both the destroyed and the remaining area (Supplementary Fig. 2).
Lost species richness ($E$) is equivalent to $PDX$ or $FDX$ when all species are phylogenetically or functionally equivalent, that is, when the dendrogram representing their similarities is rake-shaped (Fig. 3a, green), and only such tree results in a proportional loss of PD ($PDX$) that is equal to that of $E$, that is, the $PDX$AR and EAR curves are identical. We predict that if a tree has 'tippy' topology (Fig. 3a, orange), then a species that is randomly selected for extinction will, on average, represent lower proportion of the total branch lengths of the tree, compared with an extinction that occurs in a tree that has 'stemmy' or rake-like topology (Fig. 3a, green). As a consequence, the initial loss of PD should be less pronounced than the loss of species richness, and the $PDX$AR curves should be below the EAR curves (Fig. 3b). In other words, any redundancy among species' functional or phylogenetic information, that is, increasing deviation from a rake-shape topology, will result in an initial loss of PD that is less pronounced than the loss of species richness. The same principles apply for the loss of FD ($FDX$) or other dendrogram-based metrics.

Empirical extinction curves at large scales. We find that for amphibians, birds and mammals in nine regions on four continents, simulated inward area loss leads to greater loss of species richness than outward area loss, and that the randomly scattered habitat loss leads to lowest loss of richness (Fig. 4). The proportion of species predicted to go extinct in a given area is generally highest for amphibians, which corresponds with this group’s generally steeper SARs and EARs\(^{26}\). This is due to the relatively smaller ranges and higher endemicity of amphibians, which results in a predicted species loss that is almost proportional to the inward area loss. As expected, the initial loss of the PD and FD metrics $PDX$ and $FDX$ is always lower than the corresponding loss of species richness $E$ (Fig. 5) for all taxa. This difference is particularly pronounced in mammals (Supplementary Fig. 3). In contrast, PD loss is relatively high in amphibians and also in birds in selected African and Asian regions (Supplementary Fig. 3).

Predictors of regional extinction vulnerability. We use area under the extinction curve (AUC) as our measure of extinction vulnerability of a region, with steep curves, that is, high extinction vulnerability of a region, characterized by high AUC. The most important predictors of AUC were the Inward/Outward/Random geometry of the habitat loss (averaged (avg.) $\beta$ of 0, −1.4 and −1.8, respectively; Supplementary Table 2) followed by the type of diversity considered ($E$ or $PDX$; avg. $\beta = −0.4$; Supplementary Table 2), and three variables describing range geometry. Apart from the high extinction vulnerability for inward destruction and for species richness as a measure of diversity, we also found high vulnerability in taxa with relatively small mean range sizes (avg. $\beta = −0.18$), and with autocorrelated (avg. $\beta = −0.26$) and more compact (that is, relatively short perimeter; avg. $\beta = −0.123$) species geographic ranges (Fig. 6a). In contrast, lower extinction vulnerability emerges for outward and randomly scattered destruction, for PD, and in regions and taxa with large, elongated and/or scattered ranges (Fig. 6a). This confirms our expectations about the role of range size\(^{26}\) and shape. Notably, the geometry of area loss (inward versus outward or randomly scattered) had a stronger effect than all other considered factors (Fig. 6a), including mean geographic range size.

Predictors of discrepancy between inward and outward loss. Two predictors of the $EAR_{out}−EAR_{in}$ discrepancy (measured as $\Delta AUC$) had particularly high absolute values of averaged beta coefficients and occurred in the two best models (Supplementary Table 3): the mean Moran’s $I$ of the ranges (avg. $\beta = −0.43$) and the mean range size (avg. $\beta = −0.32$). Specifically, the discrepancy was higher in regions and groups with smaller and less autocorrelated ranges. These two predictors were strongly collinear (Pearson’s $\rho = 0.7$, Supplementary Table 1) and hence we were unable to discriminate between them. Because of its slightly higher absolute value of $\beta$ we report the mean Moran’s $I$ in Fig. 6b, but we stress that mean range size may play similarly important role as the autocorrelation of the ranges.

Predictors of discrepancy between EAR and $PDX$AR. The most important predictors of the discrepancy ($\Delta AUC$) between the loss of species richness (EAR) and loss of PD ($PDX$AR) were the factor describing the geometry of habitat loss (inward, outward or random with averaged $\beta$ of 0, −1.53 and −1.66 respectively; Supplementary Table 4) and the Gamma statistic characterizing the tree (avg. $\beta = 0.35$; Supplementary Table 4): phylogenetic trees characterized by higher concentration of branching events towards the tips (higher Gamma) lose their PD at a relatively slower rate. We report the model that contains these two predictors in Fig. 6c. Tree ‘stemminess’ emerges as additional
relevant predictor (avg. $\beta = 0.21$; Supplementary Table 4), suggesting that the effect of tree topology on the EAR-PDXAR discrepancy is better captured by several tree summary statistics, rather than by the Gamma alone.

Discussion

As inward versus outward extinction curves correspond to SAR-based (backward) versus EAR-based extinction estimates, our results falsify the statement by He and Hubbell\textsuperscript{12} that ‘Species–area relationships always overestimate extinction rates from habitat loss’. More precisely, our models show that the SAR-based backward method (equivalent to inward habitat loss\textsuperscript{14}) can give higher estimates of diversity loss than the direct EAR-based method, but it can also give lower estimates, depending on the specific arrangement of species ranges in the region. This ambiguity emerges at large scales where species distributions are better described by contiguous blocks rather than by sets of individuals (as in ref. 12). The issue arises even under simple null expectations of random distribution of ranges, and it critically depends on whether the realized (observed) species distributions emerge as a result of truncation of potential distributions by physical barriers\textsuperscript{29} or whether some variant of mid-domain process generates the distributions\textsuperscript{31}; our findings bring this long-standing debate from basic macroecology into the context of applied extinction science.

Our key empirical finding is that, at large geographic scales, the inward loss of habitats leads to more pronounced declines of species richness than when area is lost from within towards the edges. Our models indicate that this can happen for at least two reasons: (i) ranges may be non-randomly concentrated close to the edges for ecological reasons, for example, because of the presence of suitable habitats in those areas. (ii) Alternatively, the higher relative impact of inward area loss is expected in randomly distributed contiguous ranges, when the ranges are truncated or ‘cropped’ by region boundary, and this truncation can happen for natural reasons, for example, coast truncating potential ranges of a terrestrial species\textsuperscript{29} (Supplementary Fig. 5b), but it can also be an artefact of the study design, for example, when the focal region is part of a larger region (Supplementary Fig. 5c), so that ranges along the edge of the focal region are only parts of larger ranges, overlapping the region boundary. This can easily happen when EAR curves are constructed for small-scale plots (as in ref. 12) that are arbitrarily delineated within a substantially larger region.

Figure 4 | Loss of species richness ($E$) resulting from simulated area loss using empirical species distributions in nine regions and three taxa. Inward area loss (blue) always leads to higher proportional species loss than outward loss (red), and randomly scattered area loss (grey lines) consistently causes the lowest proportional loss. The curves are averages of multiple realizations of the habitat destruction in each of the nine regions and in each of the three vertebrate taxa (birds, mammals, amphibians). The maps at the top row show positions of the nine sampling regions. The shading in the maps indicates altitude.

Figure 5 | Loss of species richness ($E$) compared with the decrease of dendrogram-based measures of diversity (PDX and FDX) due to the simulated loss of habitable area in nine regions and three taxa. Thin transparent lines are realizations of the simulations in the nine regions, thick lines are their averages. Supplementary Fig. 3 provides detailed comparisons of the curves. Note that compared with mammals and birds the amphibian phylogeny has a weaker topological resolution and is based on a number of additional assumptions; see ref. 55 for details. We did not include the $E$ versus FDX comparison for amphibians here as available data impeded comparability.
In such a case, the discrepancy between the effect of inward and outward area loss is not particularly relevant for global species extinction, as the species that go extinct within the delineated area are mostly those that persist outside of it.

Exact quantification of the role of (i) and (ii) is beyond our scope here. Instead, we provide an inductive statistical model that predicts the shape of extinctions curves and their discrepancies by factors that are known to reflect scaling patterns of diversity. We find that the inward–outward discrepancy is highest when ranges are small and have low spatial autocorrelation (contiguity), but these two aspects are correlated and difficult to separate. Intriguingly, the geometry of area loss (inward versus outward

Figure 6 | Statistical models explaining steepness of regional extinction curves and the discrepancy between different types of curves. (a) Predictors of regional extinction vulnerability as quantified by the AUC value, (b) the discrepancy (ΔAUC) between the inward and outward loss of habitat area and (c) the discrepancy between extinction curves for species richness (EAR) and phylogenetic diversity (PDXAR). Only the single best model, respectively, is shown (based on lowest AICc score), which includes different predictors in each of the three approaches (see Supplementary Tables 2–4 for details). Betas (β) are standardized coefficients. We do not provide P-values or standard errors because of a presumed but unknown degree of pseudo-replication (the same taxon over multiple regions, and vice versa). The Gamma statistic represents ‘stemminess’ of a phylogenetic tree. Each point stands for one taxon in one of the nine regions, and/or one measure of diversity where appropriate.

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Exact quantification of the role of (i) and (ii) is beyond our scope here. Instead, we provide an inductive statistical model that
direction of loss) had a substantially stronger effect on the steepness of the extinction curves than mean geographic range size. Given the broadly recognized role of range size for extinction risk, these findings are remarkable and point to the need to jointly account for both the range size and the spatial pattern of the lost habitable area.

Although the inward versus outward dichotomy represents useful extremes, real-world habitat destruction rarely happens in such a defined and contiguous form. Instead, often both inward habitat loss (for example, from larger-scale agricultural development or sea-level rise) and outward area loss from localized centres (for example, sprawling cities or large-scale mining operations) may occur simultaneously. An extreme case of such simultaneous loss is captured by our random fragmentation scenario in which the SAR- and EAR-based extinction curves are equivalent. For this scenario, the magnitude of extinctions is always lower than in the contiguous scenarios (as also reported by refs 20,21,38), revealing the seriousness of the threat from increasing contiguous habitat transformations, as opposed to the more scattered alteration. Note, however, that the model applies only to immediate biodiversity loss. The scattered area or habitat loss may actually lead to range fragmentation, which makes species more vulnerable to extinction in the future. More realistic models that account for various biological phenomena such as coexistence mechanisms, extinction debt, or minimum area requirement could help narrow the often broad bounds on expected biodiversity loss provided by our extreme and simplified scenarios. We also see a promising new avenue in the emerging concept of countryside SAR, which realistically assumes that the new habitats replacing the original area are still to some degree habitable. Unfortunately, some of the more realistic and complex models require relatively detailed and context-specific information and will thus be less generally applicable than the more tractable scenarios presented here.

Some specific demonstrations of how PD can scale with area (PDAR) are now available. However, as we show, such PDAR curves provide no information about the sensitivity of PD to area loss in the focal region. Addressing this sensitivity requires (i) the knowledge of the PDAR outside of the focal area and (ii) the point reflection symmetry of the PDAR and PDXAR curves. These are fundamental issues that require consideration in assessments and policy addressing PD decline under area loss. As predicted (and previously qualitatively argued for PDAR curves), the discrepancy between the loss of species richness (described by EAR) and loss of PD (described by PDXAR) is determined by the shape of the underlying phylogenetic tree: the loss of PD (and other dendrogram-based metrics such as FD) is less pronounced when the extinct species have close relatives or functionally similar species in the region, that is, in a ‘stemmy’ rather than a ‘tippy’ tree shape. For instance, although a single sunbird species is lost as habitable area disappears, other members of the clade would retain a diminishing core of the group’s evolutionary and functional attributes, such as mixed nectar and insect feeding, until the extinction of the clade’s final species.

We find that for terrestrial vertebrate groups and their analysed functional traits, FD suffers a generally less steep proportional loss than PD, highlighting that FD may often, and at least initially, be more readily retained compared with PD. However, unlike PDXAR, the specifics of the FDVAR curve and the generality of this finding will depend on the traits assessed, their number and respective weighting, and the clustering algorithm (or FD metric), all of which can influence the topology of the functional dendrogram. Here, the key insight pertains to qualitative comparison, that is, we can confidently claim that the initial loss of FD (and other dendrogram-based metrics) will always be less pronounced than the loss of species richness.

Although the theory on spatial scaling of biodiversity has seen considerable progress, the scale-dependence of biodiversity loss is a complex and yet underdeveloped field, and further analyses into the associations that we uncovered are needed. In line with others, we have shown that estimates of diversity loss based solely on area lost, and ignoring spatial shape (arrangement, direction) of the loss, can be misleading. The geometry of area loss is crucial, and must be accounted for whenever dealing with extinction predictions or management decisions. Although habitat transformation of small scattered areas within a region may be relatively benign until habitat fragmentation leads to large-scale disappearance of whole species ranges, the destruction of large contiguous blocks of habitat within a region may be fatal. Similarly, estimates of counts of species are agnostic to species’ phylogenetic or functional distinctness or redundancy. Phylogenetic data, together with at least basic geographic distribution characteristics and additional trait information, is rapidly growing and should increasingly allow similar evaluations to ours for other clades and regions and enable a more inclusive conservation science that goes beyond vertebrates. As we demonstrate, such information can bound biodiversity loss expectations and can provide important baseline estimates of the multi-faceted ecological consequences of ongoing and future habitat loss.

**Methods**

**Models of range placement.** Here we describe four contrasting models of range placement that were used for our theoretical arguments (Fig. 2). The simulated realizations of Models 1–4 (Fig. 2a–d) use rectangular ranges placed on a rectangular grid, which is computationally convenient. The analytical reasoning based on Models 3 and 4 (Fig. 2e–g) assumes circular ranges placed into a circular region, which is analytically tractable.

In Model 1, we assume random placement of scattered ranges. This model uses a region consisting of 20 × 20 grid cells of the same area, where each grid cell has a probability of being occupied by an i-th species, and where Pi is constant across grid cells. The presence or absence of i-th species in each cell is then simulated as an outcome of a Bernoulli process with probability Pi. This model produces no spatial aggregation of ranges, and is similar to a random model of He and Hubbell. When averaged across many realizations, this model gives identical EARin and EARout curves. Note that He and Hubbell demonstrate this only implicitly and use different terminology; they also operate at fine scale using individuals as smallest spatial units, whereas here we consider rectangular grid.

In Model 2, we assume non-random placement of contiguous ranges. Real-world scale distributions are usually to some degree contiguous and often aggregated. Model 2 takes this to the extreme by using only contiguous ranges and placing all of them into the upper-left corner of region consisting of 20 × 20 grid cells. As a consequence, when Aear = Aearout, the difference between Eear and Eearout will simply reflect the number of ranges forced to fall completely into Aearout. This mimics, for example, the presence of strong environmental gradients or barriers constraining (truncating) species distributions, and in such a case, the difference between EARin and EARout is trivial.

Models 3 and 4 use random placement of contiguous ranges (Supplementary Fig. 4). Model 3 places each contiguous range entirely within the region, causing highest richness in the centre (mid-domain effect). Model 4 also places ranges randomly, but allows them to overlap domain edges, effectively eliminating the mid-domain effect (see ref. 26 for details of this algorithm).

**Simulations from models of range placement.** The simulations use square ranges placed on an artificial rectangular grid (region) of 20 × 20 grid cells (Fig. 2a–d; see refs 16,26 for similar approach). In each simulation run, we place 711 ranges with sizes drawn from empirical range-size frequency distribution observed in the species of birds that inhabit 2,200 × 2,200 km² placed in Western Africa (region AF1 in Fig. 4). In each run, we calculate mean extinction curves of the inward and outward scenario (EARin and EARout), as well as scattered random destruction scenarios in which grid cells are lost stepwise, one by one, and with the same probability at each step. Each simulation run was repeated 100 times, and the resulting 100 extinction curves were averaged to produce the empirical extinction curve (see below).

**Vertebrate distributional data.** We used expert-drawn range maps for terrestrial amphibians, birds and mammals in all analyses. The range maps were based on the IUCN assessment (http://www.iucnredlist.org/) for mammals and amphibians. Distributions for birds were compiled from the best available sources for a given
geographical region or taxonomic group. See also ref. 52 for more details on the data.

Grid system and study regions. We used an equal area grid originally derived in cylindrical equal-area projection with \( \pi \) degree size at the equator and a constant grid cell area \( A_{\text{cell}} \) of \( \pi \times 100 \) km\(^2\). We selected nine square regions (hereafter the regions, Fig. 4 and Supplementary Fig. 1), each of them having a total area \( A_0 \) of exactly \( 20 \times 20 \) grid cells. The regions were selected so that they lie completely within major continental landmasses and each grid cell within the region contains at least one species.

The regions were also selected to cover a broad diversity of terrestrial biomes, altitudes and latitudes. The nearly identical geometry (note that regions in higher latitudes are slightly elongated relative to the low latitudes) of the regions enabled us to control for the potentially confounding effects of area and shape, and the extinction curves are thus comparable among the nine regions. We note that the large size of the study regions is characteristic of the distinct environmental gradients, and species ranges inside the regions may aggregate along such gradients, similar to the situation in Model 2. This has the potential to enhance the inward–outward discrepancy of the EAR curves.

Extinction curves: species richness (E). We explored three scenarios of habitat area loss: inward, outward and scattered random. We adopted a strictly nested sampling design\(^{29}\) to explore the effects of inward and outward scenario (Fig. 1). We considered sampling windows of sides \( l \) and area \( A_0 = A_{\text{cell}} l^2 \), where \( l \in \mathbb{Z} \) and \( l \leq 20 \). We started with the smallest sampling window \( l = 1 \) and with the largest area outside of the sampling window \( A_{\text{area}} = A_0 - A_0 \). We moved the sampling window continually across the \( 20 \times 20 \) regional grid, and for each position, we recorded number of species with ranges exclusively within \( (E_0) \) and number of species with ranges exclusively outside of \( (E_{out}) \) the sampling window. We calculated mean \( E_0 \) and \( E_{out} \) by averaging \( E_0 \) and \( E_{out} \) values across all of the possible positions of the sampling window. We then enlarged the side of the sampling window to \( l = 2 \) and we repeated the procedure described above. We continued this procedure until \( l = 20 \) and \( A_0 = A_{\text{cell}} \), calculating mean \( E_0 \) and \( E_{out} \) for each of the window areas. We then plotted the proportions \( E_0/S_0 \) against \( A_0/(A_0 - A_{\text{area}}) \) (the red EAR\(_0\) curves in Figs 1 and 4 representing the outward destruction) and \( E_{out}/S_0 \) against \( A_0/(A_0 - A_{\text{area}}) \) (these are the blue EAR\(_{out}\) curves in Figs 1 and 4 that represent the inward destruction).

In the field of phylogenetic reconstruction, we selected the grid cells for the sampling one by one. The area within the set of selected cells was \( A_{\text{cell}} \), and the richness of species endemic to that area to \( A_0 \). In each step, each grid cell within the remaining area \( (A_0 - A_{\text{area}}) \) had the same probability of being selected for the destruction. We repeated this procedure 400 times and averaged the resulting extinction curves to get EAR\(_0\) and EAR\(_{out}\).

Extinction curves: PD. We used the most recent and dated phylogenies on the three vertebrate taxa. For birds, we chose the first tree in the posterior set (distribution) of trees in Jetz et al.\(^{25}\) (see also Jetz et al.\(^{23}\) for discussion of tree dating and robustness). We also selected one mammal super-tree from Kuhn et al.\(^{24}\). For amphibians, we used the super-tree from Isaac et al.\(^{25}\). We used the term PD for the sum of the branch lengths of a phylogenetic tree (or a sub-tree, see below)\(^{24}\). In one extreme case (the rake-shaped phylogeny), PD is equivalent to species richness (Fig. 3). Let us define several terms (see also Fig. 3 and Jetz et al.\(^{55}\)). In one extreme case (the rake-shaped phylogeny), PD is equivalent to species richness (Fig. 3). Let us define several terms (see also Fig. 3 and Jetz et al.\(^{55}\)).

Regional predictors. For each of the three major taxa in each of the nine regions, we put together nine predictors (see Supplementary Methods for technical details): (i) Gamma statistic. Tree ‘stemminess’ represented by Pybus and Harvey’s\(^{30}\) gamma statistic \( \gamma \) characterizes the distribution of branching events within the tree. Trees with \( \gamma > 0 \) have relatively longer inter-nodal distances towards the tips of the phylogeny (‘tippy’ trees), whereas trees with \( \gamma < 0 \) have relatively longer inter-nodal distances towards the root of the phylogeny (‘stemmy’ trees). (ii) Stemminess. This is an alternative measure of how ‘tippy’ (or ‘stemmy’) a tree is in a given region. It is calculated as \( I_{\text{atan}}/I_{\text{root}} \), where \( I_{\text{atan}} \) is the sum of all branch lengths in the phylogeny and \( I_{\text{root}} \) is the distance from the tips to the root of the tree, multiplied by the total number of tips. (iii) Colless’ index of imbalance\(^{37}\), which measures the branching symmetry of the phylogenetic tree of a given taxon in a given region. (iv) Mean range size, which is the arithmetic mean (calculated across all species) of the total number of grid cells in a given region in which a species was ‘detected’ according to the expert-drawn range map. (v) Mean of sqrt(range size)/perimeter. By perimeter we mean the total number of grid-cell sides that form edges of a grided area occupied by a species in a given region. We calculated the arithmetic mean of the sqrt(range size)/perimeter over all species of a given taxon that live in the region. (vi) Mean Moran’s \( I \) of the ranges. For each species in each region, we measured the autocorrelation of the 1 (occupied) and 0 (unoccupied) values by global Moran’s \( I \), which is a measure of contiguity of the ranges, and we took the arithmetic mean (across all species) of the values. (vii) Total richness (or \( S_0 \)) of given taxon in given region. (viii) Richness gradient. We created fine-grain (using \( 1^\text{st} \) cells) map of species richness for each taxon in each region. We then calculated the ordinary least square linear regression of richness on area and used it to predict the richness for each area in the region. We then measured the autocorrelation of cell-specific values of species richness. In contrast to the previous measure, the Moran’s \( I \) of richness captures short-distance autocorrelation.

Models explaining AUC and \( \Delta \text{AUC} \) by the regional predictors. We built three sets of statistical models: (i) Models that explain AUC of all of the EAR and PDXAR curves (162 data points). (ii) Models that explain \( \Delta \text{AUC} \) of all pairs of EAR and PDXAR (27 data points) with EAR\(_{in}\) and PDXAR\(_{in}\). (iii) Models that explain \( \Delta \text{AUC} \) of all pairs of EAR and PDXAR\(_{out}\) (81 data points). (iv) Models that explain \( \Delta \text{AUC} \) of all pairs of EAR\(_{in}\) and PDXAR\(_{out}\) (27 data points). (v) Models that explain PD\(_{in}\) and PD\(_{out}\) (27 data points). (vi) Models that explain AUC of all pairs of EAR\(_{in}\) and PD\(_{out}\). (vii) Models that explain AUC of all pairs of EAR\(_{out}\) and PD\(_{out}\). (viii) Models that explain AUC of all pairs of EAR\(_{in}\) and PD\(_{in}\). (ix) Models that explain AUC of all pairs of EAR\(_{out}\) and PD\(_{in}\). (x) Models that explain AUC of all pairs of EAR\(_{out}\) and PD\(_{out}\).

Representing regional extinction vulnerability by AUC. We use the AUC (or simply integral) to represent the abovementioned variation of extinction curves (Figs. 2a–d) with steep curves, that is, high extinction vulnerability of a region, characterized by high AUC.

\[ P_{\text{Din}}/P_{\text{Dout}} = \text{against} \]
shape of FDXAR curves. We therefore do not analyse these curves or FDXAR and PDXAR differences in detail and instead focus on the qualitative comparison between FDXAR and EAR curves, which is not affected by these methodological effects. All of the distributional data, phylogenies, functional dendrograms and shapefiles used for the analyses described above are also provided (see Additional Information). Further technical details are in Supplementary Methods.

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Author contributions
P.K., D.S. and W.J. designed the study and wrote the paper. W.J. provided large part of the data. P.K. led the writing, formalized the theoretical arguments, processed the data and did all analyses, simulations and visualizations.

Additional information
Complete R code, distributional data, phylogenies, functional dendrograms and shapefiles used for the analyses and simulations. The data can be downloaded from Figshare: figshare.com/s/a08c417290df11e49da06ec4d80c141 (doi:10.6084/m9.figshare.1282334). The data come with readme.txt file that contains further details and guidelines for loading the data and reproducing the analyses.

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