



# Which function describes the species–area relationship best? A review and empirical evaluation

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## ABSTRACT

**Aim** The aims of this study are to resolve terminological confusion around different types of species–area relationships (SARs) and their delimitation from species sampling relationships (SSRs), to provide a comprehensive overview of models and analytical methods for SARs, to evaluate these theoretically and empirically, and to suggest a more consistent approach for the treatment of species–area data.

**Location** Curonian Spit in north-west Russia and archipelagos world-wide.

**Methods** First, I review various typologies for SARs and SSRs as well as mathematical models, fitting procedures and goodness-of-fit measures applied to SARs. This results in a list of 23 function types, which are applicable both for untransformed ( $S$ ) and for log-transformed ( $\log S$ ) species richness. Then, example data sets for nested plots in continuous vegetation ( $n = 14$ ) and islands ( $n = 6$ ) are fitted to a selection of 12 function types (linear, power, logarithmic, saturation, sigmoid) both for  $S$  and for  $\log S$ . The suitability of these models is assessed with Akaike's information criterion for  $S$  and  $\log S$ , and with a newly proposed metric that addresses extrapolation capability.

**Results** SARs, which provide species numbers for different areas and have no upper asymptote, must be distinguished from SSRs, which approach the species richness of one single area asymptotically. Among SARs, nested plots in continuous ecosystems, non-nested plots in continuous ecosystems, and isolates can be distinguished. For the SARs of the empirical data sets, the normal and quadratic power functions as well as two of the sigmoid functions (Lomolino, cumulative beta-P) generally performed well. The normal power function (fitted for  $S$ ) was particularly suitable for predicting richness values over ten-fold increases in area. Linear, logarithmic, convex saturation and logistic functions generally were inappropriate. However, the two sigmoid models produced unstable results with arbitrary parameter estimates, and the quadratic power function resulted in decreasing richness values for large areas.

**Main conclusions** Based on theoretical considerations and empirical results, I suggest that the power law should be used to describe and compare any type of SAR while at the same time testing whether the exponent  $z$  changes with spatial scale. In addition, one should be aware that power-law parameters are significantly influenced by methodology.

## Keywords

Curve fitting, goodness-of-fit, logarithmic function, macroecology, model selection, power function, saturation function, sigmoid function, species sampling relationship, species–area relationship.

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## INTRODUCTION

Increasing species richness ( $S$ ) with increasing area of investigation ( $A$ ) is one of the most fundamental ‘laws’ in ecology (Schoener, 1976; Lawton, 1999; Lomolino, 2000). Numerous publications describe, mathematically characterize, and interpret the underlying mechanisms of species–area relationships (SARs) for nearly any biome or major taxon, and for scales ranging from square millimetres to the entire surface of the Earth (Connor & McCoy, 1979, 2001; Williamson, 1988; Rosenzweig, 1995; Lomolino, 2001; Drakare *et al.*, 2006).

The mathematical description of SARs is of great theoretical and practical interest. First, theories of island biogeography (e.g. MacArthur & Wilson, 1967; Lomolino & Weiser, 2001; Whittaker & Fernández-Palacios, 2007), species abundance distributions (e.g. Preston, 1962; May, 1975; Harte *et al.*, 1999; Ovaskainen & Hanski, 2003; Şizling & Storch, 2004; Williamson & Gaston, 2005; Pueyo, 2006) and neutral models (Bell, 2001; Hubbell, 2001; Rosindell & Cornell, 2007) predict differently shaped SARs, and thus the actual shapes of SARs provide a means for testing these theories. Moreover, it is possible to analyse how taxon, scale, ecosystem or geographic location influence the function type of the SAR and its parameters (e.g. Crawley & Haral, 2001; Keeley & Fotheringham, 2003; Storch *et al.*, 2005; Chiarucci *et al.*, 2006; Drakare *et al.*, 2006), and this in turn facilitates the testing of underlying ecological theories (e.g. Stark *et al.*, 2006). Scale-dependent processes are proposed as causes for the different shapes of portions of SARs (Preston, 1960; Shmida & Wilson, 1985; Rosenzweig, 1995; Hubbell, 2001; Whittaker *et al.*, 2001; Turner & Tjørve, 2005), and understanding the area effect in SARs allows one to test other effects on biodiversity (Buckley, 1985; Whittaker *et al.*, 2001; Price, 2004).

SARs have also been used in comparing species-richness values of different areas, in extrapolating species richness (e.g. Colwell & Coddington, 1994; He & Legendre, 1996; Plotkin *et al.*, 2000), and in producing biodiversity maps (e.g. Kier *et al.*, 2005). Finally, SARs have been applied within conservation biogeography, for example for identifying biodiversity hotspots (e.g. Veech, 2000; Fattorini, 2007), for optimal reserve planning (e.g. Desmet & Cowling, 2004), for predicting species loss after habitat loss (e.g. Connor & McCoy, 2001; Ulrich, 2005) and for assessing human impacts on biodiversity (e.g. Tittensor *et al.*, 2007).

Many models have been applied to SARs (reviewed in Tjørve, 2003). However, the two oldest, namely the power function (Arrhenius, 1920, 1921; Preston, 1962) and the logarithmic function (often erroneously termed the exponential function; Gleason, 1922), are the two most frequently applied. When different function types are compared, the best fit is most often reported for the power function (Williamson, 1988; Drakare *et al.*, 2006; Dengler & Boch, 2008), which – on untransformed axes – results in a convex upward-shaped curve without an upper limit. Despite these general findings, many authors claim that SARs should have an upper asymptote for theoretical reasons, although they usually do not provide

empirical data to substantiate this assumption (Connor & McCoy, 1979; He & Legendre, 1996; Schmitt, 1999; Lomolino, 2000, 2001; Tjørve, 2003).

Despite the long-recognized importance of species–area analyses, most existing publications on this topic share a number of serious shortcomings: (1) many new models have been proposed solely on theoretical grounds (e.g. Lomolino, 2000; Tjørve, 2003); (2) the few published empirical studies usually assume one model *a priori*, or rarely a few are compared (but see Flather, 1996, and Stiles & Scheiner, 2007, who compare nine and 15 models, respectively, but do this for species sampling relationships and not for real SARs); (3) there is no general agreement on how to select the ‘best’ model (Connor & McCoy, 1979; Fattorini, 2007); (4) despite general acknowledgement of the effect of different transformations of the dependent variable, for example as  $S$ ,  $\log S$ , or  $A/S$  (Williamson, 1988; Loehle, 1990), this effect has not been considered consistently; and (5) proper SARs and species sampling relationships (SSRs) are often confused, despite their mathematical dissimilarity (see Scheiner, 2003, 2004; Gray *et al.*, 2004a,b; Hui, 2008).

Therefore, this article aims:

- (1) to elaborate the differences between different categories of relationships, including a clear differentiation of SARs from SSRs,
- (2) to review possible SAR models comprehensively,
- (3) to provide a critique of and new ideas for the fitting and comparison of different models,
- (4) to assess a range of models and goodness-of-fit metrics theoretically and empirically (with example data sets both from continuous ecosystems and from isolates), and
- (5) to suggest a more consistent approach for the treatment of species–area data.

## THEORETICAL AND TERMINOLOGICAL BACKGROUND

### Types of curves

Scheiner (2003) initiated renewed debate (Gray *et al.*, 2004a,b; Scheiner, 2004; Whittaker & Fernández-Palacios, 2007; see Table 1) on the various types of SARs and the need to distinguish them from what he calls accumulation or rarefaction curves. His study distinguishes six variants of SARs, grouped into four major types: type I – nested data with only one measurement for each size; type II – a contiguous grid of equal-size cells; type III – a non-contiguous grid of equal-size cells; and type IV – islands of irregular shapes and sizes. Types II and III each have variants A and B, which differ in combining adjacent or randomly selected quadrats, respectively, to obtain richness values for larger areas. The same classification was recently applied by Ulrich & Buzko (2007) with, however, different names. Gray *et al.* (2004a,b) recognize only Scheiner’s type IV as a SAR, with type I coming under the category of an accumulation curve, and types II and III as rarefaction curves. In addition, they argue that it is irrelevant whether such accumu-

**Table 1** Proposed typology of species–richness relationships compared with the suggestions of Scheiner (2003, 2004), Gray *et al.* (2004a,b) and Whittaker & Fernández-Palacios (2007).

Type	Definition	Scheiner	Gray <i>et al.</i>	Whittaker & Fernández-Palacios
Species–area relationships (SARs)	Each point refers to a contiguous plot (or to a mean value of several such plots)			
A. Continuous ecosystems, nested plots	– Subplots of predefined sizes and shapes are placed within the largest plot		Species accumulation*, rarefaction*	SACs*
a. Single values	Each point refers to a single richness count	I		
b. Averaged values	Each point refers to the mean of richness counts for several equally sized plots	IIA		
i. Fully nested	Each plot is nested within the next larger plot			
ii. Partly nested	All plots are nested within the largest plot but the smaller subplots are placed independently of each other according to a systematic or random design			
B. Continuous ecosystems, non-nested plots	– Irregularly shaped units with individual sizes but adjacent to each other (e.g. countries)	IV*	Species–area*	–
C. Isolates	– True island and habitat ‘islands’	IV*	Species–area*	ISARs
Species sampling relationships (SSRs)	Each point refers to a sample (i.e. an individual, a plotless sample, or a plot) randomly drawn from a defined larger area (or to the combination of several such samples)			
A. Species accumulation curves	– Species increase according to the original sequence of recording	Species accumulation	Species accumulation*	SACs*
a. Individuals				
b. Samples				
B. Rarefaction curves	– Mean species increase based on repeated randomized re-sampling from the total sample of a species accumulation curve	Rarefaction, Species–area*	Rarefaction*	–
a. Individuals				
b. Samples		incl. IIB, IIIA, IIIB		

In Whittaker & Fernández-Palacios (2007), the acronyms SACs and ISARs denote ‘species accumulation curves’ and ‘island species–area relationships’, respectively. \*Partial correspondences. For species sampling relationships, I adopt the typology of Gotelli & Colwell (2001). For SARs type A, there are two possible subdivisions, which can be combined (e.g. subtypes A.a.ii or A.b.i). The classification of this table can be applied not only to species but also to taxa of any rank (taxon–area relationship, taxon sampling relationship).

lation and rarefaction curves are from defined areas or plotless sampling. Scheiner (2003, 2004), by contrast, restricts these two terms to plotless sampling methods. In a similar fashion to Gray *et al.* (2004a,b), Gotelli & Colwell (2001) apply ‘taxon sampling curve’ irrespective of plot-based vs. plotless methods. These authors distinguish four types of such sampling curves, depending on whether individuals or samples are the unit of replication and the use of either accumulation (successive increase of the original sampling) or rarefaction (mean values of a repeated randomized re-sampling procedure; see Table 1).

Most recently, Whittaker & Fernández-Palacios (2007) suggested a new typology similar to that of Gray *et al.* (2004a,b), but with other names. Noting that the terms ‘species–area curve’ and ‘species–area relationship’ have been used in the literature to refer to a range of very different phenomena, they argue in favour of using more precisely prescribed terms. In their view, the key distinction is between Scheiner’s type IV, which they term ‘island species–area relationships’ (ISARs), and the other three forms, all of which they regard as variants of species accumulation (or sampling) curves.

All the reviewed typologies have their merits, but fail to depict and delimit the full variety of species diversity curves. Thus, I here provide a modified typology (Table 1). I suggest distinguishing species–area relationships (SARs) from species sampling relationships (SSRs) because these two categories have fundamentally different curve shapes. Whereas SARs in this sense are always unbound functions without an upper limit (Williamson *et al.*, 2001, 2002; Dengler, 2003, 2008), SSRs necessarily approach a maximum richness value asymptotically (Gotelli & Colwell, 2001; Christensen, 2007; Dengler, 2008). For SSRs, the actual sampling may be carried out on plots of defined area, but only in SARs does each richness value of a curve refer to a contiguous area. Here, I mean ‘contiguous’ in the sense that the area is circumscribed by a single line and no part inside these bounds is excluded from the species count, although parts of this area may represent unsuitable habitat for the taxon considered. On the one hand, area is a meaningful biological parameter only when it is contiguous, because biological processes such as dispersal or lateral spread normally act much more intensively on immediately adjacent areas than on disjunct areas. On the other hand, an area of a certain size consisting of non-contiguous subplots randomly placed within some larger area (as types IIB and IIIB of Scheiner, 2003) will normally exhibit much higher richness values than will the same area in the contiguous case (e.g. Rosenzweig, 1995; Hui, 2008). This is a result of spatial autocorrelation (distance decay), which is a fundamental feature of natural systems (e.g. Williamson, 1988; Bell *et al.*, 1993; Legendre, 1993; Nekola & Brown, 2007). Thus, my delimitation of SARs deviates both from Scheiner’s (2003, 2004) by excluding his types IIB, IIIA and IIIB, and from those of Gray *et al.* (2004a,b) and Whittaker & Fernández-Palacios (2007) by including types I and IIA alongside the unquestioned type IV (Table 1).

Although it seems reasonable that for SSRs we should adopt the classification proposed by Gotelli & Colwell (2001), for SARs a new schema had to be developed because in the so-far most comprehensive classification, that of Scheiner (2003), some subtypes are inappropriately classified or missing (Table 1). Type A comprises all nested relationships (i.e. types I and IIA of Scheiner), irrespective of whether they arise from one (subtype A.a) or several (subtype A.b) subplot replications. Thus, I apply ‘nested’ in a wider sense than does Scheiner (2003, 2004), including all sampling designs where all subplots are contained within the largest. Type A is the ‘purest’ form of a SAR, with all data points representing the same environmental conditions and only plot size varying, provided that the smaller areas are analysed and averaged using an adequate number of subplots (Dengler, 2008; Dengler & Boch, 2008). As the coefficient of variation of species richness usually decreases with increasing plot size, it is reasonable to increase the number of replicates towards smaller plot sizes (Barkman, 1989; Dengler, 2006). Type C relationships, by contrast, represent isolates; that is, true islands and habitat islands. Type B is intermediate between types A and C, as it refers to continuous ecosystems (as in type A) but analyses non-nested areas of dissimilar size and shape, such as political or natural

geographical entities (as in type C). Whereas in types A and B shapes and sizes of the analysed areas are delimited by humans, the areas in type C have pre-existing bounds.

### Possible models

Tjørve (2003) has provided the most comprehensive overview of possible SAR models to date (14 types), including typology and characterization. He distinguishes between convex and sigmoid models, with all but two of the convex models approaching an upper asymptote (saturation functions). Because several relevant functions are missing in Tjørve (2003), I publish here an augmented list without repeating the details of his review (Table 2). Only for the nine newly added models (or model families) do I give brief descriptions.

The linear (1) and exponential (10) functions have been used in the literature basically because they allow linear regression (Connor & McCoy, 1979; Gitay *et al.*, 1991). Because they predict an increase of species richness with area by a factor equal to or higher than unity, they lack theoretical plausibility, although they sometimes are reported to result in good or even best fits (Connor & McCoy, 1979).

For the power (2) and logarithmic (7) functions, several extensions have been suggested that may allow a better fit but mostly have no theoretical justification. Gitay *et al.* (1991) suggested two variants of the Gleasonian (logarithmic) model (8–9), with the aim of obtaining models ‘mathematically intermediate’ between the logarithmic and power functions. They called them ‘exponential, square root’ and ‘exponential, general root’ [in Table 2 as logarithmic (quadratic) and logarithmic (general power)] and found that they both fitted their data better than the logarithmic or power function. Similarly, Chiarucci *et al.* (2006) added a quadratic term to the power function (3) and found a better fit than for the normal power function. As indicated in Table 2, one may even add terms of higher polynomial order to the power function (4). Whereas the previous additions to convex models were designed with the sole aim of better approximating real data, Plotkin *et al.* (2000) suggested a modification of the power function based on the theoretical assumption of a spatial persistence function instead of the self-similarity of the simple power function ( $S = c A^z \exp [P(A)]$ , where  $P(A)$  is an infinite polynomial in  $A$  (6)). Truncating after the first term leads to the approximation given as ‘power function (Plotkin, approximate)’ in Table 2 (5).

Regarding upper-asymptotic models applied to SARs, Tjørve (2003) covered the majority but there is some confusion over terminology. Basically, there are convex saturation functions (11–14, hereafter referred to as ‘saturation functions’) and sigmoid functions (15–23). The Michaelis–Menten function (11), called the Monod function by Tjørve (2003), was applied to SARs/SSRs for example by Schmitt (1999) and Kluth & Bruelheide (2004). Lomolino (2000) proposed a function that he claimed to be the Hill function [Morgan–Mercer–Flodin function (20)] but is not, and thus it was named the Lomolino function (21) by Tjørve

**Table 2** Overview of the major models used for fitting species–area relationships and their characteristics.

No.	Curve name	Model	Parameters	Source	Upper asymptote
1	Linear function*	$S = b_0 + b_1 A$	2	Connor & McCoy (1979)	No
2	Power function*	$S = b_0 A^{b_1}$	2	Arrhenius (1920), Tjørve (2003)	No
3	Power function (quadratic)*	$S = 10 \wedge (b_0 + b_1 \log A + b_2 (\log A)^2)$	3	Chiarucci <i>et al.</i> (2006)	No
4	Power function (general polynomial)	$S = 10 \wedge (\sum b_i A^i)$	$n + 1$	–	No
5	Power function (Plotkin, approximate)*	$S = b_0 A^{b_1} \exp(b_2 A)$	3	Plotkin <i>et al.</i> (2000)	No
6	Power function (Plotkin, full)	$S = b_0 A^{b_1} \exp(\sum b_{i+1} A^i)$	$n + 2$	Plotkin <i>et al.</i> (2000)	No
7	Logarithmic function*	$S = b_0 + b_1 \log A$	2	Gleason (1922), Tjørve (2003)	No
8	Logarithmic function (quadratic)*	$S = (b_0 + b_1 \log A)^2$	2	Gitay <i>et al.</i> (1991)	No
9	Logarithmic function (general power)	$S = (b_0 + b_1 \log A)^{b_2}$	3	Gitay <i>et al.</i> (1991)	No
10	Exponential function	$S = 10 \wedge (b_0 + b_1 A)$	2	Connor & McCoy (1979)	No
11	Michaelis–Menten (Monod) function*	$S = b_0 A/(b_1 + A)$	2	Tjørve (2003), Kluth & Bruehlheide (2004)	Yes ( $b_0$ )
12	Negative exponential function*	$S = b_0 (1 - \exp(-b_1 A))$	2	Tjørve (2003)	Yes ( $b_0$ )
13	Asymptotic regression function	$S = b_0 - b_1 b_2^{-A}$	3	Tjørve (2003)	Yes ( $b_0$ )
14	Rational function*	$S = (b_0 + b_1 A)/(1 + b_2 A)$	3	Tjørve (2003)	Yes ( $b_1/b_2$ )
15	Logistic function*	$S = b_0/(1 + \exp(-b_1 A + b_2))$	3	Tjørve (2003)	Yes ( $b_0$ )
16	He–Legendre function	$S = b_0/(b_1 + A^{-b_2})$	3	He & Legendre (1996), Fattorini (2007)	Yes ( $b_0$ )
17	Gompertz function	$S = b_0 \exp(-\exp(-b_1 A + b_2))$	3	Tjørve (2003)	Yes ( $b_0$ )
18	Extreme value function	$S = b_0 (1 - \exp(b_1 A + b_2))$	3	Tjørve (2003)	Yes ( $b_0$ )
19	Morgan–Mercer–Flodin (Hill) function	$S = b_0 A^{b_1}/(b_2 + A^{b_1})$	3	Tjørve (2003)	Yes ( $b_0$ )
20	Lomolino function*	$S = b_0/(1 + (b_1^{\log(b_2/A)}))$	3	Lomolino (2000), Tjørve (2003)	Yes ( $b_0$ )
21	Chapman–Richards function	$S = b_0 (1 - \exp(-b_1 A))^{b_2}$	3	Tjørve (2003)	Yes ( $b_0$ )
22	Cumulative Weibull function	$S = b_0 (1 - \exp(-b_1 A^{b_2}))$	3	Tjørve (2003)	Yes ( $b_0$ )
23	Cumulative beta-P function*	$S = b_0 (1 - (1 + (A/b_1)^{b_2})^{-b_3})$	4	Tjørve (2003)	Yes ( $b_0$ )

S, species richness; A, area; and  $b_0 \dots b_n$ , fitted parameters. Note that for the power functions,  $b_0$  and  $b_1$  are generally termed  $c$  and  $z$ , a terminology that is also applied in the text of this paper. For the sake of convenience, logarithms of 10 are used. Summation ( $\Sigma$ ) is always from 1 to  $n$ . The models included in the analyses of this article are marked with an asterisk (\*) after the curve name.

(2003). Similarly, He & Legendre (1996) used a function that they called the logistic function but that differs from the standard logistic function (16; see, for example, Krebs, 1985; Tjørve, 2003) and thus was named the He–Legendre function (17) by Fattorini (2007).

### Fitting and comparison of curves

During the first decades of species–area research, curve-fitting was done exclusively using linear regression (e.g. Connor & McCoy, 1979). Whereas linear and logarithmic functions can be directly fitted by linear regression, the power function ( $S = c A^z$ ) needs to be transformed logarithmically ( $\log S = \log c + z \log A$ ). Although both power function ‘versions’ are mathematically equivalent, they give different estimates for the model parameters and  $R^2$  (Loehle, 1990) because the untransformed version has an additive error term and the transformed version has a multiplicative error term (Cresswell & Vidal-Martinez, 1995). There have been vigorous discussions over which version of the power function is biologically or statistically more appropriate. Cresswell & Vidal-Martinez (1995), for example, suggested the use of the untransformed power law (i.e. the application of non-linear regression) because they saw ‘no good reason to use multiplicative error

terms’. Williamson (1988), on the other hand, suggested that the transformed power law is often statistically more appropriate because the residuals are usually less heteroscedastic after transformation. Actually, there is no *a priori* reason to fit a model for  $S$  rather than for  $\log S$  (Williamson, 1988; Quinn & Keough, 2002). It is up to the researcher to decide whether to reduce the absolute or the logarithmic deviation by choosing one of these options. However, different SAR models should be compared only when the error terms are measured in the same mathematical ‘space’ (i.e. with the same transformation of  $S$ ; Loehle, 1990; Gitay *et al.*, 1991; Fattorini, 2007). Here, two important aspects rarely considered in the literature must be pointed out: (1) apart from the power function any SAR model can be fitted both for  $S$  and for  $\log S$ ; and (2) fitting a function in one space of  $S$  and then assessing the goodness-of-fit in the other space is also possible. This, for example, allows comparison of a power function fitted for  $\log S$  with a logarithmic function fitted for  $S$ .

In comparing SAR models,  $R^2$  is still the most frequently used statistic. The use of  $R^2_{\text{adj}}$  is necessary when comparing models with different numbers of parameters (Loehle, 1990; Quinn & Keough, 2002). More recently, information criteria such as Akaike’s information criterion (AIC) and the Bayesian information criterion (BIC) have been suggested as more



powerful tools for multi-model selection (Burnham & Anderson, 2002; Quinn & Keough, 2002; Johnson & Omland, 2004). They have only rarely been applied to SARs or SSRs to date (e.g. Fridley *et al.*, 2005; Stiles & Scheiner, 2007). He & Legendre (1996) suggested that the function with the lowest *P*-value of the *F*-ratio in the ANOVA of the respective regression model should be regarded as the most suitable. This proposal, however, has two weak points: (1) the underlying null model is inappropriate as it assumes no increase of species number with area; and (2) according to the mainstream approach of hypothesis testing, a significance level should be specified *a priori*, and results with lower probabilities should then be regarded as equally significant (Quinn & Keough, 2002). Thus, in contrast to the suggestion of He & Legendre (1996), functions should not be selected based on whether the probability of erroneously rejecting  $H_0$  is, for example,  $10^{-12}$  or  $10^{-13}$ .

The visual inspection of a 'lack-of-fit' is also frequently applied in the SAR/SSR literature, be it by viewing the original graphs (Connor & McCoy, 1979) or the plots of the residuals (Flather, 1996; Fattorini, 2007). It is clear that such a visual categorization must be subjective, and McGill (2003) thus rated this approach as the weakest possible goodness-of-fit test.

Although extrapolation of species richness beyond the largest plot size is one of the most frequent applications of SARs, there are only few and unsystematic approaches to testing which model function types are most suitable for this purpose (e.g. Dolnik, 2003).

## MATERIALS AND METHODS

### Data sources

Two empirical data sets (SAR types A and C) were used to exemplify the theoretical considerations presented in this paper. For the selection of these data sets, two considerations were crucial: (1) each included SAR should cover a wide range of areas (at least two orders of magnitude, preferably more) because for narrower ranges of area, model discrimination is nearly impossible (cf. McGill, 2003); and (2) within both data sets, I aimed to include a wide array of situations. The data sets were restricted to plants because for animals and other organisms mostly SSRs and partly type C SARs, but only rarely true type A SARs are available owing to methodological limitations.

Type A is represented by nested-plot species–area data of an unusually wide plot-size range from 14 vegetation types from the Curonian Spit National Park on the Baltic coast of Russia (Dolnik, 2003). The vegetation types cover a wide ecological and structural range, from open pioneer communities of mobile dunes to species- and structurally-rich swamp forests (see Table S1 in Supporting Information). Dolnik (2003) analysed all plants (including bryophytes and lichens, and also both terricolous and non-terricolous taxa) for 16 plot sizes from 0.0001 to 900 m<sup>2</sup> (one count per size). Mean species-richness values of the two to 23 replicates per

vegetation type were used in the analyses (i.e. the data belong to subtype A.b.i according to Table 1). Detailed specifications of the data are given in Tables S1 and S2.

The type C data are for vascular plant species from islands in six lake and oceanic archipelagos, in biomes ranging from tropical to hemiarctic zones, and for sizes ranging from 1 m<sup>2</sup> to more than 10,000 km<sup>2</sup> (Buckley, 1985; Deshayé & Morisset, 1988; Rydin & Borgegård, 1988; Hobohm, 2000; Bergmeier & Dimopoulos, 2003; Price, 2004). Detailed specifications of the data are given in Table S3.

### Curve fitting

For the analyses, 12 models were selected to represent the full range of curve shapes (linear, convex-unbound, convex-saturation, sigmoid), and of numbers of fitted parameters (Table 2). Each of these 12 functions was fitted both for *S* and for log *S*. For the sake of convenience, I used log<sub>10</sub> throughout, but any other logarithm would have produced equivalent results. In addition, the Michaelis–Menten function was fitted for *A/S*, which results in a linearization of that function (Woelf transformation; see Raaijmakers, 1987; Schmitt, 1999). The regression analysis was performed with the non-linear regression model of STATISTICA 7.1 (StatSoft, Inc., 2005; settings: least squares; method of estimation: quasi-Newton; criterion of convergence: 0.0001). For starting values and step-width, the default values of the program (0.1 and 0.5) were used for all parameters unless the iterations did not converge. For these cases, the values were altered using previously established parameter values from similar situations, which always led to a satisfactory fit.

### Evaluation of the goodness-of-fit

The fitted parameters from the non-linear regressions were afterwards used to calculate goodness-of-fit metrics. To assess the goodness-of-fit within the fitted range of plot sizes, I used AICc (modification of AIC for small *n*; Burnham & Anderson, 2002; Johnson & Omland, 2004), calculated both for *S*- and for log *S*-space.

To assess the suitability of a SAR model for extrapolating species richness beyond the largest plot, I fitted the same model to the data set after omission of the largest areas and then compared the predicted with the actual species-richness values for the largest plot in the original data set. To standardize this procedure, all data for areas larger than one-tenth of the largest area were omitted. This deviation was calculated on a log *S*-scale and is termed the log error of extrapolation (LEE). In the case of type A relationships, the actual value is the one recorded for the largest plot. For curve types B and C, it is not as simple because the richness value for the largest entity usually deviates from the average curve owing to non-average environmental conditions. In such cases, for the actual value of the largest area, I used the value predicted in the full-range model by the one function that had the lowest AICc value in the *S*-space.

Rankings were calculated for each metric and each series of species–area data. These rankings were used to calculate mean ranks for each of the three metrics for both the nested-plot and the island data set. Furthermore, the mean values of metrics for these two data sets were calculated and afterwards ranked. As both methods yielded similar results, I present mostly those of the second method because they are more clearly interpretable. To condense the information further, mean ranks of all three goodness-of-fit metrics were calculated for the models in both the nested-plot and the island case.

To estimate the stability of the parameter estimates, I tested how much they changed when the data set or the analysing method was slightly altered. For this purpose, I compared the values in pairs for all fitted parameters both for models fitted in  $S$  against those fitted in  $\log S$  (the first gives more weight to large areas; the second, more weight to small areas) and for those fitted for the full range of area sizes against those fitted only for areas smaller than 1/10 of the largest area (corresponding to the criterion used for the calculation of LEE). To reflect the wide range of values an individual parameter can take (often spanning several orders of magnitude), I used log differences, which, however, were not defined in the few cases for which a parameter (partly) showed negative values.

## RESULTS

### Nested plots

According to AICc ( $S$ ), the quadratic power function fitted for  $S$  was the best model for six of the 14 analysed plant communities and worked well for the other eight, resulting in a mean rank of 1.8 for this metric and a mean  $\Delta\text{AICc}$  ( $S$ ) of 3.66 (Table 3 and Table S1). Also satisfactory were the Lomolino function, the power function (Plotkin), and the regular power function, all fitted for  $S$  (best fit in two or three communities each), as well as the  $S$ -versions of the cumulative beta-P function (mean rank: 4.9 but never the best fit) and the quadratic version of the logarithmic function (twice the best fit but only intermediate results for the other communities). The quadratic power function (fitted for  $\log S$ ) also worked well according to AICc ( $S$ ) and was ranked sixth of all 25 function–space combinations. For AICc ( $\log S$ ) (Table 3 and Table S1), the results were analogous, with the quadratic power function fitted for  $\log S$  being the best. The Lomolino, cumulative beta-P and the two other versions of the power functions fitted in the  $\log S$ -space also described the shape of the actual function satisfactorily. Again, the quadratic version of the logarithmic

**Table 3** Evaluation of the goodness-of-fit of various models and transformations of  $S$  for nested plots (curves of 14 plant communities from Dolnik, 2003; for details, see Materials and Methods).

No.	Category	Model	$S$ -space	Mean rank	AICc ( $S$ )	AICc ( $\log S$ )	LEE	$\Delta\text{AICc}$ ( $S$ )	$\Delta\text{AICc}$ ( $\log S$ )	LEE
1	Linear	Linear	$S$	20.3	19	20	22	73.47	81.69	0.92
2	Linear	Linear	$\log S$	22.0	25	18	23	103.29	75.75	1.26
3	Power	Power	$S$	5.7	5	11	1	12.16	36.26	0.03
4	Power	Power	$\log S$	7.3	11	5	6	37.95	18.37	0.13
5	Power	Power (quadratic)	$S$	3.7	1	6	4	3.66	24.89	−0.11
6	Power	Power (quadratic)	$\log S$	5.3	6	1	9	19.81	4.70	−0.05
7	Power	Power (Plotkin, approx.)	$S$	12.3	3	10	24	8.72	34.86	−1.18
8	Power	Power (Plotkin, approx.)	$\log S$	12.7	9	4	25	29.31	15.65	−2.40
9	Logarithmic	Logarithmic	$S$	17.0	15	25	11	63.36	n.d.	−0.27
10	Logarithmic	Logarithmic	$\log S$	17.0	21	13	17	80.34	58.33	−0.43
11	Logarithmic	Logarithmic (quadratic)	$S$	10.7	10	19	3	30.00	78.79	−0.12
12	Logarithmic	Logarithmic (quadratic)	$\log S$	10.7	13	9	10	54.27	31.39	−0.19
13	Saturation	Michaelis–Menten	$A/S$	17.7	18	22	13	64.69	110.72	−0.31
14	Saturation	Michaelis–Menten	$S$	17.0	14	23	14	56.82	111.05	−0.34
15	Saturation	Michaelis–Menten	$\log S$	19.3	23	15	20	86.74	68.63	−0.58
16	Saturation	Negative exponential	$S$	18.7	16	24	16	63.78	113.95	−0.37
17	Saturation	Negative exponential	$\log S$	20.3	24	16	21	88.22	70.88	−0.61
18	Saturation	Rational	$S$	13.7	12	17	12	50.55	71.34	−0.31
19	Saturation	Rational	$\log S$	16.7	20	12	18	77.34	53.41	−0.43
20	Sigmoid	Logistic	$S$	17.7	17	21	15	64.62	87.24	−0.36
21	Sigmoid	Logistic	$\log S$	18.3	22	14	19	83.86	61.89	−0.47
22	Sigmoid	Lomolino	$S$	3.7	2	7	2	8.13	27.92	−0.11
23	Sigmoid	Lomolino	$\log S$	5.7	7	2	8	22.84	8.85	−0.14
24	Sigmoid	Cumulative beta-P	$S$	5.7	4	8	5	11.94	30.18	−0.13
25	Sigmoid	Cumulative beta-P	$\log S$	6.0	8	3	7	25.52	9.23	−0.13

The naming of the models follows Table 2. Three goodness-of-fit metrics were applied: Akaike's information criterion (corrected for small  $n$ ; AICc) assessed both for  $S$ - and for  $\log S$ -space as well as log error of extrapolation (LEE; for definition, see text). For these metrics, mean values of the 14 curves (columns 9–11) as well as the corresponding ranks (1 = best fit, 25 = worst fit; columns 6–8) are presented. The column 'Mean rank' provides the average ranking of all three metrics. Positive values of LEE denote overestimation of the actual values, whereas negative values denote underestimation. Because the logarithmic function (fitted in  $S$ ) partly predicted negative richness values, AICc was not defined (n.d.) for the  $\log S$ -space.

function resulted in the best fit for two communities, and additionally the rational function gave the best fit for one community, although both curve types yielded only intermediate results for the rest of the vegetation types. On the other hand, linear, negative exponential, Michaelis–Menten and the regular logarithmic functions fitted the nested-plot SAR data poorly both for  $S$  and for  $\log S$  and for all community types.

Regarding the suitability for extrapolation, the normal power function fitted for  $S$  turned out to be the most suitable on average, and overestimated the actual species richness of a ten-fold area with a mean LEE of only 0.03 (i.e. by 7%). This model, however, accounted for only one-quarter of first rankings for LEE, and some other models had similar mean LEE values and ranks for both  $S$ -spaces, namely the Lomolino, the cumulative beta-P and the quadratic logarithmic function as well as the two other versions of the power function (see Table S1). The normal logarithmic function, the three saturation functions and the logistic function formed a group of intermediate suitability for extrapolation, whereas both the linear function and the Plotkin version of the power function turned out to be completely unsuitable, the former giving predictions *c.* 10 times too high, and the latter predictions much too low, mostly close to zero. The predicted values of the normal and quadratic power functions, irrespective of the  $S$ -space, were either slightly too high or too low. Whereas the

absolute extrapolation errors were only slightly worse for the Lomolino, cumulative beta-P and quadratic logarithmic functions, these almost always yielded estimates *c.* 30% too low. Worse were the normal exponential function, the three saturation functions and the logistic function, which underestimated the richness values of the large plot by 60% on average.

Of the functions with only two fitted parameters, the power function outperformed all other models by far. It was rated best according to AICc ( $S$ ) in all 14 community types, and for AICc ( $\log S$ ) and LEE the logarithmic function performed better in only one community for each.

## Islands

Results for the island data set were generally similar but less clear than those for the nested plots; in other words, the individual archipelagos showed more idiosyncrasies (Tables 4 and S3). Again, on average the three versions of the power function, the quadratic logarithmic function, the Lomolino function, and the cumulative beta-P function (fitted for the respective  $S$ -space) were rated as the most suitable group of functions according to AICc for  $S$  or  $\log S$ . However, for individual archipelagos other functions with on average rather poor fits proved to describe the curve shape most

**Table 4** Evaluation of the goodness-of-fit of various models and transformations of  $S$  for islands (curves of six archipelagos; for details, see Materials and Methods).

No.	Category	Model	$S$ -space	Mean rank	AICc ( $S$ )	AICc ( $\log S$ )	LEE	$\Delta$ AICc ( $S$ )	$\Delta$ AICc ( $\log S$ )	LEE
1	Linear	Linear	$S$	21.7	24	22	19	46.65	52.04	0.69
2	Linear	Linear	$\log S$	20.7	25	15	22	111.02	29.52	0.86
3	Power	Power	$S$	9.7	7	14	8	14.11	24.45	0.20
4	Power	Power	$\log S$	14.3	22	6	15	41.63	9.42	0.32
5	Power	Power (quadratic)	$S$	12.7	1	17	20	2.54	31.92	−0.29
6	Power	Power (quadratic)	$\log S$	12.0	14	1	21	23.04	3.64	−0.63
7	Power	Power (Plotkin, approx.)	$S$	13.0	3	12	24	5.31	19.67	−4.06
8	Power	Power (Plotkin, approx.)	$\log S$	13.7	13	5	23	21.27	7.74	−2.83
9	Logarithmic	Logarithmic	$S$	13.0	12	24	3	19.46	n.d.	−0.19
10	Logarithmic	Logarithmic	$\log S$	15.0	23	10	12	41.77	17.22	−0.37
11	Logarithmic	Logarithmic (quadratic)	$S$	8.7	5	20	1	10.77	37.54	−0.06
12	Logarithmic	Logarithmic (quadratic)	$\log S$	8.7	17	4	5	29.72	6.14	−0.15
13	Saturation	Michaelis–Menten	$A/S$	19.7	15	19	25	23.74	36.32	n.d.
14	Saturation	Michaelis–Menten	$S$	12.0	6	21	9	12.99	45.87	−0.18
15	Saturation	Michaelis–Menten	$\log S$	15.0	19	8	18	33.67	14.18	−0.21
16	Saturation	Negative exponential	$S$	15.7	10	23	14	16.17	54.38	−0.27
17	Saturation	Negative exponential	$\log S$	15.7	20	11	16	40.07	18.10	−0.39
18	Saturation	Rational	$S$	15.3	9	24	13	14.84	n.d.	−0.17
19	Saturation	Rational	$\log S$	11.7	18	7	10	29.88	10.43	−0.36
20	Sigmoid	Logistic	$S$	11.0	8	18	7	14.72	35.22	−0.33
21	Sigmoid	Logistic	$\log S$	15.7	21	9	17	40.79	16.79	−0.42
22	Sigmoid	Lomolino	$S$	6.7	2	16	2	4.79	30.23	−0.13
23	Sigmoid	Lomolino	$\log S$	9.7	16	2	11	26.47	4.45	−0.06
24	Sigmoid	Cumulative beta-P	$S$	7.0	4	13	4	5.81	21.70	−0.06
25	Sigmoid	Cumulative beta-P	$\log S$	6.7	11	3	6	18.62	4.63	−0.10

For details of the organization of the table, see Table 3. Undefined values are marked with 'n.d.'.



appropriately, for example the regular logarithm function for the islands in the Swedish Lake Hjälmaren (Rydin & Borgegård, 1988). Generally, the linear, the negative exponential, the logarithmic function, and all models fitted for the complementary *S*-space resulted in poor fits.

The extrapolation suitability (measured as LEE) was generally best for the quadratic logarithmic and the cumulative beta-P functions (for *S* and log *S*) as well as for the regular logarithmic and the Lomolino functions fitted for *S*. Unlike the situation for nested-plot data, the regular power function performed only moderately well (mean rank c. 11 for both transformations), and the quadratic power function intermediately if fitted for *S* (mean rank: 12.5) and rather poorly if fitted for log *S* (mean rank: 16.7). Again, the linear and the Plotkin functions were generally completely unsuitable for extrapolation, although in the case of the Macaronesian islands (Hobohm, 2000) the linear function gave the most accurate extrapolation value. Compared with the situation in the nested-plot data set, the models had the same tendencies in extrapolations towards overestimates or underestimates. However, the positive and negative deviations of the estimates from the actual value were generally more pronounced for all types of power functions, whereas underestimates were less pronounced in extrapolations from the logarithmic, saturation and sigmoid functions compared with those for nested-plot data set (Table 4).

### Stability of parameter estimates

In the nested-plot data set, the parameter estimates were relatively stable in the case of the power and logarithmic functions and their variants between *S* and log *S*, and full vs. reduced area range (Table 5). For all other function types, the estimates for at least one of the parameters were unstable or very unstable, often covering one or even several orders of magnitude (Table 5). In particular, the parameter  $b_0$  of the saturation and sigmoid functions, which corresponds to the estimated maximum richness (see Table 2), showed mean log differences of 0.15–0.97 (i.e. 1.4- to 9.3-fold differences on average; Table 5). In one community, the asymptotic richness value of the Lomolino function even differed by a factor of 1293 between the models fitted for *S* and log *S*. The situation for the island data set was basically the same (not shown); however, in this case the parameters of the derived power models (quadratic and Plotkin) also behaved very unstably.

As non-linear regression is an iterative process, it may be 'captured' at a local optimum of parameter combination. Thus, different starting or step-width values may lead to different results. In this respect, only the linear, power and logarithmic models, and their variants, as well as the Michaelis–Menten model produced 'stable' parameter estimates. For the remaining saturation functions and the sigmoid functions, there were often several solutions with practically identical AICc values but parameter estimates differing by one or several orders of magnitude (not shown).

**Table 5** Mean differences of the parameter estimates between models fitted for *S* and for log *S* as well as for those fitted for the full range of plot sizes (0.0001–900 m<sup>2</sup>) and those fitted for the reduced range used for calculating the extrapolation capability (0.0001–49 m<sup>2</sup>).

Model	S vs. log S				Full vs. reduced			
	$b_0$	$b_1$	$b_2$	$b_3$	$b_0$	$b_1$	$b_2$	$b_3$
Linear	<b>0.40</b>	<b>0.37</b>			0.27	<b>0.94</b>		
Power	0.06	0.08			0.03	0.05		
Power (quadratic)	0.01*	0.03	n.d.		0.01*	0.04	n.d.	
Power (Plotkin, approx.)	0.07	0.07	n.d.		0.07	0.06	n.d.	
Logarithmic	0.09	0.28			0.11	0.17		
Logarithmic (quadratic)	0.03	0.12			0.02	0.08		
Michaelis–Menten	0.28	<b>2.44</b>			0.25	<b>0.80</b>		
Negative exponential	0.26	<b>2.59</b>			0.25	<b>0.80</b>		
Rational	<b>0.54</b>	<b>1.11</b>	<b>1.31</b>		0.23	<b>0.65</b>	<b>0.92</b>	
Logistic	0.15	<b>1.70</b>	<b>0.30</b>		0.24	<b>0.73</b>	0.11	
Lomolino	<b>0.35</b>	0.07	<b>1.67</b>		<b>0.39</b>	0.06	<b>1.87</b>	
Cumulative beta-P	<b>0.97</b>	<b>1.95</b>	0.11	<b>1.22</b>	<b>0.91</b>	<b>1.64</b>	0.10	<b>0.83</b>

Differences were calculated as log differences, i.e.  $|\log_{10}(x_1) - \log_{10}(x_2)|$ , and are presented as means for all 14 plant communities of the nested-plot data set. Note that a log difference of more than 0.3 (set in bold italics) means a more than two-fold difference, and a log difference of more than 1.0 (bold) means a more than 10-fold difference. Owing to occurring negative values, log differences were not defined for  $b_2$  in the two derived power functions (n.d.). The values of  $b_0$  in the quadratic power function (\*) were calculated only for 13 communities because in one community this parameter took negative values and thus the log differences were undefined.

## DISCUSSION

### Criteria for model selection

As demonstrated for the two example data sets, the three applied goodness-of-fit metrics, AICc (*S*), AICc (log *S*) and LEE, resulted in clearly and consistently deviating results (Tables 3 and 4; Tables S1 and S3). This indicates that they capture different aspects of the curve fit and thus provide valuable complementary information. By contrast, other tested metrics, such as  $R^2_{adj}$ ,  $p$  or lack-of-fit measures, resulted in similar to nearly identical model rankings compared with AICc in the same *S*-space (not shown). Contrary to repeated suggestions (e.g. Connor & McCoy, 1979; He & Legendre, 1996; Fattorini, 2007), there is thus no good reason to apply these parameters additionally. Of the metrics that measure the goodness-of-fit within a fitted range, AIC (or alternatively BIC, which in this study gave nearly identical results) has the advantages of being generally accepted in recent statistical literature, of allowing the comparison of non-nested models and of adequately penalizing additional parameters (see Quinn & Keough, 2002; McGill, 2003). Although in the case of nested data the estimates of the standard errors of the regression parameters are invalid (but the same is true for all the compared metrics), the estimates of the regression parameters

themselves are unbiased (Adler *et al.*, 2005). Moreover, the model selection itself is not influenced by the nestedness of the data because the data are equally nested for all compared models (for detailed discussion, see Dengler, 2008).

Although Cresswell & Vidal-Martinez (1995) claimed that it is nonsensical to estimate goodness-of-fit metrics of SARs in the log  $S$ -space, I agree with Quinn & Keough (2002, p. 64) that the choice of the untransformed  $S$ -space is as arbitrary as that of the log  $S$ -space. It is clear that AICc ( $S$ ) gives relatively more weight to the deviations for larger areas, whereas AICc (log  $S$ ) does so for smaller areas (cf. Loehle, 1990). Because a prediction error of one species would generally be considered as high for  $S = 1$  but as negligible for  $S = 1000$ , it actually is meaningful to assess goodness-of-fit metrics (additionally) on the log  $S$ -scale.

As shown (compare Tables 3 and 4), a model that produces a good fit need not also be suitable for extrapolation. Thus, the newly proposed metric LEE adds valuable information to the model selection process, as extrapolations are one of the most fundamental applications of SARs. Moreover, one can argue that a model that produces consistently good extrapolations depicts the real nature of the SAR better than one that only fits well for a given data set within a given range of areas, as curve fitting is generally a 'weak test' (McGill, 2003). As an alternative to the proposed log error of extrapolation (LEE), one could think of a relative error of extrapolation. However, the latter would have the disadvantage of not equally weighting positive and negative deviations, but instead would range from  $-100\%$  to  $+\infty$  (non-negative species-richness values provided).

In addition to goodness-of-fit and extrapolation capability (Tables 3 and 4), other criteria are important for model selection. First, functions whose parameters have interpretable meaning and allow easy comparison between different data sets can generally be considered superior. In this respect, the linear, logarithmic, power and quadratic power functions are quite suitable. Their parameters correspond to the species richness on an area of standard size and to the steepness of the curve (i.e. to the absolute or relative rates at which new species are added when area is increased). The parameters of the Michaelis–Menten function (after transformation) also truly represent aspects of species–area relationships (Kluth & Bruehlheide, 2004). By contrast, the parameters of the negative exponential, rational and logistic functions influence more than one curve characteristic, and all but the first parameter of the Lomolino and the cumulative beta-P functions jointly define curve shape in ways that are difficult to interpret (Tjørve, 2003). Furthermore, a curve parameter may have a meaning by definition but its fitted values appear to be arbitrary. This is the case with the asymptotic richness value ( $b_0$ ) of the Lomolino and cumulative beta-P functions, which frequently exceeded the species count on the largest plot by several orders of magnitude.

Second, only the normal power function and the two logarithmic functions produced 'stable' parameter estimates throughout, meaning that they were not influenced by the settings of the non-linear regression analysis and only slightly influenced by slight modifications of the data set (see Results).

Third, some functions predict theoretically impossible values for species richness or its increment, and it is questionable whether such functions can be regarded as valid models even when they satisfactorily fit a certain range of data. For example, the logarithmic function necessarily predicts negative species richness values (for  $A < 10^{-b_0/b_1}$ ), and this mostly happens even within the fitted range. The quadratic power function also can result in negative  $S$ -values, although normally outside the fitted range. Some models also violate the limitations of the increment (corresponding to the  $z$ -value of the power function) which are  $0 \leq z \leq 1$ . This means that species–area relationships based on data from the same statistical population must be non-decreasing and cannot increase more steeply than unity (Williamson, 2003). For example, the quadratic and Plotkin modifications of the power function result either in a predicted decrease of the species richness beyond a certain size of area ( $b_2 < 0$ ) or in increments greater than unity for large areas ( $b_2 > 0$ ).

### Performance of models

Overall, the quadratic power function and the Lomolino function performed best for the nested-plot data set, followed closely by the normal power function and the cumulative beta-P function (see Table 3). From the models with only two parameters, the normal power function was by far the most adequate. Its two versions ( $S$  and log  $S$ ) behaved quite similarly, with the exception that the extrapolation capability of the first was slightly better. It should be noted that the normal power function performed very well for extrapolating richness data far beyond the largest plot throughout the wide range of vegetation types.

For the island data, the six analysed curves showed more peculiarities than did the 14 plant communities, as fundamentally different curve types were rated as most suitable, including a linear function in one case. These idiosyncrasies should, however, not be assigned to different underlying species–area relationships but to the fact that, in island data (SARs type C), the 'real' relationship (i.e. the dependence of species richness on area) is partly masked by ecological differences between the islands (i.e. the dependence of species richness on factors other than area; see, for example, Whittaker *et al.*, 2008) and also by the 'island effect' (small islands generally have fewer species than areas of the same size on continents, but this difference decreases when islands become larger and thus more similar to continents; see Whittaker & Fernández-Palacios, 2007). For the analysed islands, the Lomolino, cumulative beta-P and quadratic logarithmic functions were superior on average to power functions, but again the normal power function performed best among the two-parameter models (see Table 4).

Contrary to claims that logarithmic functions should describe small-scale SARs in continuous ecosystems better than power functions (Gleason, 1922; Stohlgren *et al.*, 1995; He & Legendre, 1996; also Dolnik, 2003, for some plant communities re-analysed in this article), I found that the

normal logarithmic function was one of the least appropriate functions to describe such SARs throughout the broad range of analysed vegetation types, which agrees with the findings of Fridley *et al.* (2005).

Apart from the Lomolino and the cumulative beta-P functions, all functions with an upper asymptote generally performed poorly for both the nested-plot and islands data set. In particular, they completely failed when extrapolating richness values beyond the largest area because most of them give richness estimates for the asymptote that lie only slightly above or even below the highest value occurring among the included data. This finding contrasts somewhat with the simulation results of McGill (2003), who found that even the Michaelis–Menten and the logistic function can fit power functions very well. However, this is only true when a narrow range of plot sizes is sampled, as the author admits. In the present study, among the saturation functions only the Lomolino and the cumulative beta-P function performed better, which, however, should rather be attributed to their high flexibility owing to three or four parameters than to the existence of an upper asymptote (cf. Tjørve, 2003). In fact, simulated data of a ‘perfect’ power function, represented by 16 data points as in the nested-plot data set, were fitted by the Lomolino function with  $R^2_{\text{adj}} = 0.999953$  and  $\text{LEE} = -0.01$  (i.e. deviation c.  $-2\%$ ) and by the cumulative beta-P function with  $R^2_{\text{adj}} = 0.999774$  and  $\text{LEE} = -0.02$  (c.  $-4\%$ ) (both examples for  $S$ -space). However, even these two flexible sigmoid functions slightly but systematically underestimated the true value in extrapolation for the nested-plot data set (see column LEE in Table 3).

### Do species–area relationships have asymptotes?

It is often claimed that SARs of different kinds should approach an upper asymptote for large areas (general: Connor & McCoy, 1979; Williams, 1995; He & Legendre, 1996; Tjørve, 2003; type A: Cain, 1938; Tüxen, 1970; Mueller-Dombois & Ellenberg, 1974; Schmitt, 1999; type C: Lomolino, 2000, 2001). If any argument for this widespread assumption is given, it usually runs as follows: ‘Because the number of species available for colonisation in any biogeographic region or geographical unit of the planet is limited, the species–area curve has to be asymptotic to some upper “number of species” bound’ (He & Legendre, 1996, p. 721). As Williamson *et al.* (2001) rightly pointed out, the fact that for any given area (even the whole Earth) there is a fixed (although often unknown) number of species does not imply that the species–area curve must approach this value asymptotically. In fact, real SARs become even steeper towards continental or intercontinental scales, i.e.  $10^7$ – $10^8$  km<sup>2</sup> (Rosenzweig, 1995; Williamson *et al.*, 2001, 2002).

For the local scale ( $10^{-4}$ – $10^3$  m<sup>2</sup>), the vast body of published data (e.g. Crawley & Harral, 2001; Fridley *et al.*, 2005) similarly contradicts the existence of asymptotes. In a recent study that by contrast claims that saturation functions nearly always fit such data better than function types without asymptotes (Stiles

& Scheiner, 2007), this finding can simply be attributed to the fact that the authors analysed type IIIB ‘species–area curves’ in the sense of Scheiner (2003), which, in fact, are SSRs. There is no sound theoretical argument why either continuous ecosystems or particular vegetation types should approach an upper limit of species for large areas (see also Dengler, 2003). On the one hand, completely homogeneous environments do not exist and owing to the universal distance decay the degree of heterogeneity on average grows with increasing area (e.g. Williamson, 1988; Bell *et al.*, 1993). On the other hand, even in completely homogeneous environments, the number of species would increase slowly but unlimitedly with increasing area, as the number of ‘atypical’ species from neighbouring ecosystems/biotas that occur in the study area by chance increases with increasing edge length. In the present study, models with an upper asymptote accordingly turned out to be unsuitable for both nested-plot and island biodiversity data (apart from the Lomolino and cumulative beta-P function; for explanation, see previous section).

The other question is whether there is a lower asymptote within SARs. Since the work of MacArthur & Wilson (1967), some biogeographers have claimed that a so-called ‘small island effect’ (SIE) should cause species richness to vary independently of island area on relatively small islands (Lomolino, 2000, 2001; Lomolino & Weiser, 2001; Whittaker & Fernández-Palacios, 2007; see also the review by Triantis *et al.*, 2006). The idea of the SIE is that below a breakpoint area  $T_1$  species richness is not affected by area (but positive), and for larger areas it follows a power or logarithmic function with  $A - T_1$  as the independent variable. In what has been to date the most comprehensive study, Lomolino & Weiser (2001) claimed that they had detected a SIE in most of their 102 analysed data sets of true and habitat islands, as they yielded higher  $R^2$  values for the breakpoint function than for the respective power or logarithm function without a breakpoint. However, they did not penalize for the extra parameter  $T_1$ , which is necessary when comparing the fit of regression models of varying complexity (e.g. Quinn & Keough, 2002). I also was not able to find a single study that demonstrated the existence of a SIE unequivocally, either because the authors rejected this effect themselves (e.g. Barret *et al.*, 2003; Panitsa *et al.*, 2006; Hannus & von Numers, 2008) or because they demonstrated it only graphically (MacArthur & Wilson, 1967) or with the same statistically flawed approach as used by Lomolino & Weiser (2001) (e.g. Gentile & Argano, 2005; Triantis *et al.*, 2006). Moreover, small areas normally will be more strongly affected by environmental heterogeneity (and thus show more scatter in the species–area plot), whereas this heterogeneity is partly levelled-off for larger areas (Williamson *et al.*, 2001). Thus, fundamentally different shapes of SARs for small islands (SAR type C) are not proven and seem improbable.

For small-scale nested-plot SARs (SAR type A) different authors have claimed a left-hand steepening or flattening of the curve (cf. Williamson *et al.*, 2001). What actually happens, however, fundamentally depends on the sampling method (Williamson, 2003; Dengler, 2008): in the any-part system

(‘shoot presence’) of sampling, all aerial parts of plants are counted with vertical projections that fall within the studied area. In the grid-point (roughly equivalent to the ‘rooted presence’) system, each ‘individual’ is treated as a point without area and thus is always assigned to only one of several adjacent areas. The consequence in both cases is a deviation from the power law (or any other SAR model) for very small areas. The exponent ( $z$  or  $b_1$  in Table 2) of the power law approaches 0 in the any-part system and 1 in the grid-point system for  $A \rightarrow 0$ . As described by Williamson (2003), the deviation from the power law ‘detected’ in the large data sets of woody species inventories by Plotkin *et al.* (2000), which caused these authors to propose a complex modification of the power law (see Table 2), is simply an artefact of the grid-point system they used. The deviations were significant up to  $10^4 \text{ m}^2$ , which probably can be attributed to the fact that they studied only very large organisms (tropical trees). In the data of Dolnik (2003) used for this study, for which ‘rooted presence’ sampling (mathematically similar to the grid-point system) was also applied but which included herbaceous plants, bryophytes and lichens, the SAR in the log–log representation became only slightly steeper towards the smallest areas ( $10^{-4} \text{ m}^2$ ); that is, the quadratic power functions had a small negative  $b_2$ . For the opposite effect in the case of the any-part system, Williamson (2003) referred to Crawley & Haral (2001), who reported decreasing  $z$ -values below areas of  $10^4 \text{ m}^2$ . However, I assume that other factors were causal there because in my own study of dry grasslands (Dengler, 2005) I could detect the small-area effect of the any-part system only below  $10^{-4} \text{ m}^2$ . Although I fundamentally agree with Williamson (2003), his prediction that the any-part system results in a lower asymptote at  $S = 1$  is correct only in his theoretical vegetation. In real vegetation, the ‘asymptotic richness’ will equal the average number of overlapping species at each point of the analysed area, which can be above or below one (Dengler, 2003, 2005).

### A general model for SARs

As shown, the normal power function was fundamentally the best two-parameter model to describe SARs at small scales ( $10^{-4}$ – $10^3 \text{ m}^2$ ) in continuous ecosystems (SAR type A) for the broad range of vegetation types studied. Among the three models with more fitted parameters that performed similarly or slightly better on average according to the mean rank in Table 3, namely quadratic power, Lomolino and cumulative beta-P, the latter two have serious shortcomings: (1) their assumption of an upper asymptote is not justified (see previous section); (2) their parameters are not easily interpretable and are very unstable; and (3) their good fit may simply be caused by their high flexibility. The quadratic power function, on the other hand, has the disadvantage that it predicts decreasing species numbers above a certain threshold area, which is in reality impossible. Although the individual SARs for islands (SAR type C) showed more peculiarities, these can be attributed to environmental differences owing to the non-nested design rather than to differences in the underlying

SAR, as argued above (see Crist & Veech, 2006). Recently, Dengler & Boch (2008) demonstrated with a re-sampling approach from continuous ecosystems that non-nested sampling actually led to more stochasticity than did nested sampling and that this improved the relative performance of other models compared with the normal power function. Knowing that power functions are most suitable for ‘pure’ SARs of nested-plot data, it seems reasonable to apply them generally for island and other non-nested data as well. When deviations from normal power functions occur in SARs of type C, they thus can be attributed to factors other than area (i.e. to ecological idiosyncrasies of the individual islands).

Based on the outlined theoretical consideration, the review of literature data, and the example data analysed in this article, I suggest using the (normal) power function as a general model for all kinds of species–area data and at any scale, but treating the exponent  $z$  as scale-dependent. This approach is similar to a recently published suggestion of Christensen (2007), who describes SARs with the function  $S(A) = c A^{\ln(\tau(A))}$ , but claims that  $\tau(A)$  decreases monotonously with increasing  $A$ . An approach that allows  $z$  to vary freely between the theoretical bounds 0 and 1 has several additional advantages, as follows. (1) The question of whether and at which point(s)  $z$  changes significantly can be addressed by standard statistical tests. For example, it could be easily tested whether or not a small area or a small island effect (see above) occurs in a data set. Similarly, it is possible to test whether SARs are ‘triphasic’ when areas over many orders of magnitude are compared. Whereas some authors have argued that SARs should follow a flat–steep–flat pattern (Lomolino, 2000, 2001; Crawley & Haral, 2001), others have supported a steep–flat–steep pattern (Preston, 1960; Hubbell, 2001; Allen & White, 2003; McGill & Collins, 2003; Fridley *et al.*, 2005). (2) A power function with flexible  $z$  can actually also describe the shapes of any other model. (3) The two parameters of the power function,  $c$  and  $z$ , and potentially the characterization of the scale-dependence of  $z$  are readily interpretable and comparable amongst the multitude of SAR studies (e.g. Drakare *et al.*, 2006).

As the estimates for both the function parameters and the goodness-of-fit metrics of power functions fitted for  $S$  or for  $\log S$  deviate from each other, it is important to report in which  $S$ -space the function was fitted and to compare only values from the same space. As discussed above, there is no prevalence for either one of these approaches, although there are arguments in favour of both. The use of  $S$  is favourable for two reasons: (1) it allows the easy treatment of entities with zero species – which could particularly occur for islands (and these then need to be included, see Williams, 1996); and (2) whereas curves fitted for  $S$  and  $\log S$  perform similarly for most parameters, the former are generally more suitable for extrapolation (see Tables 3 and 4). On the other hand, there are three arguments for fitting in the  $\log S$ -space: (1) no sophisticated statistical software for non-linear regression is needed (whereas this point certainly caused the general preference for fitting in  $\log S$ -space in the past, it should not be an ‘excuse’ today); (2) iterative, non-linear curve-fitting



procedures do not necessarily converge or may converge at a 'local optimum' only (in the present study, however, such 'problems' only occurred for function types other than power functions; see Results; cf. Stiles & Scheiner, 2007); and (3) when type A SARs are calculated, the  $z$ -value for a mean curve (for example for several series of nested-plots of the same vegetation type) remains the same, irrespective of whether the  $z$ -values for the individual plots are calculated first and then averaged, or the  $z$ -value is calculated for a data set containing all individual area–richness pairs. In contrast, the two calculations yield different results when the curves are fitted in S.

### How power-law SARs came to be

It may be questioned what causes the prevalence of power laws in SARs. Neither of the two requisites originally suggested by Preston (1962), namely (1) true isolates and (2) canonical log-normal species–abundance distributions, is actually essential. The present study joins several previous analyses in showing that the power function fits data from continuous ecosystems even better than that from islands. As regards the second aspect, May (1975) previously showed that non-canonical log-normal distributions and broken-stick distributions also result in power laws. Moreover, various authors have shown that log-normal species–abundance distributions are much rarer in nature than are power-law SARs (e.g. Williamson & Gaston, 2005). Thus recent authors have proposed other reasons for the prevalence of power laws: Harte *et al.* (1999) argued that power-law SARs are the consequence of self-similarity in the abundance distribution of species, and Šizling & Storch (2004) showed that, owing to the 'finite-area effect', this is true even when species differ in their fractal dimension. Most recently, Martín & Goldenfeld (2006) demonstrated that power-law SARs are the consequence of skewed species–abundance distributions (i.e. log-normal with higher rarity) and the clustering tendency of individuals of any given species. Hubbell (2001) and Rosindell & Cornell (2007) showed with their neutral models that stochastic events of death, dispersal and speciation are enough to produce power-law SARs over a wide range of intermediate spatial scales. In a completely different approach, Palmer (2007) mathematically deduced power-law SARs from the near-universal distance decay of features of the abiotic environment (an idea that was previously put forward but not tested by Williamson, 1988), finding that  $z$  depends on the fractal dimensions of the relevant environmental factors.

### Importance of a meaningful typology

In the literature, SARs and SSRs are often confused. For example, Inouye (1998) speaks of SARs although he analysed SSRs, and Tjørve (2003) calls Flather's (1996) species accumulation functions 'species–area models'. Although at first glance this confusion may seem to be a mere semantic problem, it actually has profound consequences as these misconceptions lead researchers to use inappropriate sampling strategies or to draw erroneous conclusions from their results.

For example, while claiming that 'not all species–area curves are power functions', Stiles & Scheiner (2007) actually studied SSRs, for which unbound functions, such as the power function, are theoretically excluded. Similarly, the general underestimation of the actual richness of combined disjunct areas by the power model in Chong & Stohlgren (2007) is not unexpected because these authors – contrary to their assumption – studied SSRs, which are initially steeper than SARs (see Hui, 2008). On the other hand, the frequent assumption that SARs should be asymptotic for large areas (see discussion on the existence of asymptotes above) probably largely emerges from incorrect analogies with SSRs.

Whereas a SAR arises from several plots or geographic units (e.g. islands) of different sizes whose species richness is known with sufficient precision, a SSR yields only one value for a single plot with defined area but unknown species richness, from which random samples are drawn to achieve this goal. Analysis of SARs aims to elucidate the relationship between area and species richness, and thus addresses a more fundamental question than that of SSRs (Gray *et al.*, 2004a). SARs are more widely applicable, such as for extrapolation, establishing a common spatial grain for analyses, deriving  $\beta$ -diversity measures, and hypothesis testing (Scheiner, 2003). SSRs, on the other hand, really only address species richness in a precisely delimited area (total plot), a property that may be extremely costly or even impossible to measure directly in certain taxa that are difficult to observe (e.g. insects, soil microbes or marine benthos). In this way, SSRs and the associated richness estimation techniques are extremely useful (Magurran, 2004). It is important to note that SSRs are basically unsuitable for analysis of the relationship of species richness to area, or for extrapolating beyond the total plot area. By contrast, if analysed appropriately, SARs may reasonably be used for extrapolation even towards much larger areas, as shown in the Results with the newly suggested parameter LEE.

### CONCLUSIONS AND OUTLOOK

In this study, I have shown that the power law generally describes different types of SARs most appropriately – which is in accordance with many previous studies. Deviating results reported in the literature can mostly be attributed either to methodological shortcomings (Dengler, 2008; Dengler & Boch, 2008) or to the fact that their authors actually studied area-based SSRs rather than real SARs. Here, the proposed new typology of species richness curves may help researchers to avoid similar misinterpretations in the future.

A variety of completely different processes are capable of producing power-law SARs, a conclusion that agrees with that of Lawton (1999), who argues that the most robust macro-ecological patterns are those that can be generated by several different mechanisms. Thus, it seems pointless to test such processes by analysing which model fits a specific SAR best, in particular, because these processes are not mutually exclusive (Turner & Tjørve, 2005; Nekola & Brown, 2007). Moreover, power-law relationships are frequently found in many complex



systems (for example number of minerals vs. area, number of unique words vs. text length), suggesting that this pattern is the consequence of shared properties of a class of complex systems (Nekola & Brown, 2007). Nevertheless, analysis of the dependence of SAR slopes on taxon, environmental conditions and spatial scale is useful, as differences in the  $z$ -values convey information on underlying processes and their relative importance in a particular case (Drakare *et al.*, 2006; Nekola & Brown, 2007; Peay *et al.*, 2007). To this end, the suggested application of the power law with flexible  $z$  offers a universal tool with which to study and compare any type of SAR – but it should be kept in mind that the parameters of the power-law SAR are also significantly influenced by methodology, particularly by the fitted  $S$ -space and the sampling procedure (any-part vs. grid-point system).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1** Detailed information for the nested-plot data set from Dolnik (2003).

**Table S2** Mean species-richness values per plot size for the nested-plot data set from Dolnik (2003).

**Table S3** Detailed information for the island data set.

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## BIOSKETCH

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