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Species-area curves revisited: the effects of model choice on parameter sensitivity to environmental, community, and individual plant characteristics

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Abstract Species-area curves are often employed to identify factors affecting biodiversity patterns. The aim of this study was to determine how model choice affects biological interpretation of SAC parameters at a small scale in wet, temperate meadows (Železné hory Mts, Czech Republic). We estimated 88 species-area curves in nested plots on areas ranging from 0.01 to 4 m^2 at 22 localities using four different models (Arrhenius, Gleason, and their log transformations). Relationships were tested between the parameters of the fitted curves (slope and intercept) and a number of environmental and vegetation characteristics (environmental—water table, pH, nutrient availability, organic matter content; community—productivity, evenness; and individual plant—shoot cyclicity, persistence of connection among ramets, multiplication rate, dispersal ability). Species diversity was calculated for 0.01, 1, and 4 m^2. The corrected Akaike information criterion was used to identify the best model. The models differed in their sensitivity to environmental, community, and individual plant characteristics. The spatial scale that was the most suitable for revealing the factors underlying species diversity was the smallest considered (0.01 m^2). The most important factors were spatial pattern in community structure (evenness, lateral spread), plant mobility (lateral spread and persistence), and soil properties. Although Gleason model showed better fit to data (both non-log and log transformation) and its intercept was more sensitive to tested biological characteristics,

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the Arrhenius model was more sensitive when correlating biological characteristics and slope. Choice of model according to best fit criteria restricts possibilities of biological interpretation and deserves further study.

Keywords Species-area curve · Arrhenius model · Gleason model · Wet meadows · Clonal growth · Akaike information criterion

Introduction

One of the most important aims in ecology is to understand species diversity and its spatial variation. One important aspect of species diversity is the relationship between the size of a considered area and the number of species it contains. The species-area relationship has been discussed since the mid-19th century and was the subject of mathematical formulations in the early 20th century (Arrhenius 1921; Gleason 1922). Despite numerous studies, many aspects of the relationship remain unclear and debated. These aspects include how data on the species-area relationship should be collected (Hill et al. 1994; Scheiner 2003), how the data should be mathematically modeled (Tjørve 2003; Dengler 2009), whether and how parameters of species-area relationships can be interpreted biologically (Connor and McCoy 1979; Hill et al. 1994), and whether common patterns of species-area relationships exist across scales and communities (Singh et al. 1996; Fridley et al. 2005).

A number of factors have been identified that may affect species-area relationships, such as successional changes (Lepš and Štursa 1989; Rejmánek and Rosén 1992), abiotic conditions (Weiher 1999; Désilets and Houle 2005), disturbance (Lepš and Štursa 1989), productivity (Pastor et al. 1996; Weiher 1999; Chiarucci et al. 2006), or management regimes (de Bello et al. 2007). However, the importance of factors may change with the considered scale (Schmida and Wilson 1985). For example, on the smallest scales, interspecific interactions (i.e., competition) are important (Grime 1973), particularly when plants are fully sessile (van der Maarel and Sykes 1993). With enlarging area, the role of interspecific interactions typically weakens and environmental heterogeneity becomes the main determinant of species richness (Schmida and Wilson 1985).

Spatial variation in species richness is commonly expressed by species-area curves (SAC), which are promising tools for testing potential factors and processes shaping diversity. They are typically estimated by one of two models: the Arrhenius model ($S = C \times A^z$, often presented as the log transformation: $\log S = \log C + z \times \log \mathrm{A}$, Arrhenius 1921) and the Gleason model ($S = C + z \times \log\ \mathrm{A}$, Gleason 1922). In these two models, S is species richness, A is area, and C and z are constants. The constant C (log C) is interpreted as (log) species richness per unit area and will be called the “intercept” hereafter. The constant z is interpreted as the rate at which species richness increases with enlarging area and will be called the “slope” hereafter. The Arrhenius and Gleason models are the most commonly used among plant ecologists, largely because they contain a small number of parameters (Connor and McCoy 1979; Lepš 2005) that can be easily and empirically understood.

However, when the aim of a study is to identify the biological factors underlying the slope and intercept of SACs, researchers should realize that the different models have different fit to data (e.g., Lepš and Štursa 1989) and that logarithmic transformation changes the relationships between intercepts, slopes, and other factors determining species-area relationships. Although studies concerning plant communities usually consider the intercept of the SAC at the area of 1 m^2 (e.g., Lepš and Štursa 1989; Chiarucci et al. 2006; de Bello et al. 2007), other sizes relevant to plant communities are equally possible (Rosenzweig 1995) and could help elucidate scale dependency of factors affecting species richness. Consequently, attempts to interpret parameters of SAC biologically require careful consideration of model choice (Tjørve 2003).

With respect to the two most commonly used SAC models (Arrhenius and Gleason model), the simple question arises: How does model choice affect biological interpretation of SAC model parameters? To answer this question, we studied species-area relationships in wet meadows in the Železné hory Mts. (Czech Republic). These wet meadows are scattered in the landscape along small streams, in spring areas, and near fish ponds. The species diversity of those marginal habitats is endangered by abandonment, eutrophication, and drainage, and we explored which factors affect the spatial pattern of species richness in these endangered habitats. Using areas ranging from 0.01 to 4 m^2 for determining the intercept, we tested the relationships among SAC parameters (intercepts and slopes as determined by the Arrhenius and Gleason functions and their logarithmic transformations) and environmental characteristics (soil chemical properties and water table depth), community characteristics (productivity and evenness in cover of resident species), and characteristics of individual plants (persistence on a spot and clonal growth). Some characteristics (soil chemical properties, water table depth, and productivity) were tested because they are commonly thought to be relevant to species richness on a plot and could affect function intercepts. Other characteristics (evenness, persistence, and clonal growth) were tested, because they are thought to be relevant to spatial pattern and hence could primarily affect function slopes.

Methods

Study area

The study area is 340–620 m above sea level in the central part of the Železné hory Mts. (East Bohemia, Czech Republic). The landscape consists of a matrix of forests, arable land, cultural meadows, and urban areas. In this matrix, wet meadows survive as small (and very often abandoned) fragments. Among these wet meadows, there is a broad range in soil moisture, soil fertility, and soil reaction. We collected data in 22 localities of various types of vegetation (alliances *Caricion gracilis*, *Calthion*, *Molinion caerulae*, *Caricion fuscaeae*, *Sphagno recurvi—Caricion canescentis* and *Sphagno warnstorfiani—Tomentypnion*, see Klimešová et al. (2011c) for detailed description; the nomenclature is according to Moravec (1995)).

Plant species richness and cover data

At each locality, we established four 2×2 m^2 plots in which vegetation was sampled. In every 2×2 m^2 "sampling plot," vegetation was assessed using phytosociological relevés (cover scale: $r =$ rare plant with 1–2 individuals; $+=$ cover less than 1 %; cover greater than 1 % was estimated to the nearest 1 % (up to 20 %) or to the nearest 5 % (over 20 %)). The cover data were used for species-evenness evaluations. For computation of SAC coefficients, we determined species composition in a nested design over a range of spatial scales from 0.01 to 4 m^2. The species richness at the largest scale (4 m^2) was extracted from the phytosociological relevés data. Data for smaller areas (0.01, 0.04, 0.09, 0.16, 0.25, 0.36, 0.49, 0.64, 0.81, and 1 m^2) were obtained using 1×1 m^2 "presence plots," which were established in the center of each sampling plot and were divided into 100 0.1×0.1 m^2 "small plots." In each small plot, all rooting species were recorded (see Klimešová et al. (2011c) for detailed information). The average species richness was calculated for all possible nested squares that could be placed in the 1×1 m^2 area of a presence plot. In total, we sampled data for 88 SACs (four replicates at 22 localities) from 11 spatial scales (0.01, 0.04, 0.09, 0.16, 0.25, 0.36, 0.49, 0.64, 0.81, 1, and 4 m^2) for every model.

SAC models

In order to test species-area relationships, we used two types of models: the Arrhenius model and the Gleason model. Our statistical analysis also included the logarithmic transformations of both models so that we could evaluate whether the log transformation of the models affects the relationships of the SAC parameters and studied characteristics. Thus, we used four models of SAC:

1) Arrhenius model

$$S = c \times A^z$$

2) Gleason model

$$S = d + y \times \log A$$

3) log Arrhenius model

$$\log S = e + x \times \log A$$

4) log Gleason model

$$\log S = \log(f + w \times \log A)$$

In order to simplify the text, we refer to the constants c, d, e, and f as "intercepts" and the constants w, x, y, and z as "slopes," although doing so is not correct in a mathematical sense.

Environmental characteristics

The main ecological factors determining the composition and diversity of meadow vegetation in Central

Europe are soil water content, nutrient availability, and soil reaction (Ellenberg 1996). We measured these abiotic parameters in the following way.

Groundwater depth

The depth of the water table was measured using perforated plastic tubes (40 mm in diameter) that were inserted to 90 cm depth and left in the soil for the duration of the sampling period. The measurements were repeated seven times per year during the years 2008–2010 at monthly intervals from April to November. Average values for the five tubes, the seven measurement dates, and 3 years at each locality were used for analyses (the dryer the locality, the greater the value for groundwater depth).

Soil characteristics

Soil was sampled from the A horizon to 15 cm depth and was analyzed for basic nutrients, soil reaction, and organic matter content. All the characteristics were determined for each sample, and the average value of five samples per locality was used for analyses. Total nitrogen was extracted using the Kjeldahl method (Novozámský et al. 1983), total phosphorus was extracted with perichloric acid (Kopáček and Hejzlar 1995), NO_3 and NH_4 ions were extracted by leaching with KCl (Anonymous 1997), and PO_4 was extracted by leaching with $CaCl_2$ (Houba 1994). Extracted nutrients were quantified with a FIAstar flow analyzer (Tecator, Sweden). Organic matter content was determined by burning the samples at 550 °C, and the exchangeable soil reaction was measured in a KCl solution according to ISO 10390 (Anonymous 1992).

Community characteristics

Productivity

The community productivity was assessed as aboveground biomass of the stand on the two $1 \times 1\ m^2$ presence plots per locality in July 2007 after species composition data were recorded. Aboveground biomass (excluding litter and mosses) was clipped 5 cm above the soil surface, dried for 12 h at 85 °C, and weighed. The average dry mass per locality was used for analyses. Data on plant productivity were log-transformed to improve normality and homoscedasticity.

Evenness

The description of community composition can be divided into two measures: species richness (i.e., how many species are present in the community) and evenness. Evenness refers to the distribution of the abundance of resident species in a community (Smith and Wilson 1996). Except for some theoretical studies and proposals (Martín and Goldenfeld 2006; Borda-de-Água et al. 2002), there is a lack of studies, especially of experimental studies exploring the patterns among evenness and the species-area relationship. Many evenness indices have been developed for the study of vegetation but the Shannon-Wiener and Simpson indexes are the most commonly used. These two indexes are species richness dependent (Smith and Wilson 1996). In order to avoid the co-varying of evenness and species richness, we used the converted index of dominance to describe species evenness:

$$E = 1/(D \times S);$$

where S is total species richness, and D is the index of dominance:

$$D = \Sigma (n_i/n)^2;$$

where n_i is cover of ith species, and n is total cover. We used cover from the phytosociological relevés for evenness computations.

Plant characteristics

We selected traits concerning the persistence/mobility of a plant (shoot cyclicity, persistence of connection, and lateral spread) and traits concerning plant aggregation (multiplication rate and lateral spread). Traits were assigned to species according to the CLO-PLA database (Klimešová and Klimeš 2006). The three or four categories for each trait from the database were merged into two broader ones, because some categories were rarely represented (fewer than five times) in the species list and because of multivalent categorization for some species (the CLO-PLA database contains multiple data from various sources). In such cases, we first averaged the values within the records and then averaged the data among the records.

Shoot cyclicity (cyclicity)

Cyclicity denotes shoot life-span, i.e., the number of growing seasons between shoot sprouting and shoot flowering and death. Two categories were used: 1 year and more than 1 year (aggregation of categories 2 and >2 in CLO-PLA).

Persistence of connection (persistence)

Persistence of connection describes how long parent and offspring ramets are interconnected. Plants with persistent connection (integrators) prefer less productive habitats than plants with less persistent connections (splitters) (Klimešová et al. 2011a). Two categories were used for persistence: 1 year and more than 1 year (aggregation of categories 2 and >2 in CLO-PLA).

Multiplication rate

Multiplication rate describes how many new shoots a parental shoot is able to produce in 1 year. This trait is relevant to meadow management, and plants with high multiplication rates tend to be favored by mowing (Klimešová et al. 2011c). Two categories were used for multiplication rate: 1 shoot or fewer per year (aggregation of categories <1 and 1 in CLO-PLA) and 2 or more shoots per year (aggregation of categories 2–10 and >10 in CLO-PLA).

Lateral spread

The horizontal spread of a clonal plant is enabled by the growth of rhizomes, stolons, etc. Lateral spread is promoted on more productive habitats (Klimešová et al. 2011a). Two categories were used for lateral spread: less than 1 cm/year and more than 1 cm/year (aggregation of categories 1–25 and >25 in CLO-PLA).

For all traits, the mean proportion of the categories in all 88 of the 2 × 2 m^2 plots was computed with all species given the same weight (i.e., abundance was ignored). Because all of the traits used only two categories, which were complementary, only one was used in computations (cyclicity> 1 year, persistence > 1 year, multiplication rate $\geq$ 2 shoots per year, and lateral spread > 1 cm/year).

Statistical analyses

Relationship among studied characteristics

In order to avoid co-linearity among explanatory variables, we calculated a correlation matrix and tolerance values for the remaining variables (Quinn and Keough 2002, online resource 1). Since soil characteristics concerning nutrient availability (total nitrogen, total phosphorus, NO_3, NH_4, PO_4, and organic matter content) were strongly and positively correlated with each other (tolerance values were <0.25), we created one variable ("soil fertility") that combined soil nutrient and organic matter contents. Soil fertility was calculated with principal component analysis (PCA) and expressed as the scores on the first ordinal axis. The soil characteristics were centered and standardized by the standard deviation value. The ordination of localities and the three groups of characteristics (environmental, community, and plant) were computed with *a*, and the characteristics were centered and standardized by the standard deviation value. All multivariate analyses were conducted in the CANOCO software (ter Braak and Šmilauer 2002).

The coefficients of SACs were computed using nonlinear regressions. In order to compare the fit of SAC parameters to empirical data, we used the Akaike information criterion. Since sample number was relatively low (SACs were constructed upon 11 points), we used the corrected form (AICc). As shown by Rosenzweig (1995), the intercept is scale dependent; therefore, we constructed SACs upon different scales (the area for which the intercept was calculated: 0.01, 1, and 4 m^2) to test whether the effect of the predicting factors on species richness differs among scales.

Similarly, the relationships among the SAC coefficients and predicting factors were analyzed by the lowest AICc criteria. The analyses were computed separately for each group of factors (environmental, community, and individual characteristics). In the first step, we created linear models: $X \sim Y$, where X was the coefficient of the SAC (slope or intercept) or the fit of the SAC (AICc) and Y was all single factors from one group (environmental, community, and individual) and all their combinations. For the group "community," for example, we created three models: $X \sim$ productivity; $X \sim$ evenness; and $X \sim$ productivity + evenness. In summary, 24 models were compared: four kinds of models (Arrhenius, Gleason, log Arrhenius, and log Gleason) × two dependent variables (slope, and intercept) × three groups of characteristics (environmental, community, and plant). The locality was assigned as a random factor. All these remaining statistical computations were conducted with the R-statistics software, version 2.13.1 (R Development Core Team, 2009). We used the function "AICcmodavg" package (Mazerolle 2011) to assess the best model from every group of created models.

Results

Fitting models

In total, 147 species were found across the 88 plots at 22 localities. Species richness ranged from 15 to 51 species at the largest scale (4 m^2) and from 0.88 to 11.23 species at the smallest scale (0.01 m^2; mean values from presence plots, see online resource 2).

The Gleason model showed better fit than the Arrhenius model in both basic (81 of 88 models) and logarithmic form (77 of 88 models) (Online Resource 2, see also the graphical illustration of fitting of the four SAC models on Fig. 1).

Slopes and intercepts of the models were significantly correlated. The correlations were negative in the Arrhenius model but positive in the Gleason model. The strength of correlations varied along the spatial scale for which the models were computed. The Arrhenius model and the log Arrhenius model showed the strongest correlations between SAC coefficients when they were computed for the smallest area (intercept at 0.01 m^2). On the other hand, correlations between SAC coefficients of the Gleason and log Gleason models were the strongest when they were computed over the largest area (intercept at 4 m^2) (Table 1).

Correlation among predicting factors

Interrelationships of the environmental, community, and individual plant characteristics are shown in Fig. 2. Soil fertility was negatively correlated with water table depth. Evenness was negatively correlated with productivity. Persistence and cyclicity were negatively correlated with lateral spread. Productivity was negatively correlated with soil fertility.

SAC slopes—predicting factors

For community characteristics, correlations between slopes and evenness were negative for all models except the log Gleason model. For individual characteristics, correlations between slopes and persistence and lateral spread were positive for the Arrhenius and log Arrhenius models (Table 2).

SAC intercepts—predicting factors

Correlations between intercepts and characteristics were significant only when they were computed upon the smallest area (intercept at 0.01 m^2), i.e., correlations were never significant at the scale of 1 or 4 m^2. For environmental characteristics, correlations between intercepts were not significant for any factor (Table 3). For community characteristics, correlations between intercepts and evenness were positive for all models except the Arrhenius model. For individual characteristics, correlations between intercepts and persistence of the connection among ramets were negative for all models except the log Arrhenius model (Table 3). We tested whether relationship between productivity and intercepts was rather non-linear; however, a quadratic model was not significant (data not shown). Despite this, relationship between species richness at a small scale (per 0.01 m^2) and productivity (average per 1 m^2) was nearly hump shaped.

Discussion

The sensitivity of the SAC model parameters to environmental, community, and individual plant factors depended on the model (Arrhenius, Gleason, log Arrhenius, or log Gleason) and on scale, i.e., on the plot size for which an intercept was calculated (0.01, 1, or 4 m^2). The slope of Arrhenius and log Arrhenius models, the intercept of Gleason and log Gleason models, and the smallest spatial scale were the most sensitive SAC model parameters for the examination of environmental, community, and individual plant characteristics. Both logarithmic and non-logarithmic versions of the models enabled consistent biological

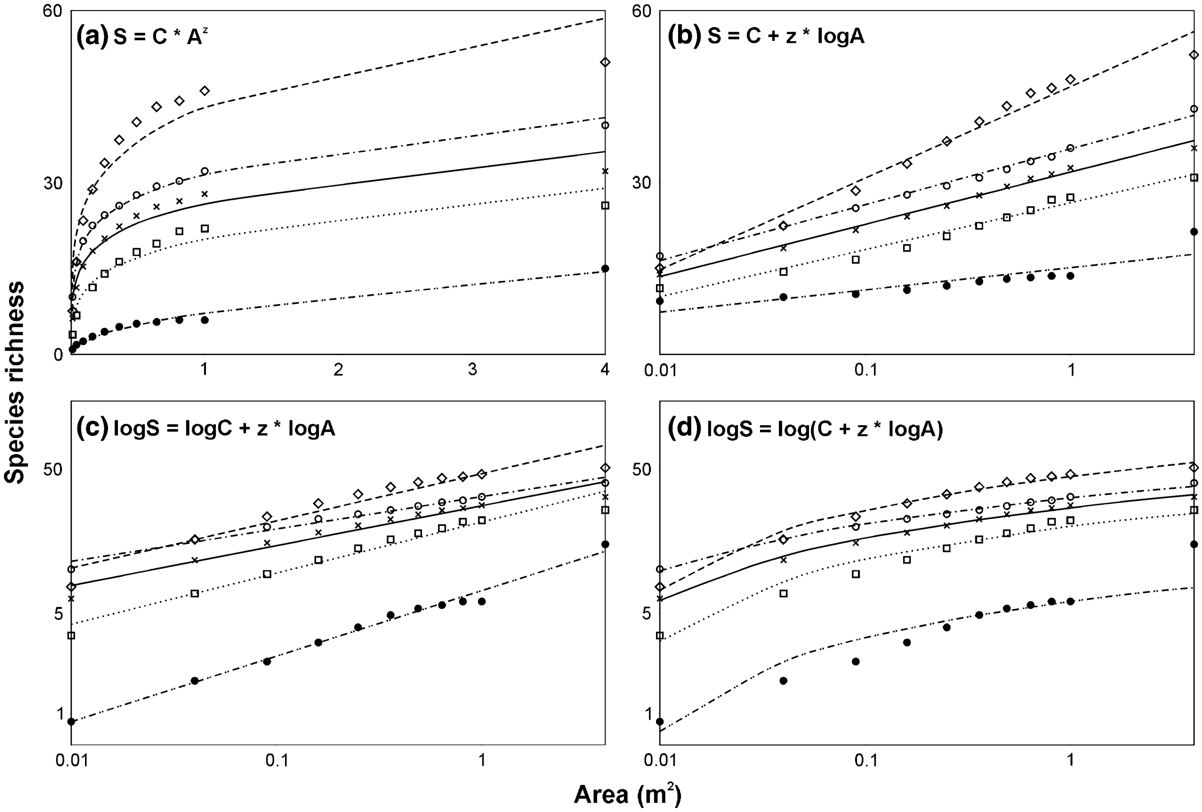

Fig. 1 Examples of SAC curves (five out of 88) fitted by four models (**a** Arrhenius, **b** Gleason, **c** log Arrhenius, and **d** log Gleason). Symbols are observed values. The five curves were selected to cover broad spectrum of vegetation types; *diamonds Caricion fuscaeae*, *empty circles* species rich *Calthion*, *crosses Molinion caerulae*, *squares Caricion gracilis*, *full circles* species poor *Calthion*

Table 1 Correlations between slopes and intercepts of four tested models

Model	Scale (area for which the intercept was calculated)					
	0.01 m^2		1 m^2		4 m^2	
	Pearson *r*	*p*	Pearson *r*	*p*	Pearson *r*	*p*
Arrhenius	−0.648	<0.0001	−0.390	0.0002	−0.253	0.0173
Gleason	0.350	0.0008	0.925	<0.0001	0.950	<0.0001
log Arrhenius	−0.691	<0.0001	−0.205	0.0549	−0.019	0.8638
log Gleason	0.618	<0.0001	0.972	<0.0001	0.981	<0.0001

interpretation of the models; this was not affected by the model fit to the data.

The slopes of the curves were affected both by characteristics that are generally thought to be relevant to species richness (soil properties) and by small-scale spatial distribution of plant individuals and their mobility (evenness, lateral spread, and persistence). These results suggest that, in our study system, a fine-grained spatial pattern of species composition was typical for high diversity plots, whereas an aggregated pattern (one with a few dominants and scattered subordinate species) was typical for low diversity plots. These patterns were associated with soil properties but not with productivity. The low importance of soil fertility in this relationship is surprising. A possible explanation is that nutrients and organic

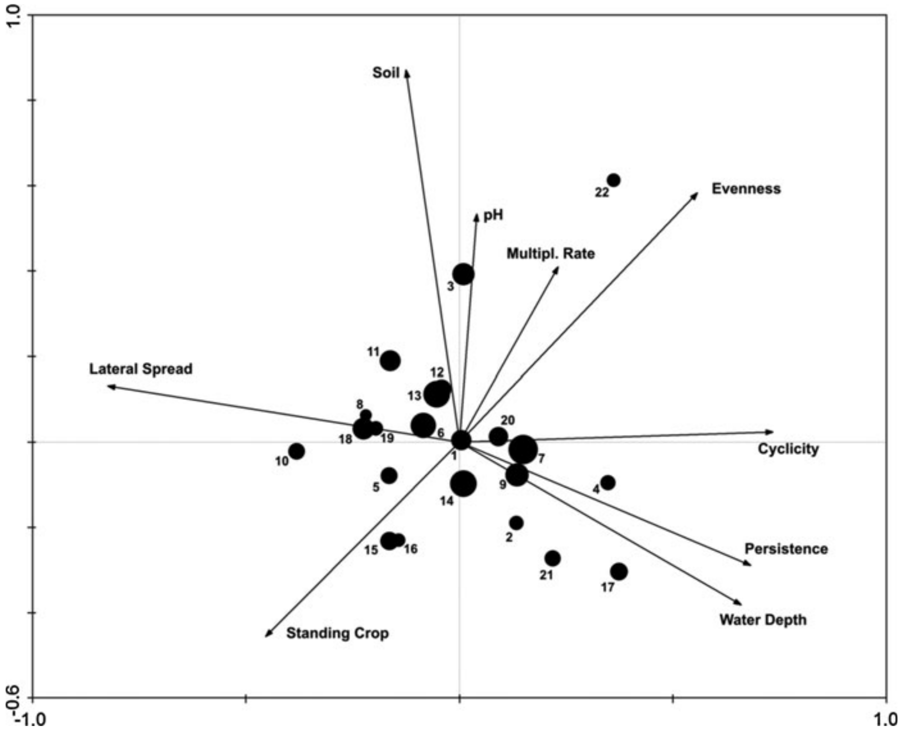

Fig. 2 Relationship among environmental characteristics (soil, pH, and water depth), community characteristics (evenness and productivity), and individual plant characteristics (cyclicity, persistence, multiplication rate, and lateral spread) for the studied data-set as visualized by a PCA ordination diagram. Six environmental characteristics were combined into the characteristic soil (organic matter, P total, N total, PO_4, NO_3, and NH_4). Points 1–22 represent centroids of four sampling plots per locality, and their diameter corresponds to mean species richness per 2 × 2 m^2 plot

Table 2 The correlations between slopes of Arrhenius, log Arrhenius, Gleason, and log Gleason models and three groups of characteristics (environmental, community, and individual plant)

Model	Environmental			Community			Individual		
	r	Factor	*p* value	*r*	Factor	*p* value	*r*	Factor	*p* value
Arrhenius	−0.02	Soil	0.0072	−0.17	Evenness	0.0001	0.38	Persistence	<0.0001
							0.41	Lateral spread	0.0001
Gleason		–	–	−2.3165	Evenness	0.0164		–	
log Arrhenius	−0.02	Soil	0.0152	−0.19	Evenness	<0.0001	0.30	Persistence	0.0020
							0.34	Lateral spread	0.0010
log Gleason		–			–			–	

– Not significant

matter are conserved by the high water table in our study area, which limits nutrient availability for plants (Verhoeven et al. 1993). This argumentation is supported by the negative correlation between soil fertility and water depth in our dataset (Fig. 2).

In contrast, none of the three environmental characteristics that are generally thought to be relevant to species richness on a plot (soil chemical properties, water table depth, productivity Ellenberg (1996)) affected SAC intercepts. Surprisingly, this basic parameter of species diversity was mainly determined by characteristics relevant to small-scale spatial pattern and mobility of species in a community (evenness and persistence). The lack of an obvious

Table 3 Correlations between intercepts of Arrhenius, log Arrhenius, Gleason, and log Gleason models (at a scale of 0.01 m^2; correlations were not significant at scales of 1 or 4 m^2) and three groups of characteristics (environmental, community, and individual plant)

Model	Environmental			Community			Individual		
	r	Factor	*p* value	*r*	Factor	*p* value	*r*	Factor	*p* value
Arrhenius		–			–		−11.02	Persistence	0.0309
Gleason		–		7.35	Evenness	0.0001	−14.11	Persistence	0.0049
log Arrhenius		–		4.26	Evenness	0.0035		–	
log Gleason		–		3.91	Evenness	0.0011	−6.65	Persistence	0.0381

– Not significant

relationship between productivity and intercepts on SAC models at any examined scale might indicate that the relationship between productivity and species richness is not linear but "hump-shaped," as has often been reported (Al-Mufti et al. 1977 and others). Depicting the relationship between species number at the smallest scale (0.01 m^2) and plot productivity partly supported this idea (Fig. 3) (although polynomial regression of intercepts and productivity at any of examined scales was not significant, data not shown). Moreover, the hump-shaped scatter of plots in the biplot indicates that productivity and species richness are clearly related to the lateral spread and persistence of connection among ramets (Fig. 3). The ascending arm of the hump-shaped diversity-productivity relationship correlates with increasing lateral spread and decreasing persistence of connection among ramets, while the descending arm correlates again with increasing lateral spread but not with persistence, which remains constant. The hump-shaped diversity-productivity relationship reported from herbaceous communities by numerous authors (Al-Mufti et al. 1977; Pastor et al. 1996) was hypothesized to be caused by plant clonality (Laanisto et al. 2008). Researchers have also proposed that the descending arm of the hump-shaped productivity-diversity relationship in grasslands can be explained by the competitive superiority of clonal plants (due to their foraging behavior) in heterogeneous environments (Eilts et al. 2011). A problem with this explanation is that most species in grasslands grow clonally (Klimeš et al. 1997), and so clonality would not result in a competitive advantage. Clonality, however, might explain various spatial patterns that result in the hump-shaped diversity-productivity relationship, as discussed in the next paragraph.

According to our study, the hump-shaped diversity-productivity relationship might be explained by the spatial mosaic caused by different combinations of clonal traits (like lateral spread and persistence). While high diversity plots in our dataset were characterized by even abundance and by plant species with intermediate lateral spread and low persistence of rhizomes, low diversity plots were characterized by an aggregation of dominants. This aggregated or clumped spatial pattern resulted in low diversity in small plots at both the low and high end of the productivity gradient. The trends mentioned above are illustrated in Fig. 3: localities located in the bottom left of the biplot are species poor and unproductive and are dominated by tussock graminoids (e.g., *Deschampsia cespitosa, Nardus stricta, Festuca filiformis*, or *Carex davaliana*) with low lateral spread and high persistence of connection among ramets; localities in the middle of the biplot have the highest species diversity and intermediate productivity and are characterized by an even distribution of abundances, intermediate lateral spread, and short-lived connection among ramets; and the less species rich and productive localities in the right of the biplot are dominated by tall herbs with long rhizomes (e.g., *Filipendula ulmaria*, *Scirpus sylvaticus*, and *Carex acuta*). Damgaard et al. (2012) found a similar relationship between plant aggregation and plant productivity/species richness in acidic grasslands, and proposed that this relationship indicates that species diversity is threatened.

Previous research has established that increasing nutrient availability is likely to have neutral effects on species-area relationships because an increase in nutrients causes an increase in shoot size but a decrease in shoot number (Oksanen 1996; Stevens and Carson 1999). Since the lateral spread of

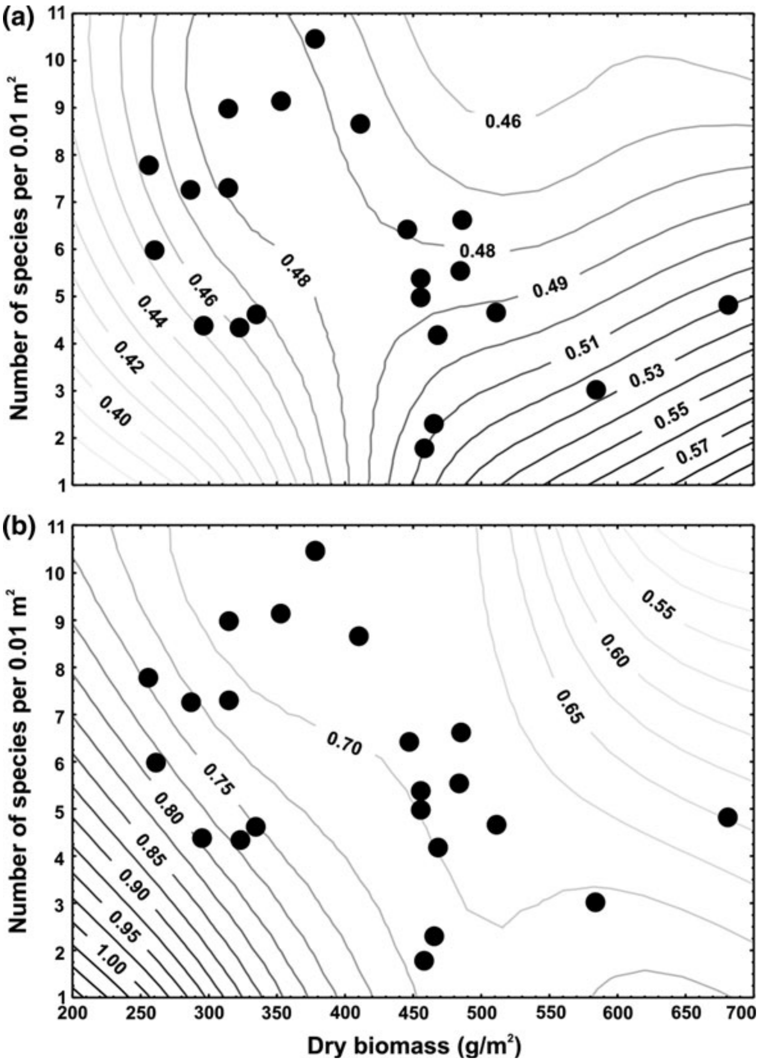

Fig. 3 Relationship between productivity (average per 1 m^2) and species richness at a small scale (per 0.01 m^2) for 22 meadows in the Železné Hory Mts. The *upper graph* shows how the relationship is affected by average lateral spread for community weighted by species abundance, and the *bottom graph* shows how the relationship is affected by persistence among ramets for community weighted by species abundance

rhizomatous plants correlates with their shoot size (Klimešová et al. 2011b) and clonal rhizomatous plants are stronger competitors than non-clonal plants, clonality also contributes to the random processes responsible for species richness decline in productive plots (Suding et al. 2005, Eilts et al. 2011).

Our results indicate that the spatial pattern generated by plant clonality affects species richness of herbaceous communities at small scales. The relevance of clonality to species-area relationships in other herb-dominated ecosystems remains to be tested.

Conclusions

The aim of this study was to determine how model choice affects biological interpretation of SAC parameters. Based on analysis of a data-set from 22 wet meadows, we showed that:

(1) The slope of Arrhenius and log Arrhenius models and the intercept of Gleason and log Gleason models were the most sensitive SAC model parameters for the examination of environmental, community, and individual plant characteristics.

(2) The spatial scale that revealed which biological factors explained species diversity in our study system was the smallest considered (0.01 m^2).

(3) The factors that most affected species richness (and hence SAC model parameters) at the small scale were the spatial pattern of community structure and soil properties. Persistence of connection among ramets and lateral spread were correlated with the parameters of species richness. Thus, as a side-result we provided the first data in support of the idea that clonal traits affect the species-area relationship by creating small-scale mosaics of species in a community.

(4) Although we found no contradictory results, the models differed in factors they were correlated with and the models with best fit were not the most sensitive to tested biological factors. We, therefore, advocate against use of the best fit criteria as the problem deserves deeper study.

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