Original Research

Assessment of Biodiversity in *Molinia* Meadows in Kampinoski National Park Based on Biocenotic Indicators

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Abstract

Communities of purple moor-grass meadows are generally decreasing. Many important problems of classification and phytogeography are connected with them. The main goal of the present study was to evaluate changes in species diversity that took place after mowing of *Molinion* meadows in Kampinoski National Park was discontinued from 1993 to 2006. Selected *Molinion* meadows in the park were evaluated in terms of their biological diversity. The data collected represented meadows that were still maintained, as well as meadows that had been abandoned at different times in the past. Biodiversity was evaluated using standard ecological indices and Disturbance Index (*Z*). In general, the Disturbance Index showed an increase in plant community forms that were abandoned or invaded by alien species. An association that was most like the typical form was seen in well maintained meadows, which suggests that the Disturbance Index continually rises with time after a meadow is abandoned. Ecological strategies and mowing tolerance were determined with the help of the BIOLFLOR database. Numerical classification revealed a highly diverse pattern of variability in the meadows examined. Correlations between ecological indicators and phytocenotic variability in *Molinion* meadows were also evaluated. Unmanaged meadows were compared to meadows in which meadow conservation management practices were carried out.

Keywords: species diversity, disturbance index, vegetation changes, mowing tolerance, abandoned meadows

Introduction

Grassland communities are threatened and in retreat everywhere in Europe [1, 2]. Diversity in a meadow community depends on many factors, and reflects habitat conditions as well as present and past agricultural uses of the meadow in question [3-10].

Molinia meadows are rich in species and develop under a particular set of conditions. In the European Union, this unique combination of species is in danger of being lost, and these meadows are therefore under protection. *Molinia* meadows differ widely over their geographical range. Their classification is therefore frequently revised [11-16]. Although many publications deal with *Molinia* meadows, further research is needed on plant succession in these communities, and on how to protect and restore them [4, 17-19].

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Diversity in *Molinia* meadows has been studied either in the context of species diversity and richness along habitat gradients, or in the context of land management [20-22]. In a particular meadow, species composition and spatial diversity are affected by endogenic and exogenic changes in the plant community. Alpha, beta and gamma diversity can be estimated on the basis of numerous ecological indicators [23-25].

Species composition and diversity have been found to be particularly affected by degeneration and disturbance [26, 27]. The degree of disturbance essentially determines the degree of diversity at both the community and species levels [28]. Semi-natural plant communities are especially sensitive to changes. One of the effects of changes is a reduction in species diversity.

In the present study, changes in species composition were estimated using the Disturbance Index [14]. This index can be used to identify meadows in which species that are non-specific for *Molinion* meadows are found, and how dominant species limit the development of other species. Changes in meadow communities are most often associated with patterns of land management practices.

Molinion meadows are a useful model plant community because they contain a large group of characteristic species, most of which are rare. All of these characteristic species have therefore been placed on local, regional or national red lists of threatened plant species [29].

Molinion meadows develop as the result of human activity in the form of irregular mowing or autumnal and winter burning. Extensive agricultural practices have made these meadows rich in plant species.

The *Molinion* meadows currently found in Kampinoski National Park have been well documented. Reliable information has been gathered on plant succession, and conservation plans have been drawn up for some of these meadows [30-32].

The aim of the present study is to describe biodiversity in *Molinion* meadows in the park from 1993 to 2006. The meadows examined were last mown in 1994. Data collected from 1993 to 1995 therefore represent the period in which human activity was still carried out.

The main goal of the present study was to evaluate the changes in species diversity that took place after mowing was discontinued. Among the changes observed in abandoned meadows is a reorganization of the species composition due to plant succession and invasion by species that are alien to the specific habitat and to the region as a whole. The study focused on the way in which species composition is affected by the development of dominant and alien species.

The definition of changed plant communities was examined, and the key factors that contribute to the formation of these communities were evaluated. Changes in diversity and species composition in the meadows were recorded throughout the observation period. Correlations between ecological indicators and phytocenotic variability in *Molinion* meadows were also evaluated. Unmanaged meadows were compared to managed meadows in which meadow conservation management practices were carried out.

Materials and Methods

From 1993 to 1999 [30], and again in 2006, selected *Molinion* meadows in the park were evaluated in terms of their biological diversity. In all, 54 phytosociological samples were collected. Data were recorded using the Braun-Blanquet quantitative scale, and entered in the TURBOVEG database [33]. Plant communities were numerically classified using the NCLAS program of the SYNTAX 5.0 software package [34]. Similarities between samples were estimated using the Jaccard formula, on the basis of the presence or absence of species in samples being compared. All samples were classified using the unweighted pair-group method with the arithmetic mean [35].

All data were analyzed using the Juice software package [36]. For each sample, the following indices were calculated: the Shannon-Wiener Diversity Index (H), the Pielou Uniformity Index (J), the General Species Richness Index (R), the Simpson Dominance Index; and the Whittaker Beta Diversity Index.

The abundance of particular species was recorded as the mean cover of cover-abundance scale transformed as follow: r = 0.1%, + = 0.5%, 1 = 5%, 2 = 17.5%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%.

The effective number of species in a particular community was estimated on the basis of the Shannon-Wiener Diversity Index. This was done to identify real differences in species diversity among the meadows examined [37].

Different forms of meadow were determined on the basis of the Disturbance Index [14]. This index is based on models simulating the stages of degeneration in natural and semi-natural plant communities [38, 39]. The value of the index depends on the overall number and cover of species that are incidental, non-specific or alien to the ecosystem in question. The Disturbance Index (Z) is calculated according to the following formula:

$$Z = \frac{\frac{d}{1+N} + A + B^2}{C}$$

...where:

d - represents the sum of the mean percentage cover of each species characteristic for the order and class to which the community belongs, multiplied (or divided) by the number of these species;

N - represents the sum of the mean percentage cover of each species characteristic for the alliance and association to which the community belongs, multiplied (or divided) by the number of these species;

A - represents the sum of the mean percentage cover of each accompanying species multiplied (or divided) by the number of these species;

B - represents the sum of the mean percentage cover of each species that act as bio-indicators of changes or disturbance multiplied (or divided) by the number of these species;

C - represents the sum of the mean percentage cover of each species characteristic for the association, alliance, order and class to which the community belongs, multiplied (or divided) by the number of these species.

In the present study, the factors listed above were calculated using multiplication. In this case, a value for the Disturbance Index between 0 and 1 indicates that the community in question is a typical undisturbed form, whereas a higher value indicates that the community is a non-typical disturbed form.

To calculate factor *B*, all of the tree and shrub species in a particular sample were taken into account, as well as herbaceous species such as *Filipendula ulmaria* and alien species such as *Solidago gigantea*. However, *Molinia caerulea* was also included when it was clearly the dominant species: that is, when the cover exceeded 62.5%, or 4 on the cover-abundance scale presented above. The effect of *Molinia caerulea* on the value of the index was not great unless the species composition was reduced.

Total cover and number of species were calculated for selected syntaxonomic and ecological groups as well as for rare and protected plant species. Ecological strategies and mowing tolerance were determined with the help of the BIOLFLOR database [40]. The number of species and species cover were calculated for each type of ecological strategy and each level of mowing tolerance. The mean values thus obtained were used to compare samples in terms of land management practice and particular forms of examined meadows.

Ten species were not taken into account because of their sporadic abundance. All of them belonged to strategy types S, R, CR and SR [41]. Level of mowing tolerance was recorded using the following scale: 1 to 3: intolerant or sensitive; 4 to 5: sensitive to moderately tolerant; 6 to 7: moderately tolerant to well tolerant; and 8 to 9: well tolerant to very tolerant.

Overall habitat conditions were evaluated by determining the proportion of species with specific habitat preferences as based on their values for selected habitat indicators [42]. The following Ellenberg indicators were calculated for each sample: light (L), moisture (M), soil reaction (R), temperature (T), nutrient level (N) and continentality (K).

All data were analyzed along a gradient of syntaxonomic variability, both as a function of time (1995, 1999, 2006) and as a function of changes in land management practice. Differences between values for diversity indices and between the types of plant communities were evaluated using non-parametric analysis of variance with the Kruskal-Wallis test and multiple comparison of mean ranks for each sample. Unpaired groups of samples were compared using the U Mann-Whitney test. The dependence between some indicators and species groups were estimated using the Pearson correlation coefficient.

De-trended correspondence analysis (DCA) was used to identify differences in species composition, as well as the main gradients of variability of the vegetation [43]. Data on the habitat consisted of 32 environmental variables. DCA was also used to identify the level of variability in the beta diversity of the plant communities [23]. In the present study, the length of the gradient was recorded using units equal to the standard deviation [26, 44]. Ordinating DCA

Table 1. Mean values of biodiversity indices for 1) typical variants; 2) variants with *Galium boreale*; 3) variants with *Carex davalliana*; and 4) variants with *Salix cinerea*.

Variant		1	2	3	4	P
Number of samples		25	9	13	7	
Mowing tolerance -species cover	1 to 3	69.29	76.74	77.49	90.64	NS
	4 to 5	63.55	42.61	48.59	35.07	NS
	6 to 7	32.43^{ab}	15.73	5.05^{a}	4.07^{b}	**
	8 to 9	14.32^{b}	25.22^{a}	6.92	0.71^{ab}	**
Mowing tolerance -species number	1 to 3	5.76	7.44	7.70	5.71	NS
	4 to 5	11.20^{b}	8.22	13.77^{a}	5.00^{ab}	**
	6 to 7	5.16^{a}	4.44^{b}	3.46	0.71^{ab}	**
	8 to 9	2.64^{b}	1.67	2.54^{a}	0.14^{ab}	**
Ecological strategy -species cover	C	58.55	71.64	43.26	41.92	NS
	CS	76.21	51.61	75.10	85.29	NS
	CSR	53.58^{a}	44.96	30.40	20.00^{a}	**
Ecological strategy -species number	C	10.00^{b}	10.33	12.15^{a}	4.57^{ab}	**
	CS	5.12	5.33	6.15	3.00	NS
	CSR	11.84^{b}	7.33	10.69^{a}	4.00 ^{ab}	**
Shannon-Wiener Index		2.59^{a}	2.42	2.45	1.69^{a}	**
Pielou Uniformity Index		0.80^{a}	0.78	0.73	0.64^{a}	*
Richness Index		26.28^{b}	23.55	29.23^{a}	13.71^{ab}	**
Simpson Dominance Index		0.85^{a}	0.83	0.81	0.64^{a}	*
Ellenberg values						
Light		7.02^{b}	6.77^{ab}	7.09^{a}	6.99	**
Moisture		7.02^{ac}	6.49^{bcd}	7.40^{ab}	7.66^{d}	**
Soil Reaction		6.24^{b}	6.08	6.26^{a}	5.42^{ab}	**
Temperature		5.30^{a}	5.37^{b}	5.14^{ab}	5.26	**
Effective number of species		14.48^{a}	12.34	12.86	6.45^{a}	**
Protected species cover		10.17^{a}	1.84^{a}	8.13	6.64	*
Protected species number		1.96	0.78	1.85	1.00	*
Woody species cover		7.33	6.68	11.31	29.00	NS
Disturbance Index		3.14^{a}	1.28^{b}	35.20	456.74^{ab}	**
Average Whittaker beta diversity		1.9467	2.357	1.8165	3.4742	

Values followed by the same letter are significantly different according to the Kruskal-Wallis test at: $^{*}P < 0.05$, $^{**}P < 0.01$.

diagrams were prepared taking the cover of species into account. The level of beta diversity was determined using canonical analysis, and was subsequently confirmed using the JUICE software package [36].

Results

Syntaxonomic Variability

Numerical classification revealed a highly diverse pattern of variability in the meadows examined (Fig. 1). All of the meadows examined belonged to the sub-association *Selino-Molinietum sanguisorbetosum.* Four local variants of this sub-association were identified: the typical variant, a variant with *Galium boreale,* a variant with *Carex davalliana*, and a variant with *Salix cinerea*. The variants differed significantly in terms of habitat preference, as reflected by their mean values for the Ellenberg indices (Table 1).

The main factor distinguishing the variants was moisture. The variant with *Galium boreale* was found in fresh and slightly moist habitats. This variant also contained the highest proportion of thermophilic species. The variants with *Carex davalliana* and *Salix cinerea* were found in the wettest habitats.

The number of species was highest in samples of the typical variant and the variant with *Carex davalliana*. Alpha diversity was highest in samples of the typical variant, and lowest in samples of the variant with *Salix cinerea* (Table 1).

The variants also differed in terms of the cover of species in the groups of species defined by their tolerance to mowing. The typical variant was characterized by the highest cover of species with a mowing tolerance of 6 to 7. The cover of species with a mowing tolerance of 8 to 9 was highest in the variant with *Galium boreale*, and lowest in the variants with *Carex davalliana* and *Salix cinerea*.

The variants that were subjected to the most intense mowing were the typical variant and the variant with *Galium boreale*. Meadows represented by the variant with *Carex davalliana* were mown only rarely. Meadows represented by the variant with *Salix cinerea* had not been mown for many years.

The number of species in Group C was highest in the variant with *Carex davalliana* and lowest in the variant with *Salix cinerea*. On the other hand, the cover of species in Group CRS type was highest in the typical variant, and lowest in the variant with *Salix cinerea*.

The main differences between the indices analyzed were between the typical variant, and the variant with *Salix cinerea* (Table 1). Differences in species composition between these variants were also evident at the level of beta diversity. Beta diversity was highest in the variant with *Salix cinerea*, and lowest in the variant with *Carex davalliana* and the typical variant.

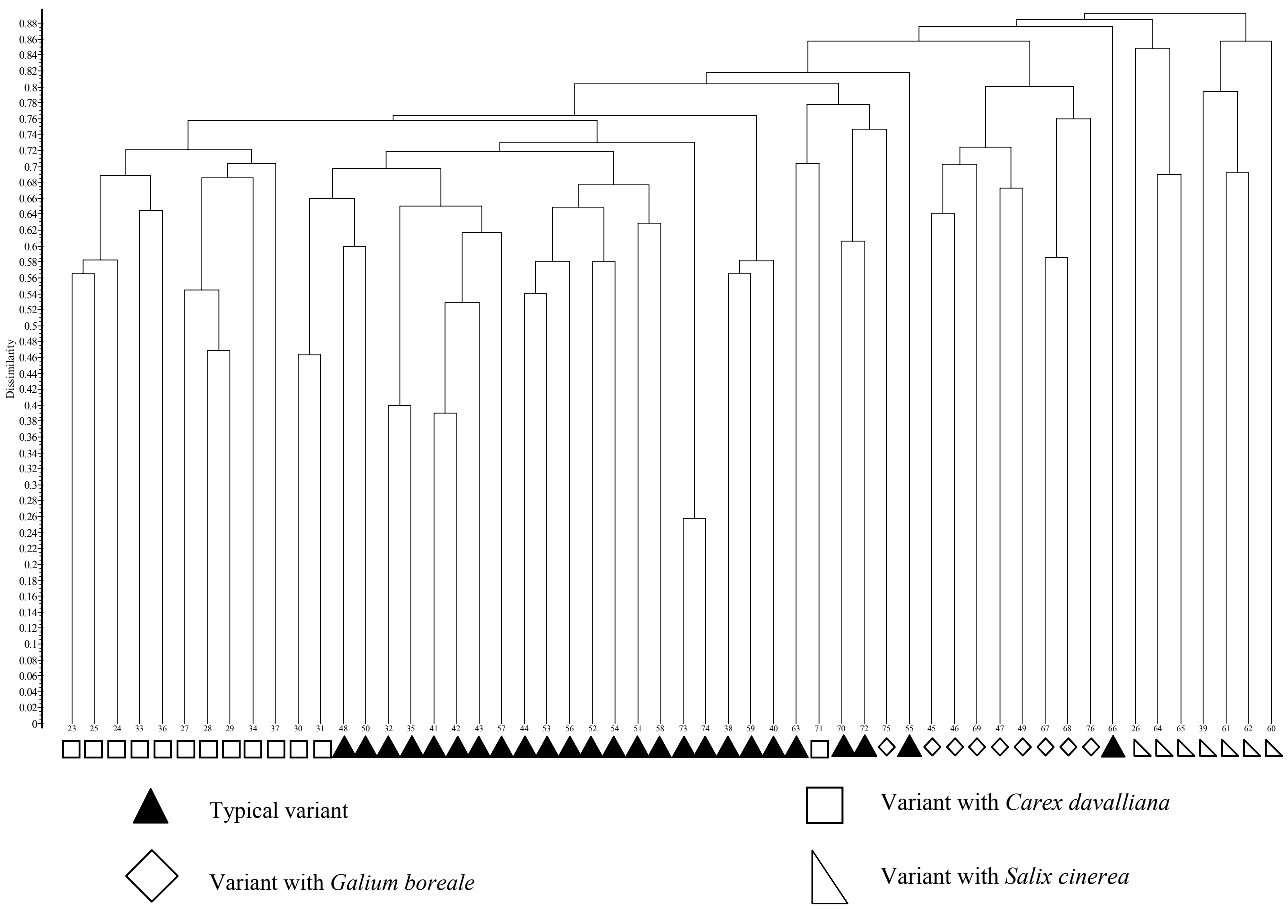

Fig. 1. Classification of *Molinion* meadows based on species composition in accordance with Jaccard's formula using the NCLAS program.

Table 2. Gamma diversity in *Molinion* meadows in Kampinoski National Park and at selected sites in Poland.

Name of region	Total number of species	Average number of species	Range of number of species	Number of samples
Kampinoski NP	185	25	8 to 44	54
Lower Silesia [12]	163	31	12 to 50	240
Upper Silesia [15]	157	37	18 to 48	20
Bolimów Primeval Forest [32]	146	30	19 to 43	28
Wielicki [1]	106	27	18 to 41	13
Przemsza Valley [34]	74	23	16 to 43	8
Noteć Valley [16]	145			16

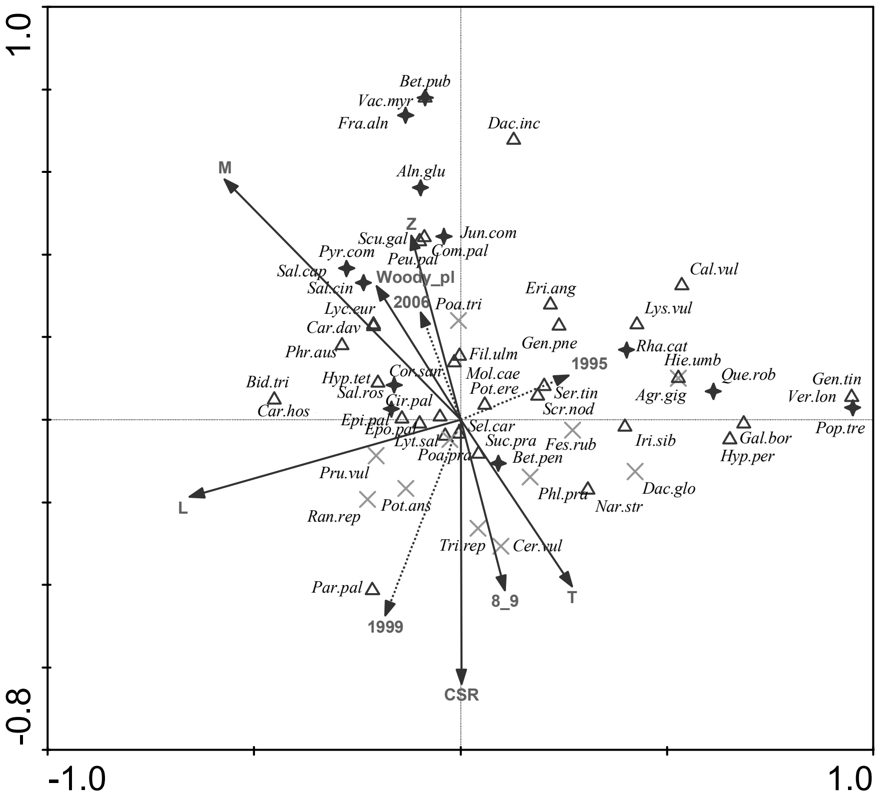

Fig. 2. Ordination diagram based on canonical correspondence analysis (CCA Axis 1 $\lambda_1 = 0.40$ and Axis 2 $\lambda_2 = 0.32$) of the species abundance of *Molinion* meadow. Nominal explanatory variables are characterized by dotted-line arrows, numeric explanatory variables by solid-line narrows (L: light, M: moisture, and T: temperature; strategy type CSR represents competitors/stress-tolerators/ruderals, mowing tolerance 8 to 9). Symbols represent different species groups: triangles: intolerant-to-sensitive to mowing, X's: well to very tolerant of mowing, and stars: woody plants.

Species codes:

Agr.gig=Agrostis gigantea, Aln.glu=Alnus glutinosa, Bet.pen=Betula pendula, Bet.pub=Betula pubescens, Bid.tri=Bidens tripartita, Calu.vul=Calluna vulgaris, Car.dav=Carex davalliana, Car.hos=Carex hostiana, Cer.vul=Cerastium vulgatum, Cir.pal=Cirsium palustre, Com.pal=Comarum palustre, Cor.san=Cornus sanguinea, Dac.glo=Dactylis glomerata, Dac.inc=Dactylorhiza incarnata, Epo.pal=Epilobium palustre, Eri.ang=Eriophorum angustifolium, Fes,rub=Festuca rubra, Fil.ulm=Filipendula ulmaria, Fra.aln=Frangula alnus, Gal.bor=Galium boreale, Gen.pne=Gentiana pneumonanthe, Gen.tin=Genista tinctoria, Hie.um=Hieracium umbelatum, Hyp.per=Hypericum perforatum, Hyp.tet=Hypericum tetrapterum, Iri.sib=Iris sibirica, Jun.com=Juniperus communis, Lyc.eur=Lycopus europaeus, Lys.vul=Lysimachia vulgaris, Lyt.sal=Lythrum salicaria, Mol.cae=Molinia caerulea, Nar.str=Nardus stricta, Par.pal=Parnassia palustris, Peu.pal=Peucedanum palustre, Phl.pra=Phleum pratense, Phr.aus=Phragmites australis, Poa.pra=Poa pratensis, Poa.tri=Poa trivialis, Pop.tre=Populus tremula, Pot.ans=Potentilla anserina, Pot.ere = Potentilla erecta, Pru.vul=Prunella vulgaris, Pyr.com=Pyrus communis, Que.rob=Quercus robur, Ran.rep=Ranunculus repens, Rha.cat = Rhamnus catharticus, Sal.cap=Salix caprea, Sal.cin=Salix cinerea, Sal.ros=Salix rosmarinifolia, Scr.nod=Scrophullaria nodosa, Scu.glu=Scutellaria galericulata, Sel.car=Selinum carvifolia, Ser.tin=Serratula tinctoria, Suc.pra=Succisa pratensis, Tri.rep=Trifolium repens, Vac.myr=Vaccinium myrtillus, Ver.lon=Veronica longifolia.

Table 3. Mean values of biodiversity indices for 1995, 1999 and 2006.

Year		1995	1999	2006	
Number of samples		18	8	28	
Mowing tolerance					
species cover	1 to 3†	58.83[a]	41.18	25.26[a]	**
	1 to 3	95.36[ab]	64.00[a]	65.21[b]	**
	4 to 5	55.89	72.88	45.11	NS
	6 to 7	20.47	43.94[a]	11.66[a]	*
	8 to 9	11.14	16.69	12.36	NS
species number	1 to 3†	5.39	4.50	6.07	NS
	1 to 3	6.11	5.38	7.07	NS
	4 to 5	7.00[a]	10.13	12.89[a]	**
	6 to 7	2.39[ab]	5.63[a]	4.68[b]	**
	8 to 9	0.94[a]	2.00	2.93[a]	**
Ecological strategy					
species cover	C	60.72	74.19	45.64	NS
	CS†	40.78	52.37	29.70	NS
	CS	77.31	75.19	69.65	NS
	CSR	50.11	60.81	31.80	NS
species number	C	5.78[a]	9.25	12.68[a]	**
	CS	4.39	5.38	5.54	NS
	CSR	7.00[a]	11.25	11.18[a]	**
Shannon-Wiener Index		2.18	2.76	2.47	NS
Pielou Uniformity Index		0.76	0.86[a]	0.73[a]	**
Richness Index		17.83[a]	25.00	29.43[a]	**
Simpson Dominance Index		0.78	0.91[a]	0.81[a]	NS
Ellenberg values					
Light		6.94	7.01	7.02	NS
Moisture		7.05	7.09	7.14	NS
Soil Reaction		6.11[a]	6.20	6.09[a]	*
Temperature		5.34[a]	5.36[b]	5.20[ab]	**
Nutrient Level		3.34[a]	3.64	3.74[a]	**
Continentality		3.88	3.81	3.88	NS
Effective number of species		10.57	16.06	13.10	NS
Protected species cover		9.33	9.75	6.32	NS
Protected species number		1.33	2.00	1.68	NS
Woody species cover		9.75	10.31	11.98	NS
Disturbance Index		98.35	1.05	70.23	NS

Values followed by the same letter are significantly different according to the Kruskal-Wallis test at $*P < 0.05$ and at $**P < 0.01$.
† designates means without *Molinia caerulea*.

Biodiversity Indices and the Disturbance Index

The *Molinion* meadows of Kampinoski National Park are characterized by a high level of gamma diversity (Table 2). Several significant differences in the indices examined were observed in successive years of the study. In 1995, the cover of species with a mowing tolerance of 6 to 7 was highest, as was the cover of species with a mowing tolerance of 1 to 3 (Table 3). The number of species with a mowing tolerance of 6 to 7, on the other hand, was lowest, as was the number of species in Group C (Table 3). The mean number of species increased significantly from 1995 to 2006. Values for the Uniformity Index were lower in 2006 than in 1999 (Table 3).

There were significant differences in the values of some of the Ellenberg indicators, especially those from 1995 and 2006 (Table 3). In 1995, the mean values for soil reaction were higher than in 2006, but values for nutrient level were lower. On the other hand, the values for temperature changed significantly in subsequent years, with the lowest values recorded in 2006.

When the vegetation of *Molinia* meadows were divided into non-typical and typical forms, many significant differences were found either between years, or in relation to the group of samples as a whole (Table 4). In 1999, the differences in mean ranks between the typical form and the non-typical forms were statistically insignificant as determined by the U Mann-Whitney test. This was because of the small amount of material collected that year. However, many significant differences were found in both 1995 and 2006 (Table 4).

The Shannon-Wiener Index, Pielou Uniformity Index, Richness and Simpson Dominance Index were significantly lower in the non-typical forms. The cover of species with a mowing tolerance of 1 to 3 was also lower in the non-typical forms, as was the cover of species with a mowing tolerance of 6 to 7 and 8 to 9. In the non-typical forms, the cover of species in Group CRS decreased from 1995 on, whereas the cover of species in Group CS increased. The increase in species belonging to Group CS can be attributed mainly to the development of *Molinia caerulea*, which had a higher cover in the non-typical forms (Table 5). When this species is not taken into account, the cover of the remaining species in Group CS decreased from 1995 on.

In most cases, the non-typical forms had significantly lower values for the cover and number of species belonging to selected groups of plants, as well as for the biocenotic indices. The only exception was with woody species, which were more abundant in samples of the non-typical forms (Tables 4 and 5).

The CCA ordination diagram revealed a high level of variability in the plant communities examined. The primary distinguishing factor was moisture. The Disturbance Index was positively correlated with moisture and with the abundance of woody species. The abundance of woody species was highest in 2006 because the smallest area of the meadows was mown in that year. On the other hand, in 1995 and 1999, the cover of species resistant to mowing

Table 4. Mean values for diversity indices in the typical and the non-typical forms for 1995, 1999 and 2006 and for meadows in use and not in use.

Year		1995		1999		2006		typical (all years)	non-typical (all years)	in use (all years)	not in use (all years)
Number of samples		9	9	6	2	14	14	29	25	34	20
Forms		typical	non-typical	typical	non-typical	typical	non-typical				
Mowing tolerance											
species cover	1 to 3†	58.78^{a}	58.89^{b}	48.50	19.25	37.92^{c}	12.59^{abc} ***	46.58	29.79 **	49.37	20.85 ***
	1 to 3	75.17	115.56^{abcd} **	69.75^{a}	46.75^{b}	65.5^{c}	65.27^{d}	69.56	81.89	81.38	64.90
	4 to 5	73.22	38.56 *	74.00	69.50	55.73	34.30 *	64.94	38.65 ***	62.96	35.44 ***
	6 to 7	30.67	10.28^{a} *	55.08^{ab}	10.50	17.76	5.55^{b} *	29.49	7.65 ***	24.64	10.44 *
	8 to 9	19.50	2.78^{a}	19.75^{a}	7.50	12.08	12.64	15.96	8.68 **	12.0	16.6
species number	1 to 3†	5.78	5.00	5.33	2.00	6.86	5.29*	6.21	4.92 *	5.50	5.80
	1 to 3	6.33	5.89	6.17	3.00	7.86	6.29 *	7.03	5.88	6.32	6.80
	4 to 5	9.22	4.78^{ab} *	10.00	10.50	13.93^{b}	11.86^{a}	11.65	9.20	9.85	11.65
	6 to 7	3.56	1.22^{ab} *	6.5^{ac}	3.00	5.07^{bc}	4.29	4.90	3.08 **	3.97	4.20
	8 to 9	1.33^{a}	0.56^{b}	2.17	1.50	4.29^{abc}	1.57^{c} ***	2.93	1.20 ***	2.0	2.35
Ecological strategy											
species cover	C	76.94	44.50	77.75	63.50	47.96	43.32	63.12	45.36 *	58.58	48.64
	CS†	54.11	27.44 *	50.75	57.25	34.45	24.95	43.92	28.43*	46.63	19.97 ***
	CS	70.50	84.11	72.00	84.75	62.03	77.27	66.72	80.33	78.5	63.8
	CSR	56.11^{a}	44.11	75.75^{b}	16.00	47.49^{c}	16.07^{abc} ***	56.03	26.16 ***	51.67	26.10
species number	C	7.33^{a}	4.22^{bc} *	9.83	7.50	14.07^{ab}	11.29^{c} *	11.10	8.44 *	8.44	12.30 **
	CS	5.67	3.11*	4.67	7.50	6.57	4.50 *	5.90	4.24 *	5.47	4.55
	CSR	8.56	5.44	13.00	6.00	12.5	9.86	11.38	7.96 *	9.71	9.95
Shannon-Wiener Index		2.62	1.74^{ab} **	2.86^{a}	2.43	2.74^{b}	2.19 **	2.72	2.05 ***	2.50	2.28 *
Pielou Uniformity Index		0.86^{ab}	0.66^{ac} **	0.88^{cd}	0.80	0.79	0.68^{bd} ***	0.83	0.68 ***	0.80	0.70 ***
Richness Index		21.77^{a}	13.88^{bc} **	26.33	21.00	32.92^{ab}	25.93^{c} *	28.10	21.20 **	23.76	26.85
Simpson Dominance Index		0.89^{ab}	0.66^{ac} **	0.92^{cd}	0.86	0.87	0.74^{bd} ***	0.89	0.72 ***	0.84	0.77 ***
Effective number of species		16.26	6.90^{ab} **	17.64^{ab}	11.32	16.25^{b}	9.94 **	15.92	8.96	13.91	10.63
Protected species cover		10.50	8.17	12.08	2.75	9.41	3.24	10.30	4.97 *	10.30	3.72 *
Protected species number		1.67	1.00	2.33	1.00	1.86	1.50	1.90	1.28	1.80	1.35
Woody species cover		4.22	15.28	3.75	30.00	3.90	20.05	3.96	19.13 *	9.34	13.79
Disturbance Index		0.35^{ab}	196.34^{acd} ***	0.30^{ce}	3.32	0.38^{df}	140.07^{bef} ***	0.35	149.39 ***	52.45	98.07

Values followed by the same letter are significantly different according to the Kruskal-Wallis Test at $P < 0.01$; Significant differences between unpaired group of samples according to the U Mann-Whitney Test are shown as: * $P<0.05$, ** $P< 0.01$ and *** $P<0.001$.
† designates means without *Molinia caerulea.*

Table 5. Mean plant cover of selected groups of species in the typical and the non-typical forms for 1995, 1999 and 2006, with breakdown by land management practice.

Year	1995		1999		2006	
Form	typical	non-typical	typical	non-typical	typical	non-typical
Number of samples	9	9	6	2	14	14
Mean plant cover						
Species characteristic of *Molinion* meadows (without *Molinia caerulea*)	53.44[ab]	20.89[a]*	21.33	14.25	25.29	8.06[b]*
Molinia caerulea	16.39[a]	56.67*	21.25	27.50	27.58	52.32[a]*
Molinietalia	31.67	22.94	55.25	50.00	36.59	15.30**
Molinio-Arrhenatheretea	54.06[a]	16.17*	69.50[ab]	15.50	30.77	18.49[b]
Accompanying species	49.39	59.00	64.25	57.00	32.31	39.36
Mean plant cover as a function of land management practice	used every year till 1993		sporadically used		mown (8 samples)	unmown (20 samples)
Species characteristic of *Molinion* meadows (without *Molinia caerulea*)	37.17		19.56		17.58	16.32
Molinia caerulea	36.53		22.81		30.33	43.8
Molinietalia	27.31		53.94		34.01	22.72
Molinio-Arrhenatheretea	35.11		56.00		24.66	24.61
Accompanying species	54.19		62.43[a]		53.6	28.73[b]*

Differences between years and type of land management practice marked by the same letter are significantly different according to the Kruskal-Wallis Test at $P < 0.01$. Differences between the typical and the non-typical forms in a given year differ according to the U Mann-Whitney Test are shown as $*P < 0.05$ and $**P < 0.01$.

and of thermophilic species was much higher. In those years, the meadows in the park were in use (Fig. 2).

In the DCA analysis, the unit length of the gradient along the first canonical axis was SD = 3.660, and the unit length of the gradient along the second canonical axis was SD = 3.415. This suggests that the level of variability was high in the meadows examined. So was the level of beta diversity, which was significantly higher in the non-typical forms (Fig. 3). On the other hand, in samples representing the typical variant and the variant with *Carex davalliana*, the level of beta diversity was low even though the level of alpha diversity was high. This is because of the high degree of homogeneity in these variants.

All of the indices analyzed were negatively correlated with the log-transformed Disturbance Index (Table 6). This was particularly true for the Shannon-Wiener Diversity Index, the Pielou Uniformity Index, and the cover of woody species. As the Disturbance Index increased, diversity decreased, and the cover of woody tree species increased (Fig. 4).

Of the Ellenberg indicators, nutrient level was positively correlated with mowing, which indicates that the trophic index is lower in mown meadows. Soil moisture, on the other hand, was positively correlated with the Disturbance Index. The cover of species in the CRS group was positively correlated with mowing, and negatively correlated with the Disturbance Index.

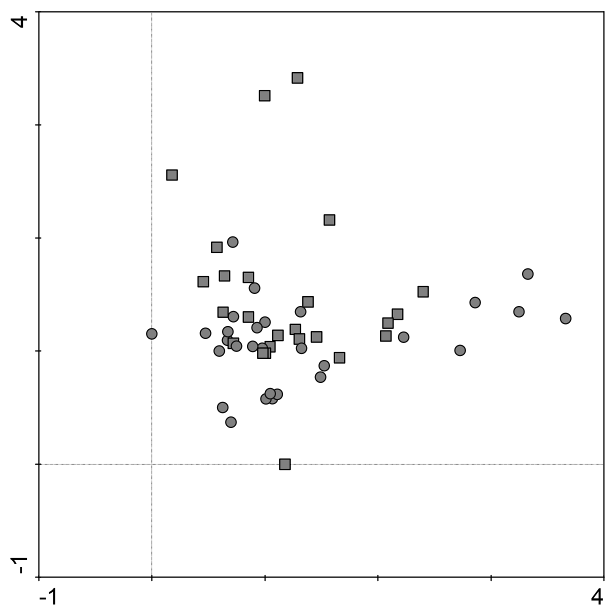

Fig. 3. Ordination of samples of the typical form (square symbols) and adjacent non-typical forms (circles) along first and second DCA axis. (Length of Gradient Axis 1: SD = 3.660; Length of Gradient Axis 2: SD = 3.415; eigenvalue for Axis 1: λ_1=0.462; eigenvalue for Axis 2: λ_2=0.344).

There were no significant differences between the typical and the non-typical forms in terms of the cover of rare and protected species.

Discussion

Molinion meadows are highly diverse plant communities both in small areas such as Kampinoski Park, as well as in larger geographical regions [13-16]. The *Molinion* meadows of the park differ from those in other parts of Poland in that they have a high number of plant species (Table 3).

Table 6. Relationship between diversity indices, usage status and Disturbance Index. Values with a Pearson correlation coefficient of P < 0.05 are marked in bold. Values for the Disturbance Index are log transformed.

	Usage status (mowing)	Disturbance Index
Shannon-Wiener Index	0.18	**-0.59**
Pielou Uniformity Index	**0.41**	**-0.58**
Richness Index	-0.17	**-0.38**
Simpson Dominance Index	0.25	**-0.61**
Moisture	-0.09	**0.38**
Nutrient Level	**-0.30**	-0.16
Effective number of species	**0.28**	**-0.55**
Species cover		
Mowing tolerance		
1-3 without *Molinia caerulea*	**0.45**	**-0.31**
4-5	**0.44**	**-0.42**
Ecological strategy		
C	0.15	**-0.31**
CSR	**0.41**	**-0.47**
Protected species	**0.33**	-0.06
Woody species	**-0.13**	**0.58**
Syntaxonomical group		
Molinion without *Molinia caerulea*	0.23	**-0.56**
Molinia caerulea	-0.20	**0.51**
Species number		
Ecological strategy		
C	**-0.43**	**-0.33**
CSR	-0.02	**-0.31**
Woody species	**-0.32**	**0.54**
Syntaxonomical group		
Molinion	-0.05	**-0.44**
Molinio-Arrhenatheretea	-0.13	**-0.51**

Although the mean number of species in a single sample from the park is close to the national average, the total number of species found in *Molinion* meadows in the park as a whole is exceptionally high. This is because the park comprises a diverse mosaic of habitats with different hydrological and agricultural conditions [4].

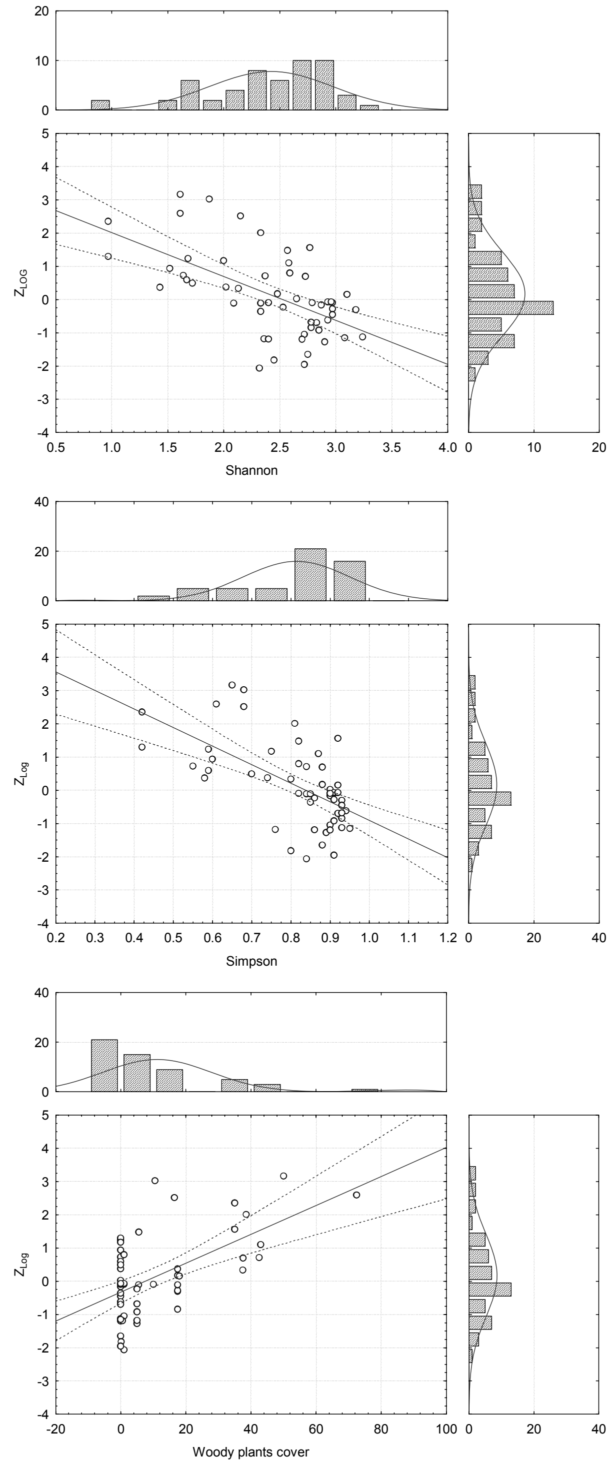

Fig. 4. The relationship between the Disturbance Index and a) the Shannon-Wiener Index, b) the Simpson Dominance Index; and c) cover of woody species in samples of *Molinion* meadows. Values for ***r*** and the levels of significance are presented in Table 6.

Furthermore, the high number of species reflects the fact that the meadows are no longer mown and are undergoing changes in species composition associated with plant succession [32, 45]. Such meadows are particularly rich because they contain species characteristic of both maintained and abandoned meadows.

In the present study, values for the Richness Index were highest in 2006. This is due to the low level of mowing carried out that year, and the fact that the Disturbance Index was increasing. On the other hand, values for the Diversity Index and the Uniformity Index were low because of the increased abundance of dominant species.

The typical form and the non-typical forms differed significantly in terms of vegetation type and species diversity. There were particularly large differences between the variant with *Salix cinerea* and the other variants. In the variant with *Salix cinerea*, the Disturbance Index and the abundance of woody species were high, whereas the Diversity Index and the Richness Index were low. Communities of this variant develop on meadows that are no longer mown, which allows trees to grow. In a previous study on abandoned grasslands, species diversity increases during the first stages of plant succession, but decreases as the trees age [46]. In the present study, samples of the variant with *Salix cinerea* differed greatly among themselves. They exhibited a high level of beta diversity.

In the non-typical forms, the cover of species from Group CS increased and the cover of species from Group CRS decreased throughout the observation period. This was true for both the variant with *Salix cinerea* and the other variants as well. A similar increase in the cover of species from Group CS was also observed in a previous study on abandoned grasslands [47]. In the meadows examined in the present study, this increase was probably due to the increase in the dominance of *Molinia caerulea*, based on the Pearson correlation coefficients.

Correlations between land management practice and diversity indices were much weaker, which shows that land management practice is not the only factor that determines the development of meadow communities (Table 6). Based on the values Disturbance Index, mown meadows can also represent non-typical forms when mowing is sporadic, or when there are changes in management level and environmental conditions.

The Disturbance Index makes it possible to precisely determine how species diversity and species composition are affected by non-meadow species such as trees, bushes and alien species. Most biocenotic indices are used to compare different sites in terms of species composition, or to determine whether the species detected are associated with a particular type of vegetation [48, 49]. The Disturbance Index, however, can be used to describe the internal organization of a plant community and the degree to which the community has changed. It does this by testing the effect of particular groups of species belonging to particular syntaxonomic or ecological groups that have already been described.

The most important change that takes place in non-typical forms of meadow communities is the loss of species specific to the habitat in question. As previous studies have shown, these changes affect diversity both above and below ground level [27, 50]. It has been hypothesized that diversity is highest at intermediate levels of disturbance [51]. In the present study, an increase in the diversity index was accompanied by a decrease in species richness and in the cover of different ecological groups of species (Table 6). This is consistent with the results of a previous study in which species richness increased as the level of species disturbance decreased [26].

Diversity changes observed in the *Molinion* meadows in Kampinoski Park are extensive. The Shannon-Wiener Index ranged from 0.97 to 3.24, which means that the effective number of species ranged from 2.6 to 25.5, according to the formula proposed by Josta [37]. In extremely changed meadows, the mean effective number of species was only one-tenth that found in typical meadows. The Disturbance Index, conversely, ranged from 0.008 to 1,445.02.

As seen in the present study, one of the most important effects of meadow changes is a decrease in the abundance of species that are specific for *Molinion* meadows. The species composition becomes monotonous, which is reflected in a decrease in alpha diversity. On the other hand, there is an increase in beta diversity because new species compositions are forming. These new compositions have fewer species in common as they lose those species that are specific for *Molinion* meadows.

Molinion meadows are exceptionally diverse and species-rich plant communities. The disappearance of *Molinion* meadows can have an adverse effect on the territorial sozofloristic value, which is an estimate of anthropogenic pressure on threatened and rare species in a given area [52]. The *Molinion* meadows in the park provide a habitat for many such plant species. Their range is being reduced as the area covered by the meadows decreases.

The park's *Molinion* meadows are a valuable habitat in the Natura 2000 program. The high level of diversity and variability in these communities is an important component of the overall biodiversity of the area around the park. Diversity in these meadows can be increased by mowing in irregular spatial-temporal patterns in order to arrest plant succession.

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