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Subalpine tall-herb vegetation patterns: a case study from the Khamar-Daban Range (southern Baikal region, Eastern Siberia)

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ABSTRACT

In this study, we present the first investigation of diversity and ecology of tall-herb vegetation (class Mulgedio-Aconitetea Hadač & Klika in Klika & Hadač 1944) on the Khamar-Daban Range, the generally assumed easternmost distribution limit of this class. We collected data of 162 relevés in the key area of the upper reaches of Bolshoi Mamai River, which is situated on the northern slope of the range. Tall-herb meadows occurred within a large altitudinal range from timberline to the watershed. We found that species richness was positively correlated with inclination and orientation of sites to warmer aspect. In contrast, strong pronounced microtopography and high organic layer thickness led to lower species richness. We divided the tall herb vegetation of the study region into seven community types, which clearly differed in ecological aspects. The results were approved by CCA ordination, which stressed the relation of clusters to elevation, aspect, inclination, microtopography and organic layer.

Keywords: tall-herb vegetation, floristic diversity, high-mountain vegetation ecology, ecological factors

РЕЗЮМЕ

Хайм Р.Ю., Чепинога В.В. Распределение субальпийской высокотравной растительности: исследование на хребте Хамар-Дабан (юг Байкальского региона, Восточная Сибирь). В статье представлены результаты первого исследования разнообразия и экологии высокотравной растительности (класс Mulgedio-Aconitetea Hadač & Klika in Klika & Hadač 1944) на хребте Хамар-Дабан, который является восточным пределом распространения сообществ этого класса. Нами выполнено 162 геоботанических описания в пределах ключевой территории в верховьях р. Большой Мамай, где высокотравные луга распространены на всем протяжении от границы леса до водраздела. Видовое богатство сообществ положительно коррелирует с крутизной склона и экспозициями, более обеспеченными теплом. Выраженный микрорельеф и мощный органический субстрат, напротив, ведут к снижению видового разнообразия. При помощи кластерного анализа выделено семь типов сообществ, хорошо различающихся экологически. Последнее подтверждено методом CCA ординации, показавшей корреляцию выделенных сообществ с такими факторами, как высота над уровнем моря, экспозиция, уклон, микрорельеф и органический субстрат.

Ключевые слова: высокотравная растительность, флористическое разнообразие, экология высокогорной растительности, экологические факторы

Tall-herb vegetation is strongly influenced by environmental factors (Odland et al. 1995, Karst et al. 2005). Humid and cool climates, as well as nutrient-rich soil conditions are essential for the formation of this vegetation type (Michl et al. 2010). Furthermore, heavy winter precipitation resulting in a long lasting snow layer, which protects the plants from frost, is important for the survival of many species that are part of these communities (Ermakov 2003, Banaš et al. 2010, Sulejman 2011). The complex of all suitable ecological peculiarities which are needed for the development of tall-herb vegetation is found on one hand in mountain ranges of the temperate and the subnemoral zone of the Northern Eurasia (Horvat et al. 1974, Rivas-Martínez et al. 1984, Grabherr & Mucina 1993, Ermakov et al. 2000, Kočí 2001, Sulejman 2011, Iakushenko et al. 2012), and on the other hand in the northern boreal zone in suboceanic Europe (MacVean & Ratcliffe 1962, Odland 1981, Dierßen 1996, Michl et al. 2010). In mountains, this kind of vegetation occurs mainly near, and sometimes above, timberline (Pott 1995, Ellenberg & Leuschner 2010). In the higher mountains of Southern Siberia, tall-herb vegetation is substituted by short-herb alpine meadows, or, in more arid conditions, by tundra vegetation (Ermakov et al. 2000).

The phytodiversity of the South Siberian Mountains is the greatest in Siberia (Malyshev et al. 1999, Belov et al. 2015). Tall-herb vegetation is phytosociologically treated within the Eurosiberian class Mulgedio-Aconitetea Hadač & Klika in Klika & Hadač 1944 (Ermakov et al. 2000) and consists out of tall-forb, tall-grass, and tall-fern communities. So far, more than 50 associations of Mulgedio-Aconitetea are described from Southern Siberia, mainly from the western part of Altai-Sayan Mts., i.e. the Altai, Western Sayan, Kuznetsky Alatau, and western margin of the Eastern Sayan (Lashchinskiy & Gorshkova 1995, Ermakov et al. 2000, Ermakov 2003, Zibzeev 2010a, 2010b, 2012, Zibzeev & Basargin 2012).

Khamar-Daban is the range on the south of Baikal rift zone, which is considered the easternmost limit of community types belonging to the class, but there is only few data available from the region (Guinochet 1982, Chytrý et al. 1993, Chytrý et al. 1995, Danihelka & Chytrý 1995, Valachovič et al. 2002).

Despite the number of publications devoted to the syntaxonomy (e. g. Ermakov et al. 2000), there is a lack of publications analyzing ecological distribution patterns of the tall-herb meadows in Southern Siberia. Communities of this biome in Siberia are influenced by continental climate, in contrast to the European ones (Ermakov 2003). Therefore, the features of Siberian tall-herb vegetation are of great interest for the understanding of ecological preferences, limits and capabilities of this type of grassland in general. Ecological studies, focusing on environmental factors and community ecology, are essential for a comprehensive description of vegetation of the continental regions of Asia.

With the intention to reveal vegetation patterns of subalpine tall-herb communities on the northern slope of the Khamar-Daban Range, we addressed following questions:

1. Which environmental variables influence species diversity of tall-herb vegetation on the northern slope of the Khamar-Daban Range?

2. How many community types can be differentiated for tall-herb vegetation in local area, floristically? And which species are indicators for those community types?

3. Are the different community types reflected by environmental variables?

STUDY AREA

The study area is situated in the east of Southern Siberia, 8 km from Lake Baikal on the northern slope of the Khamar-Daban Range in the upper reaches of the Bolshoi Mamai River, a small tributary of Lake Baikal, and covers a total area of 6.5 km^2 (Fig. 1). Southern Siberia in general, is a predominantly mountainous territory with vast Altai-Sayan Mts. (Strelkov & Vdovin 1969) on the southwest, which turn north-eastwards through the Baikal rift zone to the Stanovoy Range (Florensov 1974). These mountains are links in a transcontinental mountain chain, which stretches from Central Asia to the Beringia (Florensov 1974).

We collected data from timberline (about 900 m a.s.l.) to the top, where two sources of the Bolshoi Mamai River's watershed are found. The two highest peaks in the area, Polyana Mt. (1756 m a.s.l., 51.362400°N, 104.862447°E), and Mamai Mt. (1541 m a.s.l., 51.387197°N, 104.807840°E) are located in the south and in the west, respectively. Taking into account differences in definitions of "subalpine" by different authors (Körner 1998), we implement the subalpine belt as the transition zone between the upper limit of the closed mountain forest and the upper limit of tree species distribution. In our study area, the distribution of tall-herb meadows lies within this subalpine belt.

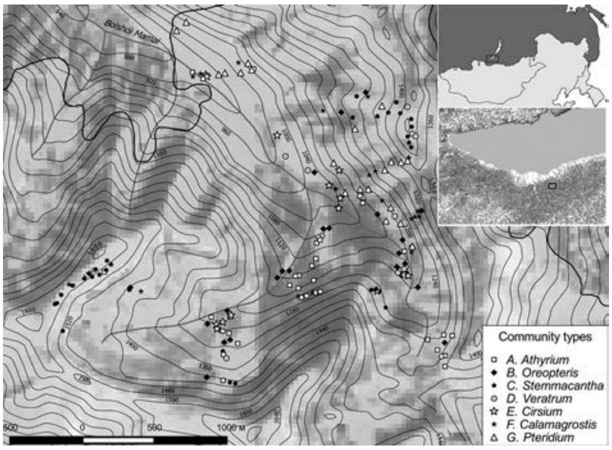

Figure 1 Localities of sample plots in upper reaches of the Bolshoi Mamai River (Khamar-Daban Range, Southern Baikal region). The timberline position is marked by the black bold line

The northern slope of the Khamar-Daban Range is composed of metamorphosed Proterozoic complexes covered by basalts (Florensov & Olyunin 1965). Sharp smaller ranges shaped by cryogenic and periglacial processes extend northwards from main mountain chain. Steep slopes (30–45°) are dissected by deep valleys.

The territory is characterized by a short and cold summer (mean July temperature: 12.7°C) and a long, comparatively cold (mean January temperature:17.9°C) winter (Ladeishchikov et al. 1977).

The Khamar-Daban Range is one of the ranges that form the rift zone around Lake Baikal. It stretches over 350 km from the south-western end of the lake (next to Kultuk town) to the Selenga River valley on the east. Sublatitudinal orientation of the range defines its barrier function on the way of the air masses, which are transferring from the Atlantic Ocean and form the climate of the western Baikal region. The central part of the northern slope of the Khamar-Daban Range intercepts the greatest amount of precipitation in the region. The only mountain meteorological station located on the western end of the Khamar-Daban Range recorded an average precipitation of 1443 mm per year (Ladeishchikov et al. 1977).

High precipitation in winter leads to a thick snow cover, which is usually more than 100 cm deep with a maximum of 190 cm (Ladeishchikov et al. 1977). The area on Bolshoi Mamai is covered by snow for at least 8 months: from the end of September until the beginning of June (personal observations). High air humidity during summer and thick snow cover during winter, provide favorable conditions for tall-herb vegetation, despite the mean annual temperature until -3.4°C (Aleksandrova et al. 1977).

The forest belt is found at lower elevations (460–600 m a.s.l.) and is composed by mixed dark coniferous forests (*Abies sibirica*, *Picea obovata*, *Pinus sibirica*) together with small-leaved birch (*Betula platyphylla*, *B.* cf. *pubescens*) and aspen (*Populus tremula*) on disturbed areas. *Pinus sibirica* predominates in mountain taiga, which is found at elevations of

600–800 m a.s.l. The upper part of the forest belt is occupied by *A. sibirica* forests accompanied by *P. sibirica*.

The range is of high refugial value for many endangered and relict mesophytic plant species absent in other parts of Baikal Siberia (Tubanova et al. 2016, Chepinoga et al. 2017). Weak human influence is typical for the mountainous highlands around Lake Baikal and contributes to the conservation of poorly disturbed subalpine vegetation.

MATERIAL AND METHODS

Sampling design

The original data set consists of 162 relevés that were sampled during the second half of July 2015. Seven relevés were sampled on the 22nd July 2014. We recorded the vegetation on plots of 25 m^2 located in representative sites. A percentage scale was used to determine plant cover. Elevation, aspect, inclination, microtopography, and thickness of organic layer (namely, O (organic) horizon) were also determined (Table 1). The term microtopography was used as ordinal variable to describe the unevenness of the ground surface (stones, protruding rhizomes, etc.), and was determined visually by estimating the difference between height of hummocks and depressions within the plot. Inclination was estimated visually as well, while we used compass and GPS navigator for determination of aspect and elevation. Aspect data were transformed to linear values (40°=0, 220°=180) because of the influence of the sun, neglecting east and west aspect (Dargie 1984, Elliott et al. 1999). Korolyuk (2006) indicator values were used for soil moisture (120 grades in full scale) and soil richness (available mineral nutrition; 30 grades) scores for every sample plot.

Data analysis

Data processing was carried out using the software package IBIS (Integrated Botanical Information System), the vegetation database management software (Zverev 2007, 2012). For statistical analyses R, Version 3.5.1. (R Core Team 2018), was used.

We analyzed interactions between species richness (dependent variable) and environmental factors (independent variables) using a general linear model assuming Poisson distribution:

Species richness ~ Elevation + Aspect + Slope + Organic Layer + Microtopography

Table 1: Variation of sampled environmental variables.

Variable	Unit	Range
Inclination	degree	0–45
Elevation (above sea level)	m	899–1589
Aspect	degree	0–360
Aspect (modified)	degree	0–180
Microtopography	cm	0–50
Thickness of organic layer	cm	0–12
Soil moisture (after Korolyuk 2006)	grades	61.1–74.2*
Soil richness (after Korolyuk 2006)	grades	9.8–11.7*

* The full scale of indicator value for mosture consists of 120 grades, and for soil richness (namely available mineral nutrition) – 30 grades.

Significant variables were selected with help of “backward selection” ($p < 0.05$) (Crawley 2013). Normal distribution and variance homogeneity of residuals was graphically tested with help of a normal probability plot (Dormann & Kühn 2009, Crawley 2013).

We divided vegetation data into community types using hierarchical agglomerative cluster-analysis using Sørensen (Bray-Curtis) indices and the Ward’s-method (Ward 1963, Oksanen et al. 2018). Incomplete cases with NAs were removed. The number of clusters was determined by optimum average silhouette width; package “fpc” (Rousseeuw 1987, Hennig 2018). Clustering algorithm output was described by the correlation between the cophenic distances and the original distances (Sneath & Sokal 1973). We analyzed community integrity with package “labdsv” (Roberts 2016). With the packages “ggplot2” (Wickham 2009), “ggdendro” (Vries & Ripley 2016), “plyr” (Wickham 2011) and “zoo” (Zeileis & Grothendieck 2005) the cluster analysis was visualized.

For community types, we determined indicator species by Dufrene-Legendre Indicator Species Analysis, using frequency tables and mean abundance (Indicator Value, $p < 0.05$) (Dufrene & Legendre 1997). Because of a lack of vegetation classification for the range and small size of the key area we avoided to link identified units to the concrete syntaxa. All distinguished community types are accepted as unranked communities belonging to the class Mulgedio-Aconitetea Hadač & Klika in Klika & Hadač 1944. Besides standard packages, the package “vegan” was used for statistical analyses of community ecology (Oksanen et al. 2018).

The significant environmental variables, which should be included in the correspondence analysis, were a priori selected with “backward selection” ($p < 0.05$) (Crawley 2013). Only plant species that occurred in at least four plots were included in the analysis ($n = 69$ remaining species). Additionally, we performed a square root transformation of cover values. After performing a DCA, which showed a first axis length of 4.45 SD unit, indicating unimodal response model with almost complete turnover in species composition we chose CCA (Leyer & Wesche 2007, Dormann & Kühn 2009) as appropriate method.

Moreover, differences between groups in regard to the environmental variables, as well as other important factors like species richness and vegetation height, were determined with the Kruskal-Wallis-test ($p < 0.05$) (Fahrmeir et al. 2016).

Nomenclature

The nomenclature of taxa mainly follows Chepinoga et al. (2008) for vascular plants, Ignatov et al. (2006) for mosses, and Konstantinova & Bakalin (2009) for liverworts.

RESULTS

Floristic diversity

The number of taxa (species and subspecies of vascular plants and bryophytes) recorded in 162 relevés consisted out of 132 species. Only 30 species exceeded the 1 % constancy and 24 species exceeded 2 %. Top ranking were (in brackets constancy percentage values) *Geranium krylovii* (86), *Veratrum lobelianum* (70), *Poa ircutica* (67), *Calamagrostis langsdorffii* (66), *Lilium pilosiusculum* (55), *Athyrium distentifolium* (53), *Rumex alpestris* (49), *Solidago dahurica* (49), *Trollius* cf. *kytmanovii* (41), *Doronicum altaicum* (40), *Anemone baicalensis* (39), *Poa sibirica* (38), *Chamaenerion angustifolium* (36), *Maianthemum bifolium* (35), *Stemmacantha carthamoides* (35).

Species diversity of individual plots varied between 6 and 37 species, depending on the community type. In addition to that, species diversity was positively correlated with inclination and orientation of plots to warmer (south and south-west) aspect, but negatively correlated with microtopography and organic layer thickness. The independent variable "Elevation" was excluded from the initial model as statistically insignificant (Table 2, Fig. 2).

Community types

Due to analysis of silhouette width, data were separated by hierarchical agglomerative cluster analysis into seven clusters (Fig. 3). The correlation between cophenetic distances and original data was 0.47. The established clusters were characterized by 45 significant indicator species (Table 3). The clusters differed significantly regarding species diversity and ecological factors, except the total cover of the herb layer (Fig. 4). The established clusters were considered as unranked communities of the class Mulgedio-Aconitetea (Table 3).

The *Athyrium distentifolium*-comm. (cluster A) was branching off from the main tree first, and is floristically most distinct from other tall-herb vegetation, in our study. It included communities characterized by the dominance of *Athyrium distentifolium*. In addition to this species, *Doronicum altaicum* was distinguished as a second indicator species. These communities were the poorest in species diversity. *A. distentifolium* stands occurred at medium elevations (mainly within 1200 and 1300 m a.s.l.) and at intermediate inclinations 10–20° of warmer west and south-west aspect. They occupy one of the poorest (concerning available mineral nutrition), often stony soils. The presence of big stones within plots lead to a strongly pronounced microtopography, with the highest differences between hummocks and depressions in comparison with other tall-herb meadows.

The *Oreopteris limbosperma*-comm. (cluster B) corresponded to stands with a well pronounced dominance of *Oreopteris limbosperma*. Other two indicator species (*Maianthemum bifolium* and *Anemone sibirica*) had lower abundance and the species diversity was relatively low in comparison to other communities. Similar to the *Athyrium distentifolium*-community, stands of *Oreopteris limbosperma* were also found at medium elevations, but they occurred on steeper but smoother slopes in a broader range of aspect at poor soils. In case of the *Oreopteris limbosperma*-comm., microtopography was formed mainly by rhizomes of *O. limbosperma* protruding above the ground. The height of fronds was also lower and usually not exceeds 60 cm.

The cluster C (*Stemmacantha carthamoides*-comm.) composed together with clusters D (*Veratrum lobelianum*-comm.) and E (*Cirsium helenioides*-comm.) the central main subclade within the tree. The *Stemmacantha carthamoides*-comm. was characterized by the highest species diversity. As indica-

Table 2. Impact of aspect, slope, microtopography and organic layer drought on number of species. The minimal adequate model explains 40% of the variance.

Independent variable	**p**	**Chi^{2} $_{1,102}$**
Aspect	<0.01	14.26
Inclination	<0.01	17.79
Microtopography	0.011	6.33
Organic layer	0.021	15.31
Elevation	0.13	-2.28

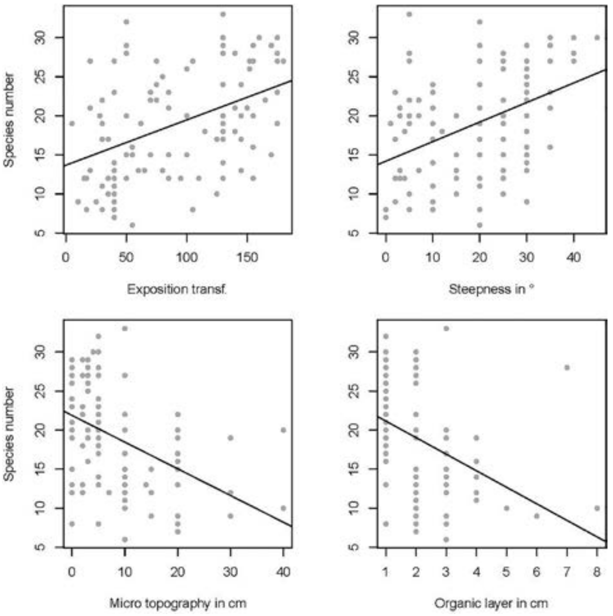

Figure 2 Number of species per plot according to the transformed aspect, slope inclination, microtopography and organic layer

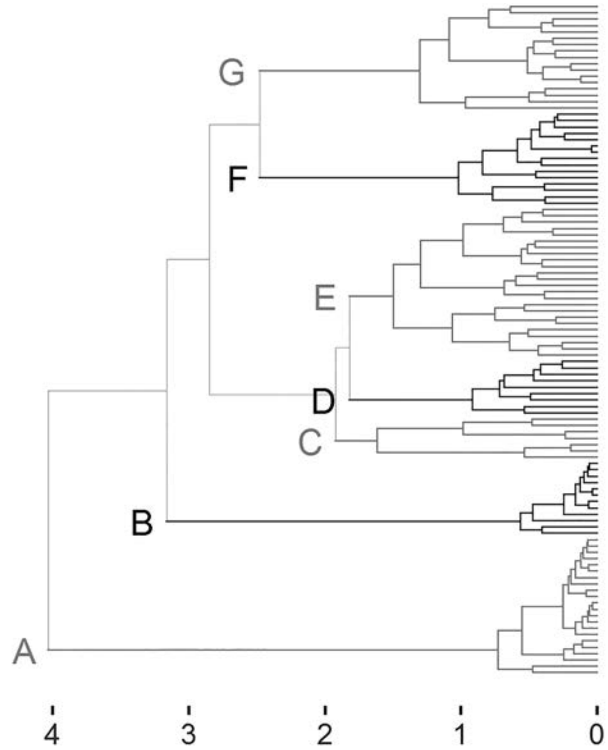

Figure 3 Dendrogram of the cluster analysis (Sørensen (Bray-Curtis) index, Ward's method) for 162 relevés of tall-herb meadows in upper reaches of the Bolshoi Mamai River. For names of the clusters (community types) see Fig. 1

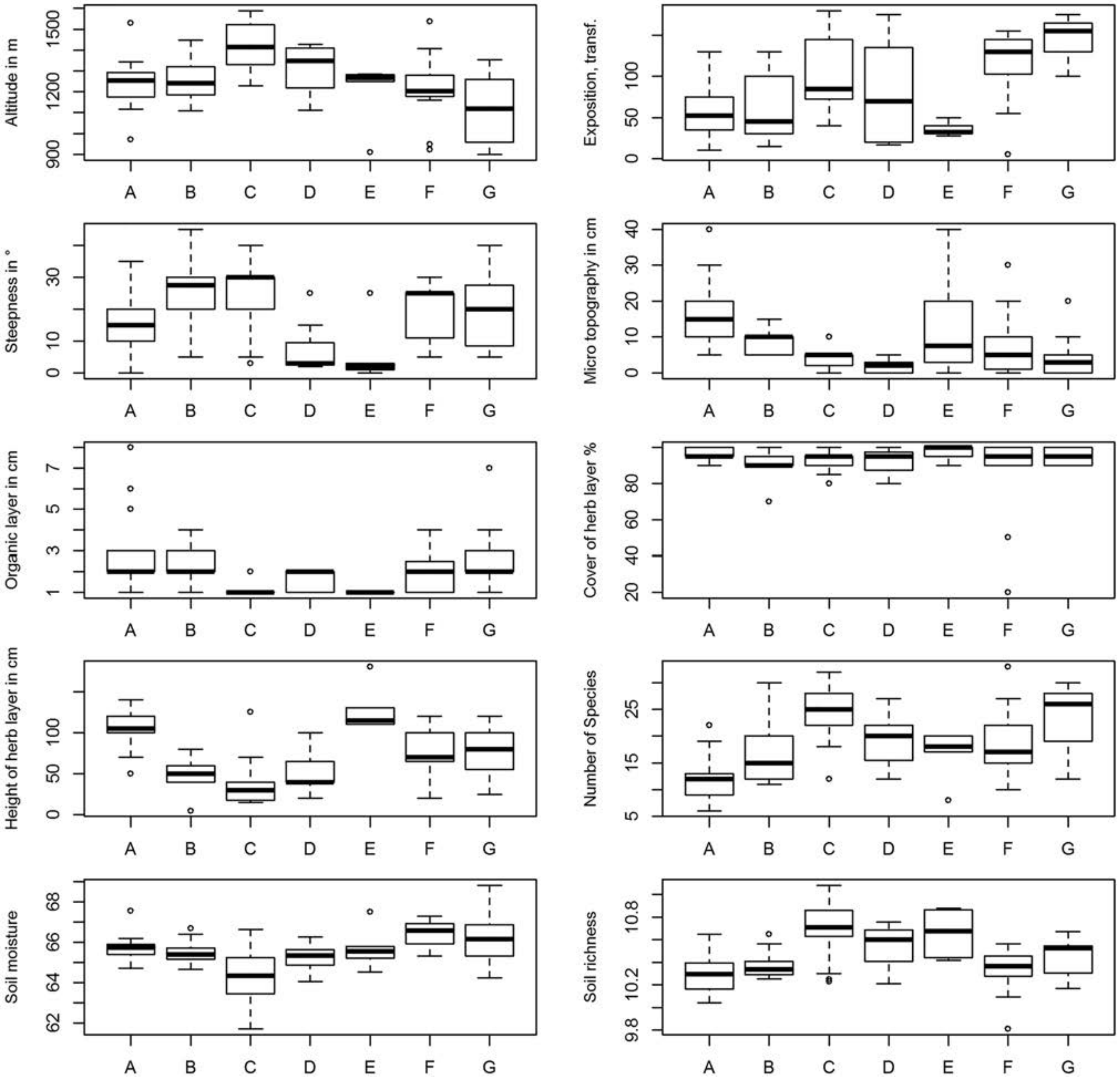

Figure 4 Ecological parameters and species richness of the established clusters. For names of the clusters (community types) see Fig. 1

tor species, 18 taxa have been distinguished. *Stemmacantha carthamoides*, *Anthoxanthum alpinum*, *Dracocephalum grandiflorum*, and *Saussurea latifolia* have highest indicator values. Besides this, these species are among the most abundant indicator species within unit. Tall-herb vegetation of the *Stemmacantha carthamoides*-comm. occupied highest elevations and steepest slopes of warmer south-east and south-west aspect. Soil moisture was comparatively low, whereas the available mineral nutrition was highest compared to other community types. The microtopography was weakly pronounced as well as the organic layer. Additionally, the mean height of herb layer of the *Stemmacantha carthamoides*-comm. stands was very low and did generally not exceed 40 cm.

The *Veratrum lobelianum*-comm. (cluster D) was very peculiar in species composition. Three species have been distinguished as indicator ones. Among them, *Poa ircutica*, the South Siberian endemic species, and *Swertia baicalensis* – a local endemic of the Khamar-Daban Range. This vegetation type occured on higher elevations but on more gentle and smooth slopes of different aspect. Rich soils with medium soil moisture characterized this cluster. Like the *Stemmacantha carthamoides*-comm., height of herb layer in stands of *Veratrum lobelianum*-comm. was low.

The physiognomy of communities belonging to cluster E (*Cirsium helenioides*-comm.) was determined by *Cirsium helenioides*, *Aconitum rubicundum* and *Delphinium elatum*, which were the dominant or codominant species on plots of this community type. Beyond these three species, eight others have been determined also as indicator species including highly indicative Saxifraga aestivalis. Habitats of this community had the largest range of microtopography associated with the presence of large stones on plots and often stretched along streams and streamlets with moderately moist soils with rich available mineral nutrition but thin organic

Table 3. Results of the indicator species analysis of units revealed in subalpine meadows of Bolshoi Mamai. Numbers indicate percentage occurrence frequency (constancy), supercase numbers indicate mean cover (in %, "+" indicates values < 0.1), gray shading indicates indicator species. The table includes only species that have an indicator value of 0.25 or higher, indicator species with an indicator value of 0.5 or higher are shown in bold. Significance levels (p) are following: *** < 0.001, ** < 0.01, * < 0.05, n.s. – not significant. For names of the clusters (community types) see Fig. 1.

Clusters	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**Indicator value**	**p**
Number of relevés	**35**	**25**	**32**	**14**	**13**	**19**	**24**		
Total number of species	**52**	**68**	**92**	**55**	**50**	**69**	**87**		
***Athyrium distentifolium*-comm.**									
Athyrium distentifolium	$100^{84.17}$	$36^{1.74}$	$34^{1.04}$	$71^{2.59}$	$23^{2.77}$	$58^{24.58}$	$29^{0.5}$	0.86	***
Doronicum altaicum	$66^{1.63}$	48^{+}	31^{+}	$50^{0.38}$	$46^{0.78}$	$16^{0.32}$	$13^{0.13}$	0.31	**
***Oreopteris limbosperma*-comm.**									
Oreopteris limbosperma	$17^{0.86}$	$100^{77.32}$	$31^{0.96}$	$50^{0.8}$	·	$16^{0.32}$	4^{+}	0.96	***
Maianthemum bifolium	$31^{0.21}$	$76^{0.68}$	$16^{0.16}$	$43^{0.17}$	8^{+}	$37^{0.28}$	$33^{0.38}$	0.27	**
Anemone sibirica	·	12^{+}	$72^{8.94}$	14^{+}	·	$5^{0.16}$	13^{+}	0.69	***
***Stemmacantha carthamoides*-comm.**									
Stemmacantha carthamoides	3^{+}	$20^{1.92}$	$97^{19.79}$	$43^{4.44}$	·	$37^{2.12}$	$33^{0.47}$	0.67	***
Anthoxanthum alpinum	·	16^{+}	$66^{1.67}$	29^{+}	·	11^{+}	13^{+}	0.59	***
Dracocephalum grandiflorum	·	·	$56^{1.2}$	7^{+}	·	·	17^{+}	0.52	***
Saussurea latifolia	3^{+}	$32^{0.89}$	$91^{6.73}$	36^{+}	8^{+}	$58^{0.75}$	$50^{0.77}$	0.50	***
Vaccinium myrtillus	·	24^{+}	$72^{3.54}$	$50^{0.39}$	·	26^{+}	$25^{1.13}$	0.49	***
Hieracium krylovii	·	20^{+}	$84^{0.96}$	$43^{0.18}$	·	$37^{0.44}$	$38^{0.19}$	0.44	***
Dianthus sajanensis	·	4^{+}	72^{+}	14^{+}	·	11^{+}	17^{+}	0.44	***
Solidago dahurica	23^{+}	$64^{0.13}$	$91^{2.81}$	$86^{0.84}$	·	$84^{0.93}$	$71^{0.58}$	0.41	***
Aquilegia glandulosa	9^{+}	$32^{0.18}$	$81^{1.03}$	$57^{0.39}$	·	$21^{0.26}$	$25^{0.22}$	0.40	***
Campanula rotundifolia	·	8^{+}	$50^{0.19}$	·	·	5^{+}	8^{+}	0.38	***
Phlojodicarpus villosus	·	4^{+}	$38^{1.61}$	·	·	·	4^{+}	0.36	***
Sanguisorba officinalis	·	·	$34^{8.66}$	·	·	·	4^{+}	0.34	***
Callianthemum sajanense	·	·	$34^{0.92}$	·	·	11^{+}	13^{+}	0.34	***
Trollius cf. *kytmanovii*	·	·	$22^{0.76}$	$7^{0.14}$	·	·	·	0.33	**
Geranium krylovii	$94^{3.1}$	$96^{3.46}$	$94^{12.28}$	$86^{7.02}$	$62^{1.38}$	$74^{3.58}$	$79^{5.13}$	0.32	**
Campanula glomerata	·	8^{+}	$44^{0.13}$	7^{+}	·	16^{+}	33^{+}	0.29	**
Pedicularis incarnata	3^{+}	20^{+}	$66^{0.24}$	29^{+}	·	47^{+}	$33^{0.18}$	0.27	**
Galium boreale	·	24^{+}	$59^{0.24}$	14^{+}	·	$32^{0.13}$	$79^{0.15}$	0.25	*
***Veratrum lobelianum*-comm.**									
Veratrum lobelianum	$86^{1.41}$	$56^{1.25}$	$66^{1.44}$	$100^{51.43}$	$54^{0.26}$	$63^{0.98}$	$63^{1.15}$	0.89	***
Poa ircutica	$91^{4.19}$	$80^{3.38}$	$69^{4.92}$	$86^{10.86}$	$46^{0.7}$	$42^{3.74}$	$38^{2.05}$	0.31	**
Swertia baicalensis	14^{+}	$60^{1.1}$	$53^{2.39}$	$64^{2.59}$	·	$16^{0.11}$	$4^{0.42}$	0.25	**
***Cirsium helenioides*-comm.**									
Cirsium helenioides	11^{+}	12^{+}	6^{+}	14^{+}	$92^{45.17}$	$26^{0.38}$	$21^{0.3}$	0.91	***
Aconitum rubicundum	$23^{1.32}$	12^{+}	$13^{0.13}$	·	$92^{25.93}$	$26^{1.59}$	$21^{1.59}$	0.78	***
Saxifraga aestivalis	$14^{0.12}$	4^{+}	9^{+}	·	$77^{1.02}$	5^{+}	·	0.68	***
Delphinium elatum	·	·	·	·	$54^{11.54}$	·	·	0.54	***
Caltha palustris	·	·	·	·	$38^{0.42}$	·	·	0.38	***
Urtica dioica	·	·	·	·	$31^{0.25}$	·	·	0.31	***
Angelica decurrens	·	·	·	·	$31^{3.15}$	·	·	0.31	***
Sciurohypnum reflexum, ml	·	·	·	·	$31^{3.69}$	·	·	0.31	***
Lescuraea patens, ml	·	·	·	·	$31^{2.23}$	·	·	0.31	***
Heracleum dissectum	$26^{0.19}$	4^{+}	9^{+}	·	$46^{3.01}$	$16^{0.43}$	$25^{0.89}$	0.30	**
Thalictrum minus	3^{+}	4^{+}	6^{+}	·	$38^{0.62}$	32^{+}	$33^{0.11}$	0.27	**
***Calamagrostis purpurea*-comm.**									
Calamagrostis langsdorffii	$77^{4.04}$	$56^{0.85}$	$19^{1.1}$	$71^{2.65}$	$85^{4.85}$	$100^{58.42}$	$83^{4.6}$	0.76	***
Chamaenerion angustifolium	$31^{0.44}$	$32^{0.1}$	$19^{0.32}$	$43^{0.46}$	$38^{0.11}$	$63^{5.23}$	$42^{1.89}$	0.39	***
Lilium pilosiusculum	$66^{0.17}$	36^{+}	$28^{0.18}$	71^{+}	$54^{0.12}$	$68^{0.72}$	$75^{0.34}$	0.29	*
***Pteridium aquilinum*-comm.**									
Pteridium aquilinum	$6^{0.6}$	$20^{2.88}$	$9^{0.94}$	$21^{2.86}$	8^{+}	$68^{11.05}$	$100^{64.71}$	0.78	***
Angelica sylvestris	3^{+}	8^{+}	6^{+}	·	8^{+}	$37^{0.18}$	$63^{0.91}$	0.51	***
Rubus saxatilis	·	8^{+}	$6^{0.47}$	$7^{0.21}$	·	16^{+}	$58^{2.27}$	0.43	***
Poa sibirica	$6^{0.15}$	$16^{0.2}$	$81^{1.33}$	$43^{0.66}$	8^{+}	$21^{0.33}$	$75^{1.8}$	0.30	**
Carex macroura	·	$8^{0.2}$	$44^{0.7}$	$7^{0.21}$	·	·	$38^{2.88}$	0.27	**
Diagnostic species of the order *Trollio-Crepidetalia sibiricae*									
Pleurospermum uralense	$3^{0.14}$	4^{+}	$22^{0.2}$	14^{+}	·	16^{+}	17^{+}		n.s.
Crepis lyrata	·	8^{+}	19^{+}	7^{+}	15^{+}	11^{+}	17^{+}		n.s.
Jacobaea nemorensis	11^{+}	4^{+}	6^{+}	·	15^{+}	$32^{0.28}$	8^{+}		n.s.
Crepis sibirica	3^{+}	16^{+}	13^{+}	·	8^{+}	$42^{0.38}$	$46^{0.32}$		n.s.
Lamium album	23^{+}	12^{+}	3^{+}	7^{+}	46^{+}	42^{+}	33^{+}		n.s.
Bupleurum aureum	6^{+}	$24^{0.29}$	$47^{0.32}$	7^{+}	·	$42^{0.38}$	$58^{0.17}$		n.s.
Anthriscus sylvestris	3^{+}	·	3^{+}	·	$23^{0.78}$	16^{+}	4^{+}		n.s.
Milium effusum	3^{+}	·	·	7^{+}	·	·	·		n.s.
Myosotis palustris	·	·	·	·	8^{+}	·	·		n.s.
Diagnostic species of the order *Schulzio crinitae-Aquilegietalia glandulosae*									
Diphasiastrum alpinum	·	·	16^{+}	·	·	·	·		n.s.
Gnaphalium norvegicum	·	4^{+}	6^{+}	·	·	·	·		n.s.
Diagnostic species of the class *Mulgedio-Aconitetea*									
Viola biflora	$51^{0.18}$	$48^{0.31}$	$16^{0.23}$	$14^{0.36}$	$69^{0.49}$	$26^{0.13}$	·		n.s.
Rumex alpestris	$43^{0.15}$	$60^{0.2}$	47^{+}	$79^{0.27}$	15^{+}	$63^{0.16}$	42^{+}		n.s.
Primula pallasii	·	·	13^{+}	·	·	·	·		n.s.

layer. The *Cyrsium helenioides*-comm. comprised very tall forb-communities.

The following F and G clusters constituted a separate subclade and correspond to two different community types.

There were three indicator species for *Calamagrostis purpurea*-community type (cluster F). The most significant indicator was the well pronounced dominant species *Calamagrostis langsdorffii*. Mean elevations were most typical for the *Calamagrostis purpurea*-comm. within the study area, but we also found a few stands at higher elevations (until 1537 m a.s.l.) in appropriate habitats. Stands belonging to this community type occupied naturally disturbed places, usually along avalanche-prone areas. Thus, they developed at rather steep slopes of southward oriented aspect. The height of the herb layer had mean values regarding the other established clusters.

Pteridium aquilinum was the main dominant species in communities of the cluster G (*Pteridium aquilinum*-comm.). There were another four indicator species, most of them are typical forest plants. This community type was characterized by high species richness. The importance of forest species reflects a confinement of these communities to lower elevations, lowest within the data set. The *Pteridium aquilinum*-comm. occurred at medium steep and smooth slopes of warmer southern aspect and occupy habitats with thick organic layer.

The general pattern of the tall-herb vegetation within the study area was following. Right above the timberline, the large habitats of the *Pteridium aquilinum*-comm. were developed. Disturbed slopes of southern aspect at different elevations were occupied by stands of the *Calamagrostis purpurea*-comm., the *Athyrium distentifolium*-comm. and the *Oreopteris limbosperma*-comm. occupied the lower and the middle parts of the slopes mainly in central part of the subalpine belt. *Stemmacantha carthamoides*-comm. vegetation developed at highest elevations and steepest slopes of valley boards. At similar elevations, but on more gentle slopes, stands of the *Veratrum lobelianum*-comm. are found. *Cirsium helenioides*-comm. were typical for banks of streams and streamlets.

Ordination

The established model for the canonical correspondence analysis included elevation, aspect (modified), inclination, microtopography and organic layer as environmental variables ($p < 0.05$) (Fig. 5). Because of NA-values, 15 relevés have been removed from the analysis. The performed CCA showed a total inertia of 3.58, from which 21.7 % was explained. The eigenvalue for the first constrained axis is 0.30, for the second 0.28 and the third 0.08. The CCA ordination was consistent with results of the cluster analysis and stresses the contribution of different ecological factors of the distinguished community types.

The strong positive correlation with microtopography of *Athyrium distentifolium*-comm. and *Cirsium helenioides*-comm. was determined by their confinement to stony habitats. In a complex together with *Oreopteris limbosperma*-comm., these community types were negatively correlated with aspect, which means, they avoid warmer slopes and prefer north-eastern or even northern aspect. A strong positive correlation of the *Stemmacantha carthamoides*-comm. with higher elevations, and steeper slopes was also evident. In contrast to that, the *Calamagrostis purpurea*-comm. and especially the *Pteridium aquilinum*-comm. avoid high elevations but were positively correlated with warmer southern and south-western aspect, as well as a well-formed

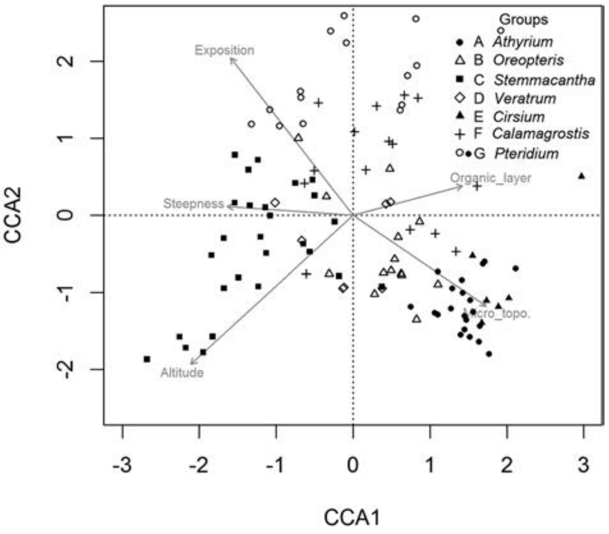

Figure 4 Canonical correspondence analysis ordination diagram for sampled relevés. Differences in sample symbols correspond to distinguished clusters. Arrows indicate the influence of environmental factors

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Other species occurence (%): *Abies sibirica* (sl): B – 4, C – 3, D – 7; *Aconitum glandulosum*: A – 3, B – 8, C – 16, F – 32, G – 13; *Aconogonon alpinum*: C – 9; *Allium chamarense*: B – 4, C – 41, D – 14, E – 8, F – 5, G – 17; *A. microdictyon*: A – 34, B – 40, C – 3, D – 57, E – 54, F – 21, G – 29; *Anemone altaica*: A – 6, B – 4, C – 6; *A. baicalensis*: A – 40, B – 56, D – 57, E – 54, F – 32, G – 58; *A. reflexa*: C – 3; *Antennaria dioica*: C– 9; *Artemisia integrifolia*: G – 4; *A. vulgaris*: F – 5, G – 4; *Bergenia crassifolia*: A – 6, B – 12, C – 31, F – 26, G – 4; *Betula* cf. × *irkutensis* (sl): F –11, G – 4; *Bistorta major*: F – 5, G – 4; *B. vivipara*: G – 8; *Brachypodium sylvaticum*: G – 4; *Calamagrostis obtusata*: G – 8; *Cardamine macrophylla*: E – 23; *Carex aterrima*: A – 3, B – 8, D – 7; *Cerastium davuricum*: A – 3, E – 8, F – 11, G – 8; *C. pauciflorum*: G – 4; *Circaea alpina*: A – 9, E – 8; *Dactylorhiza fuchsii*: A – 3, B – 12, C – 34, D – 7, F – 5, G – 21; *Dracocephalum nutans*: C – 6, G – 4; *Dryopteris expansa*: A – 9, D –7, F – 11; *D. filix-mas*: A – 3, E – 8, F – 5, G – 8; *Duschekia fruticosa* (sl): A – 6, B – 4, C – 3; *Equisetum sylvaticum*: E – 15; *Eranthis sibirica*: A – 37, B – 32, C – 28, D – 50, E – 31, G – 17; *Euphrasia syreitschikovii*: C – 25, F – 5, G – 4; *Gymnadenia conopsea*: C – 6; *Hieracium tunguskanum*: C – 9, G – 8; *Kiaeria blyttii* (ml): D – 7; *Lescuraea saxicola* (ml): C – 3; *Lycopodium clavatum*: C – 9; *Matteuccia struthiopteris*: G – 4, *Melica nutans*: F – 5, G – 8; *Moerckia blyttii* (ml): D – 7; *Oberna behen*: C – 31, D – 21, F – 11, G – 17; *Padus avium* (sl): F – 5, G –4; *Parasenecio hastatus*: G – 8; *Paris quadrifolia*: A – 9, D – 29, E – 23, F – 26, G – 38; *Parnassia palustris*: B – 4, C – 13; *Patrinia sibirica*: C – 3; *Pedicularis compacta*: C – 6, D – 7; *P. verticillata*: C – 6; *Phegopteris connectilis*: A – 3, B – 44, C –34, D – 21, F – 63, G – 71; *Phyllodoce caerulea*: C – 22; *Pinus pumila* (sl): C – 3; *Pulsatilla patens*: B – 4, C – 9; *Ranunculus propinquus*: B – 8, C – 53, D – 14, E – 8, F – 16, G – 13; *Rubus arcticus*: G – 4; *R. idaeus* (sl): A – 9, E – 8, F – 5, G – 13; *Salix caprea* (sl): G – 4; *Saussurea parviflora*: F – 11, G – 13; *Saxifraga spinulosa*: C – 9; *Sibbaldia procumbens*: C – 19; *Silene amoena*: F – 5; *Sorbus sibirica*, (sl): B – 4, G – 4; *Syntrichia ruralis* (ml): C – 3, E – 8; *Tanacetum vulgare* subsp. *boreale*: C – 6, G – 4; *Tephroseris praticola*: B – 4, G – 4; *Thesium repens*: B – 4, C – 22, G – 4; *Trientalis europaea*: A – 17, B – 12, C – 6, E – 8, F –11; *Valeriana transjenisensis*: B – 4, C – 3, E – 8, F – 5, G – 13; *Veronica densiflora*: C – 6, G – 4; *Viola uniflora*: B – 8, C – 13, G – 8.

organic layer. The *Veratrum lobelianum*-comm. did not show a strong correlation with any factors analyzed and located around the center of the diagram.

DISCUSSION

Floristic diversity

Regarding floristic diversity, it is worth to stress that only 33 species of 132 species listed in our data set have constancy-values higher than I class, i.e. recorded in more than 20 % of plots. A similar pattern was noted by Korolyuk (Korolyuk 2001) for tall-herb vegetation in Katunskii Nature Reserve (Altai Mts.). He suggested that the local diversity of dominant combinations in subalpine meadows comes amid the monotony of a comparatively low number of species (Korolyuk 2001). Although, this pattern could also be related to the dataset, as the number of species with higher frequency will decrease with addition of new data.

Higher species richness was confined to the warmest slopes with inclinations from 10 to 30 degrees of south and south-west aspect, where the topography helps to reduce superfluous soil moisture and shorten the period of snow cover. As topography is influencing snow layer in alpine regions, it evokes environmental gradients within rather small areas (Billings & Bliss 2017). Due to aspect to the sun, a longer growing season can be suggested for the species in floristically richest community types, i.e. *Stemmacantha carthamoides*-comm. at higher elevations and *Calamagrostis purpurea*-comm. and the *Pteridium aquilinum*-comm. at lower part of the subalpine belt. Besides that, Bowman (1992) supposed that vegetation below larger snow cover benefits from higher nutrient levels due to melting snow.

Community types

Tall-herb vegetation of the Bolshoi Mamai River could be clearly separated into seven community types, which were characterized by specific indicator species, in this study. We found the vegetation patterns to be strongly related to environmental factors as it was described for analogous tall-herb vegetation in Europe (Odland et al. 1995, Karst et al. 2005).

First of all, the elevation was recognized as an important factor distinguishing different types of plant communities, which is consistent with other investigations in Southern Siberia (Ermakov et al. 2000) and in Europe (Michl et al. 2010). The *Pteridium aquilinum*-comm. was characteristic for lower part of the subalpine belt within the study area. Similar communities with dominance of *Pteridium aquilinum* are known for lower elevations in Europe, too (e. g. Watt 1940). The stands of the *Stemmacantha carthamoides*-comm. were typical for higher elevations. Definitely, other mountains of Southern Siberia are ecologically more comfortable for *Stemmacantha carthamoides*, where this species is treated as diagnostic one for a number of associations in lower, middle and upper part of the subalpine belt (Ermakov et al. 2000, Zibzeev 2010a). The elevation amplitude where subalpine meadows were described in the study area comprises 600–700 m. The upper limit of their distribution was located at approximately 1600 m a.s.l. (see Tab. 1) reaching the watershed of the river basin. This distribution limit is linked to the height of the range, and not to physiological limits of the meadow plant species. For example, cryophilous tall-forb vegetation on other South Siberian Ranges described at elevations from 800 till 1900 m (Ermakov et al. 2000), or even till 2400 m a.s.l. (Korolyuk 2001).

All tall-herb communities are very productive, forming a dense and high vegetation cover (Gjærevoll 1956, Ellenberg & Leuschner 2010). For European stands of the species *Athyrium distentifolium*, for example, fronds with a size over 150 cm were recorded (Odland et al. 1995). The average height of Siberian tall-herb vegetation in general, as reported by Ermakov et al. (2000), was ranging between 80 and 140 cm but can reach up to 250 cm. In our study area, subalpine meadows are notably lower. Highest herb layer exceeding 100 cm, could be only found in *Athyrium distentifolium*-comm. and *Cirsium helenioides*-comm. *Calamagrostis purpurea*-comm. and *Pteridium aquilinum*-comm. are respectively even lower by 30 and 20 cm. The three other community types (*Oreopteris limbosperma*-comm., *Stemmacantha carthamoides*-comm., *Veratrum lobelianum*-comm.) did nearly never exceed a height of 50 cm and apparently present the most cryophilous subalpine meadows at higher elevations transitional between tall-herb subalpine and low-herb alpine meadows. Ermakov et al. (2000) consider such "middle-herb" meadows with a height of 40–80 cm in an order Schulzio crinitae-Aquilegietalia glandulosae (Ermakov et al. 2000). Despite the generally lower height of meadows in the study area, no community type from Bolshoi Mamai can be connected with the "middle-herb" order. Taking the revealed indicator species, and diagnostic species of the infraclass syntaxa into account (Ermakov et al. 2000), the distinguished community types belong to different alliances of the order Trollio-Crepidetalia sibiricae Guinochet ex Chytrý et al. 1993. The final syntaxonomic decision can be made after analysis of data from a wider area. Perhaps, the lowering of subalpine meadows in the Khamar-Daban Range in general, indirectly indicates the restrictions imposed by strong continental climate on the easternmost limit of tall-herb vegetation distribution.

A well-formed organic layer (at least 2 cm thick) was characteristic for most clusters, considered in our study. As noted before, we consider the term "organic layer" in a broad sense, including proper organic (litter) and surface soil horizons. Plants growing in tall-herb communities should be adapted to a well formed litter layer. Not only dominant species, but also associated species have to develop strongly built shoots to get through the dense litter, as it was found for *Anemone nemorosa* in Europe (Al-Mufti et al. 1977). In the same time, the well-formed organic layer suggests stable conditions, which in turn lead to the advantage of more competitive species. Consequently, this variable is inversely proportional to the species richness (see Fig. 2). Only *Stemmacantha carthamoides*-comm. and *Cirsium helenioides*-comm. showed nearly no organic layer. Steep slopes and high elevations, where stands of *Stemmacantha carthamoides*-comm. usually occur, or habitats along wet streamlets typical for *Cirsium helenioides*-comm. might explain that fact. Both habitats are too unstable to enable the assembling of a thick organic layer, but regular disturbing facilitates introduction of new species. As a result, *Stemmacantha carthamoides*-comm. and *Cirsium helenioides*-comm. are among the richest in species diversity.

In spite of the regularities revealed, the CCA ordination showed that over 70 % of the variance remained unexplained. This suggests that other environmental variables, remaining outside the analysis, are important for ecological differentiation of community types of subalpine meadows. For example, the strong correlation of some clusters with microtopography, rather a composite environmental factor, suggests that importance of substrate stoniness is left underestimated. Important for the distribution of communities are also biotic interactions, like a competition (McGill et al. 2006), which were not investigated in this study.

CONCLUSION

We studied the local vegetation pattern of subalpine tall-herb meadows on the Khamar-Daban Range, the easternmost limit of plant communities phytosociologically treated within the Eurosiberian class Mulgedio-Aconitetea Hadač & Klika in Klika & Hadač 1944. Due to broad distribution and comparatively rich vegetation diversity revealed on a small territory, the climatic conditions existing in the study area can be recognized as rather optimal for the development of subalpine tall-herb vegetation in a strong continental climate. Because of a large amplitude of elevation and different habitats in the subalpine belt of our study area, we found a comparatively high diversity of community types, which were floristically and ecologically distinguished in our research. We assume that the found community types can be a good basis for future syntaxonomic analyses of the tall-herb vegetation on the Khamar-Daban Range and that many of the indicator species will be accepted as diagnostic species.

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