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# Sub-montane semi-natural grassland communities in the Eastern Carpathians (Ukraine)

# Submontane Graslandgesellschaften in den Ost-Karpaten (Ukraine)

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**Abstract**

We performed a survey of grassland communities in the Ukrainian Carpathians with the aim of: (1) syntaxonomically classifying the meso- and subxerophilous grassland vegetation; (2) analysing the main gradients in their species composition; (3) estimating the effect of selected environmental factors on grassland species composition; (4) assessing the species richness of vascular plants and bryophytes in relation to the measured environmental variables. We collected 46 phytosociological relevés during the growing seasons of 2010 and 2011. Species composition and species richness were studied at two spatial scales (1 m² and 16 m²) in relation to soil parameters (soil depth, pH (KCl), content of P, K, Mg, N and C), management regime (mowing, grazing, ploughing in the past and burning), and other factors (altitude, litter cover, open soil, inclination, solar radiation and animal excrement). Seven grassland types were distinguished belonging to 3 classes and 4 alliances, namely the *Nardetea strictae* including the *Violion caninae* (mesic pastures at altitudes of 400–600 m mostly on moderate slopes) and the *Nardo strictae-Agrostion tenuis* (grasslands on moderate slopes at altitudes of 700–900 m usually managed by mowing and grazing the aftermath); the *Molinio-Arrhenatheretea*, including the *Arrhenatherion elatioris* (submontane grasslands originated mostly on former fields after their abandonment in the past) and the *Cynosurion cristati* (intensive pastures); and the *Festuco-Brometea* including the *Cirsio-Brachypodion pinnati* (abandoned grasslands dominated by *Brachypodium pinnatum* and *Inula salicina*). Detrended correspondence analysis indicated that the major compositional turnover was related to altitude and soil reaction. A canonical correspondence analysis confirmed that altitude had the strongest effect on species composition in the analysed dataset, followed by management treatments (former ploughing, grazing intensity). For vascular plant species richness, regression tree analysis identified grazing intensity as the most important predictor at the 1 m² scale. At the 16 m² scale, soil

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humus content was evaluated as the most important predictor of vascular plant species richness, followed by litter cover and grazing intensity. The number of bryophytes was not determined by the studied environmental factors at either of the two spatial scales. Although the number of analysed relevés in this study was limited, our results significantly contribute to the understanding of submontane grasslands in the Ukrainian Carpathians.

**Keywords:** environmental factors, *Festuco-Brometea*, grassland, management, *Molinio-Arrhenatheretea*, *Nardetea strictae*, species richness, vegetation classification

**Erweiterte deutsche Zusammenfassung am Ende des Artikels**

## 1. Introduction

The Eastern Carpathians are known for their well preserved traditional landscape structure, maintained by continuing extensive agricultural practices. Farming and grazing first began in this region in the 14–15$^{th}$ centuries, when the Walachians started to migrate from the Southern Carpathians (modern-day Romania) throughout the Eastern Carpathians (Ukraine, Poland) to the Western Carpathians (Slovakia, Moravia) (KRICSFALUSY 2013). The territory of the Ukrainian Carpathians is rich in semi-natural grasslands, which are managed mostly by hand-mowing and grazing. This area still exhibits high biodiversity concentrated in the semi-natural grassland habitats (SOLOVYEVA et al. 2011). The farming system in the Ukrainian Carpathians can be referred to as "high nature value farming", which connects the low intensity traditional farming and the conservation of nature (BEAUFOY 2007, NUPPENAU et al. 2011).

In the socialist period, land in Ukraine was owned and managed mainly by the state (LERMAN et al. 2004). Large plots of arable land and vast pastures were farmed by kolkhoz (collective farms). After the system change in 1990, agricultural land entered into the property of former workers of the former agricultural enterprises (KUEMMERLE et al. 2008). Much arable land was subdivided for subsistence farming, leading to a high level of fragmentation of the formerly extended cultivated areas in some regions (KUEMMERLE et al. 2006). As new owners lacked funds and agricultural machinery, some remote land remained unmanaged. A mosaic of small fields, meadows and fallows of various ages is typical for these landscapes (Fig. 1), which is in contrast with large areas of pastures. The original permanent (never ploughed) meadows are mainly found at higher altitudes.

The semi-natural grasslands of the Ukrainian Carpathians have so far been relatively poorly studied from a phytosociological perspective. Searching the literature, we found several studies dealing with vegetation of national nature parks or nature reserves (SOLOMAKHA et al. 2004, CHORNEY et al. 2005, KLIMUK et al. 2006, DERZHYPILSKY et al. 2011). KUZEMKO (2009) published phytosociological relevés of the *Molinio-Arrhenatheretea* class recorded by O.P. Krys during 1973–1987 in the territory of Zakarpatska, Ivano-Frankivska and Lvivska oblast. Some relevés of plant communities belonging to *Molinio-Arrhenatheretea* class were published by TOKARYUK et al. (2009) from the Bukovinian Pre-Carpathians. ROLEČEK et al. (2014) reported new sites of extremely species-rich semi-dry grasslands (belonging to the *Cirsio-Brachypodion* alliance) at the foothills of the Ukrainian Carpathians in the Southwestern Ukraine. The mountain grassland communities of subalpine and alpine belts at altitudes of 1300–2060 m were studied by MALYNOVSKI & KRICSFALUSY (2002) and KRICSFALUSY (2013). Subalpine tall-grass communities (*Calamagrostietalia villosae*) in the Ukrainian Carpathians were studied by YAKUSHENKO et al. (2012).

**Fig. 1.** A mosaic of small fields, meadows and fallows of various age forms a typical landscape scene. Grasslands near Verkhni Vorota (Photo: J. Smatanová, 08 July 2010).

**Abb. 1.** Das kleinräumige Mosaik aus Äckern, Wiesen und unterschiedlich alten Brachen bildet bei Verkhni Vorota ein typisches Landschaftsbild (Foto: J. Smatanová, 08.07.2010).

During 2010 and 2011, fifty new phytosociological relevés were recorded in meadows and pastures of the Zakarpatska oblast, Ivano-Frankivska oblast and Lvivska oblast with the purpose of distinguishing the main vegetation types and their relation to the management regimes. We used these data to address four aims: (1) to delimit the major plant community types for submontane grasslands and their syntaxonomic classification; (2) to understand the environmental factors that shape community composition; (3) to estimate the effect of selected environmental variables on grassland species composition; (4) to assess the species richness of vascular plants and bryophytes in relation to the measured environmental variables.

## 2. Study area

Sampling was carried out in the following regions of the Ukrainian Carpathians (Fig. 2): Zakarpatska oblast − Mizhhirskyi rayon, Volovetskyi rayon, Khuststkyi rayon, Tyachivskyi rayon and Rakhivskyi rayon; Ivano-Frankovskaja oblast − Dolynskyi rayon; Lvivska oblast Skolivskyi rayon (for details see Supplement E1). The Ukrainian Carpathians were formed during the Tertiary period and their predominant geological bedrock is the Carpathian Flysch composed of layers of alternating sandstone and shale with small areas of limestone and granite. The outer belt of flysch is accompanied by an inner belt of Tertiary volcanoes. All sampling localities are located in the flysch zone (KRUHLOV 2008).

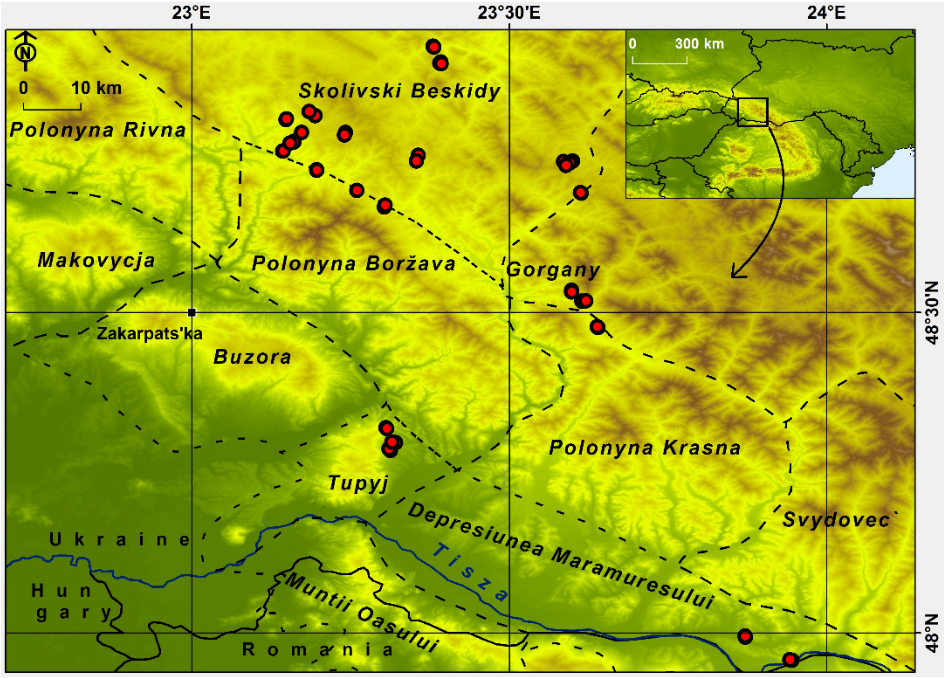



**Fig. 2.** Location of the Ukrainian Carpathians within the Europe and the distribution of relevés (Map: D. Senko).

**Abb. 2.** Lage der Aufnahmeflächen in den ukrainischen Karpaten (Karte: D. Senko).

The climate in the Ukrainian Carpathians is temperate continental. Winters are cool, with an average temperature in January of -5 °C. Summers are warm, with an average temperature in July of 18 °C (KRICSFALUSY 2013). According to the WorldClim model (HIJMANS et al. 2005), the mean annual precipitation in the sampling regions is 800 mm (680–860 mm) and annual mean temperature is 6.7 °C (5.3–9.6 °C). The Ukrainian Carpathians belong to the lower part of the Carpathians with gentle peaks that rise as high as 2061 m (Hoverla). The vegetation relevés were recorded at altitudes between 137 m and 927 m.

## 3. Methods

### 3.1 Vegetation sampling

The phytosociological relevés were recorded in July 2010 and in June 2011 following the Braun-Blanquet method (BRAUN-BLANQUET 1964). A nine-degree cover scale was used (WESTHOFF & VAN DER MAAREL 1973). For sampling, sites with homogenous species composition and environmental conditions were selected. Semi-natural grasslands were sampled in the nested plots of 1 and 16 m² (4 × 4 m) while the 1 m²-plot was situated inside this plot in the lower left corner of the 16 m²-plot. For the smaller plot size, the percentage cover of species was estimated, while the Braun-Blanquet 9-degree scale was used for the larger plot size. Altogether, 46 relevés were recorded.

The percentage cover of herb and moss layers (including lichens) as well as of litter, open soil, excrement and rocks were estimated. The information about management of each relevé was obtained either by visual observation or through an interview with landowners. The soil depth was measured with an iron rod with a diameter of 4 mm, measuring at 10 positions within each plot of 16 m². Three soil samples were taken from the uppermost 10 cm within each plot and pooled for each plot. They were used to estimate the following soil properties: soil pH measured in KCl, content of P, Mg, K, N and C. Soil pH was measured in a soil suspension prepared at a ratio of 1:5 in 1 M KCl using a pH meter with combined glass electrode (ISO 10390). The concentration of P, K and Mg was determined using the FAAS method in the soil extract according to Mehlich III. For determination of organic carbon and total nitrogen the elementary analyzer "Euro EA 3000" was used.

We followed Flora Europaea (TUTIN et al. 1968–1993) for the nomenclature of vascular plants. The nomenclature of mosses follows MARHOLD & HINDÁK (1998). For syntaxa, nomenclature is mainly according to HEGEDÜŠOVÁ VANTAROVÁ & ŠKODOVÁ (2014). For other syntaxa, the full names with authors and year of publication are given.

## 3.2 Data analysis

### 3.2.1 Vegetation classification

The phytosociological relevés were stored in TURBOVEG (HENNEKENS & SCHAMINÉE 2001) and analysed with the software JUICE 7.0.98 (TICHÝ 2002, TICHÝ & HOLT 2006). OptimClass (TICHÝ et al. 2010) determined the optimal classification algorithm, and the Ward method with relative Euclidean distance as a similarity measure and square root transformation of cover values were used for the numerical classification of relevés (using the PC-ORD programme, MCCUNE & MEFFORD 1999). Only relevés of mesic grasslands were used in the hierarchical cluster analysis. Taxa determined only at the level of genus were excluded prior to cluster analysis. We used the function "crispness of classification" proposed by BOTTA-DUKÁT et al. (2005) within the JUICE programme to identify the optimal number of clusters. As the species composition of the recorded relevés was similar to the species composition of Slovak grasslands, we classified collected relevés using the Slovak syntaxonomical system and the expert system for identification of grassland syntaxa in Slovakia was applied to assign individual clusters to the syntaxa (JANIŠOVÁ et al. 2007a, HEGEDÜŠOVÁ VANTAROVÁ & ŠKODOVÁ 2014, see also http://ibot.sav.sk/). Our decision was supported also by the fact that grassland vegetation of the submontane and lower montane zone in the Ukrainian Carpathians has not been systematically studied until now and the local phytosociological studies are very rare. We checked all relevés in the clusters if their composition and assignment by the expert system is in accordance with other relevés in the same cluster. The position of a relevé in the DCA ordination plot was also taken into account in the final syntaxonomical assigment of relevés. Two transitional relevés (no. 31 and no. 41) were shifted to another cluster.

### 3.2.2 Compositional variation

A gradient analysis was carried out in the programme CANOCO 4.5 (TER BRAAK & ŠMILAUER 2002) to display the compositional turnover between the relevés. Four outlier relevés (representing dry and semi-dry grasslands) were excluded from the data set, leaving 46 relevés of mesic grasslands for the detrended correspondence analysis (DCA). As the resulting gradient length of the first ordination axis in the DCA was 3.521, canonical correspondence analaysis (CCA) was chosen as a unimodal method of direct gradient analysis. The cover values were square-root transformed and the rare species were downweighted. For the ecological interpretation of ordination axes, the average non-weighted Ellenberg indicator values (ELLENBERG et al. 1992), altitude, management treatments and measured soil parameters for the relevés were plotted onto the DCA ordination diagram as supplementary environmental variables. There were only few taxa without a determined indicator value (*Campanula serrata*, *Centaurea rhenana*, *Dianthus barbatus*, *Ferulago sylvatica*, *Gentianella lutescens*, *Salix silesiaca*, *Scorzonera purpurea* ssp. *rosea*, *Sisyrinchium montanum*, *Trifolium pannonicum*). The Spearman correlation coefficient was used to calculate the correlation between environmental variables and the first two ordination axes. After multiple correlations, Bonferroni correction was applied to control the familywise error rate setting critical values of $\alpha$ as 0.05/14.

The relationships between species composition and environmental variables were analysed by canonical correspondence analysis. As in the previous analysis, the species cover values were square-root-transformed and the rare species were downweighted. For each relevé, information on soil parameters (pH, contents of P, K, Mg, N and C, soil depth), management regime (mowing, grazing, ploughing in the past and burning), altitude and solar radiation was obtained (Supplements E2, E3). Solar radiation (xericity) was calculated from the slope aspect and inclination according to PARKER (1988) as cosinus of the aspect in degrees minus 202.5º multiplied by the tangent of the slope in degrees). Types of management regime were analysed as categorical variables. Grazing intensity was analysed as a separate variable using the following scale: 1 – grazing of aftermath by 1–2 animals, 2 – extensive grazing, 3 – intensive grazing. Only environmental variables with significant effect on species composition (marginal, conditional or pure) were finally used in the ordination analysis.

The effect of all studied environmental variables was tested using a Monte Carlo permutation test with 9999 unrestricted permutations. Finally, the pure effect of each variable (the percentage variance explained by a variable while the remaining significant variables were used as co-variables) was calculated (TER BRAAK & PRENTICE 1988) and expressed as a percentage of the total inertia. To evaluate the independent (marginal) effect of each individual variable, the variance explained by the given variable while used as the only constraining variable was calculated. The conditional effect represents the additional variance explained by a variable at the time it was included in the forward selection. Differences in soil parameters and altitude among the delimited vegetation types were tested by Kruskal-Wallis ANOVA and multiple comparison tests of the mean ranks by STATISTICA software (StatSoft Inc. 2006). Differences in species richness were compared by ANOVA and post hoc comparison Tukey test.

### 3.2.3 Species richness-environment relationships

Relationships between species richness and 17 environmental variables were assessed using regression trees (BREIMAN et al. 1984), calculated using the STATISTICA software (StatSoft Inc. 2006). Species richness of vascular plants and bryophytes (for details see Supplement E4) were analysed. Optimal tree size was determined by a tenfold cross-validation procedure with a standard error rule set to 0.1. Each decision tree was pruned (prune of variance) after the data were split, with a minimum of 6 cases per branch and a maximum of 1,000 nodes per tree. The importance plots ranking the predictors on a 0–100 scale were used to determine which variable is the most significant predictor. Differences in species richness among the distinguished vegetation types were tested using the analysis of variance and Tukey test in the STATISTICA programme (StatSoft Inc. 2006).

## 4. Results

### 4.1 Vegetation classification and description of the associations

From the 46 recorded relevés, 44 were recorded in mesic meadows and pastures and two in semi-dry grasslands (see Supplement E1 and E2 for information about localities). Relevés from mesic grasslands were numerically classified and a crispness analysis determined the optimal number of clusters to be five. Finally, one relevé was manually set aside as a separate vegetation type different from all other clusters. Within the whole dataset, the following grassland communities were distinguished (unclear assignments are marked by "???"):

Class 1: *Nardetea strictae* Rivas Goday in Rivas Goday et Rivas-Mart. 1963

Order: *Nardetalia strictae* Oberd. ex Preising 1949

Alliance 1.1: *Violion caninae* Schwickerath 1944

Association 1.1.1: *Campanulo rotundifoliae-Dianthetum deltoidis* Balátová-Tuláčková 1980

Alliance 1.2: *Nardo strictae-Agrostion tenuis* Sillinger 1933
Association 1.2.1: *Campanulo abietinae-Nardetum strictae* (Pałczyński 1962) Hadač et al. 1988
??? Association 1.2.2: transitional between *Arrhenatherion elatioris* Luquet 1926 and *Nardo strictae-Agrostion tenuis* Sillinger 1933

Class 2: *Molinio-Arrhenatheretea* R. Tx. 1937
Order: *Arrhenatheretalia* R. Tx. 1931
Alliance 2.1: *Arrhenatherion elatioris* Luquet 1926
Association 2.2.1: *Poo-Trisetetum flavescentis* Knapp ex Oberd. 1957
Alliance 2.2: *Cynosurion cristati* R. Tx. 1947
Association 2.2.2: *Lolio perennis-Cynosuretum cristati* R. Tx. 1937

Class 3: *Festuco-Brometea* Br.-Bl. et R. Tx. ex Soó 1947
Order: *Brometalia erecti* Br.-Bl. 1936
Alliance 3.1: *Cirsio-Brachypodion pinnati* Hadač et Klika ex Klika 1951
??? Association 3.1.1: transitional between *Scabioso ochroleucae-Brachypodietum pinnati* Klika 1933 and *Festuco rupicolae-Nardetum strictae* Dostál 1933 corr. Ujházy et Kliment 2014
Association 3.1.2: *Scabioso ochroleucae-Brachypodietum pinnati* Klika 1933

**Association 1.1.1: *Campanulo rotundifoliae-Dianthetum deltoidis***
**(Supplement S1, relevés 1–17, Fig. 3)**

Characterisation: These grasslands are dominated mainly by *Festuca rubra* or *Nardus stricta*. Other low-growing grasses and sedges are also present: *Agrostis capillaris*, *Anthoxanthum odoratum*, *Carex hirta*, *Carex pilulifera*, *Cynosurus cristatus*, *Danthonia decumbens*. In some plots managed by mowing, dicotyledonous species like *Centaurea jacea*, *Thymus pulegioides* or *Leontodon hispidus* can rich higher coverage values. They include many herbs diagnostic for the *Violion caninae* alliance and *Nardetea strictae* class (*Potentilla erecta*, *Viola canina*, *Veronica officinalis*). Indicators of grazing and trampling (*Trifolium repens*, *Ononis arvensis*, *Cynosurus cristatus*) and several thermophilous species (*Thymus pulegioides*, *Pimpinella saxifraga*, *Galium verum*) are present. Species of mesic grasslands like *Achillea millefolium* agg., *Campanula patula*, *Leucanthemum vulgare* agg., *Leontodon hispidus*, *Lotus corniculatus*, *Plantago lanceolata*, *Prunella vulgaris*, *Ranunculus acris*, *Trifolium pratense* reach high constancy values. There are on average 45 vascular species per 16 m² and 31 species per 1 m² relevé (Table 2).

The moss layer is usually well developed (30–80%) with the most frequent species being *Thuidium delicatulum*, *Rhytidiadelphus squarrosus*, *Pleurozium schreberi*, *Plagiomnium affine* and *Hylocomium splendens*.

Ecology: Mesic grasslands occur at altitudes of 400–600 m mostly on moderate slopes with various aspects. The majority of these stands are intensively grazed by cattle throughout the growing season. Several plots are lightly grazed or mown with scythe. The soil analyses indicated acidic soils (average pH was 4.23). A comparison of the mean values of the measured soil parameters and altitude of all identified associations is shown in Table 1, and values for all relevés are given in Supplement E3.

**Fig. 3.** Pastures of *Campanulo rotundifoliae-Dianthetum deltoidis* association, grazed mostly by cattle (Lypovets, Khuststkyi rayon, rel. 7, Photo: K. Hegedüšová, 09 June 2011).

**Abb. 3.** Durch Rinder beweidete Weiden des *Campanulo rotundifoliae-Dianthetum deltoidis* (Lypovets, Khuststkyi rayon, Aufn. 7, Foto: K. Hegedüšová, 09.06.2011).

Classification: The floristic composition of these grasslands corresponds to communities of the *Nardetea strictae* class and *Violion caninae* alliance. These grasslands are the most similar to the west-Carpathian association *Campanulo rotundifoliae-Dianthetum deltoidis.* Submontane grasslands dominated by *Festuca rubra* from the Ukrainian Carpathians were classified as the *Festucetum rubrae* Puşcaru et al. 1956 within *Potentillo-Nardion* Simon 1957 alliance (SOLOMAKHA 2008), or *Agrostio-Festucetum rubrae* Maloch 1932 from the alliance *Agrostio-Festucion rubrae montanum* Puşcaru et al. 1956 (CHORNEY et al. 2005).

### Association 1.2.1: *Campanulo abietinae-Nardetum strictae* (Supplement S1, relevés 18–26, Fig. 4)

Characterisation: Sub-montane meadows or pastures dominated mainly by *Nardus stricta* or *Festuca rubra*. Grasses and sedges like *Agrostis capillaris*, *Anthoxanthum odoratum*, *Danthonia decumbens*, *Carex pallescens*, *Carex pilulifera*, *Luzula luzuloides* are constantly present. Diagnostic species of the *Nardo-Agrostion teniuis* alliance (*Arnica montana*, *Scorzonera purpurea* ssp. *rosea*, *Vaccinium myrtillus*, *Gentiana asclepiadea*, *Hypochoeris uniflora*, *Vaccinium vitis-idaea*, *Hieracium aurantiacum*, *Crepis conyzifolia*) are typical for these stands. Species of the *Violion caninae* alliance (*Carex pallescens*, *Danthonia decumbens*, *Dianthus deltoides*, *Polygala vulgaris*, *Viola canina*) and species of the *Nardetea strictae* class (*Potentilla erecta*, *Luzula campestris* agg., *Carex pilulifera*, *Veronica officinalis*, *Luzula luzuloides*) are also frequent. Species of mesophilous grasslands (*Ar-*

**Table 1.** Average values of soil parameters and altitude in the identified associations (Association 3.1.1 is documented by only 1 relevé).

**Tabelle 1.** Mittelwerte der Bodenparameter und Meereshöhe für die Assoziationen (von Assoziation 3.1.1 existiert nur eine Aufnahme).

| Association | pH (KCl) | Phosphorus (mg/kg) | Potassium (mg/kg) | Magnesium (mg/kg) | Humus ($C_{ox}$, %) | Nitrogen ($N_{tot}$, %) | Altitude |
|---|---|---|---|---|---|---|---|
| 1.1.1 | 4.23 | 1.6 | 135.7 | 189.0 | 4.98 | 0.47 | 604 |
| 1.2.1 | 3.78 | 0.7 | 109.1 | 88.4 | 5.11 | 0.47 | 812 |
| 1.2.2 | 4.43 | 1.0 | 69.0 | 317.0 | 4.94 | 0.49 | 775 |
| 2.2.1 | 4.51 | 2.2 | 102.7 | 228.1 | 4.06 | 0.41 | 602 |
| 2.2.2 | 4.32 | 8.1 | 120.0 | 131.5 | 2.75 | 0.29 | 439 |
| 3.1.1 | *3.70* | *0.6* | *104.0* | *37.2* | *5.26* | *0.48* | *316* |
| 3.1.2 | 6.96 | 7.8 | 280.0 | 249.0 | 4.22 | 0.37 | 308 |

**Table 2.** Average number of vascular species and bryophytes on the plots of 1 and 16 m² in the identified associations (association 3.1.1 is documented by only 1 relevé).

**Tabelle 2.** Anzahl (Mittelwerte) der Gefäßpflanzenarten und Moosarten auf 1 m²- und 16 m²-Flächen (von Gesellschaft 3.1.1 existiert nur eine Aufnahme).

| Association | Vascular plants 1 m² | Bryophytes 1 m² | Vascular plants 16 m² | Bryophytes 16 m² |
|---|---|---|---|---|
| 1.1.1 | 31 | 4 | 45 | 5 |
| 1.2.1 | 29 | 4 | 43 | 6 |
| 1.2.2 | 41 | 5 | 61 | 6 |
| 2.2.1 | 36 | 4 | 52 | 5 |
| 2.2.2 | 20 | 1 | 44 | 3 |
| 3.1.1 | *34* | *0* | *44* | *0* |
| 3.1.2 | 16 | 0 | 29 | 0 |

*rhenatherion elatioris*) are not as common as in the previously mentioned grasslands. In these grasslands there are approximately 43 vascular plant species per 16 m² and 29 species per 1 m² relevé (Table 2). The moss layer consists mostly of species like *Pleurozium schreberi*, *Rhytidiadelphus squarrosus*, *Plagiomnium affine*, *Hylocomium splendens*, *Dicranum bonjeanii*, and its cover is 30–95%.

Ecology: These grasslands occupy moderate slopes at altitudes of 700–900 m. They are usually managed by mowing and aftermath grazing. Some plots are extensively grazed during the whole vegetation season by cattle.

Classification: Montane grasslands from the Ukrainian Carpathians with very similar species composition have been usually assigned to *Hypochaerido uniflorae-Nardetum strictae* (KLIMUK et al. 2006, DERZHYPILSKY et al. 2011, SOLOMAKHA et al. 2004), which is a synonym of the *Campanulo abietinae-Nardetum strictae*.

**??? Association 1.2.2: transitional type between the *Arrhenatherion elatioris* and the *Nardo strictae-Agrostion tenuis* (Supplement S1, relevés 27–30, Fig. 5)**

Characterisation: The permanent meadows managed by mowing included in this group are rather heterogeneous. There are no marked dominant species in the community, but several grasses (*Agrostis capillaris*, *Festuca rubra*) and dicotyledonous herbs (*Alchemilla* spec. div., *Centaurea phrygia* agg., *Galium verum*, *Sanguisorba officinalis*, *Trollius europaeus*) can reach 25% coverage. Some species of the *Nardo-Agrostion caninae* alliance (*Gentiana asclepiadea*), the *Violion caninae* alliance (*Carex pallescens*, *Polygala vulgaris*, *Viola canina*), and the *Nardetea strictae* class (*Potentilla etrecta*, *Carex pilulifera*, *Veronica officinalis*, *Luzula luzuloides*) are frequently present. Some species typical for mountain meadows of the *Polygono-Trisetion flavescentis* alliance (*Astrantia major*, *Cardaminopsis hallerii*, *Trollius altissimus*) occur sporadically in this community. Species indicating increased moisture like *Deschampsia caespitosa*, *Sanguisorba officinalis*, *Myosotis scorpioides* agg. are frequently present. These meadows belong to the most species-rich communities in the Ukrainian Carpathians. There are 61 vascular species in the 16 m² plot and 41 in the 1 m² plot. The moss layer is well developed and its cover reaches usually 80–90%. The most frequent mosses are *Rhytidiadelphus squarrosus*, *Thuidium delicatulum*, *Hylocomium splendens* and *Climacium dendroides*.

Ecology: Species-rich meadows occur on moderate to steep slopes at altitudes of 700–900 m. They were mown by scythe in the past for a long time and the majority are still managed in the same way.

Classification: The classification of these grasslands has not been resolved. Relevés 27 and 28 contain a lot of species from the alliance *Nardo strictae-Agrostion tenuis*. On the other hand, they are very close to communities of the *Molinio-Arrhenatheretea* class. Relevés 29 and 30 represent a specific grassland type found in the vicinity of village Senechiv in Dolynskyi rayon. The species composition is a mixture of mesophilous species of the *Arrhenatheretalia* and *Molinietalia* orders and species of the class *Nardetea strictae*.

**Association 2.2.1: *Poo-Trisetetum flavescentis* (Supplement S1, relevés 31–41)**

Characterisation: Mesophilous grasslands on former arable fields dominated by dicotyledonous herbs such as *Centaurea phrygia* agg., *Leontodon hispidus*, *Lotus corniculatus*, *Trifolium dubium* and *Trifolium repens.* The grasses *Trisetum flavescens*, *Holcus lanatus*, *Anthoxanthum odoratum*, *Briza media* or *Agrostis capillaris* often prevail in the stands. Mesophilous species of the *Arrhenatherion* alliance (*Leucanthemum vulgare*, *Campanula patula*, *Rhinanthus minor*, *Dactylis glomerata*, *Crepis biennis*,) and species of the *Molinio-Arrhenatheretea* (*Plantago lanceolata*, *Trifolium repens*, *Ranunculus acris*, *Rumex acetosa*, *Trifolium pratense*, *Festuca pratensis*, *Carum carvi*, *Lathyrus pratensis*) are very common. *Arrhenatherum elatius* occurs only rarely. The introduced species *Sisyrinchium montanum* native to North America can occur in some stands. The mean number of vascular species is 52 in the 16 m² plot and 36 in the 1 m² plot (Table 2). Other diagnostic species of this grassland type are *Anthriscus sylvestris*, *Galium mollugo* agg., *Bromus hordeaceus*, *Veronica chamaedrys*, *Tragopogon pratensis* ssp. *orientalis*, *Myosotis arvensis*, *Taraxacum officinale*, *Lysimachia vulgaris*, *Campanula rapunculoides*, *Trifolium dubium*, *Lysimachia nummularia* and *Cerastium fontanum* ssp. *vulgare.* The moss layer cover varies from 3 to 80%, in most stands it reaches up to 50%. The most frequent species are *Rhytidiadelphus squarrosus*, *Thuidium delicatulum*, *Plagiomnium affine.*

**Fig. 4.** Mountain pastures of *Campanulo abietinae-Nardetum strictae* association (Senechiv, Dolynskyi rayon, rel. 24, Photo: K. Hegedüšová, 12 July 2010).

**Abb. 4.** Montane Weiden des *Campanulo abietinae-Nardetum strictae* (Senechiv, Dolynskyi rayon, Auf. 24; Foto: K. Hegedüšová, 12.07.2010).

**Fig. 5.** Species-rich permanent meadows, transitional between the *Arrhenatherion elatioris* and the *Nardo strictae-Agrostion tenuis* (Senechiv, Dolynskyi rayon, rel 29, Photo: I. Škodová, 12 July 2010).

**Abb. 5.** Artenreiche Wiesen im Übergang des *Arrhenatherion elatioris* zum *Nardo strictae-Agrostion tenuis* (Senechiv, Dolynskyi rayon, Auf. 29; Foto: I. Škodová, 12.07.2010).

Ecology: These grasslands developed from arable fields after their abandonment in the past. After the abolition of agricultural cooperatives in the 1990, large areas of arable land were divided among former owners and workers of cooperatives and they started to use this land. In some regions there is a special soil management regime. People grow some agricultural crops (mainly potatoes) on the field for several years, then the field is left fallow (no planting of field crops and only mowing), whilst neighbouring plots are ploughed and prepared for cultivation. This patchwork of small fields and grasslands of various ages (old field sites) is characteristic for the landscapes here (Fig. 1). The arable fields are usually manured. Grasslands of this type occur at altitudes from 300 to 900 m usually on gentle slopes up to 10 degrees.

Classification: The species composition of these grasslands corresponds to the association *Poo-Trisetetum flavescentis* within the *Arrhenatherion elatioris*. Several relevés of this community from the Ukrainian Carpathians have been published by KUZEMKO (2009). The association is listed in the national syntaxonomical survey by SOLOMAKHA (2008) as the *Trifolio-Festucetum rubrae*, which is a partial synonym of the *Poo-Trisetetum flavescentis*.

**Association 2.2.1: *Lolio perennis-Cynosuretum cristati* (Supplement S1, relevés 42–43)**

Characterisation: Intensive pastures containing species well adapted to trampling and frequent grazing like *Bellis perennis*, *Leontodon autumnalis*, *Lolium perenne*, *Taraxacum* sect. *Ruderalia*, *Trifolium pratense* and *T. repens*. The stands have a closed sward, are moderately species-rich, and the height of the herb layer is dependent on grazing intensity. There are several subdominant grasses (*Agrostis capillaris*, *Cynosurus cristatus*, *Festuca rubra* agg., *Lolium perenne*) and herbs (*Lotus corniculatus*, *Taraxacum officinale*, *Trifolium pratense*). Pastures on slopes in submontane regions contain some species of the *Nardetea strictae* class (*Veronica officinalis*, *Luzula campestris* agg., *Carex pallescens*). The mean number of vascular plant species in the 16 m² plots is 44 and 20 in the 1 m² plots (Table 2). The moss layer cover does not exceed 15%. Only *Brachythecium salebrosum* is more frequent.

Ecology: Intensively grazed pastures in submontane regions at altitudes 290–590 m grazed mainly by cows. Application of manure means that the soil contains relatively high contents of some nutrients (Table 1, Supplement E3).

Classification: Intensive pastures of this type belong to the *Lolio perennis-Cynosuretum cristati* from the *Cynosurion cristati* alliance. KUZEMKO (2009) published similar relevés recorded by O.P. Krys from the Ukrainian Carpathians classified within the *Festuco-Cynosuretum*, which is a synonym of the *Lolio perennis-Cynosuretum cristati* (JANIŠOVÁ et al. 2007b). Relevés belonging to the *Lolio-Cynosuretum* were recorded also in the national natural parks of Hutzulshchyna, Vizhnytsky and Skolivski Beskydy (DERZHYPILSKY et al. 2011, CHORNEJ et al. 2005, SOLOMAKHA et al. 2004) and under the name of the *Festuco-Cynosuretum* also from the Gorgany National Nature Reserve (KLIMUK et al. 2006).

**??? Association 3.1.1: transitional type between the *Scabioso ochroleucae-Brachypodietum pinnati* and the *Festuco rupicolae-Nardetum strictae* (Supplement S1, relevé 44)**

Characterisation: Grassland dominated by *Festuca rupicola* containing many *Festuco-Brometea* species (*Agrimonia eupatoria*, *Brachypodium pinnatum*, *Carex caryophyllea*, *Carlina vulgaris*, *Euphorbia cyparissias*, *Festuca valesiaca*, *Galium verum*, *Linum catharticum*, *Pimpinella saxifraga* agg., *Polygala comosa*, *Scabiosa ochroleuca*). Other subdominant grasses are *Agrostis capillaris* and *Briza media*. Species of the *Violion caninae* alliance (*Carex pallescens*, *Danthonia decumbens*, *Viola canina*) are also present. The occurrence of the fringe species *Trifolium medium* with a relatively high cover (2b) and other species of *Trifolio-Geranietea* class (*Melampyrum nemorosum*, *Stachys officinalis*) is probably caused by the absence of regular management. There are an average of 44 vascular plant species per 16 m² relevé. The moss layer is largely absent.

Ecology: The community was recorded in the southern part of the Ukrainian Carpathians near the village of Dibrova on the south-western slope at an altitude of 316 m. Recently, the pasture has become rather degraded and only lightly grazed by cows. Formerly (70 years ago), it was also grazed by sheep and mown.

Classification: The syntaxonomical classification of such degraded grasslands has not been resolved. It is a transitional community between the alliances of the *Cirsio-Brachypodion pinnati* (*Scabioso ochroleucae-Brachypodietum pinnati*, *Festuco-Brometea*) and *Violion caninae* (*Nardetea strictae*). It is similar to the west-Carpathian association *Nardo strictae-Festucetum rupicolae* from the *Violion caninae* alliance.

**Association 3.1.2: *Scabioso ochroleucae-Brachypodietum pinnati* Klika 1933 (Supplement S1, relevés 45–46)**

Characterisation: Abandoned grasslands dominated by *Brachypodium pinnatum* and *Inula salicina*. Species of the *Cirsio-Brachypodion pinnati* alliance (*Coronilla varia*, *Carlina vulgaris*) and *Festuco-Brometea* class (*Asperula cynanchica*, *Euphorbia cyparissias*, *Agrimonia eupatoria*, *Salvia verticillata*, *Scabiosa ochroleuca*, *Veronica spicata*, *Stachys recta*, *Polygala comosa*, *Centaurea scabiosa*) prevail in these grasslands. *Carex flacca* and *Lotus corniculatus* reach coverages of 5–15%. Abandonment supports occurrence of fringe species like *Origanum vulgare* and *Galium glaucum* from the *Trifolio-Geranietea* class. The number of vascular species per relevé is between 26 and 32. The stands were repeatedly burned in the past, which is why there was no herb litter or moss layer.

Ecology: Grasslands dominated by *Brachypodium pinnatum* are rare in the Ukrainian Carpathians. We found only one locality near the village of Bila Tserkva close to the border with Romania. These grasslands on a steep SW slope were used as pastures in the past.

Classification: The species composition of these grasslands corresponds to the association *Scabioso ochroleucae-Brachypodietum pinnati* partly degradated by abandonment and fire.

### 4.3 Compositional variation

The first DCA axis explained 9.2% of variance in the species composition, the second axis 6.6% and the first four axes together explained 22.5% of variance. The selected Ellenberg inditator values for relevés (temperature, moisture, light), altitude, measured soil variables ($N_{tot}$, P, K, Mg, Cox, pH) and the management variables (mowing, intensity of grazing, ploughing in the past and burning) were post-hoc correlated with the ordination axes to reveal the main environmental gradients in our data (Fig. 6). The first axis was significantly positively correlated with pH (correlation coefficient 0.50), phosphorus (0.48), and indicator values for temperature (0.76) and light (0.54); and negatively correlated with altitude (-0.49). The main environmental gradient was related to altitude and soil parameters, especially soil reaction. The left side of the ordination plot contains relevés of the *Nardo-Agrostion* alliance occurring at higher altitudes and on acid nutrient-poor soil, while relevés from lowland pas-

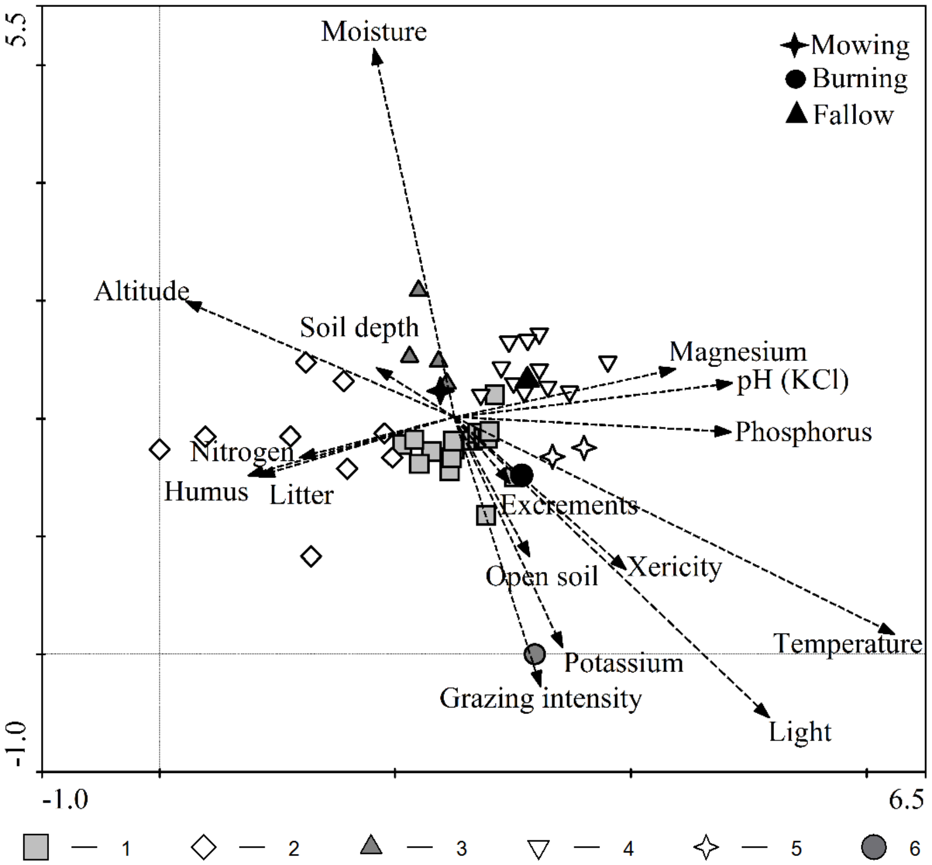



**Fig. 6.** Detrended correspondence analysis of phytosociological relevés. Environmental variables (Ellenberg indicator values, altitude and type of management) were plotted onto the diagram as supplementary data. Plant communities are marked as follows: 1 – *Campanulo rotundifoliae-Dianthetum deltoidis*, 2 – *Campanulo abietinae-Nardetum strictae*, 3 – transitional type between the *Arrhenatherion elatioris* and the *Nardo strictae-Agrostion tenuis*, 4 – *Poo-Trisetetum flavescentis*, 5 – *Lolio perennis-Cynosuretum cristati*, 6 – transitional between the *Scabioso ochroleucae-Brachypodietum pinnati* and the *Festuco rupicolae-Nardetum strictae*.

**Abb. 6.** *Detrended correspondence analysis* der Vegetationsaufnahmen. Die Umweltvariablen (Ellenberg-Zeigerwerte, Meereshöhe, Bewirtschaftungstyp) wurden als supplementäre Daten über das DCA-Diagramm gelegt. Die Bedeutung der Pflanzengesellschaften siehe in der englischen Abbildungsunterschrift.

tures (*Cynosurion cristati*, *Lolio perennis-Cynosuretum cristati*) and meadows on former arable fields (*Arrhenatherion elatioris*, *Poo-Trisetetum flavescentis*) hosting species demanding higher nutrient concentrations are concentrated on the right side of plot.

The second axis is significantly positively correlated with the indicator values for moisture (0.75) and negatively correlated with grazing intensity (-0.52), and indicator values for light (-0.49). Grasslands managed by mowing in relatively moist habitats in mountain regions (transitional type between the *Arrhenatherion elatioris* and the *Nardo strictae-Agrostion tenuis*) are shifted along the second axis to the upper part of the ordination space.

In contrast, the relevés of intensively grazed pastures belonging to the *Violion caninae* alliance (*Campanulo rotundifoliae-Dianthetum deltoidis* association) are concentrated on the opposite side.

Canonical correspondence analysis (CCA) was carried out to assess of the effect of measured environmental variables on species composition of grasslands. The first canonical axis explained 9.8% of the variance in the species composition data and 33.4% of the variance in the species-environment relationship, which means that 33.4% of the variability of our data set caused by selected environmental variables was reflected by the first ordination axis. The second axis explained 5.3% of the variance in the species data and 18.9% of the variance in the species-environment relationship. Seven environmental variables passed the forward selection: altitude, fallow (i.e. ploughing in the past), soil reaction (pH), intensity of grazing, burning and content of phosphorus and magnesium. Altogether, these variables explained 29.3% of the variance in the species data. The pure effect of significant environmental factors was 22.5% (Table 3). Altitude had the strongest influence on species composition of the analysed dataset (5.3%), together with some management treatments (ploughing in the past – 5.2%, intensity of grazing – 4.9%). Burning had a significant effect on species composition (3.0%) but was not significant if tested as the only constraining variable. On the other hand, mowing was not significant in the forward selection, but was significant when tested as the only environmental variable. Among the soil parameters, soil reaction (pH) was the most important (5.1%).

The differences in soil parameters and altitude among the described vegetation types are shown by the boxplots in Figure 7 (see also Table 1). Grasslands classified within the *Campanulo abietinae-Nardetum strictae* association significantly differ from almost all other vegetation types as they have the lowest soil reaction. The phosphorus and magnesium con-

**Table 3.** CCA variance explained by each environmental variable. ***, $p \leq 0.001$; ** $p \leq 0.01$; *, $p \leq 0.05$; ns, not significant. Values in collumns 1, 3, 5 are eigenavalues of single variables in forward selection. Significant values in bold.

**Tabelle 3.** Durch die jeweiligen Umweltfaktoren erklärte CCA-Varianz. ***, $p \leq 0{,}001$; **, $p \leq 0{,}01$; *, $p \leq 0{,}05$; ns, nicht signifikant. Signifikante Werte sind fett dargestellt.

| Environmental variable | Marginal effect | % | Conditional effect (selection order) | % | Pure effect | % |
|---|---|---|---|---|---|---|
| Altitude | **0.126 ***** | **5.3** | **0.126 ***** | **5.3** | **0.109 ***** | **4.6** |
| Fallow | **0.116 **** | **4.9** | **0.124 ***** | **5.2** | **0.113 ***** | **4.7** |
| pH (KCl) | **0.125 **** | **5.2** | **0.121 ***** | **5.1** | 0.063 ns | 2.6 |
| Intensity of grazing | **0.121 ***** | **5.1** | **0.118 ***** | **4.9** | **0.107 ***** | **4.5** |
| Phosphorus | 0.123 ns | 5.1 | **0.074 *** | **3.1** | **0.073 *** | **3.1** |
| Burning | 0.081 ns | 3.4 | **0.072 *** | **3.0** | **0.071 *** | **3.0** |
| Magnesium | **0.109 **** | **4.6** | **0.066 *** | **2.8** | **0.066 *** | **2.8** |
| Potassium | **0.105 **** | **4.4** | 0.054 ns | 2.3 | 0.054 ns | 2.3 |
| Humus ($C_{ox}$) | **0.080 *** | **3.3** | 0.043 ns | 1.8 | 0.043 ns | 1.8 |
| Nitrogen | 0.068 ns | 2.8 | 0.042 ns | 1.8 | 0.042 ns | 1.8 |
| Mowing | **0.119 ***** | **5.0** | 0.033 ns | 1.4 | 0.036 ns | 1.5 |
| Sum of variances | - | 49.0 | - | 36.5 | - | 32.5 |
| Sum of significant variances | - | **37.7** | - | **29.3** | - | **22.5** |

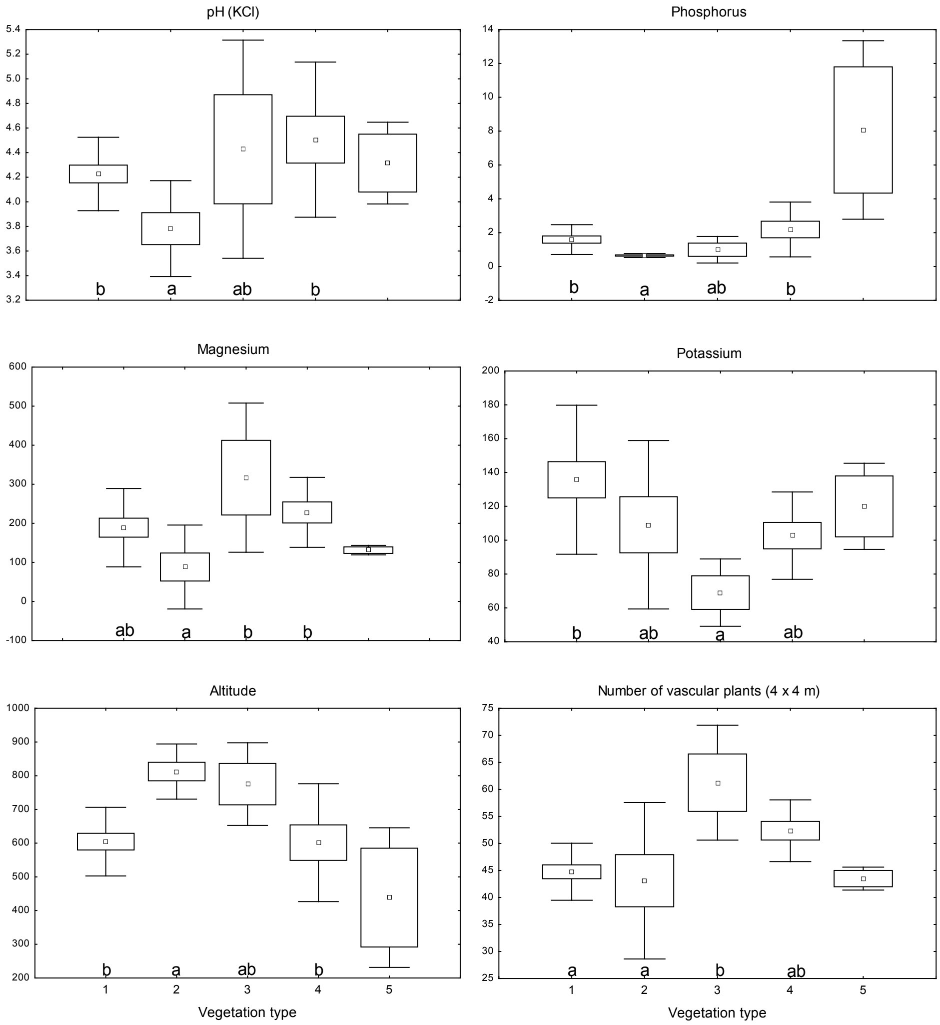



**Fig. 7.** Comparison of soil parameters, altitude and number of vascular plant species for the studied plant communities. Mean, standard deviation and standard error are shown. 1 – *Campanulo rotundifoliae-Dianthetum deltoidis*, 2 – *Campanulo abietinae-Nardetum strictae*, 3 – transitional type between the *Arrhenatherion elatioris* and the *Nardo strictae-Agrostion tenuis*, 4 – *Poo-Trisetetum flavescentis*, 5 – *Lolio perennis-Cynosuretum cristati* (the last community was not used in comparison test as it contains only two relevés). Significant differences are marked using different letters.

**Abb. 7.** Vergleich von Bodenkennwerten, Meereshöhe und Pflanzenartenreichtum zwischen den untersuchten Gesellschaften. Mittelwert, Standardabweichung und Standardfehler sind dargestellt. Die Pflanzengesellschaften siehe in der englischen Abbildungsunterschrift. Gesellschaft 5 ist nur mit zwei Vegetationsaufnahmen vertreten. Signifikante Unterschiede sind durch unterschiedliche Buchstaben gekennzeichnet.

tent was lower in comparison to other grasslands. Montane meadows were found on soils with a lower potassium content compared to montane pastures of the *Nardo-Agrostion* alliance.

Pastures of the *Campanulo abietinae-Nardetum strictae* were found at the highest altitudes and pastures of *Lolio perennis-Cynosuretum cristati* were found at the lowest altitudes. There were no differences in humus and nitrogen contents in soil of the studied communities.

### 4.4 Species richness-environment relationships

For vascular plant species richness, regression tree analysis identified grazing intensity as the most important predictor at the 1 m² scale (Fig. 8). The only split of the regression tree based on grazing intensity separated more intensively grazed species-poorer plots (with 27 vascular plant taxa on average) from non-grazed or seasonally grazed plots with higher species richness (35 taxa on average). At the 16 m² scale, soil humus content was evaluated as the most important predictor of vascular plant species richness, followed by litter cover, grazing intensity, inclination and pH (Fig. 9A). The optimal regression tree (Fig. 9B) had six terminal nodes. The first split was based on inclination, separating plots on the steepest slopes with the highest absolute species richness (66 vascular plant taxa on average). The second split was based on humus content with the lowest absolute species richness (35 taxa

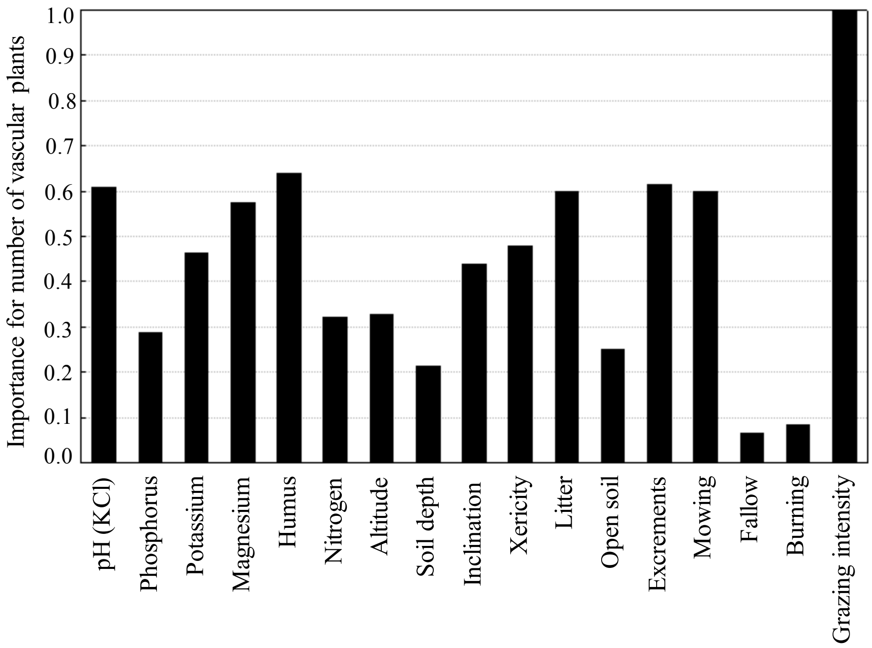
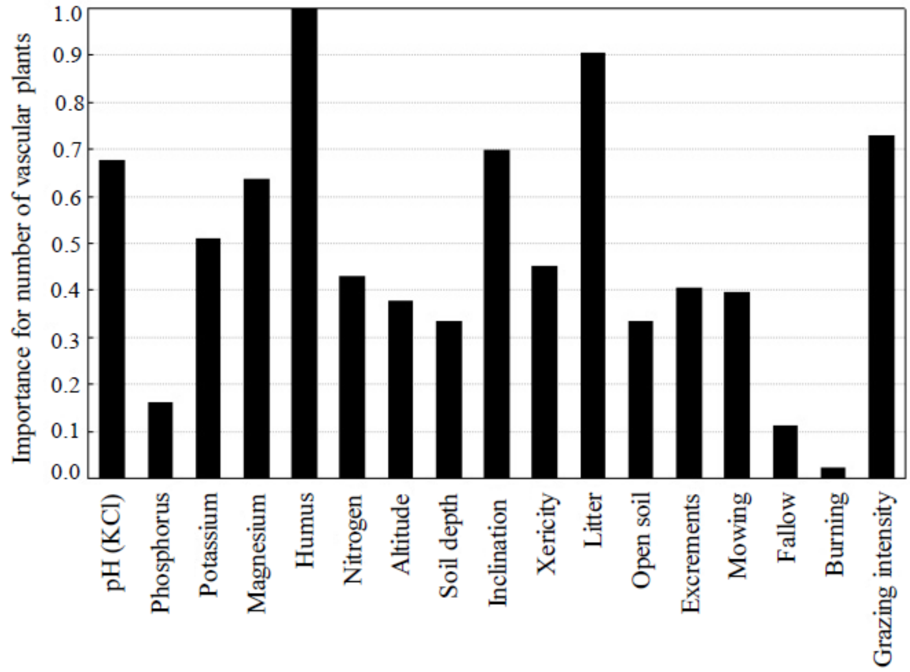


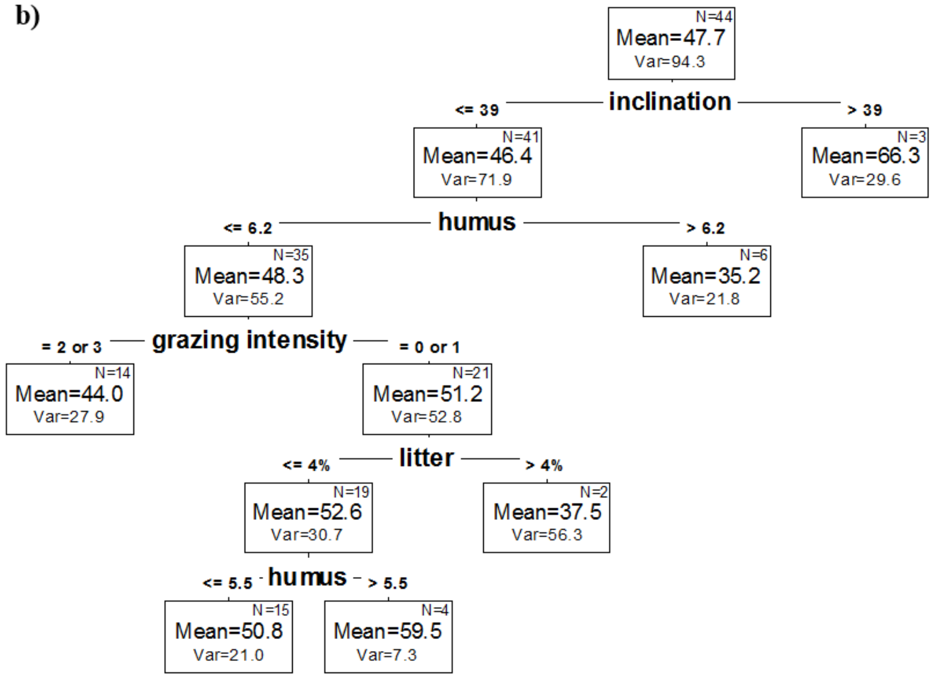

**Fig. 8.** Relative importance of the studied environmental variables for prediction of species richness of vascular plants in 1 m² plots by a regression tree. The predictors are ranked on a 0–1 scale, whereby the most significant predictor has the value 1.

**Abb. 8.** Relative Bedeutung der untersuchten Umweltvariablen zur Vorhersage des Pflanzenartenreichtums auf 1 m²-Flächen durch den Regressionsbaum. Die Prediktatoren reichen von 0–1; der Wert 1 zeigt die wichtisten Prediktatoren an.

a)


Importance for number of vascular plants
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
pH (KCl)
Phosphorus
Potassium
Magnesium
Humus
Nitrogen
Altitude
Soil depth
Inclination
Xericity
Litter
Open soil
Excrements
Mowing
Fallow
Burning
Grazing intensity

b)


N=44
Mean=47.7
Var=94.3
<= 39
inclination
> 39
N=41
Mean=46.4
Var=71.9
N=3
Mean=66.3
Var=29.6
<= 6.2
humus
> 6.2
N=35
Mean=48.3
Var=55.2
N=6
Mean=35.2
Var=21.8
= 2 or 3
grazing intensity
= 0 or 1
N=14
Mean=44.0
Var=27.9
N=21
Mean=51.2
Var=52.8
<= 4%
litter
> 4%
N=19
Mean=52.6
Var=30.7
N=2
Mean=37.5
Var=56.3
<= 5.5
humus
> 5.5
N=15
Mean=50.8
Var=21.0
N=4
Mean=59.5
Var=7.3

on average) in the dataset associated with humus-rich grasslands. The group of humus-poor grasslands was further split by grazing intensity separating species-poorer intensively grazed plots from other plots. These species-poor plots were further divided to extremely species-poor plots with high litter cover and a group of plots with low litter cover, which was further divided based on humus content again. The number of bryophytes was not affected by the studied environmental factors at either of the two spatial scales (1 m² or 16 m²).

Among the four evaluated grassland types, permanent montane meadows were species-richest (on average 61 taxa of vascular plants in 16 m²), followed by former fields transformed to meadows (52 taxa). Pastures of the *Violion caninae* and *Nardo-Agrostion* aliaces were species-poorer (45 and 43 taxa, respectively, Fig. 7).

## 5. Discussion

### 5.1 Syntaxonomical classification

We did not perform a common numerical classification and direct comparison of our phytosociological relevés with those published by other authors from the studied territory here because Ukrainian phytosociologists usually used plot sizes of 100 m² (in some cases 400 m² or even larger), while we used much smaller plots of 16 m², different classification approaches and cover scales.

During the last decade, phytosociological research of plant communities has been carried out in some national parks and nature reserves in Ukrainian Carpathians. Within the class *Molinio-Arrhenatheretea*, phytosociological relevés classified as the *Lolio perennis-Cynosuretum cristati* and *Festuco-Cynosuretum* R. Tx. have been published in Büker 1942 (Chorney et al. 2005, Derzhypilsky et al. 2011, Tokaryuk et al. 2009). Several communities without a specified rank belonging to the *Arrhenatheretalia* order have been published, e.g. com. *Festuca pratensis*, com. *Festuca rubra*, com. *Dactylis glomerata* and com. *Brachypodium pinnatum-Trifolium pannonicum* (Chorney et al. 2005); com. *Laserpitium alpinum-Agrostis tenuis*, com. *Luzula luzuloides-Festuca rubra* (Klimuk et al. 2006); com. *Poa pratensis-Festuca rubra* (Tokaryuk et al. 2009). Other communities belonging to this order have also been identified, e.g. the *Arrhenatheretum elatioris* Scherrer 1925, *Anthoxantho odorati-Agrostietum tenuis*, *Centaureo-Trifolietum pannonici*, *Anthyllido vulnerariae-Trifolietum montani* (Derzhypilsky et al. 2011, Tokaryuk et al. 2009).

Phytosociological relevés carried out by O.P. Krys and published by Kuzemko (2009) were classified to the associations *Poo-Trisetetum flavescentis*, *Anthoxantho odorati-Agrostietum tenuis nardetosum* Jurko 1970, *Festuco-Cynosuretum* R. Tx. in Büker 1942, *Brizeto-Anthoxanthetum* Kmoníček 1936 within the class *Molinio-Arrhenatheretea*. The

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**Fig. 9.** Relative importance of the studied environmental variables for the prediction of species richness of vascular plants in 16 m² plots by a regression tree **a)** and the corresponding regression tree **b)**. The predictors are ranked on a 0–1 scale, whereby the most significant predictor has the value 1.

**Abb. 9.** Relative Bedeutung der untersuchten Umweltvariablen für den Artenreichtum der Gefäßpflanzenarten von 16 m²-Flächen durch den Regressionsbaum **a)** und den entsprechenden Regressionsbaum **b)**. Die Prediktatoren reichen von 0–1; der Wert 1 zeigt die wichtisten Prediktatoren an.

species composition of these communities differs from the communities that we recorded in this study. The species composition of the majority of relevés recorded by O.P. Krys is rather heterogeneous and in many cases consists of species belonging to several ecological groups (pasture species together with species of wet meadows, as well as species of mesic or semi-dry grasslands). It is probably caused by the fact that the size of plots was too large (400 m²) and the sampled grasslands were not homogenous.

Within the class *Nardetea strictae* and the order *Nardetalia*, com. *Nardus stricta-Agrostis tenuis*, com. *Deschampsia caespitose-Nardus stricta* and com. *Nardus stricta-Trifolium pannonicum* have been published (CHORNEY et al. 2005). Phytosociological relevés classified as the *Hypochoeridi uniflorae-Nardetum strictae* and com. *Deschampsia caespitose-Nardus stricta* were published by DERZHYPILSKY et al. (2011) and KLIMUK et al. (2006).

### 5.2 Compositional variation

Based on the results of indirect ordination analysis (DCA) the major compositional gradient is correlated with soil pH. This result is in accordance with the results of several studies on the vegetation of mesic and semi-dry grasslands (CACHOVANOVÁ et al. 2012, CRITCHLEY et al. 2002, WAGNER 2009).

Some other studies suggest that the main floristic gradient in grasslands is related to annual precipitation (BRUELHEIDE & JANDT 2007, ŠKODOVÁ et al. 2011, JANIŠOVÁ et al. 2010). Our research was focused mainly on mesic grasslands, thus the sampled relevés have only a short moisture gradient. In the DCA analysis, we used indicator values for moisture to express the requirements for water supply, which were correlated with the second ordination axis.

In the direct ordination (CCA), of the seven environmental variables that passed the forward selection, altitude explained 5.3% of species variability. Other important variables in the forward selection were "fallow" (5.2% of species variability), soil pH (5.1%) and intensity of grazing (4.9%). All these variables are closely related. In the study area, grasslands at higher altitudes are mostly used as pastures (*Nardo-Agrostion* alliance), while at lower altitudes there are fallows of various ages, i.e. former arable fields, on which grasslands of the *Arrhenatherion elatioris* alliance developed. Soil chemical properties and management are generally considered to be the most important factors affecting species composition and diversity in grassland ecosystems, whereby soil chemical properties are often considered to be the result of management (MYKLESTAD 2004). In our study, soil pH is significantly lower at higher altitudes. Of the other soil properties, only the magnesium content passed the forward selection of variables. Content of phosphorus, potassium, total nitrogen and carbon had significant effects on species composition only when each of these variables was used as the only constraining variable.

From the analysis of soil samples it is obvious that soil pH decreases with increasing altitude. This fact is also discussed by STRONG at al. (2011). Soil properties generally reflected the climate data, in particular higher moisture and cooler temperatures experienced at the higher altitudes. This produced a general decrease in nutrients and pH with increased altitude. In contrast, soil moisture, organic matter content and soluble aluminium increased with increasing altitude. Decreasing pH of soil is connected with higher precipitation at higher altitudes, which causes intensive leaching of alkaline cations from the soil. Decreasing content of potassium cations is also related to this phenomenon. Content of available phosphorus is also dependent on pH. The availability of plant nutrients such as phosphorus (P) and calcium (Ca) can be limiting at low soil pH (ASP & BERGGREN 1990, KIDANEMARIAM et al. 2012). When soil pH is low, iron and aluminium react with phosphorus, producing insoluble phosphates that are unusable for plants. In contrast, the content of organic carbon increases with increasing altitude. The intensity of mineralisation decreases with the lower average temperature at higher altitudes and raw humus accumulates. The same trend is observed in the content of nitrogen. Lower content of carbon in soils of the *Poo-Trisetetum flavescetis* could be caused by former ploughing. It is known that cultivation decreases natural content of carbon in soil (POST & KWON 2000). Aeration of the soil increases the mineralisation of organic matter.

### 5.3 Species richness-environment relationships

There is no major difference in the effect of environmental factors on species richness at the two studied spatial scales. Vascular plant species richness was determined mainly by the management regime (grazing intensity and intensity of agricultural utilisation indicated by litter cover) and soil nutrient content (humus). At a smaller scale (1 m²), only grazing intensity was shown to be significant. Moreover, regularly mown permanent montane meadows not affected by former ploughing and intensive grazing had the highest species richness of the grassland communities in the study region. These results are in accordance with numerous studies indicating higher species richness in mown vs. grazed grasslands (e.g. TURTUREANU et al. 2014). However, similarly to the effect of grazing intensity, mowing intensity is also important and a high cutting frequency is expected to decrease species richness (SOCHER et al. 2012) in a similar way to intensive grazing (PROULX & MAZUMDER 1998). Our results also support the idea that the species richness of vascular plants and bryophytes respond clearly to different environmental signals and are determined by different combinations of environmental variables (e.g. HETTENBERGEROVÁ et al. 2013).

## 6. Conclusions and outlook

Thanks to the continuation of traditional agriculture, semi-natural grasslands form an important component of the rural Carpathian landscape. Based on our research, we distinguished five well-delimited grassland communities at the association level. The syntaxonomical classification of two units represented only by few relevés remained unresolved and should be reexamined after recording further relevés. Although the number of analysed relevés in this study was limited and their classification should be considered as preliminary, our findings contribute to the understanding of submontane grasslands in this region. We gathered 46 high quality phytosociological relevés including both vascular plants and cryptogam species. Moreover, the detailed data on soil properties and management regime were gathered for individual relevés. This is the first time that such detailed phytosociologial relevés have been published from this area. For the first time we recorded the association *Campanulo rotundifoliae-Dianthetum deltoidis* and the alliance *Violion caninae* in the Ukrainian Carpathians.

During our research, we collected a lot of information about the management and conservation of the studied grasslands. At present, the major threats to grasslands in the Ukrainian Carpathians are changes in traditional land-use, and mainly abandonment (KRICSFALUSY 2013, SOLOVYEVA et al. 2011). In some abandoned pastures *Pteridium aquillinum* is spreading. On the other hand, there are some regions where overgrazing has degraded the grasslands. Regularly mown permanent montane meadows not affected by former ploughing and intensive grazing were the most species-rich of the grassland communities in the study region.

Regarding to the conservation of biodiversity, the best management treatment is a combination of mowing once or twice a year, with low-intensity grazing by cows, sheep, horses or goats. In spite of the continuing decline in traditional land-use, the Ukrainian Carpathians belong to one of the few European regions with a large proportion of high nature value grasslands.

## Erweiterte deutsche Zusammefassung

**Einleitung** – In den ukrainischen Karpaten existieren noch große Flächen naturnahen Graslands, das größtenteils von Hand gemäht oder beweidet wird. Das Gebiet besitzt eine hohe Biodiversität die sich im Grasland stark konzentriert. Das landwirtschaftliche System in den ukrainischen Karpaten entsprichte dem *high nature value farming*, einem Konzept der EU-Agrarpolitik zum Erhalt einer hohen Biodiversität auf landwirtschaftlichen Flächen (BEAUFOY 2007, NUPPENAU et al. 2011). Bislang war das naturnahe Grasland der ukrainischen Karpaten pflanzensoziologisch kaum untersucht. Daher erstellten wir dort in den Jahren 2010 und 2011 insgesamt 46 Vegetationsaufnahmen um (1) das meso- und subxerophile naturnahe Grasland syntaxonomisch einzuordnen, (2) die floristischen Hauptgradienten zu analysieren und ökologisch zu interpretieren, und um den Einfluss verschiedener Umweltfaktoren auf (3) die Artenzusammensetzung und (4) den Artenreichtum der Gefäßpflanzen und Moose einzuschätzen.

**Untersuchungsgebiet** – Die Studie wurde in folgenden Regionen der ukrainischen Karpaten durchgeführt: Zakarpatska Oblast-Mizhhirskyi Rayon, Volovetskyi Rayon, Khuststkyi Rayon, Rayon und Tyachivskyi Rakhivskyi Rayon, Ivano-Frankovskaja Oblast-Dolynskyi Rayon und Lvivska oblast Skolivskyi Rayon (Abb. 2). Das Ausgangsgestein in den ukrainischen Karpaten wird von wechselnden Schichten des Flysch-Schiefers und Flysch-Sandsteins gebildet; kleinräumig existiert auch Kalkstein oder Granit. Das Klima ist gemäßigt kontinental. Das Untersuchungsgebiet gehört zu den unteren Karpaten mit moderat-hohen Gipfeln (bis 2061 m ü. NN: Hoverla). Die hier präsentierten Vegetationsaufnahmen wurden in Höhenlagen von 137–927 m ü. NN erstellt.

**Methoden** – Während der Vegetationsperiode 2010 und 2011 wurden 46 Vegetationsaufnahmen nach der Braun-Blanquet-Methode mit allen Gefäßpflanzen- und Moosarten erstellt. Die Vegetation wurde auf 1 m²- und 16 m² (4 × 4 m)-Flächen aufgenommen, wobei die 1 m²-Flächen innerhalb der 16 m²-Flächen lagen. Auf den 1 m²-Flächen wurde die Deckung der Arten in Prozentschritten geschätzt während auf den 16 m²-Flächen die neunstufige Braun-Blanquet-Skala verwendet wurde. Für jede Aufnahmefläche wurden die folgenden Bodenparameter und Standortmerkmale erfasst: Bodentiefe, pH (KCl), Gehalte an P, K, Mg, N und C, aktuelle Landnutzung (Mahd, Beweidung, Abbrennen) sowie frühere Ackernutzung, Meereshöhe, Streudeckung, Deckung offener Boden, Hangneigung, Trockenheit und die Präsenz von Tierexkrementen. Die Vegetationsaufnahmen wurden in JUICE 7.0.98 analysiert (TICHÝ 2002, TICHÝ & HOLT 2006). Die Deckungswerte wurden vor den Analysen quadratwurzeltransformiert und die Vegetationsaufnahmen anschließend mit der Ward-Methode mit relativen euklidischen Distanzen analysiert. Eine mit dem Programm CANOCO 4.5 (TER BRAAK & ŠMILAUER 2002) durchgeführte Gradientenanalyse sollte Unterschiede in der Artenzusammensetzung zwischen den Vegetationseinheiten visualisieren. Beziehungen zwischen dem Artenreichtum der Gefäßpflanzen und Moose und 17 Umweltvariablen wurden mit Hilfe von Regressionsbäumen analysiert (BREIMAN et al. 1984).

**Ergebnisse** – Sieben Vegetationstypen aus drei Klassen und vier Ordnungen wurden unterschieden (Beilage S1): Klasse *Nardetea strictae* → Ordnung *Nardetalia strictae* → Verbände *Violion caninae* (Weiden in Höhenlagen von 400–600 m vorwiegend an sanften Hängen) und *Nardo strictae-Agrostion tenuis* (in Höhenlagen von 700–900 m an sanften Hängen; in der Regel gemäht und anschließend beweidet). Klasse: *Molinio-Arrhenatheretea* → Ordnung *Arrhenatheretalia* → Verbände *Arrhenatherion elatioris* (submontane Wiesen, vorwiegend auf früheren Ackerflächen) und *Cynosurion cristati* (Intensivweiden); Klasse *Festuco-Brometea* → Ordnung *Brachypodietalia* → Verband *Cirsio-Brachypodion pinnati* (Brachen mit Dominanz von *Brachypodium pinnatum* und *Inula salicina*).

Korrelationen der DCA-Ordinationsachsen mit Ellenberg-Zeigerwerten, Bodenvariablen und Landnutzungstypen deuteten auf die Meereshöhe und den pH-Wert des Bodens als wichtigste Umweltfaktoren für die Vegetation hin (Abb. 6). Eine kanonische Korrespondenzanalyse (CCA) deutete ebenfalls auf die Meereshöhe als wichtigste Umweltvariable hin, gefolgt von den Landnutzungsvariablen ehemalige Ackernutzung und Beweidungsintensität sowie pH-Wert des Bodens, Abbrennen sowie Phosphor- und Magnesiumgehalt (Tab. 3).

Der Gefäßpflanzenartenreichtum war auf den 1 m²-Flächen am stärksten mit der Beweidungsintensität korreliert (Abb. 8) und auf den 16 m²-Flächen mit dem Bodenhumusgehalt, der Streudeckung und Beweidungsintensität (Abb. 9A). Der Moosartenreichtum konnte auf keiner der beiden Raumskalen durch die untersuchten Umweltfaktoren erklärt werden. Am artenreichsten (im Mittel 61 Gefäßpflanzentaxa pro 16 m²) waren montane, regelmässig gemähte Wiesen, die offenbar niemals als Acker genutzt worden waren oder auch nicht intensiv beweidet wurden. Wiesen auf ehemaligen Ackerstandorten zeigten mit 52 Taxa einen mittleren Gäßpflanzenartenreichtum (Tab. 2) während Weiden des *Violion caninae* und *Nardo-Agrostion* am artenärmsten waren (45 bzw. 43 Taxa; Abb. 7).

**Diskussion** – Ein direkter Vergleich unserer phytosoziologischen Einteilung mit bereits aus dem Untersuchnugsgebiet publizierten Syntaxa wurde nicht vorgenommen, da die betreffenden ukrainischen Pflanzensoziologen einen anderen Klassifikationsansatz, eine andere Skala bei der Schätzung der Deckungsgrade sowie grössere Aufnahmeflächen (100 m² bis ≥400 m²) verwendetet haben. Mit dieser Methodik wurden in den letzten 10 Jahren die Vegetationstypen einiger Nationalparks und Naturschutzgebiete in den ukrainischen Karpaten pflanzensoziologisch klassifiziert (CHORNEY et al. 2005, KLIMUK et al. 2006, TOKARYUK et al. 2009, DERZHYPILSKY et al. 2011). Die Ergebnisse der Studien entsprechen jedoch nur teilweise unseren Einheiten.

**Schlussfolgerungen** – Naturnahes Grasland bildet einen prägenden Bestandteil der Vegetation der Karpaten. Ihre größte Bedrohung sind Änderungen der traditionellen Landnutzung, vor allem aber die Aufgabe der Landnutzung überhaupt. In einigen Regionen ist Intensivierung (meist Überweidung) ein Problem wodurch die Diversität des Graslands erodiert und die Wiesen degradieren. Trotz dieser negativen Entwicklungen stellen die ukrainischen Karpaten für naturnahes Graslands immer noch eine naturschutzfachlich sehr wertvolle Region dar. Die Erkenntnisse dieser Studie sollen zur besseren Kenntnis und zum besseren Verständnis der unterschiedlichen Graslandtypen der Region beitragen.

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## Supplements

**Supplement S1.** Phytosociological relevés of grassland vegetation in Ukrainian Carpathians.

**Beilage S1.** Vegetationsaufnahmen des Graslands in den ukrainischen Karpaten.

**Additional supporting information may be found in the online version of this article.**
**Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.**

**Supplement E1.** List of localities of relevés.

**Anhang E1.** Liste der Lokalitäten der Aufnahmen.

**Supplement E2.** Additional information on altitude, slope, aspect and percenage cover of layers for each relevé.

**Anhang E2.** Angaben zu Meereshöhe, Hangneigung, Hanglage und Deckungen der Schichten pro Aufnahme.

**Supplement E3.** Measured soil parameters for relevés and applied management treatments.

**Anhang E3.** Bodenkennwerte und Bewirtschaftungsmerkmale der Aufnahmen.

**Supplement E4.** Number of species in plots of size 1 × 1 m and 4 × 4 m.

**Anhang E4.** Artenzahlen pro Aufnahme der Größe 1 × 1 m und 4 × 4 m.

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