

Geometry and scale in species–area relationships

ARISING FROM F. He & S. P. Hubbell *Nature* **473**, 368–371 (2011)

He and Hubbell developed a sampling theory for the species–area relationship (SAR) and the endemics–area relationship (EAR)¹. They argued that the number of extinctions after habitat loss is

described by the EAR and that extinction rates in previous studies are overestimates because the EAR is always lower than the SAR. Here we show that their conclusion is not general and depends on the geometry of habitat destruction and the scale of the SAR. We also question their critique of the Millennium Ecosystem Assessment estimates, as those estimates are not dependent on the SAR only, although important uncertainties remain due to other methodological issues.

In several studies of extinction rates^{2–4}, the proportion of extinctions after a habitat loss of area a from a total area A has been estimated from the power-law model of the SAR, $S_{SAR}(A) = cA^z$, as:

$$\lambda_{SAR}(a) = \frac{S_{SAR}(A) - S_{SAR}(A-a)}{S_{SAR}(A)} = 1 - \left(1 - \frac{a}{A}\right)^z \quad (1)$$

He and Hubbell call this method the backward SAR, as it uses estimates from the SAR in a backward way (from large to small areas) of how the SAR is constructed¹. They argue that, instead, the number of extinctions is given by the proportion of endemics in a relative to A , which can be approximated by

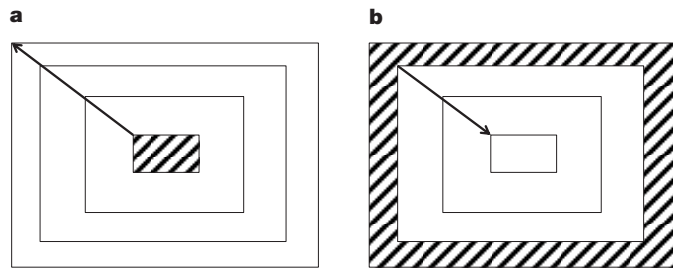


Figure 1 | The outward EAR and the inward EAR. **a**, The outward EAR is calculated by counting the number of the endemic species to a rectangle from the centre to the periphery. **b**, The inward EAR is calculated by counting the number of endemics to an outer ring from the periphery to the centre. It is the inward EAR that replicates the geometry of the backward SAR.

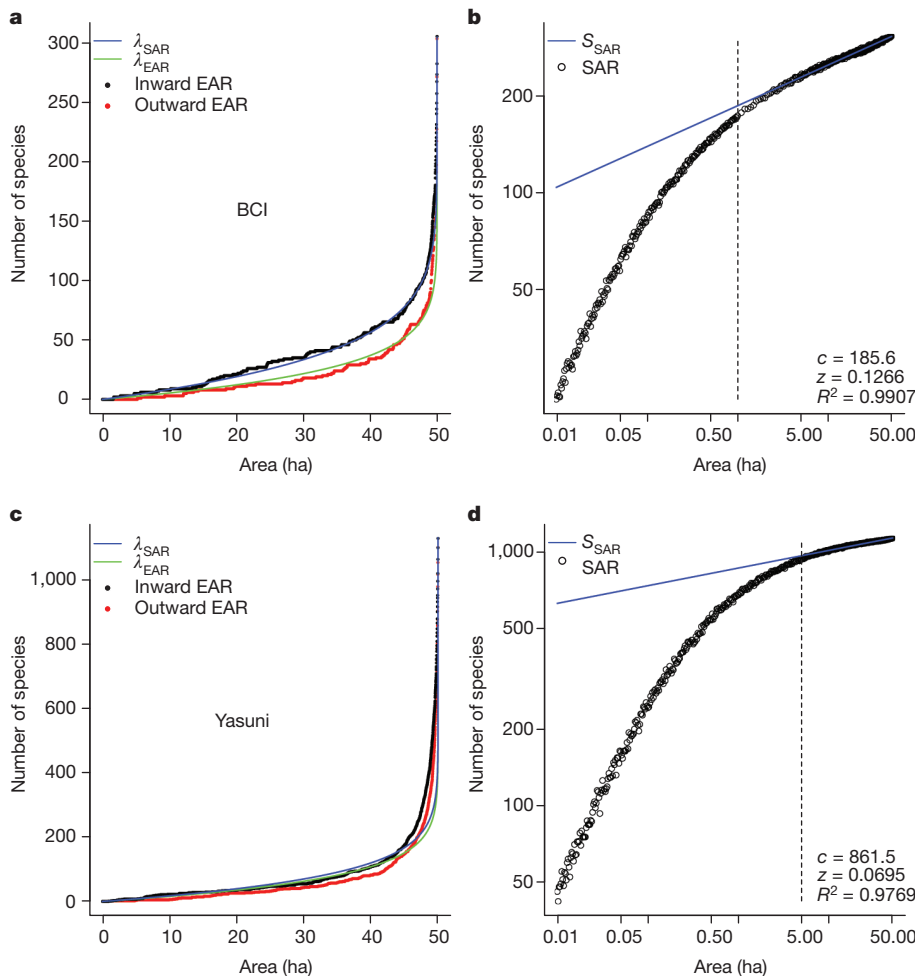


Figure 2 | The influence of scale and geometry on the EAR and the SAR. **a, c**, The graphs compare the outward EAR and the inward EAR with the backward SAR model (λ_{SAR}) and the forward EAR model (λ_{EAR}) fitted to the data of each plot. Points correspond to the value of the EAR for each area size, sampled as in Fig. 1. The z value for λ_{EAR} comes from He and Hubbell¹, whereas the z value for the λ_{SAR} comes from the fit of the power law to the linear region of the SAR. **b, d**, Fit of the power-law SAR (S_{SAR}) to the data on a log–log scale. Each point corresponds to the average number of species for randomly placed rectangles with a given area size. The SAR sampled from the centre to the periphery (Fig. 1a) gives similar z values ($z_{BCI} = 0.1265$ and $z_{Yasuni} = 0.0625$). All z values were obtained by nonlinear least squares. The dashed vertical line marks the minimum area included in the fit. The top plots are for the tree and shrub species in the 50 ha plot in Barro Colorado Island (BCI), Panama, whereas the bottom plots are for the 50 ha plot in Yasuni, Ecuador.

$$\gamma_{\text{EAR}}(a) = 1 - \left(1 - \frac{a}{A}\right)^z \quad (2)$$

where z' is fit from the EAR and is always lower than the z from the SAR. The EAR is built in a forward fashion, counting the endemic species in progressively larger areas.

It is uncontroversial that the species that go extinct immediately after habitat destruction are the endemic species to the area removed^{5,6}. However, both λ_{EAR} and λ_{SAR} describe the proportion of endemics in an area a , although of different geometry⁵. If destruction starts from the centre of the patch (Fig. 1a), then λ_{EAR} describes the number of extinctions because it approximates the proportion of endemics in progressively larger rectangles, the outward EAR (Fig. 2a). In contrast, if destruction occurs in the periphery (Fig. 1b), it is λ_{SAR} that describes extinctions because it approximates the number of endemics in outer rings towards the centre of the plot, the inward EAR (Fig. 2a). This happens because only the inward EAR backtracks the geometry of how the SAR is built. This backtracking is exact if the SAR is built as in Fig. 1a, or approximate if the SAR is built from sampling several rectangles for each area size, but the z values of both methods are almost the same (Fig. 2).

Note that, depending on the spatial structure of the distribution of species in the plot, the outward EAR may be similar to the inward EAR (Fig. 2c), but λ_{SAR} is always a good approximation of the inward EAR as long as the SAR data points fit the power law. This fit depends on the scale of the SAR. Several studies have shown that at very small scales the SAR is curvilinear in a log–log scale⁷, as can be observed in the Barro Colorado Island and Yasuni plots (Fig. 2b, d). Therefore, the z of the SAR must be calculated for the linear region that is relevant for the extinction projections.

There are many other sources of uncertainties in estimating future extinction rates. For instance, both the SAR and EAR project that all species go extinct after all native habitat is lost, ignoring that many species persist in human-modified habitats. The countryside SAR addresses this problem by tracking the number of species with similar habitat affinities in multiple habitats⁸. Another open question is what type of SAR better describes long-term extinctions after habitat loss. After a first stage of extinction of endemics, described by the EAR or the backward SAR, many species that still occur in the landscape will go extinct because the habitat left for them is smaller than their minimum required habitat size⁶. In this case, it has been proposed that future extinction rates are better described by the island SAR (built from counting the number of species in different islands)⁶.

The Millennium Ecosystem Assessment drew in a wide range of extinction projections to identify the envelope of those uncertainties⁹. The SAR projections^{2,4} were consistent with estimates from other methods, such as assessing the extinction risk of currently threatened

species^{10,11}. In 2010 there was a revised assessment with more recent global extinction projections¹², in which SAR-based projections again had a limited role, and new approaches such as the overlap of species ranges with habitat loss¹³, ecophysiological models¹⁴ and the correlation between elevational range and extinction risk, were included¹⁵. The range of uncertainty across models and scenarios was close to three orders of magnitude, compared to which the uncertainty now identified by He and Hubbell¹ is negligible. In all cases models and scenarios supported the Millennium Ecosystem Assessment conclusions that biodiversity will continue to decline, and in most cases at increasing rates relatively to the recent past.

Henrique Miguel Pereira¹, Luís Borda-de-Água¹ & Inês Santos Martins¹

¹Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisboa, Portugal.

email: hpereira@fc.ul.pt

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Extinction and climate change

ARISING FROM F. He & S. P. Hubbell *Nature* **473**, 368–371 (2011)

Statistical relationships between habitat area and the number of species observed (species–area relationships, SARs) are sometimes used to assess extinction risks following habitat destruction or loss of climatic suitability. He and Hubbell¹ argue that the numbers of species confined to—rather than observed in—different areas (endemics–area relationships, EARs) should be used instead of SARs, and that SAR-based extinction estimates in the literature

are too high. We suggest that He and Hubbell's SAR estimates are biased, that the empirical data they use are not appropriate to calculate extinction risks, and that their statements about extinction risks from climate change² do not take into account non-SAR-based estimates or recent observations. Species have already responded to climate change in a manner consistent with high future extinction risks.

Most of He and Hubbell's results involved analysis of the number of tree species in 0.2 ha and successively larger subplots within forest stands of 20–50 ha. By only counting the tree stems present in a plot (rather than canopies), they underestimate the true number of species present in small subplots. This artefact exaggerates SAR slopes when subplots smaller than ~2.5 ha are included³.

We suggest that the data He and Hubbell¹ use are not appropriate to calculate SAR or EAR slopes that are relevant to extinction. To calculate extinction risks, it is necessary to consider how many species might be lost if a habitat becomes isolated; however, He and Hubbell used data for forest plots that are surrounded by more forest, and for bird distributional cells that are surrounded by other land where birds also live. He and Hubbell¹ consider the instantaneous presence of species in sample plots within contiguous areas, not the expected long-term persistence of species if these habitats were isolated. On average, 31 species of birds bred each year in Eastern Wood in England (instantaneous number), but only 16 species bred in every one of 25 years (persistent species)⁴. Were this woodland completely isolated from other breeding habitats, the number of species would about halve in 25 years, resulting in much steeper SAR slopes. It is not known whether SAR and EAR estimates would steepen equally or converge for true isolates, so He and Hubbell's¹ main conclusion that SARs overestimate extinction remains unsubstantiated.

He and Hubbell¹ consider that previous² SAR-based estimates of species 'committed to extinction' from climate change (18–35% by 2050) are too high. However, most published estimates of extinction risk from climate change do not derive from SAR⁵. For example, it has been estimated⁶ that "5%, 8% and 16% (mean of dispersal scenarios) of the species considered would have lost 100% of their climatically suitable area by 2050, for minimum, mid-range and maximum climate warming, respectively" and that "15%, 22% and 40%... are projected to have lost more than 90%... by 2050." Given the near-linear continuation of global warming projected before and after 2050, most species losing >90% of their climatically suitable areas over the period ~1970–2050 (and many additional species losing 70–90%) would lose 100% of their area long before 2100. With time lags in both human and climate systems, at least 15–40% of the species analysed are effectively committed to extinction by 2050.

He and Hubbell¹ also argue that projected extinctions exceed those observed, but high population-level extinction rates have already been observed: ~20% climate-related losses within 500 km of retreating latitudinal boundaries⁷, 34% loss of populated areas at retreating elevation boundaries⁸, and loss of an estimated 4% of worldwide lizard populations, consistent with 20% loss of lizard species by 2080⁹. Cloud forest moth species on Mount Kinabalu in Borneo have contracted at both lower and upper boundaries¹⁰ at a rate that, if sustained, would extinguish ~45% of the endemic species by 2100. Amphibians and reptiles have shifted higher in Tsaratanana Massif in Madagascar, where three (5.9% of 51 species considered) of the highest elevation species were not found in 2003¹¹. At Monteverde in Costa Rica, two high elevation anole lizard species became extinct from the study area,

and two high elevation frog/toad species became globally extinct, after dry years¹². The pathogen-induced extinction of ~2.2% of New World amphibian species (harlequin frogs) coincided with unusually hot years¹³. A third of the world's coral species are threatened by a combination of temperature-induced bleaching, ocean acidification and other pressures¹⁴.

Anthropogenic warming so far is less than or equal to half of that expected by 2050, and modelled biodiversity losses accelerate with increased warming. Recently observed range shifts have tracked levels of climate change¹⁵, and these empirical trends are concordant with projected 2050/2100 losses. Although many uncertainties remain, we believe that He and Hubbell's conclusions about extinction risks are unjustified.

Chris D. Thomas¹ & Mark Williamson¹

¹Department of Biology, University of York, Heslington, York, YO10 5DD, UK.

email: chris.thomas@york.ac.uk

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He and Hubbell reply

REPLYING TO H. M. Pereira, L. Borda-de-Água & I. Santos Martins *Nature* **482**, doi:10.1038/nature10857; C. D. Thomas & M. Williamson *Nature* **482**, doi:10.1038/nature10858

Pereira *et al.*¹ argue that our conclusion² that species–area relationships (SARs) always overestimate extinction is not general because the spatial configuration of landscape destruction can influence the results.

Thomas and Williamson³ argue that there are many other causes of extinction besides habitat loss. We agree with the latter comment, but show that the arguments of Pereira *et al.* are not substantiated.

BRIEF COMMUNICATIONS ARISING

Conservation biologists make wide use of SARs to estimate species extinction caused by habitat loss. The mathematics underpinning this application is²

$$\text{EAR}(a) = \text{SAR}(A) - \text{SAR}(A - a) \quad (1)$$

where $\text{EAR}(a)$ is the number of species endemic to subarea a that is nested within the regional area A , $\text{SAR}(A)$ is the total number of species in the region, and $\text{SAR}(A - a)$ is the number of species in the complementary area $A - a$.

$\text{EAR}(a)$ is the number of species immediately lost if habitat area a is destroyed. $\text{EAR}(a)$ is usually not known because data on the global distribution of species are not available. Traditionally, $\text{EAR}(a)$ is obtained by substituting a SAR model, usually the power-law SAR model, into equation (1). However, by making this substitution, our paper² shows that one inevitably overestimates the average, or expected, extinction rate. This so-called backward SAR method is a method for estimating endemic species, not 'extinction debt'. The backward SAR method has nothing to do with, and does not measure, extinction debt. We do not question the existence of extinction debt, but to measure extinction debt it is necessary to use other methods.

There are four reasons that the arguments of Pereira *et al.* are not substantiated. First, Pereira *et al.*¹ commit a statistical error by confusing a specific configuration of landscape destruction with the statistical expectation. The SAR is a macroecological pattern defined as the expected number of species as a function of area. The word 'always' in the title of our paper² refers to the fact that the expectation of extinction rate is always biased too high if one uses the backward power-law SAR method. One certainly cannot trust any single specific case of the extinction rate estimated in this manner to be reliable, and our result is a general proof that shows that the average extinction rate so estimated is always an overestimate.

Second, if what Pereira *et al.* say is correct, then the outward EAR and the inward EAR must be different, but they are not different in their own analysis of the Yasuni plot (figure 2c in ref. 1), undermining their claim. The configuration of destruction can matter only to specific samples, but does not eliminate the bias we show exists in the statistical expectation. It is unclear why outward-inward destruction should be so special, versus, for example, left-to-right or up-to-down destruction. Clearly, a specific destruction pattern cannot represent the general expectation because it is just one sample of many possible patterns of destruction.

Third, Pereira *et al.* compare the SARs between the inward and outward configurations for the Barro Colorado Island (BCI) and Yasuni plots and argue that the inward EAR can be predicted by the backward SAR for the two plots because the z_{SAR} values for both configurations are similar. However, a close scrutiny of the method used to calculate these z values shows that the result is the outcome of post-hoc selected ranges of area over which they chose to fit the SARs. For the BCI plot, they used 1 ha as the minimal area, but they used a 5 ha minimum for the Yasuni plot (figure 2b, d in ref. 1). The problem is that one can obtain practically any z value by arbitrarily varying the minimal area. This is because in small areas the SAR is only approximately a power law, and including small areas when fitting the power-law SAR model inflates the z value. This arbitrary post-hoc selection

of z values invalidates their comparison. The minimum area in our study² is consistently set to be ≥ 0.2 ha across all plots to ensure that the analyses are standardized and comparable and that the log-log SARs are adequately linear with $R^2 > 0.92$. Using a consistent minimum area, one does not obtain their result.

Fourth, Pereira *et al.* argue that island SARs are more appropriate models for estimating extinction rates. This is not correct. Regardless of what you call the SAR or the reason why island SARs generally have steeper slopes than continental SARs, people use the same backwards SAR model to estimate extinction rates on continents and in island archipelagoes. In instances in which z values are not available, researchers universally use $z = 0.25$ (refs 4, 5).

We do not disagree with Thomas and Williamson³ that extinction is caused by many factors, not just habitat loss, including climate change, and we also agree that extinction is real and happening at elevated rates. All we have shown is that the backward SAR method is not appropriate for estimating extinction rates caused by habitat loss. Any extinction rates estimated from that method are questionable. We are well aware that species extinction can be evaluated by a variety of methods. Not all of the extinction estimates in the Millennium Ecosystem Assessment used the flawed backwards power-law method. We did not question or assess the validity of those methods because our study does not apply to them. We also did not criticize the methods used by the Intergovernmental Panel on Climate Change or the International Union for Conservation of Nature to estimate extinctions, contrary to misquotes in the press.

For further information, a JAVA program written by G. Acevo that computes SAR and EAR curves and expectations for model communities is available for download from <http://shubbell.eeb.ucla.edu/earsar.php>.

Fangliang He^{1,2} & Stephen P. Hubbell^{3,4}

¹State Key Laboratory of Biocontrol, and SYSU-Alberta Joint Lab for Biodiversity Conservation, School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, China.

²Department of Renewable Resources, University of Alberta, Edmonton, Alberta, T6G 2H1, Canada.

email: fhe@ualberta.ca

³Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California 90095, USA.

⁴Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, Republic of Panama.

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