

Determination of diagnostic species with statistical fidelity measures

Chytrý, Milan¹; Tichý, Lubomír¹; Holt, Jason² & Botta-Dukát, Zoltán³

¹Department of Botany, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic; Fax +420541211214; E-mail chytry@sci.muni.cz, tichy@sci.muni.cz; ²Merhautova 151, CZ-613 00 Brno, Czech Republic; ³Institute of Ecology and Botany, Hungarian Academy of Sciences, H-2163 Vácrátót, Hungary; E-mail bdz@botanika.hu

Abstract. Statistical measures of fidelity, i.e. the concentration of species occurrences in vegetation units, are reviewed and compared. The focus is on measures suitable for categorical data which are based on observed species frequencies within a vegetation unit compared with the frequencies expected under random distribution. Particular attention is paid to Bruelheide's u value. It is shown that its original form, based on binomial distribution, is an asymmetric measure of fidelity of a species to a vegetation unit which tends to assign comparatively high fidelity values to rare species. Here, a hypergeometric form of u is introduced which is a symmetric measure of the joint fidelity of species to a vegetation unit and *vice versa*. It is also shown that another form of the binomial u value may be defined which measures the asymmetric fidelity of a vegetation unit to a species. These u values are compared with phi coefficient, chi-square, G statistic and Fisher's exact test. Contrary to the other measures, phi coefficient is independent of the number of relevés in the data set, and like the hypergeometric form of u and the chi-square it is little affected by the relative size of the vegetation unit. It is therefore particularly useful when comparing species fidelity values among differently sized data sets and vegetation units. However, unlike the other measures it does not measure any statistical significance and may produce unreliable results for small vegetation units and small data sets. The above measures, all based on the comparison of observed/expected frequencies, are compared with the categorical form of the Dufrene-Legendre Indicator Value Index, an index strongly underweighting the fidelity of rare species.

These fidelity measures are applied to a data set of 15 989 relevés of Czech herbaceous vegetation. In a small subset of this data set which simulates a phytosociological table, we demonstrate that traditional table analysis fails to determine diagnostic species of general validity in different habitats and large areas. On the other hand, we show that fidelity calculations used in conjunction with large data sets can replace expert knowledge in the determination of generally valid diagnostic species. Averaging positive fidelity values for all species within a vegetation unit is a useful approach to measure quality of delimitation of the vegetation unit. We propose a new way of ordering species in synoptic species-by-relevé tables, using fidelity calculations.

Keywords: Character species; Differential species; Frequency; Indicator species; Non-parametric statistics; Phytosociological database; Plant community; Vegetation classification.

Nomenclature: Ehrendorfer (1973).

Introduction

The diagnostic species is an important concept in vegetation classification (Whittaker 1962; Westhoff & van der Maarel 1973). Diagnostic species include species which preferably occur in a single vegetation unit (character species) or in a few vegetation units (differential species). Most frequently, diagnostic species are considered *a posteriori*, i.e. vegetation samples (relevés) are first classified by expert judgement or a numerical method, and then species with the highest concentration in particular vegetation units are determined as diagnostic. Diagnostic species are useful for identification of previously distinguished vegetation units in field surveys.

In European phytosociology, the concept of diagnostic species has been associated with fidelity, which is a measure of species concentration in vegetation units. However, hardly any attempt has been made to develop and apply a statistical measure of fidelity since Szafer & Pawłowski (1927) published a quantitative (yet intuitive and not statistical) guide to fidelity determination, which was taken over by Braun-Blanquet (1928) and also by some recent reviews and textbooks of vegetation classification (Westhoff & van der Maarel 1973; Dierschke 1994). Another intuitive approach was proposed by Bergmeier et al. (1990) who defined diagnostic (character) species as those whose frequency in the vegetation unit was at least two times higher and two frequency classes higher than in the other vegetation units. Generally, the intuitive approaches failed to find a balance between the frequency proportions and frequency differences within and outside the vegetation units and ignored the number of relevés in vegetation units and in the total data set (Barkman 1989).

A statistical measure related to fidelity was developed by Brisse et al. (1995). They used information on species co-occurrences (called fidelities in their terminology) in a large database to define 'species discrimi-

nation capability' (or 'discriminant power') for a vegetation unit. However, this measure evaluates each species on the basis of its co-occurrences with other species rather than according to its actual occurrence within and outside the vegetation unit. As a result, even a species absent from a particular vegetation unit can have a high positive discrimination capability for the vegetation unit. This approach is similar to the Index of Sociological Favourability proposed by Beals (1984) but it is not a direct measure of fidelity.

In this paper, we focus on fidelity measures suitable for categorical data. In vegetation data sets, species presences/absences give a more robust fidelity estimation than covers/abundances as they are less affected by temporal fluctuations and observer bias. In addition, arbitrary weighting of species abundances is avoided by using categorical data (Bruehlheide 2000). A promising approach to fidelity measuring is comparison of observed frequencies of species occurrence in the vegetation unit with the frequencies that would be expected if the species distribution was random. This is the theoretical basis of the fidelity measure u , developed by Bruehlheide (1995, 2000). Besides u there are more traditional methods which can be used to measure fidelity, e.g. the chi-square statistic (Goodall 1953; Juhász-Nagy 1964) or G statistic of the likelihood ratio test (also called G test or $2I$ test; Botta-Dukát & Borhidi 1999). Except for the implementation of the chi-square statistic in the TABORD program (van der Maarel et al. 1978), the use of statistical fidelity measures was limited to pilot studies and did not become widespread in vegetation science. Recently, Dufrêne & Legendre (1997) proposed an Indicator Value Index which is also suitable for measuring fidelity and is available in the PC-ORD package (McCune & Mefford 1999).

Determination of diagnostic species does not only depend on the appropriate fidelity measure but also on the data set structure. Usually, diagnostic species are determined in data sets which include only relevés of a single alliance, order or class, or of a few closely related vegetation units. Such diagnostic species may have a low potential for generalization, as species affinities to other vegetation units not included in the data set are ignored. With the availability of large phytosociological databases in recent years (Hennekens & Schaminée 2001), diagnostic species of more general validity should be preferably determined in data sets that include relevés of most vegetation types occurring in a wide area.

The objectives of this paper are (1) reviewing statistical methods suitable for measuring fidelity with categorical data; (2) defining relationships between different fidelity measures and testing their performance in data sets of varying structure; (3) discussing applications of statistical fidelity measures for determining

diagnostic species, evaluating vegetation units and ordering species in classified relevé tables.

u -values and other statistical measures of fidelity

Variables and contingency tables

We will use the same notation as Bruehlheide (1995, 2000):

- N = number of relevés in the data set;
 N_p = number of relevés in the particular vegetation unit;
 n = number of occurrences of the species in the data set;
 n_p = number of occurrences of the species in the particular vegetation unit.

Each relevé in which the species is present is counted as an occurrence of the species. We compare the observed distribution of these occurrences within the data set to what would theoretically be expected if such occurrences were distributed randomly. Observed frequencies can be summarized in the following 2×2 contingency table. They will be further referred to as $f(o)_i$, where $i = 1, 2, 3$, and 4 for the four fields of the table:

Number of relevés ...	in the vegetation unit	not in the vegetation unit
containing the species	n_p	$n - n_p$
not containing the species	$N_p - n_p$	$N - N_p - n + n_p$

Corresponding expected frequencies, further referred to as $f(e)_i$ are:

Number of relevés ...	in the vegetation unit	not in the vegetation unit
containing the species	$n \cdot N_p / N$	$n \cdot (N - N_p) / N$
not containing the species	$(N - n) \cdot N_p / N$	$(N - n) \cdot (N - N_p) / N$

u values

Bruehlheide (1995, 2000) proposed the fidelity measure u , which compares the observed number of occurrences of the species in the vegetation unit (n_p) with the expected number of occurrences ($\mu = n \cdot N_p / N$). The u value is defined as the deviation of the observed frequency of the species occurrence in the vegetation unit from the expected frequency, compared with the standard deviation (σ):

$$u = (n_p - \mu) / \sigma \quad (1)$$

In the 2×2 contingency table above, assuming that N , N_p and n are fixed quantities, which is the case in databases, the random variable n_p will have a hypergeometric distribution if occurrence of the species is independent of the vegetation unit. Therefore, we use

the standard deviation for a hypergeometric random variable (Sokal & Rohlf 1995: 94):

$$\sigma_{hyp} = \sqrt{n \cdot N_p \cdot (N - n) \cdot (N - N_p) / (N^2 \cdot (N - 1))} \quad (2)$$

We denote the corresponding u value as u_{hyp} . If the species and the vegetation unit co-occur more often than is expected, u_{hyp} will be positive and will indicate some degree of joint fidelity of the species to the vegetation unit and of the vegetation unit to the species (Juhász-Nagy 1964; Botta-Dukát & Borhidi 1999).

Bruehlheide (1995, 2000) used a binomial approach. For a binomial random variable,

$$\sigma_{bin} = \sqrt{K \cdot P \cdot (1 - P)} \quad (3)$$

where K is the number of trials and P is the probability of success (Sokal & Rohlf 1995: 77).

In Bruehlheide's approach, a trial is a relevé containing the species in question. There are n such relevés. Success is the event that the relevé belongs to the vegetation unit in question, and the probability of success is $P = N_p / N$. The assumption of this approach is that n and the relative size of the vegetation unit within the data set (N_p / N) are fixed quantities. Thus the standard deviation is computed as follows:

$$\sigma_{binB} = \sqrt{n \cdot (N_p / N) \cdot (1 - N_p / N)} \quad (4)$$

where the subscript *binB* indicates that this is Bruehlheide's binomial approach. The corresponding u value will be denoted as u_{binB} . If successes occur more frequently than expected, u_{binB} will be positive. This indicates that relevés containing the species are found to belong to the vegetation unit more often than would be expected by chance. This represents a degree of fidelity of the species to the vegetation unit.

There is an alternative binomial approach. We may take the set of N_p relevés belonging to the vegetation unit as our trials and let success be the event that a relevé contains the species in question. The probability of success estimated from the data is $P = n / N$. Here, we assume that N_p and the frequency of the species within the data set (n / N) are fixed. The standard deviation is

$$\sigma_{binA} = \sqrt{N_p \cdot (n / N) \cdot (1 - n / N)} \quad (5)$$

where the subscript *binA* denotes that this is the alternative binomial approach. The corresponding u value will be denoted as u_{binA} . If u_{binA} is positive, the species occurs in the vegetation unit more often than would be expected by chance. This represents a degree of fidelity of the vegetation unit to the species. Note that in either binomial case, as with the hypergeometric case, the

expected value $\mu = K \cdot P = n \cdot N_p / N$.

For completeness, we present here the formula for the standard deviation of a hypergeometric random variable as it is presented in Sokal & Rohlf (1995: 94):

$$\sigma_{hyp} = \sqrt{K \cdot P \cdot (1 - P) \cdot (N - K) / (N - 1)} \quad (6)$$

Regardless of whether the definitions of trial and success are chosen according to Bruehlheide's approach or the alternative approach, we get the value of σ_{hyp} given in Eq. 2. Because u_{hyp} is a measure of joint fidelity, the roles of the vegetation unit and the species can be reversed without affecting the u_{hyp} value.

The binomial u values are related to u_{hyp} by the following equations:

$$u_{binB} = u_{hyp} \cdot \sqrt{(N - n) / (N - 1)} \quad (7)$$

$$u_{binA} = u_{hyp} \cdot \sqrt{(N - N_p) / (N - 1)} \quad (8)$$

Phi coefficient

The value u_{hyp} is a measure of statistical significance, and thus it depends upon N , the number of relevés in the data set. More relevés give the results greater statistical significance and u_{hyp} is larger. As an example, consider the case of perfect joint fidelity: the species occurs exclusively within the vegetation unit and every relevé from the vegetation unit contains the species. In this case $n_p = n = N_p$. Calculation shows that $u_{hyp} = \sqrt{N - 1}$, regardless of the value of n_p . Perfect joint fidelity is given greater value if the data set is larger.

To compare u_{hyp} values from data sets of different sizes, we can normalize by dividing by the maximum value u_{hyp} can achieve within the database:

$$\Phi = \frac{u_{hyp}}{\sqrt{N - 1}} = \frac{N \cdot n_p - n \cdot N_p}{\sqrt{n \cdot N_p \cdot (N - n) \cdot (N - N_p)}} \quad (9)$$

This quantity is the phi coefficient of association (Sokal & Rohlf 1995: 741, 743). It is independent of the size of the data set. It takes values from -1 to $+1$. Positive values indicate that the species and the vegetation unit co-occur more frequently than would be expected by chance. Larger values indicate a greater degree of joint fidelity. The value 1 indicates that the species and the vegetation unit are completely faithful to each other.

chi-square statistic

The phi coefficient is closely related to the chi-square statistic (Sokal & Rohlf 1995: 697, 736). Computed for our 2×2 contingency tables above, the chi-square statistic can be reduced to the following form:

$$X^2 = \sum \frac{(f(o)_i - f(e)_i)^2}{f(e)_i} = \frac{N \cdot (N \cdot n_p - n \cdot N_p)^2}{n \cdot N_p \cdot (N - n) \cdot (N - N_p)} \quad (10)$$

Comparing X^2 with u_{hyp} ,

$$X^2 = u_{hyp}^2 \cdot N / (N - 1) \quad (11)$$

we see that the two statistics are essentially the same. An advantage of u_{hyp} over X^2 is that, whereas X^2 will take on positive values if the species and vegetation unit co-occur more often or less often than is expected, u_{hyp} distinguishes between positive and negative fidelity by taking positive values in the former case and negative values in the latter.

G statistic

The G statistic is an alternative to the chi-square statistic (Sokal & Rohlf 1995; Botta-Dukát & Borhidi 1999). Here, we express it in a computational form:

$$G = 2 \sum f(o)_i \cdot \ln[f(o)_i / f(e)_i] \quad (12)$$

Estimating probabilities and continuity corrections

If the species and the vegetation unit occur independently, both X^2 and G statistics have, approximately, a X^2 distribution with one degree of freedom. The hypergeometric distribution of u_{hyp} can be approximated by a standard normal distribution. If the statistics are sufficiently large, we can reject the null hypothesis of independence. For example, the probability that a normally distributed random variable will take on a value more than 1.96 standard deviations from the mean is less than 5%. Because u_{hyp} measures how many standard deviations n_p is distant from what would be expected if the species and the vegetation unit were independent (Eq. 1), we can say that values of $|u_{hyp}| > 1.96$ are statistically significant at $P < 0.05$.

The binomial u values will also have, approximately, a normal distribution under the appropriate null hypothesis. For u_{binB} , the null hypothesis is that among relevés containing the species, relevés belonging to the vegetation unit occur with probability $P = N_p / N$. For u_{binA} , the null hypothesis is that among relevés belonging to the vegetation unit, relevés containing the species occur with probability $P = n / N$.

These statistics are often used with a continuity correction to get more accurate estimates of the probability (P -value) that the observed results could have occurred by chance under the given null hypothesis. In the case of u values, Bruelheide (1995, 2000) used the following correction:

If $n_p - n \cdot N_p / N > 0.5$, then $u_{adj} = u - 0.5/\sigma$.
 If $n_p - n \cdot N_p / N < -0.5$, then $u_{adj} = u + 0.5/\sigma$.
 If $|n_p - n \cdot N_p / N| \leq 0.5$, then $u_{adj} = 0$.

Note that this correction can be substantial when σ is small.

X^2 can be adjusted by the Yates correction (Sokal & Rohlf 1995: 737):

$$X^2_{adj} = \frac{N \cdot \left(\left| N \cdot n_p - n \cdot N_p \right| - (N/2) \right)^2}{n \cdot N_p \cdot (N - n) \cdot (N - N_p)} \quad (13)$$

For the G statistic, the Williams correction can be used (Sokal & Rohlf 1995: 731):

$$G_{adj} = \frac{G}{1 + \frac{1}{6N} \left(\frac{N}{n} + \frac{N}{N-n} - 1 \right) \left(\frac{N}{N_p} + \frac{N}{N-N_p} - 1 \right)} \quad (14)$$

Fisher's exact test

With modern computing machinery, it is not necessary to resort to approximations and continuity corrections. Fisher's exact test for a right-tail hypothesis precisely calculates the probability of obtaining $f(o)_i \geq n_p$ (Sokal & Rohlf 1995: 730, 733). The calculation is based on the hypergeometric distribution. The smaller the calculated probability, the higher the fidelity.

$$P(f(o)_i \geq n_p) = \sum \frac{n! \cdot N_p! \cdot (N - n)! \cdot (N - N_p)!}{i! \cdot N! \cdot (n - i)! \cdot (N_p - i)! \cdot (N - N_p - n + i)!} \quad (15)$$

where the sum is taken over all $i \geq n_p$. In larger phytosociological data sets, Fisher's exact test may yield very small probability values, including those smaller than 10^{-100} , which are difficult to cope with in practical work. For this reason, $-\log_{10} P(f(o)_i \geq n_p)$ is a more practical quantity to use for a measure.

Dufrêne-Legendre Indicator Value Index

Dufrêne & Legendre (1997; see also Legendre & Legendre 1998: 369) proposed the Indicator Value Index (*IndVal*) which is also suitable for determination of fidelity. Unlike the above measures, it is not derived from the comparison of observed and expected frequen-

cies. A potential advantage of this index is that it considers species abundances; the disadvantage is that it ranges from 0 to 1, not distinguishing negative fidelity. Because it is becoming increasingly popular in ecology, we include it here in its categorical form for comparison. In Dufrêne & Legendre's (1997) use of this index, fidelity of a species to a vegetation unit is dependent on the delimitation of other vegetation units in the rest of the data set. In our case, we determine species fidelity by comparing the vegetation unit with the rest of the data set as a whole, disregarding any information about the partitions of the data set outside the vegetation unit in question. In this case, using our symbols, the Indicator Value Index for categorical data is expressed as

$$IndVal = \frac{n_p(N - N_p)}{n \cdot N_p - 2n_p \cdot N_p + n_p \cdot N} \cdot \frac{n_p}{N_p} \quad (16)$$

Material and Methods

To test the performance of statistical fidelity measures, we used a data set of 502 relevés of rock-outcrop dry grasslands (alliances *Festucion pallentis* and *Diantho lumnitzeri-Seslerion*) of the Czech Republic, classified into 8 vegetation units (Chytrý et al. unpubl.), called A-H in this paper. Classification was performed by the Cocktail method (Bruehlheide 1995, 2000). The number of relevés assigned to particular vegetation units has a wide range, from 11 to 204, which is a typical situation for classified relevé data sets. In some analyses, we added 15487 relevés of different types of herbaceous vegetation from the Czech National Phytosociological Database (Chytrý 1997) in order to investigate properties of different fidelity measures in data sets of larger size and different structure. These additional relevés include dry grasslands on deeper soils (not on rock outcrops), meadows, pastures, mountain grasslands, ruderal vegetation, wet grasslands and some other vegetation types. Only vascular plant records were considered because cryptogams were not sampled in some relevés.

Fidelity measures discussed in the previous section were calculated for all species and each of the 8 vegetation units by the computer program JUICE (Tichý 2001), which is freely available at the web site <http://www.sci.muni.cz/botany/juice.htm>. The statistics X^2 , G and all three types of u were each calculated both with and without continuity correction. Where continuity correction was applied, the measure is denoted as adjusted (*adj*). For each vegetation unit, species were ranked by decreasing fidelity, and species ranks produced by different measures were compared. Cluster

analysis (UPGMA, Chord Distance) of the fidelity measures based on standardized species ranks was calculated using the PC-ORD 4 package (McCune & Mefford 1999). The species ranks were standardized by dividing each rank value by the sum of all rank values for that species. Calculations were performed only with those species which were ranked among the 20 most faithful by at least one fidelity measure.

To demonstrate how fidelity calculations can be used for species ordering in phytosociological tables and to investigate the effect of data set structure on fidelity, we prepared two synoptic tables using JUICE. The first table (Table 5) includes only 502 relevés of the rock-outcrop-dry grasslands, each belonging to one of the 8 vegetation units. The second table (Table 6) includes the same relevés and 15487 additional relevés. For defining diagnostic species in these tables, the phi coefficient was used. Threshold Φ values for species to be diagnostic were arbitrarily set so as to yield 50 diagnostic species in each table. The threshold values were 0.417 for Table 5 and 0.154 for Table 6. For the latter data set, a lower threshold was necessary because the fidelity of several species decreased due to their occurrence in the additional relevés. The tables were shortened by deleting species without diagnostic capacity.

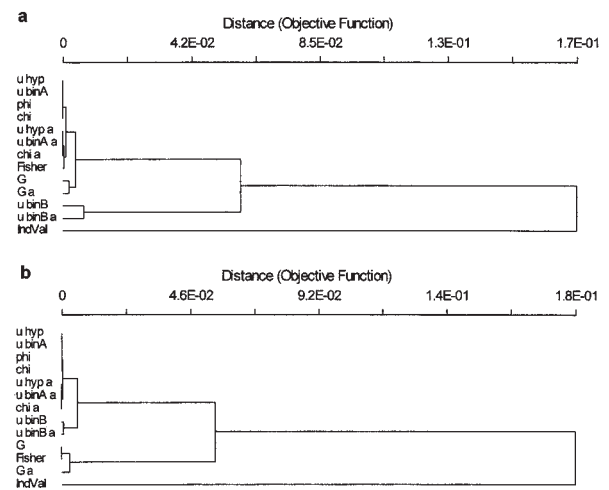


Fig. 1. Dendrogram based on standardized species ranks resulting from different fidelity measures (see Tables 1 and 2), determined for the vegetation unit A (204 relevés) in the data set of 502 relevés (a) and in the data set of 15898 relevés (b). The distance measure is Relative Euclidean (Chord Distance), the group linkage method is Group Average (UPGMA). The letter *a* denotes measures applied with the continuity correction.

Table 1. Ranks of species by decreasing fidelity with respect to vegetation unit A (204 relevés), calculated by different fidelity measures in the data set of 502 relevés. Only species ranked among the 20 most faithful according to at least one measure are included and species not ranked among 80 most faithful according to at least one measure are excluded. n = number of species occurrences in the entire data set, n_p = number of species occurrences in the vegetation unit.

	u_{hyp}	u_{hyp} adj	u_{binB}	u_{binB} adj	u_{binA}	u_{binA} adj	Φ	X^2	X^2 adj	G	G adj	Fisher	Ind Val	n	n_p
<i>Asplenium septentrionale</i>	1	1	1	1	1	1	1	1	1	1	1	1	2	190	154
<i>Aurinia saxatilis</i>	2	2	2	2	2	2	2	2	2	2	2	2	1	205	160
<i>Hieracium pallidum</i>	3	3	3	3	3	3	3	3	3	3	3	3	8	101	81
<i>Sedum reflexum</i>	4	4	4	4	4	4	4	4	4	4	4	4	6	144	103
<i>Thymus pulegioides</i>	5	5	5	5	5	5	5	5	5	5	5	5	7	126	89
<i>Artemisia campestris</i>	6	6	6	6	6	6	6	6	6	6	6	6	4	202	122
<i>Hieracium cymosum</i>	7	7	7	7	7	7	7	7	7	7	7	7	23	63	44
<i>Pulsatilla pratensis</i>	9	9	9	9	9	9	9	9	9	10	10	10	19	76	50
<i>Festuca pallens</i>	8	8	29	26	8	8	8	8	8	8	8	8	3	334	161
<i>Veronica dillenii</i>	10	10	8	8	10	10	10	10	10	9	9	9	38	27	23
<i>Hieracium umbellatum</i>	11	11	10	10	11	11	11	11	11	11	11	11	33	46	33
<i>Galium glaucum</i>	12	12	21	19	12	12	12	12	12	12	12	12	9	217	112
<i>Campanula rotundifolia</i> agg.	13	13	11	11	13	13	13	13	13	13	13	13	20	82	51
<i>Verbascum lychnitis</i>	15	14	15	15	15	14	15	15	14	15	15	14	17	98	57
<i>Hieracium sabaudum</i>	14	15	12	12	14	15	14	14	15	14	14	15	29	59	38
<i>Rumex acetosella</i> agg.	17	16	16	16	17	16	17	17	16	17	17	16	22	84	50
<i>Stipa joannis</i>	16	17	13	13	16	17	16	16	17	16	16	17	36	46	31
<i>Lychnis viscaria</i>	18	18	14	14	18	18	18	18	18	18	18	18	45	23	18
<i>Potentilla neummanniana</i>	19	19	18	17	19	19	19	19	19	19	19	19	35	51	33
<i>Anthericum liliago</i>	21	20	20	20	21	20	21	21	20	21	21	20	28	70	42
<i>Hieracium pilosella</i>	22	21	24	24	22	21	22	22	21	22	22	22	18	105	58
<i>Hieracium bauhini</i>	20	22	17	18	20	22	20	20	22	20	20	21	55	17	14
<i>Artemisia absinthium</i>	25	25	19	22	25	25	25	25	25	24	24	25	52	21	16
<i>Dianthus carthusianorum</i> agg.	28	28	35	34	28	28	28	28	28	29	29	28	11	179	89
<i>Euphorbia cyparissias</i>	27	27	49	42	27	27	27	27	27	28	28	27	5	324	148
<i>Sedum maximum</i>	46	44	48	46	46	44	46	46	44	46	44	44	15	151	72
<i>Allium montanum</i>	79	74	80	77	79	74	79	79	74	79	78	77	10	271	113

Results and Discussion

Empirical comparison of fidelity measures

Species ranks yielded by different fidelity measures for a single vegetation unit are compared in Fig. 1 and Tables 1 and 2. Two cases are shown: a vegetation unit which is (a) large and (b) small relative to the size of the data set. Both cases are represented by vegetation unit A (204 relevés), treated in the data sets of 502 and 15 989 relevés, respectively.

Due to the relationships among them, u_{hyp} , u_{binA} , Φ , and X^2 yield exactly the same species ranks in both cases. If u_{hyp} , u_{binA} and X^2 are corrected for continuity, the ranks for adjusted measures are again identical, but differ from the ranks yielded with unadjusted measures. This is due to the tendency of adjusted measures to give slightly lower fidelity values to rare species. Species ranks produced by u_{binB} and G remarkably differ from those produced by the above measures and have also a low similarity to one another. In u_{binB} , this difference is because it tends to underweight fidelity of common species (e.g. *Euphorbia cyparissias* and *Dianthus carthusianorum* agg. in Tables 1 and 2). This is in accordance with Eq. 7, which shows that u_{binB} deviates from u_{hyp} (and related measures) unless the number of species occurrences in the data set (n) is small

relative to the total number of relevés (N). By contrast, the G statistic tends to underweight fidelity of rare species, particularly if the vegetation unit is small relative to the data set size (e.g. *Hieracium cymosum*, *H. sabaudum*, and *Asplenium trichomanes* in Table 2). The same, but a much stronger tendency was found in the categorical form of the Indicator Value Index which gives the most deviating results compared with the other measures (note that it yields high values for common species such as *Euphorbia cyparissias*, *Artemisia campestris*, and *Dianthus carthusianorum* agg. in Tables 1 and 2).

Joint fidelity measures

Botta-Dukát & Borhidi (1999) emphasized the distinction between the joint fidelity and two asymmetric fidelity measures. We believe that the traditional understanding of phytosociological fidelity is close to the joint fidelity and, to some extent, also to the fidelity of a species to a vegetation unit. First, we discuss properties of the joint fidelity measures, i.e. u_{hyp} , Φ , X^2 , G and Fisher's exact test. Table 3 compares these measures in six test cases. Cases 1, 3 and 5 represent perfect joint fidelity, i.e. any relevé belonging to the vegetation unit contains the species and any relevé containing the species belongs to the vegetation unit. In Cases 2, 4 and 6 fidelity is still high

Table 2. Ranks of species by decreasing fidelity with respect to vegetation unit A (204 relevés), calculated by different fidelity measures in the data set of 15 898 relevés. Only species ranked among the 20 most faithful according to at least one measure are included. n = number of species occurrences in the entire data set, n_p = number of species occurrences in the vegetation unit.

	u_{hyp}	u_{hyp}^{adj}	u_{binB}	u_{binB}^{adj}	u_{binA}	u_{binA}^{adj}	Φ	X^2	X^2 <i>adj</i>	G	G <i>adj</i>	Fisher	<i>Ind</i> <i>Val</i>	n	n_p
<i>Asplenium septentrionale</i>	1	1	1	1	1	1	1	1	1	2	2	2	2	279	154
<i>Aurinia saxatilis</i>	2	2	2	2	2	2	2	2	2	1	1	1	1	307	160
<i>Hieracium pallidum</i>	3	3	3	3	3	3	3	3	3	4	5	4	12	133	81
<i>Festuca pallens</i>	5	5	5	5	5	5	5	5	5	3	3	3	3	891	161
<i>Sedum reflexum</i>	4	4	4	4	4	4	4	4	4	5	4	5	8	353	103
<i>Allium montanum</i>	6	6	6	6	6	6	6	6	6	6	6	6	6	578	113
<i>Galium glaucum</i>	8	8	8	8	8	8	8	8	8	7	7	7	7	841	112
<i>Sedum album</i>	9	9	9	9	9	9	9	9	9	10	10	10	10	735	95
<i>Artemisia campestris</i>	10	10	12	12	10	10	10	10	10	8	8	8	5	1265	122
<i>Hieracium cymosum</i>	7	7	7	7	7	7	7	7	7	14	14	14	25	137	44
<i>Seseli osseum</i>	11	11	11	11	11	11	11	11	11	9	9	9	9	953	105
<i>Jovibarba sobolifera</i>	12	12	10	10	12	12	12	12	12	13	13	13	19	306	57
<i>Sedum maximum</i>	13	13	13	13	13	13	13	13	13	12	12	12	16	558	72
<i>Melica transsilvanica</i>	14	14	14	14	14	14	14	14	14	15	16	15	22	411	56
<i>Vincetoxicum hirsutiflorum</i>	16	16	16	16	16	16	16	16	16	16	15	16	18	568	63
<i>Euphorbia cyparissias</i>	20	20	26	26	20	20	20	20	20	11	11	11	4	3376	148
<i>Pulsatilla pratensis</i>	17	17	18	17	17	17	17	17	17	20	20	20	24	430	50
<i>Asplenium trichomanes</i>	15	15	15	15	15	15	15	15	15	23	23	23	35	156	133
<i>Verbascum lychnitis</i>	19	19	19	19	19	19	19	19	19	19	19	19	23	597	57
<i>Hieracium sabaudum</i>	18	18	17	18	18	18	18	18	18	24	25	24	32	260	38
<i>Anthericum liliago</i>	21	21	20	20	21	21	21	21	21	26	26	26	29	352	42
<i>Thymus pulegioides</i>	26	25	27	27	26	25	26	26	25	18	18	18	13	1526	89
<i>Potentilla arenaria</i>	28	27	28	28	28	27	28	28	27	17	17	17	11	1980	101
<i>Dianthus carthusianorum</i> agg.	33	32	36	34	33	32	33	33	32	21	21	21	14	1803	89
<i>Asperula cynanchica</i>	35	35	37	35	35	35	35	35	35	22	22	22	15	1799	88
<i>Echium vulgare</i>	34	33	34	33	34	33	34	34	33	28	28	28	20	1022	64

but not perfect, with the target species being absent in some relevés of the vegetation unit and present in some relevés outside the vegetation unit.

By increasing the number of relevés in the vegetation unit (N_p) from 20 to 200 while maintaining the perfect joint fidelity (Cases 1 and 3) the P -value calculated by Fisher's exact test decreases from 10^{-42} to 10^{-216} . Case 4 does not represent perfect joint fidelity, but because the vegetation unit is larger, the results are statistically less probable than the perfect fidelity of Case 1. That is, the probability of the results occurring by chance is lower in Case 4 than in Case 1. By increasing the size of the entire data set (Cases 5 and 6), the results become even less probable. Intuitively, however, Cases 3 and 5, or Cases 4 and 6, respectively, can be treated as the same. Therefore, probability may not be considered as the most appropriate measure of fidelity in some cases.

The G statistic behaves in the same way as Fisher's exact test. The measures u_{hyp} and X^2 are not as dependent on the size of the vegetation unit as Fisher's exact test or the G statistic. However, their values increase with the increasing size of the data set. Therefore they produce roughly comparable results for differently sized vegetation units but not for differently sized data sets.

The phi coefficient is independent of the size of the data set. It is equal to 1 for all cases of perfect joint fidelity and yields roughly comparable values for Cases 2, 4 and 6, which seems more in accordance with intui-

tion. It should be noted, however, that unlike u_{hyp} , X^2 , G or Fisher's exact test, the phi coefficient contains no information about statistical significance. For small data sets or small vegetation units, use of the phi coefficient to measure fidelity may lead to invalid conclusions. By contrast, in large data sets the fidelity values for the most faithful species are usually far beyond the conventional significance levels. In the latter case, the phi coefficient is a particularly appropriate fidelity measure as it yields comparable values among differently sized vegetation units and among differently sized data sets.

Table 3. Comparison of the joint fidelity measures in six test cases, with Cases 1, 3 and 5 being the perfect joint fidelity of the species and the vegetation unit to each other. N = number of relevés in the data set; N_p = number of relevés in the vegetation unit; n = number of species occurrences in the data set; n_p = number of species occurrences in the vegetation unit.

	Case 1	Case 2	Case 3	Case 4	Case 5	Case 6
N	1000	1000	1000	1000	10 000	10 000
N_p	20	20	200	200	2000	2000
n	20	20	200	200	2000	2000
n_p	20	15	200	150	2000	1500
u_{hyp}	31.61	23.54	31.61	21.73	100.00	68.75
Φ	1	0.74	1	0.69	1	0.69
X^2	1000	555	1000	473	10 000	4727
G	196	111	1000	402	10 000	4018
Fisher	10^{-42}	10^{-24}	10^{-216}	10^{-88}	$<10^{-1000}$	10^{-874}

It is important to note that, within a given database, the phi coefficient and u_{hyp} will give the same ranks of fidelities, although the values will not be the same (Eq. 9). The X^2 statistic will also yield the same results (Eq. 11), assuming we ignore the pairs which are negatively faithful to each other.

Asymmetric fidelity measures

Botta-Dukát & Borhidi (1999) derived three variants of the G statistic to measure joint fidelity, fidelity of the species to the vegetation unit and fidelity of the vegetation unit to the species. These three forms of fidelity can be also measured, in turn, by u_{hyp} , u_{binB} and u_{binA} .

Table 4 shows three test cases, representing the three forms of fidelity. In Case 1 the species and the vegetation unit are perfectly jointly faithful to each other. In Case 2 the species is faithful to the vegetation unit, but the vegetation unit is not faithful to the species. Case 3 is the opposite of Case 2. All measures have high values in Case 1. Cases 2 and 3 cannot be distinguished by u_{hyp} because it is a joint fidelity measure. By contrast, u_{binB} yields higher values in Case 2 than in Case 3, which demonstrates its suitability for measuring the fidelity of a species to a vegetation unit. The opposite pattern is shown for u_{binA} , which indicates that it gives a higher weight to the fidelity of a vegetation unit to a species.

In Tables 1 and 2 (see also Fig. 1), u_{binA} yields the same species ranks for one vegetation unit as u_{hyp} , X^2 , and Φ . This is explained by Eq. 8 which shows that u_{binA} is related to these measures through variables N and N_p which are the same for all species, but not through n or n_p which vary among species. If we theoretically ranked vegetation units by their fidelity to a single species, identical ranks would be yielded for u_{hyp} , X^2 , Φ , and u_{binB} , whereas u_{binA} would deviate (Eq. 7).

In conclusion, u_{binB} can also be used as an appropriate fidelity measure, provided there is an intention to give a higher value to the phenomenon of species-to-vegetation unit fidelity, i. e. to highlight the species which occur in few relevés of a vegetation unit due to their overall rarity, but are hardly found outside this unit. By contrast u_{binA} does not have a practical value for measuring fidelity. If strong downweighting of fidelity of rare species is required, which is perhaps rarely the aim in phytosociology, the categorical form of the Dufréne-Legendre Indicator Value Index can be used. This index, however, may be advantageous when working with abundance/cover values.

Fidelity-based sorting of species in phytosociological tables

Phytosociological tables are a common tool for visualization of vegetation data (Westhoff & van der

Maarel 1973; Dierschke 1994). Species sorting in these tables is usually done by intuitive comparison of differences in species frequencies among vegetation units. Following the ideas pioneered in recent studies based on u values (Bruehlheide 1995; Bruehlheide & Jandt 1995, 1997; Jandt 1999; Pflume 1999; Bruehlheide & Chytrý 2000; Täuber 2000), we suggest an automatic procedure for fidelity-based species sorting in phytosociological tables, which is available in the JUICE program (Tichý 2001). In the test examples of Tables 5 and 6, we demonstrate this new method on synoptic tables sorted by the phi coefficient. It can be also applied in combination with any other fidelity measure and to any table of individual relevés which has been previously partitioned by some classification method.

In phytosociological tables, diagnostic species for particular vegetation units are usually clustered into diagonally arranged blocks. Diagnostic species to be included into these blocks can be defined as those exceeding some arbitrary threshold value of fidelity. The lower the threshold value is set, the more species will be considered as diagnostic and the larger proportion of the table's species will be assigned to the blocks. In Tables 5 and 6, the aim was to have 50 diagnostic species in each and the thresholds were selected accordingly.

As the aim of species blocks is displaying differentiation of vegetation units, it is reasonable to rank species within blocks by decreasing fidelity (i.e. differentiation capacity) rather than by decreasing percentage frequency which is the option commonly used in traditional tables. Tables 5 and 6 are sorted by fidelity. They clearly show that there is no perfect correlation between species fidelity and frequency.

Properties of the fidelity measures determine an important feature of Tables 5 and 6 which has never been considered in the traditional tables prepared intuitively by experts. Some species which are relatively common in the data set do not have diagnostic value for vegetation

Table 4. Comparison of the performance of u_{hyp} , u_{binB} , and u_{binA} in three test cases, representing different forms of fidelity. N , N_p , n and n_p as in Table 3.

	Case 1	Case 2	Case 3
Joint fidelity	High	Moderate	Moderate
Fidelity of the species to the vegetation unit	High	High	Low
Fidelity of the vegetation unit to the species	High	Low	High
N	100	100	100
N_p	10	50	10
n	10	10	50
n_p	10	10	10
u_{hyp}	9.95	3.32	3.32
u_{binB}	9.49	3.16	2.36
u_{binA}	9.49	2.36	3.16

Table 5. Synoptic table of 502 relevés of the Czech rock-outcrop dry grasslands, based on fidelity comparison without additional relevés. Diagnostic species (values grey-shaded) are those with $\Phi \geq 0.417$; they are ranked by decreasing value of Φ . Dots in part (a) indicate species absence, dashes in part (b) of the table indicate negative fidelity. Asterisks before species names indicate species which are also diagnostic in Table 6.

Vegetation unit	(a) percentage frequency								(b) phi coefficient $\times 1000$							
	A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H
Nr. of relevés	204	78	25	30	66	73	11	15	204	78	25	30	66	73	11	15
Nr. of diagnostic species	2	0	13	14	2	2	8	13	2	0	13	14	2	2	8	13
Diagnostic species of the vegetation unit A																
* <i>Asplenium septentrionale</i>	75	23	.	.	3	22	.	.	642	-	-	-	-	-	-	-
* <i>Aurinia saxatilis</i>	78	36	.	.	9	15	.	.	633	-	-	-	-	-	-	-
Diagnostic species of the vegetation unit C																
* <i>Achillea setacea</i>	.	3	48	-	-	629	-	-	-	-	-
<i>Agrostis stricta</i>	2	1	56	.	.	1	.	.	-	-	609	-	-	-	-	-
* <i>Helichrysum arenarium</i>	1	.	40	-	-	564	-	-	-	-	-
<i>Jasione montana</i>	5	.	56	-	-	550	-	-	-	-	-
<i>Carex supina</i>	.	.	28	-	-	519	-	-	-	-	-
<i>Rumex acetosella</i> agg.	25	6	100	.	.	.	36	.	172	-	511	-	-	-	79	-
<i>Erophila verna</i> agg.	0	3	36	.	2	.	.	.	-	-	482	-	-	-	-	-
* <i>Hieracium echioides</i>	6	3	56	.	5	.	.	.	-	-	474	-	-	-	-	-
<i>Avenochloa pratensis</i>	2	.	52	.	3	5	45	.	-	-	463	-	-	-	260	-
* <i>Gagea bohemica</i>	0	.	24	-	-	441	-	-	-	-	-
* <i>Scleranthus perennis</i>	13	.	64	.	.	3	.	.	124	-	441	-	-	-	-	-
Diagnostic species of the vegetation unit D																
* <i>Teucrium montanum</i>	.	.	.	97	5	3	.	.	-	-	-	902	-	-	-	-
* <i>Scorzonera austriaca</i>	.	.	.	73	6	1	.	.	-	-	-	759	12	-	-	-
* <i>Poa badensis</i>	.	4	.	80	8	4	.	.	-	-	-	723	-	-	-	-
* <i>Campanula sibirica</i>	.	.	.	63	5	3	.	.	-	-	-	692	-	-	-	-
* <i>Fumana procumbens</i>	.	.	.	53	2	1	.	.	-	-	-	675	-	-	-	-
* <i>Minuartia setacea</i>	1	4	4	100	18	23	.	.	-	-	-	648	58	124	-	-
* <i>Melica ciliata</i>	1	5	.	77	8	15	.	.	-	-	-	597	-	88	-	-
* <i>Dorycnium germanicum</i>	.	.	4	70	8	7	55	.	-	-	-	595	-	-	266	-
* <i>Allium flavum</i>	3	3	8	77	14	11	45	.	-	-	-	525	31	-	163	-
<i>Medicago falcata</i>	.	4	4	47	6	.	7	.	-	-	-	507	28	-	-	18
* <i>Alyssum montanum</i>	7	14	8	87	24	15	18	.	-	-	-	480	83	-	-	-
<i>Stipa capillata</i>	6	8	.	60	8	1	.	.	-	-	-	463	-	-	-	-
<i>Astragalus austriacus</i>	.	.	.	33	3	4	.	.	-	-	-	449	-	27	-	-
<i>Inula ensifolia</i>	.	.	.	33	6	4	.	.	-	-	-	417	58	16	-	-
Diagnostic species of the vegetation unit E																
* <i>Helianthemum canum</i>	.	3	.	3	32	5	.	7	-	-	-	-	434	-	-	-
Diagnostic species of the vegetation unit F																
* <i>Saxifraga paniculata</i>	18	41	.	.	-	-	-	-	138	488	-	-
Diagnostic species of the vegetation unit G																
* <i>Asplenium cuneifolium</i>	100	.	-	-	-	-	-	-	1000	-
* <i>Thlaspi montanum</i>	3	.	73	.	-	-	-	-	29	-	758	-
<i>Rumex acetosa</i>	2	1	55	.	-	-	-	-	-	-	633	-
* <i>Biscutella laevigata</i>	1	3	12	3	14	19	100	.	-	-	28	-	70	156	489	-
<i>Festuca ovina</i>	7	5	12	.	5	5	82	.	-	-	41	-	-	-	426	-
Diagnostic species of the vegetation unit H																
* <i>Cirsium acaule</i>	87	-	-	-	-	-	-	-	929
<i>Ononis spinosa</i>	3	1	.	80	-	-	-	-	-	-	-	794
* <i>Coronilla vaginalis</i>	40	-	-	-	-	-	-	-	627
<i>Brachypodium pinnatum</i>	2	.	.	.	12	7	.	93	-	-	-	92	-	-	-	625
<i>Inula salicina</i>	.	1	40	-	-	-	-	-	-	-	578
<i>Gentianella ciliata</i>	33	-	-	-	-	-	-	-	572
<i>Scorzonera hispanica</i>	33	-	-	-	-	-	-	-	572
<i>Prunella grandiflora</i>	33	-	-	-	-	-	-	-	572
<i>Carex flacca</i>	33	-	-	-	-	-	-	-	572
<i>Cirsium pannonicum</i>	2	1	.	33	-	-	-	-	-	-	-	478
<i>Carlina vulgaris</i> agg.	0	.	4	.	2	5	.	47	-	-	17	-	-	67	-	468
<i>Bromus erectus</i>	20	-	-	-	-	-	-	-	442
<i>Centaurea jacea</i>	20	-	-	-	-	-	-	-	442
Common diagnostic species of two vegetation units																
* <i>Armeria elongata</i>	1	.	52	.	.	.	91	.	-	-	495	-	-	-	591	-
* <i>Genista pilosa</i>	0	.	60	.	2	14	82	.	-	-	469	-	-	104	433	-
* <i>Sesleria varia</i>	2	1	.	40	98	100	100	100	-	-	-	21	506	549	199	234

Table 6. Synoptic table of 502 relevés of Czech rock-outcrop dry grasslands, based on fidelity comparison with 15487 additional relevés of various grassland types of the Czech Republic. Diagnostic species (values grey-shaded) are those with $\Phi \geq 0.154$; they are ranked by decreasing value of Φ . Dots in part (a) indicate species absence, dashes in part (b) of the table indicate negative fidelity. Asterisks before species names indicate species which are also diagnostic in Table 5.

Vegetation unit	(a) percentage frequency								(b) phi coefficient $\times 1000$							
	A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H
Nr. of relevés	204	78	25	30	66	73	11	15	204	78	25	0	66	73	11	15
Nr. of diagnostic species	16	7	8	16	13	14	7	3	16	7	8	16	13	14	7	3
Diagnostic species of the vegetation unit A																
* <i>Asplenium septentrionale</i>	75	23	.	.	3	22	.	.	640	114	-	-	-	104	-	-
<i>Hieracium pallidum</i>	40	5	4	.	8	14	.	.	487	33	14	-	48	96	-	-
<i>Sedum reflexum</i>	50	13	24	.	6	29	.	.	373	51	59	-	17	122	-	-
<i>Hieracium cymosum</i>	22	3	.	.	9	15	.	.	255	13	-	-	57	104	-	-
<i>Artemisia campestris</i>	60	42	44	57	18	10	.	.	218	89	53	78	24	-	-	-
Diagnostic species of the vegetation unit C																
* <i>Hieracium echinoides</i>	6	3	56	.	5	.	.	.	47	-	195	-	19	-	-	-
* <i>Gagea bohemica</i>	0	.	24	-	-	188	-	-	-	-	-
* <i>Helichrysum arenarium</i>	1	.	40	-	-	167	-	-	-	-	-
* <i>Scleranthus perennis</i>	13	.	64	.	.	3	.	.	85	-	166	-	-	-	-	-
* <i>Achillea setacea</i>	.	3	48	-	-	154	-	-	-	-	-
Diagnostic species of the vegetation unit D																
* <i>Teucrium montanum</i>	.	.	.	97	5	3	.	.	-	-	-	701	45	27	-	-
* <i>Scorzonera austriaca</i>	.	.	.	73	6	1	.	.	-	-	-	561	66	13	-	-
* <i>Fumana procumbens</i>	.	.	.	53	2	1	.	.	-	-	-	532	20	18	-	-
* <i>Poa badensis</i>	.	4	.	80	8	4	.	.	-	30	-	458	60	32	-	-
* <i>Minuartia setacea</i>	1	4	4	100	18	23	.	.	-	20	12	427	110	150	-	-
* <i>Melica ciliata</i>	1	5	.	77	8	15	.	.	-	29	-	331	43	96	-	-
* <i>Campanula sibirica</i>	.	.	.	63	5	3	.	.	-	-	-	263	22	11	-	-
* <i>Allium flavum</i>	3	3	8	77	14	11	45	.	14	-	19	248	58	47	87	-
* <i>Alyssum montanum</i>	7	14	8	87	24	15	18	.	32	52	14	234	90	55	26	-
<i>Diplotaxis muralis</i>	.	.	.	7	-	-	-	182	-	-	-	-
* <i>Dorycnium germanicum</i>	.	.	4	70	8	7	55	.	-	-	-	165	16	14	77	-
Diagnostic species of the vegetation unit E																
* <i>Helianthemum canum</i>	.	3	.	3	32	5	.	7	-	14	-	12	224	36	-	20
<i>Stachys recta</i>	31	53	4	47	86	18	.	7	122	140	-	76	222	35	-	-
Diagnostic species of the vegetation unit F																
<i>Cardaminopsis petraea</i>	0	.	.	.	3	11	.	.	17	-	-	-	69	269	-	-
<i>Viola collina</i>	3	.	.	.	8	16	.	.	48	-	-	-	77	179	-	-
<i>Cardaminopsis arenosa</i>	10	3	.	.	18	19	.	.	137	17	-	-	141	157	-	-
Diagnostic species of the vegetation unit G																
* <i>Asplenium cuneifolium</i>	100	.	-	-	-	-	-	-	782	-
* <i>Thlaspi montanum</i>	3	73	.	.	-	-	-	-	50	-	514	-
<i>Stellaria holostea</i>	1	.	.	.	2	1	36	.	19	-	-	-	18	17	206	-
Diagnostic species of the vegetation unit H																
* <i>Coronilla vaginalis</i>	40	-	-	-	-	-	-	-	225
* <i>Cirsium acaule</i>	87	-	-	-	-	-	-	-	168
Common diagnostic species of two vegetation units																
* <i>Aurinia saxatilis</i>	78	36	.	.	9	15	.	.	634	173	-	-	34	65	-	-
<i>Sedum maximum</i>	35	58	4	.	17	19	73	.	197	207	-	-	46	58	99	-
<i>Melica transsilvanica</i>	27	45	4	3	14	14	.	.	179	187	-	-	45	48	-	-
<i>Galium glaucum</i>	55	35	.	33	74	22	20	.	253	92	-	54	199	50	-	20
<i>Asplenium trichomanes</i>	16	14	.	.	17	48	18	.	176	93	-	-	103	324	46	-
* <i>Genista pilosa</i>	0	.	60	.	2	14	82	.	-	-	206	-	-	74	187	-
* <i>Armeria elongata</i>	1	.	52	.	.	.	91	.	-	-	167	-	-	-	195	-
<i>Anthericum ramosum</i>	8	10	8	90	56	49	33	.	22	20	-	183	164	150	-	44
<i>Asplenium ruta-muraria</i>	14	18	.	7	38	47	.	.	132	109	-	22	219	284	-	-
<i>Cotoneaster integerrimus</i>	17	12	4	.	38	37	.	.	140	55	-	-	186	190	-	-
* <i>Saxifraga paniculata</i>	18	41	.	.	-	-	-	-	173	417	-	-
<i>Biscutella laevigata</i>	1	3	12	3	14	19	100	.	13	18	58	15	109	163	338	-
Common diagnostic species of more than two vegetation units																
<i>Allium montanum</i>	55	100	.	30	56	47	.	.	315	362	-	61	181	156	-	-
<i>Sedum album</i>	47	88	.	90	64	62	.	.	228	280	-	177	181	184	-	-
<i>Seseli osseum</i>	51	62	52	100	83	82	.	.	218	164	77	172	210	218	-	-
<i>Festuca pallens</i>	79	44	100	100	53	64	18	.	363	116	163	178	133	174	14	-
<i>Jovibarba sobolifera</i>	28	33	4	87	38	29	.	.	216	161	-	268	169	133	-	-
<i>Vincetoxicum hirsutinaria</i>	31	21	4	7	55	68	.	.	168	64	-	-	177	238	-	-
* <i>Sesleria varia</i>	2	1	.	40	98	100	100	100	-	-	-	108	408	436	169	197

units with few relevés, even though they have a high frequency in these vegetation units. For example, *Sedum maximum* in Table 6 is diagnostic for vegetation units A and B where its frequency is 35% and 58%, respectively, but is not diagnostic for vegetation unit G where its frequency is 73% (note that unit A includes 204 relevés, B 78, and G only 11). A similar pattern is shown by *Sesleria varia* in Table 5 and *Asplenium trichomanes*, *Seseli osseum* and *Jovibarba sobolifera* in Table 6. This is in accordance with the well-known statistical rule that observed phenomena (in this case species occurrence in a vegetation unit) are more significant if observed in more cases (i.e. in more relevés).

Determination of diagnostic species in large data sets

During the history of phytosociology, diagnostic species could have hardly been determined from real data because even large tables only included relevés of a few related vegetation types or relevés from restricted areas. Expert judgement was the only way to determine diagnostic species of more general validity before large phytosociological data sets and corresponding computer technology became available. Table 5, compiled from a data set which includes only 502 relevés of the rock-outcrop dry grasslands, represents this traditional approach. In this table diagnostic value is given to several species with broad ecological ranges which are frequently found in many different vegetation types. Many of them have their ecological optima outside the rock outcrops (e.g. *Jasione montana*, *Rumex acetosella*, *R. acetosa*, *Festuca ovina*, *Brachypodium pinnatum*, *Carex flacca*, *Bromus erectus* and *Centaurea jacea*). These species can be valuable for differentiating particular vegetation units against the others in the rock-outcrop grassland data set, but not against the units outside the data set.

With currently available phytosociological databases, it is possible to determine diagnostic species in large data sets which include not only relevés of target vegetation types but also relevés of most vegetation types occurring in a wider area. This approach yields diagnostic species of more general validity. Table 6 shows diagnostic species of the same vegetation units as in Table 5, however, these diagnostic species were determined in a data set where several thousands of relevés of different types of herbaceous vegetation were added. It is evident that species with broad ecological ranges are no longer indicated as diagnostic. In addition, ecologically specialized species which occur in many types of rock-outcrop grasslands but are rare in other vegetation types are indicated as diagnostic in Table 6 but not in Table 5. For example, *Allium montanum*, *Sedum album*, *Seseli osseum*, *Festuca pallens*, and *Jovibarba sobolifera* are indicated as diagnostic for 4-5 vegetation units in Table 6 but for no single unit in

Table 5. These results suggest that for determination of diagnostic species generally valid over a large area, fidelity calculation in a large data set is a promising alternative to expert knowledge.

Effects of data set structure on diagnostic species

A conspicuous discrepancy is found in vegetation units with relatively many relevés (A, B, E and F), which have few diagnostic species if considered in a small data set (Table 5) but several diagnostic species if considered in the large data set with additional relevés (Table 6). Numbers of diagnostic species between the two tables are directly comparable because each table contains a total of 50 diagnostic species.

Let us consider vegetation unit A (204 relevés) in a data set of 502 relevés (Table 5). In this small data set, vegetation unit A is relatively large. To be diagnostic for this unit, a species must be rather common in the data set and most of its occurrences must be concentrated in the vegetation unit. As most species are relatively rare in phytosociological data sets, very few species exceed the threshold fidelity value.

In the data set of 15 989 relevés, vegetation unit A has the same absolute size but becomes small relative to the data set size. As the additional relevés belong to other vegetation types, there are several species which occur in the vegetation unit but are quite rare or absent in the additional relevés. Thus, relative concentration of these species in the vegetation unit increases and they eventually exceed the threshold fidelity value.

In conclusion, it is necessary to realize that the diagnostic capacity of species can be underestimated in vegetation units which are large relative to the data set size. However, this may be a problem only of using small data sets, because in large data sets with additional relevés all vegetation units are relatively small.

Well defined and poorly defined vegetation units

When evaluating classifications, phytosociologists often think in terms of 'good' and 'bad' vegetation units (Pignatti et al. 1995). Vegetation units containing several faithful species are usually considered as 'good' and the others as 'poor'. 'Goodness' of a vegetation unit can be quantified by calculating the average positive fidelity

Table 7. Averages of positive values of the phi coefficient ($\times 1000$) for all species occurring in vegetation units from Tables 5 and 6.

Vegetation unit	A	B	C	D	E	F	G	H
Table 5 (small)	86	81	193	209	96	104	241	228
Table 6 (large)	57	38	54	88	48	52	95	47

value for all species occurring in this vegetation unit (Table 7). Vegetation units C, D, G, and H appear as the 'best' in the small data set (Table 5) but if the large data set with additional relevés (Table 6) is considered, it becomes clear that only units D and G are really 'good', while H is rather 'poor'. This indicates that many species which appeared to be faithful to communities C and H in the small data set have their main ecological optimum outside this data set, in vegetation types other than the rock-outcrop grasslands. Vegetation unit B is indicated as the 'poorest' in both tables; this reflects the fact that it is mainly defined by the absence of diagnostic species of other units, combined with dominance of a single species, *Allium montanum*.

Acknowledgements. Our thanks are due to Helge Bruelheide, Jörg Ewald, and two anonymous referees for stimulating comments on the previous version of the paper. We appreciated the help by Maruška Rafajová and other colleagues involved in computerization of our database. This research was funded from projects GA ČR 206/99/1523 and MSM 143100010 (Working Group Biodiversity).

References

- Barkman, J.J. 1989. Fidelity and character-species, a critical evaluation. *Vegetatio* 85: 105-116.
- Beals, E.W. 1984. Bray-Curtis-ordination: an effective strategy for analysis of multivariate ecological data. *Adv. Ecol. Res.* 14: 1-55.
- Bergmeier, E., Härdtle, W., Mierwald, U., Nowak, B. & Peppler, C. 1990. Vorschläge zur syntaxonomischen Arbeitsweise in der Pflanzensoziologie. *Kiel. Not. Pflanzenk. Schleswig-Holst. Hamburg* 20: 92-103.
- Botta-Dukát, Z. & Borhidi, A. 1999. New objective method for calculating fidelity. Example: The Illyrian beechwoods. *Ann. Bot. (Roma)* 57: 73-90.
- Braun-Blanquet, J. 1928. *Pflanzensoziologie. Grundzüge der Vegetationskunde*. Springer, Berlin, DE.
- Brisse, H., De Ruffray, P., Grandjouan, G. & Hoff, M. 1995. The Phytosociological Database 'SOPHY'. Part I: Calibration of indicator plants. Part II: Socio-ecological classification of relevés. *Ann. Bot. (Roma)* 53: 177-190.
- Bruelheide, H. 1995. Die Grünlandgesellschaften des Harzes und ihre Standortbedingungen. Mit einem Beitrag zum Gliederungsprinzip auf der Basis von statistisch ermittelten Artengruppen. *Diss. Bot.* 244: 1-338.
- Bruelheide, H. 2000. A new measure of fidelity and its application to defining species groups. *J. Veg. Sci.* 11: 167-178.
- Bruelheide, H. & Chytrý, M. 2000. Towards unification of national vegetation classifications: a comparison of two methods for analysis of large datasets. *J. Veg. Sci.* 11: 295-306.
- Bruelheide, H. & Jandt, U. 1995. Survey of limestone grassland by statistically formed groups of differential species. *Coll. Phytosoc.* 23: 319-338.
- Bruelheide, H. & Jandt, U. 1997. Demarcation of communities in large databases. *Phytocoenologia* 27: 141-159.
- Chytrý, M. 1997. Czech National Phytosociological Database: initial state and perspectives. *Zpr. Čes. Bot. Společ., Mat.* 15: 27-40. (In Czech.)
- Dierschke, H. 1994. *Pflanzensoziologie*. Ulmer, Stuttgart, DE.
- Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67: 345-366.
- Ehrendorfer, F. (ed.) 1973. *Liste der Gefäßpflanzen Mitteleuropas*. 2nd ed. G. Fischer, Stuttgart, DE.
- Goodall, D.W. 1953. Objective methods for the classification of vegetation II. Fidelity and indicator value. *Aust. J. Bot.* 1: 434-456.
- Hennekens, S.M. & Schaminée, J.H.J. 2001. TURBOVEG, a comprehensive data base management system for vegetation data. *J. Veg. Sci.* 12: 589-591.
- Jandt, U. 1999. Kalkmagerrasen am Südharrand und im Kyffhäuser. Gliederung im überregionalen Kontext, Verbreitung, Standortverhältnisse und Flora. *Diss. Bot.* 322: 1-246.
- Juhász-Nagy, P. 1964. Some theoretical models of cenological fidelity I. *Acta Biol. Debrec.* 3: 33-43.
- Legendre, P. & Legendre, L. 1998. *Numerical ecology*. 2nd English ed. Elsevier, Amsterdam, NL.
- McCune, B. & Mefford, M.J. 1999. *PC-ORD. Multivariate analysis of ecological data. Version 4*. MjM Software Design, Gleneden Beach, OR, US.
- Pflume, S. 1999. *Laubwaldgesellschaften im Harz. Gliederung, Ökologie und Verbreitung*. M. Galunder-Verlag, Wiehl, DE.
- Pignatti, S., Oberdorfer, E., Schaminée, J.H.J. & Westhoff, V. 1995. On the concept of vegetation class in phytosociology. *J. Veg. Sci.* 6: 143-152.
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry*. 3rd ed. Freeman, New York, NY, US.
- Szafer, W. & Pawłowski, B. 1927. Die Pflanzenassoziationen des Tatra-Gebirges. Bemerkungen über die angewandte Arbeitstechnik. *Bull. Int. Acad. Polon. Sci. Lettres B* 3, Suppl. 2: 1-12.
- Täuber, T. 2000. *Zwergbinsen-Gesellschaften (Isoëto-Nanojuncetea) in Niedersachsen – Verbreitung, Gliederung, Dynamik, Keimungsbedingungen der Arten und Schutzkonzepte*. Cuvillier, Göttingen, DE.
- Tichý, L. 2001. *JUICE 4.0. Software user's guide*. Department of Botany, Masaryk University, Brno, CZ.
- van der Maarel, E., Janssen, J.G.M. & Louppen, J.M.W. 1978. TABORD, a program for structuring phytosociological tables. *Vegetatio* 3: 143-156.
- Westhoff, V. & van der Maarel, E. 1973. The Braun-Blanquet approach. In: Whittaker, R.H. (ed.) *Ordination and classification of plant communities*, pp. 617-737. W. Junk, The Hague, NL.
- Whittaker, R.H. 1962. Classification of natural communities. *Bot. Rev.* 28: 1-239.

Received 16 February 2001;
Revision received 9 October 2001;
Accepted 27 November 2001.
Coordinating Editor: H. Bruelheide.