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Pitfalls in Small-Scale Species-Area Sampling and Analysis

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Abstract Analyses of the dependency of species richness (*S*) on area (*A*), the so-called species-area relationships (SARs), are widespread approaches to characterize and compare biodiversity patterns. This article highlights – with a focus on small-scale SARs of plants in continuous ecosystems – how inappropriate sampling methods or theoretical misconceptions can create artifacts and thus may lead to wrong conclusions. Most of these problems have been recognized before but continue to appear regularly in the scientific literature. The following main points are reviewed and discussed: *i*) Species richness values and SARs depend on the measurement method (any-part vs. grid-point system); *ii*) Species-richness values depend on the shape of the analyzed plots; *iii*) Many published SARs are not true SARs but instead represent species sampling curves or their data points consist of richness totals for incontiguous subplots; *iv*) Nested-plot design is the preferred sampling method for SARs (the claim that this approach would cause pseudoreplication is erroneous); *v*) SARs should be constructed using mean values of several counts for the smaller areas; *vi*) SAR functions can be fitted and selected both in the *S*- and the log *S*-space but this must be done consistently for all compared function types. It turns out that the finding of non-power function SARs in many studies is due to a lack of awareness of one or several of the named points. Thus, power-function SARs are even more widespread than a recent review would suggest. I therefore propose to use the power law as a universal model for all types of SARs but to test whether the slope z varies with spatial scale. Finally, I urge readers to be aware of the many pitfalls in SAR studies, to fully disclose methodology, and to apply a meaningful and consistent terminology, especially by restricting the terms "species-area relationship" and "species density" to situations in which each data point represents a contiguous area.

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Introduction

Analyses of the dependency of species richness (*S*) on area (*A*), the so-called species-area relationships (SARs; for terminology, see Table **1**), are widespread approaches to characterize and compare biodiversity patterns (Williamson 1988; Rosenzweig 1995; Dengler, in press). Such studies focus on three basic goals (see Scheiner 2003; Gray et al. 2004a; Dengler, in press): *i*) to characterize and compare models of different SARs and their parameters in order to understand underlying processes; *ii*) to standardize richness values to a certain spatial scale via interpolation; and *iii*) to estimate the species richness of a larger area via

Table 1 Important terms in biodiversity research that are used in this paper with their definitions as applied here (mostly following Dengler, in press)

Term	Definition and explanation
Species richness	Number of species found in any kind of entity, e.g. a certain sample, area, geographical, ecological, or phyologentic unit
Species density	Species richness of an area of standardized size
Species-area relationship (SAR;=species-area curve)	Relationship between species richness and area; here restricted to such curves that are constructed from contiguous plots
Species-sampling curve (SSC)	Empirical relationship between species richness and sampling effort; the latter could be expressed e.g. as number of analysed individuals or samples, or as cumulative area of incontiguous plots that are summed up; species accumulation curves and rarefaction curves represent the two fundamental types of SSCs
Continuous ecosystem	Term used to refer to ecosystems whose spatial extent is (far) beyond the largest analyzed plot size (although these ecosystems may exhibit some degree of internal heterogeneity)
Isolates	Term used to refer to ecosystems that are considered as entities with sharp boundaries (i.e., true islands and habitat islands)
Contiguous area/plot	Area in one piece, i.e., species richness is measured for all areas located within a certain boundary line (although not all included habitats need to be suitable for the taxonomic group studied)
Incontiguous area/plot	Area that consists of several unconnected subplots
Any-part system (=shoot-presence system)	Each plant indivual is assigned to the whole area of the vertical projection of its aerial parts and thus can be counted in more than one non-overlapping plot
Grid-point system	Each plant individual is assigned to one point (located in its centre or where it roots) and thus can only be counted in one of several non-overlapping plots
Rooted-presence system	Each plant individual is counted only in those plots in which it roots; this system is not precisely defined in mathematical terms and has somehow intermediate features between the two previous systems, but is closer to the grid-point system

Note that all compound names with "species" are often also used for other terminal taxa, such as subspecies or varieties. Additionally, these concepts can be applied similarly to any supra-specific rank, e.g. one can speak of genus richness, family richness, or generically, of taxon richness extrapolation. Moreover, SAR analyses play a vital role in applied biodiversity research, for example for identifying biodiversity hotspots (e.g. Veech 2000), for optimal reserve planning (e.g. Kunin 1997; Desmet and Cowling 2004; Williams et al. 2005), or for assessing human impacts on biodiversity (e.g. Tittensor et al. 2007).

Palmer et al. (2008, this issue) raise the point that despite the boom in biodiversity research, theoretical misconceptions and misapplication of methods frequently still lead researchers to report true but trivial patterns (*artifacts*; e.g. caused by mathematical relationships and not by ecological "laws") or even non-existing patterns (termed *artifictions* by Palmer et al.; e.g. caused by the wrong application of statistical methods). Such artifacts and artifictions are often seen as support for equally wrong theoretical concepts (see Palmer et al. 2008, this issue and many additional examples in this article). As Palmer et al. (2008, this issue) admit, their report on artifacts and artifictions is far from complete. Actually, there have been some other valuable seminal papers that highlight similar pitfalls or illustrate good practice in biodiversity research in general and in species-area analyses in particular (e.g. Palmer 1995; Gotelli and Colwell 2001). Methodological problems in species-area studies range from mistakes that have frequently been pointed out in the literature but nevertheless regularly appear in scientific articles (e.g. the incorrect comparison of R^2 values determined in S- and log S-space) to only recently described and thus still widely unknown aspects, which nevertheless may cause major artifacts (e.g. the effect of any-part *vs*. grid-point sampling; Williamson 2003).

With this paper, I seek to provide a complementary critical treatment of methodologies in the field of species-area relationships (SARs) as do Gotelli and Colwell (2001) for species sampling curves (SSCs; for terminology, see Table **1**) and Palmer et al. (2008, this issue) for some other aspects of biodiversity research. In some respect, the present article thus represents an update and deepening of Palmer (1995). Regarding the methodologies used for sampling and analysis of species-area data, I particularly aim at *i*) evaluating the possible effects of different approaches; *ii*) assessing which empirical patterns and derived theoretical concepts may be caused by inappropriate methodologies; and *iii*) advocating an improved approach for this type of research (accompanied by a list of common pitfalls to avoid). I pursue these goals mainly through critical review of the existing literature to unravel the pitfalls that are hidden along the usual steps in species-area studies.

Although this paper focuses on small-scale (i.e., 1 mm^2–1 ha) SARs of plants in continuous ecosystems (for terminology, see Table **1**), it suggests that most arguments also hold for animals and other biota as well as for larger scales as I rarely ever refer to specific properties of plants or scale in my reasoning. Moreover, some points are equally relevant for biodiversity studies on individual spatial scales.

Any-Part *vs*. Grid-point System

When recording plant species composition of a plot, two fundamentally different systems are applicable (Kilburn 1966; Greig-Smith 1983; Williamson 2003; Christensen 2007): A species is either recorded as present when it "roots" within the plot (rooted presence and similarly grid-point system; for terminology, see

Table 1) or when the vertical projection of its aerial parts falls within the plot (shoot presence, any-part system; for terminology, see Table 1). The second terminology by Williamson (2003) is preferable because it is also applicable to rootless plants and because it depicts the fundamental difference between the two sampling systems more clearly. While in the grid-point system every plant "individual" is treated as an arealess point, in the any-part system it is referred to as an area. One single plant "individual" can only be attributed to a single plot of a certain size in the first system but to several adjacent plots in the second system when a larger area is divided into grid cells of consecutively smaller sizes.

At first glance, the differences between the two systems seem to be negligible, and this may be why several of the most comprehensive textbooks on methodology in vegetation science do not even mention this contrast (Westhoff and van der Maarel 1973; Mueller-Dombois and Ellenberg 1974; Knapp 1984; Dierschke 1994). Also, in the methods sections of biodiversity studies the choice of one of the two alternative recording methods is rarely ever mentioned. Exceptions are Condit et al. (1996: grid-point), Dolnik (2003: rooted-presence below 1 m^2, any-part above), Dengler (2006: any-part throughout). Peet et al. (1998) use "rooted" presence, but it remains unclear whether a tree with a basal area of 1 m^2 would be counted in several grid cells of 0.01 m^2. I know of only two papers that compare species-richness values of both approaches. Kilburn (1966) analyzed six 900 m^2 plots (one prairie, one deciduous forest, four coniferous forests) with both approaches and found very regular patterns despite the large structural differences among communities. The deviation between both approaches was largest at 0.01 m^2 (+1.7 species on average with the any-part system) and gradually diminished both towards smaller and larger areas with a mean difference of +1.2 in 1 m^2 and +0.3 in 100 m^2. In the dry grassland communities studied by Sykes et al. (1994), the any-part system resulted in 1–2 additional species in 0.001 m^2, in 0.5–1 additional species in 0.01 m^2, but had negligible effects above this plot size. These differences still appear unimportant on the absolute scale, but they increase rapidly towards smaller plot sizes when percentage differences are considered. In the study of Kilburn (1966), the any-part system resulted in an average richness "gain" of 0.4% on 100 m^2, 8.6% on 1 m^2, nearly 180% on 0.01 m^2 and more than 400% on 0.0001 cm^2. Moreover, Dengler (2003) and Williamson (2003) showed that the differences between both approaches greatly affect the left-end shape of SARs: While the z value (i.e., the slope of a SAR in the log-log representation) approaches zero for the any-part system, it approaches one for the grid-point system. In other words, any-part SARs inevitably become flatter and grid-point SARs steeper towards very small plot sizes. Species richness, on the other hand, asymptotically approaches a straight line with $S = S_0$, where S_0 is a positive value for the any-part system and 0 for the grid-point system. Contrary to the assumption of Williamson (2003), the approached positive value in the any-part system is not necessarily 1 but equals the number of overlapping species averaged across all points of the plot (Dengler 2003). Many researchers seem to be unaware of this artifact. In one case, authors even developed a complicated new model for a "species-area relationship" to fit their grid-point data with increasing steepness to the left (Plotkin et al. 2000).

So, when do differences between the two systems really matter and which of these approaches is preferable? As indicated, the relative and even the absolute differences in species richness increase towards smaller areas. However, “small” is to be seen relative to the size of the studied organisms as the following examples illustrate. For the grid-point system, Plotkin et al. (2000), who considered only trees, found significant deviations from a regular power-law SAR up to plot sizes of 1 ha (10,000 m^2), whereas Löbel et al. (2004) found a steepening of the SAR only below 0.1 m^2 in dry grasslands, when including also bryophytes and lichens. For the any-part system, the deviations are generally milder (Williamson 2003), and Dengler et al. (2004) found a slight flattening of the curves in dry grasslands (also with consideration of non-vascular plants) only below 0.0001 m^2. Thus, the any-part system is the preferable one, even more so because it avoids terminological problems with rootless plants and the definition of “individuals” in clonal species.

Plot Shape

While several studies consider the effect of area shape on species richness at larger spatial scales, for example in view of reserve design (e.g. Kunin 1997; Hill and Curran 2003; Williams et al. 2005), less is known about how shape affects species richness on smaller spatial scales. From a theoretical point of view it is clear that species richness for a given plot size on average should increase with decreasing compactness of the plot, i.e., an elongated plot should contain more species than a square or circular one (Harte et al. 1999; Dengler 2003). This effect generally can be attributed to the “distance decay” of environmental conditions (e.g. Williamson 1988; Bell et al. 1993; Stohlgren 1995) and increased vicinism (e.g. Zonneveld 1995; Heegaard et al. 2007) due to relatively longer borders of elongated plots. While these two factors hold for both sampling systems described in the previous section, there is an additional effect of sampling strategy for the any-part system. As Dengler (2003) has shown it would be possible in the any-part system to capture all plant species of the Earth in one single plot of 10 m^2 if this were extremely long and thin and spirally twisted around the globe.

However, what are the real effects of practically applied shapes? Stohlgren (2007: 51) found that species density (for terminology, see Table 1) was significantly increased by 40% in 4:1 rectangular plots of 1 m^2 compared to squares of the same size. Bossuyt and Hermy (2004) reported that richness for 4:1 rectangles was increased in relation to squares by 1.4% (P=0.009) for 0.25 m^2 and by 1.6% (n.s.) for 1 m^2. For 16 m^2, Kunin (1997) found a statistically insignificant increase of species richness by 5.5% in 16:1 line plots compared to both square and 4:1 rectangular plots, whereas the latter two did not differ. Keeley and Fotheringham (2005) did not find significant species richness differences of 4:1 rectangles compared to squares (1 m^2 and 100 m^2). In contrast, Stohlgren et al. (1995) reported pronounced and significant richness increases from squares to 4:1 or 2.5:1 rectangles of 1 m^2 and 100 m^2 size, respectively, but this result is confounded because they studied cumulative richness values of 10 plots each and varied not only the shape but also the spatial aggregation of the plots between the variants (compare Keeley and Fotheringham 2005). A conclusion that can be drawn both from the theoretical considerations and the few available empirical studies is that an elongated plot shape leads to higher species richness but that for plots with a width/length ratio of less than 5:1 the differences normally will be low enough not to confound results unless one searches for very small effects on diversity. For future studies, however, even such minor distorting effects should be avoided by using identical plot shapes at all spatial scales. I suggest the use of squares as standard shape because (apart from circles, which are rather impractical in most situations) they are the most compact form and thus on average comprise the least environmental heterogeneity, and because any elongated shape would necessitate replicated measurements with the rectangles orientated in different directions. Additionally, squares also in the past were the most frequently used shape and thus provide optimal comparability. In this respect, both the original Whittaker plot (Shmida 1984) and the modified Whittaker plot (Stohlgren et al. 1995) are less appropriate because they use different length/width ratios at different spatial scales. Likely the best sampling schemes are those that use squares throughout (e.g. Dolnik 2003; Dengler et al. 2004) or nearly so such as the North Carolina Vegetation Survey (NCVS; Peet et al. 1998: squares from 0.01 to 100 m^2 and elongated plots only for 1,000 m^2).

Contiguous *vs.* Incontiguous Plots

Frequently, cumulative species-richness values of several incontiguous subplots were treated as equivalent to those of contiguous plots of the same size (e.g. Stohlgren et al. 1995; Öster et al. 2007; for terminology, see Table **1**). However, both cases are not at all interchangeable, and area is a biologically meaningful measure only when it is contiguous (Dengler, in press) because biological processes such as dispersal or lateral growth mainly or exclusively affect adjacent and not distant areas, randomly chosen by the researcher. It is an established fact in ecology that incontiguous plots normally will host more species than contiguous plots of the same size and that the difference will increase with increased distance between the cumulated subplots (e.g. Keeley and Fotheringham 2005; Christensen 2007; Hui 2008; see also the section on plot arrangement below). If the spatial arrangement of the cumulated subplots is fixed, the resulting richness value still is biologically meaningless but at least allows for statistically valid comparison between different sites. If the spatial arrangement of the subplots (i.e., their dispersion) differs, no statistical inference can be validly drawn, and any reported effects will be mainly artifacts of an inadequate sampling scheme. For example, the reported richness increases in elongated *vs*. square plots of Stohlgren et al. (1995) can at least mainly be attributed to the fact that the elongated subplots were at the same time further apart from each other than the square plots (Keeley and Fotheringham 2005). The finding of Öster et al. (2007) that their "species density" at 10 m^2 was highly positively correlated with both size of the total grassland patch and the number of vegetation types on these patches is trivial as their count for 10 m^2 actually consisted of the summation of ten 1-m^2 plots that were randomly placed within the grassland patches (i.e., with greater distances between in the larger patches). Many additional similar misinterpretations from the recent literature could be added. I urge researchers to be aware of the effect of contiguous vs. incontiguous plots in biodiversity research, and to restrict the term "species density" exclusively to species-richness counts from contiguous plots of a certain size.

Species-Area Curves *vs.* Species-sampling Curves

The long-standing debate on the adequate typology of species-area relationships vs. species-sampling curves (Gotelli and Colwell 2001; Connor and McCoy 2001; Scheiner 2003, 2004; Gray et al. 2004a,b; Christensen 2007; for terminology, see Table **1**) firstly seems to be a solely semantic problem. Because, however, this controversy involves various wide-spread misconceptions, which in turn lead to inappropriate sampling designs or false interpretations of obtained results, I have recently proposed a new typology that aims at resolving the different standpoints and to draw terminological distinctions where there are major biological and/or statistical differences (Dengler, in press). Because that paper reviews and discusses this topic in detail, I provide only a short outline of the major aspects here: According to Dengler (in press) the two fundamental types of curves are species-area relationships (SARs) and species-sampling curves (SSCs). SARs in this sense are exclusively constructed from points, each of which refers to a contiguous area (which may, however, contain interspersed parts of "unsuitable" habitat; see Table **1**). There are strong theoretical arguments that such SARs can never reach an asymptote (e.g. Williamson et al. 2001, 2002; Dengler 2003, in press), and the vast body of empirical data is consistent with this claim. SSCs, by contrast, aim to estimate the total richness of a single area by analyzing repeated subsamples, when a direct recording of this value is not feasible. The subsamples can be of different type, namely individuals and plotless samples (e.g. animals collected with any type of trap), but also subplots with defined area (Gotelli and Colwell 2001; Ugland et al. 2003; Gray et al. 2004a; Dengler, in press). Much of the dispute and confusion seems to be because SSCs derived from subsamples of defined area nevertheless are not true SARs (Gotelli and Colwell 2001; Hui 2008; Dengler, in press). This distinction is important as such "pseudo-SACs" (i.e., SSCs with plots as samples = types IIB and IIIB of Scheiner's 2003 "species-area curves") have completely different mathematical properties from real SARs (Dengler, in press, compare also Christensen 2007). SSCs are usually analyzed in the form of so-called rarefaction curves, which are generated from the original accumulation curves by randomized resampling to get a smooth and "averaged" curve (Gotelli and Colwell 2001). The resampling can be done with or without replacement, the former including the possibility that the same sample is "drawn" more than once. In the first case the curve must approach the total richness value of the analyzed statistical population (e.g. a certain larger area) asymptotically (e.g. Christensen 2007). In the second case (without replacement) the situation is slightly different because the curve actually will reach the maximum value with an angle >0° (Christensen 2007). In practice, this difference is irrelevant because it is marginal and because it only affects the right-hand end of the curve, whereas on the left-hand end the two types of curves are practically indistinguishable (and only left-end data are normally used to fit rarefaction curves as rarefaction would be superfluous if data on the right-hand end were available!). Thus, irrespective of whether the resampling is done with or without replacement, such curves must always (closely) follow a saturation function (i.e., a function that asymptotically approaches an upper limit of S; precisely which type of saturation function is irrelevant here, but see Christensen 2007 for detailed discussion). It is important to be aware that it is not a consequence of the underlying biodiversity data, but only of the resampling procedure (thus an artifact) that rarefaction curves are always saturation functions.

One problem in biodiversity literature is that evidently many researchers are not aware of these fundamental differences between real SARs and area-based SSCs and thus frequently attribute findings for the latter function type to properties of the first. For example, Inouye (1998) and Stiles and Scheiner (2007) analyzed area-based SSCs and logically found saturation functions to fit their data best but then argued that species-area relationships have an upper asymptote. Sometimes, even plotless sampling schemes, such as the bird sighting data of Flather (1996; correctly named accumulation curves therein) are interpreted as SARs by subsequent authors (Tjørve 2003).

Plot Replication, Arrangement, and Size Distribution

As regards the arrangement of plots for creating small-scale SARs, two fundamentally different approaches are available, nested-plot and random (or at least non-nested) placement (Barkman 1989; Connor and McCoy 2001; Stohlgren 2007). The first approach is much more widely used because it is more practical and time-efficient but several authors claim that only non-nested placement allows for statistical treatment such as regression analysis. They argue that with nested plots, when each smaller plot is contained in the next-larger plot, the richness values of the different plot sizes were not independent (Barkman 1989; Connor and McCoy 2001; Stohlgren 2007). I see this common argument as a misunderstanding: First, even with non-nested placement, plots are still not independent of one another because they are located in the same area and thus share similar environmental features and the same species pool (compare Ricotta 2007; Wilson 2007). Thus, what matters is not a general independence but only a statistical independence, meaning that the dependent variable (i.e., species richness) can vary at one plot size irrespective of the values at another plot size. This is obviously not realized in the case of nested-plots because species richness of the larger plot cannot possibly be smaller than the one of the contained smaller plot. But is this a problem? I think it is not. Actually, curve fitting as well as the estimation of model parameters and goodness-of-fit metrics are unaffected by violation of this *a priori* assumption of a regression (Quinn and Keough 2002; Adler et al. 2005). Only the standard errors of the parameter estimates become unreliable and thus hypothesis testing is impossible (Quinn and Keough 2002; Adler et al. 2005). Randomly sampled plots allow a test of the null hypothesis that there is no change of species richness with increasing plot size. This, however, is of little interest because most researchers accept the overwhelming theoretical arguments and empirical evidence in favour of increasing species richness with increasing plot size. Thus, we normally do not ask whether there is an increase but which function describes the relationship best and which are the function parameters in the specific case (see Dengler, in press). And these questions can be addressed satisfactorally with nested-plot data, too. Actually, nested-plots even from a statistical point of view may be considered preferable to non-nestedly placed plots: It is usual practice in sampling protocols for statistical analyses to vary only the factor of interest and control for all other factors. Thus, if we wish to analyze the shape of the relationship between area and species richness we should only vary area but keep environmental conditions as similar as possible. Obviously, this aim can best be achieved by a nested-plot design.

Within the framework of nested plots, there are still different possible layouts. Most often, textbooks and seminal texts offer the least appropriate solution (Mueller-Dombois and Ellenberg 1974; Dolnik 2003; Scheiner 2003; Stohlgren 2007: 96), that is: start with one square and enlarge it subsequently into one direction. With such a design the environmental conditions in the smallest plots will rarely ever correspond to the average values in the largest plot. If only one replicate is possible for each plot size, a more reasonable approach would be to enlarge the plots subsequently in the direction of all four corners of the first plot because such a spiral arrangement will place the smallest plot approximately in the centre of the largest. Even then the smaller plots cannot represent the whole environmental variability of the larger one. Contrary to the claim of Dolnik and Breuner (2008, this issue), it is thus advisable to sample all areas besides the largest using several subplots equally spread within the main plot. The designs of Peet et al. (1998) and Dengler et al. (2004) aim at meeting these requirements. A second argument in favor of sampling a higher number of subsamples of smaller areas is that the coefficient of variation of the species richness increases with decreasing plot size (Barkman 1989; Dengler 2006). If mean species densities per plot size are calculated, the derived curve in this case actually represents the relationship of species richness to area, liberated from both stochasticity and environmental heterogeneity. Use of average richness values has two additional advantages. (1) While richness counts do not follow a normal but a Poisson distribution and thus violate the assumptions of usual regression analyses, averaging always leads to normally distributed data (central limit theorem; Quinn and Keough 2002). (2) Averaging a sufficient number of counts avoids plot sizes with zero species, which need to be included in the analysis (Williams 1996) but would pose serious problems for regression analysis in log S-space because log(0) is not defined. The addition of a constant has been proposed to circumvent the problem of undefined logarithms (Quinn and Keough 2002), it is, however, highly controversial whether such a step is justified (Wilson 2007).

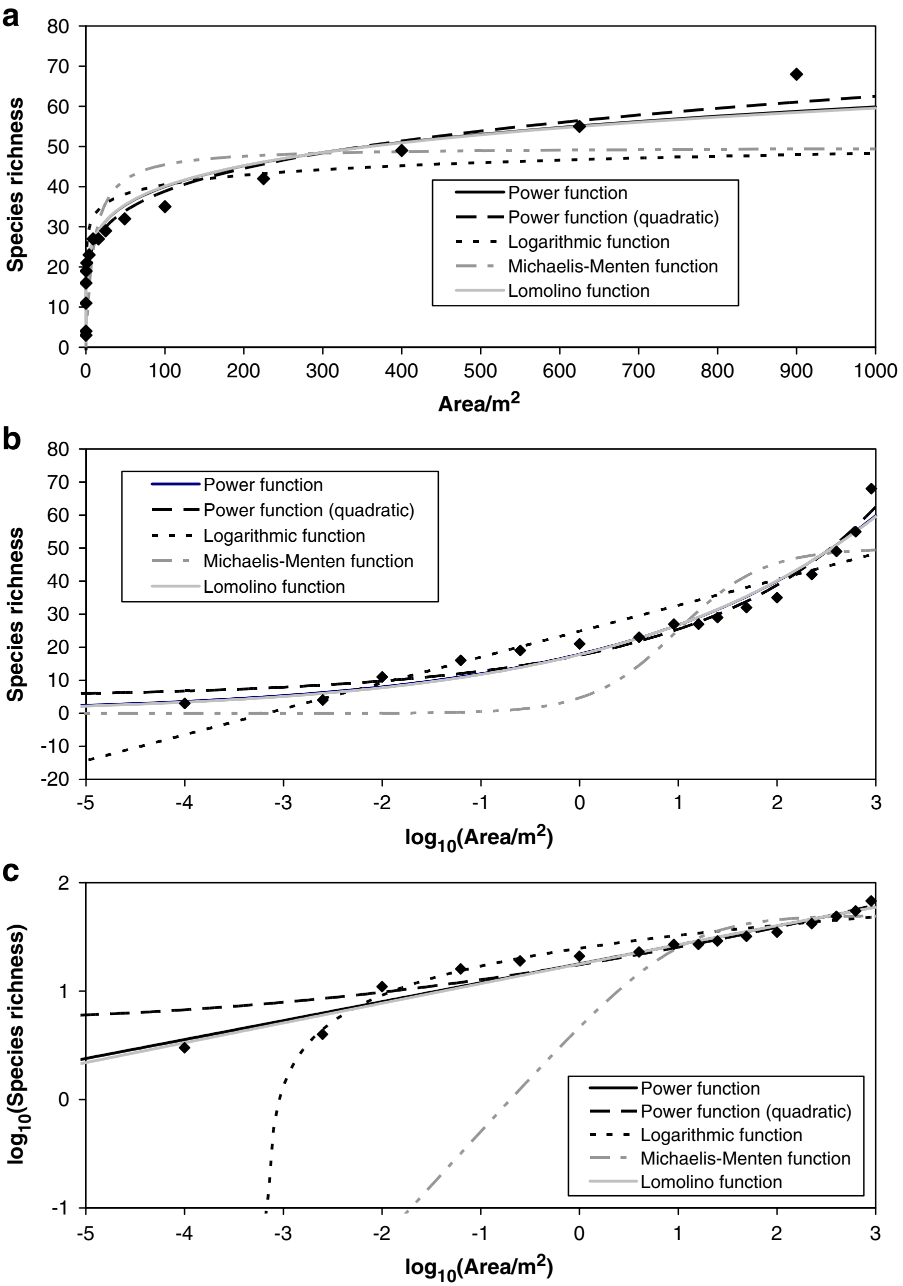
One final aspect should be addressed here: the analyzed plot sizes. First, if the aim of the study is to discern between different possible species-area functions, a wide range of spatial scales is indispensable because for narrower ranges the possible models become nearly indistinguishable (cf. McGill 2003). Analyses of hundreds of SARs of different types (Dengler, in press) as well as the simulations of McGill (2003) suggest that one should preferably cover five orders of magnitude or more. Second, one should pay attention to an equal spacing of the analyzed areas on the log scale, i.e., they should form a geometric series. Usual approaches are tenfold (e.g. Peet et al. 1998, Dengler et al. 2004) and fourfold increments (e.g. Chiarucci et al. 2006) between subsequent plot sizes. Less appropriate are varying factors between subsequent sizes as applied for example by Kilburn (1966) or Dolnik (2003: Fig. 1) because here different parts of the curve receive different weight in the regression analysis in an unintended manner.

Fitting Procedures and Goodness-Of-Fit Metrics

As I recently reviewed and discussed these topics in detail (including an overview of possible function types for SARs; Dengler, in press), only major aspects shall be outlined here. *i*) R^2 and other goodness-of-fit metrics cannot be compared between

Fig. 1 Curve shapes of five different models for species-area relationships (for details of the models, see Table **2**) in linear (**a**), semi-logarithmic (**b**), and double-logarithmic (**c**) representations. The curves shown are models fitted with non-linear regression in *S*-space to the empirical data represented by the black squares. The empirical data are plant species-richness values (non-vascular and non-terricolous taxa included) of a stand of the *Helichryso-Jasionetum* (sandy dry grassland) on the Curonian Spit on the Baltic coast of Russia (plot Nr. 70, unpublished original data of Dolnik 2003). Note that power function and Lomolino function are practically indistinguishable in the upper two graphs and that the logarithmic model predicts negative richness values for areas below 7 cm^2 and thus log(*S*) is not defined there. According to AICc (*S*), in this example the quadratic power function is the best model, followed by the regular power function (ΔAICc=0.43), the Lomolino function (ΔAICc=4.67), the logarithmic function (ΔAICc=21.24), and the Michaelis-Menten function (ΔAICc=33.01) ▶

the *S*-scale and the log *S*-scale. Although this caution has frequently been given in the SAR literature (e.g. Loehle 1990; Gitay et al. 1991; Cresswell and Vidal-Martinez 1995; Fattorini 2007), papers are still published that ignore this point (e.g. Sagar et al. 2003; Keeley and Fotheringham 2005; Chong and Stohlgren 2007). *ii*) Similarly, the parameter estimates (e.g. *c* and *z* in the case of the power function) differ depending on whether the curve has been fitted in *S*- or in log *S*-space (Loehle 1990; Dengler, in press). *iii*) When comparing models with different numbers of parameters, it is necessary to use a goodness-of-fit-measure that adequately penalizes for the extra parameters (Quinn and Keough 2002), with Akaike's Information Criterion (corrected for small *n*; AICc) being one of the most appropriate measures (Burnham and Anderson 2002; Johnson and Omland 2004; Dengler, in press). *iv*) In considering different *S*-spaces, there is – in contrast to the claims of Cresswell and Vidal-Martinez (1995) – no biological or statistical preference for either *S* or log *S* (Williamson 1988; Quinn and Keough 2002; Dengler, in press). Additionally, both the curve fitting and the goodness-of-fit evaluation can be done in both spaces, and the same goodness-of-fit measures for the two spaces provide valuable complementary information (Dengler, in press). *v*) Extrapolation beyond the largest plot size is a prominent application of SARs but goodness-of-fit within the fitted range of areas does not necessarily coincide with good extrapolation capability (Dengler, in press). Accordingly, I introduced the log error of extrapolation (LEE) as a third informative quality parameter besides AICc (*S*) and AICc (log *S*) (see Dengler, in press), thus applying a formalized expression to the ideas of Dolnik (2003) and Sagar et al. (2003). *vi*) Regressions in SAR analyses should not be forced through the origin or any other point. While "forced" regressions are questionable even when there are strong theoretical arguments to assume a specific value of the dependent variable for a certain value of the predictor variable (Quinn and Keough 2002), they become nonsense in cases in which such a theoretical justification is missing. While it is clear with the grid-point system that there are zero species on 0 m^2, this is not the case for the preferred any-part system (see section on this topic). There is even less reason to assume *a priori* a certain richness value for a positive area as did Désilets and Houle (2005), who argue that "by forcing the regressions through the origin (of the log-log representation), we made the reasonable assumption that there would be only one species per 1-m^2 plot" (the smallest analyzed plot in this study was 6.25 m^2). Most biodiversity researchers will agree that this assumption lacks any empirical support as in most plant communities much more than one species are found on 1 m^2 (e.g. Dolnik 2003; Fridley et al. 2005), in few communities perhaps less, but certainly not the same number of species in all



vegetation types of a broad range of environmental conditions as covered in that study. Forcing all their regressions through the origin renders the published results of Désilets and Houle (2005) artifictional despite their otherwise innovative approach. The extremely high *z* values (0.7–0.8) reported in this article, give an additional indication that there was something wrong with the analyses, because these values lie far out of the usual ranges for continuous vegetation (0.1–0.5; e.g. Crawley and Harral 2001; Dolnik 2003; Fridley et al. 2005).

How Methodological Artifacts Affect the Shape of Species-Area Relationships

All the numerous methodological issues outlined in the previous review sections evidently will influence the perceived shape of species-area relationships. In the following, I discuss how certain artifacts actually alter the curve shape and how this may bias the model selection when different function types are compared. To enable the reader to follow the arguments more easily, I visualize the shape characteristics of five prominent SAR models in Fig. **1**. I selected these five types because they are most frequently reported to give the best fit and/or they represent a whole class of curves having similar behaviour (Table **2**; compare Dengler, in press).

Species-Sampling Curves

Based on a study of Sonoran Desert plant communities, Stiles and Scheiner (2007) recently claimed that "not all species-area curves are power functions". Actually, when fitting 12 different models to their "species-area data" of 25 habitat islands, power and logarithmic function fitted best only in one case each, while saturation functions such as the logistic, Hill, and Lomolino function proved to be most appropriate for the remaining 23 datasets. However, the sampling design was type IIIB of Scheiner (2003), thus actually a species accumulation curve despite the fact that sampling was done on plots with a certain area. Therefore, saturation functions are exactly as expected (see review section above). A similar artifact obviously underlies the difference Stohlgren et al. (1995) reported for the "species-area curves" recorded with their modified Whittaker plots compared to the traditional Whittaker plot design. While their SAR for traditional Whittaker plots seemingly corresponded well to a power law (they only calculated regressions for the logarithmic function but

Table 2 Five models typically used to fit species-area relationships, varying in general shape (see also Fig. **1**) and number of fitted parameters (for more details, see Dengler, in press)

Curve Name	Model	General shape	Number of parameters	Upper asymptote
Power (regular)	$S = b_0\, A^{\,b_1}$	Unbound, convex	2	no
Power (quadratic)	$S = 10\verb|^|\left(b_0 + b_1 \log A + b_2 (\log A)^2\right)$	u-shaped (b_2>0) or inverse u-shaped (b_2<0)	3	no
Logarithmic	$S = b_0 + b_1 \log A$	Unbound, convex	2	no
Michaelis-Menten	$S = b_0 A/(b_1 + A)$	Saturation, convex	2	yes (b_1/b_2)
Lomolino	$S = b_0 \Big/ \left(1 + \left(b_1^{\log(b_2/A)}\right)\right)$	Saturation, sigmoid	3	yes (b_0)

S − species richness; A − area; b_i − fitted parameter, log − logarithm of a certain base (normally $\log_{10}$ is used). Note that for the u-shaped or inverse u-shaped quadratic power functions the point beyond which richness would decrease with increasing area normally lies far outside the fitted range of areas.

their graph shows the typical pattern of observed *vs*. predicted values that occurs when a power-law relationship is fitted with a logarithmic law, compare Fig. **1b**), their data for the modified Whittaker plot closely follow a logarithmic function. As already pointed out by Keeley and Fotheringham (2005), the plotted values of the two smallest plot sizes (1 m^2 and 10 m^2) are not for contiguous plots but sums for ten or two widely dispersed subplots of the respective size, which is a situation similar to SSCs (the second flaw here is that the correct area is not 1 m^2 and 10 m^2 as given in the graph of Stohlgren et al. 1995 but 10 m^2 and 20 m^2).

Grid-Point vs. *Any-Part System*

That these two sampling schemes can have major influence on the shape of species-area relationships became evident when I compared the results of two of my diploma students, Swantje Löbel and Steffen Boch. Both studied SARs of dry grassland communities in the hemiboreal zone on the islands of Öland (Sweden) and Saaremaa (Estonia), respectively. Although the geology, land-use history and vegetation types are very similar, they found consistently different shapes in their SACs. Throughout the range of different community types, on Öland a quadratic power function with a significant negative quadratic term gave the best fit (see Löbel et al. 2004), whereas on Saaremaa we found near-perfect (regular) power functions throughout (Dengler and Boch 2008). What was the reason for this striking difference? It turned out that the data on Öland had been sampled with the grid-point system and those on Saaremaa with the any-part system. Actually, the quadratic power function (with $b_2 < 0$) is suitable to approximate the left-hand steepening of grid-point SAR data (note that in Fig. **1** the parameter b_2 of the quadratic power function is positive and thus the curve becomes flatter towards smaller plot sizes). Towards smaller plot sizes, the shape of quadratic power functions is very similar to that of the Plotkin variant of the power function (Dengler, in press), a function type that has been specifically designed to model the artifacts of grid-point SAR data by Plotkin et al. (2000) though the authors believed that they would describe the fundamental shape of SARs. In their analysis of nearly 1,500 SARs from the United States, Fridley et al. (2005: Figure 2A) also found that the curve in the double-logarithmic representation had a slight but consistent downward curvature, exactly what is to be expected when the grid-point system is used as they did. It can be safely assumed that they would have found even better fits of the regular power function and higher scale-invariance of z if they had used the any-part system instead. When Dolnik (2003: 77) reported a better fit of the logarithmic function compared to the power function for a considerable part of the analyzed plant communities, this similarly can at least partly be attributed to artifacts of the rooted-presence system (similar to the grid-point system) he used for areas below 1 m^2 (there are also other confounding aspects in this study, see below). Similar to the quadratic and Plotkin variants of the power function, the logarithmic function exhibits a pronounced steepening towards small areas (see Fig. **1c**) and thus is likely to fit grid-point or rooted-presence data on small scales better than the regular power function. Whether the grid-point system is also causal for the mostly better fit of the quadratic vs. the regular power function reported by Chiarucci et al. (2006) remains unclear because these authors do not specify their sampling procedure in this respect.

Single-Value vs. *Average-Value Curves*

As argued in the review section of this paper, SARs constructed from one single richness value per area size are considerably influenced by stochasticity, which should frequently lead to erroneous selection of a function as the best model. So far, however, only few empirical data sets are available to assess the practical importance of such effects. Dengler (in press) found that using mean values instead of individual richness counts, favoured the power model in several of those communities, for which Dolnik (2003) reported a better fit of the logarithmic model. In a comprehensive study of SARs in European dry grasslands (Dengler, Boch, Chytrý, Dolnik, Löbel, Jeschke, Kiehl and Otýpková, in prep.), we found that the regular and quadratic power functions were the best of five compared models (the same as in Table **2**) in most cases. Of the 18%–24% of SARs for which one of the other three models was rated best according to the three criteria AICc (S), AICc (log S), and LEE (see review section above) the vast majority were recorded with single values per plot size. Thus, finding non-power functions in small-scale SARs is closely associated with non-averaged richness-values (Dengler, Boch, Chytrý, Dolnik, Löbel, Jeschke, Kiehl and Otýpková, in prep.). I know of only one study that compares the effect of single-value vs. average-value on the same plots (Dengler and Boch 2008). These authors showed that the performance of the logarithmic function improves relative to the power function when single values are used instead of average values, although in this study the power function remained superior also in nearly all single-value curves.

Non-Nested Plots vs. *Nested Plots*

In the only analysis of this aspect known to me, Dengler and Boch (2008) showed a slightly but significantly better performance of the logarithmic function and Michaelis-Menten function (a convex saturation function) relative to the power function when non-nested sampling was used. However, the regular power function was by far the most appropriate model in both sampling designs, indicating that non-nested sampling probably is not a major cause for reported superior fits of the logarithmic model.

Other Aspects

For most of the other artifacts and artifictions outlined in the review section (different plot shapes, comparison of goodness-of-fit measures calculated in different S-spaces, unequal spacing of analysed plot sizes along the log A axis, insufficient range of analysed plot sizes), it is presently unclear how strong their effects will be with real data and whether they only increase stochasticity – and thus occasionally lead to selection of the wrong model from time to time – or whether they bias the model selection in a certain direction by giving bias to specific function types. As regards failure to penalize for additional parameters, it is well known that this will artifictionally favour the more complex models (Burnham and Anderson 2002; Quinn and Keough 2002). I do not know of an example from small-scale SARs, but the reported better fits of power or logarithmic functions with an additional breakpoint parameter T_1 for island data compared to the respective “pure” function (Lomolino and Weiser 2001) probably are largely caused by the missing penalization.

Conclusions and Outlook

In SAR studies that compare different potential models, the power function most frequently, but not always, turns out to be the most suitable function for practically any taxon and any scale (e.g. Connor and McCoy 1979; Rosenzweig 1995; Fridley et al. 2005). Still there are frequent arguments that for theoretical reasons models other than the power function should be more adequate. For example, many authors claim that SARs should reach an asymptote (e.g. Connor and McCoy 1979; Williams 1995; He and Legendre 1996; Lomolino 2000, 2001; Tjørve 2003) while others reject this idea as unjustified (Williamson et al. 2001, 2002; Dengler, in press). Others argue that a so-called small-island effect (Lomolino 2000, 2001; Lomolino and Weiser 2001) or a lack of self-similarity on small scales (Plotkin et al. 2000) should cause deviations from the power law towards the left-hand end of the curve. Moreover, it is not seldom assumed in the biodiversity literature that the logarithmic function better describes the real relationship between area and species richness particularly on small scales in continuous ecosystems (Stohlgren et al. 1995; He and Legendre 1996; van der Maarel 1997). This claim goes back to Gleason (1922) and Williams (1943) but these authors only provided weak theoretical arguments and few empirical data. Thus it is surprising that these authors could influence subsequent generations of ecologists so lastingly, all the more so as the vast body of empirical data for small-scale SARs in continuous ecosystems also predominantly favours the power model (e.g. Crawley and Harral 2001; Fridley et al. 2005; Dengler, in press; see also Hopkins 1955, who fitted logarithmic functions throughout but whose empirical curves deviated from the logarithmic function in a way similar to the data in Fig. **1b** and thus obviously conform to the power model much better).

It can be concluded that contrary to frequently published claims, empirical evidence for a better fit of other models than the regular power function in specific cases is relatively rare. Non-power functions as best-fitting models become even more rare when all those cases in which other functions performed better only due to those artifacts and artifictions discussed above are subtracted. The uncovered examples are probably only the tip of the iceberg. When Rejmánek and Rosén (1992) reported that they found the logarithmic function rather than the power function to better fit their data of dry grasslands with shrub encroachment, I have the impression that this is due to sampling with the grid-point approach because I myself never found logarithmic functions in similar communities. However, I cannot explore this further because the authors have not documented their methods sufficiently.

Thus, we can conclude that power-function SARs are even more common than a review of the present literature would suggest but I do not argue that all SARs across all spatial scales from square millimetres to the surface of the Earth can be represented adequately by power functions with constant z value. Although the slope of power function (z) is often astonishingly constant within a wide range of plot sizes (e.g. across six orders of magnitude in the examples treated in Dengler and Boch

2008), there are also clear indications of scale-dependency of z in many situations (e.g. Rosenzweig 1995; Crawley and Harral 2001; Fridley et al. 2005; Allers and Dengler 2007). My suggestion for a universal treatment of SARs therefore is to use power functions throughout (preferably fitted in S, i.e. with non-linear regression) but to allow z to vary with scale (see also Dengler, in press). Such an approach would allow the treatment of all different kinds of SARs within the same framework and provide the easily interpretable and comparable parameters c and z (see e.g. the vast review by Drakare et al. 2006), while it would not presuppose that all SARs are actually power functions with fixed slope. Instead, we could statistically test if and where z changes significantly, and also any other function type can be described as a power function with variable z (see also Christensen 2007).

Let me finish this article with three proposals to authors, editors, and referees: *i*) be vigilant about the many pitfalls that are hidden along the course of species-area sampling and analysis and try to avoid them; *ii*) report your methodological approaches so comprehensively that others can assess whether your documented SARs are real patterns, artifacts, or artifictions; and *iii*) use a precise and meaningful terminology, in particular restrict “species-area relationship” and “species-area curve” to curves constructed of points each of which represents a contiguous area and “species density” to species richness counts for contiguous areas of a certain size.

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