

Choice of Species-Area Function Affects Identification of Hotspots

JOSEPH A. VEECH

Department of Biology, Ecology, Evolution, and Conservation Biology Program, University of Nevada, Reno, NV 89557, U.S.A., email javeech@scs.unr.edu

Abstract: *I tested the reliability of species-area curves for use in identifying hotspots, political or geographical regions of high species richness. On a species-area plot, hotspots are points (regions) that appear above the curve to a greater extent than other points. Because several different curves can be fit to species-area data, identification of hotspots may differ depending on the curve-fitting function used. I tested this hypothesis by comparing hotspots identified by the power function, the extreme value function, a linear function, and the exponential function. I examined several species-area data sets varying in size and in the presence of endemics. I defined hotspots as the highest 25% for small data sets and highest 10% and 25% for large data sets of standardized residuals from each function fitted to each data set. For some data sets, the functions agreed in identification of hotspots in that they identified 75% or more of the same hotspots. The extreme value function tended to identify hotspots not identified by the other three functions. For most data sets, the functions did not agree completely in identifying hotspots. Therefore, species-area curves should not be used as the sole means of identifying hotspots of species richness, although they can be used to examine the effect hotspot area has on richness for hotspots identified by other methods.*

La Selección de la Función Especie-Área Afecta la Identificación de Zonas Clave

Resumen: *Determiné la confiabilidad de curvas de especie-área a ser usadas en la identificación de zonas clave, regiones políticas o geográficas de alta riqueza de especies. En gráficas de especie-área las zonas clave son puntos (regiones) que aparecen por arriba de la curva con una extensión relativamente mayor que los otros puntos. Debido a que hay diferentes curvas que pueden ajustarse a datos de especie-área, la identificación de zonas clave puede diferir dependiendo de la función de ajuste de curva utilizada. Examiné esta hipótesis al comparar zonas clave identificadas por una función de potencia, la función de valor extremo, la función lineal y la función exponencial. Examiné series de datos de especie-área que variaron en tamaño y en presencia de especies endémicas. Definí las zonas clave como aquellas con porcentajes de residuos estandarizados de cada función ajustada en cada base de datos de 25% mayor para juegos de datos pequeños y 10% y 25% mayor para juegos de datos grandes. Para algunos juegos de datos, las funciones coincidieron en la identificación de zonas clave en las que las funciones identificaron 75% o más de ellas. La función de valores extremos tendió a identificar zonas clave que no fueron identificadas por las otras tres funciones. Para la mayoría de los juegos de datos las funciones no coincidieron completamente en la identificación de zonas clave. Por lo tanto, las curvas de especie-área no deberían ser usadas como medio único para la identificación de zonas clave de riqueza de especies, aunque pueden ser utilizadas para examinar los efectos que las zonas clave tienen sobre la riqueza para zonas clave identificadas por otros métodos.*

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Introduction

Myers (1988) originally defined hotspots as areas of tropical forest that have exceptionally large numbers of endemic plant species and that also have an exceptionally high probability of being partially or completely destroyed. Myers (1990) later expanded this definition to include areas in the Mediterranean type of biome. In recent years, the definition of a biodiversity hotspot has become even broader and includes areas with a large number of species in general (of any taxonomic group), not just endemics, that may not be faced with an immediate threat of destruction (Reid 1998). Initially, hotspots were identified in an informal, descriptive sense that involved a simultaneous assessment of the percent endemism of a region's flora along with an estimate of the size of the area encompassed by the vegetation (N. Myers 1988, 1990). These assessments sometimes included an identification of the factors or conditions threatening the hotspot, an estimate of the rate at which species or area was being lost, an evaluation of current protection of the hotspot, and a prognosis on the future of the hotspot (N. Myers 1988, 1990).

A clearly defined and universal protocol for identifying hotspots has yet to be developed, although analyses based on geographic information systems show some promise (Scott et al. 1993; Kiester et al. 1996; Flather et al. 1997). For instance, one could use GAP analysis (Scott et al. 1993) to identify areas where the ranges of many species overlap, with the added benefit that the analysis may include information—size and location of protected areas and disturbed areas—that could be used to assess the feasibility and urgency of protecting the hotspots. The TWINSPLAN methods (Hill 1979) used to identify endemic bird areas (EBAs) are noteworthy for their scope and rigor (Bibby et al. 1992). After identifying the EBAs, Bibby et al. (1992) ranked them on the basis of many factors, including whether or not an EBA contained more species than expected based on its area, as interpolated from a species-area curve.

Other researchers have continued to use species-area curves to identify hotspots. Pomeroy (1993) used a species-area curve to identify Cameroon, Gabon, South Africa, and Tanzania as African countries with an exceptional richness of flowering plants. Ceballos and Brown (1995) found an exceptional richness of endemic mammals in Australia, Madagascar, Mexico, and the Philippines by using a species-area curve with data from 155 countries. In neither study do the authors refer to these countries as hotspots, but both studies identify "exceptionally species-rich countries" as those displaced above the species-area curve (those having a positive residual). Ceballos and Brown (1995) refer to those countries as outliers on their species-area plots, and Pomeroy (1993) calculates relative species richness for each country by ranking each country's displacement from a species-area curve. Moreover, the authors of both studies conclude

that their methods, which rely on species-area curves, can be used to identify key areas of conservation concern and can "provide a basis for setting priorities for allocating limited resources" (Ceballos & Brown 1995).

The use of species-area curves as a method of identifying hotspots has not been discussed or studied as much as the application of species-area curves to reserve design and to predicting species losses. In addition, any method of identifying hotspots must take into account the effect of area on species richness (Bibby et al. 1992; A. A. Myers 1996). Therefore, the purpose of my study is to test whether species-area curves can be used reliably to identify hotspots of species richness. Hereafter, the term "hotspot" is used solely to indicate a region having an exceptional richness of species; I am not using the more inclusive definition of Reid (1998).

Using species-area curves to identify hotspots is fundamentally different than using them to estimate species richness for reserve design or species losses due to habitat destruction. Both reserve design and the estimation of species extinction require accurate prediction or interpolation from the curve. The use of species-area curves in the identification of hotspots, however, depends upon an accurate and consistent estimate of the displacement of an area (a country or other geographical unit) above the curve. But, therein lies a potential problem with using this means of identifying hotspots. The displacement depends on how well the curve fits the data, and the trust we put into the residuals as indicators of hotspots depends on how accurately the curve is estimated. The hotspots revealed by a particular curve-fitting function could be different (or displaced more or less) if the same data were fit with a different function. I tested this possibility by fitting four functions to several species-area data sets, some of which are important to conservation efforts. The four models I examined were a simple linear function, the power function (Preston 1962), the exponential function (Gleason 1922), and the extreme value function (Williams 1995). I then compared the hotspots revealed by the functions. If the functions agree in identifying hotspots, one could conclude that, in practice, using species-area curves to identify hotspots is generally robust to the particular curve-fitting function chosen.

Methods

Species-Area Functions

The simplest species-area function is an untransformed linear relationship between species richness (S) and area (A): $S = (\text{slope} \times A) + \text{y-intercept}$. But ecologists typically have used the power function, $S = cA^z$, to describe species-area relations, where both c and z are constants specific to the data set being analyzed; in other

words, a particular group of species distributed among a particular set of islands or habitat fragments has a unique c and z . One can determine c and z by log-transforming both species number and area so as to fit the linear form of the power function, $\log S = \log c + z \log A$, to the data. The power function as a species-area curve is unbounded (Williams 1995), however. In other words, there is no limit on S , species richness. Also, because the log of zero is undefined, islands and fragments with zero species cannot be included in the log-log curves unless transformed. A typical transformation is to add 1 to all log S , but this transformation of data can be problematic when it comes to obtaining accurate estimates of c and z (Williams 1996). The exponential or semi-log function $S = \text{slope} \times \log(\text{area}) + \text{y-intercept}$ is an alternative to the power function, although it is not as widely applied as the power function.

The extreme value function, EVF, is considerably different from the previous three functions, particularly because it gives a species-area curve that is sigmoidal—that is, it has an asymptote. Because of this, species richness is bounded and the slope of the curve is not constant over the entire range of area. Williams (1995) presented the EVF as an alternative to the power function and went on to suggest the EVF has important ramifications for studies concerned with the conservation of species richness. Specifically, because the EVF-fitted species-area curve is asymptotic, a decrease in area will not always lead to a decrease in species richness, and an increase in area (as in enlargement of a reserve) will not necessarily lead to an increase in species richness (Williams 1995; Fig. 1).

The EVF as a species-area curve is based on Coleman et al.'s (1982) random placement model (Williams 1995), which assumes that individuals of all species are distributed independently (of other conspecifics and heterospecifics) and randomly (Williams 1995). The probability that at least one individual of species j is found within an island (or habitat fragment) is proportional to the area of the island (A_x) compared with the cumulative area of all islands (A_t) and the number of individuals of species j (n_j). When two or more species are considered simultaneously we can determine the expected species richness (S) for a given area by summing each species' probability of occurrence in the area (Williams 1995). As noted above, a species' probability of occurrence in an area is the probability that at least one individual of the species exists in the area. Thus the expected species richness of an area is given by $S = P - \sum [1 - (A_x / A_t)^{n_j}]$, where P is the total number of species in the pool (Coleman et al. 1982; Williams 1995). For example, if a data set consists of 20 species distributed among habitat fragments that together have a total area of 1000 ha and one wants to know the expected species richness of a fragment that is 200 ha in area, then we calculate $1 - (A_x / A_t)$ as 0.8, and if we know

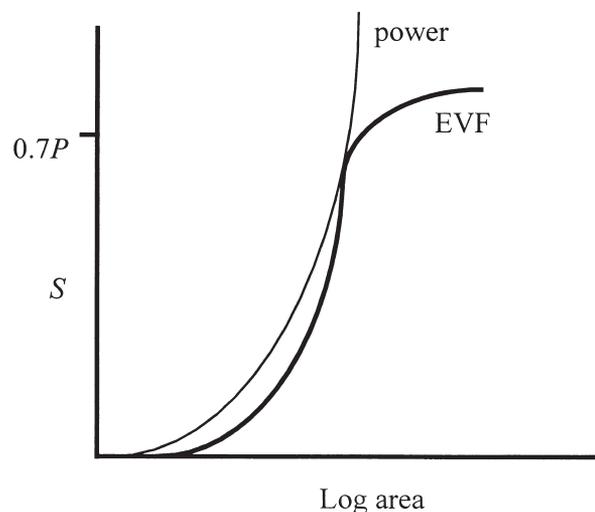


Figure 1. The power function and the extreme value function (EVF) as species-area curves. The power function provides no limit to species richness (S); the curve is unbounded. The EVF does limit species richness because the EVF curve is asymptotic. The two curves are similar except when S is $\geq 0.7P$ where P is the total number of species in the data set. The figure is modified from Williams (1995).

(or assume) that all 20 species are equally abundant with 10 individuals each, then $S = 20 - 2.1 = 17.9$ species. But we rarely know the abundances (n_j) of each (or any) of the species. Williams (1995) circumvented this problem by proposing that the EVF, which does not require census data, is a good approximation to Coleman's random placement model. Williams's (1995) derivation of the EVF as a species-area curve is as follows: $S = P(1 - \exp[-\exp(m \log A + \log b)])$, where m is the slope, $\log b$ is the y-intercept, and $\exp(x)$ denotes e^x . Williams (1995) validated the use of the EVF by testing whether it gave better fit to previously published data sets of species area than the power function did. He found that goodness of fit as measured by r^2 values is not much improved by use of the EVF, but expected species richness based on the EVF is closer to the actual species richness than is expected species richness based on the power function. Because the EVF is bounded (asymptotic) and it can include areas that have zero species, the EVF may differ from the other functions in identifying hotspots.

Identifying Hotspots with Species-Area Functions

I used all four functions to fit species-area curves to several previously published data sets of species richness for different political regions (e.g., butterflies in Oregon, mammals in Asia) (Table 1, Appendix). Some of the data sets included only endemic species, whereas others included endemic species richness and total species richness. The data sets also differed in total number of species and in to-

Table 1. Data sets used to create species-area curves.

<i>Data set</i>	<i>Description</i>	<i>Species included^a</i>	<i>Number of species</i>	<i>Number of areas</i>	<i>Source</i>
1	birds on tropical Pacific islands	A	485	30	Adler 1992
		E	292	30	
2	butterflies on tropical Pacific islands	A	285	26	Adler & Dudley 1994
		E	100	26	
3	skinks on tropical Pacific islands	A	100	27	Adler et al. 1995
		E	66	27	
4	mammals in Indo-Pacific region	E	483	23	Dinerstein & Wikramanayake 1993
5	plants in Indo-Pacific region	E	51835	22	Dinerstein & Wikramanayake 1993
6	birds in Indo-Pacific region	E	892	23	Dinerstein & Wikramanayake 1993
7	isopods on islands in Aegean Archipelago	A	71	43	Sfenthourakis 1996
8	butterflies in Oregon (U.S.A.)	A	214	36	Fagan & Kareiva 1997
9	threatened vertebrate and arthropod species in Venezuela ^b	A	306	23	Rodriguez & Rojas-Suarez 1996
10	endemic vertebrate and arthropod species in Venezuela ^b	E	102	23	Rodriguez & Rojas-Suarez 1996
11	high-risk vertebrate and arthropod species in Venezuela ^b	A	46	23	Rodriguez & Rojas-Suarez 1996
12	tiger beetles throughout the world	A	2024	130	Pearson & Cassola 1992
		E	1230	130	
13	endemic bird areas (EBA) throughout the world	E	2484	221	Bibby et al. 1992
14	mammals throughout the world	E	1535	107	Sisk et al. 1994
15	butterflies throughout the world	E	2149	107	Sisk et al. 1994

^aData set includes only endemic species (E) or endemic and nonendemic species (A).

^bSee Rodriguez and Rojas-Suarez (1996) for definitions of threatened, endemic, and high-risk species.

tal number of areas (islands, counties, states, or countries). An alternative strategy would have been to generate hypothetical data sets in some way and then determine how well each function identifies known hotspots in the data. I rejected that approach because I could find no method of creating hotspots (in hypothetical data) that would be independently of all species-area models. Hotspots do not exist independently of some assumed relationship between area and species richness. Instead, I used real data sets and operated under the assumption that hotspots exist in all the data sets used in the study. The purpose of the study was to determine how well the four functions agree in identifying hotspots and to evaluate the performance of each function separately by determining if it could identify "known" hotspots identified by the other three functions.

After fitting the species-area curves, I ranked the displacement of each area from each curve, based on the value of its standardized residual. For each data set I then selected the highest 25% of ranks (and highest 10% for large data sets) from all four functions. The areas corresponding to each of these ranks were considered hotspots. So each data set gave four groups of hotspots, each group corresponding to one of the four species-area functions. For each data set, the percent similarity among the four groups was determined as the number of hotspots identified by all four functions, divided by the total number of hotspots in a group. For example, the highest 25% of ranks in a data set consisting of 32

countries includes eight hotspots in each group. If three hotspots (countries) occur in all four groups, then the percent similarity among the four groups is 37.5%. Percent similarity was also determined pairwise for all four functions for each data set. For those pairs for which percent similarity was >75%, I applied a Spearman rank correlation test to compare the rankings of the hotspots identified by the two functions. A significant correlation indicates that the two curve-fitting functions agree in identifying hotspots of species richness.

Results

The percent similarity of identified hotspots was never more than 67% among the four functions, and sometimes the groups of hotspots identified by the four functions had no members common to all four groups (i.e., percent similarity was zero; Table 2). The pairwise comparisons of functions revealed many instances of percent similarity >75%, with some functions in complete agreement in identifying hotspots (i.e., percent similarity equal to 100%; Table 2). Among all the data sets, however, there were 144 pairwise comparisons of the hotspot groups identified by the functions, but percent similarity was >75% in only 42 out of the 144 comparisons. Percent similarity tended to be >75% when the power, linear, and exponential functions were com-

Table 2. Percent similarity among hotspots identified by the four species-area functions.^a

Data set ^b	Number of hotspots in highest 25% and 10%	All four functions	Power vs.			EVF vs.		Linear vs. exponential
			EVF	linear	exponential	linear	exponential	
1A	8	0	37.5	50	25	0	75	12.5
1E	8	25	37.5	62.5	50	12.5	87.5	25
2A	7	29	57	71	57	29	100	29
2E	7	29	57	43	71	71	29	29
3A	7	14	29	71	71	14	57	43
3E	7	29	57	57	71	43	43	29
4E	6	67	100*	67	67	67	67	67
5E	6	50	50	67	67	50	67	67
6E	6	67	67	83*	83	83*	67	83
7A	11	0	45	36	55	0	36	18
8A	9	56	100	67	100*	67	100	67
9A	6	50	67	83*	100	50	67	83
10E	6	67	67	100	100	67	67	100*
11A	6	67	67	100***	100***	67	67	100***
12A	13 ^c	46	62	54	54	92**	92**	85**
	33 ^d	64	88**	70	73	79**	73	76**
12E	13 ^c	0	8	85**	85**	0	15	85**
	33 ^d	12	27	85**	76**	12	39	67
13E	22 ^c	0	0	77**	95**	0	0	86**
	55 ^d	20	29	91**	95**	20	24	95**
14E	11 ^c	0	0	73	55	0	27	55
	27 ^d	15	22	93**	59	19	59	52
15E	11 ^c	0	0	91*	91*	0	9	91**
	27 ^d	11	26	89**	67	19	52	59

^aFunctions examined include power function, extreme value function (EVF), linear function, and exponential function (see Methods). For cases in which percent similarity is >75%, Spearman rank correlation tests were performed (*p < 0.05, **p < 0.01, ***perfect correlation).

^bData set code explained in Table 1.

^cHighest 10%.

^dHighest 25%.

pared to one another (pairwise) than when either of the three was compared to the EVF (Fig. 2).

There were no apparent differences between small data sets (data sets 1-11), defined as those with fewer than 50 areas, and large data sets (12-15) in percent similarity between functions. Of the 60 pairwise comparisons represented among the large data sets, 22 comparisons revealed percent similarity of 75% or more, but some of the comparisons were not strictly independent given that the large data sets included hotspot groups based on the highest 10% of ranks along with the highest 25% of ranks; the former is a subset of the latter. Therefore, the 22 instances (of percent similarity >75%) out of 60 comparisons among large data sets is not very different from 20 out of 84 comparisons among small data sets. Similarly, no differences were found between data sets that included only endemic species (25 instances of >75% similarity out of 90 comparisons) and those that included all species (17 instances of >75% similarity out of 54 comparisons).

I performed a Spearman rank correlation test on pairs of hotspot groups that were more than 75% similar. The results of these tests indicate that even when two functions identify the same hotspots, they often do not agree in the ranking of those hotspots, particularly if the data set is small (Table 2). For large data sets, however, functions of

ten do agree in the ranking of hotspots, as indicated by highly significant correlations between the ranks (Table 2).

Discussion

The four species-area functions failed to agree on identifying hotspots of species richness. Most of the lack of agreement was due to the EVF identifying a different set of hotspots than that identified by the other three functions, regardless of which data set was being examined. The EVF tended to overestimate species richness along the entire range of area in a given data set. This overestimation was lowest for small areas, so the EVF typically identified the smallest counties, countries, and islands as hotspots. It is not readily apparent why the EVF should behave in this way. According to Williams (1995) the EVF is a good approximation of the random placement model of Coleman et al. (1982); even if the data violate the assumption of random placement of individuals, the EVF accurately estimates species richness (Williams 1995). Individuals of endemic species are certainly not randomly placed; by definition, endemic species can occur in only one place. Perhaps data sets that include only endemic species so severely violate random placement that the EVF is not appropriate for them.

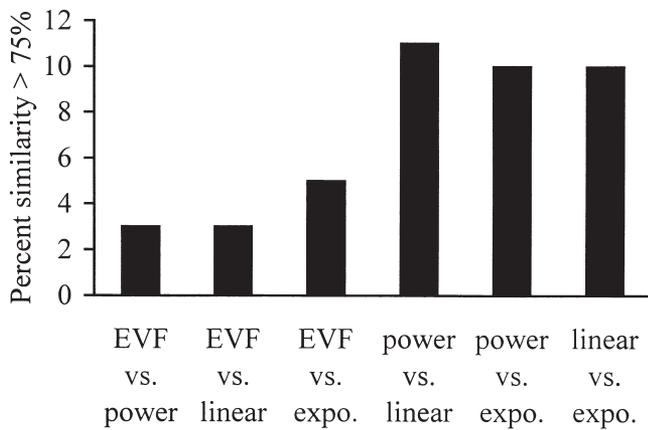


Figure 2. The number of pairwise comparisons in which percent similarity was >75% for each function (extreme value [EVF], power, linear, and exponential [expo.]) compared with each of the others. Including all data sets, there were 24 pairwise comparisons for each pair of functions.

When I removed the EVF results from the analysis, I was left with 31 instances of percent similarity >75% out of a total of 72 pairwise comparisons. Therefore, even without the EVF included, the three remaining functions did not exhibit much agreement in identifying hotspots. Also, the functions rarely agreed on the ranking of the hotspots, although they sometimes shared 75% or more of the hotspots. Hotspots identified in large data sets were an exception; the rankings were often significantly correlated. But the significant correlation should not be taken as a perfect or near-perfect correspondence between the rankings from two functions. Indeed, a significant correlation may exist even though no hotspot had the same rank from either function, given that the data set was large enough. The power, linear, and exponential functions gave identical rankings of hotspots in only one data set (11).

Based on my results, one might conclude that species-area functions have little value in identifying hotspots of species richness. Such a conclusion would follow similar assessments of the application of species-area curves to other conservation-related tasks, such as reserve design (Simberloff & Abele 1976; Margules et al. 1982; Soulé & Simberloff 1986; Zimmermann & Bierragaard 1986; Saunders et al. 1991; Lomolino 1994; Boecklen 1997) and the prediction of species losses (Simberloff 1986, 1992; Reid & Miller 1989; Heywood & Stuart 1992; Reid 1992). Such a conclusion might overlook the most appropriate use of species-area curves.

Not including the EVF, the species-area curves examined in this study typically identified groups of hotspots that were at least 50% similar in composition as revealed by the pairwise comparisons. So perhaps the most appropriate use of species-area curves will be in determin-

ing those areas (counties, countries, islands, etc.) that are identified as hotspots of species richness regardless of the type of curve-fitting function applied to the data. In other words, we can use species-area curves to find hotspots that are robust to the various species-area models instead of using them to try to find all the hotspots in a data set or rank how hot a spot is. The former objective is much more realistic than the latter two. If a particular region or country is consistently identified as a hotspot by all species-area models, then we can be confident in concluding that it is one, regardless of how well the model fits the data. Somewhat ironically, if a species-area model fits the data extremely well then the standardized residuals will be small. From that we might conclude that none of the regions has a significantly better-than-average species richness because all of the standardized residuals are small. In other words, we could mandate that a standardized residual must exceed some predetermined value in order for the region to be labeled a hotspot. I did not use this alternative to ranking the standardized residuals because it also leads to the unsettling conclusion that the functions that fit the data the poorest are also the best at identifying hotspots, in that they are the ones that return the largest residuals.

We should be careful in picking hotspots. Attempts to identify hotspots based solely on the species-area relationship or to rank hotspots solely on the basis of area may be misguided. The use of species-area curves in these ways does not include a consideration of what is to be accomplished by identifying and ranking hotspots. We could do so as a simple academic pursuit, as in the present study. We could use any criteria in doing this and not have to worry too much about the real-world implications of our rankings. But there is more at stake when we seek to identify hotspots, such as the allocation of funds to protect such places (Abramowitz 1991; Reid 1998). Because of this, the method used to identify and rank hotspots (the hotspot analysis) must explicitly include an assessment of the feasibility and urgency of protecting the hotspot (Dinerstein & Wikramanayake 1993; Sisk et al. 1994). For instance, species-area curves as used in this study do not include estimates of habitat availability, current and future habitat destruction, or biases in the data due to incomplete sampling. This does not mean that species-area curves should be excluded from hotspot analyses. Species-area curves can serve as a way of assessing whether previously identified (and ranked) hotspots have a better-than-average species richness based on their areas (e.g., Bibby et al. 1992). Such knowledge could then contribute to decisions regarding the protection of the hotspots. The results of this study suggest that the different species-area curves will often disagree on which countries (or regions, counties, states, islands, etc.) have better-than-average species richness. This disagreement highlights the importance of not choosing just one function and suggests using the power, linear, and exponential functions, espe-

cially given that none of these three consistently fits species-area data better than the others (Conner & McCoy 1979; Sfenthourakis 1996).

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Appendix

The equations for each of the four functions (power, extreme value [EVF], linear, and exponential) used to fit curves to each species-area data set.*

Data set	Power ($\log S = m \log A + y$)		EVF $S = P(1 - \exp$ $[\exp(m \log A + \log b)])$			Linear ($S = m A + y$)		Exponential ($S = m \log A + y$)	
	m	y	P	m	log b	m	y	m	y
1A	0.536	-0.377	485	0.998	-1.636	0.003	9.859	29.45	-50.17
1E	0.434	-0.493	292	1.0	-0.860	0.001	3.405	10.66	-18.68
2A	0.453	-0.338	285	1.0	-2.119	0.003	6.581	24.85	-46.41
2E	0.345	-0.677	100	1.0	0.561	0.001	-0.696	5.58	-11.96
3A	0.272	0.010	100	1.0	-2.233	0.001	4.722	6.30	-8.60
3E	0.273	-0.498	66	1.0	0.258	0.0003	0.630	3.12	-6.26
4	0.474	-1.141	483	1.0	-1.267	6.6×10^{-5}	15.50	20.55	-63.93
5	0.680	0.050	51835	1.0	-2.908	0.011	1438.1	2231.2	-6863.8
6	0.329	-0.416	892	1.0	-1.546	6.4×10^{-5}	33.48	30.60	-87.70
7	0.204	0.969	71	0.943	-1.911	0.065	12.56	7.02	10.63
8	0.309	0.830	214	1.0	-2.865	0.006	59.55	50.15	-89.82
9	0.139	1.018	306	1.0	-2.779	0.0002	36.90	14.40	-17.11
10	-0.227	1.806	102	1.0	-3.222	-1.9×10^{-5}	9.20	-3.96	25.30
11	0.033	0.562	46	1.0	-3.092	3.6×10^{-6}	5.46	0.16	4.92
12A	0.361	1.170	2028	0.962	-4.742	0.521	29.78	23.00	26.60
12E	0.275	0.399	1230	0.970	-0.459	0.218	7.25	8.49	6.33
13	0.115	0.825	2484	1.0	-4.307	-0.002	13.45	3.23	9.97
14	0.532	-1.762	1535	1.0	-0.658	9.3×10^{-5}	5.20	21.44	-81.80
15	0.403	-1.194	2150	1.0	-0.489	6.2×10^{-5}	14.02	22.02	-78.77

*The power, linear, and exponential equations were obtained with the options available in EXCEL. The EVF curves were fit to species-area data by the LOGISTIC regression procedure available in the SAS ASSIST option of SAS System for Windows (6.12). The link function used was the complementary log-log because it "linearizes" the EVF (Williams 1995). The SAS output provides estimates of the y-intercept (log b) and slope (m) which are needed in the equation: $S = P(1 - \exp[-\exp(m \log A + \log b)])$. Data set designations are explained in Table 1.

