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Long-term dynamics of plant communities in subalpine and alpine zone of the Eastern Giant Mts

Dlouhodobá dynamika rostlinných společenstev subalpinského a alpinského stupně východních Krkonoš

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Abstract The main aim of the study is the evaluation of the long-term (1977–2008) changes in plant communities in the Eastern Giant Mts. Total 34 plots (with 102 relevés) were established in the grasslands (with dominant species *Avenella flexuosa*, *Nardus stricta* and *Calamagrostis villosa*), in the communities with *Vaccinium myrtillus*, *V. uliginosum* as well as *Pinus mugo* stands, in altitudes 1225–1504 m a.s.l. The herb layers of the communities prevail poor in both species richness (S = 4 to 23) and total diversity (Shannon-Wiener's index H' = 0.67 to 3.92). Communities overgrown by patchy dwarf pine show similar species structure of herb layer as grasslands in respective site conditions. It points to the origin of such stands in pastures without woods or with low cover of woods. Grasslands and similar communities in the investigated subalpine and alpine regions of the Giant Mts are highly stable in the species structure during period of last 16–29 years regardless of regular pasture was excluded and changes in the man-influenced disturbances (paths near to some plots were closed).

Abstrakt Cílem této práce je hodnocení dlouhodobých změn (1977–2008) v rostlinných společenstvech východních Krkonoš. Celkem 34 ploch (s celkem 102 snímky) bylo založeno v loukách (s dominantami *Avenella flexuosa*, *Nardus stricta* a *Calamagrostis villosa*), ve společenstvech s *Vaccinium myrtillus*, *V. uliginosum* a v porostech s *Pinus mugo*, ve výšce 1225–1504 m nad mořem. Bylinné patro společenstev bývá zpravidla chudé jak z hlediska druhové bohatosti (S = 4 až 23), tak celkové diversity (Shannon-Wienerův index H' = 0.67 až 3.92). Společenstva s mezerovitou klečí vykazují podobnou druhovou strukturu jako luční společenstva v podobných podmínkách. To ukazuje na původ takových porostů v pastvinách bez dřevin nebo s jejich nízkou pokryvností. Louky a podobná společenstva ve zkoumaných subalpinských a alpinských polohách Krkonoš jsou vysoce druhově stabilní během posledních 16–29 let bez ohledu na skutečnost, že byla vyloučena pastva a proběhly změny v disturbančním režimu (cesty u některých ploch byly uzavřeny).

Keywords: alpine grassland, beta-diversity, community dynamics, diversity, succession
Klíčová slova: alpinské trávníky, beta-diversita, dynamika společenstev, diversita, sukcese

INTRODUCTION

Subalpine and alpine grasslands in the Giant Mts (Krkonoše Mts) are under long term man influence. Big areas were mowed or pastured for several centuries (Hejcman et al. 2007b, Vacek et al. 2007b, Matějka 2010). These activities influenced upper altitudinal limit of forests (Treml 2004). Changes in the management practice lead to succession in grasslands (e.g. Blažková 1988, 2003, Galvanek & Lepš 2009, Krahulec et al. 1996). Abandonment of grassland mowing in the Giant Mts was frequent during second half of 20th century. The touristic-activity boom and nature conservation impact increase led to changes in distribution of paths in the region. Some paths had been closed thus connected trampling effect on adjacent plant communities decreased. All these changes lead to development in structure and processes in these communities (Málková 1997a, b, 1998, 2000). First results of the plant community dynamics investigation was published without precise quantification of changes (Málková 1992, 1993, 1994a, b).

There are several leading grass species with typical ecology and syntaxonomy in the (sub)alpine grasslands: *Nardus stricta* (Klečka 1930, Štursová 1974, Krahulec 1988, Klimešová 1992, Hejcman et al. 2005), *Avenella flexuosa* and *Calamagrostis villosa* (Pyšek 1993, Hejcman et al. 2009) in the first line. Syntaxonomical classification of grassland and similar communities in the Giant Mts was described by Krahulec et al. (1996). The system of these communities within the Czech Republic was listed in Moravec et al. (1995). The most actual revised system can be found in Chytrý (2007).

The main aim of the study is the evaluation of long-term changes in subalpine and alpine plant communities (prevailing grasslands) on the base of permanent plots in the Eastern Giant Mts. Dynamics of communities is quantified with data of the repeated phytosociological relevés. The permanent plots were established within several different projects. It results in some methodical obstacles (e.g. length of the observation period varies). Evaluation of changes in diversity of different communities is one of the goals of the project BiodivKrŠu (www.infodatasys.cz/biodivkrsu) within the ecosystem biodiversity level (Matějka 2010).

METHODS

STUDY AREA AND PLOT SAMPLING

The selected 34 permanent plots are localized in sub-alpine and alpine altitudinal zones of the Eastern Giant Mts, in localities Úpské rašeliniště peatland, Kaple, Modrý důl valley and Studniční hora Mt (Fig. 1). These localities are concerned on top of the landscape transect which is under investigation

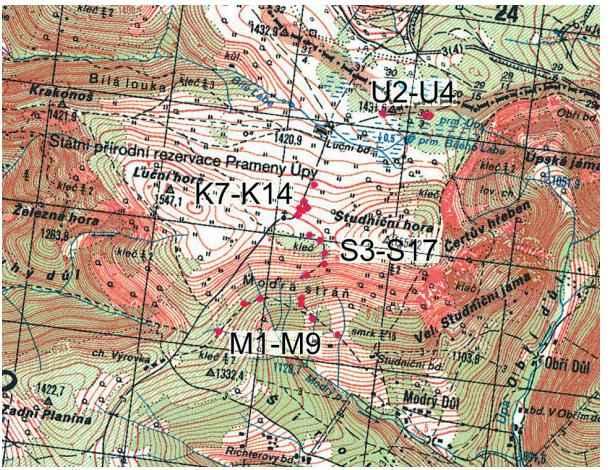

Fig. 1 Localization of the selected permanent plots in the Eastern Giant Mts.

Obr. 1. Lokalizace vybraných trvalých ploch ve východních Krkonoších.

Tab. 1 List of the selected permanent plots, their features and associated vegetation units. Association: AfCv – *Avenello flexuosae-Callunetum vulgaris*; CFs – *Cetrario-Festucetum supinae*; CbN – *Carici bigelowii-Nardetum strictae*; CbNm – *Carici bigelowii-Nardetum* subas. *molinietosum*; CcCv – *Crepido conyzifoliae-Calamagrostietum villosae*; FsNs – *Festuco supinae-Nartedum strictae*; TaN – *Thesio alpini-Nardetum strictae*; FsVm – *Festuco supinae-Vaccinietum myrtilli*; MPm – *Myrtillo-Pinetum mughi*. Several communities represent transition between associations or they are not assigned. Dominant species: Af – *Avenella flexuosa*, Cb – *Carex bigelowii*, Cl – *Calluna vulgaris*, Cv – *Calamagrostis villosa*, Dc – *Deschampsia cespitosa*, Mc – *Molinia coerulea*, Ns – *Nardus stricta*, Vm – *Vaccinium myrtillus*, Pm – *Pinus mugo* in the shrub layer, * – without dominance of any species. The classification group is assigned according to the Ward's classification (Fig. 2).

Seznam vybraných trvalých ploch, jejich vlastnosti a přiřazené vegetační jednotky. Asociace: AfCv – *Avenello flexuosae-Callunetum vulgaris*; CFs – *Cetrario-Festucetum supinae*; CbN – *Carici bigelowii-Nardetum strictae*; CbNm – *Carici bigelowii-Nardetum* subas. *molinietosum*; CcCv – *Crepido conyzifoliae-Calamagrostietum villosae*; FsNs – *Festuco supinae-Nartedum strictae*; TaN – *Thesio alpini-Nardetum strictae*; FsVm – *Festuco supinae-Vaccinietum myrtilli*; MPm – *Myrtillo-Pinetum mughi*. Některá společenstva představují přechod mezi asociacemi nebo jednotku nebylo možno přiřadit. Dominantní druhy: Af – *Avenella flexuosa*, Cb – *Carex bigelowii*, Cl – *Calluna vulgaris*, Cv – *Calamagrostis villosa*, Dc – *Deschampsia cespitosa*, Mc – *Molinia coerulea*, Ns – *Nardus stricta*, Vm – *Vaccinium myrtillus*, Pm – *Pinus mugo* v keřovém patře, * – bez dominance určitého druhu. Klasifikační skupina je přiřazena podle Wardovy klasifikace (Obr. 2).

No.	Locality	Altitude (m)	Inclination (°)	Exposition	Association	Dominant species	Classification group	Sampling years
1	M7N	1340	12	SE	FsNs	Af	A0	1990, 2008
2	S3P	1456	18	SSE	CbN	Af	A0	1990, 95, 2006
3	K8	1476	10	N	CbN	Af	A0	1977, 89, 95, 2006
4	K11	1487	6	NNE	CbN	Af	A0	1977, 89, 95, 2006
5	K7	1455	8	N	CbN	Af (Ns)	A0	1977, 89, 95, 2006
6	S7L	1486	21	SSE	CbN	Vm (Cv)	A0	1990, 95, 2006
7	K13	1487	6	N	CbN	Af (Ns)	A0	1977, 89, 95, 2006
8	K12	1483	6	NNE	CFs	Af	A1	1977, 89, 95, 2006
9	K14	1495	8	NNE	CFs	Af	A1	1977, 89, 95, 2006
10	S17L	1504	0	–	CFs	Af	A1	1990, 95, 2006
11	S13L	1500	0	–	AfCv	Af (Cl)	A1	1990, 95, 2006
12	S13P	1500	0	–	AfCv	Af (Cl Cb)	A1	1990, 95, 2006
13	S17P	1504	0	–	AfCv	Af (Cb)	A1	1990, 95, 2006
14	M2P	1331	20	SSE	FsVm / CcCv	Vm / Pm	B0	1990, 2007
15	M7D	1340	12	SE	FsVm / CcCv	Vm (Af Cv)	B0	1990, 2008
16	M1D	1412	30	SE	FsVm	Vm (Af)	B0	1990, 95, 2006
17	M8D	1345	2	SE	FsVm	Vm	B0	1990, 2008
18	S7P	1486	21	SSE	FsVm / MPm	Vm (Cv) / Pm	B0	1990, 95, 2006
19	M4C	1270	10	SSE	FsNs / FsVm	Af (Cv Vm)	B1	1990, 2007
20	M1N	1412	25	SE	FsNs / FsVm	Af (Vm)	B1	1990, 95, 2006
21	M3P	1317	17	SSE	FsNs / FsVm	Af (Vm Ns)	B1	1990, 2007
22	M2L	1331	20	SSE	FsNs / FsVm	Af (Vm Ns)	B1	1990, 2007

No.	Locality	Altitude (m)	Inclination (°)	Exposition	Association	Dominant species	Classification group	Sampling years
23	M8N	1345	2	SE	MPm	Cv / Pm	C	1990, 2008
24	M9N	1345	5	SE	CcCv	Cv	C	1990, 2008
25	M4M	1270	10	SSE	FsNs	Ns (Cv)	D0	1990, 2007
26	M3L	1317	17	SSE		Ns (Vm)	D0	1990, 2007
27	M5D	1225	8	S	TaN / CcCv	*	D0	1984, 89, 90, 95, 2006
28	M9D	1345	0	–		Af Dc Ns	D1	1990, 2008
29	U1	1431	0	–	FsNs	Ns (Af)	D1	1977, 89, 95, 2006
30	U2	1431	0	–	FsNs	Ns (Af)	D1	1977, 89, 95, 2006
31	S3L	1456	18	SSE	FsNs	Dc (Af)	D1	1990, 95, 2006
32	U4	1431	0	–	CbNm	Mc Ns	D2	1977, 89, 95, 2006
33	U3	1432	0	–	CbNm	Mc (Af)	D2	1977, 89, 95, 2006
34	M5N	1225	8	S		Cl	D3	1990, 95, 2006

of a wide scope (Matějka 2010). Altitudes vary between 1225 and 1504 m a.s.l. Geological bedrock consists of the mineral-poor rocks-schists, granite partially covered by deluvial sediments and peat. The soils are acidic to strongly acidic with lack of base cations, especially mountain humus podsols, with the peat accumulation in wet localities. Basic features of the plots and their vegetation are summarized in Tab. 1. The plot selection was important because of some other plots (not included in this study) are very close and similar to another ones.

Each plot was permanently stabilized by big iron nail at time of first sampling. Plot size was 16 m^2. Plot sampling was carried out in time of the well-developed vegetation. Species representations were assessed directly in per-cents or in grades of the Braun-Blanquet's scale using inter-grades (e.g. +–1, 1–2...). These differences have occurred regarding to different studies, within which plots were established. Data of both scales are comparable because a standardization method has been applied (see below).

DATA PROCESSING

Phytosociological relevés were stored in the DBreleve database (Matějka 2009). The species cover grades of used scale were transformed to average percentage cover as value of species representation. Data of species representation were standardized on sum of representations of all species in the etage to be equal to total cover of the etage. All community features described in the following text are related to composition of the herb layer. Diversity indices were calculated: species richness (S) – number of presented species, total diversity – Shannon-Wiener's index

$$H' = -\sum_i p_i \cdot \log_2 p_i$$

and species equitability

$$e = H' / \log_2 S$$

(Maguran 2004). This diversity represents a measure of the α-diversity. In case of repeated sampling, summary sample (which is calculated as an average over all relevés) shows diversity within whole (temporal) gradient – similar index is H_{tot}. Change of community structure over whole period (temporal β-diversity) can be calculated as $dH = H_{tot} – avg(H_i)$ in absolute value or relatively as dH/H_{tot}. All indices of diversity and richness were calculated in the DBreleve software.

Changes in species composition over time can be visualized as shifts of the respective point in the ordination space of several first axes. Ordination was made as detrended correspondence analysis (DCA). CANOCO version 4.5 was employed (ter Braak & Šmilauer 2002). Each relevé in the plot represents a point in the ordination space. All such points during succession in the plots are a set of random points (e.g. DCA_{1r} – ordination score along 1st axis in r-th relevé) with average and variance (equal to square of standard deviation) according to each ordination axis. Changes in the species composition of the community were evaluated as sums of the ordination score variances using first i ordination axes: where $var(x_i)$ indicates variance of random variables x_i. Regarding to varying number of relevés representing each plot, estimation of population variance (calculate with dividing by n–1 instate n) is better to compare values V_i.

$$V_i = \sum_{j=1}^{i} var(DCA_{jr})$$

All plots were classified (Ward's hierarchical method with square of Euclidean distance) according to the average (over all relevés) cover of species in the herb layer. Statistical analysis was processed in the software Statistica, version 8 (product of StatSoft, Inc.).

Plant species nomenclature follows Kubát (2002).

RESULTS AND DISCUSSION

PLANT COMMUNITIES AND THEIR BASIC FEATURES

Observed plant communities can be assigned to the syntaxonomical system of units corresponding with Chytrý (2007) and Moravec (1995):

- Class *Loiseleurio-Vaccinietea* Eggler ex Schubert 1960, Alliance *Loiseleurio procumbentis-Vaccinion* Br.–Bl. in Br.–Bl. et Jenny 1926, Assoc. *Avenello flexuosae-Callunetum vulgaris* Zlatník 1925
- Class *Juncetea trifidi* Hadač in Klika et Hadač 1944, Alliance *Juncion trifidi* Krajina 1933, Assoc. *Cetrario-Festucetum supinae* Jeník 1961, Alliance *Nardo strictae-Caricion bigelowii* Nordhagen 1943, Assoc. *Carici bigelowii-Nardetum strictae* (Zlatník 1928) Jeník 1961
- Class *Mulgedio-Aconitetea* Hadač et Klika in Klika et Hadač 1944, Alliance *Calamagrostion villosae* Pawłowski et al. 1928, Assoc. *Crepido conyzifoliae-Calamagrostietum villosae* (Zlatník 1925) Jeník 1961
- Class *Calluno-Ulicetea* Br.–Bl. et Tüxen ex Klika et Hadač 1944, Alliance *Nardion strictae* Br.–Bl. 1926, Assoc. *Festuco supinae-Nartedum strictae* Šmarda 1950, Assoc. *Thesio alpini-Nardetum strictae* Jeník et al. 1980, Alliance Genisto pilosae-Vaccinion Br.–Bl. 1926, Assoc. *Festuco supinae-Vaccinietum myrtilli* Šmarda 1950, Class *Vaccinio-Piceetea* Br.–Bl. in Br.–Bl., Sissingh et Vlieger 1939, Alliance *Pinion mughi* Pawłowski et al. 1928, Assoc. *Myrtillo-Pinetum mughi* Hadač 1956

Several communities are assigned to an alliance only. Transition communities are common. Regardless this article would not be concerned in the syntaxonomy, numerical classification should be useful background to evaluate community dynamics. Four basic community (plot) groups were distinguished (Fig. 2):

The group A represents alpine communities (classes *Loiseleurio-Vaccinietea* and *Juncetea trifidi*) where species as *Melampyrum pratense*, *Trientalis europaea*, *Dryopteris dilatata* (partly species of the Norway spruce forest zone) and *Pinus mugo* are missing. The subgroup A0 includes plots of association *Carici bigelowii-Nardetum*, prevailing on hangs. The subgroup A1 embraces communities mainly with opened herb layer in the flat terrain. The lower altitudinal limit of communities of the group A lays near 1400 m a.s.l. (Matějka 2010), which coincides with elevation of alpine timberline (1360 m a.s.l.; Treml 2004).

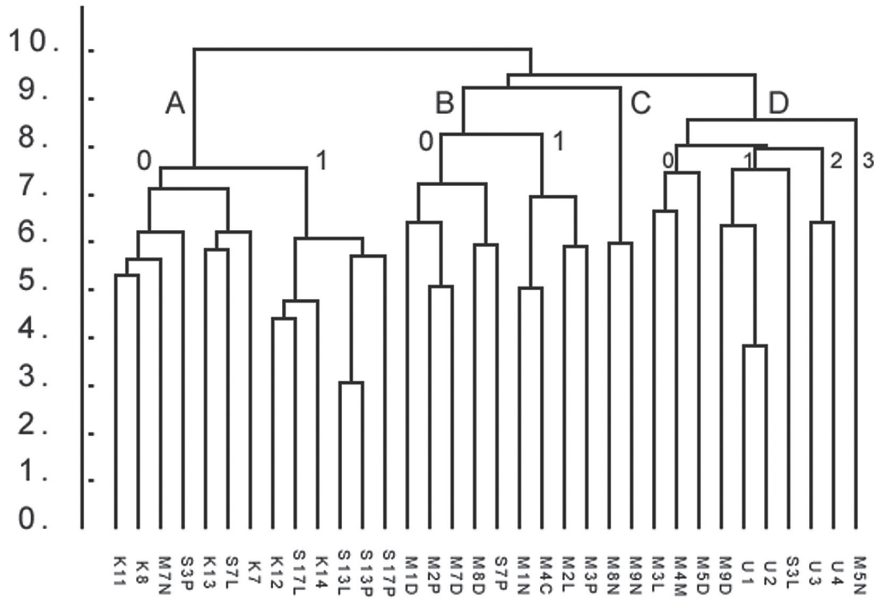

Fig. 2 Classification of the plots using Ward's hierarchical method with square of Euclidean distance. Logarithms of dissimilarities are plotted in the vertical axis. A to D are basic classification groups: A – alpine communities, B – communities of the alliance *Genisto pilosae-Vaccinion myrtilli* with transitions, C – communities with dominant *Calamagrostis villosa*, D – wet or mesic communities of the subalpine zone.

Obr. 2. Klasifikace ploch za použití Wardovy metody hierarchické klasifikace se čtvercem euklidovské vzdálenosti. Logaritmus nepodobnosti je vynesen na vertikální ose. A až D jsou základní klasifikační skupiny: A – alpinská společenstva, B – společenstva svazu *Genisto pilosae-Vaccinion myrtilli* s přechody, C – společenstva s dominancí *Calamagrostis villosa*, D – vlhká až mezická společenstva subalpinské zóny.

The group B represents subalpine and high montane grassland communities, partly overgrown by dwarf pine. It is typical of the presence of *Vaccinium myrtillus* and species listed as missing in the community group A. The communities typically belong to alliance *Genisto pilosae-Vaccinion*.

The small group C (two plots) is typical with high cover of *Calamagrostis villosa*.

The heterogeneous group D includes localities in subalpine and high montane zones on wet or mesic soils, mainly of the class *Calluno-Ulicetea*. Species as *Molinia coerulea*, *Deschampsia cespitosa*, *Juncus filiformis* and *Gentiana asclepiadea* occur in these communities typically.

All relevés are accessible via Internet as accompanying data set (www.infodatasys.cz/data/GePK2009_matejka_malkova.htm).

The first DCA axis is correlated with plot altitude (Fig. 3A). Higher values of the ordination score along the second axis indicate probably increase in soil moisture and other stand features producing deviations in the community structure. This picture can be elucidated by localization of species in the ordination space. Species *Trichophorum cespitosum*, *Molinia caerulea*, *Eriophorum vaginatum*, *Luzula sudetica* and *Juncus filiformis* are on the left site (with the lowest values of ordination score along 1st axis). On the contrary, species typically growing in high montane forests and in dwarf pine stands as *Maianthemum bifolium*, *Melampyrum sylvaticum*, *Picea abies*, *Pinus mugo*, *Trientalis europaea*, *Dryopteris dilatata*, *Carex nigra* and *Juncus effusus* occupy right part of the ordination space (Fig. 3B).

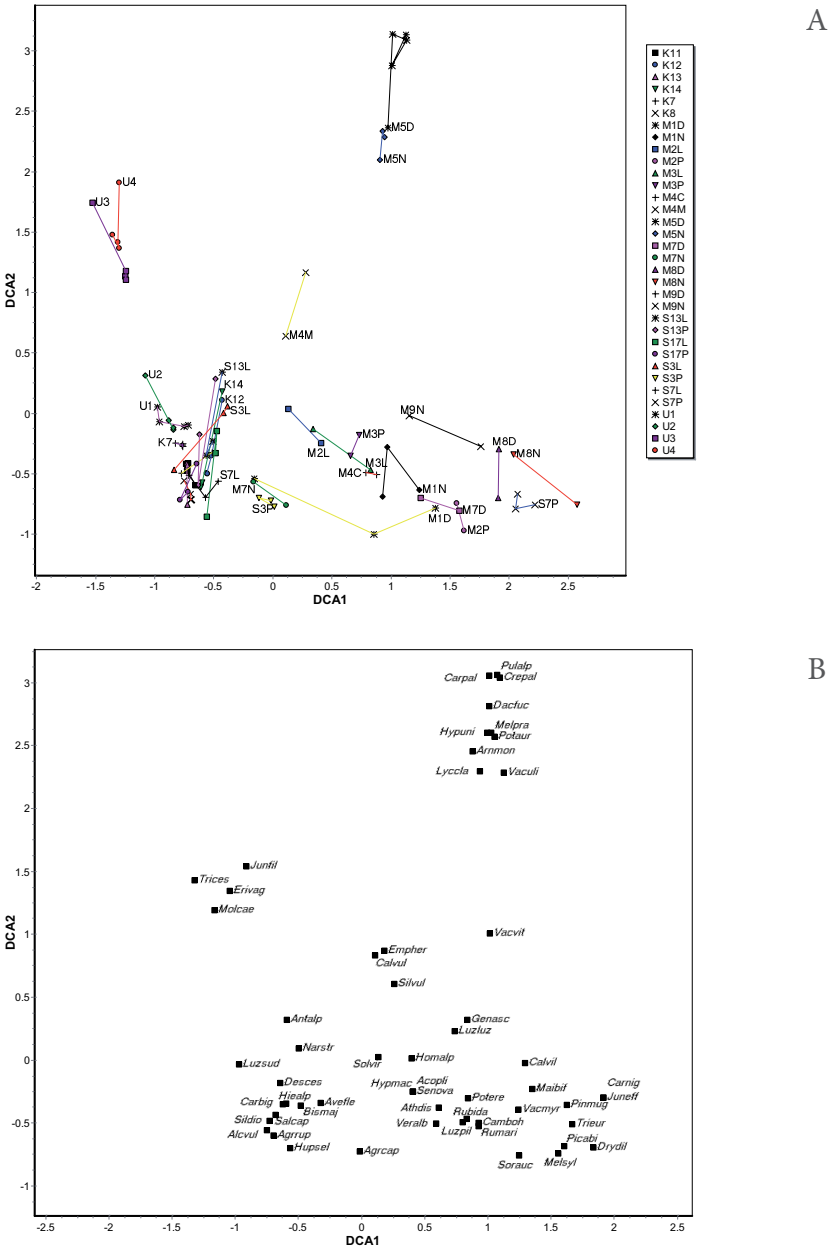

Fig. 3 DCA ordination of all relevés (A) and distribution of species within this ordination space (B). Points representing relevés from a plot are connected by line. The point representing the last relevé is marked by the plot name.

Obr. 3. Odinace DCA všech snímků (A) a rozmístění druhů v ordinačním prostoru (B). Body reprezentují snímky na jedné ploše, které jsou spojené linií. Bod odpovídající poslednímu snímku je označen jménem plochy.

Tab. 2 The herb layer diversity parameters and dynamics within selected permanent plots. Indices of the community dynamics would be typed in bold if value is higher than 95 % confidential limit of the respective mean over all observed plots.

Parametry diversity bylinného patra a jeho dynamika ve vybraných trvalých plochách. Indexy dynamiky společenstva vytištěné tučně jsou vyšší než 95 % konfidenční interval průměru pro všechny pozorované plochy.

No.	Locality	N	S_{min}	S_{avg}	S_{max}	S_{tot}	H_{min}	H_{avg}	H_{max}	H_{tot}	e_{min}	e_{avg}	e_{max}	dS	dS/ S_{tot}	dH	dH/ H_{tot}	V_1	V_2	V_3	V_4
1	M7N	2	8	8.5	9	9	1.66	1.78	1.89	1.88	0.52	0.58	0.63	0.5	0.06	0.1	0.055	**0.194**	0.236	0.257	0.441
2	S3P	3	8	11.3	13	15	2.04	2.06	2.09	2.19	0.55	0.6	0.7	**3.7**	**0.24**	0.12	0.055	0.068	0.078	0.284	0.364
3	K8	4	8	9.3	10	11	1.47	1.58	1.75	1.62	0.44	0.49	0.55	1.8	0.16	0.05	0.028	0.028	0.081	0.129	0.151
4	K11	4	10	11.3	12	12	1.74	1.82	1.9	1.86	0.48	0.52	0.57	0.8	0.06	0.04	0.021	0.035	0.091	0.146	0.178
5	K7	4	8	9.5	11	12	1.85	1.91	2.04	1.95	0.55	0.59	0.62	2.5	0.21	0.04	0.021	0.031	0.033	0.185	0.187
6	S7L	3	7	9.3	11	15	1.56	1.78	2.11	1.89	0.48	0.56	0.64	**5.7**	**0.38**	0.1	0.055	0.124	0.157	0.236	0.276
7	K13	4	6	6.5	7	8	1.53	1.81	1.94	1.84	0.54	0.67	0.73	1.5	0.19	0.03	0.017	0	0.165	0.172	0.209
8	K12	4	7	8.5	9	10	1.43	1.57	1.8	1.65	0.47	0.51	0.57	1.5	0.15	0.08	0.047	0.061	0.294	0.384	0.407
9	K14	4	8	9	11	12	1.6	1.68	1.85	1.78	0.53	0.53	0.53	**3**	**0.25**	0.1	0.056	0.09	**0.4**	0.484	0.519
10	S17L	3	7	8.3	9	11	0.67	1.8	2.48	1.98	0.24	0.58	0.78	**2.7**	**0.24**	**0.18**	**0.09**	0.046	**0.373**	0.513	0.615
11	S13L	3	7	7.7	8	9	1.87	2.03	2.12	2.14	0.62	0.69	0.75	1.3	0.15	0.11	0.049	0.066	**0.374**	**0.649**	0.657
12	S13P	3	6	6.7	7	9	1.56	1.96	2.35	2.1	0.6	0.72	0.84	2.3	**0.26**	0.14	0.065	0.08	**0.448**	0.51	0.546
13	S17P	3	8	8	8	9	1.92	2.06	2.26	2.21	0.64	0.69	0.76	1	0.11	**0.16**	**0.071**	0.07	0.171	0.36	0.376
14	M2P	2	12	13	14	16	2.03	2.11	2.19	2.17	0.53	0.57	0.61	**3**	0.19	0.06	0.028	0.045	0.17	0.171	0.473
15	M7D	2	9	9.5	10	10	1.71	2.2	2.69	2.37	0.51	0.68	0.85	0.5	0.05	**0.17**	**0.073**	**0.232**	0.243	0.344	**0.983**
16	M1D	3	9	9.7	11	12	1.53	2.06	2.74	2.38	0.44	0.64	0.86	2.3	0.19	**0.33**	**0.137**	**0.779**	**0.813**	**1.1**	**1.628**
17	M8D	2	9	13.5	18	18	2.25	2.25	2.26	2.47	0.54	0.63	0.71	**4.5**	**0.25**	**0.21**	**0.086**	0	0.287	0.331	**1.769**
18	S7P	3	4	5.7	7	8	1.14	1.32	1.42	1.39	0.44	0.55	0.71	2.3	**0.29**	0.07	0.052	0.09	0.11	0.118	0.447
19	M4C	2	12	13.5	15	16	2.18	2.28	2.39	2.34	0.61	0.61	0.61	2.5	0.16	0.06	0.024	0.066	0.068	0.068	0.072
20	M1N	3	6	8.7	11	14	2.09	2.22	2.42	2.4	0.61	0.74	0.84	**5.3**	**0.38**	**0.18**	**0.074**	0.169	0.28	0.283	0.853
21	M3P	2	9	10	11	11	2.75	2.81	2.86	2.87	0.83	0.85	0.87	1	0.09	0.06	0.021	0.049	0.127	0.211	0.388
22	M2L	2	8	11	14	14	2.61	2.71	2.81	2.77	0.74	0.8	0.87	**3**	**0.21**	0.06	0.023	**0.194**	0.279	0.431	0.451
23	M8N	2	4	5.5	7	7	1.24	1.38	1.51	1.65	0.44	0.6	0.76	1.5	**0.21**	**0.27**	**0.165**	**0.382**	**0.481**	0.546	**2.842**

No.	Locality	N	S_{min}	S_{avg}	S_{max}	S_{tot}	H_{min}	H_{avg}	H_{max}	H_{tot}	e_{min}	e_{avg}	e_{max}	dS	dS/S_{tot}	dH	dH/H_{tot}	V_1	V_2	V_3	V_4
24	M9N	2	7	10.5	14	14	1.52	1.89	2.27	2.02	0.54	0.57	0.6	**3.5**	**0.25**	0.12	0.061	**0.429**	**0.465**	0.497	0.518
25	M4M	2	17	17	17	18	2.74	2.94	3.13	3.11	0.67	0.72	0.77	1	0.06	**0.17**	0.054	0.12	**0.39**	0.461	0.597
26	M3L	2	13	14	15	15	2.05	2.47	2.9	2.66	0.52	0.65	0.78	1	0.07	**0.18**	**0.069**	**0.345**	**0.419**	**0.62**	0.822
27	M5D	5	20	22.2	23	24	3.58	3.82	3.92	3.89	0.83	0.85	0.87	1.8	0.08	0.07	0.018	0.073	**0.338**	0.35	0.492
28	M9D	2	10	11	12	12	2.65	2.75	2.84	2.81	0.79	0.8	0.8	1	0.08	0.06	0.022	0.186	0.224	0.238	0.283
29	U1	4	7	7.8	9	10	1.93	2.18	2.42	2.34	0.69	0.74	0.8	2.3	**0.23**	**0.16**	0.068	0.137	0.157	0.467	0.561
30	U2	4	6	6.3	7	7	1.79	1.98	2.37	2.1	0.69	0.75	0.85	0.8	0.11	0.12	0.056	0.114	0.24	0.456	0.515
31	S3L	3	6	9.3	12	12	1.21	2.23	2.74	2.6	0.47	0.68	0.82	2.7	0.22	0.37	0.142	0.251	0.382	2.267	2.283
32	U4	4	10	11	12	12	2.52	2.59	2.65	2.74	0.74	0.75	0.76	1	0.08	0.15	0.056	0.028	0.251	0.412	0.659
33	U3	4	7	7.8	8	9	1.74	2.08	2.25	2.11	0.58	0.71	0.77	1.3	0.14	0.03	0.015	0.14	**0.333**	0.348	0.416
34	M5N	3	10	11.3	12	12	2.42	2.58	2.79	2.63	0.71	0.74	0.78	0.7	0.06	0.05	0.019	0.017	0.129	0.173	0.231

VEGETATION DIVERSITY AND DYNAMICS

Basic findings according to plots are written in Tab. 2. The communities are species poor (Tab 3). Total 57 species in the herb and shrub layers were recorded in all relevés. Average number of species in the relevé varies between 4 and 23. Total number of species in the plot (in all recorded relevés) was between 12 and 24. Average number of species in relevé was 10.1 (median 9.4). Average Shannon-Wiener's index of diversity was 2.14 (median 2.31). Average species equitability was 0.66, with interval 0.44–0.87 for the individual relevés (decrease to e = 0.24 was observed in one relevé).

Approximately two species are responsible for observed succession change in the plot (compare values dS). Minor species changes were observed in a high portion of plots: dH was observed in the interval 0.03–0.37, dH/H_{tot} varies between 1 and 17 %. Exchange in species richness was slightly higher (dS was between 0.5 and 5.7). Indices dS and dS/S_{tot} are correlated with community richness and diversity, while other indices (dH, dH/H_{tot} and $V_1 – V_4$) represent the other correlated group (Tab. 4). While index dS was positively correlated with total diversity (H_{tot}), this index decreased with equitability (e_{tot}). In other words, communities without important dominance of some species are more stabile in species composition.

Tab. 3 Basic statistics of the community dynamics calculated for all observed plots.

Základní statistiky dynamiky společenstev počítané pro všechny pozorované plochy.

	Mean	Median	Minimum	Maximum	Std.Dev.
S_{tot}	12.1	12	7	24	3.6
H_{tot}	2.26	2.18	1.39	3.89	0.5
dS	2.1	1.8	0.5	5.7	1.3
dH	0.12	0.11	0.03	0.37	0.08
dH/H_{tot}	0.056	0.055	0.015	0.165	0.036
V_1	0.14	0.09	0	0.78	0.15
V_2	0.27	0.25	0.03	0.81	0.16
V_3	0.42	0.35	0.07	2.27	0.38
V_4	0.65	0.48	0.07	2.84	0.61

Tab. 4 Correlations (r) for parameters of the community diversity (calculated for average species composition in the plot during whole investigation period) and dynamics for all plots (N=34). Marked correlations are statistically significant on the level α ≤ 5 %.

Korelační koeficienty (r) pro parametry diversity společenstva (pořítané pro průměrné druhovéí složení na ploše v průběhu celé sledované periody) a pro jeho dynamiku u u všech ploch (N=34). Označené koeficienty jsou statisticky průkazné na hladině α ≤ 5 %.

	S_{tot}	H_{tot}	e_{tot}	dS	dS/S_{tot}	dH	dH/H_{tot}	V_1	V_2	V_3
H_{tot}	0.665 *									
e_{tot}	0.152	0.834 *								
dS	0.389 *	–0.123	–0.431 *							
dS/S_{tot}	0	–0.403 *	–0.525 *	0.895 *						
dH	–0.016	0.114	0.166	0.167	0.2					
dH/H_{tot}	–0.19	–0.139	–0.035	0.18	0.303	0.946 *				
V_1	–0.051	0.04	0.078	0.035	0.072	0.616 *	0.614 *			
V_2	0.02	0.149	0.178	0.027	0.078	0.656 *	0.635 *	0.756 *		
V_3	–0.047	0.167	0.241	0.049	0.102	0.784 *	0.674 *	0.482 *	0.575 *	
V_4	–0.066	0.033	0.107	0.119	0.181	0.858 *	0.887 *	0.527 *	0.588 *	0.655 *

Indices dS, dH and dH/H_{tot} are not dependent on classification of the plot into groups A to D.

Cumulative percentage variance of species data in DCA analysis was 15.3 %, 25.2 %, 34.7 % and 41.0 % for 1st to 4th ordination axis respectively. Indices V_1 to V_4 are growing more steeply than these percentages. It implies that observed changes in the communities would not be very well mirrored by the ordination results. Indices V_1 and V_4 are probably dependent on classification of the plot into groups A to D (F-test of one-way ANOVA, p = 0.019 and 0.023 respectively), but this is caused by difference of two plots in the group C, only. If the plot groups A, B and D are taken into account only, the lowest probabilities of the ANOVA F-test have been observed for indices based on species richness (p = 0.052 and 0.070 for dS/S_{tot} and dS respectively; Figs. 4–5). The lowest indices were calculated for communities in the classification group D. Temporal β-diversity do not differ among groups of plots.

Four plots (S17L, M8D, M1N and S3L) show higher changes indicated by all indices of temporal β-diversity (dH and dH/H_{tot}) and species exchange (dS, dS/S_{tot}). Only the last mentioned plot has increased values V_1 to V_4. These plots represent all three main classification groups of vegetation (A, B and D). In the plot S17L, decrease of the *Avenella flexuosa* coverage is prominent. Species intolerant to trampling and mowing (*Calluna vulgaris* and *Vaccinium myrtillus*) have occurred newly (Tab. 5). Plot M8D is peculiar by many species recorded at the end of observation. All these species have only small representation. In spite of that, the total diversity (H') was constant. Soil became moderately moist probably (Tab. 6). Changes in the plot M1N are connected with the increase of the *Vaccinium myrtillus* coverage and partial exclusion of *Calamagrostis villosa* (Tab. 7). Succession from the secondary subalpine grassland dominated by *Deschampsia cespitosa* to the association *Festuco supinae-Nartedum* was described in the plot S3L (Tab. 8). This plot represents an example of succession leading to relatively rich seminatural grassland communities after exclusion of trampling in the subalpine zone.

Calculated indices are measures of change, they do not tell about a trend in the community. Therefore average annual changes in species richness and total diversity were enumerated (Tab. 9). Little mean increase in species richness was observed. More important increase was approximately 15 years ago. Average change of species richness was lower during 11 year period (0.021 per year). Slightly higher value (0.088 per year) was observed during approximately 18 year period. Average total species

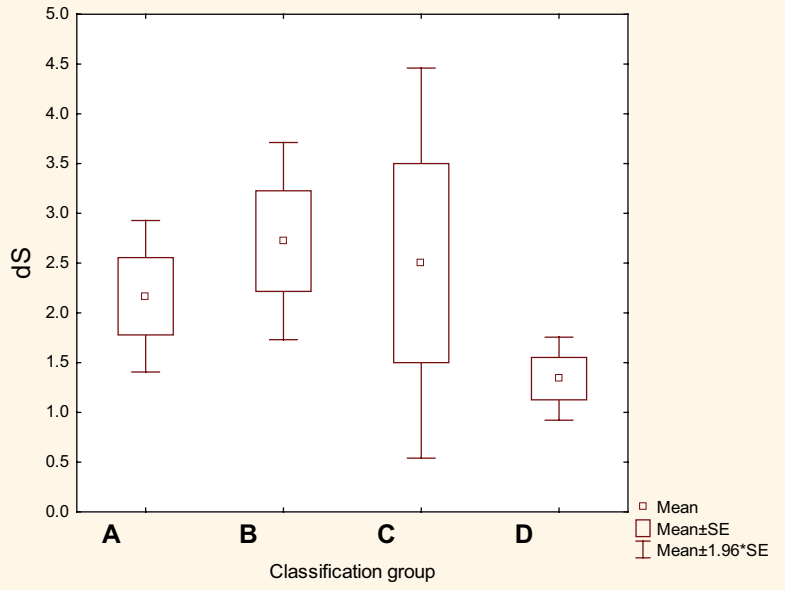

Fig. 4 Differentiation among the groups of plots on the base of index dS (average number of the exchanged species).

Obr. 4. Diferenciace mezi skupinami ploch na základě indexu dS (průměrný počet vyměněných druhů).

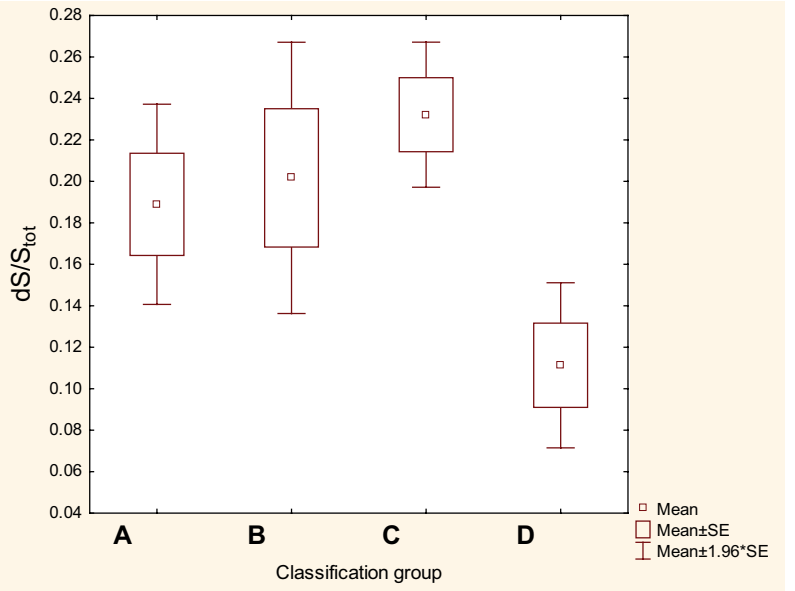

Fig. 5 Differentiation among the groups of plots on the base of index dS/S_{tot} (relative share of the exchanged species).

Obr. 5. Diferenciace mezi skupinami ploch na základě indexu dS/S_{tot} (relativní podíl vyměněných druhů).

Tab. 5 Vegetation changes in the plot S17L. Transformed species cover in per-cents.

Vegetační změny na ploše S17L. Transformovaná pokryvnost druhů v %.

Year	1990	1995	2006
Avenella flexuosa	80	20	41
Bistorta major	1	3	0.41
Carex bigelowii	3.1	5	14
Homogyne alpina	0.2		0.081
Nardus stricta	1	7.5	8.1
Solidago virgaurea subsp. *minuta*	2	0.2	
Vaccinium vitis-idaea	1		
Calamagrostis villosa		2	0.081
Calluna vulgaris		9	14
Hieracium alpinum		4	8.1
Vaccinium myrtillus		0.2	4.1

Tab. 6 Vegetation changes in the plot M8D. Transformed species cover in per-cents.

Vegetační změny na ploše M8D. Transformovaná pokryvnost druhů v %.

Year	1990	2008
Avenella flexuosa	5.4	11
Calamagrostis villosa	10	11
Homogyne alpina	1.5	0.33
Picea abies	2.3	0.33
Pinus mugo	1.5	11
Potentilla erecta	7.7	0.066
Vaccinium myrtillus	51	41
Vaccinium vitis-idaea	7.7	0.066
Veratrum album subsp. *lobelianum*	7.7	0.33
Anthoxanthum alpinum		0.33
Bistorta major		0.066
Calluna vulgaris		0.33
Carex nigra		0.066
Juncus effusus		0.33
Melampyrum pratense		0.33
Molinia caerulea		0.33
Trientalis europaea		0.066
Vaccinium uliginosum		6.6

Tab. 7 Vegetation changes in the plot M1N Transformed species cover in per-cents.

Vegetační změny na ploše M1N. Transformovaná pokryvnost druhů v %.

Year	1990	1995	2006
Avenella flexuosa	37	34	31
Calamagrostis villosa	17	16	8.9
Campanula bohemica	5	4.5	
Gentiana asclepiadea	5	4.5	8.9
Homogyne alpina		0.45	0.89
Melampyrum pratense			0.89
Nardus stricta			0.89
Potentilla aurea		4.5	
Potentilla erecta	5		
Solidago virgaurea subsp. *minuta*			0.89
Trientalis europaea			0.89
Vaccinium myrtillus	17	16	45
Vaccinium vitis-idaea		0.45	0.89
Veratrum album subsp. lobelianum		4.5	0.89

Tab. 8 Vegetation changes in the plot S3L Transformed species cover in per-cents.

Vegetační změny na ploše S3L. Transformovaná pokryvnost druhů v %.

Year	1990	1995	2006
Avenella flexuosa	4.1	24	33
Bistorta major	3.1	2.4	2.2
Calamagrostis villosa	7.1	16	8.9
Deschampsia cespitosa	71	24	16
Homogyne alpina	0.2	1.6	4.4
Nardus stricta	6.1	13	8.9
Anthoxanthum alpinum		3.1	0.44
Carex bigelowii		0.79	0.44
Molinia caerulea		9.4	16
Solidago virgaurea subsp. *minuta*		2.4	0.44
Silene vulgaris			0.089
Vaccinium myrtillus			8.9

Tab. 9 Annual change of species richness (b_S) and total diversity (Shannon-Wiener's index) (b_H) according to main classification groups (A to D, Fig. 2) in eleven-year period and in seventeen (16–18) year period ending in 2000's. Arithmetic means ± standard deviations are written. n – number of pairs.

Roční změna druhové bohatosti (bS) a celkové diversity (Shannon-Wienerův index) (bH) podle hlavních klasifikačních skupin (A až D, obr. 2) v jedenáctileté periodě a v sedmnáctileté (16 až 18 let) periodě končící v desetiletí 2000. Jsou uvedeny aritmetický průměr ± směrodatná odchylka. n – počet datových párů.

period		**11 years**			**18 years**	
	n	bS	bH	n	bS	bH
group A	12	0.015±0.101	0.015±0.028	13	0.048±0.123	0.015±0.029
group B	3	0.091±0.157	–0028±0.006	9	0.209±0.146	–0.015±0.031
group D	7	0.000±0.166	–0.007±0.030	11	0.037±0.153	0.002±0.039
post-hoc comparison			B <A		A <B	
(using LSD-test at α≤5 %)					D <B	
all plots	22	0.021±0.128	0.002±0.030	33	0.088±0.155	0.002±0.034

diversity was constant. Alpine (classification group A) and subalpine (group B) communities show different dynamics of species richness – stable average values in alpine communities and increasing in subalpine ones. Average slight decrease of total diversity together with positive change in number species in the plots of subalpine zone points to prevailing increase in dominance of selected species.

Some communities (example of plots S3L and M9D; often classified as *Festuco supinae-Nartedum*) can be secondary overgrown by *Deschampsia cespitosa*. Such communities can be stabile (M9D) or temporary (S3L).

Stability of communities with *Nardus stricta* is connected with durability of several features of this dominant species within an interval (e.g. regarding to nutrient addition). Rapid changes were observed out of this interval (Štursová 1974). Long-term influence of fertilization in subalpine grasslands was described (Hejcman et al. 2007a, Klaudisová et al. 2009, Semelová et al. 2008).

All communities occupy localities from forest-subalpine transition zone to alpine zone. Tree invasibility of such grasslands is lower. Typical succession of abandoned grasslands (e.g. Blažková 1988, 2003, Hrivňák & Ujházy 2005) is absent in this altitudinal zone. However dwarf pine represents woody species which would be dangerous for long-time existence of these communities. Scattered pine distribution does not endanger these stands and their species composition while pine cover is low with sufficient gaps (Pašťalková et al. 2002, Málková et al. 2002). Dynamics of spatial structure plays important role in such communities (Wild & Winkler 2008).

Relative stability of species composition in subalpine zone can be linked to higher stability of herb layer in the Norway spruce climax forest comparing beech-mixture forests in lower altitudes (Matějka & Vacek 2007).

Indices of community dynamics were used in forests, for instance Matějka in Vacek et al. 2007a: pp 164–165. It is possible to compare above presented data and dynamics of the undamaged Norway spruce forest in the Giant Mts during 1980–2005: Species composition changes in the forests were more important (average dS = 4.0 and 2.1 in forests and grasslands, respectively), although β-diversity was similar (dH = 0.19 and 0.12, respectively). Shifts in ordination spaces were more than two times higher in the (sub)alpine grasslands (Tab. 3) comparing the forests (V_1 = 0.03, V_2 = 0.15, V_3 = 0.19 and V_4 = 0.30). It points to slightly much systematic changes of species structure in the grasslands.

Other dynamical processes cannot be revealed on the base of phytosociological relevés because of they run in lower hierarchical level and are manifested in the community spatial structure (Herben et al. 1993, 1995).

Trends in vegetation changes observed in arctic communities (Wilson & Nilsson 2009), were not revealed in the (sub)alpine communities, because situation in the Central European mountains is much complicated. Possible global warming is completed by changes in man influence (mowing, trampling, changes in air pollution etc.).

CONCLUSIONS

The species-poor grassland and similar communities of the subalpine and alpine zone of the Giant Mts are relatively stabile; observed temporal β-diversity was very low. Range of dynamics in subalpine and alpine grasslands is similar. Exchange in composition of accompanying species with minor coverage is much important than changes in representation of dominant species.

The used system of community change indices describes dynamics in sense of temporal β-diversity and temporal gradients (Müller 1998) very well.

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