

Become a part of the AAAS
community. Join today.

AIDScience

SCIENCE ONLINE SCIENCE MAGAZINE HOME SCIENCE NOW NEXT WAVE STKE/AIDS/SAGE SCIENCE CAREERS E-MARKETPLACE

MARIALUZ CALDERON | [Change Password](#) | [Change User Info](#) | [CiteTrack Alerts](#) | [Subscription Help](#) | [Sign Out](#)

Science
magazine

HELP

SUBSCRIPTIONS

FEEDBACK

SIGN IN

SEARCH

BROWSE

▶ ORDER THIS ARTICLE

ECOLOGY:

Species-Area Relations in Tropical Forests

Robert M. May and Michael P. H. Stumpf*

One of the earliest accomplishments of theoretical ecology was the discovery of a relationship between the number of species (of plants, birds, beetles, or whatever) on a given island and the area of that island (1). For example, a 10-fold increase in island area approximately doubles the number of species. This species-area relationship (SAR) is often used by conservation biologists to assess the long-term effects of the fragmentation of tropical forests, or other reductions in habitat area, upon species diversity (2). The SAR, as first enunciated by MacArthur and Wilson in their influential book *Theory of Island Biogeography* (1) and by others [see (3) and references therein], was phenomenological, based on observations.

The islands described by the SAR may be real islands in the ocean, or virtual islands such as hilltops (where the surrounding lowland presents a barrier to many species), lakes, or wooded tracts surrounded by open land. In such island groups, plotting the number of species S in a particular taxonomic category against the area A results in a power-law relation of the form $S = cA^z$ (see the graph below). The constant c is characteristic of the taxonomic group, but the exponent z tends usually to lie between 0.2 and 0.3. Such a sweeping generalization inevitably requires qualifications. For example, the linear $\log S$ - $\log A$ relation tends to fail (the graph curves downward) if the island area is very small; on the other hand, the exponent z tends to have lower values if the islands are very large (particularly on the scale of a continent). But, despite occasional carping, this SAR with a $z \approx 1/4$ applies to such a wide collection of taxa and island groups that a theoretical explanation is called for. Enter Plotkin *et al.* (3) with just such a theoretical explanation, reported in their new study of more than 1 million trees from five tropical forests on three different continents.

But Plotkin and colleagues are not the only investigators with a contentious theoretical explanation for SAR. The earliest explanation (1, 4) was prompted by the observation that the distribution of numbers

- ▶ [Summary of this Article](#)
- ▶ dEbate: [Submit a response](#) to this article
- ▶ Similar articles found in:
[SCIENCE Online](#)
[ISI Web of Science](#)
[PubMed](#)
- ▶ [PubMed Citation](#)
- ▶ Search Medline for articles by:
[May, R. M.](#) || [Stumpf, M. P. H.](#)
- ▶ Search for citing articles in:
[ISI Web of Science \(2\)](#)
- ▶ Alert me when:
[new articles cite this article](#)
- ▶ [Download to Citation Manager](#)
- ▶ Collections under which this article appears:
[Ecology](#)

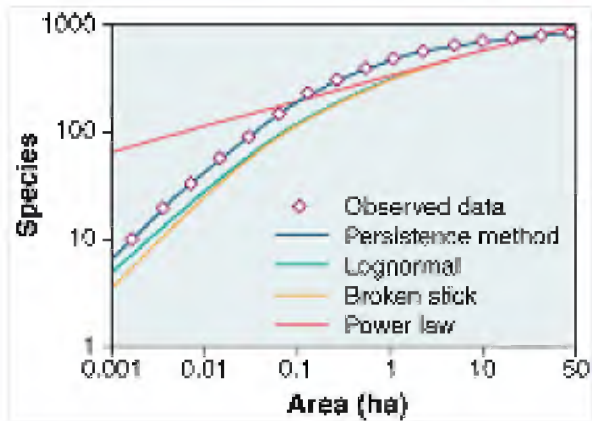
of individuals (N) among species (S) is likely to be influenced by the multiplicative interplay of many different ecological factors. This results in a lognormal distribution for the relative abundance of species within a particular area (see the graph below). Earlier, Preston (5) documented such lognormal distributions; he observed that they were commonly one particular or "canonical" member of this one-dimensionally infinite family, and that for a large number of species they corresponded to the numbers of species and individuals related by $S \approx (\text{constant}) \times N^{0.25}$. Later work (4) demonstrated that, for essentially all lognormal distributions with a sufficiently large number of species, this relation was roughly $S \approx (\text{constant}) \times N^z$, with z in the range 0.2 to 0.3. Add the further rough assumption that the number of individuals (N) is linearly proportional to the island's area (A), and you have the observed SAR power law. An additional refinement is that, although such lognormal distributions of relative abundance of species imply a power law for a large number of species, at lower values of N (and thus A) the curves turn downward. Sugihara (6) later argued that Preston's canonical shape with its exponent $z \approx 1/4$, is more accurate than May's (4) arm-waving can justify, and he proposed a "sequential broken stick" model (7) for the relationship between number of individuals (N) and abundance of species (S). This, I think, gives a better, although still debatable, explanation of observed SAR (see the graph). More recently, Harte *et al.* (8) have offered an explanation for a pure power-law SAR that assumes "self-similarity"--the fraction of a species found in an area A , which is also found in one-half A , is independent of A . This attractive assumption certainly supports the power law, but it has the disadvantage that it gives no reason for why the z exponent is so consistently in the range 0.2 to 0.3, nor does it agree with the observed departure from a pure power law at low values of A .



The diversity of species. The species-area relation (SAR) observed by Plotkin *et al.* (3) in the Pasoh tropical forest site in Malaysia compared with the predictions of four theoretical models. Specifically, all four models have a scaling parameter (c) that essentially depends on overall species richness. For the Plotkin "persistence method," the curve (which involves at least two adjustable parameters) is taken from their paper (3). The self-similarity assumption gives a pure power law, with an arbitrary exponent z ; here, $z = 0.25$. The canonical lognormal and the sequential broken stick graphs have uniquely determined shapes (which asymptotically give power laws with $z = 0.25$), and thus have no adjustable parameters beyond c .

Now come Plotkin and co-workers with their new study (3). They begin with an especially valuable collection of data on the diversity of tropical tree species within each of five 50-ha study sites--in India, Panama, Thailand, and Malaysia (see the figure). Motivated by the work of Harte, Plotkin *et al.* calculate, for each plot, a spatial persistence function, $a(A)$, which describes the average fraction of species present in A that are found (or "persist") in one-half A . For Harte's self-similarity assumption, $a(A)$ is constant. To the contrary, Plotkin *et al.* find that the persistence function depends on A , in a way

that is fairly similar for each of their 50-ha plots. From this analysis, they suggest that the plots have SAR patterns that roughly obey the relation $S = cA^z \exp(-kA)$, where the usual c and z , along with the additional parameter k , can be estimated from the empirical $a(A)$ curves. Interestingly, z and k estimated in this way from any one plot give a good description (to within 5 to 10%) of the shape of the SAR on any of the other plots. That is, the five SARs have similar shapes, although the absolute number of species for a given value of A , which depends on the parameter c , varies significantly among them.



Seeing the forest and the trees. The locations of five tropical forest plots, each 50 ha in size. In each plot, every woody stem greater than 1 cm in diameter was identified by species and counted in the census. Boxes show the total number of trees and the total number of species for each plot. [Adapted from (3)]

The data presented by Plotkin *et al.*--the outcome of a long-term research program coordinated by the Smithsonian Institution's Center for Tropical Forest Science--are immensely useful. As emphasized by the authors, their observed SARs on average roughly conform to a power law with $z \approx 1/4$, but such a simplistic statement underestimates the slope when the area is smaller (as noted by others) and overestimates the slope when the area is larger. The similarity in SAR shapes, despite the differences in overall species richness among the five plots, suggests that we can estimate the diversity of tree species in other unstudied tropical places, on the basis of sampling in just one relatively small area.

Turning from phenomenological usefulness to theoretical underpinnings, there are a number of nagging questions. First, it is not surprising that, with two adjustable parameters (z and k), Plotkin *et al.* can fit observed SAR observations better than the earlier theorists who used one-parameter models (z only). (Give me five parameters, and I will fit elephants.) Second, although Plotkin *et al.* (9) have begun to explore possible theoretical bases for their observed persistence functions, this work is itself phenomenological, based largely on observed clustering patterns of trees.

Third, as is true for other work oriented toward conservation biology, Plotkin *et al.* are not truly dealing with species-area relations, but rather with sampling effects (4). In the original body of work on SAR, which dealt with archipelagos of islands, the rough equilibrium numbers of plants or animals found on islands of different sizes were determined. This is clearly similar to asking about subplots within a larger tropical forest plot, but it is not exactly the same question. Before taking phenomenological rules and theoretical ideas about SAR (from real or virtual islands) and applying them to problems in conservation such as the fragmentation of tropical forests, I would like to see more careful discussion of the similarities and differences between these two ecological situations.

The new work certainly is important from the point of view of the empirical patterns it has uncovered and for the theoretical questions it raises. With the world's tropical forests currently disappearing at an overall rate of between 0.8 and 2% each year--even the rate is uncertain--we desperately need ambitious projects, such as the Tropical Forest Science project on which this work is based, to ensure that effective conservation action is taken.

References and Notes

1. R. H. MacArthur, E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, NJ, 1967).
2. Essentially all estimates of "the number of species becoming extinct this year" are based on a rather wild extrapolation of the SAR, along with estimates of the fraction of tropical forest loss each year. This is, for example, the source of the often quoted "27,000 species will become extinct this year" estimate, a number having embarrassing specificity given that we are unsure, to within a factor of 10, of how many eukaryotic species are alive on Earth today [see R. M. May *et al.*, in *Extinction Rates*, J. H. Lawton, R. M. May, Eds. (Oxford Univ. Press, Oxford, 1995), pp. 1-24] [[publisher's information](#)].
3. J. B. Plotkin *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 10850 (2000) [[Medline](#)].
4. R. M. May, in *Ecology of Species and Communities*, M. Cody, J. M. Diamond, Eds. (Harvard Univ. Press, Cambridge, MA, 1975), pp. 81-120.
5. F. W. Preston, *Ecology* **43**, 185 (1962); *Ecology* **43**, 410 (1962).
6. G. Sugihara, *Am. Nat.* **116**, 770 (1980).
7. In the sequential broken stick model, the "niche space" of the community of species is visualized as some multidimensional volume, which is sequentially broken up by the component species; each of the fragments of the resulting "sequentially broken volume (or stick)" represents the relative abundance of a species.
8. J. Harte, A. Kinzig, J. Green, *Science* **284**, [334](#) (1999).
9. J. B. Plotkin *et al.*, *J. Theor. Biol.* **207**, 81 (2000) [[Medline](#)].

The authors are in the Zoology Department, Oxford University, Oxford OX1 3PS, UK. E-mail: robert.may@zoo.ox.ac.uk; michael.stumpf@zoo.ox.ac.uk

- ▶ [Summary of this Article](#)
- ▶ **dEbate:** [Submit a response to this article](#)
- ▶ Similar articles found in:
[SCIENCE Online](#)
[ISI Web of Science](#)
[PubMed](#)
- ▶ [PubMed Citation](#)
- ▶ Search Medline for articles by:
[May, R. M.](#) || [Stumpf, M. P. H.](#)
- ▶ Search for citing articles in:
[ISI Web of Science \(2\)](#)

- ▶ Alert me when:
[new articles cite this article](#)
- ▶ [Download to Citation Manager](#)

- ▶ Collections under which this article appears:
[Ecology](#)

Volume 290, Number 5499, Issue of 15 Dec 2000, pp. 2084-2086.

Copyright © 2000 by The American Association for the Advancement of Science. All rights reserved.

[STKE](#)

[Resume Database](#)

▲ [PAGE TOP](#)