

Species constancy depends on plot size – a problem for vegetation classification and how it can be solved

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Abstract

Question: While it is well known that species richness depends on plot size, it is not generally recognised that the same must be true for constancy. Accordingly, many authors use varying plot sizes when classifying vegetation based on the comparison of constancies between groups of plots. We ask whether the constancy-area relationship follows a general rule, how strong the effect of plot sizes is on constancies, and if it is possible to correct constancies for area.

Location: For empirical evaluation, we use data from plant communities in the Czech Republic, Sweden and Russia.

Methods: To assess the potential influence of differences in plot size on constancies, we develop a mathematical model. Then, we use series of nested plot species richness data from a wide range of community types (herbaceous and forest) to determine the parameters of the derived function and to test how much the shape of the constancy-area relationship depends on taxa or vegetation types.

Results: Generally, the constancy-area relationship can be described by $C(A) = 1 - (1 - C_0)^{(A/A_0)^d}$, with C being constancy, A area, C_0 known constancy on a specific area A_0 , and d a damping parameter accounting for spatial autocorrelation. As predicted by this function, constancies in plant communities always varied from values near 0% to near 100% if plot sizes were changed sufficiently. For the studied vegetation types, a two- to fourfold increase in plot size resulted in a change of conventional constancy classes, i.e. an increase of constancy by 20% or more.

Conclusions: Vegetation classification, which largely relies on constancy values, irrespective of whether traditional or modern fidelity definitions are used, is strongly prone to

distorting scale effects when relevés of different plot sizes are combined in studies. The constancy-area functions presented allow an approximate transformation of constancies to other plot sizes but are flawed by idiosyncrasies in taxa and vegetation types. Thus, we conclude that the best solution for future surveys is to apply uniform plot sizes within a few *a priori* delimited formations and to determine diagnostic species only within these formations. Finally, we suggest that more detailed analyses of constancy-area relationships can contribute to a better understanding of species-area relationships because the latter are the summation of the first for all species.

Keywords: Constancy-area relationship; Fidelity; Phytosociology; Presence degree; Scale dependence; Species-area relationship; Synoptic table; Syntaxonomy; Vegetation database.

Abbreviations: A = area; C = constancy; d = damping coefficient.

Introduction

The scale of observation is important in community ecology in general (see Peterson & Parker 1998; Storch et al. 2007), and the species-area relationship is only the most obvious representation (e.g. Connor & McCoy 2001; Crawley & Harral 2001; Dengler 2009). Spatial scale also affects many other aspects of community composition and structure, such as species co-occurrence patterns (e.g. Otýpková & Chytrý 2006), species turnover along environmental gradients (e.g. Reed et al. 1993; Grytnes et al. 2008), spatial patterns of diversity

metrics (e.g. Kallimanis et al. 2008), and species frequency distributions (e.g. Gleason 1929; Dengler 2003). Moreover, different processes affect species richness patterns at different spatial scales (e.g. Cornell & Karlson 1997; Turner & Tjørve 2005). Last, but not least, scale also influences the “completeness” and reliability of observations (e.g. Chytrý 2001).

An increasing number of large databases provide vegetation plot data for many countries from all over the world (Ewald 2001). Such databases could potentially be the basis for well-founded supra-regional vegetation classifications, as well as for various other kinds of meta-analyses (Ewald 2003). Recently, several authors have developed approaches that allow the consistent classification of such large amounts of relevés (e.g. Bruelheide 2000; Chytrý et al. 2002; Dengler 2003; Knollová et al. 2005; Illyés et al. 2007; for review, see Dengler et al. 2008). Vegetation classifications that are consistent over larger geographical areas or even whole continents are thus a realistic aim for the future (e.g. the European Vegetation Survey, cf. Rodwell et al. 2002, and VegBank in North America, cf. Peet et al. 2001).

However, large differences in sizes of plots in these databases pose a serious, though commonly ignored, problem and the reliability of any classification or other data analysis based on them may be questioned. Chytrý & Otýpková (2003) found that, at the Europe-wide level, plot sizes used within one vegetation class differ by a factor of up to 50 000, with a median of 800. Plot sizes recommended by standard textbooks (Westhoff & van der Maarel 1973; Dierschke 1994; van der Maarel 2005) for different vegetation types span an immense range from $<0.1 \text{ m}^2$ for terricolous bryophyte and lichen communities to $>10\,000 \text{ m}^2$ for tropical rain forests. Even in many individual phytosociological studies, plots of varying size are used to sample vegetation of the same type. This lack of standardisation is probably due to the general belief that plot sizes are irrelevant as long as they exceed the so-called “minimal area”. This is defined as the smallest area that contains the total number of species of a plant community or a certain high proportion of it, e.g. 90% (Braun-Blanquet 1964; Westhoff & van der Maarel 1973; Dierschke 1994). However, the numerous proposed methods for determining “minimal areas” (e.g. Hopkins 1957; Moravec 1973; Barkman 1989) ignore the nature of species-area curves, which usually follow a power function (Arrhenius 1921; Preston 1962; Crawley & Harral 2001) and thus cannot exhibit an asymptote (e.g. Williamson et al. 2001; Dengler 2009).

It is likely that plot size has an important effect on the results of vegetation classification, but few authors have mentioned this problem (e.g. Jandt & Bruelheide 2002; Dengler 2003). First, plot size determines the “spatial grain” (Wiens 1989), i.e. whether a small-scale mosaic of vegetation is considered as one or as several communities (e.g. hollows and hummocks in a bog). Second, following from the species-area relationship, increasing plot sizes result in increasing constancy values of species.

“Constancy”, as the proportion of relevés containing a certain taxon within a set of relevés, is a fundamental concept in vegetation science. While Westhoff & van der Maarel (1973) restricted the term “constancy” to even-sized plots and suggested the use of the term “presence degree” when plot sizes vary, we apply “constancy” in both cases, following widespread practice. Most often constancy values are used in synoptic tables for a brief characterisation of vegetation units. Apart from this descriptive use, constancy values are important analytical tools for the delimitation and definition of vegetation types in the vast majority of approaches to vegetation classification, both in traditional phytosociology and in numerical classification. Traditional phytosociology uses the concept of fidelity to recognise character species (e.g. Braun-Blanquet 1964; Westhoff & van der Maarel 1973; Dierschke 1994), which requires the comparison of constancy values of species among communities. This comparison is either directly applied to percentage constancies (Schaminée et al. 1995; Dengler 2003; Willner et al. 2009) or to constancy classes (Szafer & Pawłowski 1927; Westhoff & van der Maarel 1973; Bergmeier et al. 1990; Willner 2001). Likewise, statistical approaches to determine diagnostic species (e.g. Hill 1979; Bruelheide 2000; Chytrý et al. 2002) are mostly based on the implicit comparison of constancy values of species in different sets of relevés. Statistical fidelity measures (u value, phi coefficient and Fischer’s exact test, for example) are now widely used in numerical vegetation classification (see Willner et al. 2009). These compare the observed frequency in a vegetation unit with the expected frequency under the assumption of random distribution using 2×2 contingency tables (Sokal & Rohlf 1995; Bruelheide 2000; Chytrý et al. 2002; de Cáceres et al. 2008). Because frequency is simply the product of constancy and number of relevés, the classification outcome is directly linked to the determined constancy values.

Changes in constancy values from near 0% to near 100% with increasing plot size have been mentioned and described several times in contexts other

than classification (Du Rietz 1922; Gleason 1929; Hopkins 1957; Moravec 1973; Nosek 1986). Still, this fact and its potentially distorting effects are largely ignored in vegetation classification (but see Dengler 2003). In this paper, we investigate the scale dependence of species constancies and its potential effect on classification results, both theoretically and empirically. Specifically, we address the following questions:

- How strongly are constancy values affected by spatial scale?
- Do changes in constancy values with plot size follow a general rule?
- Is it possible to correct constancy values for plot size?

Theoretical approach to constancy-area relations

While constancy (in the strict sense) is defined as the proportion of plots within a set of even-sized plots in which a certain species occurs, it can also be seen as the probability of this species to be present in a randomly chosen plot of this set. With this probabilistic interpretation, we come to the following notions for constancy values on a specific plot size A_0 :

C_0	= constancy value of species i for a given plot size A_0 = probability that species i occurs in a randomly chosen plot of size A_0
$1 - C_0$	= probability that species i does not occur in a randomly chosen plot of size A_0
$1 - (1 - C_0)^x$	= probability that species i occurs in at least one of x randomly chosen plots of size A_0

Those x plots of size A_0 together would cover a total area of size $A = x \cdot A_0$. However, if each of the A_0 plots were chosen randomly from the total area of the respective vegetation unit (referred to as “random case”), they together normally would not form a contiguous area. Theoretically, these subplots could even overlap or match, leading to a total area less than $x \cdot A_0$. Since the total area of a vegetation type commonly far exceeds that of the largest single plot, this potential reduction of the area becomes unimportant. With $A = x \cdot A_0$ and $x \in \{1; 2; 3; \dots\}$ we thus can note:

$$C(A) = 1 - (1 - C_0) \left(\frac{A}{A_0}\right) \quad (1)$$

This general expression does not directly apply to vegetation plots because they are normally contiguous (Dengler et al. 2008). This means that a larger vegetation plot of size A can be derived from a

smaller one of size A_0 by adding neighbouring areas of size A_0 (“contiguous case”). Such a contiguously added area A_0 will more closely resemble the small plot in its species composition than a randomly chosen second area of the same size, which can lie far away (for illustration of the idea, see Supporting Information, Appendix S1). This spatial autocorrelation (Legendre 1993) is due to the distance decay of both abiotic conditions and dispersal rates (e.g. Williamson 1988; Nekola & White 1999). Thus, in the “contiguous case”, the enlargement of the area will result in fewer additional species than in the “random case”. Consequently, the constancy values will increase more slowly with increasing plot size when dealing with real plots than with “plots” consisting of randomly distributed subplots (compare Supporting Information, Appendix S1):

$$C_{\text{contiguous}}(A) \leq C_{\text{random}}(A) \quad (2)$$

This relation can be modelled by introducing a damping coefficient d in Eq. 1, which accounts for the spatial autocorrelation. We then obtain:

$$C_{\text{contiguous}}(A) = 1 - (1 - C_0) \left(\frac{A}{A_0}\right)^d, \text{ with} \quad (3)$$

$$0 \leq d \leq 1$$

This function is also defined for areas that are non-integer multiples of the arbitrary base size A_0 , and, since there is no hysteresis, it is also applicable to areas smaller than A_0 (Fig. 1a).

Besides the decreasing mean similarity in species composition with increasing distance between plots, the “random model” deviates from reality in another aspect: plots combined in a constancy column are, in general, not randomly distributed in space and time. However, this can also be accounted for by the damping coefficient d in the contiguous model, so that no additional parameters are necessary.

With this conceptual model, we can tackle the following questions:

- Is d a constant or a function of C ?
- Does d depend on the identity of the species (e.g. taxonomic group, rarity) or the vegetation type?

Empirical evaluation of the conceptual model

Data sources

For evaluation of the model, we used nested plot series of species composition from different vegetation types and regions. The plot sizes of each series spanned several orders of magnitude. Twelve

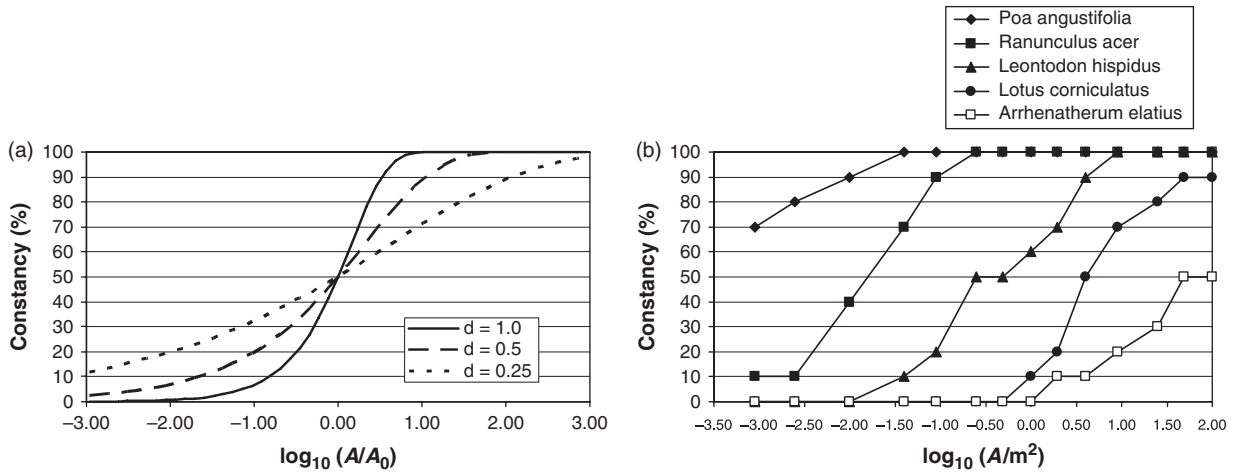


Fig. 1. Changes in the constancy values of species with increasing plot size. (a) Theoretical functions for $C_0 = 0.5$ and $d = 1, 0.5$ and 0.25 . (b) Exemplary empirical constancy transitions for five species of different commonness in the *Sanguisorbo-Deschampsietum* in the Czech Republic (data from Moravec 1973).

Table 1. Nested plot species composition data used for the analyses. For details of the plot arrangement, see the respective references. The data are from 12 communities at the level of association, four of which (*) constitute the suballiance *Tortello-Helianthemion*. Communities are arranged in three groups from top to bottom, namely various herbaceous communities, dry grasslands and forests. Minimum and maximum plot sizes as well as number of different plot sizes ($n_{Plot\ sizes}$) are given for each series of data. Both the total number of species ($n_{Species}$) and the proportion of these with constancy transitions that allowed inclusion in the calculations ($n_{Species, used}$) are indicated. The sample size, i.e. the number of nested plot series available per vegetation type, is indicated in the last column ($n_{Replicates}$). For Löbel (2002), also see Löbel & Dengler (2008).

Plant community	Class	Country	Source	Plot sizes (m ²)	$n_{Plot\ sizes}$	$n_{Species}$	$n_{Species, used}$	$n_{Replicates}$
<i>Caricetum vesicariae</i>	<i>Phragmito-Magno-Caricetea</i>	Czech Republic	Moravec (1973)	0.0625–64	11	15	6	10
<i>Sanguisorbo-Deschampsietum</i>	<i>Molinio-Arrhenatheretea</i>	Czech Republic	Moravec (1973)	0.0009–100	14	53	25	10
<i>Corispermum-Ammophila</i> comm.	<i>Ammophiletea</i>	Russia	Dolnik (2003)	0.01–900	14	15	9	9
<i>Crepido-Allietum*</i>	<i>Koelerio-Coryneporetea</i>	Sweden	Löbel (2002)	0.0001–9	11	145	83	10
<i>Fulgensio-Poetum*</i>	<i>Koelerio-Coryneporetea</i>	Sweden	Löbel (2002)	0.0001–9	11	83	51	4
<i>Helianthemo-Galietum*</i>	<i>Koelerio-Coryneporetea</i>	Sweden	Löbel (2002)	0.0001–9	11	127	54	5
<i>Gypsophilo-Globularietum*</i>	<i>Koelerio-Coryneporetea</i>	Sweden	Löbel (2002)	0.0001–9	11	141	79	6
Suball. <i>Tortello-Helianthemion</i>	<i>Koelerio-Coryneporetea</i>	Sweden	Löbel (2002)	0.0001–9	11	205	143	25
<i>Veronico-Avenetum</i>	<i>Festuco-Brometea</i>	Sweden	Löbel (2002)	0.0001–9	11	95	62	6
<i>Alnion glutinosae</i> comm.	<i>Alnetea glutinosae</i>	Russia	Dolnik (2003)	0.0001–900	16	265	178	20
<i>Dicrano-Pinion</i> comm.	<i>Vaccinio-Piceetea</i>	Russia	Dolnik (2003)	0.0001–900	16	238	119	12
<i>Luzulo-Fagetum</i>	<i>Quercetea robori-petraeae</i>	Czech Republic	Moravec (1973)	0.01–400	10	29	13	10
<i>Luzulo-Quercetum</i>	<i>Quercetea robori-petraeae</i>	Czech Republic	Moravec (1973)	0.0625–512	11	41	25	10

datasets were derived from three different studies (Table 1). We included vascular plants, terricolous bryophytes and lichens in the analyses, except for the dataset of Moravec (1973) as he only recorded vascular plants.

Determination of the damping coefficient d

The damping coefficient d can be obtained by solving Eq. 3: Let C_0 and C_1 denote the empirical

constancy values (i.e. contiguous case) for plots of two different sizes, A_0 and A_1 . Then

$$(1 - C_0) \left(\frac{A_1}{A_0}\right)^d = 1 - C_1 \quad (4)$$

$$\left(\frac{A_1}{A_0}\right)^d = \frac{\log_{10}(1 - C_1)}{\log_{10}(1 - C_0)} \quad (5)$$

$$d = \frac{\log_{10} \left(\frac{\log_{10}(1 - C_1)}{\log_{10}(1 - C_0)} \right)}{\log_{10} A_1 - \log_{10} A_0} \quad (6)$$

For every species occurring in one of the analysed vegetation types, we calculated d for each pair of possible neighbouring values of C . For example, when sample size was ten, only C values that are integer multiples of 10% occurred, and we calculated d values for the constancy transitions 10% \rightarrow 20%, 20% \rightarrow 30%, etc. using the values of C_0 , C_1 , A_0 and A_1 .

If we found the same constancy value for several subsequent plot sizes, we assigned the geometric mean of these plot areas to that constancy value. If, on the other hand, a certain constancy value between two other plots was not realised at all in our dataset, we used a semi-log interpolation between the neighbouring pairs of values to calculate it. Both interpolations are based on our conceptual model (Eq. 3), according to which constancy is a strictly monotonously increasing function of $\log(A)$. We therefore regarded all deviations from this strict monotony as a consequence of the small numbers of replicates that necessarily lead to stepped curve shapes. In the analyses, the constancy transitions from and towards the endpoints (0%, 100%) were excluded because the theoretical function (Eq. 3) can never reach these values.

The mean d values for a certain constancy transition within one vegetation type were calculated as geometric means of all species that showed this constancy transition in our dataset. The geometric mean was used because the data were usually strongly right-skewed. We assigned them to the mean constancy value of the start and end point of this constancy transition.

General results

With few exceptions, the constancies of all species in all communities increased with increasing plot size. The exceptions mostly occurred in communities represented by a particularly low number of replicates. In the community type with the highest number of available replicates, the *Alnion glutinosae*, for example, the constancy of all 265 species increased between 0.0001 and 900 m², but many species also showed increases for much smaller ranges of plot sizes (Table 2).

The shapes of individual constancy-area curves (Fig. 1b; see also Supporting Information, Appendix S2) matched the theoretical curves (Fig. 1a) in two fundamental aspects. Both were generally s-shaped in the semi-logarithmic representation, and they always exhibited a transition from constancy values at or near 0% to constancy values at or near 100% when plot size was sufficiently increased. None of the hundreds of species in the communities studied showed a different pattern, such as an invariant constancy at intermediate levels over several orders of spatial magnitude. Other differences concern a moderate variation of the steepness of the empirical curves in comparison with theoretical curves with a d value below 1. Finally, due to the finite number of replicates, only discrete values of C can occur in the empirical curves, leading to less smooth shapes than in the theoretical curves. Thus, the basic difference between different species was in the position of their curve along the x -axis, i.e. at which plot size they reached 50% constancy (Fig. 1b).

Table 2. Comparison of constancies of the *Alnion glutinosae* data (cf. Table 1, Fig. 2) for selected pairs of different plot sizes ($n = 20$ for each plot size). Number of species differs between the columns because some species are encountered only in the largest plots. The proportion of species showing no, insignificantly or significantly increased constancy in the larger plots is indicated according to Fisher's exact test (see Chytrý et al. 2002; $P < 0.05$). In the final six lines, the "fidelity" of the species to the larger plots is given when the two plot sizes were treated as different entities. The fidelity is assessed with the phi coefficient (see Chytrý et al. 2002), and the rating of the species into non-diagnostic, diagnostic and highly diagnostic species is done with thresholds of 0.25 and 0.50, following Chytrý (2007). The columns in bold roughly correspond to the plot size ranges used in Chytrý (2007) for all vegetation types (4–1000 m²) and forest vegetation (50–1000 m²).

Smallest plot (m ²)	0.0001	4	49	49	100	100	225
Largest plot (m ²)	900	900	900	100	400	225	400
Number of species	265	265	265	183	230	213	230
Proportion of species with no change in constancy	0%	3%	11%	58%	27%	47%	53%
Proportion of species with insignificant increase	60%	66%	77%	42%	73%	53%	47%
Proportion of species with significant increase	40%	30%	12%	0%	1%	0%	0%
phi coefficient (mean)	0.35	0.27	0.19	0.05	0.11	0.06	0.05
phi coefficient (min)	0.16	0.00	0.00	0.00	0.00	0.00	0.00
phi coefficient (max)	1.00	0.75	0.55	0.25	0.38	0.23	0.25
Proportion of non-diagnostic species	46%	58%	76%	100%	97%	100%	100%
Proportion of diagnostic species	35%	32%	23%	0%	3%	0%	0%
Proportion of highly diagnostic species	19%	9%	1%	0%	0%	0%	0%

The damping coefficient d decreased with increasing constancy for five of the 12 studied communities (for an example, see Fig. 2), while it showed no significant changes for the other seven (Supporting Information, Appendix S3). When, however, the four closely related associations of the *Tortello-Helianthemion*, which were represented by only a few replicates and individually did not show a significant pattern, were combined in this superior vegetation unit, they also exhibited a significant negative relationship (Supporting Information, Appendix S3). The damping coefficient for the study communities at 50% constancy was 0.46 ± 0.12 (mean \pm SD; Supporting Information, Appendix S3).

In a joint analysis of all communities – one point in the graph representing a mean of all species for a certain constancy transition in an individual community – we found a weak, yet significant, negative relationship between d and C (Fig. 3).

While the previous trends hold true for all species, individual species showed peculiarities in the parameters of the species-constancy relationship. The variation between species increased with increasing differences in plot size, especially when moving from larger to smaller plot sizes (for examples, see Supporting Information, Appendix S2).

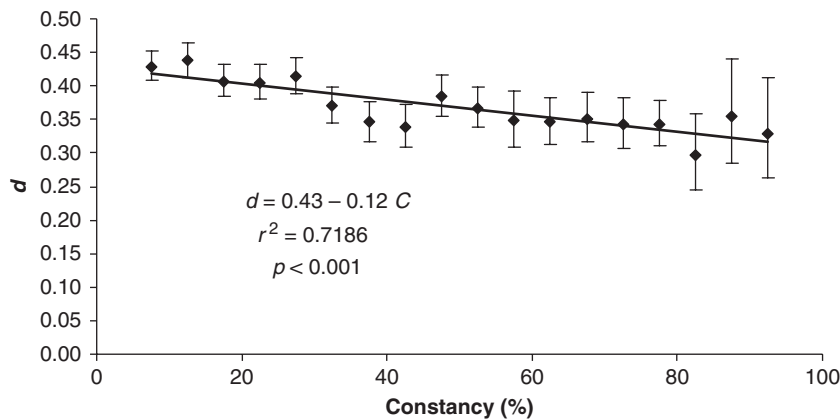


Fig. 2. Linear regression of the damping coefficient d versus the constancy C for *Alnion glutinosae* stands in Russia (data from Dolnik 2003). Each point represents the geometric mean for a certain constancy transition. The bars indicate the standard errors of the means. The larger standard errors towards higher constancies are mostly caused by the fact that fewer constancy transitions were available from those data for the calculation.

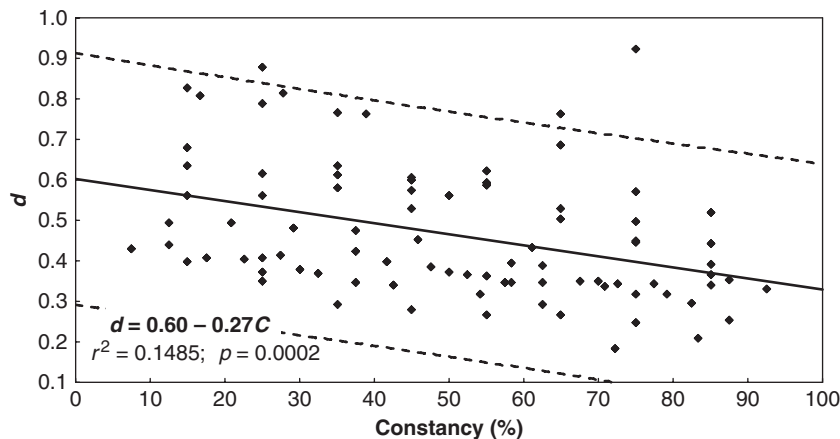


Fig. 3. Linear regression of the damping coefficient d versus the constancy C for all studied communities (see Table 1). Each point represents the mean value for a certain constancy transition in an individual community. The dashed lines indicate 95% prediction intervals.

Variability of the damping coefficient d

To evaluate whether these general findings on averages of species and communities also apply for specific situations, we compared subsets of species within the communities and analysed the differences between communities.

Common versus rare species

For five communities (*Sanguisorbo-Deschampsietum*, *Crepido-Allietum*, *Alnion glutinosae*, *Dicrano-Pinion*, *Luzulo-Quercetum*) we had sufficient data to test the dependence of d on the rarity of species (Supporting Information, Appendix S4). While species of all rarity classes showed the same fundamental curve shape as described above, they varied greatly and idiosyncratically regarding the slope of different parts of the d -constancy curve. Using d (50%) as an overall parameter for comparison, it turned out that this value either increased with rarity or did not show significant changes (Supporting Information, Appendix S4). This means that rarer species tended to have higher d values, that is, their constancy-area curves were slightly steeper.

Taxonomic groups

For four vegetation types (*Tortello-Helianthemion*, *Veronico-Avenetum*, *Alnion glutinosae*, *Dicrano-Pinion*), sufficient data were available to test whether d values differ between major taxonomic groups (vascular plants, bryophytes, lichens). The d -constancy curves were decreasing with similar slopes for vascular plants and bryophytes in three of the vegetation types, while in the fourth both showed a positive but insignificant increase (Supporting Information, Appendix S5a). The d values of bryophytes tended to be slightly lower than those of vascular plants, although this difference was significant only in one case (Supporting Information, Appendix S5b). By contrast, the d values of lichens never depended significantly on constancy, and they were not significantly different from either vascular plants or bryophytes (Supporting Information, Appendices S5a and Sb).

Species density

While species density of the vegetation types at 1 m² negatively influenced the intercept of the d -constancy curves ($P = 0.021$; Supporting Information, Appendix S6a), their slope was not significantly affected (Supporting Information, Appendix S6b). Generally, these relationships were

dominated by differences between the three distinguished major vegetation types.

Vegetation types

The d -constancy curves showed no clear and consistent differences between herbaceous and forest associations (Supporting Information, Appendix S7a). However, within the herbaceous vegetation, dry grassland associations had significantly flatter slopes and lower intercepts than other associations (Supporting Information, Appendix S7b).

Case study of plot size effects on fidelity

We used the best-documented community type of our study (*Alnion glutinosae*) to exemplify the effects of varying plot sizes on species constancy and statistical fidelity measures (Table 2). According to phi values and Fisher's exact test, comparing two series of plots of exactly the same community, but recorded with different plot sizes, would lead to the column with the larger plots being regarded as positively differentiated by a range of species. Their number increased with increasing ratio of the plot sizes. While approximately doubling the plot size (49 to 100 m²; 100 to 225 m² and 225 to 400 m²) did not yield any "diagnostic species" for the larger plots, a four-fold increase (100 to 400 m²) already gave eight (3%) such species. For the widest plot size range recorded (0.0001 to 900 m²), 54% of all 265 species were rated "diagnostic" or "highly diagnostic", including 40% for which this constancy increase towards larger plots was significant.

Discussion

How plot sizes affect classification

Using the regression function of Fig. 3, we calculated the expected average changes in constancy with increasing plot size for a broad range of different vegetation types (Table 3). Accordingly, every two- to fourfold increase in plot size would result in a change of constancy class. To visualise the potential impact of this scale-dependence on classification results, one may assume a certain species with 20% constancy in community A and 50% constancy in community B (see grey cells in Table 3). According to the definitions of Bergmeier et al. (1990) and Dengler (2003), this species would be accepted as a differential species of community B. If, however, the first community was recorded on plots half the size of those of the second, this assignment would prove

Table 3. Changes in the constancy values resulting from subsequent doubling of the plot size (from left to right), based on the regression function $d = 0.60 - 0.27 C$, derived for an array of different plant communities (see Fig. 3). The dashed lines delimit constancy ranges of 20% width, corresponding to the common five constancy classes in phytosociology. The values referred to in the text are highlighted in grey.

	A_0	$2A_0$	$4A_0$	$8A_0$	$16A_0$	$32A_0$	$64A_0$	$128A_0$
	0.05	0.07	0.11	0.16	0.24	0.34	0.47	0.61
	0.10	0.15	0.22	0.31	0.43	0.57	0.72	0.86
	0.15	0.22	0.31	0.43	0.58	0.73	0.86	0.95
	0.20	0.29	0.40	0.54	0.69	0.83	0.93	0.98
	0.25	0.35	0.48	0.63	0.78	0.90	0.97	1.00
	0.30	0.42	0.56	0.71	0.85	0.94	0.99	1.00
	0.35	0.48	0.63	0.78	0.90	0.97	0.99	1.00
	0.40	0.54	0.69	0.83	0.93	0.98	1.00	1.00
	0.45	0.60	0.75	0.88	0.96	0.99	1.00	1.00
	0.50	0.65	0.80	0.91	0.97	1.00	1.00	1.00
	0.55	0.70	0.84	0.94	0.99	1.00	1.00	1.00
	0.60	0.75	0.88	0.96	0.99	1.00	1.00	1.00
	0.65	0.80	0.91	0.97	1.00	1.00	1.00	1.00
	0.70	0.84	0.94	0.98	1.00	1.00	1.00	1.00
	0.75	0.88	0.96	0.99	1.00	1.00	1.00	1.00
	0.80	0.91	0.98	1.00	1.00	1.00	1.00	1.00
	0.85	0.94	0.99	1.00	1.00	1.00	1.00	1.00
	0.90	0.97	0.99	1.00	1.00	1.00	1.00	1.00
	0.95	0.99	1.00	1.00	1.00	1.00	1.00	1.00

to be wrong when removing the scale effect, because doubling the plot size in community A to obtain the same plot size as in community B would lead to an approximative constancy of 29% in community A. Thus, according to the differential species criterion (> twofold constancy), this species would actually not be differential for B. If the plots of community A were eight-times smaller, the species would be even more frequent in this community (54% versus 50%), despite the contrary impression that an uncorrected constancy table of both community types would give. As plot size also affects all other species' constancies, the two "communities" might be identical, and the differences highlighted in the synoptic table an artefact of differing plot sizes.

The picture is similar for statistical fidelity measures. As shown in Table 3, a fourfold difference in plot size already yielded eight "diagnostic" species for the larger plot relevés of the same community, a figure many researchers would accept as sufficient for the delimitation of an association (see Chytrý 2007). Thus, a simple increase in plot size by a factor of four could create such an artificial "association". While some of the "diagnostic species" in Table 2 were not valid according to Fisher's exact test due to the low number of replicates, this effect would not occur in large

vegetation tables with often hundreds or even thousands of relevés per column. However, the number of artificial diagnostic species may be much larger for those maximum plot size differences that have been accepted by recent vegetation monographs such as Chytrý (2007; see bold columns in Table 2).

Varying plot sizes as a problem

Despite peculiarities of species and vegetation types, constancy-area curves show a constancy transition from near 0% to near 100% if plot sizes are altered sufficiently. The shapes of the empirical curves could be well described by our conceptual model. Thus, constancy is not a fixed property of a certain taxon in a certain vegetation type, but a highly scale-dependent feature. For practical vegetation science, this means that it only makes sense to combine even-sized plots in constancy columns, and to compare constancy values between units that have been sampled with the same plot sizes.

The last decade brought enormous methodological developments towards statistically sound classification of vegetation relevés (e.g. Bruelheide 2000; Chytrý et al. 2002; Tichý 2005; Tichý & Chytrý 2006; Illyés et al. 2007; de Cáceres et al. 2008),

many of which are implemented in the freely available software package JUICE (see Tichý 2002). However, the quality and suitability of the relevé data has received much less attention. The problems of non-random sampling (e.g. Botta-Dukát et al. 2007; Roleček et al. 2007) and geographic biases (e.g. Knollová et al. 2005) have attracted at least some discussion and found partial solutions, but the distorting effects of varying plot sizes have largely been ignored. It has been common practice in large-scale vegetation overviews to include all available relevé data, irrespective of their plot sizes. Even the methodologically most advanced treatise of Chytrý (2007), though discarding the most extreme plot sizes, still accepts 4 to 100 m² for herbaceous vegetation and 50 to 1000 m² for forest vegetation. This means that the relevés within one structural type may differ by a factor of 20 or more in size. Since, however, species fidelity is assessed across all structural types in Chytrý (2007), there may even be a 250-fold difference in plot size.

Similarly, results of other studies relying on vegetation data with widely differing plot sizes may be distorted. For example, the differences in establishment of exotic species in different European riparian forest types reported by Schnitzler et al. (2007) could easily be an artefact because the authors did not check and correct for the different plot sizes applied in the vegetation studies used in their meta-analysis.

How to deal with the problem in old data

One way to use old vegetation data is to select only relevés within relatively narrow plot size ranges in order to minimize distorting effects of scale dependence. How much variance caused by plot size differences is acceptable depends on the requirements of a specific analysis. Table 3 can be used to set limits for maximum acceptable variation of plot sizes in a specific study. As a rule of thumb, our results indicate that serious problems are to be expected when mean plot sizes between compared units differ by more than a factor of two, or when constancy columns are based on relevés whose plot sizes vary by much more than a factor of five. To allow posterior assessment of possible plot size effects, the presentation of mean plot sizes (e.g. Berg et al. 2001) should be regarded as indispensable for any publication of synoptic vegetation tables.

Another way to overcome this problem is to transform constancy values to standard plot sizes. As described, an empirically parameterised constancy-area function based on our conceptual

model – be it a general one or one specifically derived for a certain vegetation type – can be used for this purpose. Empirical studies analysing constancy-area relationships for a much wider array of vegetation types and species than in our study would thus be desirable. However, the presented data already show that there is so much variation in *d* between vegetation types and taxa that the extrapolation of constancy values will always be prone to considerable error and will be reliable within relatively small plot size ranges at best.

How to deal with the problem in the future

For future surveys, the only appropriate solution is to apply uniform plot sizes for all vegetation types that will be jointly classified, or whose constancy values, species richness values or other scale-dependent properties will be otherwise compared. Here, proposals for standardisation for plots sampled for classification purposes such as those of Chytrý & Otýpková (2003) or Dengler (2003) show a way to go. These authors suggest two, three or four structural vegetation types that are distinguished *a priori* and then recorded with specific plot sizes for each. One single standard plot size for classification of all vegetation types worldwide would not be reasonable for many reasons (see Dengler 2003) and has not been proposed so far. It is important that the delimitation of such “formations” is unambiguous and that the new standard areas correspond to prevailing sizes in historical data in order to allow comparisons with these. While classification needs such standardisations that are widely agreed upon, for many other purposes it is highly desirable to study community patterns at different or various spatial scales because patterns and causations may vary depending on scale (Turner & Tjørve 2005). However, also in such studies, it would be advantageous to include the “standard sizes” to allow a wider use of the data beyond the original purpose.

As a consequence of applying different plot sizes in different structural vegetation types, the determination of “absolute” character species (e.g. Willner 2001, 2006) is impossible, at least when fidelity is essentially based on constancy comparisons (see Dengler 2003). It is important to note that it is only possible to determine the diagnostic value of species within sets of relevés with identical (or at least similar) plot sizes. For example, the proposal of Chytrý & Otýpková (2003) to record the alliance *Alyso-Sedion* with 4-m² plots but the other alliances

of the class *Koelerio-Corynephoretea* on 16-m² plots would prevent the sound determination of differential species between these units. Similarly, long-standing debates in phytosociology on whether certain species were diagnostic for woodland or herbaceous vegetation types appear meaningless as long as forest communities are recorded on much larger plots than herbaceous communities. When the diagnostic value of species is defined independently in *a priori* distinguished structural types, the same species can be a character species in more than one structural type (Dierschke 1992; Dengler 2003; Berg et al. 2004).

Constancy-area relationships in a wider context

In a recent synthesis, Storch et al. (2008) showed how various scale-dependent macroecological patterns are interrelated. Among the nine macroecological patterns mentioned by them is the occupancy-area relationship (*P*-area relationship), which in fact is quite similar to the constancy-area relationship explored in this article. The only differences are that these authors had much larger areas in mind (grid cells of 100 km² and more; see Šizling & Storch 2004) and that constancy is normally not based on random or systematic placement of the plots. Similar to occupancy-area relationships (Šizling & Storch 2004; Storch et al. 2008), constancy-area relationships are closely related to species-area relationships, with the latter being simply the summation of the constancy-area relationships of all species in a system. Because occupancy/constancy of a species cannot exceed a value of 1 (Šizling & Storch 2004), the usual unbound species-area relationships closely following power laws over many orders of magnitude (e.g. Williamson et al. 2001; Dengler 2009) can only emerge when species differ widely in their frequency (Šizling & Storch 2004; Tjørve et al. 2008). However, the latter seems to be a typical feature of real communities, as can be seen in Fig. 1b, where the five exemplary species differ by more than six orders of magnitude in the plot size on which they reach 50% constancy.

Based on the assumption of self-similar species distributions within finite areas, Šizling & Storch (2004) postulate that occupancy-area relationships should linearly increase in log-log scale until they reach $P = 1$, where they abruptly bend to the horizontal. The conceptual model for constancy-area relationships developed under different assumptions in this article results in a similar curve shape, with the only difference being that the change from the

linearly increasing to the horizontal branch of the curve in the log-log representation happens gradually (see Supporting Information, Appendix S8). According to the empirical data analysed in this study the gradual model seems to be more realistic. Actually, in most cases the *d* values decreased with increasing constancy (see Supporting Information, Appendix S3), meaning that the transition from the increasing to the horizontal branch of the constancy-area curve is usually even more gradual than suggested by our conceptual model. It will be a promising task for future studies to analyse the shapes of probability/constancy-area curves of various species in more detail and over a wider range of spatial scales because this can help to understand how (power law) species-area relationships come into being.

Acknowledgements. We are very grateful to Ingolf Kühn (Halle), Jörg Ewald (Freising), Norm Kenkel (Winnipeg), Erik Christensen (Probsteierhagen) and two anonymous reviewers, as well as Anna Augustin, Niels Dreber, Wiebke Hanke, Jens Oldeland, Ute Schmiedel, Tene Kwetche Sop and Dirk Wesuls (all Hamburg) for their valuable comments on earlier versions of this paper. Toby Spribille (formerly Göttingen), Curtis Björk (Clearwater) and Aiko Huckauf (Kiel) kindly improved our English.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Illustration of the idea underlying the conceptual model for constancy-area relationships.

Appendix S2. Effect of increasing and decreasing plot size on constancy values, exemplified with data of the *Sanguisorbo-Deschampsietum* from the Czech Republic (Moravec 1973).

Appendix S3. Dependence of the damping coefficient d on constancy C , tested with linear regression analysis.

Appendix S4. Dependence of the damping coefficient d on the rarity of species analysed for those five communities with sufficient data (i.e. ≥ 10 replicates and ≥ 25 species available for calculations; see Table 1).

Appendix S5. Comparison of the damping coefficients (d) and their dependence on constancy (C) between vascular plants, bryophytes, and lichens for four plant communities.

Appendix S6. Dependence of the function parameters of the d -constancy curves (a: intercept; b: slope) of the 12 communities at association level on mean species densities at 1 m^2 , tested with linear regression analysis.

Appendix S7. Comparison of the function parameters of the d -constancy curves between associations belonging to different structural types.

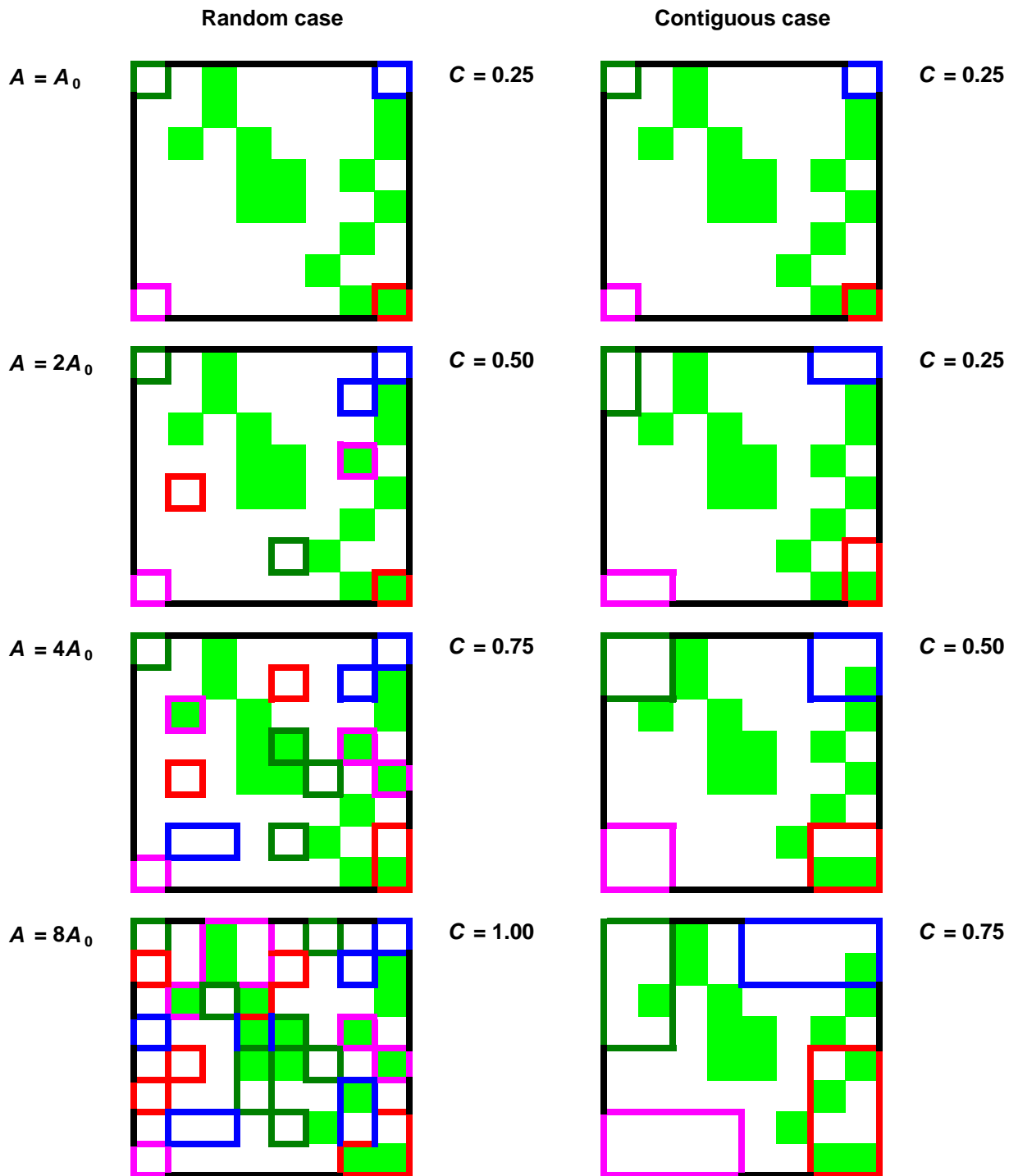
Appendix S8. Constancy-area relationships according to the conceptual model of this article compared to the model of Šizling & Storch (2004).

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Received 4 July 2008;

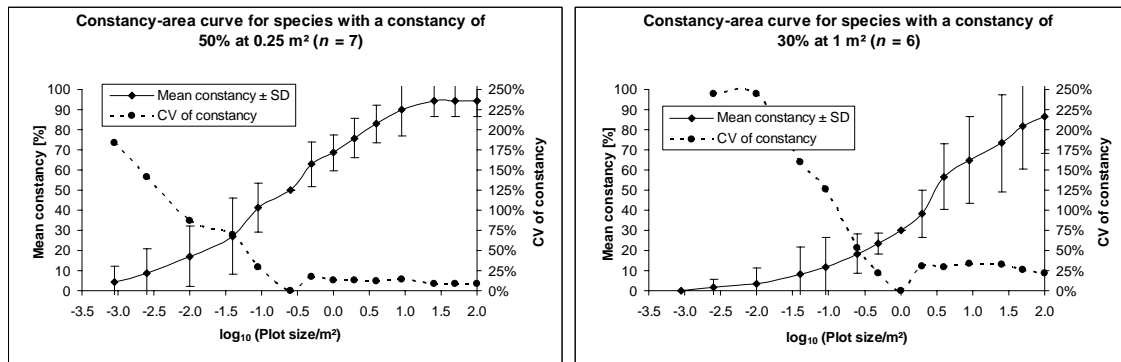
Accepted 26 March 2009.

Co-ordinating Editor: I. Kühn.



Electronic Appendix 1. Illustration of the idea underlying the conceptual model for constancy–area relationships. Imagine that the eight illustrations above each show the same 8 m × 8 m sector of a plant community. The light green 1-m² cells represent (the slightly autocorrelated) occurrences of a particular species with 25% (0.25) constancy at the 1-m² scale (A_0). In each figure, the combined areas outlined by one of the four colours (pink, red, blue, green) indicate a single ‘plot’ of sizes A_0 , $2A_0$, $4A_0$, and $8A_0$, respectively. In both columns, each outline colour corresponds to one successively increased plot (‘nested plot’). In the ‘random case’, each ‘plot’ of size $A = x \cdot A_0$ consists of x randomly placed subplots of size A_0 . In the contiguous case, corresponding to the practice in vegetation sampling, the larger sized plots are also contiguous. Note that such plot series do not need to start in the corners of the study sector and that subplots of different series can overlap. It is evident that constancy (C) necessarily

increases with increasing plot size in both cases, provided that constancy calculation is based on a sufficiently high number of replicates. However, the increase is faster in the 'random case' than in the 'contiguous case', provided that the occurrences of the species are somehow spatially autocorrelated. The precise C values (i.e. based on an infinite number of nested plot series) in the 'random case' would be 0.25, 0.44, 0.68 and 0.90.



Electronic Appendix 2. Effect of increasing and decreasing plot size on constancy values, exemplified with data of the *Sanguisorbo-Deschampsietum* from the Czech Republic (Moravec 1973). In both graphs, all those species were combined that had a certain constancy value at a certain plot size (as given in the header). Apart from mean constancies for all smaller and larger plot sizes, standard deviations (SD) and coefficients of variation (CV) among the species are also displayed in the figures.

Electronic Appendix 3. Dependence of the damping coefficient d on constancy C , tested with linear regression analysis. The number of data points (n) used for the regression is $n_{\text{Replicates}} - 2$. For the regression functions, explained variance, p value, slope, as well as predicted d values for three levels of constancy are presented. Communities are arranged in three groups from top to bottom, namely various herbaceous communities, dry grasslands and forests. The four associations constituting the suballiance *Tortello-Helianthemenion* are marked with an asterisk (*). At the bottom, summarizing statistics for all communities (except the suballiance) are provided.

Plant community	n	r^2	p	slope	d (0%)	d (50%)	d (100%)
<i>Caricetum vesicariae</i>	8	0.8156	0.002	-0.76	0.98	0.60	0.22
<i>Sanguisorbo-Deschampsietum</i>	8	0.7859	0.004	-0.28	0.70	0.56	0.42
<i>Corispermum-Ammophila</i> comm.	7	0.9207	0.001	-1.09	1.08	0.54	-0.01
<i>Crepido-Allietum</i> *	8	0.3229	0.149	-0.12	0.37	0.31	0.25
<i>Fulgensio-Poetum</i> *	2	1.0000	-	-0.14	0.48	0.41	0.34
<i>Helianthemo-Galietum</i> *	3	0.9380	0.121	-0.07	0.40	0.37	0.33
<i>Gypsophilo-Globularietum</i> *	4	0.6689	0.233	-0.13	0.42	0.36	0.29
Suball. <i>Tortello-Helianthemenion</i>	23	0.5087	<0.001	-0.23	0.41	0.30	0.19
<i>Veronico-Avenetum</i>	4	0.3776	0.460	0.07	0.38	0.41	0.45
<i>Alnion glutinosae</i> comm.	18	0.7186	<0.001	-0.12	0.43	0.37	0.31
<i>Dicrano-Pinion</i> comm.	10	0.8471	<0.001	-0.35	0.57	0.39	0.22
<i>Luzulo-Fagetum</i>	8	0.1519	0.331	0.22	0.52	0.63	0.74
<i>Luzulo-Quercetum</i>	8	0.4278	0.071	-0.30	0.76	0.61	0.46
Mean				-0.26	0.59	0.46	0.33
SD				0.36	0.24	0.12	0.18

Electronic Appendix 4. Dependence of the damping coefficient d on the rarity of species analysed for those five communities with sufficient data (i.e. ≥ 10 replicates and ≥ 25 species available for calculations; see Table 1). Rarity is expressed as $\log_{10}(A)$, with A being the area on which a species achieved a certain ‘starting constancy’, namely 10%, 30% or 50% (the number of available data points was too low to calculate it for larger constancies). This approach is based on the fact that constancy of every species increases with increasing plot size. For example, a species that reaches 10% constancy at a certain plot size can be termed more common (less rare) than another species that reaches the same constancy only for a larger plot size. Accordingly, for the presented analyses, species were grouped by their shared constancy values (first column) at a certain plot size. Second, mean damping coefficients for all constancy transitions were calculated for each such group according to the procedure given in the text. If the species group yielded values for at least 50% of the possible constancy transitions, these values were used to calculate a linear regression of d against C . With this regression function, the predicted d value was then determined at 50% constancy, as in Electronic Appendix 1. Finally, these d (50%) values were regressed against $\log_{10}(A)$. The results of the latter regressions are shown in the following tables for the five analysed communities. In these tables, n denotes the number of data points available for each regression. The intercept of the regression functions corresponds to d at 1 m² and the slope to the change in d when plot size is increased tenfold. Note that positive values of slope indicate increasing d values with increasing rarity of species.

a – *Sanguisorbo-Deschampsietum*

Starting constancy	n	intercept	slope	p
10%	10	0.700	0.033	0.007
30%	9	0.672	0.112	0.002
50%	10	0.451	-0.074	0.116

b – *Crepido-Allietum*

Starting constancy	n	intercept	slope	p
10%	7	0.569	0.079	0.015
30%	9	0.468	0.066	0.034
50%	8	0.259	-0.041	0.155

c – *Alnion glutinosae* community

Starting constancy	n	intercept	slope	p
10%	12	0.470	0.066	0.008
30%	12	0.331	0.024	0.518
50%	10	0.393	0.026	0.415

d – *Dicrano-Pinion* community

Starting constancy	n	intercept	slope	p
8%	13	0.709	0.182	0.021
33%	11	0.436	0.073	0.065
50%	13	0.454	0.041	0.209

e – *Luzulo-Quercetum*

Starting constancy	n	intercept	slope	p
10%	8	0.676	0.286	0.019
30%	7	0.382	0.145	0.493
50%	7	0.401	0.059	0.108

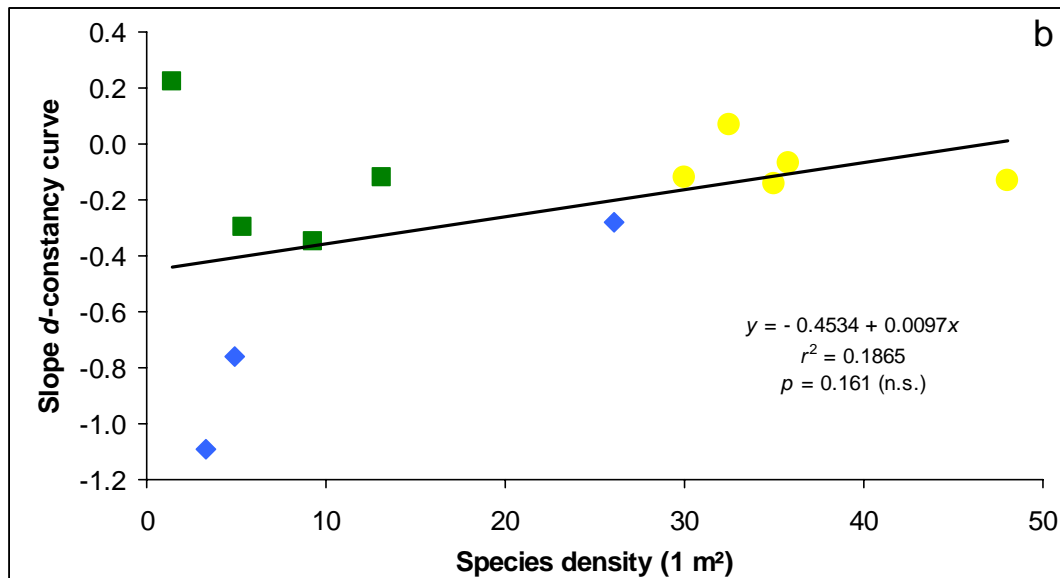
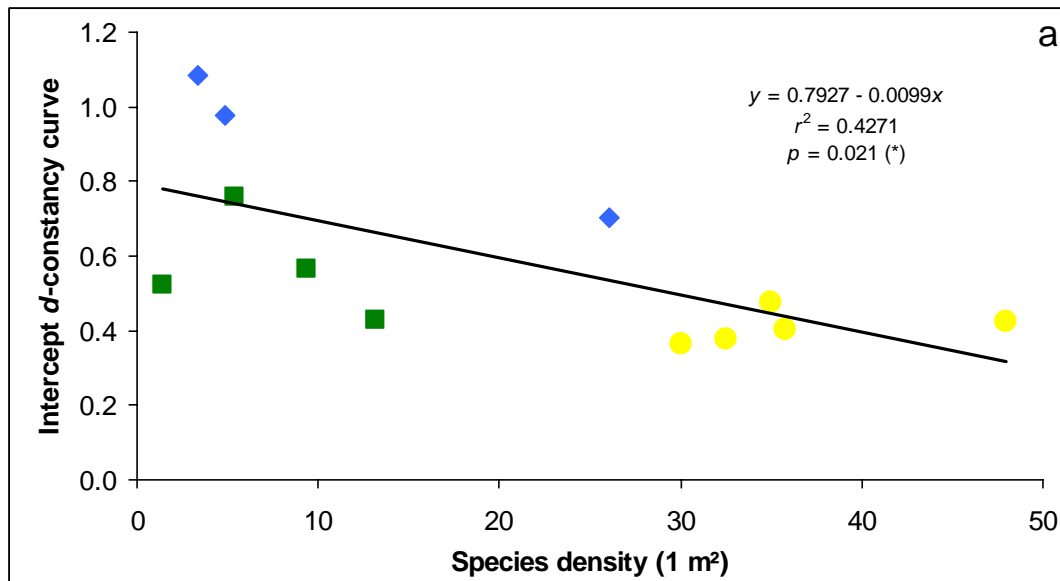
Electronic Appendix 5. Comparison of the damping coefficients (d) and their dependence on constancy (C) between vascular plants, bryophytes and lichens for four plant communities. In the upper part (a), the results of linear regression analyses of d on C are presented for the three taxonomic groups. In each case, the number of data points, the regression function, the p value, and the explained variance (r^2) are presented. The lower part (b) shows the results of pairwise t -tests between the d values of the three groups. Here, the number of data pairs, the mean difference in d (Δd) and the significance are provided. The p values of significant results at $\alpha = 0.05$ (for the multiple t -tests after Bonferroni correction) are in bold face in both tables.

a

Vegetation type	Vascular plants	Bryophytes	Lichens
Suball. <i>Tortello-Helianthemenion</i>	$n = 21$ $d = 0.433 - 0.212 C$ $p = 0.001$ $r^2 = 0.433$	$n = 23$ $d = 0.448 - 0.289 C$ $p < 0.001$ $r^2 = 0.356$	$n = 18$ $d = 0.353 - 0.110 C$ $p = 0.212$ $r^2 = 0.095$
<i>Veronico-Avenetum</i>	$n = 4$ $d = 0.403 + 0.073 C$ $p = 0.321$ $r^2 = 0.461$	$n = 4$ $d = 0.239 + 0.206 C$ $p = 0.404$ $r^2 = 0.356$	$n = 4$ $d = 0.385 - 0.054 C$ $p = 0.805$ $r^2 = 0.038$
<i>Alnion glutinosae</i> comm.	$n = 18$ $d = 0.455 - 0.153 C$ $p < 0.001$ $r^2 = 0.693$	$n = 18$ $d = 0.368 - 0.082 C$ $p = 0.144$ $r^2 = 0.129$	–
<i>Dicrano-Pinion</i> comm.	$n = 10$ $d = 0.583 - 0.347 C$ $p < 0.001$ $r^2 = 0.885$	$n = 10$ $d = 0.518 - 0.322 C$ $p = 0.026$ $r^2 = 0.483$	$n = 3$ $d = 0.749 - 1.259 C$ $p = 0.064$ $r^2 = 0.990$

b

Vegetation type	Vascular plants – bryophytes	Vascular plants – lichens	Bryophytes – lichens
Suball. <i>Tortello-Helianthemenion</i>	$n = 21$ $\Delta d = +0.019$ $p = 0.263$	$n = 18$ $\Delta d = +0.018$ $p = 0.338$	$n = 18$ $\Delta d = +0.017$ $p = 0.375$
<i>Veronico-Avenetum</i>	$n = 4$ $\Delta d = +0.097$ $p = 0.080$	$n = 4$ $\Delta d = +0.082$ $p = 0.119$	$n = 4$ $\Delta d = -0.016$ $p = 0.622$
<i>Alnion glutinosae</i> comm.	$n = 18$ $\Delta d = +0.051$ $p = 0.008$	–	–
<i>Dicrano-Pinion</i> comm.	$n = 10$ $\Delta d = +0.053$ $p = 0.086$	$n = 3$ $\Delta d = +0.016$ $p = 0.823$	$n = 3$ $\Delta d = -0.040$ $p = 0.541$



Electronic Appendix 6. Dependence of the function parameters of the d -constancy curves (a: intercept; b: slope) of the 12 communities at association level on mean species densities at 1 m^2 , tested with linear regression analysis. The different symbols of the communities indicate their structural type (green: forest communities; yellow: dry grassland communities; blue: other herbaceous communities).

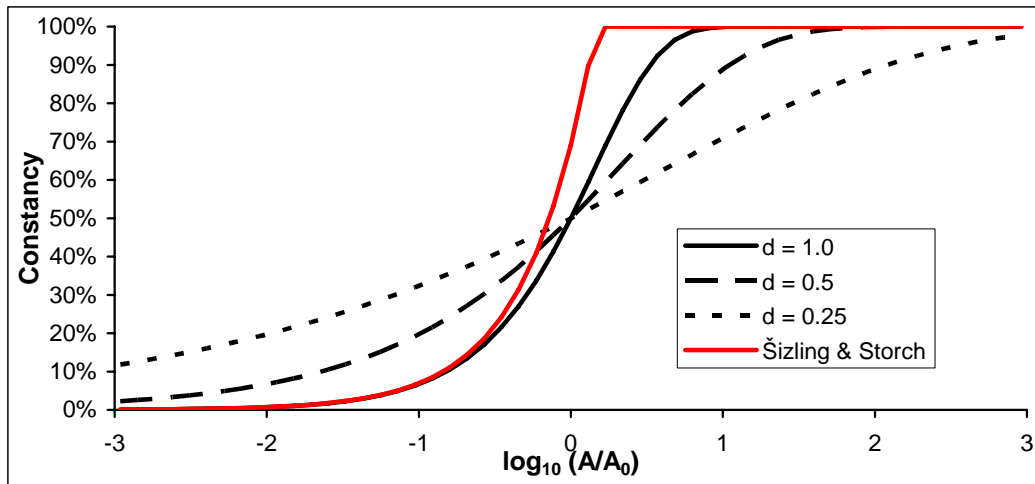
Electronic Appendix 7. Comparison of the function parameters of the d -constancy curves between associations belonging to different structural types. Slope as well as predicted d values for 0%, 50% and 100% constancy were tested using one-way ANOVAs. In the upper table (a), all herbaceous vegetation types are compared with the forest communities, while in the lower table (b) various other herbaceous types are compared to dry grasslands. In both cases, mean values for the parameters as well as p values are provided.

a

Parameter	Herbaceous types ($n = 8$)	Forest types ($n = 4$)	p
Slope	-0.32	-0.14	0.442
d (0%)	0.60	0.57	0.843
d (50%)	0.45	0.50	0.462
d (100%)	0.29	0.43	0.197

b

Parameter	Other herbaceous types ($n = 3$)	Dry grasslands ($n = 5$)	p
Slope	-0.71	-0.08	0.012
d (0%)	0.92	0.41	0.001
d (50%)	0.57	0.37	<0.001
d (100%)	0.21	0.33	0.273



Electronic Appendix 8. Constasy–area relationships according to the conceptual model in this article (with different d values as in Fig. 1a; in black) compared to the model of Šizling & Storch (2004; in red).