

THE INFLUENCE OF FOREST SITE FERTILITY AND SAMPLING SCALE ON SPECIES-AREA CURVES

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Abstract: The floristic data were collected using a nested sampling design in two different forest understories. The shape of the curves ($S = c \times A^z$) usually used to fit the distribution of species richness (S) as a function of sampled area (A) was analysed by means of the values of parameters *c* and *z*. The influence of sampling scale was assessed manipulating two of its components: grain size and extent. The estimate of parameter *c* resulted larger on richer soils and it is responsible for the higher slope of the curve at small scales (<50 m²). Increasing the grain size, while keeping the extent constant, may causes a strong deformation of the species-area curve, which is especially important at large scales (>400 m²) by underestimating the species richness. Decreasing the extent, while grain size is held unvaried, produces little effect on the slope of species-area curves, but can lead to overestimating species richness in habitats with low spatial heterogeneity. The exhaustive assessment of the influence of sampling scale on these curves requires further considerations such as the interaction between grain and extent, the number of samples and the spatial autocorrelation between quadrats.

Introduction

One of the oldest relationships revealed in ecology has been that between species richness and area sampled, or the species-area curve [2]. Its shape has been used to define methodologically the ‘minimum area’ of a plant community [7,10,17], to optimally design the natural reserves [5,6], to estimate the biodiversity over large regions or preserves [18,27] and to infer biological processes such as disturbance [11], competition [14] or division of niche space [26].

The distribution of species richness (S) as a function of area (A) is generally fitted by means of a power function: $S = c \times A^z$, in which *c* and *z* are positive regression parameters. However, Coleman (1981) stressed that the power function model assumes a random distribution of both species and individuals, which is not always the case in natural communities. Whereas the values of *z* (generally between 0.15 and 0.45) are positively related with the habitat heterogeneity [1,23], the parameter *c* has a more hidden ecological interpretation.

The convex shape of the species-area curve has been thought to be rather similar across different plant communities, i.e. a steep increase followed by a more

or less flatten tail. The first, sheer part of the curve is the effect of the intrinsic increase of area (niche space), whereas the tail steepness depends on the habitat heterogeneity. However, there are also many examples of species-area curves that do not show any tendency to flatten, simply because the spatial structure of some communities is course-grained. That's why the importance of the scale of observation on our perception of vegetation patterns has been stressed recurrently in the literature [4,22,25]. Scale dependence can be defined as the degree to which ecological phenomena (in the present case, species richness) vary as a function of grain, extent, number of samples or other components of observation scale [20]. The grain is associated with the size of the smallest sampling unit, while the farthest distance between these ones gives the extent.

The purpose of this study is to evaluate the influence of forest site fertility and scale of observation (grain and extent) on the shape of species-area curves. In particular, we intend to see how and to what extent the slope of these curves is modelled by the single variation of the previous mentioned factors in case of forest floor vegetation.

Study area

The fieldwork was performed in two woodlots ("Făget" and "Zăpodie") that are parts of the Cluj Forest District and precisely, in the subparcels 53C and 18A, respectively [8]. These forest stands (hereinafter referred to as "Făget" and "Zăpodie") are almost entirely pure and physiognomically very similar as the tree layer is dominated (over 80%) by even-aged populations (50-60 years) of hornbeam (*Carpinus betulus*). The herb layer covers about 80% in "Făget" and 70% in "Zăpodie".

Whereas the "Făget" stand is located on a north slope at about 500 m a.s.l. (the potential natural vegetation being represented by *Carpino-Fagetum* Paucă 1941), the "Zăpodie" stand lies at an elevation of about 400 m facing east (the potential natural vegetation being considered *Lathyro hallersteinii-Carpinetum* Coldea 1975). Despite the two study sites share many edaphic similarities, the forest soil from "Făget" evolved on a base-richer substrate (marns) and displays typical pseudogley features in the upper horizon.

Materials and methods

The fieldwork was performed in May-June 2001 in order to clearly identify both the remains of prevernal-vernal plants and the first leaves of late-season plants. The following criteria were used to choose the area to be sampled: 1) relative ecological and phytocoenotic homogeneity; 2) a minimum distance of 50 m from the forest edge; 3) absence of any visible trampling traces; 4) no gaps in the tree canopy. One 0.1 ha plot was placed accordingly in each of the two study sites [10,15].

The 20 x 50 m plots were delimited using a red string sustained on metal stakes. In addition, 3 nested quadrats of 1, 10 and 100 m² were also marked at each

corner of the large plot. Vegetation sampling was carried out following a nested design, i.e. in 1, 10, 100 and 1000 m² subplots [21]. The presence of all vascular plants with less than 1 m height was recorded in each subplot. The species occurrence per 200 m² was deduced from joining the data collected in the adjacent 100 m² subplots.

Within both plots (“Făget” and “Zăpodie”), 3 soil samples from the depth of 10 cm were randomly collected. As a surrogate of a complex index of soil fertility we employed the pH value, which was measured for each soil sample using the digital pH-meter MV-87. Only the mean calculated over each plot was subsequently employed in comparisons (Tabs. 1 and 2).

The species richness-area relationship becomes linear in a log-log space: $\log S = z \times \log A + \log c$. As the logarithm is not defined for $A=0$, we can actually use a slightly modified form of the previous equation, in order to estimate the species richness when area has vanished: $\log S = z' \times \log(A+1) + \log c'$. Consequently, c' equals theoretically the number of species at a point and may be interpreted in terms of ‘species packing’ or community saturation. Higher values of c' should be obtained in case of mature communities developed on fertile sites, because species coexistence is promoted by a greater range of resources, which are expected to be more fully exploited [3]. By extrapolation, we hypothesized that the parameter c might have a similar ecologic determination as c' .

In order to understand the effect of parameters c and z on the shape of species-area curves, two sets of simulations on artificial data were performed. Different values of one parameter were used while keeping constant the value of the other parameter in the power function usually used to fit species-area curves. By plotting the resulting curves on the same axes, we could estimate the effect of increasing (decreasing) one parameter on curvilinearity, while controlling for the other one (Fig. 1).

The real species-area curves were built by fitting the distribution of mean species richness at different scales. The effects of grain and extent on the shape of these curves were evaluated by comparing the complete curves with those fitted at a larger grain (10 m²) and at a lower extent (200 m²), respectively.

The non-linear (power) models were considered satisfactory and their parameters statistically significant in regression analysis, only if the probabilities associated with the F and t-tests resulted lower than the 0.01 threshold. All statistical analyses were run using the SAS/STAT 7.0 software [24].

Results

The tails of the curves in Fig. 1A are almost parallel suggesting that the parameter c has a visible effect only at fine scales. In fact the slope of the first part of curves becomes higher and higher as the value of c increases. On the other hand, z influences drastically the steepness of the curves at all scales (Fig. 1B). These findings support the hypothesis according to which c is close related to alpha-

diversity, but also reveal the confounding effect of the two parameters (c and z) on species richness at community level.

Table 1: Mean soil pH value and occurrence of vascular species within the 20x50 m² plot (ABCD) located in the “Făget” stand.

Area (m ²)	1				10				100				1000
Plot corner	A	B	C	D	A	B	C	D	A	B	C	D	ABCD
<i>Hepatica nobilis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Anemone nemorosa</i>	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Lamium galeobdolon</i>	1	1	1	0	1	1	1	1	1	1	1	1	1
<i>Polygonatum odoratum</i>	0	0	1	1	1	1	1	1	1	1	1	1	1
<i>Asarum europaeum</i>	0	0	1	1	0	1	1	1	1	1	1	1	1
<i>Aposeris foetida</i>	0	0	0	1	0	1	1	1	0	1	1	1	1
<i>Carpinus betulus</i> (S)	1	0	0	0	1	1	0	0	1	1	1	0	1
<i>Viola reichenbachiana</i>	0	0	1	0	1	0	1	0	1	1	1	0	1
<i>Viola hirta</i>	0	0	1	0	0	0	1	0	0	1	1	0	1
<i>Stellaria holostea</i>	0	0	1	0	0	0	1	0	0	1	1	0	1
<i>Pulmonaria officinalis</i>	0	0	0	0	0	1	1	1	0	1	1	1	1
<i>Acer campestre</i> (S)	0	0	0	0	0	1	1	0	1	1	1	1	1
<i>Milium effusum</i>	0	0	0	0	0	0	1	1	1	0	1	1	1
<i>Fagus sylvatica</i> (S)	0	0	0	0	0	1	0	1	1	1	0	1	1
<i>Ranunculus auricomus</i>	0	0	0	0	0	0	0	1	1	1	1	1	1
<i>Cardamine impatiens</i>	0	0	0	0	1	0	0	0	1	1	1	0	1
<i>Acer pseudoplatanus</i> (S)	0	0	0	0	0	1	0	0	1	1	0	1	1
<i>Ranunculus cassubicus</i>	0	0	0	0	0	1	0	0	0	1	0	1	1
<i>Galium odoratum</i>	0	0	0	0	0	0	1	0	0	1	1	0	1
<i>Quercus petraea</i> (S)	0	0	0	0	0	0	0	1	0	0	0	1	1
<i>Ajuga reptans</i>	0	0	0	0	0	0	0	0	1	1	1	1	1
<i>Euphorbia amygdaloides</i>	0	0	0	0	0	0	0	0	1	1	1	1	1
<i>Galium aparine</i>	0	0	0	0	0	0	0	0	1	1	1	0	1
<i>Carex sylvatica</i>	0	0	0	0	0	0	0	0	0	1	1	1	1
<i>Prunus avium</i> (S)	0	0	0	0	0	0	0	0	1	0	1	0	1
<i>Maianthemum bifolium</i>	0	0	0	0	0	0	0	0	1	0	1	0	1
<i>Crataegus monogyna</i> (S)	0	0	0	0	0	0	0	0	1	0	1	0	1
<i>Evonymus europaeus</i> (S)	0	0	0	0	0	0	0	0	0	1	0	1	1
<i>Geum urbanum</i>	0	0	0	0	0	0	0	0	0	0	1	1	1
<i>Alliaria petiolata</i>	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Sanicula europaea</i>	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Melica nutans</i>	0	0	0	0	0	0	0	0	0	0	1	0	1
<i>Lathyrus vernus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Luzula pilosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	1
Total species richness	4	3	8	5	7	11	13	11	19	25	25	19	34
Mean species richness	5.0				10.5				22.0				-
Mean pH	-				-				-				5.7

The presence of species in the 1, 10 and 100 m² nested quadrats is indicated for each corner of the rectangular plot (S = saplings less than 1 m height).

Apart from the difference in soil fertility between “Făget” and “Zăpodie”, the former stand is conspicuously more mesic as indicated by its floristic composition (Tabs. 1 and 2). Both the lower species richness and herb layer cover

recorded in the “Zăpodie” stand are clearly related with the overall higher resource availability in the “Făget” stand.

Table 2: Mean soil pH value and occurrence of vascular species within the 20x50 m² plot (ABCD) located in the “Zăpodie” stand.

Area (m ²)	1				10				100				1000
Plot corner	A	B	C	D	A	B	C	D	A	B	C	D	ABCD
<i>Viola reichenbachiana</i>	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Hepatica nobilis</i>	0	1	1	0	1	1	1	1	1	1	1	1	1
<i>Acer campestre</i> (S)	0	0	1	1	1	0	1	1	1	1	1	1	1
<i>Crataegus monogyna</i> (S)	0	0	1	1	1	0	1	1	1	1	1	1	1
<i>Rosa canina</i> (S)	0	0	0	1	0	0	1	1	0	1	1	1	1
<i>Hypericum perforatum</i>	0	0	0	1	0	0	0	1	0	0	0	1	1
<i>Melica nutans</i>	0	0	0	0	1	1	1	0	1	1	1	1	1
<i>Lamium galeobdolon</i>	0	0	0	0	1	1	1	0	1	1	1	1	1
<i>Evonymus europaeus</i> (S)	0	0	0	0	1	0	1	1	1	1	1	1	1
<i>Quercus cerris</i> (S)	0	0	0	0	0	1	1	0	1	1	1	1	1
<i>Polygonatum odoratum</i>	0	0	0	0	0	1	1	0	0	1	1	1	1
<i>Euphorbia amygdaloides</i>	0	0	0	0	0	0	1	1	0	0	1	1	1
<i>Melica uniflora</i>	0	0	0	0	0	0	1	1	0	0	1	1	1
<i>Geum urbanum</i>	0	0	0	0	0	1	0	0	0	1	1	1	1
<i>Prunus avium</i> (S)	0	0	0	0	0	0	1	0	0	0	1	1	1
<i>Mercurialis perennis</i>	0	0	0	0	0	1	0	0	0	1	0	0	1
<i>Campanula persicifolia</i>	0	0	0	0	0	0	0	1	0	0	0	1	1
<i>Ranunculus auricomus</i>	0	0	0	0	0	0	0	1	0	0	0	1	1
<i>Pulmonaria officinalis</i>	0	0	0	0	0	0	0	0	0	0	1	1	1
<i>Helleborus purpurascens</i>	0	0	0	0	0	0	0	0	0	0	1	1	1
<i>Stellaria holostea</i>	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Acer platanoides</i> (S)	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Melittis melissophyllum</i>	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Neottia nidus-avis</i>	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Aposeris foetida</i>	0	0	0	0	0	0	0	0	0	0	0	0	1
Total species richness	1	2	4	5	7	8	13	11	10	12	16	19	25
Mean species richness	3.00				9.75				12.50				-
Mean pH	-				-				-				5.1

The presence of species in the 1, 10 and 100 m² nested quadrats is indicated for each corner of the rectangular plot (S = saplings less than 1 m height).

The main distinction between the species-area curves fitted for the two study sites is mostly due to the larger value of *c* in case of the “Făget” stand (Fig. 2), which determines a much steeper curve in the domain of small scales (below 50 m²). The hypothesis of a positive relationship between the *c* value and the level of soil resources in the two study stands is fully confirmed, especially because the difference in *z* values is negligible. This is also confirmed by the almost parallel tails of the two curves toward large scales (over 500 m²), and suggests the existence of similar spatial patterns of habitat microheterogeneity within the two stands.

The increase in grain size (keeping constant the extent) causes a deformation of species-area curves: the value of *c* and *z* is larger and respectively, lower than its counterpart determined previously (Fig. 3A and B). However, the error in the

estimation of species richness is very low at small-medium scales, but increases proportionally with the augmentation of the area considered. In particular, species richness is likely to be largely underestimated at the forest community level ($>400 \text{ m}^2$).

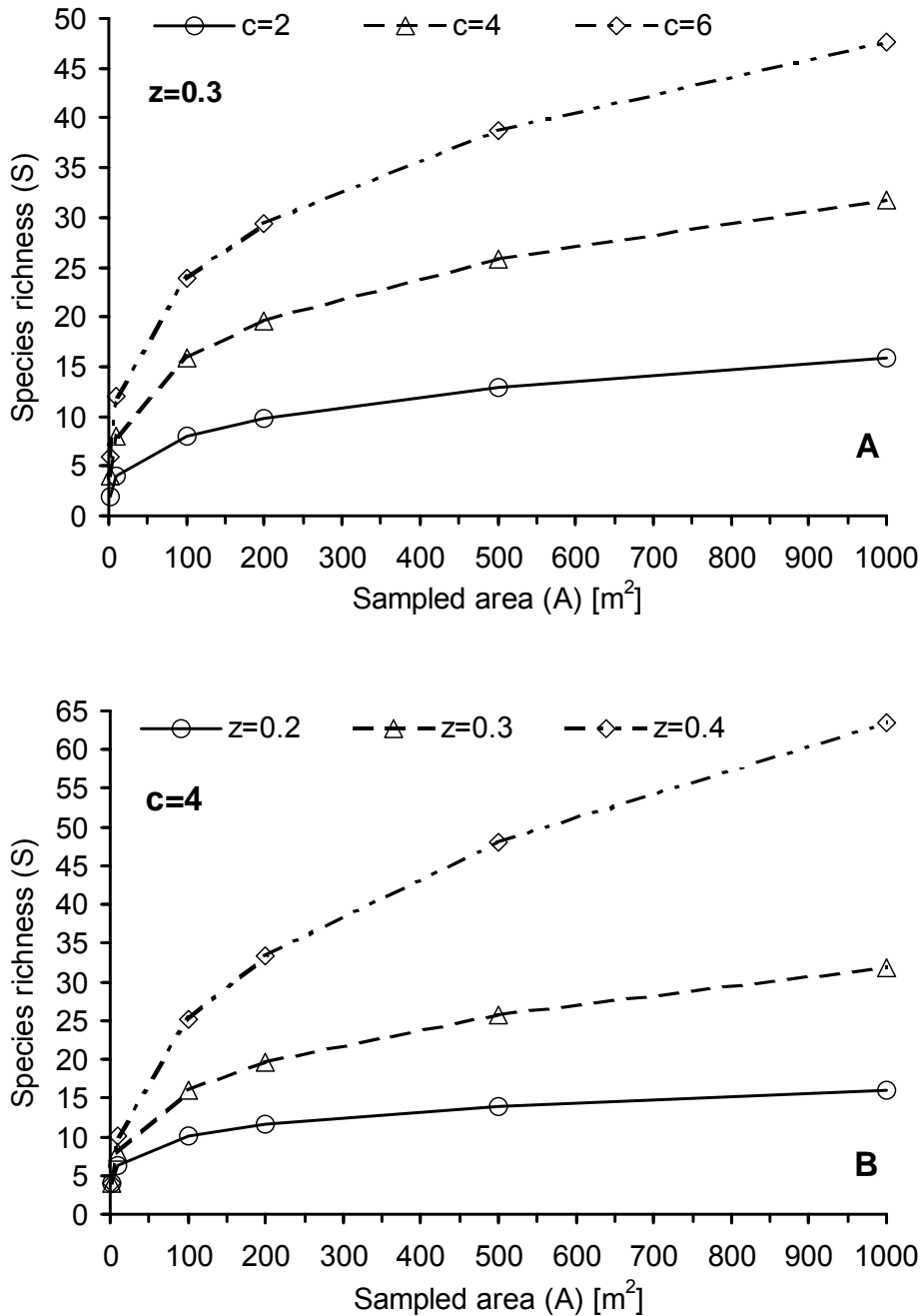


Fig. 1: Simulated changes in shape (slope) of species-area curves determined by the independent variation in c and z parameters of the related power equation (A – z is fixed and c is varied; B – c is kept constant and z takes different values).

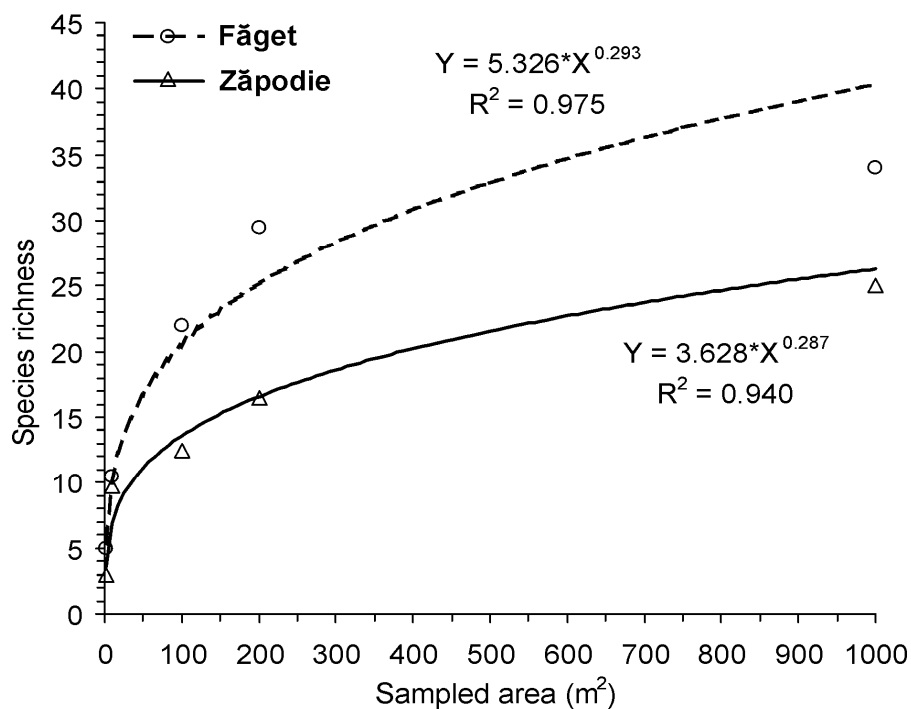


Fig. 2: Fitted species-area curves based on mean species richness in nested quadrats for the two forest understory stands (“Făget” and “Zăpodie”).

Decreasing the extent while grain size is held invaried, produces an opposite effect on the shape of species-area curves (Fig. 3A and B). However, in this case there is almost no variation in c values comparing with the reference equations. This is probably because the parameter c is influenced by the size of samples with low degree of nestedness (i.e., the small ones). The last inference is consistent with the observation that the c values affect the slope of the first part of species-area curves. By using a lower extent the species richness can be overestimated, although the errors are not significant as long as the decrease in slope of the species-area curve is gradual. In case of communities with a low habitat microheterogeneity, but developed on fertile sites (as the “Făget” stand), the slope changes abruptly and the errors may become larger (Fig. 3A).

Discussion

None of the fitted species-area curves show any tendency to flatten, despite the largest sampling plot (1000 m²) is twice the size of minimum area assumed for most temperate forest communities [9,28]. This outcome does not seem to be a bias due to the incomplete inventory of species composition (i.e., within herb layer only), as we have neglected one-two woody species at most, considering the absence of a shrub layer and the homogeneity of the tree canopy. A patchy distribution of disturbance patterns within the study forest stands may be responsible for the steady increase of species even at large scales. Similar elevated

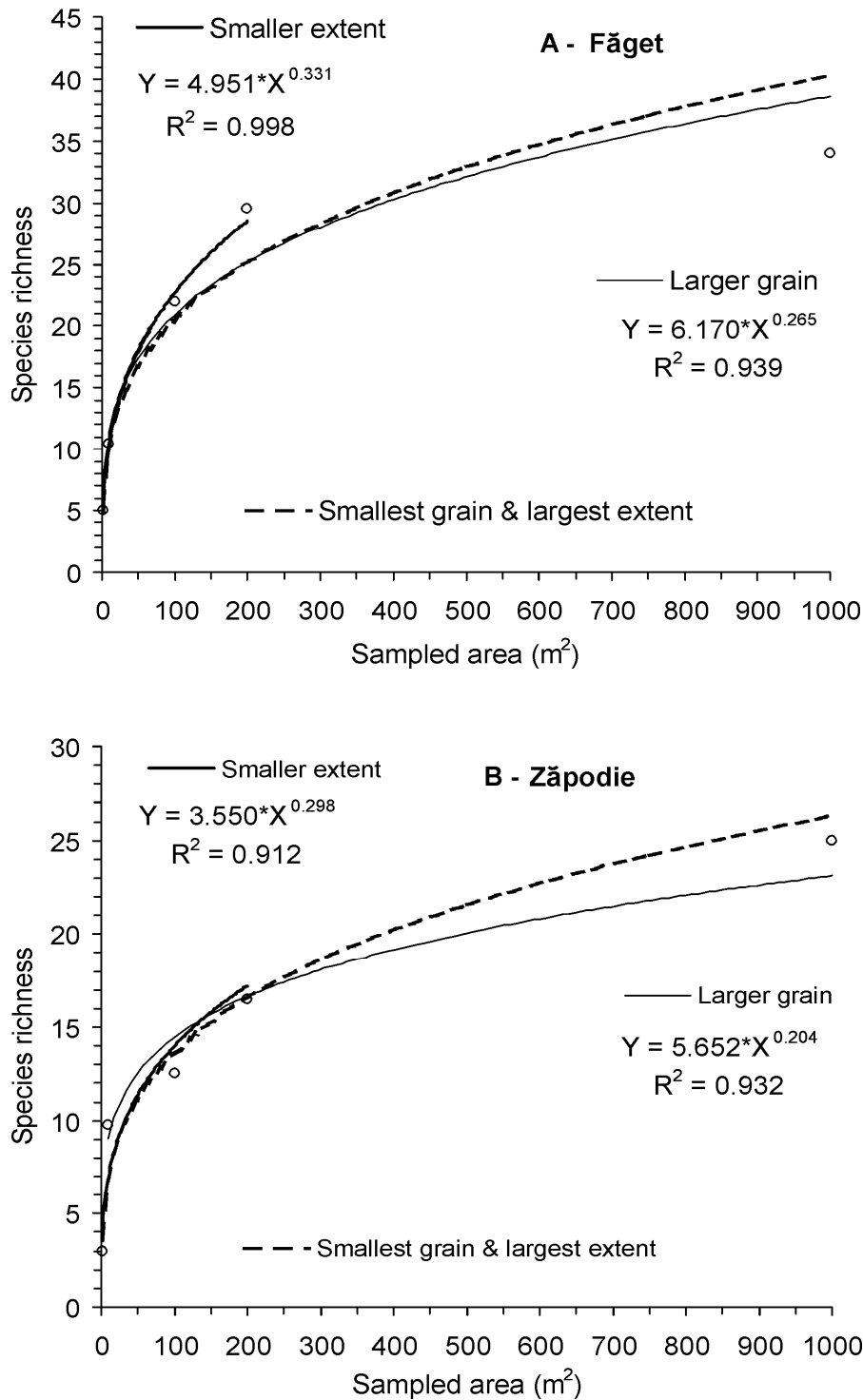


Fig. 3: Fitted species-area curves for the “Făget” (A) and “Zăpodie” (B) stands at different grains or extents (the complete curve corresponding to the smallest grain and largest extent is drawn for reference).

slopes (z values) of species-area curves have also been found in man-disturbed forest communities by Kwiatkowska (1994).

We do found the value of parameter c being larger in case of forest floor vegetation developed on fertile sites, but other factors may interfere with this

complex ecological relationship. In particular, the observed pattern may be completely overcome by the strong dominance of one or two herb species, which may occur in certain disturbed forests via nitrophization, intensive trampling and so on.

Between the two components of scale considered here, the grain has the largest effect on the shape of species-area curves. It should be stressed that the influence of grain upon the slope of these curves depends also on the size of individual plants or clumps [20]. In fact, species-area curves for small grains begin with very low slopes, simply because few individuals can fit into a sampling quadrat. The grain size used in the present study (1m^2) was large enough to avoid that species richness be constrained by such kind of disproportion.

The magnitude of the effect exerted by extent seems to be controlled by site fertility, but specific and detailed investigations should be undertaken in order to confirm this hypothesis. Apart from this, it is likely to exist a hidden and subtle influence of extent, which is related to distance decay (also known as spatial autocorrelation). Many authors have been recently highlighted an almost universal property of spatially based data, i.e. nearby environments are generally more similar to each other than distant ones [12,13,19]. In our specific case, sampling quadrats farther apart are floristically more different and contain more species in aggregate than closer quadrats. That's why the plot size (the sample with the highest degree of nestedness) as well as its shape (perimeter/area ratio) can influence the species richness estimated at a given scale.

We have discussed so far the role played by grain and extent assuming they affect independently the species richness estimation. However, there are some evidences of an interaction between them, e.g. the extent enlargement only increases the number of new species if the grain is large [20]. In addition, other components of scale (not considered here) cannot be fully controlled when varying the grain and/or extent. For example, if the total area (extent) is held constant, decreasing grain is necessarily accompanied by a reduction in the number of samples.

The above considerations indicate that the species-area relationship is quite complex, because of the combined influences of site conditions (overall fertility and spatial heterogeneity), plant species traits (size and vegetative spreading patterns), community structure (species spatial patterns and distribution of abundances) and scale (grain, extent, number of samples). Therefore, these curves tend to estimate species richness poorly, especially at scales larger than the extent of sampling, and their classic use for minimum area detection seems to be misleading [16,18]. Nevertheless, the species-area curves possess certain regularities and will continue to represent a useful tool for searching patterns at community, landscape and regional scales.

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INFLUENȚA FERTILITĂȚII STAȚIUNII FORESTIERE ȘI SCĂRII EȘANTIONAJULUI ASUPRA CURBEI AREAL-SPECIE

(Rezumat)

Atât fertilitatea stațiunii, evaluată expeditiv prin intermediul acidității solului și valorii indicatoare de umiditate a speciilor vasculare, cât și scara de observație, exprimată prin mărimea eșantionului elementar (rezoluția) și extinderea suprafeței inventariate, au o influență sensibilă asupra formei curbei areal-specie. Aceasta a fost modelată pe baza valorilor parametrilor c și z ai ecuației de regresie $S = c \times A^z$, folosită pentru ajustarea distribuției numărului de specii (S) în funcție de suprafață (A).

Spre deosebire de parametrul z care afectează panta curbei pe întreaga ei lungime, parametrul c controlează exclusiv panta primei părți a curbei, corespunzătoare suprafețelor mici. Valoarea mai ridicată a parametrului c obținut în cazul arboretului din Făget se poate atribui în totalitate condițiilor staționale mai favorabile, întrucât valorile parametrului z sunt foarte apropiate între cele două ecuații de regresie ("cozile" curbilor sunt aproape paralele).

Folosirea unui eșantion elementar de mărime superioară a determinat o deformare sensibilă a curbei corespunzătoare arboretului din Zăpodie, datorită căreia erorile de subestimare a bogăției specifice la scări de peste 400 m² devin semnificative. Reducerea suprafeței inventariate a produs o deformare mai slabă a curbilor, în special datorită variației reduse a parametrului c . Cu toate acestea, erori semnificative de supraestimare a bogăției specifice pot apare tot la scări relativ mari, în cazul fitocenozelor situate în stațiuni fertile, dar cu heterogenitate spațială redusă (curbele cu aplatizare bruscă).

Deși curbele areal-specie obținute prin regresie neliniară nu au tendința să se aplatizeze până la o suprafață inventariată de 1000 m², pare neverosimil ca aceasta să se datoreze efectuării releveelor floristice exclusiv în stratul ierbos (mai ales că stratul arbuștilor era absent, iar stratul arborilor este aproape monospecific), ci mai degrabă antropizării care a condus probabil la o mozaicare secundară a biotopului prin îmbogățirea în azot, băcătorirea solului, etc.

Observațiile noastre, ca și alte studii anterioare, par să indice că influența scării de observație asupra preciziei de estimare a numărului de specii pe o suprafață de o anumită mărime se manifestă și prin interacțiunea dintre eșantionul elementar și extindere, numărul suprafețelor de probă și autocorelația spațială dintre acestea.