

## **Vegetation of oak-hornbeam, scree and ravine forests at lower altitudes in Transcarpathia, Western Ukraine**

### **Vegetation der Eichen-Hainbuchen- sowie Hangschutt- und Schluchtwälder der unteren Lagen Transkarpatiens, West-Ukraine**

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#### **Abstract**

Transitional between the Pannonian Basin and the Eastern Carpathians the Transcarpathian Ukraine (Transcarpathia) has a diverse geology including Quaternary sediments, volcanites, limestones and flysch, and its climate at low altitudes is relatively warm and humid. We conducted a field survey in June 2016 focusing on mesophilous forest vegetation along a transect covering almost the whole low-altitudinal part of Transcarpathia. We recorded 54 relevés in the field and further digitized 22 relevés from literature. Using classification analysis, we distinguished three clusters of oak-hornbeam forests (alliance *Carpinion betuli*; 1–3) and three clusters of scree and ravine forests (alliance *Tilio platyphylli-Acerion*; 4–6): (1) Slightly wet Pannonian oak-hornbeam forests occurring in the lowland part of the region (*Circaeo-Carpinetum*); (2) Mesophilous oak-hornbeam forests (*Carici pilosae-Carpinetum*); (3) Xero-mesophilous oak-hornbeam forests (a drier subtype of the *Carici pilosae-Carpinetum* and the association *Primulo veris-Carpinetum*); (4) Mesophilous scree forests (*Phyllitido-Aceretum*); (5) Forests of steep slopes (*Aceri-Tilietum*) and transitions to mesophilous oak-hornbeam forests (*Carici pilosae-Carpinetum*); (6) Cool and wet scree and ravine forests (*Arunco dioici-Aceretum pseudoplatani*). Using indirect ordination analysis, three environmental variables (altitude, heat load index and slope) were identified as factors of significant influence on the species composition. These factors well distinguish oak-hornbeam forests from scree and ravine forests.

**Keywords:** *Carpinion betuli*, Eastern Carpathians, forest vegetation, Pannonian Basin, phytosociology, syntaxonomy, *Tilio platyphylli-Acerion*

**Erweiterte deutsche Zusammenfassung am Ende des Artikels**

### **1. Introduction**

Mesophilous forests are considered natural vegetation with a wide potential distribution across Central Europe (BOHN et al. 2000–2003). Due to deforestation of lowland regions and the occurrence of endangered biota, some types of these forests have been recorded on the European Red List of Habitats (JANSSEN et al. 2016).

The Carpathians and their foothills are regarded as one of the centres of diversity of deciduous forest vegetation in Europe (OSZLÁNYI et al. 2004, WILLNER et al. 2009). Many regional and national phytosociological studies considering Carpathian forests have been conducted in all the Carpathian countries including Ukraine (e.g., ONYSHCHENKO 2007,

ŠEBESTA et al. 2011). Yet relatively little attention has been paid to oak-hornbeam, scree and ravine forests, which typically occur below the beech forest belt (ONYSHCHENKO 2009). Therefore, our aim was to fill this gap and describe the diversity of forest vegetation at the lower altitudes of Transcarpathia, a region in Western Ukraine comprising the southwestern slopes of the Ukrainian Carpathians and the adjacent part of the Pannonian Basin.

Local oak-hornbeam forests have been surveyed near the towns of Uzhhorod and Mukacheve, though no attention has been paid to scree and ravine forests in the studies published so far (KRAMARETS et al. 1992, ONYSHCHENKO & LUKASH 2005, VOROBYOV et al. 2008, ONYSHCHENKO 2009). In contrast, the forest vegetation in adjacent areas of the Pannonian-Carpathian transitional zone in neighbouring countries has been investigated fairly intensively in eastern Slovakia (e.g., HADAČ & TERRAY 1989) and north-western Romania (e.g., RAȚIU & GERGELY 1979, MARIAN 2008).

The main goals of our study are: (1) to survey the studied vegetation based on numerical analyses and to compare it with syntaxa previously described in Ukraine and adjacent countries; (2) to provide clearer understanding of the environmental factors that drive the floristic composition of the studied vegetation types in Transcarpathia.

## 2. Study area

The study area comprises the flat margins of the Pannonian Basin filled by Quaternary sediments and the Carpathian foothills. The Carpathian foothills are formed of three geologically distinct zones (from lowland to upland parts) starting with the Vihorlat–Gutâi Belt composed of volcanic hills and ridges with prevailing andesite, basalt and dacite. Towards the north-east, this belt is followed by a large region of Carpathian flysch comprising the highest peaks of the Ukrainian Carpathians. Between these two zones, the Pieniny Klippen Belt composed of Mesozoic limestone appears locally at the surface (ANDÓ 1999). Relevés were recorded at sites of various types of bedrock with the exception of flysch.

The region is situated in a climatically transitional zone between the continental Pannonian Basin with dry and hot summers and the mountain climate of the Carpathians with lower mean temperatures and higher precipitation (800–1,000 mm). The mean annual temperature ranges between 7 and 9.5 °C, the mean July temperature between 17 and 20 °C and the mean January temperature between -4 and -2 °C (ANDÓ 1999).

Transcarpathia is one of the most forested regions of Ukraine, though the Pannonian part has been strongly deforested in the past and current forest cover is predominantly restricted to patches in the agricultural landscape. Alluvial hardwood and willow-poplar forests in the flat lowlands and oak-hornbeam forests in the lower parts of the Carpathian foothills are regarded as natural vegetation. Beech forests prevail at higher altitudes (BOHN et al. 2000–2003, DIDUKH & SHELYAG-SOSONKO 2008). Thermophilous oak forests are locally developed on the steep and sunny slopes of volcanic hills (FODOR 1958, STOYKO 2009). Relevés were recorded along the whole altitudinal gradient of oak-hornbeam forests and in the lower part (120–625 m a.s.l.) of the altitudinal range of scree and ravine forests.

Flora and vegetation of the Transcarpathian lowlands differ significantly from the rest of Ukraine due to strong influences from neighbouring Pannonian and Carpathian regions (e.g., FODOR 1958, 1974, KRICSFALUSY 1999, ONYSHCHENKO 2009). This is reflected in the geobotanical zonation of Ukraine, where the lower altitudes of Transcarpathia belong to the distinctive Pannonian Province, which is part of the Eurasian Steppe Region (DIDUKH & SHELYAG-SOSONKO 2008).

## 3. Methods

### 3.1 Vegetation sampling

In June 2016, we conducted an extensive field survey in a transect 80 km long and 30 km wide between the cities of Mukacheve and Bushtyno (48°03'–48°35' N, 22°36'–23°37' E) and the study area (approximately 2,400 km<sup>2</sup>) thus comprises a major part of the low-altitudinal areas of Transcarpathia. The survey focused on the vegetation of oak-hornbeam (alliance *Carpinion betuli*) and scree and ravine forests (*Tilio platyphylli-Acerion*). These forests have a tree layer dominated by *Carpinus betulus*, *Quercus petraea*, *Q. robur* or noble hardwood trees such as *Acer* spp., *Fraxinus excelsior*, *Tilia* spp. and *Ulmus glabra*.

Vegetation was sampled following the Braun-Blanquet approach (DENGLER et al. 2008). Each relevé ( $n = 54$ ) had a uniform area size of 100 m<sup>2</sup>. First, the percentage cover of each vegetation layer was estimated. Subsequently, the cover of each species was estimated using the extended nine-degree Braun-Blanquet cover-abundance scale (DENGLER et al. 2008). Cryptogams were not determined. Basic environmental variables (aspect and inclination of slope, percentage of rocks) were recorded for all relevés, as well as coordinates (WGS-84) taken using a GPS receiver. Furthermore, we took a mixed soil sample within each relevé (from the uppermost 15 cm at four places within the site). Subsequently, the pH of dried soil samples was measured in a water suspension (2:5) by portable instruments (GMH Greisinger). The heat load index (HLI) indicating the potential heat load of a given site based on its slope and aspect was calculated for each relevé using Equation 3 in MCCUNE & KEON (2002). Relevés from our field work were saved in TURBOVEG 2.0 (HENNEKENS & SCHAMINÉE 2001) and further analysed, primarily with the use of JUICE 7.0 (TICHÝ 2002). To obtain a more representative dataset, we included and digitized relevés of oak-hornbeam or scree and ravine forests ( $n = 22$ ) from the study area published by ONYSHCHENKO & LUKASH (2005). Although the area size of these relevés (150–1,600 m<sup>2</sup>) differed from ours, their species richness was similar. Sampled twice – in spring and summer – relevés from ONYSHCHENKO & LUKASH (2005) contain several vernal species that we missed during our field work carried out in June. Therefore we excluded vernal species (VYMAZALOVÁ et al. 2016) from relevés originating from the given study in order to make the two datasets comparable.

We did not include relevés of oak-hornbeam forests from Transcarpathia published by VOROBYOV et al. (2008) due to the lack of any site information other than species covers.

The final dataset used for numerical analyses contained 76 relevés of oak-hornbeam, scree and ravine forest vegetation from Transcarpathia. Tree and shrub species recorded in the herb layer were deleted from all the relevés and subsequently all layers were merged into a single layer prior to analyses. The nomenclature of taxa follows the Euro+Med PlantBase (<http://ww2.bgbm.org/EuroPlusMed/>; accessed 2017-01-12) and supplemented by The Plant List (<http://www.theplantlist.org>; accessed 2017-01-12) for those families not yet covered in Euro+Med PlantBase.

### 3.2 Data analyses

#### 3.2.1 Classification analyses

For classification, we first computed TWINSpan with pseudospecies cut levels set at 0, 1, 5 and 25% cover (HILL & ŠMILAUER 2005) to distinguish the two main vegetation types the study is concerned with – oak-hornbeam forests (*Carpinion betuli*) and scree and ravine forests (*Tilio platyphylli-Acerion*). Due to the different levels of heterogeneity within each of those two main clusters, we classified each of them separately.

We tried several approaches with various classification algorithms, intersample distance measures and cover-abundance transformations. All methods used produced relatively similar results. Finally, we followed the formalized OptimClass 1 method (TICHÝ et al. 2010). Subsequently, we selected the final number of subclusters being relatively homogeneous from both the ecological and geographical point of view. Within each of the two main clusters, the optimal classification was achieved using a different classification method. For classification of oak-hornbeam forests, we used the beta-flexible algorithm

(beta = -0.25) and Bray-Curtis index as a measure of distance between relevés, with logarithmically transformed cover values. The classification was performed using PC-ORD (MCCUNE & MEFFORD 1999) incorporated in JUICE. For the classification of scree and ravine forests, we applied modified TWINSpan (ROLEČEK et al. 2009) with the same cut levels as in the first case. The final number of subclusters within each of the main clusters was three.

The interpretation of the species composition and structure of subclusters was based on diagnostic, constant and dominant species. The *phi* coefficient (SOKAL & ROHLF 1995) was calculated for the identification of diagnostic species. Species with a *phi* coefficient higher than 0.5 were accepted as being highly diagnostic and species with a *phi* coefficient higher than 0.2 were considered diagnostic. Fisher's exact test (alpha = 0.01) was used to exclude rarely occurring species from the lists of diagnostic species. As the identification of diagnostic species depends on the size of the given subcluster, the sizes of all subclusters were virtually standardized so as to be equal (TICHÝ & CHYTRÝ 2006). The diagnostic species of the two main clusters were identified in the same way.

Differences in Borhidi indicator values (BIVs; BORHIDI 1995), the covers of each layer, environmental variables and species richness among distinguished subclusters were tested using Kruskal-Wallis ANOVA in the software Statistica (STATSOFT 2006). As BIVs are connected with species composition, ANOVA results were checked using a permutation approach (ZELENÝ & SCHAFFERS 2011;  $p_{\text{modif}} \leq 0.05$ ). Subsequently, multiple comparison tests of mean ranks were calculated to distinguish groups of homogenous subclusters for variables with significant differences among subclusters (alpha = 0.05). Boxplots of selected variables with the most significant differences within subclusters are shown.

The results were syntaxonomically interpreted using the Ukrainian phytosociological literature (mainly ONYSHCHENKO 2009) and selected studies from nearby countries (e.g., HADAČ & TERRAY 1989, OBERDORFER 1992, MATUSZKIEWICZ 2001, JAROLÍMEK & ŠIBÍK 2008, WILLNER & GRABHERR 2007, BORHIDI et al. 2012, CHYTRÝ 2013, COLDEA et al. 2015).

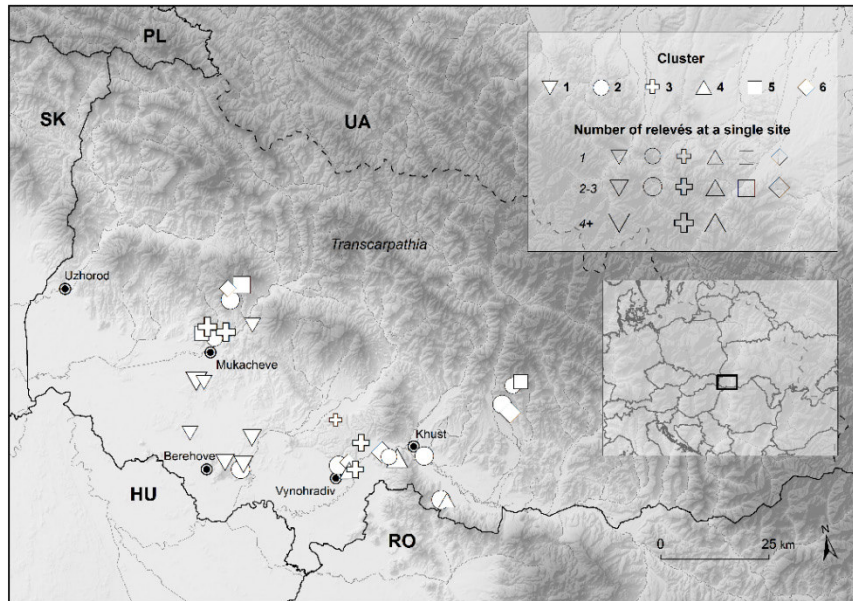
### 3.2.2 Ordination analysis

We performed Detrended Correspondence Analysis (DCA) in CANOCO 4.5 (TER BRAAK & ŠMILAUER 2002) to facilitate the ecological interpretation of subclusters. Species cover values were logarithmically transformed before the analysis. The length of the first DCA axis was 3.469 which suggested that ordination methods assuming the unimodal response of species to the environmental gradient were appropriate. Both the environmental variables (only those available for all relevés – altitude, heat load index and slope) and covers of all vegetation layers that were significantly correlated (Spearman's correlation,  $r_s$ , alpha = 0.01) with at least one of the first two axes were passively projected onto the ordination space. Borhidi indicator values for continentality, light, moisture, nutrients, soil reaction and temperature were used. BIVs were proposed for the flora of Hungary which is highly similar to the low-altitudinal parts of Transcarpathia, which is why we preferred these values over the Didukh indicator values (DIDUKH 2011) calibrated for the territory of Ukraine. We worked with unweighted means of BIVs for each relevé. The significance of the correlations of BIVs with the two first DCA axes was checked using the permutation approach (ZELENÝ & SCHAFFERS 2011).

## 4. Results and discussion

### 4.1 Overview of species composition and forest types

In total, the dataset contained 210 species. The most frequent species were: *Carpinus betulus* (71 records), *Rubus* subgen. *Rubus* (58), *Lamium galeobdolon* (53), *Anemone nemorosa* (49), *Cardamine bulbifera* (43), *Galium odoratum* (41), *Polygonatum multiflorum* (40), *Fagus sylvatica* (38), *Dryopteris filix-mas* (37), *Carex pilosa* (35), *Viola reichenbachiana* (34), *Corylus avellana* (32), *Hedera helix* (31) and *Stellaria holostea* (31). Forest meso-



**Fig. 1.** Distribution map of relevés of subclusters 1–6 (for corresponding associations see text) based on analysed dataset ( $n = 76$ ).

**Abb. 1.** Verbreitungskarte der klassifizierten Vegetationsaufnahmen ( $n = 76$ ) der Teilgruppen 1–6 (korrespondierende Assoziationen siehe Text).

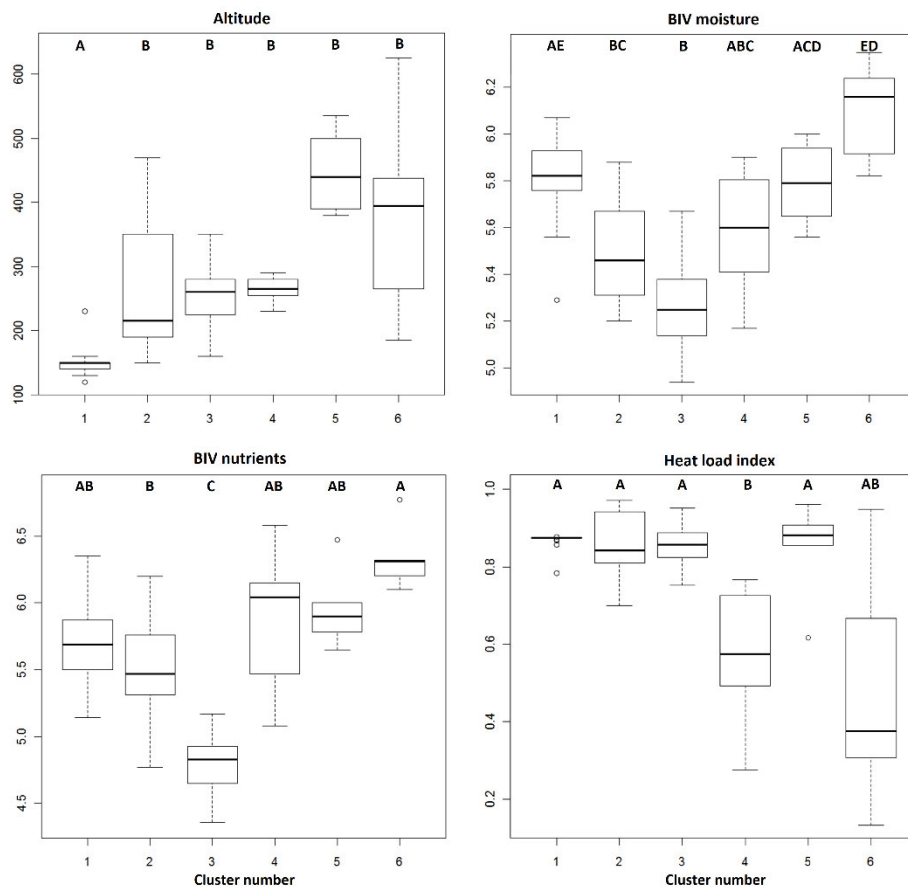
phytes obviously highly prevailed. Besides common species, several species of the Red List of the Ukrainian flora (DIDUKH 2009) were recorded (*Asplenium adiantum-nigrum*, *Cephalanthera longifolia*, *Drymochloa drymeja*, *Lathyrus transsilvanicus*, *Lunaria rediviva*, *Scopolia carniolica*). *Geranium lucidum* was discovered as a new species for Transcarpathian Ukraine (cf. FODOR 1974).

Using TWINSpan, we distinguished two main clusters that corresponded well to phytosociological alliances: the first cluster of 54 relevés to *Carpinion betuli*, the second cluster of 22 relevés to *Tilio platyphylli-Acerion*. Three subclusters were identified in each of these two clusters and further interpreted at association level. A list of the diagnostic species of each cluster and subcluster as well as frequent species of the dataset are shown in Supplement S1. For relevés recorded in 2016 see Supplements E1–E3. The distribution of all vegetation types is summarized in Figure 1. The ecological interpretation of subclusters follows measured environmental variables and BIVs (Fig. 2 and Supplement E4). Photos of all vegetation types are provided in Figure 3.

#### 4.1.1 Main cluster 1 – Oak-hornbeam forests

##### Subcluster 1 – Eutrophic slightly wet oak-hornbeam forests (*Circaeo-Carpinetum*)

This subcluster represents oak-hornbeam forests of the lowland part of Transcarpathia. They occur on relatively fertile and deep soils with high moisture, probably due to temporarily high groundwater level, which are developed on lowland alluvial sediments. Their mean pH value is 5.1.



**Fig. 2.** Comparison of selected environmental variables and BIVs among subclusters. Mean, quartiles, standard deviation and outliers are plotted. Homogenous groups are signed with the same letters. 1 – *Circaeo-Carpinetum*, 2 – *Carici pilosae-Carpinetum*, 3 – *Carici pilosae-Carpinetum* and *Primulo veris-Carpinetum*, 4 – *Phyllitido-Aceretum*, 5 – *Aceri-Tilietum* and transitions to *Carici pilosae-Carpinetum*, 6 – *Arunco dioici-Aceretum pseudoplatani*.

**Abb. 2.** Ausgewählte Umweltvariablen und Zeigerwerte nach Borhidi im Vergleich der Teilgruppen 1–6 (Assoziationen). Die Boxplot-Diagramme zeigen Mittelwerte, Quartile, Standardabweichungen und statistische Ausreißer. Gleiche Buchstaben weisen auf nichtsignifikante Unterschiede zwischen Gruppen.

The tree layer is composed mainly of *Carpinus betulus* and *Quercus robur*. The shrub layer (cover usually below 25%) contains common shade-tolerating species (e.g., *Cornus sanguinea* and *Corylus avellana*). The herb layer is relatively dense and is dominated by forest mesophytes. In addition to these, there are also numerous moisture- and nutrient-demanding species (e.g., *Aegopodium podagraria*, *Carex brizoides* and *Circaea lutetiana*). Several subcontinental species (e.g., *Acer tataricum*, *Oenanthe banatica*) also occur in this community. The moss layer has predominantly very low cover.

We assign these relevés to the *Circaeo-Carpinetum* reported in the Pannonian Basin in Hungary including Transcarpathian borderlands (BORHIDI et al. 2012). ONYSHCHENKO (2009) describes forests of this association as zonal vegetation on the flatlands of the Pannonian Basin in Transcarpathia, and this is in agreement with our results.

#### **Subcluster 2 – Mesophilous oak-hornbeam forests (*Carici pilosae-Carpinetum*)**

This community is characteristic for the Carpathian foothills in the studied area (up to 470 m). It occurs on mesic sites, often on mild slopes. The bedrock is volcanic or limestone, the soils are rather deep and usually strongly acidic (mean soil pH 5.2).

The canopy of these forests is relatively closed, dominated mainly by *Carpinus betulus*, although the admixture of *Fagus sylvatica* and *Quercus petraea* is frequent. Common occurrence of beech could indicate the origin of some growth from beech forests under strong human pressure. The shrub layer is often well developed (mean cover approximately 10%) and mainly contains species of the tree layer and *Corylus avellana*. Concerning the herb layer (cover ranging from 15 to 70%), in addition to common forest mesophytes, there is also notable co-occurrence of subcontinental (*Carex pilosa*, *Galium intermedium*) and sub-mediterranean (e.g., *Euphorbia amygdaloides*, *Primula vulgaris*) mesophilous forest species. The moss layer is usually developed, though only with low cover.

The species composition of these forests corresponds to the *Carici pilosae-Carpinetum* which is characteristic of the western part of the Carpathian arc. It has been reported in the area between the Czech Republic and Ukraine (ONYSHCHENKO 2009, CHYTRÝ 2013).

#### **Subcluster 3 – Xero-mesophilous oak-hornbeam forests (*Carici pilosae-Carpinetum* and *Primulo veris-Carpinetum*)**

This community comprises xero-mesophilous oak-hornbeam forests on volcanic hills above the Pannonian lowland around the towns of Mukacheve and Vynohradiv. It grows mainly on warm mild slopes with strongly acidic soils (pH ranging from 4.7 to 5.3).

The tree layer is relatively open, reaching a mean cover of approximately 70%. It is predominantly composed of *Carpinus betulus* and *Quercus petraea*, with the latter even prevailing in some relevés. The shrub layer (cover mainly up to 5%) contains various species, including thermophilous ones (e.g., *Cornus mas* and *Ligustrum vulgare*). The herb layer of these forests is dominated by forest mesophytes as in Subcluster 2. In addition, there is a notable presence of xero-mesophilous acidotolerant (e.g., *Hieracium laevigatum*, *Pteridium aquilinum*) as well as slightly thermophilous species (e.g., *Lathyrus niger* and *Melittis melissophyllum*).

The majority of relevés can be assigned to a xerophilous subtype of the *Carici pilosae-Carpinetum*. In addition, some relevés (nos. 31 and 33) containing more thermophilous species are similar to the thermophilous oak-hornbeam forests of the *Primulo veris-Carpinetum* described in the volcanic hills of south-central Slovakia (NEUHÄUSL & NEUHÄUSLOVÁ-NOVOTNÁ 1964), comprising thermophilous oak-hornbeam forests of Central Europe with a distribution centre on the northern edge of the Pannonian Basin. It is recognized mainly in the Czech Republic and Slovakia, including the eastern part of the country (HADAČ & TERRAY 1989), and, according to some studies, also in Austria (CHYTRÝ 2013). Several similar associations are also recognized in Hungary (BORHIDI et al. 2012). It has not yet been distinguished in Ukraine (cf. ONYSHCHENKO 2009) and is, therefore, the first record based on original field data.



**Fig. 3.** Photos of forest vegetation of particular subclusters distinguished in Transcarpathian Ukraine **a)** Lowland slightly wet oak-hornbeam forests of the association *Circaeo-Carpinetum* (Subcluster 1) near the village of Pavshino in the Mukacheve District; **b)** Mesophilous oak-hornbeam forests of the association *Carici pilosae-Carpinetum* (Subcluster 2) on the western slope of the Chorna hora Mt. above the town of Vynohradiv; **c)** Xero-mesophilous oak-hornbeam forest of the association *Carici pilosae-Carpinetum* (Subcluster 3) on the upper terrace of the Tisa River at the village of Velyka Kopanya in the Vynohradiv District; **d)** Scree forest of the association *Phyllitido-Aceretum* (Subcluster 4) on slope above of the Tisa River near the village of Kryva in the Khust District; **e)** Slope forest from the Subcluster 5 in Matekova River valley near the village of Syniak in the Mukacheve District and **f)** Edge of a scree forest with *Aruncus dioicus* of the association *Arunco-Aceretum* (Subcluster 6) developed on the slope above the Tisa River near the village of Kryva in the Khust District (All photos: P. Novák, June 2016).



#### 4.1.2 Main cluster 2 – Scree and ravine forests

##### Subcluster 4 – Mesophilous scree forests (*Phyllitido-Aceretum*)

This group comprises scree forests of lower volcanic hills in the deep Tisa River valley between the towns of Khust and Vynohradiv. Relevés of this group were recorded predominantly on slopes of inclinations from 10 to 45° with strongly acidic soil (pH ranging from 4.4 to 7.2).

The canopy cover of these forests varies among sites, ranging from 55 to 95%. They are dominated by *Acer pseudoplatanus* and *Carpinus betulus* with *Fagus sylvatica* or *Ulmus glabra* being frequent admixtures. The shrub layer is often well developed, containing mainly *Corylus avellana* and young trees. The cover of the herb layer varies greatly among the studied sites (15–70%), depending on the occurrence and size of boulders and blocks of rock. The presence of scree favours chasmophytes, both herbs (e.g., *Arabidopsis arenosa* and *Hylotelephium maximum*) and ferns (e.g., *Asplenium scolopendrium*, *Cystopteris fragilis* and *Polypodium vulgare*). In addition to chasmophytes, nutrient-demanding species (e.g., *Geranium robertianum* and *Scopolia carniolica*) are also frequent. The moss layer is developed and its cover varies from 3 to 55% in the sites of our relevés.

Scree forests with frequent occurrence of the ferns *Asplenium scolopendrium*, *Polypodium vulgare* and *Polystichum aculeatum* have been classified as *Phyllitido-Aceretum* Moor 1945 (MATUSZKIEWICZ 2001, WILLNER & GRABHERR 2007, ONYSHCHENKO 2009). This association comprises scree forests of narrow ravines mainly on limestone. It includes moisture-demanding species among others. Our relevés lack most of these species, though they are characterized by the frequent occurrence of several diagnostic species of this association (mainly the above-mentioned fern species). The relatively warm climate of the sampled sites could be the reason for the lower frequency of species with higher moisture requirements. We therefore consider most of the relevés of this subcluster as being on the margin of the variation range of the *Phyllitido-Aceretum*.

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**Abb. 3.** Fotos der Waldvegetation bestimmter in der transkarpatischen Ukraine unterschiedener Untercluster **a)** Feuchter Eichen-Hainbuchenwald des Tieflands des *Circaeo-Carpinetum* (Subcluster 1) beim Dorf Pashino im Distrikt Mukacheve; **b)** Mesophiler Eichen-Hainbuchenwald des *Carici pilosae-Carpinetum* (Subcluster 2) am Westabhang der Chomabergs oberhalb der Stadt Vynohradiv; **c)** Xeromesophiler Eichen-Hainbuchenwald des *Carici pilosae-Carpinetum* (Subcluster 3) auf der oberen Terasse des Tisa-Flusses beim Dorf Velyka Kopanya im Distrikt Vynohradiv; **d)** Blockschuttwald des *Phyllitido-Aceretum* (Subcluster 4) auf einem Hang über dem Tisa-Fluss beim Dorf Kryva im Distrikt Khust; **e)** Hangwald im Subcluster 5 im Matekova-Flusstal beim Dorf Syniak im Distrikt Mukacheve und **f)** Saum eines zum *Arunco-Aceretum* gehörenden Blockschuttwaldes mit *Arunco dioicus* (Subcluster 6) auf dem Hang über dem Tisa-Fluss beim Dorf Kryva im Distrikt Khust (Alle Fotos: P. Novák, Juni 2016).

#### **Subcluster 5 – Slope forests (*Aceri-Tilietum*) and transitions to mesophilous oak-hornbeam forests (*Carici pilosae-Carpinetum*)**

This group includes several relevés of forests on slopes of moderate inclination (15–25°) and of relatively flat places at the foot of slopes with skeletal soil. The community was recorded in the Krychovo and Mukacheve surroundings. The bedrock of this vegetation is volcanic or limestone, though the soils tend to be rather acidic (mean pH approximately 4.9).

The canopy of this group is relatively closed (75–95%), dominated by *Carpinus betulus*, with *Acer pseudoplatanus* or *Fagus sylvatica* usually admixed. The shrub layer has a mean cover of approximately 10%, containing predominantly younger individuals of the tree species and *Corylus avellana*. The herb layer is usually dense, with a cover above 60% – the highest of all the subclusters. It is composed mainly of oak-hornbeam forest elements (e.g., *Anemone nemorosa*, *Cardamine bulbifera* and *Carex pilosa*) with a notable presence of species with higher nutrient requirements (e.g., *Aegopodium podagraria*, *Mercurialis perennis* and *Pulmonaria obscura*). Ferns (mainly *Dryopteris filix-mas*) are also common. Mosses cover up to 5%.

Central European slope forests of lower altitudes with a high proportion of *Carpinus betulus*, noble hardwood tree species, oak-hornbeam forest species and nitrophytes are usually assigned to the *Aceri-Tilietum* Faber 1936. This association is recognized in Germany (OBERDORFER 1992), Austria (WILLNER & GRABHERR 2007), the Czech Republic (CHYTRÝ 2013), Poland (MATUSZKIEWICZ 2001) and, under the name *Aceri-Carpinetum* Klika 1941, Slovakia (JAROLÍMEK & ŠIBÍK 2008). However, if we examine the data in more detail, only relevé no. 45 with noble hardwoods prevailing can be clearly assigned to the *Aceri-Tilietum*, while the other four relevés of this group are dominated by *Carpinus betulus*. Moreover, one of these four relevés is dominated by *Festuca drymeja* and another two relevés are co-dominated by *Carex pilosa*, indicating that they should rather be classified into the alliance *Carpinion betuli*. On the other hand, these relevés contain species typical for scree and ravine forests (e.g., *Lunaria rediviva*, *Polystichum aculeatum* and *Symphytum cordatum*), in addition to other nutrient-demanding species and ferns. We assume, therefore, that relevé no. 45 belongs to the *Aceri-Tilietum*, while the other relevés of this subcluster are transitional between *Aceri-Tilietum* and oak-hornbeam forests of the *Carici pilosae-Carpinetum*.

#### **Subcluster 6 – Cool and wet scree and ravine forests (*Arunco dioici-Aceretum pseudoplatani*)**

This community comprises scree and ravine forests recorded on the slopes of the Tisa River valley and in narrow ravines above streams. It is developed on rather steep slopes (usually between 30 and 50°) on sites where beech is probably suppressed by solifluction. Mean soil pH of the sites is approximately 5.9, the highest among studied communities.

The tree layer of this group has variable cover (40–95%) and is composed mainly of *Acer pseudoplatanus* and *Fagus sylvatica*, while other tree species are less frequent (e.g., *Carpinus betulus*, *Fraxinus excelsior* and *Ulmus glabra*). The shrub layer is usually well-developed, composed of *Corylus avellana*, *Sambucus nigra* and young tree. The herb layer is also typically dense (50–75%), and is comprised of moisture- and nutrient-demanding species (e.g., *Arunco dioicus*, *Impatiens noli-tangere* and *Lunaria rediviva*), typical herbs of the Carpathian beech forests (*Cardamine glanduligera*, *Symphytum cordatum*) and ferns (*Athyrium filix-femina*, *Dryopteris filix-mas*, *Polystichum aculeatum*). The cover of the moss layer varies among our relevés.

Two possible associations correspond to the relevés in this subcluster: *Arunco dioici-Aceretum pseudoplatani* Moor 1952 and *Lunario-Aceretum* Schlüter in Grüneberg et Schlüter 1957. However, some authors consider them synonyms (e.g., ONYSHCHENKO 2009, CHYTRÝ 2013) or the latter as a subtype of the former (WILLNER & GRABHERR 2007). Since both associations occur on similar sites and their species composition is very similar (as also documented by the assignment of our relevés with *Aruncus dioicus* to the same subcluster as those with *Lunaria rediviva*), we agree that the *Lunario-Aceretum* should be considered a synonym of the *Arunco dioici-Aceretum pseudoplatani*.

#### 4.1.3 Syntaxonomical system

The syntaxonomical interpretations of clusters, on which the syntaxonomical system stated below is based, were adopted from syntaxa recognized in the Western Carpathians and surrounding regions (e.g., ONYSHCHENKO 2009, BORHIDI et al. 2012, CHYTRÝ 2013). Comparing the studied vegetation in Transcarpathia with analogous vegetation in adjacent areas in Romania (COLDEA et al. 2015), it was obvious that relevés in Romania are richer in Eastern Carpathian and Balkan elements (e.g., *Galium pseudaristatum*, *Melampyrum bihariense*, *Lathyrus hallersteinii*), for what reason we worked mainly with syntaxa distinguished in the western part of the Carpathians. Above association level, the system follows MUCINA et al. (2016).

Class *Carpino-Fagetea* Jakucs ex Passarge 1968

Order 1. *Carpinetalia betuli* P. Fukarek 1968

Alliance 1.1. *Carpinion betuli* Issler 1931

Association 1.1.1. *Circaeo-Carpinetum* Borhidi 2003

Association 1.1.2. *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964

Association 1.1.3. *Primulo veris-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964

Order 2. *Aceretalia pseudoplatani* Moor 1976

Alliance 2.2. *Tilio platyphylli-Acerion* Klika 1955

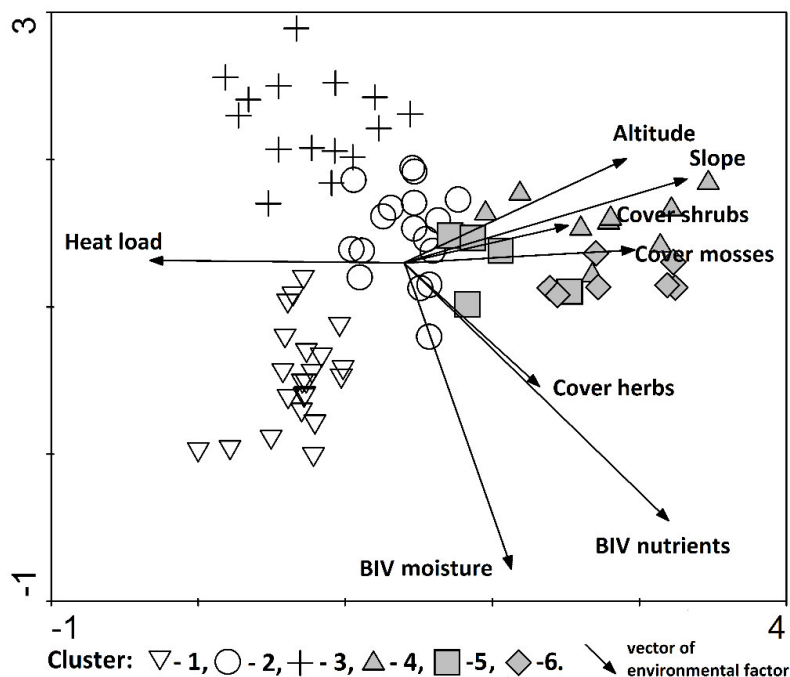
Association 2.2.1. *Phyllitido-Aceretum* Moor 1945

Association 2.2.2. *Aceri-Tilietum* Faber 1936

Association 2.2.3. *Arunco dioici-Aceretum pseudoplatani* Moor 1952

#### 4.2 The relationship between vegetation and measured environmental factors

The first DCA ordination axis explained 7.4% of the variance in the species composition of relevés (Fig. 4). The second axis explained 5.0% of variance, and the first four axes together explained 18.3% of variance. The first ordination axis was positively correlated ( $p \leq 0.01$ ) with the cover of the moss layer ( $r_s = 0.73$ ), slope (0.71), altitude (0.62), cover of shrub layer (0.42) and the indicator value for nutrients (0.51). A negative correlation ( $p \leq 0.01$ ) was shown for the heat load index (-0.44). The first axis is interpreted to visualize a complex environmental gradient specifying the local distribution of oak-hornbeam and scree and ravine forests in the landscape of Transcarpathia (zonal habitats vs. shady rocky slopes, respectively).



**Fig. 4.** Detrended Correspondence Analysis (DCA) of relevés from the final dataset. Environmental variables correlated with at least one of the first two ordination axes ( $p \leq 0.01$ ) were plotted into the diagram. Subcluster numbers as in Figure 2.

**Abb. 4.** Detrended Correspondence Analysis (DCA) der Vegetationsaufnahmen. Umweltvariablen, die mit wenigstens einer der beiden Ordinationsachsen korreliert sind, wurden nachträglich im Diagramm aufgetragen. Nummern der Teilgruppen wie in Abbildung 2.

The second axis was positively correlated with altitude (0.51) and slope (0.49) and negatively with indicator values for moisture (-0.79), nutrients (-0.60) and the cover of the herb layer (-0.39). The second axis can be interpreted to represent a complex gradient combining soil moisture and nutrient availability.

The main clusters are fairly well distinguished by their position along the first ordination axis. Oak-hornbeam forests, situated on the left side of the plot, prefer flat terrain or mild slopes and sites with higher heat load. On the other hand, scree and ravine forests, situated on the right side of the plot, are confined mainly to steep and shady slopes, often with rock outcrops as is indicated by higher moss cover.

The DCA results corresponded well with our classification of oak-hornbeam forests in which associations were distinguished mainly by soil moisture and nutrients. Relevés of the wetter type (Subcluster 1) were situated in the lower part of the diagram, those of the mesophilous type (Subcluster 2) in the central part, and those of the drier type (Subcluster 3) in the upper part.

Scree and ravine forests represented a rather homogeneous group within our dataset. They were distributed mainly along the first axis. Relevés of Subcluster 5 were distributed mainly between oak-hornbeam forests and the rest of scree and ravine forests, indicating their transitional character between the two alliances. The results of indirect gradient analysis were in agreement with the results of classification.

#### 4.3 Previously reported associations in Transcarpathia – a comparison with the proposed classification system

As we performed numerical classification of our relevés with previously published data from the Mukacheve surroundings (ONYSHCHENKO & LUKASH 2005), relevés from both sources were clustered together and their syntaxonomical interpretation was similar.

In recent decades, several phytosociological studies considering the forest vegetation of Transcarpathia have been carried out. Within the *Carpinion betuli*, the previously mentioned central position of mesophilous oak-hornbeam forests of the *Carici pilosae-Carpinetum* in Transcarpathia (KRICSFALUSY 1999, ONYSHCHENKO & LUKASH 2005, ONYSHCHENKO 2009) was confirmed by our study. This vegetation has also been reported under the synonym *Brachypodio sylvatici-Quercetum petraeae* (KRAMARETS et al. 1992, VOROBYOV et al. 2008). It is also a leading type of oak-hornbeam forests in the adjacent part of Eastern Slovakia (HADAČ & TERRAY 1989). In addition to *Carici pilosae-Carpinetum*, KRICSFALUSY (1999) mentioned the *Melampyro nemorosi-Carpinetum* Passarge 1962, which is currently believed to be a synonym of the association *Galio sylvatici-Carpinetum*, including the oak-hornbeam forests of the western part of Central Europe (CHYTRÝ 2013). They contain species characteristic of western Central Europe (e.g., *Galium sylvaticum* or *Potentilla sterilis*) which are rare or missing in the flora of Transcarpathia (cf. FODOR 1974). We conclude that the *Galio sylvatici-Carpinetum* does not occur in the study area.

Lowland slightly wet oak-hornbeam forests have been reported in Transcarpathia as *Fraxino pannonicae-Carpinetum* Soó & Borhidi 1962 in some studies (ONYSHCHENKO & LUKASH 2005, OMELCHUK 2016). This association was described in the Illyrian part of Hungary and comprises slightly wet oak-hornbeam forests with a higher frequency of submediterranean elements (BORHIDI et al. 2012) which do not occur in the study area (cf. FODOR 1974). The more suitable name *Circaeo-Carpinetum* was used for these forests in the synopsis of mesophilous forest vegetation in Ukraine (ONYSHCHENKO 2009).

Some xero-mesophilous oak-hornbeam forests are close to the *Primulo veris-Carpinetum*; this association has not yet been mentioned on the basis of Ukrainian field data (ONYSHCHENKO 2009). There is a single mention in a study by OMELCHUK (2016), accompanied only by a list of diagnostic species. According to these species and the indicated ecology (river banks), it seems to be similar to the *Circaeo-Carpinetum*.

Concerning the alliance *Tilio-Acerion*, ONYSHCHENKO (2009) reported four associations of the alliance *Tilio platyphylli-Acerion* occurring in Ukraine, though only two of these can be expected to occur in the Carpathians: *Arunco-Aceretum* and *Phyllitido-Aceretum*. Although his work lacks relevés from the study area, we can confirm that these associations occur in this area. In addition, there is a single report of the association *Aceri-Carpinetum* in Transcarpathia (KRICSFALUSY 1999), though without relevés. Our results confirm that this association, believed to be a synonym of the *Aceri-Tilietum*, occurs in this area.

### Erweiterte deutsche Zusammenfassung

**Einleitung** – Mesophile Wälder Transkarpatiens (Karpaten-Ukraine) sind bisher kaum untersucht worden, obwohl sie ausgedehnt und recht gut erhalten sind. Wir haben daher im Juni 2016 die Eichen-Hainbuchen-Wälder, Hangschutt- und Schluchtwälder untersucht.

**Untersuchungsgebiet** – Wir untersuchten die niederen Lagen Transkarpatiens zwischen 120 und 625 m ü.M. Das Gebiet umfasst die weitgehend entwaldete Quartärebene des Pannonischen Beckens und das bewaldete Karpatenvorland. Die Aufnahmen aus dem Karpatenvorland stammen von Standort-

ten über Vulkangestein und mesozoischem Kalk. Das Klima zeichnet sich durch heiße Sommer und relativ milde Winter aus. Das Temperatur-Jahresmittel liegt bei 7 bis 9,5 °C; die Jahresniederschläge (800–1000 mm) sind selbst in den tieferen Lagen relativ hoch.

Methoden: Der Datensatz wurde aus eigenen Vegetationsaufnahmen von 2016 (54 Probeflächen; jeweils 100 m<sup>2</sup>; mit pH-Messungen) und Aufnahmen aus einer Untersuchung von ONYSHCHENKO & LUKASH (2005; 22 Flächen) zusammengestellt. Ungewichtete mittlere Zeigerwerte nach Borhidi (1995) wurden berechnet. Eichen-Hainbuchen-Wälder wurden mit einem agglomerativ-hierarchischen Verfahren (*beta-flexible algorithm*) klassifiziert, Hangschutt- und Schluchtwälder mit TWINSPAN (modifiziert nach ROLEČEK et al. 2009). Beziehungen zwischen Artenzusammensetzung und Umweltfaktoren wurden mittels der indirekten Gradientenanalyse DCA dargestellt.

**Ergebnisse** – Der Datensatz enthält 210 Gefäßpflanzenarten. Sechs Teilgruppen wurden klassifiziert (Fig. 1, Anhang S1), nämlich drei Gruppen von Eichen-Hainbuchen-Wäldern und drei Gruppen Hangschutt- und Schluchtwälder. Erstere umfassen folgende Gruppen: a) Schwach feuchte eutrophe Ei-Hb-Wälder des pannonischen Beckens mit *Carpinus betulus* und *Quercus robur* (*Circaeo-Carpinetum*), b) Mesophile Ei-Hb-Wälder mit Buchen-Beimischung auf Kalk und Vulkanit im Karpatenvorland (*Carici pilosae-Carpinetum*) und c) Xero-mesophile Ei-Hb-Wälder an warmen Vulkangesteinshängen des Karpatenvorlandes mit thermophilen Arten in der Krautschicht und *Quercus petraea* als kodominanter Baumart (*Carici pilosae-Carpinetum* und *Primulo veris-Carpinetum*).

Die azonalen Hangschutt- und Schluchtwälder, gekennzeichnet durch Edellaubbäume, nährstoffanspruchsvolle Arten sowie Farne, umfassen folgende Gruppen: a) Mesophile Blockhangwälder mit Felsspaltpflanzen (*Phyllitido-Aceretum*) und b) Schluchtwälder im Übergang von mesophilen Ei-Hb-Wäldern (*Carici pilosae-Carpinetum*, *Carpinion betuli*) und *Aceri-Tilietum* (*Tilio platyphylli-Acerion*) - Steilhangwälder oberhalb von Wasserläufen mit Feuchtezeigern und Arten der karpatischen Buchenwälder (*Arunco dioici-Aceretum pseudoplatani*).

Eine indirekte Gradientenanalyse (DCA) zeigte, dass Ei-Hb-Wälder vor allem entlang der zweiten Ordinationsachse angeordnet sind, welche einen Feuchte- und Nährstoffgradienten nachzeichnet. Hangschutt- und Schluchtwälder verteilen sich vor allem entlang der ersten Ordinationsachse. Diese Achse lässt sich als Gradient der Verteilung in der Landschaft deuten, da diese Wälder kühlere Lagen und felsige Steilhänge in höheren Lagen bevorzugen.

**Diskussion** – Die unterschiedenen Gruppen ließen sich im Kontext zentraleuropäischer Syntaxa interpretieren, wie sie in den nationalen Übersichten von WILLNER & GRABHERR (2007), BORHIDI et al. (2012) und CHYTRÝ (2013) publiziert wurden. Zwei Assoziationen – *Primulo veris-Carpinetum* (thermophile Ei-Hb-Wälder) und *Aceri-Tilietum* (Schluchtwälder des Tieflandes) – wurden erstmals für die Ukraine mit Aufnahmen belegt (cf. ONYSHCHENKO 2009). Mittels Gradientenanalyse (DCA) wurden Höhe ü.M., *heat load* und Hangneigung als für die Artenzusammensetzung wichtige Umweltfaktoren erkannt. Diese Faktoren trennen die beiden Hauptgruppen deutlich – Ei-Hb-Wälder sowie Hangschutt- und Schluchtwälder, und sie bestimmen ihre weitere Verbreitung in den tieferen Lagen des südlichen Zentraleuropas.

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## Supplements

**Supplement S1.** Synoptic table of subclusters (associations) and main clusters (alliances).

**Beilage S1.** Synoptische Tabelle der klassifizierten Teilgruppen (Assoziationen) und Hauptgruppen (Verbände).

**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.** Table of relevés recorded in 2016 and classification of relevés published in ONYSHCHENKO & LUKASH (2005) which were used in analyses.

**Anhang E1.** Tabelle der 2016 angefertigten Vegetationsaufnahmen und in ONYSHCHENKO & LUKASH (2005) publizierte Klassifikation der Aufnahmen, die für die Analysen verwendet wurden .

**Supplement E2.** Localities of relevés recorded in 2016.

**Anhang E2.** Lokalitäten der 2016 angefertigten Vegetationsaufnahmen.

**Supplement E3.** Additional information about altitude, slope, aspect, soil pH, cover of each layer and number of species for relevés recorded in 2016.

**Anhang E3.** Zusätzliche Informationen über Höhenlage, Inklination, Exposition, Boden-pH, Wärmebelastungsindex, Deckungsgrad der Schichten und Artenzahl für die 2016 angefertigten Vegetationsaufnahmen.

**Supplement E4.** Comparison of BIVs, cover of all vegetation layers, environmental variables and number of species amongst clusters.

**Anhang E4.** Vergleich der Zeigerwerte nach Borhidi (BIVs), Deckungsgrad aller Vegetationsschichten, Umweltvariablen und Artenzahlen zwischen den Clustern.

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**Supplement E2.** Localities of relevés recorded in 2016.**Anhang E2.** Lokalitäten der 2016 angefertigten Vegetationsaufnahmen.

Relevé number	date	locality (municipality)	latitude (degrees N)	longitude (degrees E)
1	11 June 2016	Pavshyno	48.38825	22.6747222
2	11 June 2016	Mala Byihan	48.2839139	22.6132778
3	6 June 2016	Kvasovo	48.2004722	22.7624167
4	10 June 2016	Nizhni Remety	48.2529167	22.8013889
5	10 June 2016	Kidesh	48.2093333	22.7048611
6	10 June 2016	Vilkhovytsia	48.4816944	22.8617778
7	6 June 2016	Kvasovo	48.1995611	22.7605278
8	10 June 2016	Nyzhni Remety	48.2538194	22.7998194
9	10 June 2016	Kidesh	48.2159306	22.7082889
10	6 June 2016	Kvasovo	48.1998917	22.7609444
11	7 June 2016	Vynohradiv	48.1619667	23.0520833
12	9 June 2016	Shaian	48.0583	23.354025
13	9 June 2016	Chust	48.1679722	23.2956944
14	9 June 2016	Shaian	48.0599	23.3549389
15	9 June 2016	Shaian	48.0598306	23.3549306
16	10 June 2016	Mukacheve	48.4688056	22.7375278
17	9 June 2016	Khust	48.1666806	23.2962
18	6 June 2016	Kvasovo	48.1968056	22.7588889
19	10 June 2016	Dubino	48.5409167	22.8005556
20	10 June 2016	Dubino	48.5390833	22.7992778
21	8 June 2016	Kryva	48.1707667	23.20925
22	8 June 2016	Rososh	48.2292778	23.5938889
23	7 June 2016	Bukove	48.766333	23.0772
24	7 June 2016	Vynohradiv	48.16125	23.0535833
25	6 June 2016	Kvasovo	48.1977222	22.757875
26	9 June 2016	Mala Uholka	48.2566944	23.62575
27	8 June 2016	Rososh	48.2203333	23.5920556
28	7 June 2016	Velika Kopanya	48.2034333	23.1314
29	8 June 2016	Vilkhivka	48.2585667	23.0671833
30	7 June 2016	Mala Kopanya	48.1626667	23.0790056
31	6 June 2016	Vynohradiv	48.1566944	23.0930556
32	7 June 2016	Velyka Kopanya	48.2028	23.1326167
33	7 June 2016	Mala Kopanya	48.1632917	23.0817917
34	8 June 2016	Kryva	48.1698833	23.2133167
35	6 June 2016	Vynohradiv	48.1517778	23.08375
36	8 June 2016	Kryva	48.1690333	23.2193833
37	8 June 2016	Kryva	48.1694333	23.2150667
38	8 June 2016	Kryva	48.16855	23.2175167
39	7 June 2016	Vynohradiv	48.1617167	23.0507833
40	8 June 2016	Kryva	48.1691	23.2158833
41	9 June 2016	Shaian	48.0637694	23.3587
42	8 June 2016	Kryva	48.1689	23.2179
43	6 June 2016	Vynohradiv	48.1515833	23.0839167
44	8 June 2016	Mala Uholka	48.2618611	23.6320556
45	10 June 2016	Syniak	48.5624361	22.8404667
46	10 June 2016	Syniak	48.56075	22.8412222
47	10 June 2016	Syniak	48.5736667	22.8439722
48	8 June 2016	Kryva	48.17575	23.19525
49	10 June 2016	Dubyno	48.5646944	22.8045556
50	8 June 2016	Kryva	48.16995	23.209
51	7 June 2016	Mala Kopanya	48.1622222	23.0811389
52	8 June 2016	Kryva	48.1780833	23.1884667
53	9 June 2016	Rososh	48.2201556	23.5946861
54	9 June 2016	Rososh	48.22925	23.5929444

**Supplement E3.** Additional information about altitude, slope, aspect, soil pH, heat load index, cover of each layer and number of species for relevés recorded in 2016.

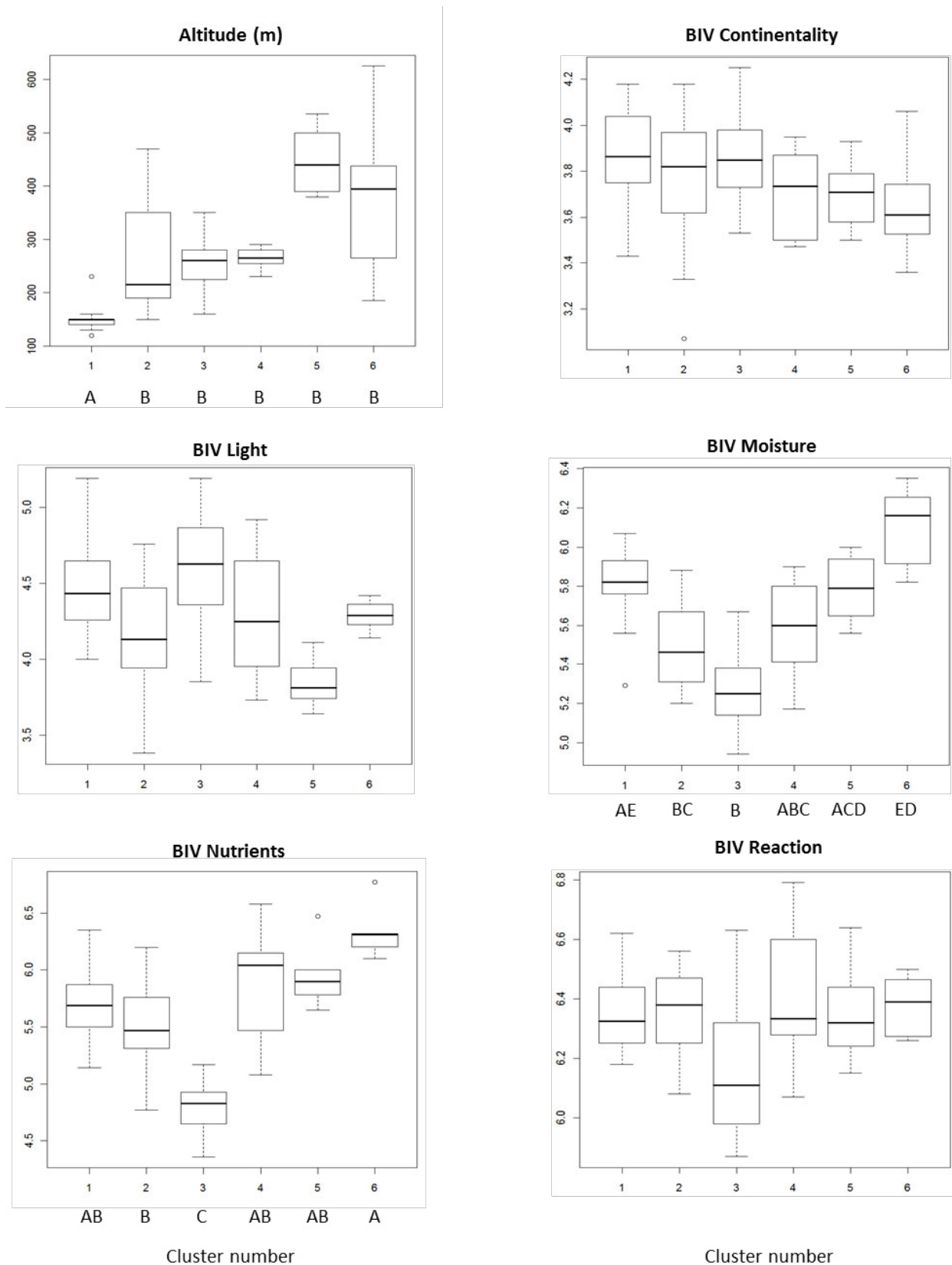
**Anhang E3.** Zusätzliche Informationen über Höhenlage, Inklination, Exposition, Boden-pH, Wärmebelastungsindex, Deckungsgrad der Schichten und Artenzahl für die 2016 angefertigten Vegetationsaufnahmen.

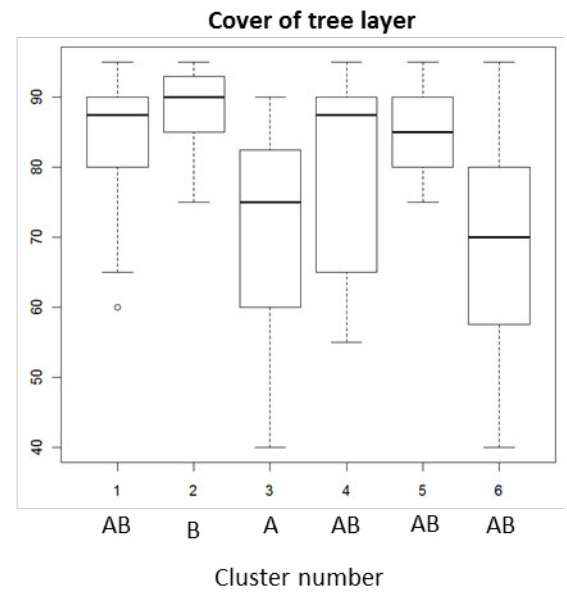
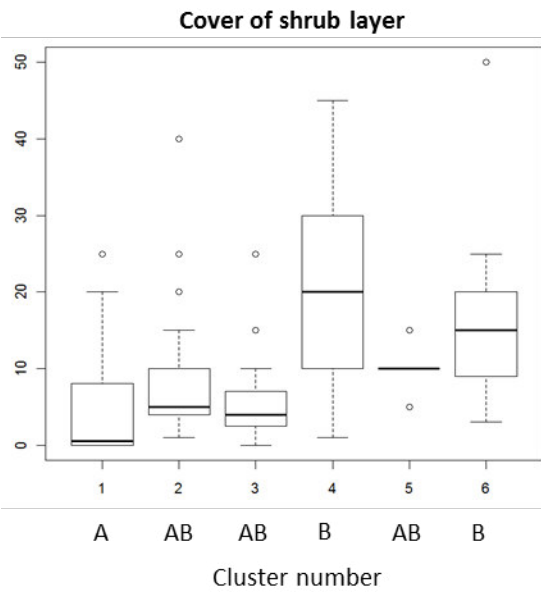
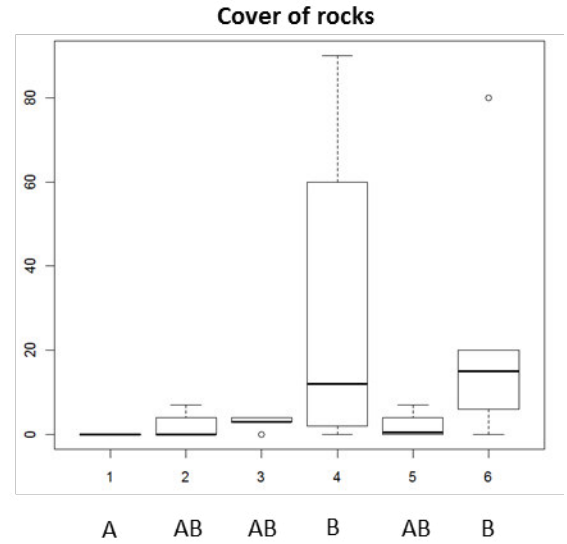
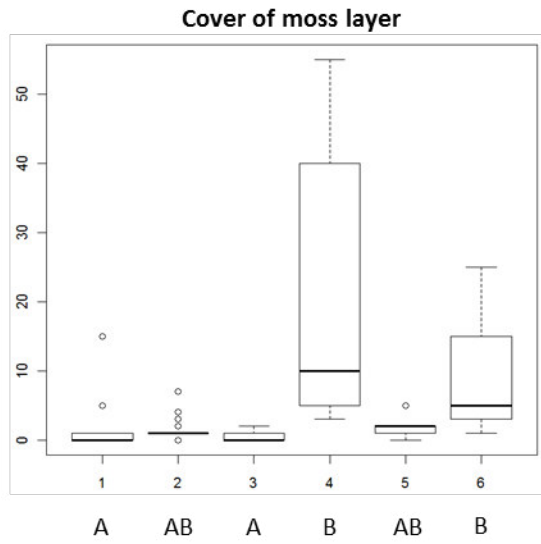
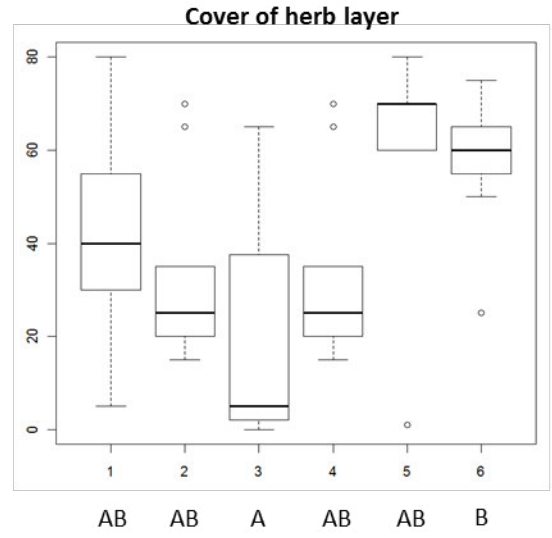
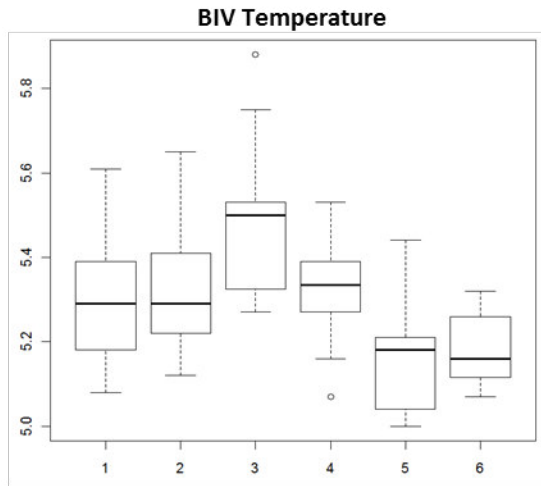
Relevé number	Altitude (m)	Slope (°)	Aspect (°)	Soil pH	Heat load index	Cover E3 (%)	Cover E2 (%)	Cover E1 (%)	Cover E0 (%)	Cover of rocks (%)	Number of species
1	140	0	-	5.54	0.876	85	0	65	1	0	36
2	120	0	-	5.09	0.877	95	5	35	1	0	28
3	130	0	-	5.15	0.878	65	8	35	1	0	28
4	160	10	360	4.34	0.784	80	25	35	1	0	21
5	130	2	320	4.26	0.871	85	10	70	1	0	26
6	230	5	300	5.94	0.871	85	4	30	15	0	34
7	140	0	-	5.45	0.878	90	1	15	0	0	28
8	157	2	80	5.2	0.858	85	8	55	5	0	40
9	155	1	80	4.59	0.868	80	6	75	1	0	20
10	140	0	-	5.81	0.878	90	10	25	0	0	22
11	235	15	315	6.5	0.822	85	4	25	1	0	30
12	215	25	120	4.56	0.714	90	2	15	1	0	22
13	190	10	270	4.35	0.904	95	10	65	1	2	21
14	210	35	200	5.41	0.948	95	25	20	1	7	31
15	210	35	200	6.06	0.948	90	10	15	1	0	22
16	190	15	220	6.14	0.943	95	6	30	0	0	19
17	175	35	220	5.11	0.972	85	15	70	1	0	30
18	150	3	45	4.57	0.844	85	5	35	1	0	43
19	370	0	-	4.91	0.874	90	3	20	4	0	35
20	350	10	240	5.09	0.921	90	4	30	1	0	21
21	230	15	320	4.46	0.811	93	1	25	1	4	11
22	420	30	160	5.5	0.834	90	10	35	1	7	58
23	180	15	20	4.74	0.709	93	4	15	2	3	19
24	280	15	320	5.81	0.811	75	5	20	1	3	22
25	150	5	45	5.25	0.821	80	2	30	1	0	28
26	470	20	100	5.16	0.7	95	40	35	7	7	34
27	390	25	240	5.48	0.962	90	20	15	3	7	37
28	260	10	180	4.93	0.903	90	3	35	1	4	14
29	210	15	300	4.83	0.853	90	10	50	1	4	16
30	350	20	120	4.89	0.753	85	1	30	2	3	36
31	240	15	130	5.26	0.811	75	15	65	1	3	30
32	270	10	248	4.73	0.921	75	4	40	1	0	17
33	340	15	120	5.14	0.789	75	4	55	2	3	34
34	270	20	23	4.6	0.643	65	30	65	40	50	27
35	260	45	45	5.15	0.276	90	30	20	5	3	37
36	230	10	23	5.12	0.767	90	3	15	55	80	33
37	285	35	23	4.55	0.44	55	25	70	10	20	31
38	275	30	23	4.38	0.509	65	20	25	50	90	19
39	230	35	340	7.23	0.58	95	20	20	7	4	28
40	290	20	340	4.66	0.726	85	10	30	40	60	20
41	280	25	30	6.83	0.57	90	1	25	3	2	21
42	260	10	30	4.62	0.763	90	10	25	10	0	21
43	255	30	45	5.74	0.492	55	45	35	5	2	28
44	500	15	270	5.12	0.909	95	5	60	1	7	33
45	390	25	90	4.43	0.617	75	15	80	5	1	20
46	380	2	90	4.66	0.856	90	10	70	2	0	20
47	440	2	200	5.22	0.883	85	10	70	2	0	35
48	270	45	360	5.6	0.376	95	10	25	1	7	15
49	625	30	248	4.73	0.95	70	8	75	20	15	34
50	260	30	338	4.92	0.638	40	50	50	25	80	32
51	395	15	45	6.92	0.697	70	25	70	3	5	23
52	185	45	23	6.6	0.301	90	15	60	10	20	20
53	430	50	360	6.6	0.312	50	3	60	3	0	35
54	445	55	45	6.2	0.133	65	15	60	5	20	44

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**Supplement E4.** Comparison of BIVs, cover of all vegetation layers, environmental variables and number of species amongst clusters. Homogenous groups according to the multiple comparison tests of the mean ranks are marked with the same letter.

**Anhang E1.** Vergleich der Zeigerwerte nach Borhidi (BIVs), Deckungsgrad aller Vegetationsschichten, Umweltvariablen und Artenzahlen zwischen den Clustern. Homogene Gruppen entsprechend den multiplen Vergleichstests der mittleren Ränge sind mit dem gleichen Buchstaben markiert.





Cluster number

Cluster number

