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Phytosociology and dynamics of calcareous grasslands in Ķemeri National Park, Latvia

Agnese Priede

Institute of Biology, Laboratory of Geobotany, Miera Street 3, Salaspils, LV-2169, Latvia; agnesepriede@hotmail.com

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Abstract. Ecology, phytosociology, and regional characteristics of and management effects on calcareous grasslands in Ķemeri National Park (Latvia) were studied. The data set included 181 phytosociological relevés. According to TWINSPAN division and mean Ellenberg values the relevés were classified into four major groups at association level and classified as *Sesleria caerulea–Primula veris* community (alliance *Bromion*), *Sesleria caerulea–Inula salicina* community, *Molinietum caeruleae* community, and *Carex hostiana* community (alliance *Molinion*). Environmental factors were analysed by DCA using the mean Ellenberg values. The variances in species composition were mainly influenced by moisture, the only factor significantly differing among the phytosociological groups. The recent management has not directly affected the present species richness and vegetation structure at community level. Some aspects of grassland dynamics and conservation are discussed.

Key words: *Molinion caerulea*, *Festuco–Brometea*, *Bromion erecti*, Ķemeri National Park, Latvia.

INTRODUCTION

Semi-natural grasslands, both hay meadows and pastures, have significantly decreased in Latvia due to the decline of traditional grassland management practices (Rūsiņa, 2007, 2008). Both abandonment and intensive agriculture have influenced the cover of low-productive grasslands, which have been ameliorated and cultivated or abandoned during the last half a century.

Semi-natural calcareous grasslands in Latvia are formed on dolomite or limestone bedrocks, carbonate-rich moraine, or carbonate-rich peat soils, and are dominated by a complex of calcareous species. Calcareous grasslands in Latvia harbour many rare and specialist plant species. Today all semi-natural calcareous grassland types are rare in Latvia, and are therefore protected both by national and European legislative acts. In 2003 the total area of semi-natural grasslands was estimated at only 17 323 ha or 0.3% of the territory of Latvia. Of these approximately 6.4% (1116 ha) was classified as dry calcareous grasslands *Bromion erecti*, 4.88% (846 ha) as humid oligotrophic grasslands *Molinion caerulaea*, and 0.27% (47 ha) as calcareous dwarf sedge communities *Caricion davallianae* (Kabucis et al., 2003).

Dry calcareous grasslands belong to the class of sub-continental dry grasslands *Festuco–Brometea* Br.-Bl. et Tüxen ex Soó 1947 being one of the most species-rich vegetation types in Europe, hereto rich in rare, protected plant species (Löbel & Dengler, 2008). *Festuco–Brometea* communities are found in nutrient-poor, calcareous xeric or mesic soils; usually the sites are exposed to extreme micro-climatic conditions such as draught and high temperature amplitudes, which have facilitated the presence of many stress-tolerant species (Schubert, 2001; Janišová, 2007). In Latvia, drier calcareous grasslands belong to the alliance *Bromion erecti* Koch 1926 with a distribution range falling into West and Central European oceanic and sub-oceanic regions.

In Europe a large proportion of humid calcareous grasslands belong to the alliance *Molinion caerulaea* Koch 1926 and are found in poorly drained alkaline or acidic to slightly acidic peat or clayey, nutrient-poor soils, predominantly in lowlands with relatively high precipitation, occasionally also in sub-alpine regions (Anon., 1995; Hájková et al., 2007; Rodwell et al., 2007). Throughout their distribution range *Molinion* grasslands are endangered, being thus one of the priorities in the conservation of European grassland habitats (Anon., 1995; Hájková et al., 2007; Řezničková, 2007).

There are few studies on calcareous grasslands in Latvia. Over the last century, calcareous grasslands in Latvia have been classified according to the dominant species method (Sabardina, 1957), which is hardly comparable with the Central European phytosociological approach applied later and used by e.g. Rūsiņa (Rusina, 2003; Rūsiņa, 2007) for xerophytic and mesophytic grasslands. In terms of EU protected habitats, the characteristics and regional variation of dry calcareous grasslands (EU habitat code 6210) and *Molinia* grasslands on soils with fluctuating water tables (6410) were described also by Rūsiņa (2010) and Rūsiņa & Kabucis (2010).

Although not covering large areas, semi-natural calcareous grassland communities are well represented in Ķemeri National Park. The relatively small patches of calcareous vegetation are highly important in order to protect the particular habitat types and the affiliated species.

The aim of this study was to analyse the ecology, phytosociological affiliation, and regional characteristics of and management effects on calcareous grasslands in Ķemeri National Park.

MATERIAL AND METHODS

The study was performed in Ķemeri National Park (KNP), Latvia, which lies in the contact zone of the Coastal Lowland to the south of the Gulf of Riga and the northern edge of the Zemgale Lowland, 56°55′14″ N, 23°26′30″ E. The area is mostly flat, the average altitude reaches only a few metres above sea level. The soils are formed mainly of Devonian dolomite, dolomite marlstone, and clay bedrocks, moraine clayey material, sandy eolic and alluvial deposits. Large areas are covered by acidic peat soils; in small patches outflows of carbonate-rich spring waters have created specific conditions with carbonate-rich, sulphurous carbonatic peat deposits. The flora of the area contains floristic sub-atlantic elements typical for the Coastal Lowland and West Latvia. The park is very rich in plant species including botanical rarities and is particular with its high habitat diversity (Priede, 2008).

The area is predominantly covered by forests, raised bogs, and lakes. At the end of the 20th century the total area of semi-natural and ameliorated grasslands made up about 7% (2483 ha) of the total area of KNP. The dynamics of the grassland area over the 20th century cannot be precisely detected due to lack of data; however, according to retrospective analysis of cartographic materials (Priede, 2009) the total area of semi-natural grasslands in the mid-20th century may have been about 25% larger than at the beginning of the 21st century. At the beginning of the 21st century calcareous grasslands covered about 118 ha.

The study included mapping and classification of grassland habitats (2007 to 2009) and description of vegetation plots. The grassland areas were calculated on the basis of the orthophoto maps of 2007 using ESRI ArcGIS 9.0 software.

The vegetation was sampled in 2 m × 2 m plots located from each other at a distance of 10 to 20 m along a transect in a randomly chosen direction crossing the grassland patch. Vegetation plots were sampled using the Braun-Blanquet method: all vascular plant species occurring within the plot and their coverage in percentages were taken into account. The approximate area of the grassland where the vegetation plots were described was 80 ha, which covers about 70% of the patches of similar vegetation type in KNP. The location of plots in relation to the distribution of calcareous grasslands is given in Fig. 1.

A total of 181 plots were extracted from a larger grassland vegetation data set (552 relevés), where calcareous grasslands were distinguished by two-way indicator species analysis (TWINSPAN; Hill, 1979) on the basis of similarity of species composition and presence of indicator species. Then the selected TWINSPAN group of calcareous grassland plots was classified into vegetation units according to the similarity of species composition. Indirect ordination method DCA (PC-ORD program package; McCune & Mefford, 1999) was applied in analysing the ecological factors. As the explanatory variables the mean Ellenberg values (light, temperature, continentality, moisture, reaction, nitrogen) (Ellenberg et al., 1992) were calculated for each plot and then the mean values for the relevé groups were used. The parameters acquired in field (total moss layer, total litter layer, total number of species per relevé, and management) were included in the analysis. Independent samples *t*-test was used for comparing the significance of differences between the mean Ellenberg values of both major vegetation groups.

The classification of vegetation follows the Central European Braun-Blanquet system. The nomenclature for vegetation units is according to Weber et al. (2000). The species nomenclature follows Gavrilova & Šulcs (1999).

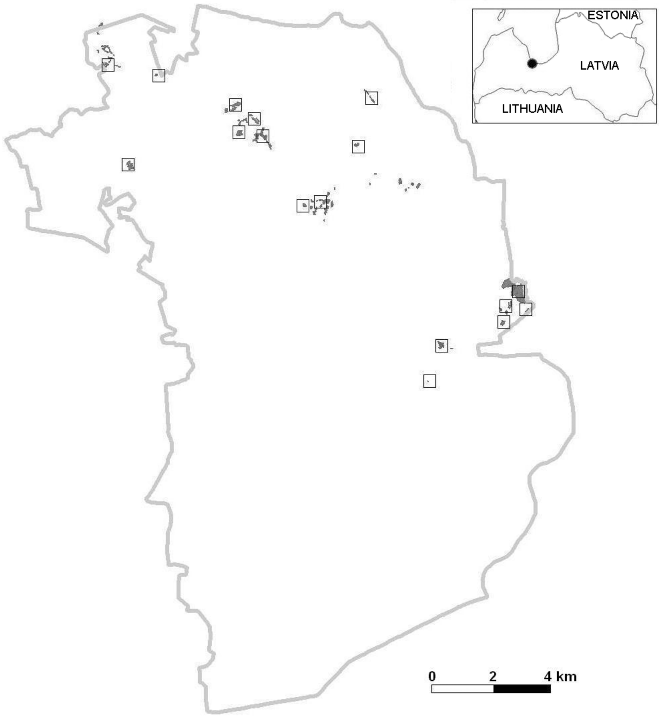

Fig. 1. Study area with the distribution of calcareous grasslands (patches) and location of vegetation plots (quadrates).

RESULTS AND DISCUSSION

Mapping results

Among the calcareous grasslands the largest areas were covered by *Molinion* grasslands, while *Bromion* grasslands were found mainly in small, relatively isolated patches or enclosed as mosaic patches in *Molinion* grasslands. Therefore the exact areas of these vegetation types could not be determined, and many locations contain elements of both types. About half of the *Molinion* and *Bromion* grasslands had representative vegetation, while the rest were partly overgrown or partly transformed into species-poor fen-like moist grasslands, fens, and/or shrublands. The causes of transformation include both abandonment and paludification. Over the period 2006–2009, about 40% of the *Molinion* and *Bromion* grasslands in KNP were mown at least once over the 4-year period. Some of the currently managed grasslands were classified as fallows rather than calcareous grasslands several years after cessation of arable cultivation; however, these have a high potential for renaturalization into calcareous grassland communities.

Classification of relevés

According to TWINSPAN analysis, the data set was split into two major groups: (1) xerophytic to mesophytic communities of *Sesleria caerulea* group (128 relevés in total); and (2) mesophytic communities with *Molinia caerulea* or *Carex hostiana* as dominant species (53 relevés in total). Both groups were divided into two sub-units: *Sesleria caerulea* group into *Sesleria caerulea–Bromion* and *Sesleria caerulea–Molinion* subgroups, and *Molinia caerulea* group into *Molinia caerulea* and *Carex hostiana* sub-groups (Fig. 2).

DCA Axis 1 explained 67.7% of variation, Axis 2 43%, and Axis 3 27% of variation. The only statistically significant environmental gradient was moisture, which distinguished *Sesleria caerulea* and *Molinia caerulea* groups. Moisture was followed by the total number of species (Fig. 3, Table 1).

Comparison of the mean Ellenberg values in the *S. caerulea* and *M. caerulea* groups shows that none of the factors significantly differs between the groups. Both groups are found on moderately warm, neutral to slightly acidic, nutrient-poor soils with little variations in the mean Ellenberg values except that the *S. caerulea* group occurs on slightly drier soils than the *M. caerulea* group (Table 2).

Comparison of species richness among the four sub-groups shows that the *S. caerulea* group is constantly richer in species than the *M. caerulea* group. The recent management has not directly affected the present species richness and vegetation structure at community level (Table 3).

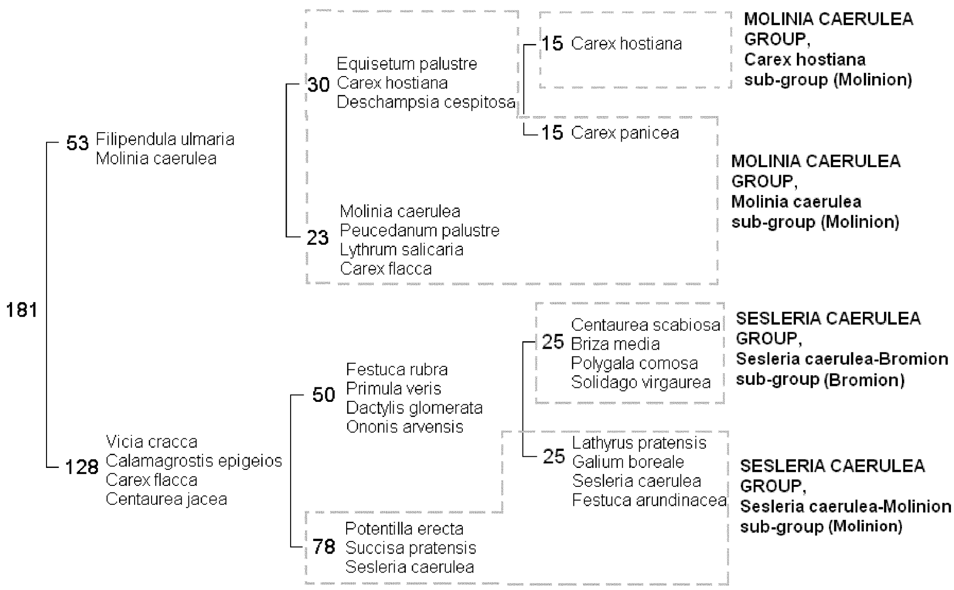

Fig. 2. TWINSPAN division of relevés.

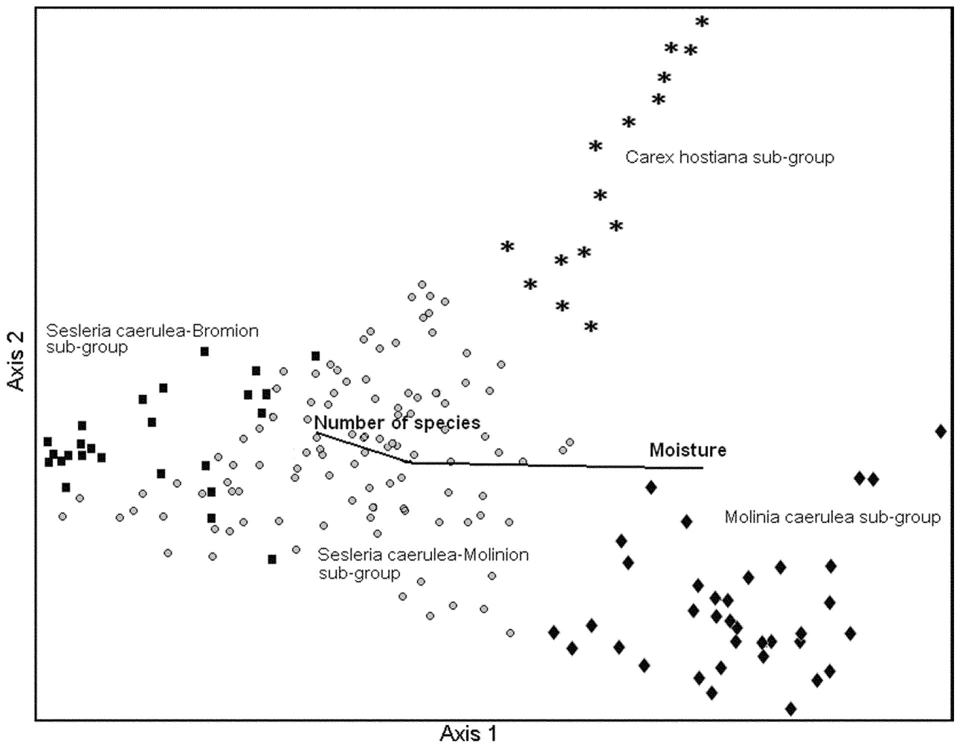

Fig. 3. DCA ordination of relevés and the major gradients.

Table 1. Pearson correlation coefficients between the mean Ellenberg values on the first two DCA axes

Environmental factor	DCA Axis 1	DCA Axis 2
Light	0.181	–0.127
Temperature	–0.278	–0.205
Continentality	–0.337	–0.344
Moisture	0.794*	0.075
Reaction	–0.337	–0.205
Nitrogen	–0.413	0.266
Total herbaceous cover	0.122	0.157
Total moss cover	–0.107	0.033
Total litter cover	–0.150	–0.128
Total number of species	–0.453	0.027
Management	–0.108	0.083

* Significant at 0.05 level.

Table 2. Comparison of the mean Ellenberg values in two major TWINSPAN groups

	Light	Temperature	Continentality	Moisture	Reaction	Nitrogen
Sesleria caerulea–Bromion sub-group	6.90	5.30	3.90	7.10	6.60	3.80
Sesleria caerulea–Molinion sub-group	7.10	5.20	3.60	6.90	7.10	3.10
Mean of *Sesleria caerulea* group	7.00	5.15	3.75	7.00	6.85	3.45
Standard Deviation	0.14	0.07	0.21	0.14	0.35	0.49
Molinia caerulea sub-group	7.10	5.30	3.90	7.50	6.60	3.30
Carex hostiana sub-group	7.10	5.10	3.40	7.80	6.10	3.70
Mean of *Molinia caerulea* group	7.10	5.20	3.65	7.65	6.35	3.50
Standard deviation	0	0.14	0.35	0.21	0.35	0.28
t-value	1.00	0.44	0.34	–3.60	1.40	–0.12
p-value*	0.42	0.69	0.76	0.07	0.29	0.91

* Significant at 0.05 level.

Table 3. Species richness at abandoned and mown sites

	Sesleria caerulea–Bromion sub-group $n = 25$	*Sesleria caerulea–Molinion* sub-group $n = 103$	*Molinia caerulea* sub-group $n = 38$	*Carex hostiana* sub-group $n = 15$
Mean number of species per relevé	21.6 ($n = 25$)	16.7 ($n = 103$)	12 ($n = 38$)	12.7 ($n = 15$)
Total number of species per relevé at abandoned sites	25 ($n = 12$)	16 ($n = 74$)	12 ($n = 17$)	13 ($n = 2$)
Total number of species per relevé at mown sites	20 ($n = 13$)	18 ($n = 29$)	12 ($n = 21$)	13 ($n = 13$)

n, number of samples.

Sesleria caerulea group

Most commonly, *S. caerulea* communities occurred on shallow mineral soils, less frequently on peaty soils, rarely on rendzina soils with gravelly dolomite admixture. Xerophytic to mesophytic communities belonging to the *S. caerulea* group were the richest in species. The total number of species per relevé varied from 7 in abandoned, considerably overgrown sites to 37 in managed sites per 4 m^2. The vegetation was differentiated into two layers; the sward was typically dense and medium low. The moss layer was absent or its cover was very small.

The *S. caerulea* group was rather variable in species composition and ecological conditions, and contained character species of several vegetation classes and lower syntaxonomical units. The group was largely formed by mesophytic grassland species belonging to the class *Molinio–Arrhenatheretea* R. Tx. 1937, order *Arrhenatheretalia* R. Tx. 1937, less frequently accompanied by character species of the orders *Calthion palustris* R. Tx. 1937 and *Deschampsion cespitosae* Horvatič 1930. The group was dominated by species of mesophytic to hygrophytic grassland communities of the alliance *Molinietalia caerulaea* Koch 1926 and xerophytic to mesophytic continental calcareous grassland species of the class *Festuco–Brometea*, rarely accompanied by species of forest edge communities of *Trifolio–Geranietea* T. Müller 1961 (Appendix).

Syntaxonomy of Sesleria caerulea *grasslands*

The *S. caerulea* group belongs to the alliances *Bromion* (*Festuco–Brometea*) and *Molinion* (*Molinio–Arrhenatheretea*). The affiliation to lower syntaxonomical units is disputable, since they contain character species of both vegetation classes and associated lower syntaxonomical units (orders, alliances). Affiliation to *Festuco–Brometea* or *Molinio–Arrhenatheretea* was based on presence/absence of the character species in the TWINSPAN division. The communities were named after two dominant differential species.

The proposed syntaxonomy of the *S. caerulea* group is as follows:

Class *Festuco–Brometea* Br.-Bl. et Tüxen ex Soó 1947
- Order *Brometalia erecti* Br.-Bl. 1936
  - Alliance *Bromion erecti* Koch 1926
    - *Sesleria caerulea–Primula veris* community (25 relevés, = TWINSPAN *Sesleria caerulea–Bromion* sub-group)

Class *Molinio–Arrhenatheretea* R. Tx. 1937
- Order *Molietalia* Koch 1926
  - Alliance *Eu-Molinion* Koch em. Passarge 1964
    - *Sesleria caerulea–Inula salicina* community (103 relevés, = TWINSPAN *Sesleria caerulea–Molinion* sub-group)

The *S. caerulea–P. veris* community (*Bromion*) differs from the moister *S. Caerulea–I. salicina* community (*Molinion*) in including several xerophytes and mesoxerophytes, e.g., *Primula veris*, *Polygala comosa*, *Carlina vulgaris*, *Agrimonia eupatoria*. The moister *S. caerulea–I. salicina* community (*Molinion*) has a high frequency of *Succisa pratensis*, *Galium boreale*, *Inula salicina*, and *Geum rivale*, which are absent or very rare in the *S. Caerulea–P. veris* community.

Both *S. caerulea* communities are variable due to microhabitat conditions. Patches with *S. caerulea* as a co-dominant species along with *Carex flacca* and/or *C. hostiana* and other character species of *Molinion* were found. In such cases, along with natural succession the role of *Molinia caerulea* increases. In sites with well-pronounced dominance of *S. caerulea* and a small number of accompanying species the species composition can be perhaps explained by overgrowing and impoverishment of the vegetation structure and species composition.

A polydominant mesophytic community with *S. caerulea* as a co-dominant or frequent accompanying species of the alliance *Calthion* or absence of *S. caerulea* were found in moister sites. Along with natural succession, in moister depressions the role of *Filipendula ulmaria* increased, on drier elevations *Festuca arundinacea* could prevail. Rarely the cover of *Deschampsia cespitosa* increased at abandoned sites. In drier conditions *S. caerulea* was a co-dominant species along with mesophytic grass species of *Arrhenateretalia*, e.g., *Helictotrichon pubescens*, *Festuca pratensis*, *Briza media*. Constant accompanying species of *Molinion* and *Festuco–Brometea* formed a small proportion in the community. On dry forest edges and partly overgrown grasslands the community was usually polydominant with *S. caerulea* as an accompanying species or *S. caerulea* was absent. Several character species of *Trifolio–Geranietea* were present.

Both communities in the *S. caerulea* group in KNP were somewhat similar to the *Filipendula vulgaris–Helictotrichon pratense* association and its *caricetum flaccae* sub-association described by Rūsiņa (2007). The typical sub-association of *Filipendula vulgaris–Helictotrichon pratense* was not present in the study area, and the typical character species *Helictotrichon pratense*, *Filipendula vulgaris*, and *Fragaria viridis* were very rare. The ecological conditions of the *S. caerulea* community in KNP and the communities of the *Filipendula vulgaris–Helictotrichon pratense* association described by Rūsiņa (2007) mostly in West and Central Latvia were rather similar except for moisture, which was notably lower in the communities described by Rūsiņa (2007). The communities described by Rūsiņa (2007) are drier and contain more species of *Festuco–Brometea*, while *S. caerulea* grasslands in KNP were richer in species of *Molinion*; besides, most of the typical *Filipendula vulgaris–Helictotrichon pratense* grasslands are located on slopes of river valleys on drier, well-drained soils than those in the lowland with often poorly drained soils in KNP.

Using the dominant species method, Sabardina (1957) separated 16 semi-natural grassland associations with *S. caerulea* in Latvia occurring in various moisture conditions varying from wet fens and fen-like grasslands to extremely dry soils (Dítě et al., 2007; Rūsiņa, 2007) and thus proving the high tolerance of *S. caerulea* for different levels of moisture in soils. Although *S. caerulea* is an excellent indicator of carbonates in soil, its high tolerance for moisture conditions does not allow its use as a differentiating species in classification of plant communities.

Central European dry calcareous grassland associations of *Festuco–Brometea* are found mainly on dry rendzina soils and are basically formed of continental and sub-continental species (Chytrý et al., 2007; Škodová, 2007; Molnár et al., 2008), from which many are absent in Latvia. The *S. caerulea* communities in KNP resemble more alvar grasslands of Estonia and Swedish islands (Pärtel et al., 1999; Rosén, 2006); however, the communities in KNP differ in having deeper soils, less extreme climate conditions, lower species richness, lack of endemic species, and different land use history.

In KNP, the moistest types of grassland communities of the *S. caerulea* group are somewhat similar to those of Central European calcareous fens with *S. caerulea* as a dominant species belonging to the association *Seslerietum uliginosae* Klika 1934 (class *Scheuchzerio–Carietea nigrae* (Nordh. 1937) R. Tx. 1937, order *Caricetalia davalliana* Br.-Bl. 1949, alliance *Caricion davallianae* Klika 1934). However, a peculiarity of fen communities is moister soils and perhaps also different bedrock, while the described *S. caerulea* communities in KNP occur on dry to moderately moist soils, rarely on soils with fluctuating water tables, and therefore are accompanied by mesophytes.

Xerophytic grasslands with *S. caerulea* as a dominant or co-dominant species with a large proportion of sub-continental xerophytic or mesoxerophytic species were rare in KNP and occurred only as small patches. Their distribution pattern was largely defined by varying small-scale micro-relief conditions, while communities where species of the comparatively moister *Molinion* species prevailed were more widespread.

The *S. caerulea* communities with dry forest edge species of *Trifolio–Geranietea* covered small patches in dry, sunny sites along the forest–grassland edges and often contained several forest edge species such as *Agrimonia eupatoria*, *Trifolium medium*, *Origanum vulgare*, *Melampyrum nemorosum*, *Solidago virgaurea*.

Management of Sesleria caerulea *grasslands*

Currently management measures are applied to a small part of the *S. caerulea* grasslands. The majority of these localities are found in the surroundings of villages, which were formerly regularly used both as hay meadows and pastures. Some of the *S. caerulea* grasslands occur in distant areas surrounded by forests and were used as hay meadows in the past, perhaps half a century ago. Over the last 50 years, the degree of isolation of the forest meadows has significantly increased. In the period of the survey (2007–2009) mowing was applied in three meadows only, while the last pasture was abandoned around 2000. As suggested by the known history of the grassland management in KNP, regular grass cutting with removal of litter, preferably once a year or once every two years, has to be assured to maintain the grasslands rich in species. Mixed cutting–moderate grazing management is acceptable.

Effects of abandonment in Sesleria caerulea *grasslands*

The species composition and community structure in both *S. caerulea* communities were in many cases associated with management history and intensity over the last decades. As a result of succession, the vegetation structure became poorer: a well-pronounced vegetation layer consisting of expansive grasses and herbs developed, while the lower layer with low dicotyledons was poorly represented and the species richness had significantly decreased. The low, light-demanding species vanished as they became suppressed by the tall grasses and herbs. The maximum species richness per 4 m^2 was 37 species, while in later successional stages in abandoned grasslands the number of species per plot reached only 7 or even fewer species per 4 m^2, although the species-poorest grasslands not containing any character species were not classified under any groups of calcareous grassland vegetation and therefore were not included in the analysis. Contrary to the observed effects of abandonment in field, in the described plots the species richness at abandoned and mown sites did not differ significantly. In the *Sesleria caerulea–Primula veris* community the species richness was even higher at the abandoned sites than at the mown sites (Table 3).

In both *S. caerulea* communities some expansive species, e.g., *Calamagrostis epigeios*, *Festuca arundinacea*, *Brachypodium pinnatum*, and *Inula salicina* appeared to be good indicators of abandonment. In dry forest edges some species of *Trifolio–Geranietea* indicated natural transformation towards forest communities, e.g., *Trifolium medium* and *Agrimonia eupatoria* were often accompanied by *C. epigeios* and thus outcompeting the low, light-demanding species. While in drier sites the transformation was well represented by the expansion of *C. epigeios*, *I. salicina*, and *F. arundinacea*, in moister locations some *Calthion* and *Deschampsion* species might occur, e.g., *Filipendula ulmaria*, *Deschampsia cespitosa*, *Geum rivale*, and *Phragmites australis*.

In West and Central Europe, and also in Estonian and Swedish calcareous dry grasslands, expansion of *Brachypodium pinnatum* due to abandonment is reported (e.g., Bobbink & Willems, 1993; Hurst & John, 1999; Butaye et al., 2005), indicating a successional phase between open grassland and forest stage (Rūsiņa, 2007). In the study area the dominance of *B. pinnatum* was just fragmentary in small patches at abandoned forest–grassland edges. In Central and West Europe expansion of *B. pinnatum* is associated not only with abandonment, but also with large airborne deposits of nitrogen (Hurst & John, 1999), which is not a priority cause in Latvia.

As suggested by the results of many grassland restoration trials in European calcareous grasslands (Willems & Bik, 1998; Von Blanchenhagen & Poschlod, 2005), if appropriate preconditions such as rich soil seed bank, propagule sources in the vicinity, and suitable soil conditions exist, grassland restoration might be successful. Re-establishment of mowing in calcareous grasslands has given promising results also in KNP, although the current management, mowing and mulching the cut grass, does not exactly imitate the traditionally practised haymaking with biomass removal. Mulching does not decrease nutrients in soil and litter, therefore it is not sustainable in the management and restoration of semi-natural grassland communities (Rūsiņa, 2008).

The overgrowing of *S. caerulea* grasslands leads to the pre-forest phase with an expansion of several tree and shrub species, most commonly *Frangula alnus*, *Betula pubescens*, and *B. pendula*, various *Salix* species, and on drier sites *Pinus sylvestris*. On moister sites, *Lonicera caerulea* subsp. *pallasii* is rarely present as a co-dominant species. Seldom expansion of *Juniperus communis* was observed on drier sites, where they sometimes formed *J. communis*-dominated shrublands, although they covered small areas. Some of the dry calcareous *S. caerulea* grasslands were afforested with *Picea abies* in the 1970s, currently forming dense stands with very sparse or without any vegetation cover.

Some abandoned forest hay meadows were still very rich in indicator species and contained many rare species. Mowing ceased at least 50 years ago, yet grasslands still existed as open patches with high species richness. Similar results were obtained by Rēriha & Rūsiņa (2009) in Slītere National Park in North-West Latvia, who found up to 50 species per 1 m^2 in a partly overgrown calcareous grassland massif. Although the species richness in forest hay meadows in KNP was comparatively lower (up to 37 species per 4 m^2), in both cases probably wild large herbivores play an important role in maintaining the open patches.

Reference to EU-level protected habitats of Sesleria caerulea *grasslands*

The majority of the studied grasslands were classified as habitat 6410 *Molinia* meadows on calcareous, peaty or clayey-silt-laden soils (European Commission, 2007). The driest calcareous grasslands with the highest proportion of *Festuco–Brometea* species were classified as 6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates.

Molinia caerulea group

Molinia caerulea grasslands lie on shallow peat soils formed on low-permeable dolomite bedrock. The soils are seasonally flooded, while in summers they might dry out. The local moisture conditions depend also on the micro-relief. These grasslands were rarer in the study area but less fragmented than *Sesleria caerulea* communities. Compared to the *S. caerulea* group, *M. caerulea* grasslands were comparatively species-poorer and less variable (Table 3, Appendix).

In the *M. caerulea* sub-group the number of species per 4 m^2 varied from 6 to 25. The vegetation was usually structured in one or two layers, sometimes with different flowering periods, e.g., *Viola uliginosa* formed the flowering cover in late spring, while the majority of taller plants bloomed in late summer, creating shade and thus not allowing full development of lower herbs.

The *Carex hostiana* community was separated as a sub-group differing in ecological conditions and consequently also in species composition (Appendix). This sub-group was peculiar with relatively low species richness (9 to 19 species per 4 m^2 plot). The vegetation structure was similar to the *M. caerulea* sub-group. Calcareous grassland communities with *C. hostiana* as a dominant or co-dominant species were rarely found also on mesic carbonate-rich soils or soils with a fluctuating water table, although in such cases mesophytic to hygrophytic species of *Calthion* were not present or were rare.

According to mean Ellenberg values, the soils under the *C. hostiana* sub-group were slightly more acidic and moister than those of the *M. caerulea* sub-group (Table 2). Probably the dominance of *C. hostiana* is promoted by a higher water table and/or differences in management regimes, respectively, the succession stage (Rūsiņa & Kabucis, 2010).

Syntaxonomy of Molinia caerulea *grasslands*

The *M. caerulea* group belongs to the class *Molinio–Arrhenatheretea*, order *Molinietalia*, alliance *Molinion*. This alliance is commonly divided into two groups (Mucina et al., 1993). The *Molinia caerulea* sub-goup belongs to *Eu-Molinion* Koch em. Passarge 1964, the association *Molinietum caeruleae* Koch 1926. The species-poorer *C. hostiana* sub-group in moister and slightly more acidic soils coincides with the higher syntaxonomical unit at the alliance level *Junco-Molinion* Korneck ex Passarge 1964.

The proposed syntaxonomy of the *M. caerulea* group is as follows:

Class *Molinio–Arrhenatheretea* R. Tx. 1937
- Order *Molietalia* Koch 1926
  - Alliance *Eu-Molinion* Koch em. Passarge 1964
    - Association *Molinietum caeruleae* Koch 1926 (38 relevés, = TWINSPAN *Molinia caerulea* sub-group)
  - Alliance *Junco-Molinion* Korneck ex Passarge 1964
    - *Carex hostiana* community (15 relevés, = TWINSPAN *Carex hostiana* sub-group)

In *Molinietum caeruleae* in KNP some *Festuco–Brometea* species were present, while they were absent in the moister *Carex hostiana* community. Typical species in *Molinietum caeruleae*, *Galium boreale* and *Inula salicina*, were absent or very rare in the *Carex hostiana* community.

In both communities the ecological conditions were often similar to those of fens on shallow peat soils; sometimes transitional moist to wet grassland–fen communities could be found. Both in the *M. caerulea* and *S. caerulea* communities species of alkaline fens belonging to the class *Scheuchzerio–Carietea nigrae*, order *Caricetalia davalliana*, alliance *Caricion davallianae*, e.g., *Eriophorum latifolium*, *Primula farinosa*, *Carex flava*, *Schoenus ferrugineus*, and *Epipactis palustris* were rather frequent. Also *S. caerulea*, a co-dominant or an accompanying species, was rather frequent as it is tolerant of various moisture conditions.

Additionally, some species of other classes or lower syntaxonomical units of fen communities (e.g., *Caricion lasiocarpae* Van den Berghen ap. Lebrun et al. 1949 and *Magnocaricion elatae* Koch 1926) were present. As a regional peculiarity, high frequency of species typical for West and West-coastal Latvia – *Viola uliginosa* and *Myrica gale* – should be mentioned. Some of the frequent species such as *Carex hostiana*, *C. flacca*, *Ononis arvensis*, and *Cirsium acaule* are rather frequent in West Latvia, but rare or absent in other regions of the country (Fatare, 1992).

Management of Molinia caerulea *grasslands*

Formerly, *M. caerulea* grasslands were commonly utilized as hay meadows, pastures, or mixed mowing–late summer grazing management was applied. Only a few *M. caerulea* grasslands have been managed in recent years by mulching. In order to maintain the *M. caerulea* grasslands open and species-rich, preferably cutting once a year or once every two years with hay removal or mixed cutting–moderate grazing should be applied.

Effects of abandonment of Molinia caerulea *grasslands*

No significant differences were found in the species richness at mown and abandoned sites (Table 3). Due to overgrowing the dominance of *M. caerulea* increases, therefore it is a good indicator of transformation processes affecting the vegetation structure. Along with natural succession of the community the nutrients are being accumulated in the root system allowing *M. caerulea* becoming a dominant species (Mucina et al., 1993). Such grasslands are characteristic with low species richness and hummocky micro-relief.

In some cases, *Carex buxbaumii* expands in abandoned grasslands, although this species is rare in Latvia, including the study area. In moister sites *Carex lasiocarpa* and *C. elata* increase accompanied by the expansion of *Phragmites australis*. Hydrological changes sometimes result in a spread of the *Calamagrostis canescens* cover, indicating paludification. In a *Carex hostiana* community, the cover of some tall herbs such as *Eupatorium cannabium* and *Senecio paludosus* may increase.

In KNP abandonment has led to an expansion of *Myrica gale* shrublands, which syntaxonomically belong to the *Myricetum gale* Jonas 1932 association. The *M. gale* shrublands are a successional pre-forest stage, followed by a proliferation of higher woody species, e.g., *Frangula alnus*, *Salix aurita*, *S. cinerea*, *Betula pubescens*, *Alnus glutinosa*, and *Lonicera caerulea* subsp. *pallasii*. The last species is typical for coastal areas only.

Abandonment and perhaps also the currently practised mulching lead to accumulation of litter, thus diminishing germination of light-demanding species and increasing the fire hazard. Fires increase the aboveground biomass, seed production, and germinability of *M. caerulea* (Brys et al., 2005), promoting its dominance. Irregular grass burning at the end of the 20th century and at the beginning of the 21st century has affected few *M. caerulea* grasslands in KNP, although the possible effects are controversial and cannot be unambiguously judged as negative. The effects of burning at a community level are not documented; however, it has evidently maintained the open landscape without dense shrublands, while as negative effects increased dominance of *M. caerulea* and formation of hummocks should be mentioned. Since the burned areas are frequently inundated in spring floods, the dead litter does not form a thick layer.

Irregular cutting of *M. gale* shrubs does not significantly change the community structure and composition, since the shrubs are able to regenerate in a few years, while cutting may significantly decrease the dominance of shrubs and offsprings of *Salix* and *Betula* spp.

Reference to EU-level protected habitats of the Molinia caerulea *group*

All grasslands belonging to the *M. caerulea* group are classified as habitat 6410 *Molinia* meadows on calcareous, peaty, or clayey-silt-laden soils (European Commission, 2007).

Representativity of the results on a national scale

The results should not be generalized as representing the whole territory of Latvia, although the species composition and vegetation structure can be extrapolated to grasslands in similar environmental conditions in most of the Coastal Lowland and West Latvia. The species composition of calcareous grasslands in Latvia varies also due to an uneven regional distribution of quite numerous character species; for example, many of them are common in West Latvia, but absent or very rare in Central and East Latvia. Nevertheless, the main natural transformation processes are similar throughout the country and the whole region reflects the tendencies of changes in biodiversity closely related to altering lifestyles of inhabitants and agricultural practices.

Conservation aspects

According to Rūsiņa (2010), dry calcareous grassland habitats (EU code 6210) cover about 0.02% of the territory of Latvia, while *Molinia* grasslands (EU code 6410) cover 0.015% of the country (Rūsiņa & Kabucis, 2010). The estimated numbers illustrate the low frequency and bad conservation status of both these habitat types in Latvia. These grassland communities and relevant ecological conditions are rarely and fragmentarily found throughout Latvia. The distribution pattern largely coincides with river valleys and the Coastal Lowland (Rūsiņa, 2010). In KNP dry calcareous grassland communities are very rare, while more mesophytic calcareous contact communities of *Molinion* and *Bromion* are more widely distributed. According to a rough estimate, *Molinion* grasslands in KNP make up about 12% of the total cover of this habitat in Latvia.

Calcareous grasslands in KNP contain many Red List species. Along with the declining cover of calcareous grasslands and fens, the distribution of *Sesleria caerulea* is shrinking (Medene, 2009; Rēriha & Rūsiņa, 2009). In KNP some species associated to calcareous grasslands are present also in some derivate communities on roadsides on carbonate-rich substrates. Although not representing the community structure of semi-natural grasslands, they are important regarding the species migration and connectivity of habitats, particularly in a situation when semi-natural grasslands are becoming more and more isolated (Adriaens et al., 2006).

In KNP in some cases grassland habitats can naturally transform into other threatened and rare vegetation types; for example, *Molinia caerulea* communities transform into *Myrica gale* shrubland. However, considering the rapid decline of semi-natural grasslands, conservation of those threatened communities should be considered as priority instead of preserving a pre-forest shrubland successional phase.

According to analysis of historical maps from the early and mid-20th century, a considerable proportion of today's semi-natural grasslands in KNP with high species richness were previously utilized as temporary arable lands (Priede, 2009). In species- and community-rich regions with good connectivity of semi-natural grasslands plowing of grasslands and temporary use as arable lands without significant changes in the soil nutrient level need not significantly decrease the regional species pool. Therefore fragmentary plowing can be accepted as appropriate land use if the soils are not intensively fertilized or ameliorated.

Studies by Kalamees & Zobel (1998) in Estonian semi-natural grasslands show that a relatively rich soil seed bank may persist several decades after abandonment or afforestation allowing successful grassland restoration. Similar conclusions can be derived from studies by Blanckenhagen & Poschlod (2005) in Belgium. However, Kalamees & Zobel (1997) found that the number of species and seeds in the seed bank significantly decline from managed grasslands to closed overgrown community. Similarly, a study by Rosén (2006) in Swedish alvars shows that the soil seed bank in abandoned overgrown calcareous grasslands is significantly reduced and contains widespread grassland species, while the specialist species have vanished. The richness of the soil seed bank does not always play a crucial role in conditions with a high degree of habitat isolation. Grassland connectivity and presence of species-rich grasslands in the neighbourhood are equally important in the restoration of heavily overgrown grasslands. The possibility of restoration, taking into account the above-mentioned preconditions, is still high in KNP. Species richness and its preservation in calcareous grasslands are related to regular management (e.g. Aavik et al., 2008), therefore continuous management, preferably mowing with hay removal or mixed mowing–moderate grazing regimes should be applied in order to keep the semi-natural calcareous grasslands species-rich and diverse.

APPENDIX

SYNOPTIC TABLE (NUMBER OF SPECIES OCCURRENCES PER GROUP)

	Sesleria caerulea–Primula veris community (*Bromion*)	*Sesleria caerulea–Inula salicina* community (*Molinion*)	*Molinietum caeruleae* community (*Molinion*)	*Carex hostiana* community (*Molinion*)
Number of relevés	25	103	38	15
Mean number of species per relevé	21.6	16.7	12	12.7
Total number of species	50	92	66	33
Class Molinio–Arrhenatheretea				
Achillea millefolium	76	45	5	·
Centaurea jacea	52	60	5	·
Dactylis glomerata	52	23	·	·
Festuca pratensis	16	24	5	20
Lathyrus pratensis	28	49	11	13
Phleum pratense	12	8	·	·
Plantago lanceolata	56	14	·	·
Poa pratensis	36	31	·	·
Prunella vulgaris	4	13	·	·
Ranunculus acris	8	33	8	20
Trifolium pratense	28	12	3	·
Vicia cracca	56	63	16	·
Order Arrhenatheretalia				
Anthoxanthum odoratum	4	11	·	·
Galium album	52	45	3	·
Heracleum sibiricum	12	4	·	·
Leucanthemum vulgare	12	9	3	·
Lotus corniculatus	16	7	5	·
Order Molinietalia				
Angelica sylvestris	·	9	16	13
Cirsium oleraceum	·	5	·	20
Cirsium palustre	·	7	16	53
Deschampsia cespitosa	·	10	·	60
Equisetum palustre	·	8	24	67

APPENDIX. *Continued*

	Sesleria caerulea–Primula veris community (*Bromion*)	*Sesleria caerulea–Inula salicina* community (*Molinion*)	*Molinietum caeruleae* community (*Molinion*)	*Carex hostiana* community (*Molinion*)
Filipendula ulmaria	·	26	68	73
Galium uliginosum	·	2	32	53
Lathyrus palustris	·	9	39	·
Selinum carvifolia	4	28	16	13
Valeriana officinalis	·	7	11	27
Alliance Molinion				
Carex flacca	76	80	50	·
Carex panicea	8	35	29	80
Galium boreale	24	69	37	7
Inula salicina	24	56	32	·
Molinia caerulea	·	18	100	7
Potentilla erecta	8	66	76	80
Sesleria caerulea	48	87	58	73
Succisa pratensis	·	35	42	33
Alliance Calthion				
Caltha palustris	·	·	·	53
Geum rivale	4	47	3	33
Lysimachia vulgaris	·	4	26	47
Alliance Arrhenatherion				
Helictotrichon pubescens	52	38	·	·
Alliance Cynosurion				
Briza media	92	54	13	27
Festuca rubra	68	23	·	·
Class Scheuchzerio–Caricetum nigrae				
Order Caricetala nigrae				
Carex lasiocarpa	·	·	13	·
Carex nigra	·	1	·	40
Comarum palustre	·	·	13	13
Primula farinosa	·	5	·	·
Alliance Caricion davallianae				
Carex hostiana	·	16	·	67
Epipactis palustris	8	19	13	13
Class Festuco–Brometea				
Anthylis vulneraria s.l.	36	1	3	·
Centaurea scabiosa	60	2	·	·
Campanula glomerata	12	11	3	·
Carlina vulgaris	32	5	3	·
Poygala comosa	45	7	3	·
Order Bromion erecti				
Carex ornithopoda	8	9	·	·
Cirsium acaule	16	9	3	·
Gymnadenia conopsea	8	8	5	·
Leontodon hispidus	40	11	·	·
Linum catharticum	24	5	3	·
Ononis arvensis	68	28	5	·

APPENDIX. *Continued*

	Sesleria caerulea–Primula veris community (*Bromion*)	*Sesleria caerulea–Inula salicina* community (*Molinion*)	*Molinietum caeruleae* community (*Molinion*)	*Carex hostiana* community (*Molinion*)
Ophioglossum vulgatum	16	22	3	·
Pimpinella saxifraga	80	31	8	·
Plantago media	44	12	·	·
Primula veris	84	15	3	·
Trifolium montanum	32	8	3	·
Class Trifolio–Geranietea				
Agrimonia eupatoria	52	4	·	·
Origanum vulgare	16	1	·	·
Solidago virgaurea	36	·	·	·
Trifolium medium	16	1	·	·
Class Phragmito–Magnocaricetea				
Lythrum salicaria	·	1	34	·
Phragmites australis	·	3	8	·
Alliance Magnocaricion elatae				
Carex buxbaumii	·	·	11	·
Peucedanum palustre	·	·	39	·
Other species				
Aegopodium podagraria	·	5	·	·
Alchemilla vulgaris s.l.	24	27	·	·
Betula pubescens	·	7	5	·
Calamagrostis epigeios	56	46	8	
Campanula rapunculoides	20	3	·	·
Carex flava	·	·	3	·
Carex hirta	·	5	·	·
Equisetum pratense	8	17	3	7
Eupatorium cannabium	·	·	5	33
Festuca arundinacea	52	35	·	·
Festuca ovina	4	5	3	·
Frangula alnus	·	4	11	·
Hepatica nobilis	4	4	·	·
Knautia arvensis	44	6	·	·
Listera ovata	·	12	3	·
Luzula multiflora	16	12	3	13
Medicago lupulina	32	12	·	·
Melampyrum nemorosum	36	12	3	
Myrica gale	·	·	24	·
Pinus sylvestris	·	5	3	·
Potentilla anserina	4	8	3	20
Ranunculus auricomus	·	13	3	13
Ranunculus polyanthemos	24	10	·	·
Rumex acetosa	12	15	·	7
Salix aurita	·	4	13	·
Scorzonera humilis	·	5	3	·
Veronica chamaedrys	32	25	·	·
Viola uliginosa	·	3	37	·

Rare species (with less than 2 occurrences per TWINSPAN group). Abbreviations used: SB – *Sesleria caerulea–Primula veris* community; SM – *Sesleria caerulea–Inula salicina* community; CM – *Carex hostiana* community; MM – *Molinietum caeruleae* community.

Agrostis stonolifera (MM), *Agrostis tenuis* (SM, MM), *Alnus incana* (SM), *Arrhenatherum elatius* (SM), *Artemisia campestris* (SB), *Astragalus glycyphyllos* (SB), *Bella perennis* (SM), *Brachypodium pinnatum* (SB), *Calamagrostis arundinacea* (MM), *Calamagrostis canescens* (MM), *Carex capillaris* (SB, CM), *Carex caryophyllea* (SB), *Carex diandra* (MM), *Carex elata* (MM), *Carex lepidocarpa* (CM, MM), *Carex pallescens* (SM), *Carex sylvatica* (MM), *Carex vesicaria* (MM), *Carum carvi* (SB), *Cerastium holosteoides* (SB, SM), *Cirsium arvense* (SB), *Clinopodium vulgare* (MM), *Convallaria majalis* (CM), *Convolvulus arvensis* (MM), *Dactylorhiza baltica* (SM), *Dactylorhiza fuchsii* (CM), *Dactylorhiza incarnata* (SM, CM, MM), *Dactylorhiza maculata* (CM), *Daucus carota* (SB), *Elytrigia repens* (SB), *Equisetum variegatum* (MM), *Eriophorum latifolium* (CM, MM), *Fragaria vesca* (SB), *Galium palustre* (SM, MM), *Geranium palustre* (SM, MM), *Geranium pratense* (SM), *Glechoma hederacea* (SM), *Hieracium* sp. (SM), *Hierochloe odorata* (MM), *Holcus lanatus* (SM), *Hypericum perforatum* (SB, SM), *Juncus articulatus* (CM, MM), *Leontodon autumnalis* (SM, CM), *Luzula campestris* (SM), *Lychnis flos-cuculi* (SM), *Lycopus europaeus* (MM), *Lysimachia nummularia* (SM, MM), *Melica nutans* (SM), *Melilotus officinalis* (SB), *Mentha aquatica* (CM, MM), *Orchis mascula* (MM), *Parnassia palustris* (CM, MM), *Picea abies* (SM), *Pilosella officinarum* (SB, SM), *Poa compressa* (SM), *Poa palustre* (MM), *Polemonium caeruleum* (SM), *Populus tremula* (SM), *Potentilla reptans* (SB), *Quercus robur* (SM), *Ranunculus repens* (SM), *Rhamnus cathartica* (SB), *Rubus caesius* (SB, SM), *Rubus saxatilis* (SM, CM), *Salix purpurea* (SM), *Schoenus ferrigineus* (MM), *Scutellaria galericulata* (SM, CM), *Senecio paludosus* (MM), *Sieglingia decumbens* (SM, CM), *Taraxacum officinale* (SB, SM), *Thalictrum aquilegifolium* (SM), *Thalictrum flavum* (SM, MM), *Thalictrum lucidum* (MM), *Thelypteris palustris* (MM), *Thymus ovatus* (SB, SM), *Thymus serphyllum* (SM), *Tragopogon pratensis* (SB), *Trifolium repens* (SB, SM), *Triglochin palustris* (MM), *Trollius europaeus* (SM), *Tussilago farfara* (SB, SM), *Veronica longifolia* (MM), *Veronica officinalis* (SM), *Vicia sepium* (SM), *Vicia tetrasperma* (SB, SM), *Viola mirabilis* (SM).

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Lubjarikaste rohumaade fütosotsioloogia ja dünaamika Ķemeri rahvuspargis (Läti)

Agnese Priede

Uuriti Ķemeri rahvuspargi lubjarikaste niitude ökoloogiat, fütosotsioloogiat, regionaalseid iseärasusi ja majandamismõjusid. Andmestiku moodustasid 181 prooviala. TWINSPAN jaotas need Ellenbergi väärtarvude alusel assotsiatsiooni tasandil nelja suuremasse gruppi: *Sesleria caerulea–Primula veris*'e kooslus, *Sesleria caerulea–Inula salicina* kooslus, *Molinietum caeruleae* ja *Carex hostiana* kooslus. Keskkonnatingimusi analüüsiti Ellenbergi väärtarvude alusel ordinatsioonimeetodeid kasutades. Varieeruvus liigilises koosseisus oli tingitud põhiliselt niiskustingimustest. See oli ainuke faktor, mis usaldusväärselt erines eri fütosotsioloogiliste gruppide vahel. Viimaste aegade majandamine pole otseselt tänast liigirikkust ja taimkatte struktuuri koosluse tasandil mõjutanud. Käsitlemist leiavad ka erinevad aspektid rohumaade dünaamikast ja kaitsest.