Methodological aspects in the study of species richness, diversity and homotony of grass cover

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ABSTRACT

This work proposes a new method for the assessment of species richness, diversity, and homotony in related vegetation relevés of grass swards. Hypothetical vegetation relevés with identical species number but differing constancy were generated to compare the techniques describing the species variety and diversity. By calculating these theoretical values in combination with data from real swards of *Alopecuretum* meadows, it has been shown that the determination of the constancy of particular species is essential for the evaluation of species diversity of grass swards. The relationship between the share of different combinations of vegetation relevés in the whole sample and corresponding total number of plant species were expressed by generating regression equations and the mid values of these curves were worked out and evaluated for individual sets of relevés; it was then possible to create homotony/heterotony indices for these sets. The indices of heterotony can be used, e.g., for expressing biotope diversity within a set of vegetation relevés from different stands.

Keywords: species richness; species diversity; grass stand; stands homotony; methodological approaches

One of the most important non-production functions of grass stands is their protective function with respect to both plant and animal genetic resources (Rychnovská et al. 1985). This significant non-production function can be developed only by efficient farming and utilization of grass stands (Opitz von Boberfeld 1994, Klimeš 1997).

Several quantitative approaches are used in viewing the genetic resource richness of individual cenoses. In addition to the elementary formulation of the number of species in individual communities (species variety), one of the most common indicators of species diversity is the Shannon-Wiener index of species diversity, which takes into account not only species quantity but also the shares of individual species in the formation of a community (Jeník 1998). Another view of forms of species diversity is Simpson's index concerning a participation of individual species in a community formation. Recently, the rank-abundance diagram (Begon et al. 1997) has been used in the study of community variety.

While carrying out phytocenological analyses of vegetation relevés it is also reasonable to assess, besides the constancy of particular species, the homotony of the community (Moravec et al. 1994). The present work therefore focuses on the methodology developed for evaluating the species richness, diversity and homotony in sets of vegetation relevés of grass stands.

MATERIAL AND METHODS

While studying methodological questions of dynamic models of species variety and their analyses (Klimeš 2000) in grass swards we intended to solve the problem of bringing species variety

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into a formula helpful for experimental grassland management applications and for observational studies of grass stands with limited databases. These studies arose from the comparison of existing methodological approaches and analyses of quantitative phytocenological models (Klimeš 1997, 2000, Klimeš et al. 2001) with respect to the possibilities of their further development. For the requirements of methodological studies, model hypothetical files were also generated (stand I, II and III). The verification of the process for designed evaluation of species variety was carried out on the file of *Alopecuretum* meadows (stand IV, blind experiment with a consecutive study of groundwater contamination with nitrates: Klimeš and Kužel 2004) which belong to the subassociation *Trifolio-Festucetum alopecuretosum* (Neuhäusl 1972), submontane region of Bohemian Forest, altitude 545 m, annual mean air temperature 6.3°C, long-term mean annual rainfall 675 mm, sandy loamy soil, pH_{KCl} 6.0. Our technique for viewing species variety and homotony of grass stands is described in the next chapter.

RESULTS AND DISCUSSION

We made a hypothetical set of grass stands for comparing the techniques describing the plant species variety and diversity. There were 5, 10, 20 and 100 plant species in the grass stands and these were absolutely balanced in the grass stands, i.e. about 20%*D*, 10%*D*, 5%*D* and 1%*D* (Table 1). After comparing various techniques describing the species variety, we concluded that the values of the species variety (*Q* – number of plant species in the grass stand) and the values of Simpson's index of the species diversity of the grass stand (*D*) showed the same tendency with increasing numbers of plant species in grass stands. Comparisons between relative values of particular characteristics showed that the values of Shannon-Wiener index of species diversity were quite different from the others. The values of the plant species variety and diversity (Table 1) show that the data of the species variety (*Q*) and Simpson's index of species diversity (*D*) are more suitable and complement each other.

These methods however present some problems. Only one vegetation relevé is evaluated at a time while we need a set of vegetation relevés (a selected set) for a complex characteristic of a grass sward. Another problem concerning the evaluation of species diversity consists in finding a way of estimating the number of various plant species in the grass stands. Some cannot be used for a high number of grass species (for example sprouting species). The use of dominance is also questionable because the plants greatly differ in size. For example, one plant can occupy an area larger than 1 m^2 (e.g. *Phalaroides arundinacea*), on the other hand the area of 1 m^2 can be occupied by thousands of very small plants. We drew the conclusion that the most important parameter for the evaluation of grass stands could be the constancy of particular species (i.e. their repetitive occurrence in a particular vegetation). In many important respects, this idea has already been used for solving numerous syntaxonomic questions at the early stages of establishing the Zürich-Montpellier school.

Brockmann-Jerosch (1907) and later Moravec et al. (1994) introduced the term "constancy of the species" referring to the share of plant stands with particular species in the total number of

Table 1. Comparison of various techniques describing species variety and species diversity at the absolute constancy of individual species in a grass stand

Parameter of species variety and species diversity	Method of expression	Value parameters of species variety and species diversity			
Q	abs	5	10	20	100
	rel	1.000	2.000	4.000	20.000
H	abs	1.609	2.303	2.996	4.605
	rel	1.000	1.431	1.862	2.862
D	abs	5	10	20	100
	rel	1.000	2.000	4.000	20.000

Q = number of plant species; *H* = Shannon-Wiener index of species diversity; *D* = Simpson's index of species diversity

Table 2. The presence (1) or the absence (0) of a particular vascular plant species [$S_{ij(k)}$] in particular (k = 1) and combined (k > 1) replicates of a grass stands I, II and III and analytical process for calculation of species variety in a certain share of relevés [Q_p]:

$$Q_p = \binom{n(1)}{k}^{-1} \sum_{j(k)=1}^{n(k)} \sum_{i=1}^{m_{j(k)}} \left\{ \left[-1 \left| \prod_{j(1)=1}^{k} \left(S_{ij(1)} - 1 \right) \right| \right] + 1 \right\}$$

$$p = \frac{k}{n(1)} \qquad [k = 1; 2; \ldots; n(1)]$$

Species	i	Grass stand														
		I					II					III				
		replicate														
		a	b	c	d	C_i	a	b	c	d	C_i	a	b	c	d	C_i
		j(1)				Q	j (1)				Q	j (1)				Q
		1	2	3	4		1	2	3	4		1	2	3	4	
A	1	1	0	1	1	0.75	1	0	0	0	0.25	1	1	1	1	1.00
B	2	1	1	1	0	0.75	0	0	0	1	0.25	1	1	1	1	1.00
C	3	1	1	1	1	1.00	0	1	0	0	0.25	1	1	1	1	1.00
D	4	1	1	0	1	0.75	1	0	0	0	0.25	1	1	1	1	1.00
E	5	1	0	1	1	0.75	0	0	0	1	0.25	1	1	1	1	1.00
F	6	1	1	1	0	0.75	0	0	1	0	0.25	1	1	1	1	1.00
G	7	0	1	1	1	0.75	0	1	0	0	0.25	1	1	1	1	1.00
H	8	1	1	0	1	0.75	0	0	1	0	0.25	1	1	1	1	1.00
I	9	1	0	1	1	0.75	1	0	0	0	0.25	1	1	1	1	1.00
J	10	1	1	1	0	0.75	0	0	0	1	0.25	1	1	1	1	1.00
K	11	0	0	1	1	0.50	0	1	0	0	0.25	1	1	1	1	1.00
L	12	1	1	1	1	1.00	0	1	0	0	0.25	1	1	1	1	1.00
M	13	1	0	1	0	0.50	0	1	0	0	0.25	1	1	1	1	1.00
N	14	1	1	1	1	1.00	0	0	0	1	0.25	1	1	1	1	1.00
O	15	0	1	0	1	0.50	1	0	0	0	0.25	1	1	1	1	1.00
$Q_{0.25}$		12	10	12	11	11.25	4	4	3	4	3.75	15	15	15	15	15
$Q_{0.50}$		14 (*)		15 (*)		14.5	8 (*)		7 (*)		7.5	15 (*)		15 (*)		15
$Q_{1.00}$		15				15	15				15	15				15

C_i = constancy (constancy of particular plant species; 100% = 1)

Q = number of vascular plant species

(*) = only selected combinations

k = the value k represents a subset of k elements singled out of a set of $n(1)$ elements (i.e. set of all replicates)

i = 1; 2; ...; m — $j(k) = \{j(k) \sim [j(1)]\}$

$j(1) = \{1 \sim [1]\}; \{2 \sim [2]\}; \ldots; \{n(1) \sim [n(1)]\}$

$j(k)$ = 1; 2; ...; $n(k)$ — $j(2) = \{1 \sim [1, 2]\}; \{2 \sim [1, 3]\}; \ldots; \{n(2) \sim [n - 1(1), n(1)]\}$

$n(k) = \binom{n(1)}{k}$ — $j[n(1)] = \{1[1, 2, \ldots, n(1)]\}$

$S_{ij(k)}$ = 0; 1

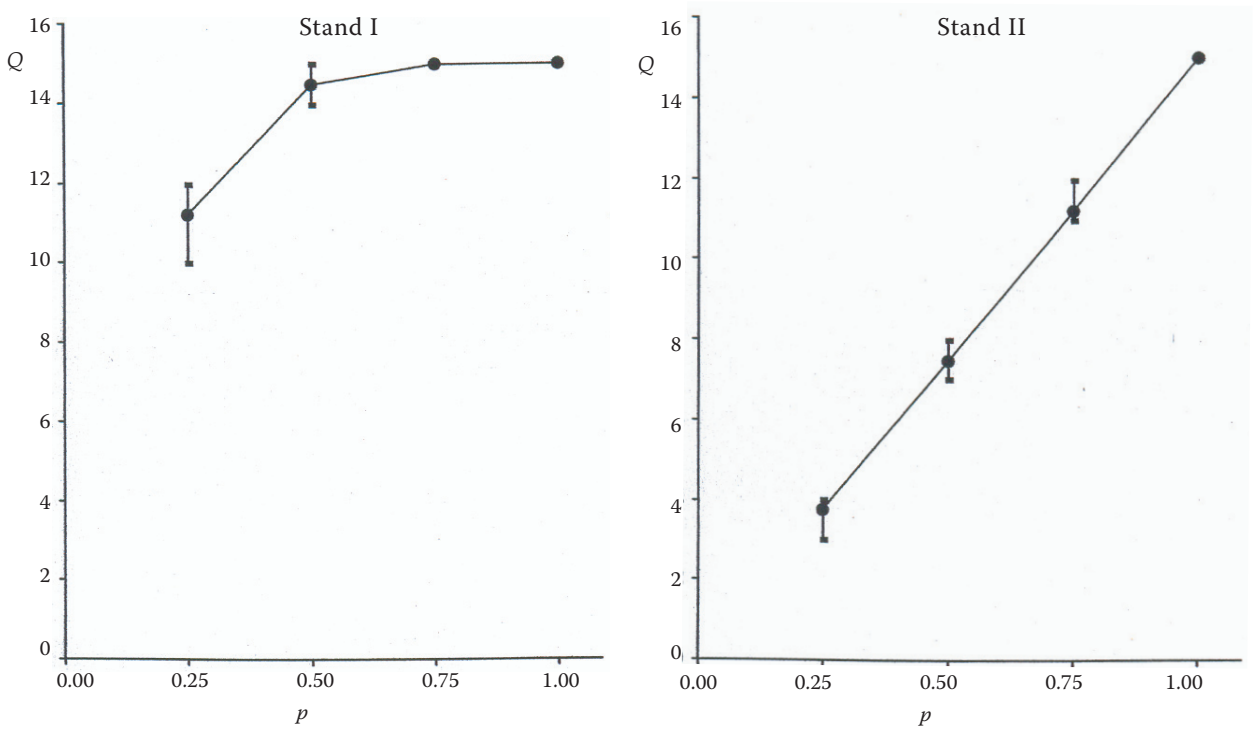

Figure 1. The horizontal distribution profile of species variety in grass stands I and II

p – share of sample elements of the whole sample (total number of replicates); Q – number of plant species (with variation span)

Table 3. The number of plant species in particular replicates and various combinations of the replicates in the grass stands I, II and III

Number of replicates	Replicate	Grass stand		
		I	II	III
1	a	12.00	4.00	15
	b	10.00	4.00	15
	c	12.00	3.00	15
	d	11.00	4.00	15
	$\bar{x}$	11.25	3.75	15
2	a–b	14.00	8.00	15
	c–d	15.00	7.00	15
	b–c	15.00	7.00	15
	a–d	15.00	8.00	15
	a–c	14.00	7.00	15
	b–d	14.00	8.00	15
	$\bar{x}$	14.50	7.50	15
3	a–b–c	15.00	11.00	15
	a–c–d	15.00	11.00	15
	b–c–d	15.00	11.00	15
	a–b–d	15.00	12.00	15
	$\bar{x}$	15.00	11.25	15
4	a–b–c–d	15.00	15.00	15

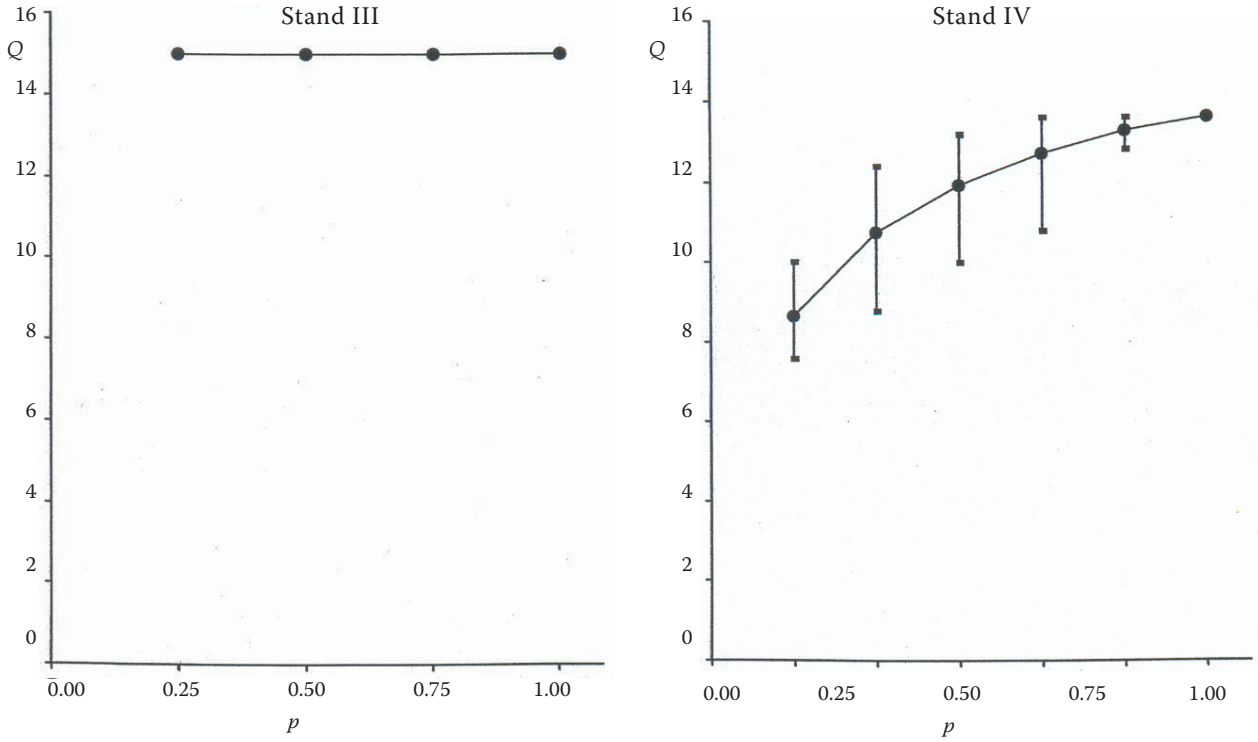

Figure 2. The horizontal distribution profile of species variety in grass stands III and IV

p – share of sample elements of the whole sample (total number of replicates); Q – number of plant species (with variation span)

plant stands analysed. Using the figures showing the constancy of species considered for the evaluation of species diversity of plant stands would not provide a complex plant species spectre in a particular location, in location sets, in repeated meadow experiments, etc. For this reason, we started to develop a new method that would take into account the horizontal distribution of species diversity. This method was tested with hypothetical sets (grass stands I, II and III) consisting of the same number of plant species (15). In the set No. III, all 15 species show 100% constancy. In the grass stand I various species differ in their constancy from 50 to 100%. In the grass stand II, all plant species occur only once and their constancy is 25%. The evaluation is shown in Table 2 and Figures 1 and 2. Gradually, we established the number of plant species in a single replicate, in pair replicates, in triple replicates and finally in the whole set (Table 3). Figures 1 and 2 are a graphic description of the horizontal profile distribution of species variety in the grass stands I, II and III. The average values are completed with a variation span (R_Q). Table 4 shows the data of the plant species variety for a certain share of the replicates in total sets (P = 0.25, 0.50, 0.75, 1).

Table 4. The quantitative parameters of area distribution of species variety and diversity (Q_p, SQ') in the grass stands I, II, III and IV

Parameter	Grass stand			
	I	II	III	IV
$Q_{0.25}$	11.25	3.75	15	24.38
$Q_{0.50}$	14.50	7.50	15	28.94
$Q_{0.75}$	15.00	11.25	15	31.61
$Q_{1.00}$	15.00	15.00	15	33.51
SQ'	12.35	7.50	15	27.61

The relationship between the proportion of relevés out of the whole set of relevés evaluated (p) and the number of vascular plant species (Q) is expressed by the following regression equation:

$$Q' = f(p) \quad (1)$$

This expression is suitable for a detailed analysis of grass stands.

The mid values of these curves (SQ') were worked out and evaluated for individual sets:

$$SQ' = \frac{1}{b-a}\int_a^b f(p)\,dp \quad (2)$$

$a = 0$, $b = 1$ (boundary values of curves)

The value $a = 0$ was chosen to prevent a misrepresentation of different numbers of vegetation relevés (replicates).

Regression models [$Q' = f(p)$] and mid values (SQ') were set for grass stands I, II and III:

$$Q'_{\mathrm{I}} = 0.042 + 63.861p - 88.863\,502p^2 + 40.003\,287p^3 \quad (3)$$

$I_{pQI} = 0.989^{**}$

$$SQ_{\mathrm{I}} = \frac{1}{1-0}\left[0.042\int_0^1 dp + 63.861\int_0^1 p\,dp - 88.863\,502\int_0^1 p^2\,dp + 40.003\,-287\int_0^1 p^3\,dp\right] = \left[0.042\,p\right]_0^1 + \left[63.861\frac{p^2}{2}\right]_0^1 - \left[88.863\,502\frac{p^3}{3}\right]_0^1 + \left[40.003\,287\frac{p^4}{4}\right]_0^1 = \left[0.042-0\right] + \left[\frac{63.861}{2}-0\right] - \left[\frac{88.863\,502}{3}-0\right] + \left[\frac{40.003\,287}{4}-0\right] =$$

$$= 0.042 + 31.931 - 29.621 + 10.001 = \underline{12.353} \quad (4)$$

$$Q'_{\mathrm{II}} = 15p \left[r_{pQ_{\mathrm{II}}} = +0.993^{**}\right] \quad (5)$$

$$SQ_{\mathrm{II}} = \frac{1}{1-0}15\int_0^1 p\,dp = \left[15\frac{p^2}{2}\right]_0^1 = \left[7.500-0\right] = \underline{7.500} \quad (6)$$

$$Q'_{\mathrm{III}} = 15 - 0p = 15 \left[r_{pQ_{\mathrm{III}}} = 1.000^{**}\right] \quad (7)$$

$$SQ_{\mathrm{III}} = \frac{1}{1-0}\left[15\int_0^1 dp\right] = \left[15\,p\right]_0^1 = \left[15-0\right] = \underline{15.000} \quad (8)$$

Verification of the analytical method was carried out on a set of real stands of *Alopecuretum* meadows (*Trifolio-Festucetum alopecuretosum* Neuhäusl 1972 – grass stand IV). This set consisted of six vegetation relevés (Table 5). Data about the number of vascular plants are given in Table 5 and Figure 2. Figure 2 can also be used for the specification of the number of replicates needed (i.e. particular vegetation relevés – particular research areas) or the specification of the species variety of the grass stands. The theoretical reconstruction of empirical data for the set of grass stand IV – the regression model (9) and the calculation of the mid value (10) for the curve (9) are as follows::

$$Q'_{\mathrm{IV}} = 34.436 + 7.158\ln p \left[r_{pQ_{\mathrm{IV}}} = 0.999^{**}\right] \quad (9)$$

$$SQ_{\mathrm{IV}} = \frac{1}{1-0.01}\left[34.436\int_{0.01}^1 dp + 7.158\int_{0.01}^1 \ln p\,dp\right] =$$

$$= \frac{1}{0.99}\left\{\left[34.436\,p\right]_{0.01}^1 + \left[7.158\left(p\ln p - p\right)\right]_{0.01}^1\right\} =$$

$$= 1.010\left\{\left[34.436-0.344\right] + \left[-7.158-\left(-0.056\times 7.158\right)\right]\right\} =$$

$$= 1.010 = \left(34.092 - 6.757\right) = \underline{27.608} \quad (10)$$

This method is closely related to the Zürich-Montpellier phytocenological school (Braun-Blanquet 1964, Moravec et al. 1994). It is important that the data on the repetitive presence of particular species in particular grass stands are unambiguous (as opposed to the estimates of cover degree). This method may be used for the evaluation of plant community relevés at a quantitative and also semiquantitative level. It is suitable for the evaluation of species variety and species diversity also in other ecosystems (forests, marshes), and for some zoocenoses and whole biocenoses.

The numerical expression of the species variety and diversity is suitable for research of the grass stand composition. At an absolute grass stand constancy (grass stand III) = all plant species would show 100% constancy. The values of Q' model (1) = constant (c):

$$Q' = f(p) = c \quad (11)$$

We evaluated a larger number of homotonic sets of relevés and the curves of horizontal distribution of the species variety have a concave shape.

A practical use of the proposed simultaneous assessment of plant communities can provide information on their biodiversity and environmental state. In addition to assessments of quantity it is also important to assess quality parameters, i.e., the occurrence and role of various populations and cenoses in a landscape.

One of the important questions of experimental and observation studies aimed at the evaluation of

Table 5. Sample of vegetation relevés of meadows No IV (*Trifolio-Festucetum alopecuretosum)*

PhU	Species	Replicate						C_i / Q
		a	b	c	d	e	f	
		%*D*						
Trifolio-festucetum rubrae	*Festuca rubra*	4	10	12	10	8	4	1.00
	Alchemilla xanthochlora	+	2	1	1	2	3	1.00
	Veronica chamaedrys	+	1	+	.	1	+	0.83
	Achillea millefolium	.	.	1	+	+	.	0,33
	Ranunculus acris	.	.	+	.	+	.	0.33
Subassociation: alopecuretosum	*Alopecurus pratensis*	50	35	40	30	42	40	1.00
	Poa pratensis	8	3	6	1	3	5	1.00
	Lathyrus pratensis	1	+	+	9	4	3	1.00
	Sanguisorba officinalis	+	+	+	3	2	7	1.00
	Ranunculus repens	+	.	+	+	+	1	0.83
	Lychnis flos-cuculi	+	.	+	.	.	+	0.50
	Poa trivialis	.	.	+	.	.	+	0.33
	Vicia sepium	.	.	+	1	.	.	0.33
	Cardamine pratensis	.	+	.	.	.	.	0.17
Molinio-Arrhenatheretea	*Holcus lanatus*	1	+	1	1	1	2	1.00
	Festuca pratensis	4	5	3	8	4	1	1.00
	Poa angustifolia	4	4	3	2	2	4	1.00
	Plantago lanceolata	.	1	1	+	+	1	0.83
	Cerastium holosteoides	.	1	1	+	+	+	0,83
Arrhenatheretalia and *Arrhenatherion*	*Trisetum flavescens*	10	12	12	12	7	10	1.00
	Pimpinella major	10	8	8	10	12	9	1.00
	Avenastrum pubescens	+	3	2	.	2	2	0.83
	Heracleum sphondylium	.	+	+	+	+	+	0.67
	Chrysanthemum leucanthemum	.	+	.	+	.	+	0.50
	Saxifraga granulata		.	+	+	.	+	0.50
	Dactylis glomerata	+	+	.	.	.	.	0.33
	Galium mollugo	+	1	.	.	.	.	0.33
	Taraxacum officinale	+	.		.	.	.	0.17
	Campanula patula	.	+	.	.	.	.	0.17
	Arrhenatherum elatius	1	.	.	.	.	.	0.17
	Anthriscus silvestris	.	.	.	.	.	+	0.17
Molinion and subordinate units	*Deschampsia caespitosa*	+	+	.	.	.	.	0.33
	Elytrigia repens	1	2	1	.	.	.	0.50
	Agrostis stolonifera	.	+	+	.	.	.	0.33
Gaps		6	12	9	12	10	8	
$Q_{0.17}$		21	24	24	19	19	21	21.33
$Q_{0.33}$		28 (*)		26 (*)		24 (*)		26.00
$Q_{0.50}$		32 (*)				25 (*)		29.00
$Q_{1.00}$		34						34.00

PhU = phytocenological units
C_i = constancy (constancy of particular plant species; 100% = l)
Q = number of vascular plant species
%*D* = cover degree
(*) = only selected combinations

phytocenological relationships within grass stands is the assessment of relevés. While solving these problems we focused our attention on the potential of the methods proposed for the analysis of species variety distribution ($S_{Q'}$ Q_p) and for the specification of homotony of relevés. On the basis of a set with zero homotony (grass stand II) and a set with absolute homotony (grass stand III) (Table 2) we derived the following relationship between SQ' and $Q'_{1.0}$ values, which expresses homotony (ε') of these sets (the calculation also includes the standardization of the relationship):

$$\varepsilon' = \frac{2S_Q}{Q'_{1.0}} - 1 \quad (12)$$

For grass stand II, the homotony index (ε') thus calculated is:

$$\varepsilon'_{II} = \frac{2 \times 7.50}{15} - 1 = 0 \quad (13)$$

and for grass stand III it is:

$$\varepsilon'_{III} = \frac{2 \times 15}{15} - 1 = 1 \quad (14)$$

The presented relations also justify the use of all the methods described above for the analysis of species variety (SQ', Q_p) in grass swards.

For grass stand I, the homotony index (ε') is:

$$\varepsilon'_I = \frac{2 \times 12.353}{15} - 1 = 0.647 \quad (15)$$

and for grass stand III it is:

$$\varepsilon'_{IV} = \frac{2 \times 27.608}{33.51} - 1 = 0.648 \quad (16)$$

While verifying the proposed method for the assessment of sward homotony, we gradually linearly changed the homotony of model stands between the sets represented by grass stands II and III. We found out that the homotony index (ε') was not changing linearly. Therefore we elaborated a method for determining the corrected value of this index (cor ε'), which varies in the same proportions as the homotony changes in the studied sets. The formula for achieving linear development (cor ε') of ε' is as follows:

$$cor\ \varepsilon' = \exp_{\varepsilon'}(5.807\varepsilon^{0.333})^{-1} \quad (17)$$

This correction seems to be suitable for all cases where $0 < \varepsilon' < 1$. For set I (generated as a simplified form of set IV for solving methodological problems within sets I, II, III and IV) the corrected value of the homotony index is cor ε' = 0.917, as well as for set IV. Correction is not necessary for sets II and III, where $\varepsilon' = 0$ or $\varepsilon' = 1$. Experimental practice will indicate which homotony index is to be applied. In our opinion, it is advisable to apply both indices (ε', cor ε').

As the values of the homotony index (ε') and corrected homotony index (cor ε') are standardised for the span 0 to 1, it is also possible to express heterotony by means of the heterotony index (ξ'), or a corrected heterotony index (cor ξ'), in the following way:

$$\xi' = 1 - \varepsilon' \quad (18)$$

$$cor\ \xi = 1 - cor\ \varepsilon' \quad (19)$$

The indices of heterotony could be used, e.g. for expressing biotope diversity within a set of relevés from different stands.

By solving methodological problems of the analysis of species variety and grass sward diversity we come to another analytical characteristic of a set of relevés – δ diversity, which can be characterized as a variation span of species variety within particular relevés or particular swards (Q) classified in the studied set:

$$\delta_{abs} = Q_{max} - Q_{min} \quad (20)$$

or in relative expression:

$$\delta_{rel} = \frac{Q_{max}}{Q_{min}} \quad (21)$$

or in its inversion form:

$$i(\delta_{rel}) = \frac{Q_{min}}{Q_{max}} \quad (22)$$

In set IV the values of δ diversity (Table 6) are as follows:

$$\delta_{abs} = Q_{0.17max} - Q_{0.17min} = 26 - 17 = 9 \quad (23)$$

$$\delta_{rel} = \frac{Q_{0.17max}}{Q_{0.17min}} = \frac{17}{26} = 1.529 \quad (24)$$

$$i(\delta_{rel}) = \frac{Q_{0.17max}}{Q_{0.17min}} = \frac{17}{26} = 0.654 \quad (25)$$

All the analytical procedures presented above become parts of the computer programme Species Richness – FA SU, which can be downloaded freely on the address: http://www2.zf.jcu.cz/~klimes/; the programme is supplemented by freely acces-

sible detailed instructions, including the proposed algorithm for an analysis of soil diversity (pedodiversity) or agrodiversity.

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