

Species–area relationships always overestimate extinction rates from habitat loss

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Extinction from habitat loss is the signature conservation problem of the twenty-first century¹. Despite its importance, estimating extinction rates is still highly uncertain because no proven direct methods or reliable data exist for verifying extinctions. The most widely used indirect method is to estimate extinction rates by reversing the species–area accumulation curve, extrapolating backwards to smaller areas to calculate expected species loss. Estimates of extinction rates based on this method are almost always much higher than those actually observed^{2–5}. This discrepancy gave rise to the concept of an ‘extinction debt’, referring to species ‘committed to extinction’ owing to habitat loss and reduced population size but not yet extinct during a non-equilibrium period^{6,7}. Here we show that the extinction debt as currently defined is largely a sampling artefact due to an unrecognized difference between the underlying sampling problems when constructing a species–area relationship (SAR) and when extrapolating species extinction from habitat loss. The key mathematical result is that the area required to remove the last individual of a species (extinction) is larger, almost always much larger, than the sample area needed to encounter the first individual of a species, irrespective of species distribution and spatial scale. We illustrate these results with data from a global network of large, mapped forest plots and ranges of passerine bird species in the continental USA; and we show that overestimation can be greater than 160%. Although we conclude that extinctions caused by habitat loss require greater loss of habitat than previously thought, our results must not lead to complacency about extinction due to habitat loss, which is a real and growing threat.

The Millennium Ecosystem Assessment¹ predicts that near-term extinction rates could be as high as 1,000 to 10,000 times background rates (see also ref. 7). Most predictions of species extinction rates, including those in the Millennium Ecosystem Assessment, are inferred from applying the SAR to rates of habitat loss^{8–14}. The wide discrepancy between the rates of species extinction predicted by this method and the extinction rates actually recorded, has fuelled a continuing debate about how to explain the discrepancy^{2,4,15–20}. The main issue is that, almost always, more species are left after a given loss of habitat than the number of species predicted to remain, based on the SAR. The most frequent interpretation is that the excess species are ‘committed to extinction’. The term ‘extinction debt’ was coined to refer to species’ populations that were no longer viable but were facing certain extinction due to habitat destruction that had already occurred^{3,6,17}. The consensus on the most likely reason for the extinction debt is that there is a time lag for populations to go extinct after severe losses in population size^{6,21}.

Here we show that extinction rates estimated from the SAR are all overestimates. We define extinction rate as the fractional loss of species over a defined period accompanied by a given loss of habitat. These overestimates are due to the false assumption that the sampling problem for extinction is simply the reverse of the sampling problem for the SAR. The area that must be added to find the first individual of a species is in

general much smaller than the area that must be removed to eliminate the last individual of a species (Fig. 1). Therefore, on average, it takes a much greater loss of area to cause the extinction of a species than it takes to add the species on first encounter, except in the degenerate case of a species having a single individual. We show mathematically that this is a necessary result of fundamental sampling differences between the SAR and the endemics–area relationship (EAR). Only in a very special and biologically unrealistic case, when all species are randomly and independently distributed in space, is it possible to derive the EAR from the SAR. Although this special case almost never occurs in nature, we examine this simple case first to clarify the nature of the problem. Then we relax these assumptions and consider the general case of aggregated species distributions.

The problem has gone unnoticed for so long because the traditional method for estimating extinction uses the power-law SAR, $S = cA^z$, which has no sampling theory relating it to species distributions (Supplementary Information A). To develop a sampling theory, we must consider the spatial distribution of species explicitly (Supplementary Information B and C). We derive the SAR and EAR from nearest-neighbour distances under two situations, random dispersion and clumped dispersion. We construct a SAR from the probability of encountering the first nearest neighbour of a species (a new species is added every time the sampling frame a encounters the first individual of the given species). In contrast, we construct the EAR from the probability of encountering the last neighbour of a species (a species is added only after all individuals are contained within frame a). We arrive at the species–area curve for randomly and independently distributed species as (Supplementary Information B):

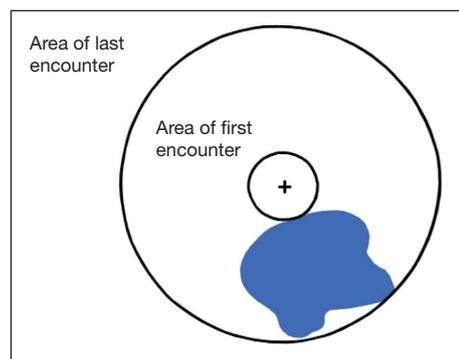


Figure 1 | Sampling differences for SAR and EAR. Range distribution of a species (blue area), and an arbitrary starting sample point, indicated by +. Regardless of the starting location, a sampling frame of arbitrary shape (here circular) with an area of a size sufficient to contact the species for the first time is always less than the sample area needed to encompass the entire range of the species. The SAR (species accumulation) is constructed from sample areas of first contact, and the EAR (species extinction) is constructed from areas of last contact.

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$$S_a^1 = S - \sum_{i=1}^S \left(1 - \frac{a}{A}\right)^{N_i} \tag{1}$$

and the endemics–area curve as:

$$S_a^N = \sum_{i=1}^S \left(\frac{a}{A}\right)^{N_i} \tag{2}$$

where N_i is the total abundance of species i and S is the total number of species in the region A . Equations (1) and (2), derived from nearest-neighbour distances, are identical to the classical random placement models^{22–25}.

Let the total area be A and let a sub-area a be lost. For randomly and independently distributed species, we can calculate the expected number of species lost with a loss of area a from the SAR (equation (1)) as $S_{\text{loss}} = S - S_{A-a}$. This is identical to the EAR calculated directly from equation (2): $S_{\text{loss}} = S - S_{A-a}^1 = \sum_{i=1}^S \left(\frac{a}{A}\right)^{N_i} = S_a^N$. This proves that, for the special case of species distributed randomly in space, extinction rates estimated from the backward random placement SAR and from the forward random placement EAR are the same, and the SAR and EAR are mirror images (Fig. 2 and Supplementary Fig. 1). This case is true because, under random placement, the total area A is equal to the sum of the areas of encountering the first individual and the last individual of a species. From the probability models of the nearest-neighbour distance, the expected area needed to sample the first individual is $a^1 = A/(N + 1)$, and the expected area for the last individual is $a^N = NA/(N + 1)$ (Supplementary Information B). Thus $a^1 + a^N = A$. Note that $a^N > a^1$ is always true except when $N = 1$.

This mirror-image relationship only holds for randomly distributed species, however. Almost all species in nature are clumped, not randomly distributed²⁶. For aggregated species, one can show that $a^1 + a^N < A$ with $a^N \geq a^1$ remaining true (Supplementary Information C and Supplementary Fig. 2). This leads to $S - S_{A-a}^1 \neq S_a^N$. The more spatially aggregated species distributions are, the stronger the inequality $a^N \geq a^1$ becomes. These results are completely general and explain the discrepancy between the backward SAR and forward EAR methods as well as why the backward SAR method systematically overestimates extinction rates.

These results apply to sample areas on any spatial scale. We can assess the magnitude of overestimation by the backward SAR method precisely in cases where we know the species composition and spatial location of each individual of each species or spatial range of each species. To illustrate this, we use spatially explicit data from eight large stem-mapped plots from a global forest dynamics network. We also perform the analysis on biogeographical spatial scales for passerine species in the continental USA (see Methods). The results show that the classic power-law SAR model, $S = cA^z$, and its corresponding EAR model (Supplementary Information A),

$$\lambda = S_{\text{loss}}/S_A = 1 - (1 - a/A)^z \tag{3}$$

are not mirror-image curves. In equation (3), S_{loss} is the number of species lost (endemic) to destroyed sub-area a . Because of the difference in sampling procedure of encountering species and losing species, the slopes z of the power-law model $S = cA^z$ and EAR (3) are not the same. The fit of the power-law SAR and EAR to species–area and endemics–area data respectively lead to two very different slopes

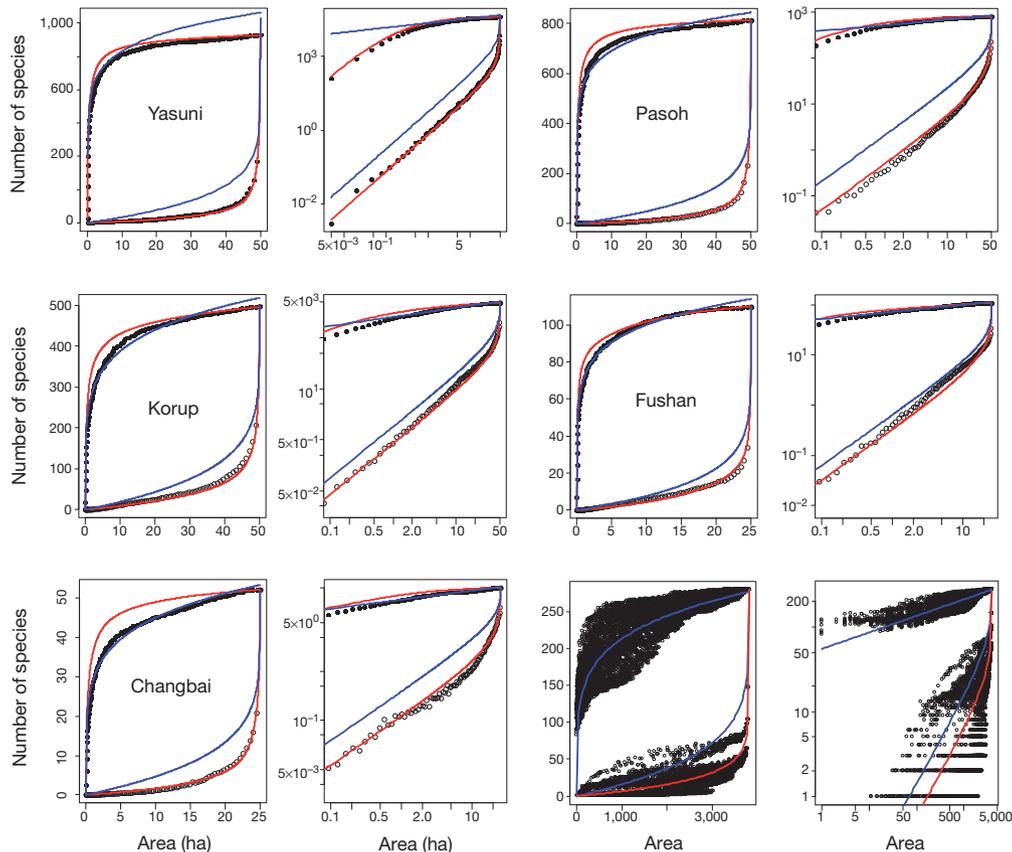


Figure 2 | Species- and endemics–area curves for six of the nine data sets in Table 1. The second and fourth columns are the plots on a log–log scale. The upper and lower blue curves are the fits of the power-law SAR and EAR (equation (3)), respectively. The upper and lower red curves are the predictions of the random placement SAR (equation (1)) and EAR (equation (2)), respectively. Unlike for the other data sets, the red curve for US passerine data

(cell size 0.48° latitude \times 0.48° longitude) is the fit of equation (3) because the abundances of the passerine species are not known (so equation (2) cannot be used). The cloud of points represent 100 repeated random samples of the SAR and EAR. The SAR and EAR curves for the Barro Colorado Island plot are shown in Supplementary Fig. 1.

Table 1 | Eight stem-mapped forest plots across the world and distributions of passerine birds in the continental USA

Plot	Forest type	Size (ha)	Number of trees	Number of species	z_{SAR}	z_{EAR}	Bias _{0.52} (%)	Bias ₂₅ (%)
Barro Colorado Island, Panama	Lowland tropical forest	50	325,549	316	0.133 (0.00202)	0.0803 (0.000611)	65.61	64.38
Yasuni, Ecuador	Lowland tropical forest	50	307,279	1,128	0.126 (0.00473)	0.0623 (0.00189)	102.21	100.41
Pasoh, Malaysia	Lowland tropical forest	50	323,262	814	0.124 (0.00374)	0.0536 (0.00158)	131.30	129.02
Korup, Cameroon	Lowland tropical forest	50	328,973	496	0.179 (0.00369)	0.113 (0.00116)	58.38	56.92
Dinghu, China	Subtropical evergreen broad-leaved forest	20	71,617	210	0.274 (0.00180)	0.193 (0.000880)	41.94	40.34
Fushan, Taiwan	Subtropical evergreen broad-leaved forest	25	114,508	110	0.142 (0.00199)	0.0922 (0.000838)	53.99	52.92
Tiantong, China	Subtropical evergreen broad-leaved forest	20	94,603	152	0.200 (0.00214)	0.0994 (0.00175)	101.15	98.34
Changbai, China	Temperate forest	25	38,902	52	0.184 (0.00296)	0.0905 (0.00233)	103.27	100.62
USA	Passerine birds (0.24° × 0.24°)	14,904	–	279	0.187 (0.00101)	0.0766 (0.000516)	144.06	140.31
USA	Passerine birds (0.48° × 0.48°)	3,830	–	279	0.195 (0.00106)	0.0791 (0.000421)	147.39	143.39

The 'bias' is the overestimation calculated by comparing the extinction rates estimated from the z_{SAR} values with those from the endemic z_{EAR} values: $(\lambda_{SAR} - \lambda_{EAR})/\lambda_{EAR}$. We calculated percentage bias by assuming 0.52% and 25% habitat loss^{1–29}, respectively. Equation (3) gives λ_x . To analyse passerine distributions, we divided the lower 48 states of the USA into a grid of 14,904 cells with cell size of 0.24° latitude × 0.24° longitude and into 3,830 cells with cell size of 0.48° latitude × 0.48° longitude.

(the SAR z_{SAR} versus the EAR z_{EAR}) (Table 1). In some cases, z_{SAR} can be more than double z_{EAR} . This result is independent of the spatial scale of the data, as is evident for the passerine case shown in Table 1.

This analysis demonstrates that the most widely used method of estimating species extinction rates due to habitat loss, the backward SAR calculation, is not correct. For non-randomly distributed species, the SAR and EAR are not mirror images, so that one cannot be used to infer the other. This result holds regardless of how well the power-law SAR fits species–area data (Supplementary Information D). Even for randomly distributed species, the backward power-law SAR model is still not appropriate for estimating extinction rates because in this case equation (1) is the only correct SAR, not the power-law SAR (Supplementary Fig. 2), and equation (2) is the only correct EAR model. These results show that the concept of an 'extinction debt' (that is, the extinctions lost to biotic relaxation due to habitat destruction) based on the backward SAR model is not conceptually sound. Note that these results say nothing about whether an extinction debt exists, only that such a debt as might exist is not appropriately measured by the backward SAR method. To model the process of biotic relaxation will require a dynamic theoretical framework different from the current static SAR model. Currently, no such theory is available. The EAR curve is consistent with the concept of 'imminent extinction', which states that predictions of near-term extinctions due to habitat loss should focus on species endemic to the area of destroyed habitat^{4,7,27,28}.

Previous estimates of extremely high extinction rates, – for example, one species per hour to one species a day⁸, 33–50% of all species between the 1970s and 2000 (ref. 9), from half to several million species by 2000 (refs 10, 12) or 50% of species by 2000 (ref. 11) – have not been observed. There is also reason to question the recent estimates of extinction rates made by the Millennium Ecosystem Assessment¹ and those by Thomas *et al.*¹⁹. In the latter case, the loss of habitat and the shift of species' ranges are driven by climate change. However, the use of the flawed backward SAR in Thomas *et al.* raises a legitimate question about the validity of their conclusion that 18–35% of species will be committed to extinction by 2050. We suggest that their estimated rates of extinction should be regarded as a high-end possibility rather than as supported by hard scientific evidence.

By how much have we overestimated extinction rates? Precise answers to this question require information about the EAR curve, which is generally not known. However, we can make a first approximation from the results shown in Table 1, for which we know the EAR curves in stem-mapped samples of forests and range distributions of passerines. We calculated the z_{EAR} and z_{SAR} averaged over the data in Table 1, leading to $z_{EAR} = 0.0940$ and $z_{SAR} = 0.174$. We then used two estimates of forest habitat loss, the annual deforestation rate of $(a/A)100\% = 0.52\%$ for humid tropical forests²⁹ and the estimated 25% conversion of original forest habitat into agricultural land¹. The

SAR backward method (equation (3)) overestimates extinction rates by 85.07% and 83.00% in these respective cases, compared with the rates estimated by the forward EAR method. Conservation biologists often use a z value of 0.25 in cases where z values are not available^{18,19}. Using this value inflates extinction rate estimates much more, being 165.85% and 160.10% for the two deforestation rates, respectively (see also Supplementary Fig. 1).

Are better methods available for estimating extinction rates? Our results show that the random placement EAR curve describes the empirical EAR curves for the forest plots very well. This result is remarkable and provides a simple method for estimating extinction (Supplementary Information E). Note that the theoretical random placement EAR for each plot is not data-fitting but a genuine prediction from equation (2).

These results might receive a mixed reaction from the conservation community. On the one hand, the good news is that all extinction rate estimates based on the backward SAR method are overestimates. Because it is derived from sample areas of first contact with each species, the backward SAR method makes the previously unrecognized assumption that any loss whatsoever of population due to habitat loss commits a species to extinction, which clearly is not true. On the other hand, there is likely to be concern that these results could jeopardize conservation efforts and be falsely construed in some quarters to imply that habitat loss is not a problem. Nothing could be further from the truth. There is no doubt whatsoever that the Millennium Ecosystem Assessment¹ has correctly identified habitat loss as the primary threat to conserving the Earth's biodiversity, and the sixth mass extinction might already be upon us or imminent³⁰. Our results do indicate, however, that the backward SAR is not the correct way to estimate the magnitude of the current extinction event. To help mitigate contemporary extinctions and strengthen the science behind conservation planning, we need far better geographical data on endemism and species' distributions to improve forecasts of extinction rates⁷. Improving geographical databases on the distribution of biodiversity on Earth should be an urgent international priority.

METHODS SUMMARY

We analysed data from eight 20–50 ha (1 hectare (ha) = 10⁴ m²), stem-mapped plots of the Center for Tropical Forest Science global plot network to construct SAR and EAR curves (<http://www.ctfs.si.edu/>). These data sets are suitable because (1) our analysis is independent of spatial scale, (2) they are among the few data sets in which individuals are mapped on a landscape scale and (3) the EAR curve, which must be known, cannot be calculated from SAR curves (see text).

We obtained the SAR and EAR curves as follows: (1) grid the plot into cells of some minimum size (for example 5 m × 5 m); (2) count the number of species and the number of endemic species (species completely confined to the sample area) in each cell; (3) average the number of species per cell and the number of endemic species across all cells of a given size; and (4) construct species–area and endemics–area

curves by repeating steps 1–3, increasing cell size from $5\text{ m} \times 5\text{ m}$, $10\text{ m} \times 5\text{ m}$, $10\text{ m} \times 10\text{ m}$, etc. up to the entire plot.

We estimated z_{SAR} by nonlinear fit of the power-law SAR model to the observed species–area data. We limited fitting to areas of at least 0.2 ha because the power-law model is not considered applicable at small spatial scales (including them inflates z values and worsens overestimation). We estimated z_{EAR} by directly fitting equation (3) to the observed endemics–area data (see Table 1).

We analysed SAR and EAR curves for 279 passerine species in the lower 48 states of the USA using individual species' range maps from Natureserve (<http://www.natureserve.org/getData/birdMaps.jsp>). We divided the USA into grids at two respective cell sizes, 0.24° latitude \times 0.24° longitude (14,904 cells) and 0.48° latitude \times 0.48° longitude (3,830 cells), to confirm that our analysis is robust to scale change, as predicted by the analytical results. We computed SAR and EAR curves using presence–absence data following the above procedure.

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