Sampling-Design Effects on Properties of Species-Area Relationships – A Case Study from Estonian Dry Grassland Communities

Jürgen Dengler · Steffen Boch

Abstract Despite widespread use of species-area relationships (SARs), dispute remains over the most representative SAR model. Using data of small-scale SARs of Estonian dry grassland communities, we address three questions: (1) Which model describes these SARs best when known artifacts are excluded? (2) How do deviating sampling procedures (marginal instead of central position of the smaller plots in relation to the largest plot; single values instead of average values; randomly located subplots instead of nested subplots) influence the properties of the SARs? (3) Are those effects likely to bias the selection of the best model? Our general dataset consisted of 16 series of nested-plots (1 cm^2–100 m^2, any-part system), each of which comprised five series of subplots located in the four corners and the centre of the 100-m^2 plot. Data for the three pairs of compared sampling designs were generated from this dataset by subsampling. Five function types (power, quadratic power, logarithmic, Michaelis-Menten, Lomolino) were fitted with non-linear regression. In some of the communities, we found extremely high species densities (including bryophytes and lichens), namely up to eight species in 1 cm^2 and up to 140 species in 100 m^2, which appear to be the highest documented values on these scales. For SARs constructed from nested-plot average-value data, the regular power function generally was the best model, closely followed by the quadratic power function, while the logarithmic and Michaelis-Menten functions performed poorly throughout. However, the relative fit of the latter two models increased significantly relative to the respective best model when the single-value or random-sampling method was applied, however, the power function normally remained far superior.

J. Dengler (✉)
Plant Systematics, Biocentre Klein Flottbek, University of Hamburg,
Ohnhorststr. 18, D-22609 Hamburg, Germany
e-mail: dengler@botanik.uni-hamburg.de

S. Boch
Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland
e-mail: steffen.boch@ips.unibe.ch

These results confirm the hypothesis that both single-value and random-sampling approaches cause artifacts by increasing stochasticity in the data, which can lead to the selection of inappropriate models.

Keywords Artifact · Biodiversity · Estonia · Logarithmic function ·
Nested-plot design · Power function · Statistical analysis

Introduction

Species-area relationships (SARs) are widely used to describe the relationship of species richness (S) on area analyzed (A), to disentangle underlying mechanisms, to standardize richness values to a common spatial "grain", to extrapolate species richness values to areas larger than those analyzed, and to develop efficient conservation strategies (e.g. Williamson 1988; Rosenzweig 1995; Connor and McCoy 2001; Desmet and Cowling 2004; Fridley et al. 2005; Kier et al. 2005; Drakare et al. 2006; Dengler, in press). Despite the widespread application of SAR analyses, the best functional model for describing this relationship is still subject to robust debate. While some authors advocate that species-area relationships should follow a saturation function (He and Legendre 1996; Lomolino 2000; Tjørve 2003), others claim that real SARs never have an upper asymptote (e.g. Rosenzweig 1995; Williamson et al. 2001, 2002; Dengler 2003, in press). For small-scale (mm^2 – ha) SARs in continuous vegetation, the controversy focuses more on whether the logarithmic model (Gleason 1922; He and Legendre 1996; van der Maarel 1997) or the power model (Arrhenius 1920; Crawley and Harral 2001; Fridley et al. 2005; Dengler, in press) describe real patterns more closely.

In this Special Issue, Palmer et al. demonstrated how analytical artifacts in biodiversity research in general may lead to faulty conclusions. More specifically for sampling and analysis of species-area data, Dengler (2008, this issue) showed that many such "pitfalls" are also hidden along the course of analysis of species-area data but general awareness of these is widely lacking. As argued by Dengler (2008, this issue), several of these methodological artifacts should favour other SAR models such as logarithmic function, saturation functions, or modified versions of the power function over the regular power function. Thus, a considerable part of best fits reported for non-power functions in small-scale SACs (e.g. Rejmánek and Rosén 1992; Stohlgren et al. 1995; Dolnik 2003; Stiles and Scheiner 2007) may be caused rather by methodological inadequacies than by differences in the actual SARs. However, only a few studies have comparatively analyzed the effects of different methodological approaches on the perception of SARs, namely the any-part vs. the grid-point system and the use of square vs. rectangular plots (review in Dengler 2008).

For other aspects that according to Dengler (2008, this issue) theoretically should also cause artifacts, we know of no empirical studies that try to assess whether the predicted effect really occurs or how influential it is. In this study, we aim to address three of these open points. *i*) In a single-value nested design, plots that are enlarged in only one direction (e.g. Mueller-Dombois and Ellenberg 1974; Dolnik 2003; Scheiner 2003; Stohlgren 2007: 96), the smaller-sized plots should be less

representative for the area of the largest plot than subplots placed centrally (Dengler 2008, this issue). *ii*) While some authors construct SARs from nested-plot data with one count per area size (Mueller-Dombois and Ellenberg 1973; Dolnik 2003; Scheiner 2003; Dolnik and Breuer 2008), others argue that at least the smaller plots should be represented by several subplots, whose richness values are averaged (Barkman 1989; Peet et al. 1998; Dengler 2006, 2008, this issue). *iii*) There is a long-standing debate in SAR research whether nested-plot design or random (non-nested) placement of all subplots is more appropriate. For example, Barkman (1989), Connor and McCoy (2001), and Stohlgren (2007) favour the second solution because they see basic prerequisites of statistical analysis being violated in the first approach. According to Dengler (2008, this issue, see detailed discussion therein), this position, however, may be a misunderstanding, and nested-plot design could even be advantageous from a statistical point-of-view. In cases *i*)–*iii*), Dengler (2008, this issue) suggests that artifacts caused by what he identifies as less appropriate sampling strategies (i.e., smallest plot in the corner instead of the center of the largest plot, single-value instead of nested-value, random-plot design instead of nested-plot design) all act in the same direction. They should increase stochasticity and thus the chance of erroneous selection of SAR models.

In this study, we use small-scale species-richness data from dry grassland communities in Estonia to address the following questions:

- Which model describes the empirical SACs of these communities best when a methodology is applied that according to Dengler (2008, this issue) minimizes artifacts?
- How do deviating sampling procedures with respect to points *i*)–*iii*) influence the properties of the SARs?
- Do differences in the properties of SARs sampled with different approaches bias SAR model selection?

Material and Methods

Field Data

We collected 16 series of nested-plot species-richness data of visually homogeneous stands from the whole range of dry grassland types occurring on the island of Saaremaa (Estonia; hemiboreal zone, 21°45′–23°30′ E/57°50′–58°40′N). The analyzed stands belong to six associations from five phytosociological orders (see Table 1). Each series of nested plots was located in a different dry grassland area (see Table 1). We used a sampling design similar to that outlined in Dengler et al. (2004, but without plot sizes below 0.0001 m^2), i.e., square plots of 0.0001 m^2, 0.0009 m^2, 0.01 m^2, 0.09 m^2, 1 m^2, 9 m^2, and 100 m^2, with all sizes but the largest represented by five subsamples nested within the 100-m^2 plot. These five subseries of smaller plots were located in the four corners and in the center of the 100-m^2 plot. All macroscopically visible "plants" (including bryophytes, lichens, "algae", and also non-terricolous plants) were recorded with the any-part approach (see Dengler 2008, this issue).

Table 1 Overview of the 16 series of nested plots

Series Nr.	X coordinate	Y coordinate	Association	Order	(Sub-) Class
B10	553,264	6,481,823	*Caricetum arenariae**	*Corynephoretalia canescentis*	*Koelerio-Corynephorenea*
B13	553,994	6,457,198	*Sileno-Festucetum*	*Trifolio arvensis-Festucetalia ovinae*	*Koelerio-Corynephorenea*
B01	573,781	6,448,848	*Festucetum polesicae*	*Sedo acris-Festucetalia*	*Koelerio-Corynephorenea*
B02	574,556	6,450,459	*Festucetum polesicae*	*Sedo acris-Festucetalia*	*Koelerio-Corynephorenea*
B03	568,842	6,474,769	*Festucetum polesicae*	*Sedo acris-Festucetalia*	*Koelerio-Corynephorenea*
B06	563,894	6,475,496	*Festucetum polesicae*	*Sedo acris-Festucetalia*	*Koelerio-Corynephorenea*
B04	570,082	6,473,200	*Cladonio-Sedetum***	*Alysso alyssoidis-Sedetalia*	*Sedo-Scleranthenea*
B08	584,200	6,455,832	*Crepido-Allietum*	*Alysso alyssoidis-Sedetalia*	*Sedo-Scleranthenea*
B11	558,094	6,476,048	*Crepido-Allietum*	*Alysso alyssoidis-Sedetalia*	*Sedo-Scleranthenea*
B12	556,838	6,455,864	*Crepido-Allietum*	*Alysso alyssoidis-Sedetalia*	*Sedo-Scleranthenea*
B14	570,411	6,490,202	*Crepido-Allietum*	*Alysso alyssoidis-Sedetalia*	*Sedo-Scleranthenea*
B05	576,417	6,465,338	*Helictotrichon pratense* comm.	*Brachypodietalia pinnati*	*Festuco-Brometea*
B07	577,482	6,465,170	*Helictotrichon pratense* comm.	*Brachypodietalia pinnati*	*Festuco-Brometea*
B09	577,871	6,463,993	*Helictotrichon pratense* comm.***	*Brachypodietalia pinnati*	*Festuco-Brometea*
B15	612,570	6,467,809	*Helictotrichon pratense* comm.	*Brachypodietalia pinnati*	*Festuco-Brometea*
B16	607,534	6,480,890	*Helictotrichon pratense* comm.	*Brachypodietalia pinnati*	*Festuco-Brometea*

Coordinates of the central subplot according to UTM (WGS-84) and phytosociological assignment following Boch and Dengler (2006) are given. The full association names are *Caricetum arenariae* Christiansen 1927, *Sileno otitae-Festucetum brevipilae* Libbert 1933 corr. Kratzert and Dengler 1999 nom. invers. propos., *Festucetum polesicae* Regel 1928, *Cladonio symphicarpiae-Sedetum albi* Tx. 1951 nom. invers. propos., *Crepido pumilae-Allietum alvarensis* Krahulec et al. ex Dengler and Löbel 2006. The fact that in three series the five subplots were subdivided between two associations in the classification of Boch and Dengler (2006) does not mean that these plots are less homogeneous than the others.

*) Two of the five subplots were assigned to the *Helichryso arenarii-Jansionetum litoralis* Libbert 1940
**) One of the five subplots was assigned to the *Helictotrichon pratense-[Brachypodietalia pinnati]* community
***) Two of the five subplots were assigned to the *Helianthemo oelandici-Galietum oelandici* Krahulec et al. ex Dengler and Löbel 2006

Data Analyses

For the comparison of different SAR functions, we selected five of the 23 SAR models described in Dengler (in press). With this choice we aimed to include those models that normally result in best fits and to represent models with fundamentally different shapes and different numbers of fitted parameters (Table 2, for a visualisation of the shapes of these functions, see Dengler 2008, this issue: Fig. 1). All functions were fitted both in S-space and in log S-space (in this article, we use $\log_{10}$ throughout), resulting in 10 models to be compared. Model fitting was done with the non-linear regression module of STATISTICA 7.1 (StatSoft, Inc. 2005; settings: least squares; method of estimation: quasi-Newton; criterion of convergence: 0.0001). We used $b_0=5$, $b_1=0.1$, and $b_2=0.1$ as starting points and 0.1 as step-width throughout unless the iterations did not converge or got caught in a local optimum (indicated by unreasonably low R^2 values below 0.4). In the latter cases,

Table 2 The five function types used to model the species-area relationships in this study and their characteristics (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)	$S = 10 \wedge (b_0 + b_1 \log A + b_2 (\log A)^2)$	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_0)
Lomolino	$S = b_0 \left/ \left(1 + \left(b_1^{\log(b_2/A)}\right)\right)\right.$	Saturation, sigmoid	3	yes (b_0)

S − species richness; A − area; b_i − fitted parameter, log − logarithm of a certain base (here $\log_{10}$ is used). In the case of the power function, b_0 and b_1 are often termed c and z. 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

* The logarithmic function is often erroneously termed "exponential function".

the starting values were altered using previously established parameter values from similar situations, which always led to stable results with satisfactory fit (indicating that the global optimum was found). As goodness-of-fit metrics, we basically applied AICc (Akaike's Information Criterion corrected for small n) calculated for both S-spaces, and log error of extrapolation (LEE; Dengler, in press). These three measures contain valuable complementary information and thus should be used jointly for quality assessment (Dengler, in press). While the two AICc measures assess the goodness-of-fit within the fitted range of A (AICc [S] with additive error terms and AICc [log S] with multiplicative error terms), LEE provides a quantification of the extrapolation capability beyond the largest plot size (which does not necessarily coincide with fitting quality; Dengler; in press). LEE is simply the difference (on $\log_{10}$ scale) between the richness value predicted for the largest plot when fitting the same model to all data apart from the largest plot and the actual richness value of this plot.

These calculations were first done for the mean richness values of the 16 series of nested plots (i.e., each value except the one for 100 m² represented the arithmetic mean of the species densities in five subplots of equal size). Second, the same analyses were applied to single-value nested-plot data, namely to the central subplot series and to two marginal subplot series (located at opposite corners). Finally, for comparison between nested-plot and random-plot SARs for each of the 16 series of nested plots, two subseries with nested-plot design and two with random-plot design were generated from the whole data set. In this case, the 100-m² plots were excluded from the calculation because no replicate measures were available for this plot size within the 16 series. Both in the nested-plot and in the random-plot cases, arithmetic means of two species-richness counts were used. In the nested-plot case, these were simply the two combinations of the series in opposite corners of the 100-m² plot. In the random-plot case, random data were gained by "bootstrapping" (compare Quinn and Keough 2002), i.e., resampling the available five values of each size. Contrary to claims of some authors (Connor and McCoy 2001; Stohlgren 2007) fully randomized sampling for statistical (not physical!) independence includes the possibility of sampling overlapping areas or even sampling the same area twice.

Thus, the two series of pairs of subplots were drawn using random numbers and the sampled subplots were returned to the sampling pool for each subsequent iteration. Consequently, the SACs of the random-plot data are not necessarily non-decreasing. LEE for nested plot *vs.* random plot (as for the two other comparisons) was calculated as the extrapolation capability of the model for the range 0.0001–9 m^2 to the actual richness value of 100 m^2.

A comparison of parameter estimates for the average-value nested-plot SARs between *S*- and log *S*-space or against zero were calculated with the appropriate *t*-tests in STATISTICA 7.1 (StatSoft, Inc. 2005). For comparison of different sampling designs with (partly) more than one replicate per nested-plot series, two-factorial analyses of variance (ANOVAs) were applied with STATISTICA 7.1 (StatSoft, Inc. 2005). Here, sampling design was treated as one factor (d.f.=1) and the identity of the nested-plot series as another factor (d.f.=31), with potential interactions accounting for further 31 d.f. Only the results for sampling design are shown as only these are relevant to our questions.

Results

General Characterization of the SARs

Species richness on the studied plot sizes differed considerably between vegetation types (Table 3). The maximum values (eight species on 1 cm^2; 24 species on 1 dm^2; 52 species on 1 m^2, and 140 species on 100 m^2) were all found in one stand (B11) of the *Crepido pumilae-Allietum alvarensis*. In this community, bryophytes and lichens constituted the largest proportion of plant diversity (i.e., 38 bryophytes and 65 lichens compared to 36 vascular plants and one alga on 100 m^2).

In all analyzed dry grassland stands, either the power function or the quadratic power function fitted for the respective *S*-space were the best models according to AICc (*S*) and AICc (log *S*) (Table 3 and 5). With additive error terms (AICc/*S*) the regular power function was prevailing, whereas with multiplicative error terms (AICc/log *S*) the quadratic power function was slightly more frequently selected. With respect to extrapolation capability (LEE), again the power function (*S*) performed best, followed by the three other variants of the power function included in this comparison (Table 3 and 5). On average, only the regular power function (log *S*) overestimated the real richness value of the largest plot (but insignificantly; *P*= 0.134), whereas all other models tended to underestimate the real value. The degree of underestimation ranged through minor and insignificant in the regular power function fitted for *S* (*P*=0.054), moderate in quadratic power and Lomolino functions, and high in the variants of the logarithmic and Michaelis-Menten model (all highly significant; *P*<0.002). Combining the various aspects of fitting quality (column "mean of mean ranks" in Table 4), the regular power function fitted for *S* was the best model. It is followed by the three other variants of the power function and then the two variants of the Lomolino function, which generally also performed moderately to well. By contrast, both variants of the logarithmic and Michaelis-Menten function proved to be unsuitable for fitting the real data as well as for extrapolating.

Table 3 Characterization of the 16 series of nested plots, arranged by phytosociological similarity (for details, see Table 1)

Series Number	Order	Species density [0.0001 m²]	Species density [0.01 m²]	Species density [1 m²]	Species density [100 m²]	Best model [AICc (S)]	Best model [AICc (log S)]	Best model [LEE]	c [S]	z [S]
B10	*Corynephoretalia*	2.0±1.4	6.8±2.6	15.8±2.7	35	Power, quadr. (S)	Power, quadr. (log S)	Power, quadr. (S)	15.8	0.176
B13	*Trifolio-Festucetalia*	2.8±0.8	8.8±2.9	20.4±4.6	54	Power (S)	Power (log S)	Lomolino (S)	21.2	0.203
B01	*Sedo-Festucetalia*	2.2±0.8	8.8±2.4	21.0±4.3	44	Power (S)	Power, quadr. (log S)	Power (S)	19.5	0.174
B02	*Sedo-Festucetalia*	1.2±0.8	5.6±2.1	15.8±2.6	36	Power, quadr. (S)	Power, quadr. (log S)	Power (S)	15.1	0.192
B03	*Sedo-Festucetalia*	2.2±0.8	6.6±1.1	16.4±3.2	49	Power (S)	Power (log S)	Power (S)	16.8	0.232
B06	*Sedo-Festucetalia*	1.4±1.5	5.4±1.1	15.2±4.3	56	Power, quadr. (S)	Power (log S)	Power (log S)	15.3	0.278
B04	*Alysso-Sedetalia*	3.0±1.0	7.4±2.9	28.6±2.6	99	Power (S)	Power, quadr. (log S)	Power (S)	27.0	0.281
B08	*Alysso-Sedetalia*	4.2±1.8	14.8±3.6	41.4±7.1	108	Power (S)	Power, quadr. (log S)	Power (S)	40.1	0.214
B11	*Alysso-Sedetalia*	6.2±2.5	19.0±3.4	48.8±3.1	140	Power (S)	Power (log S)	Power (log S)	49.8	0.222
B12	*Alysso-Sedetalia*	2.6±1.5	16.4±3.8	38.0±3.6	89	Power (S)	Power, quadr. (log S)	Power (S)	36.0	0.195
B14	*Alysso-Sedetalia*	3.6±2.2	10.4±3.2	29.4±5.2	100	Power, quadr. (S)	Power (log S)	Power, quadr. (S)	30.0	0.260
B05	*Brachypodietalia*	5.2±2.3	11.0±4.5	32.6±5.9	92	Power (S)	Power, quadr. (log S)	Power, quadr. (S)	32.2	0.227
B07	*Brachypodietalia*	4.8±2.2	12.8±1.3	33.6±3.8	90	Power (S)	Power (log S)	Power (log S)	33.3	0.214
B09	*Brachypodietalia*	2.0±1.6	12.2±1.3	40.6±5.4	116	Power (S)	Power, quadr. (log S)	Power (S)	38.3	0.240
B15	*Brachypodietalia*	3.6±1.8	10.4±4.2	30.8±3.1	84	Power (S)	Power (log S)	Power (log S)	29.4	0.227
B16	*Brachypodietalia*	4.4±0.5	14.4±3.0	37.6±5.3	84	Power, quadr. (S)	Power, quadr. (log S)	Power (S)	35.6	0.188
Overall range		0–8	3–24	9–52	35–140					

Species densities (arithmetic mean ± s.d.) are given for four of the analyzed plot sizes. The best fitting model among the 10 compared models (i.e., the five function types of Table 2 modelled for both S and log S) is given for mean richness data according to three major goodness-of-fit measures (for definitions, see text). Finally, the parameters of the power function fitted for S are listed. In the last line, the observed extreme values of species density are given ($n=80$ for smaller plot sizes; $n=16$ for 100 m²)

Table 4 Overview of the performance of the 10 SAR models for the 16 series of nested-plot mean-value SAR data of Table 3

Model	Mean of mean ranks	ΔAICc (S, mean rank)	ΔAICc (S)	ΔAICc (log S, mean rank)	ΔAICc (log S)	Log Error of Extrapolation (LEE) [absolute, mean rank]	Log error of extrapolation (LEE)
Power (S)	**2.4**	**1.4**	**0.8±1.7**	4.0	8.9±6.0	**1.7**	**−0.02±0.03**
Power (log S)	3.2	4.1	11.4±7.3	1.9	2.6±3.8	3.5	0.03±0.08
Power, quadr. (S)	3.3	1.9	3.8±3.1	4.8	11.3±5.1	3.0	−0.06±0.06
Power, quadr. (log S)	3.4	4.5	11.8±4.5	**1.8**	**2.5±3.2**	3.8	−0.07±0.08
Logarithm (S)	8.0	7.3	30.3±7.7	10.0	n.d.	6.6	−0.22±0.06
Logarithm (log S)	8.1	9.0	36.8±8.7	6.4	23.3±11.7	8.8	−0.34±0.09
Michaelis-Menten (S)	8.3	7.6	30.6±5.3	9.0	54.7±9.4	8.2	−0.29±0.04
Michaelis-Menten (log S)	9.3	9.9	41.7±6.7	7.9	30.8±9.2	10.0	−0.56±0.09
Lomolino function (S)	4.4	3.5	7.2±2.9	5.9	14.8±5.0	3.8	−0.07±0.05
Lomolino function (log S)	4.9	5.8	16.7±5.6	3.3	6.0±2.4	5.6	−0.11±0.06

For ΔAICc (S), ΔAICc (log S), and LEE, mean values and s.d. are given (n.d. − not defined). Additionally, mean ranks are listed for these three fundamental, complementary metrics. ΔAICc is the difference in AICc between the particular model and the best model, i.e., ΔAICc of the best model is zero. LEE is negative when the true richness value for the largest plot is underestimated, and positive when it is overestimated. In the second column from the left, the combined mean rank of these three measures is presented as an overall assessment of the suitability of the different models. The best performing models according to the different criteria are marked in bold face.

Focusing on the power function (S) as the best model (see Table 3), it turns out that explained variance ($R^2_{adj.}$) was extremely high throughout (more than 99% with one exception, not shown). While the intercept (c value) distinctly differed between the analyzed community types (15.1–41.8), the slope in the log-log representation (z

Table 5 Proportion of best fits (according to AICc/S) found for different sampling approaches

Model	Average-value (0.0001–100 m²) n=16	Single-value (0.0001–100 m²) n=48	Nested-plot (0.0001–9 m²) n=32	Random-plot (0.0001–9 m²) n=32
Power (S)	69%	90%	78%	91%
Power, quadr. (S)	31%	8%	16%	3%
Logarithm (S)	–	2%	–	3%
Michaelis-Menten (S)	–	–	–	–
Lomolino (S)	–	–	6%	3%

Note that best fits for AICc (S) necessarily can only occur in models fitted in S and not in the corresponding models fitted in log S. Accordingly, the five models fitted in log S are not listed here. Average-value data (each data point represents a mean of five subsamples, except for 100 m²) and single-value data were both recorded with the nested-plot approach, while nested-plot SARs and random-plot SARs were both based on averaged values (each data point represents a mean of two subsamples).

value) showed less variance, and the ranges of values found in the different phytosociological orders were similar (Table 3). The z values showed a minor albeit significant (P=0.009) difference between fitting in S (mean±s.d.=0.220±0.033; see Table 3) and fitting in log S (0.229±0.023; not shown). Regarding the quadratic power models (S and log S) for individual plant communities, the quadratic terms were partly positive (upward curvature) and partly negative (downward curvature). The quadratic term (b_2) was significantly higher if fitted in S (mean±s.d.=0.0009± 0.0064) than if fitted in log S (−0.0066±0.0107) (P=0.001) but only the latter was significantly different from zero (P=0.587 for S; P=0.026 for log S).

Average-Value SARs vs. *Single-Value SARs*

Goodness-of-fit measured with AICc (S), AICc (log S), and LEE did not differ significantly between single-value SARs of the central and marginal subseries for any of the 10 SAR models (not shown). Thus, for the subsequent analyses, the two marginal and the central subseries of each nested-plot series were pooled as single-value SACs and contrasted to those SARs obtained for average richness values (Table 6). The power function (S) fitted best according to AICc (S) in most cases both for average-value and for single-value SARs, followed by the quadratic power function (S), but the relative proportion of the regular power function was higher for single values (Table 5). In the case of the four power-function and the two Lomolino variants, the average absolute fit within the modelled range (measured as AICc) was significantly better for SARs constructed from average values than for those constructed from single values (Table 6). This was equally true for both S-spaces (i.e., AICc/S and AICc/log S). By contrast, the average absolute curve fit was not significantly influenced by sampling method for the four other models (variants of the logarithmic and the Michaelis-Menten models; Table 6). The picture is nearly reversed when instead of the absolute goodness-of-fit, the relative goodness-of-fit compared to the best model is considered (ΔAICc/S and ΔAICc/log S; Table 6). Here, the first-named six models showed no significant differences between the two compared sampling designs, whereas single-value SARs increased their relative performance compared to the respective best models. As with average-value SARs (see previous section), single-value SARs performed best according to AICc (S) (in this case, only five of 48 best models were not power functions fitted for S; Table 5). However, the lower ΔAICc values for the logarithmic and Michaelis-Menten models in this case indicate that they did not perform as poorly as in the first case. Regarding the extrapolation capability (measured as LEE), the two sampling approaches did not differ significantly among the 10 SAR models, however, the variance of LEE increased for all of them. Finally, the estimates for the fitted parameters (b_0 ... b_2) did not differ in any systematic manner between average-value and single-value SARs, except for b_2 of both Lomolino models, which was significantly higher in the first case (not shown).

Nested-Plot SARs vs. *Random-Plot SARs*

The power function (S) fitted best according to AICc (S) in most cases, both for nested-plot and for random-plot SARs, followed by the quadratic power function (S), but the

Table 6 Results of two-factorial ANOVAs for differences in goodness-of-fit measures between average-value SARs and single value SARs in the case of 10 different SAR models ($n_{total}=64$; $n_{average}=16$; $n_{single}=48$)

Goodness-of-fit measure	Sampling design	Power (S)	Power (log S)	Power, quadr. (S)	Power, quadr. (log S)	Logarithm (S)	Logarithm (log S)	Michaelis-Menten (S)	Michaelis-Menten (log S)	Lomolino function (S)	Lomolino function (log S)
AICc (S)	Average	11.50±6.71	22.12±10.55	14.44±8.26	22.53±10.17	40.94±7.67	47.01±7.72	41.29±5.79	52.35±6.44	17.90±7.77	27.35±9.67
	Single	19.37±6.73	28.45±7.98	22.97±8.03	29.28±9.68	41.08±8.42	47.09±8.14	40.82±6.60	52.23±6.69	25.38±7.99	33.31±9.36
	Significance	***	**	***	**	n.s.	n.s.	n.s.	n.s.	***	*
AICc (log S)	Average	−29.29±9.69	−35.60±8.69	−26.84±9.37	−35.70±7.49	n.d.	−15.88±3.65	16.49±2.34	−7.39±1.93	−23.42±8.94	−32.18±7.04
	Single	−22.96±8.28	−28.36±7.20	−19.18±8.47	−26.10±7.16	n.d.	−15.04±4.73	16.22±3.47	−7.16±2.49	−16.87±7.64	−23.28±6.10
	Significance	**	***	**	***	n.d.	n.s.	n.s.	n.s.	**	***
ΔAICc (S)	Average	0.81±1.70	11.43±7.28	3.75±3.09	11.84±4.51	30.25±7.69	36.32±7.69	30.60±5.28	41.66±6.68	7.21±2.93	16.66±5.57
	Single	0.86±2.78	9.94±7.11	4.46±2.45	10.77±5.56	22.57±8.13	28.58±8.20	22.31±5.95	33.71±6.88	6.87±2.81	14.80±6.74
	Significance	n.s.	n.s.	n.s.	n.s.	***	**	***	**	n.s.	n.s.
ΔAICc (log S)	Average	8.88±6.02	2.57±3.75	11.33±5.13	2.47±3.21	n.d.	22.29±9.81	54.66±9.38	30.78±9.22	14.75±4.96	5.99±2.40
	Single	6.85±5.44	1.45±2.74	10.64±5.02	3.72±2.76	n.d.	14.77±8.43	46.03±9.11	22.66±7.84	12.95±6.17	6.53±3.18
	Significance	n.s.	n.s.	n.s.	n.s.	n.d.	***	***	***	n.s.	n.s.
LEE	Average	−0.02±0.03	0.03±0.08	−0.06±0.06	−0.07±0.08	−0.22±0.06	−0.34±0.09	−0.29±0.04	−0.56±0.09	−0.07±0.05	−0.11±0.06
	Single	−0.02±0.07	0.03±0.11	−0.08±0.11	−0.07±0.11	−0.23±0.08	−0.35±0.12	−0.29±0.07	−0.57±0.11	−0.09±0.09	−0.13±0.09
	Significance	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

The effect of sampling design (d.f.=1) is shown. Plot series is treated as a second factor (d.f.=31), with interactions between sampling design and plot series as a third potential cause of variance (d.f.=31). Arithmetic means ± s.d. are given for the two sampling designs in each case. Significant differences are indicated in the line below (n.s. − $P≥0.05$; * − $P<0.05$; ** − $P<0.01$; *** − $P<0.001$). The abbreviation "n.d." (not defined) denotes cases where the respective metric was not defined due to logarithms of negative values.

relative proportion of the regular power function was higher for random plots (Table 5). The average goodness-of-fit for the modelled range of areas (measured with AICc) was better for data sampled with nested-plot design than for those sampled with random-plot design (Table 7). This difference occurred for all SAR models and in both S-spaces (except for AICc [log S] for the Michaelis-Menten function fitted in S), but was significant only for the variants of the Lomolino function and the power function (except for AICc [S] of the power function fitted in log S). For the relative goodness-of-fit (ΔAICc), the converse is true (Table 7): For the logarithmic and Michaelis-Menten models, distance toward the best model decreased significantly in the random case, although they still fitted real data much less well than the respective best model (mostly a variant of the power function). Regarding LEE, both sampling approaches showed no systematic difference (Table 7). The same is true for estimates of all fitted parameters (b_0 … b_2) in any of the models (not shown).

Discussion

General Characterization of the SACs

The finding that of the ten models tested, the regular power function (fitted for S) was overall the best to describe small-scale SARs for the different Estonian dry grassland communities is in line with results of other comparative studies for a much wider range of community types (e.g. Fridley et al. 2005; Dengler, in press). Apart from the regular power function, however, the quadratic power function also worked well and was even the best for some stands and some goodness-of-fit measures (see Table 4), particularly when assessed in log S-space where often a small but significant negative quadratic term was found (see Results). Although the exponent z of the power-law SARs showed an astonishingly high constancy within the analyzed wide range of spatial scales (six orders of magnitude), some scale-dependency remained even when avoiding methodological artifacts. The occurrence of scale-dependency is in line with findings by, for example, Crawley and Harral (2001) and Fridley et al. (2005), and theoretical suggestions by others (e.g. Rosenzweig 1995; Turner and Tjørve 2005).

Our finding that the logarithmic function performed very poorly throughout in fitting our species-area data contrasts to the frequent assumption that specifically on small spatial scales the logarithmic function should be the more adequate model (Gleason 1922; Williams 1943; Hopkins 1955; He and Legendre 1996; van der Maarel 1997). While some authors (Hopkins 1955; van der Maarel 1997) fitted logarithmic functions to their data even though their graphs showed such deviations from that curve type that a power model probably would have been more adequate, in other cases, the selection of the logarithmic function as the best model may have been correct but caused by methodological artifacts (Dengler 2008, this issue; see also the next section). It is not surprising that the Michaelis-Menten function (as representative of convex saturation models) generally performed very poorly in all respects because real SARs do not have asymptotes (Williamson et al. 2001, 2002; Dengler 2008, this issue). Given this argument, it is somewhat surprising that the Lomolino function (as representative of sigmoid saturation functions) on average performed only slightly worse than the variants of the power function but much

Table 7 Results of two-factorial ANOVAs for differences in goodness-of-fit measures between nested-plot and random-plot sampling in the case of 10 different SAR models ($n_{total}=64$; $n_{nested}=32$; $n_{random}=32$)

Goodness-of-fit measure	Sampling design	Power (S)	Power (log S)	Power, quadr. (S)	Power, quadr. (log S)	Logarithm (S)	Logarithm (log S)	Michaelis-Menten (S)	Michaelis-Menten (log S)	Lomolino function (S)	Lomolino function (log S)
AICc (S)	Nested	11.83±7.56	19.61±10.62	15.31±7.43	20.14±8.17	28.12±6.68	33.25±6.93	31.23±4.48	39.79±5.05	16.41±7.59	22.04±10.06
	Random	18.11±7.01	23.11±7.88	24.27±7.95	28.40±7.98	29.58±7.51	33.83±6.93	31.54±4.49	40.06±5.39	24.53±7.72	28.93±7.96
	Significance	***	n.s.	***	***	n.s.	n.s.	n.s.	n.s.	***	***
AICc (log S)	Nested	−20.27±9.44	−24.73±8.13	−16.91±8.25	−22.32±7.00	n.d.	−14.70±4.33	11.44±2.62	−6.43±2.16	−15.41±10.31	−20.53±8.63
	Random	−16.25±7.58	−19.18±7.11	−9.58±9.35	−13.57±8.21	n.d.	−13.11±5.29	11.05±2.70	−5.98±2.75	−9.40±8.90	−12.73±8.20
	Significance	*	**	***	***	n.d.	n.s.	n.s.	n.s.	**	***
ΔAICc (S)	Nested	1.56±5.71	9.34±8.13	5.05±3.51	9.88±4.66	17.85±8.00	22.99±7.89	20.96±7.53	29.53±7.30	6.14±3.57	11.77±6.14
	Random	0.57±2.17	5.57±5.39	6.72±2.87	10.85±4.36	12.03±7.04	16.29±6.61	14.00±6.33	22.51±6.25	6.98±2.76	11.39±5.12
	Significance	n.s.	*	**	n.s.	***	***	***	***	n.s.	n.s.
ΔAICc (log S)	Nested	7.35±7.67	2.89±6.42	10.70±4.53	5.30±3.85	28.91±10.38	12.92±8.32	39.05±7.98	21.19±7.98	12.20±5.06	7.09±3.37
	Random	4.78±4.93	1.86±3.45	11.45±5.21	7.46±3.41	22.65±8.16	7.92±6.09	32.08±6.47	15.05±6.48	11.63±4.41	8.30±3.53
	Significance	*	n.s.	n.s.	*	***	**	***	***	n.s.	n.s.
LEE	Nested	−0.01±0.04	0.04±0.10	−0.05±0.07	−0.08±0.12	−0.22±0.06	−0.34±0.10	−0.29±0.05	−0.56±0.09	−0.07±0.06	−0.12±0.09
	Random	−0.02±0.05	0.04±0.10	−0.06±0.10	−0.07±0.17	−0.22±0.06	−0.35±0.12	−0.29±0.05	−0.56±0.10	−0.08±0.08	−0.13±0.11
	Significance	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

The effect of sampling design (d.f.=1) is shown. Plot series is treated as a second factor (d.f.=31), with interactions between sampling design and plot series as a third potential cause of variance (d.f.=31). Arithmetic means±s.d. are given for the two sampling designs in each case. Significant differences are indicated in the line below (n.s. − $P \geq 0.05$; * − $P<0.05$; ** − $P<0.01$; *** − $P<0.001$). The abbreviation "n.d." (not defined) denotes cases where the respective metric was not defined due to logarithms of negative values.

better than the Michaelis-Menten function. According to Dengler (2008, in press), this can be attributed to the high flexibility of the Lomolino function, which can nearly perfectly "simulate" a power function over many orders of magnitude (compare the practically indistinguishable curves of the two functions in Fig. 1 of Dengler 2008, this issue). Thus, the generally good suitability of the Lomolino function is not due to its basically sigmoid shape (because the power function is not sigmoid!), nor that real SARs have an upper asymptote (both arguments brought forward by Tjørve 2003) but simply to the ability of this model to "mimic" the power function (see Dengler, in press). Actually, Dengler (in press) demonstrated that while the Cumulative-beta-P function (another highly flexible sigmoid saturation model) showed similar performance as the Lomolino function, the sigmoid but less flexible logistic function performed as badly as the convex Michaelis-Menten function.

The z values (log S) of power-function SARs with a mean of 0.229 (see Results) and a rather small variance compare well to the situation in other European dry grasslands as reviewed by Dengler (2005), who found a mean z value of 0.210 (range: 0.193–0.249) for similar plot size ranges as in the present study. Thus, dry grassland communities, despite their pronounced differences in soil pH, soil depth, and openness of the sward, behave similarly in this respect, whereas z values of other temperate plant communities cover a much wider range of values. Hobohm (1998) and Dolnik (2003), for example, reported values of 0.045–0.306 for a wide variety of European vegetation types, and Fridley et al. (2005) found a 95% confidence interval of z values from 0.217 to 0.538 in plant communities of SE United States.

As regards species densities on the analyzed spatial scales, the studied communities in Estonia partly exceed even the maximum values compiled by Dengler (2005) for European dry grasslands: 8 species is the new "record" on 1 cm^2 (Dengler 2005: 6 species), and 140 species by far exceeds the maximum value of 69 given by Dengler (2005) for 100 m^2 (but only a few data of this plot size were included there; on 9 m^2, the maximum value was 84). Although we have intensively searched the literature for extreme values of species densities worldwide, we did not find other records that exceed either eight species on 1 cm^2 or 140 species on 100 m^2. At the larger scale, some meadow steppe communities probably show equal total plant density because in these just the vascular plants may sum up to 117 on 100 m^2 (Walter and Breckle 1986: meadow steppe in the Ukraine) or 103 on 24 m^2 (Klimeš 1997: *Brachypodio pinnati-Molinietum arundinaceae* in the Czech Republic; in both cases no records with cryptogam treatment were available but bryophytes and lichens probably do not play as large a role in such communities).

Effect of Sampling Design

We could not find the hypothesized decrease in goodness-of-fit when single-value SARs are constructed from marginal instead of central subplots. This does not mean that such an effect is non-existent but that in this case study was too small to be detected with our relatively few replicates. Additionally, the 100-m^2 plots were chosen according to homogeneity criteria, and the centers of the marginal and central 9-m^2 subplots were only approx. 5 m apart. The two approaches would probably deviate more if the largest plot were bigger (thus the distances between marginal and central subplots larger) and less homogeneous (as e.g. in the study of Dolnik 2003).

By contrast, the two other aspects of sampling design had exactly the predicted effects. Interestingly, the deviations of single-value *vs.* average-value and random-plot *vs.* nested-plot were nearly identical (see the extensive similarities between Table 6 and 7). Thus, we discuss them jointly. As hypothesized, both single-value and random-plot design gave rise to an increase in stochasticity compared to the preferred average-value nested-plot approach. This increase of stochasticity has opposite effects for well fitting and poorly fitting models. Those SAR models that fit the data well, namely the power function, the quadratic power function, and the Lomolino function, showed a significantly decreased absolute fit in sampling designs with more stochasticity, while their relative fit remained largely unaffected. Those SAR models that fit the data poorly, namely the logarithmic and the Michaelis-Menten function, did not, however, alter their absolute goodness-of-fit but improved relatively to the six other models. Despite this relative improvement on average by approximately 5–8 units on the log scale of AICc, the logarithmic function only very rarely and the Michaelis-Menten function never could surpass the variants of the power function in fitting quality even with "added stochasticity" (see Table 5). As expected, sampling schemes that involve more stochasticity caused no systematic bias either in estimated function parameters (except for one parameter of the Lomolino function in one case, see Results) or in the tendency to over- or underestimate richness values when used for extrapolation, though they sometimes increased the variance.

To conclude, for two of the three pairs of different sampling approaches the methodology that inherently encompassed more environmental stochasticity caused a relative improvement in fitting quality of less suitable SAR models. This is consistent with the theoretical prediction of Dengler (2008, this issue). This tendency will increase the chance of erroneously selecting a certain SAR model. However, the effect – at least in this case study – was so small that it is not likely a major reason for the better fits of logarithmic than power models for small-scale SARs that are sometimes reported in the literature, and which Dengler (2008, this issue) assumes to be largely due to methodological artifacts. According to the available data (see Dengler 2008, this issue), grid-point *vs.* any-part system and use of incontiguous instead of contiguous areas seem to cause much stronger deviations from the regular power function in small-scale SARs towards logarithmic and saturation functions or power models with decreasing z value (e.g. quadratic and Plotkin variants of the power function, cf. Dengler 2008, in press). For example, Löbel (2002; also see Löbel et al. 2004), who with the grid-point system analyzed dry grassland communities on the Swedish island of Öland very similar to those of our study, reported an average value of the parameter b_2 of the quadratic power function (fitted in log S) of −0.056, which exceeds the value found in the present study (−0.0066) by nearly one order of magnitude. Nevertheless, it seems reasonable to avoid even such minor distorting effects in future studies and therefore to apply nested-plot sampling with a sufficient number of subplots for the smaller areas equally spread within the largest plot.

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