

# Taxonomic and regional uncertainty in species-area relationships and the identification of richness hotspots

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Edited by Michael P. H. Stumpf, Imperial College London, London, United Kingdom, and accepted by the Editorial Board August 22, 2008 (received for review April 14, 2008)

**Species-area relationships (SARs) are fundamental to the study of key and high-profile issues in conservation biology and are particularly widely used in establishing the broad patterns of biodiversity that underpin approaches to determining priority areas for biological conservation. Classically, the SAR has been argued in general to conform to a power-law relationship, and this form has been widely assumed in most applications in the field of conservation biology. Here, using nonlinear regressions within an information theoretical model selection framework, we included uncertainty regarding both model selection and parameter estimation in SAR modeling and conducted a global-scale analysis of the form of SARs for vascular plants and major vertebrate groups across 792 terrestrial ecoregions representing almost 97% of Earth's inhabited land. The results revealed a high level of uncertainty in model selection across biomes and taxa, and that the power-law model is clearly the most appropriate in only a minority of cases. Incorporating this uncertainty into a hotspots analysis using multimodel SARs led to the identification of a dramatically different set of global richness hotspots than when the power-law SAR was assumed. Our findings suggest that the results of analyses that assume a power-law model may be at severe odds with real ecological patterns, raising significant concerns for conservation priority-setting schemes and biogeographical studies.**

conservation biology | ecoregions | model selection | vascular plants | vertebrates

Species-area relationships (SARs), the change in species numbers with increasing area, are fundamental to the present understanding of many key and high-profile issues in conservation biology. They have, for example, variously been used to predict regional species extinction rates after habitat loss, as a consequence of such pressures as deforestation and climate change (1–4) and to predict species extinction rates in blocks of remnant habitat, including protected areas, as a consequence of their isolation (5). More fundamentally, the SAR is an essential tool used to estimate broad patterns and to identify hotspots of species richness when regions differ in area (6–13).

In the main, applications of SARs have assumed that these relationships take the classical form of a log-linearizable power function,  $S = cA^z$ , where  $S$  is species richness,  $A$  is area, and  $c$  and  $z$  are constants (14). Depending on the objectives and opportunities, the parameters of this function (notably the exponent, or rate,  $z$ ) are derived from theory (15–18), from particular datasets or from broad collations of datasets (19–22). However, although the power function has been applied extremely widely, in practice there is much variation in the basic form of SARs (23, 24). Attention has focused foremost on how this form changes with spatial scale (25–27) or assemblage properties (28). Other kinds of systematic variation may also exist, but analyses have principally only rather narrowly addressed these by comparing the

parameter values estimated from fitting a power function relationship (e.g., space, refs. 21, 29, 30; environment, ref. 31; and anthropogenic threats, ref. 22).

Given that a single generic form for SARs is widely assumed to pertain, of particular concern for conservation biology would be if the underlying form actually differed markedly between major taxonomic groups and/or biomes (global-scale biogeographic regions distinguished by unique collections of ecosystems and species assemblages; ref. 32). Whether such variation was systematic, it could have significant implications particularly for the fundamental understanding of the distribution of biodiversity that underlies much of the prioritization of lands for conservation investment and action (33). For example, studies have variously sought to incorporate the effects of variation in area on species richness at large spatial scales (often ecoregions) when considering the concordance of spatial variation in richness of different higher taxa (13, 34), patterns of protected area coverage (35), the impacts of urbanization on biodiversity (36), and the allocation of conservation resources (37, 38).

In this article, we conduct an analysis of global-scale SARs with two aims. First, we investigate the uncertainty about the best-fitting SAR model by quantifying the relative probabilities that different models best describe SARs and determine whether those probabilities vary systematically for the same higher taxon in different biomes and for different higher taxa in the same biome. Second, we conduct a global identification of hotspots of richness, incorporating the uncertainty about the best-fit SAR model, and compare these results with those obtained when it is assumed that the power model is the best-fitting SAR model. We use data on the species richness of vascular plants and vertebrates across the world's terrestrial ecoregions (13, 39) [supporting information (SI) *Text* and *Table S1*]. Ecoregions are large units of land containing geographically distinct species assemblages and experiencing geographically distinct environmental conditions and have proven valuable for addressing a range of issues in conservation prioritization (13, 40, 41).

## Results

**Taxonomic and Regional Uncertainty in Species-Area Relationships.** The relative fit of eight different potential forms for SARs (*Table S2*) was evaluated for each combination of higher taxon

Author contributions: F.G., O.G., K.J.G., and D.M. designed research; F.G., O.G., K.J.G., and D.M. performed research; F.G., O.G., K.J.G., and D.M. analyzed data; and F.G., O.G., K.J.G., and D.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. M.P.H.S. is a guest editor invited by the Editorial Board.

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This article contains supporting information online at [www.pnas.org/cgi/content/full/0803610105/DCSupplemental](http://www.pnas.org/cgi/content/full/0803610105/DCSupplemental).

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and biome. These forms encompassed convex, sigmoid, asymptotic, and nonasymptotic models, with the fit being evaluated using nonlinear regressions in the so-called model selection framework (42). This emerging approach in the context of SARs (43) aims to evaluate, for a given dataset, the strength of evidence for alternative explanatory models (44). Furthermore, by averaging across statistically valid models, this framework allows the construction of robust inferences incorporating uncertainty regarding both model selection and parameter estimation (multimodel SARs; see *Materials and Methods* for details).

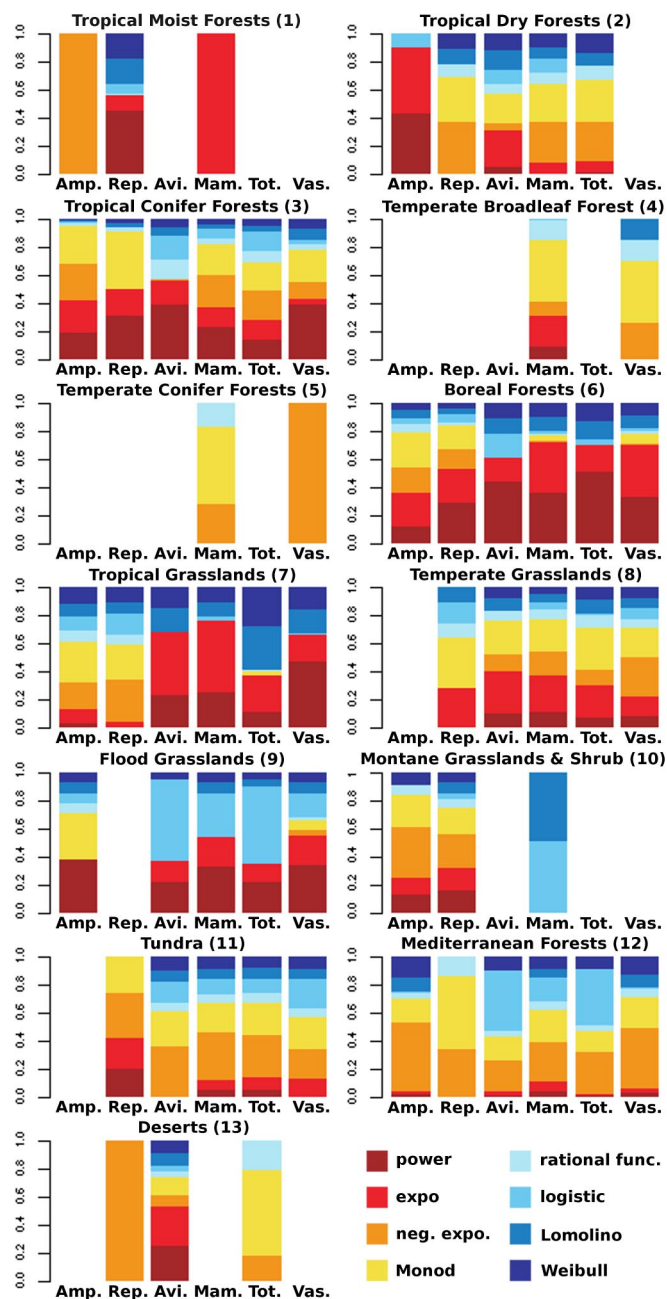
Surprisingly, given the apparent generality of the SAR, the analysis revealed substantial variation in the strength of the effect of area on species richness. Although the  $R^2$  for multimodel SARs had an overall mean of 0.30, values for different combinations of higher taxa and biomes ranged from 0.02 for amphibians in Tropical Dry Forests to 0.69 for total vertebrates in Tropical Grasslands (Table S3). Furthermore, for several datasets (21 of 78), the SAR cannot be adequately described by any of the candidate models (Fig. 1, Table S4). This latter tendency was not limited to those datasets with narrower ranges of variation in species richness or area but is more obvious for biomes than for higher taxa. For example, SARs were statistically validated across temperate forest ecoregions only for mammals and vascular plants.

The best-fitting model varied markedly across biomes for all higher taxa and across higher taxa for each biome (Fig. 1, Table S4). It was the asymptotic negative exponential (convex) and the Monod (convex) models in 18 and 13 cases, respectively, the nonasymptotic power and exponential models in 10 cases each, and the logistic and Lomolino models in five and one case, respectively. The rational function and the cumulative Weibull models never provided the best fit. However, with the exception of four datasets (amphibians and mammals in Tropical and Subtropical Moist Broadleaf Forests, vascular plants in Temperate Conifer Forests, and reptiles in Deserts), there was a substantial degree of uncertainty about the best-fitting SAR model (Fig. 1, Table S4). For most of the datasets, no single model was clearly superior.

Furthermore, for almost all higher taxa, model probabilities differed markedly across biomes (Fig. 1, Table S4). Although for almost all biomes, model probabilities also differed markedly across higher taxa (Fig. 1, Table S4), summing these probabilities across the different models revealed some coarse tendencies. Indeed, for Boreal Forests, except for amphibians, the sum of the probabilities of nonasymptotic models that best describe the SAR was always  $>0.5$ . In contrast, for the Tundra and Mediterranean Forests, the SAR was likely to be asymptotic for most higher taxa (Fig. 1, Table S4).

**Hotspot Detection.** Using multimodel SARs could result in a rather different set of species richness hotspots being recognized than was the case when it was assumed that the power model was the best-fitting SAR model (Fig. 2). For example, using the frequent (but arbitrary) cut-off of distinguishing the richest 2.5% of ecoregions as hotspots, between 30% (birds) and 78% (amphibians) of the hotspots identified by the two approaches were the same. Inevitably, the similarity in the composition of the hotspots increased as the cut-off was increased, but it remained quite variable even when this cut-off was rather high (Fig. 2).

The differences in the hotspots recognized were especially marked when focusing on particular combinations of higher taxa and biomes. In one of many possible examples, for birds in Tropical Grasslands, the five richest ecoregions (approximately the richest 10%) were, with one exception, entirely different when determined using multimodel SARs and when using a power model (Fig. 3, Table 1).



**Fig. 1.** SAR model selection patterns. Patterns of model selection are presented for each biome for amphibians (Amp.), reptiles (Rep.), birds (Avi.), mammals (Mam.), total vertebrates (Tot.), and vascular plants (Vas.). The height of each fraction of the colored band is proportional to the probability (Akaike weight) that each model [see color legend, exponential (expo.), negative exponential (neg. expo.), rational function (rational func.)] is the best in explaining the dataset. A lack of colored band means that none of the eight SAR models was statistically valid for the corresponding dataset.

### Discussion

Although it has long been apparent that the assumption of a single generic form for SARs was potentially problematic (19, 23, 43), the practice has remained widespread. In part, this has been because of the understandable demand to address important, and often urgent, conservation issues in circumstances for which information on the actual form of SARs is wanting and difficult to obtain. The results of the analyses reported here highlight several key issues that result from such an approach.





**Statistical Analyses.** All statistical analyses conducted in this study were implemented within the R statistical programming environment (R 2.7, ref. 48).

**Toward Consensual Inference.** We discriminated the different SAR models in the so-called model selection framework (42, 49), which is now widely used across biological fields (44, 50–52). Through the use of information theoretic criteria such as the Akaike Information Criterion (AIC, ref. 42), it provides a rigorous way in which to evaluate and compare the relative support of nonnested differently parameterized models of a given dataset. In this study, we use Akaike weights derived from the AIC to evaluate the relative likelihood of each SAR model given the data and the set of models. Akaike weights (normalized by construction across the set of candidate models to sum to one) are directly interpreted in terms of probabilities of a given model being the best of a defined set of alternative models in explaining the data (42, 50).

In the model selection framework, model selection uncertainty arises when the data at hand support several models with a similar strength. In such a case, relying on only the best model is inadequate, and multimodel inference is recommended as a way to construct a robust final inference (42). As advocated for differently parameterized models, we use model averaging and consider the weighted average of model predictions with respect to model weights.

One of the most important challenges in information theoretic analyses is the construction of a consistent set of models (42, 52). Here, we propose a set (Table S2), including four convex models (power, exponential, negative exponential, and Monod) and four sigmoidal models (rational function, logistic, Lomolino, and cumulative Weibull). This includes convex, sigmoid, asymptotic, and nonasymptotic functions, thus encompassing the various shapes attributed to SARs in the literature. The linearized forms (via logarithmic transformations) of the power and exponential models were not included in the set because of nonequivalence in the study of the variation in a variable and in its transformation (23, 53) and bias of back-transformed results obtained on a logarithmic scale (54). Furthermore, the nonlinear form of the power equation leads to a more realistic detection of biodiversity hotspots than does the log-linearized power equation (54).

AIC and other model selection criteria that estimate Kullback–Leibler information (see *SI Materials and Methods*) are used widely in the ecological literature, but other criteria such as the Bayesian Information Criterion (BIC) are also commonly used to carry out model selection (42, 50). AIC and BIC were not derived in similar contexts [AIC is based on the Kullback–Leibler information theory, whereas BIC was derived in a Bayesian context (42, 50)] and have different properties: AIC aims to select the best model approximating reality given the sample size and the set of models, whereas BIC was devised to select the true model that generates the data independently of sample size and given that this true model is one of the candidate models. Although AIC and BIC do not share the same conceptual bases and penalize differently for the dimension of the models (BIC tends to select models with fewer parameters than AIC), the results of our analyses were robust to the criterion used for model selection and averaging. Using the BIC, the model ranks were globally maintained across the datasets, and the substantial uncertainty revealed by the AIC analysis persists (Fig. S1).

**Fitting the Models.** Nonlinear regression models were fitted by minimizing the residual sum of squares (RSS) using the unconstrained Nelder–Mead optimization algorithm (55). Assuming normality of the observations, this approach produces optimal maximum likelihood estimates of model parameters (56). Regressions were evaluated by statistical examination of normality and homoscedasticity of residuals: a model was excluded from final averaging if the Lilliefors extension of the Kolmogorov normality test or the Pearson's product moment correlation coefficient with areas was significant at the 5% level. To avoid numerical problems, such as local minima, and speed up the convergence process, we paid particular attention to the starting values that were used to run the optimization algorithm. We obtained initial values for those parameters that were directly interpretable (e.g., an asymptote) by taking corresponding values in the datasets (e.g., the observed maximum of species richness in the case of an asymptote) and calculated initial values for the remaining parameters using the standard procedures of Ratkowsky (57, 58). Although the selection of nonlinear regression models through the use of the coefficient of determination ( $R^2$ ) is not advocated (53, 57), these indices were useful indicators of the proportion of variation in intrabiome species richness explained by area.

**Confidence Intervals and Ecoregion Ranking.** By synthesizing and extending recent advances and solving major concerns about the methodology of hotspot detection (6–9, 11, 12, 54), ecoregions were ranked with respect to their positions in the confidence interval of the model-averaged SAR (Fig. 3, *SI Materials and Methods*). To fully incorporate uncertainty in this process, confidence intervals were calculated by using a nonparametric bootstrapping procedure (59, 60). As advocated for regression (59, 61), we generated bootstrap resamples from the modified residuals (in the sense of ref. 60), and we applied the model selection and averaging procedure to each of these resamples. In so doing, we generated robust confidence intervals explicitly incorporating uncertainty regarding both model selection and parameter estimation.

**Comparison of Hotspot Detection Methods.** To investigate the effect of accounting for uncertainty in richness comparison among places of varying area, we assessed the similarity between the ranking obtained from our approach and that obtained from usual methods (e.g., ref. 13). Classical methods rank regions according to their residuals in a log-linear power regression: the higher the residual, the higher the region in the ranking. The percentage similarity was defined as the number of ecoregions identified as hotspots by the two methods, divided by the total number of ecoregions in a set of hotspots (6). For all higher taxa studied and for a varying proportion of ecoregions identified as hotspots, the percentage similarity between the two methods was averaged across the fitted biomes.

**ACKNOWLEDGMENTS.** We thank S. Buckland, K. L. Evans, L. Marini, and three anonymous reviewers for helpful comments and/or discussions. K.J.G. holds a Royal Society-Wolfson Research Merit Award.

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