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## Coenology of the stands of the endangered *Lilium bulbiferum* subsp. *bulbiferum* on the north-eastern border of its range in Europe

### Zönologie von Beständen des gefährdeten *Lilium bulbiferum* subsp. *bulbiferum* an seiner nordöstlichen Arealgrenze in Europa

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#### Abstract

Orange lily *Lilium bulbiferum* subsp. *bulbiferum* occurs in the mountains of Western and Central Europe. Within almost the entire area of distribution, it is considered to be rare and endangered. The main purpose of the present study is to analyse the variability of environmental conditions of sites of the orange lily that are considered natural on its north-eastern border of occurrence. Using vegetation databases from Poland, the Czech Republic and Slovakia and our material collected during field work in the Western Carpathians and the Sudetes, we analysed the variability of species composition within communities with the occurrence of *L. bulbiferum* subsp. *bulbiferum*. The classification was performed using a modified TWINSpan algorithm in the JUICE software. Ecological analysis was performed on the basis of Ellenberg indicator values with a Zelený-Schaffers modified permutation test. In general, the findings indicate that in the study area there are at least seven plant communities, within three separate classes, with the occurrence of the orange lily. All vegetation units distinguished here are semi-natural communities, which are maintained through extensive and traditional agricultural practices. Microclimatic conditions, which indicate a narrow ecological tolerance of the species to light availability and temperature, may have a crucial effect on the distribution of *L. bulbiferum* subsp. *bulbiferum* on the north-eastern border of its range in Europe. These factors significantly reduce the possibility of penetration of the species into forest or scrub communities. On the other hand, owing to far wider ranges of tolerance to moisture conditions and soil reaction than previously considered typical of the species, the orange lily can occur in different light-demanding communities, from acidic pastures up to calcareous thermophilous grasslands. An almost exclusive presence of *L. bulbiferum* subsp. *bulbiferum* in semi-natural habitats suggests that active management and protection are crucial to protect its full genetic variation on the European continent.

**Keywords:** Central Europe, classification, Ellenberg Indicator Value, endangered species, mountain vegetation, semi-natural communities

**Erweiterte deutsche Zusammenfassung am Ende des Artikels**

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## 1. Introduction

The orange lily *Lilium bulbiferum* L. occurs at natural sites in the mountains of Western and Central Europe: in the Alps, the Ore Mts, the Bohemian Forest, the Sudetes, the Western Carpathians, the Apennines and Corsica (MEUSEL et al. 1965) and Northern Germany (ROTHMALER 1963). It is also recorded at isolated sites in the Southern and Eastern Carpathians as well as in the Polish lowlands but the occurrences are synanthropic in character (MEUSEL et al. 1965, ZAJĄC & ZAJĄC 2001, CIOCĂRLAN 2009). *Lilium bulbiferum* has diversified into two subspecies: *L. bulbiferum* subsp. *bulbiferum* (Fig. 1) occurring in the north-eastern part of the range of the species (DOSTÁL 1989, DANIHELKA et al. 2012) and *L. bulbiferum* subsp. *croceum* (Chaix) Nyman recorded from the Apennines and Corsica (CONTI et al. 2005) northwards to the river Elbe in the Northern Germany (<http://www.floraweb.de/webkarten/karte.html?taxnr=3401>). In the central part of the range, both subspecies occur simultaneously (MOSER et al. 2002).

Throughout most of its distribution range, *L. bulbiferum* subsp. *bulbiferum* is considered to be rare and endangered. The species is recognized as vulnerable to extinction in Austria (GRIMS et al. 1997), Switzerland (MOSER et al. 2002), Slovenia (ANONYMOUS 2002), Croatia (NIKOLIĆ 2009), Germany (KORNECK et al. 1996), Slovakia (FERÁKOVÁ et al. 2001), and endangered in the Czech Republic (GRULICH 2012) and Poland (KOCZUR & ŚWIERKOSZ 2014).

In the north-eastern part of the range, in the Western Carpathians and the Sudetes, the origin of the species is uncertain. Although the known sites of orange lily there were originally considered natural (MEUSEL et al. 1965), some researchers question that view and list *L. bulbiferum* subsp. *bulbiferum* as a naturalized archeophyte (ONDRÁČEK 2010, DANIHELKA et al. 2012, PYŠEK et al. 2012). This is supported by the fact that the species has been cultivated in the gardens of Central Europe since the 16<sup>th</sup> century (PELKONEN et al. 2007, SIGIEL-DOPIERAŁA & JAGODZIŃSKI 2011, VAN TUYL et al. 2011).



**Fig. 1.** Orange lily *Lilium bulbiferum* subsp. *bulbiferum* in the *Gladiolo-Agrostietum caninae* in the Spisko-Gubałowskie Foothills (South Poland) (Photo: A. Koczur, 8 July 2010).

**Abb. 1.** Wiesen-Feuerlilie *Lilium bulbiferum* subsp. *bulbiferum* im *Gladiolo-Agrostietum caninae* in der Gebirgskette Spisko-Gubałowskie (Südpolen) (Foto A. Koczur, 8.07.2010).

In the Carpathians and the Sudetes, *L. bulbiferum* subsp. *bulbiferum* is mainly a component of meadow and grassland communities. Apart from them, it has also been sporadically recorded in thickets and forest margins as well as fields, fallows and roadsides (GRODZIŃSKA & PANCER-KOTEJOWA 1960, DOSTÁL 1989, ONDRÁČEK 2010). In the Carpathians, orange lily is vulnerable to extinction (VU – TASENKEVICH 2003), whereas in the Polish part of this mountain range it is critically endangered (CR – KOCZUR 2008). In the Polish part of the Sudetes the species is considered to be endangered (EN – FABISZEWSKI & KWIATKOWSKI 2002), while in the Karkonosze Mts it is critically endangered (CR – ŠTURSA et al. 2009).

The main purpose of the present study is to analyse the variability of environmental conditions of sites of *L. bulbiferum* subsp. *bulbiferum* which are considered natural in the Western Carpathians and the Sudetes and define the north-eastern border of the species range. The recognition of the habitat preferences of this endangered taxon and distribution in plant communities are essential to the maintenance of the orange lily on the edge of its range and to the protection of its full genetic variation on the European continent.

## 2. Methods

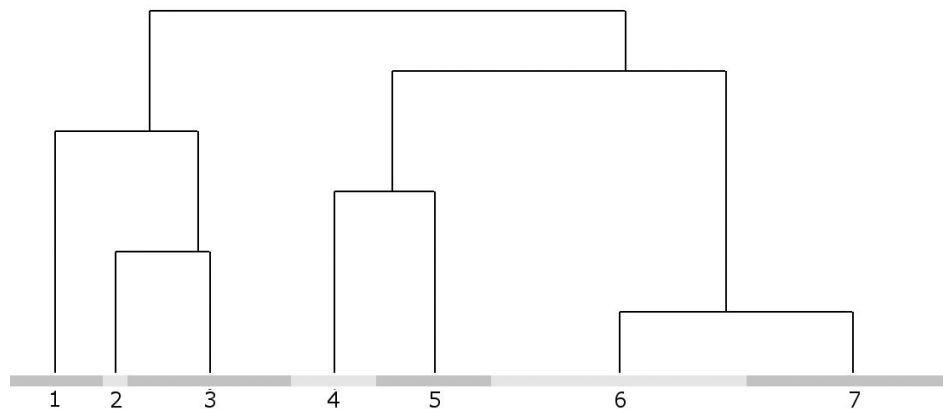
### 2.1 Data sampling

Communities with *Lilium bulbiferum* subsp. *bulbiferum* were studied in the Sudetes and the Western Carpathians between 2009 and 2013. Phytosociological relevés were collected according to Braun-Blanquet approach (MUELLER-DOMBOIS & ELLENBERG 2002) at all sites where orange lily occurred, regardless of the type of habitat. The area of the plots was adapted to those proposed by CHYTRÝ & OTÝPKOVÁ (2003), suitable for meadow and grassland communities (25 m<sup>2</sup>; exceptionally 40 or 100 m<sup>2</sup>). During field work, 30 relevés were collected and stored in a TURBOVEG database (HENNEKENS & SCHAMINE 2001). The author's relevés were transferred to the Grasslands in the Polish Carpathians Database (GIVD ID: EU-PL-002; KORZENIAK 2013) and to Polish Vegetation Database (GIVD ID: EU-PL-001 Database; KAČKI & ŚLIWIŃSKI 2012), to allow repetition of the study. In order to include comparative material from Central Europe, relevés excerpted from the literature sources and vegetation databases were used. Of them, 101 relevés originated from Slovakia (EU-SK-001 Database; ŠIBÍK 2012), 24 from the Czech Republic (EU-CZ-001 Database; CHYTRÝ & RAFAJOVÁ 2003) and 2 from Poland (EU-PL-001 Database). From the external databases we retrieved all plots with the respective species, with no additional criteria concerning their phytosociological classification or species abundance. In total, 157 relevés were used in the analysis (Supplement S1, E1).

### 2.2 Numerical analyses

The numerical classification of collected relevés, based on their species composition, was performed using a modified algorithm of TWINSpan (ROLEČEK et al. 2009) available in the JUICE program (TICHÝ 2002). The cover-abundance scale was transformed into a three-step interval scale (pseudospecies cut levels 0%, 5%, 25%). Cluster heterogeneity was measured by the Total inertia (ROLEČEK et al. 2009). As a measure of fidelity,  $\Phi$  coefficient for clusters of equalized size was used (CHYTRÝ et al. 2002). Only species with both a significant concentration in the particular cluster (using the Fisher's exact test at the significance level  $p < 0.05$ ) and a  $\Phi$  coefficient  $> 0.3$  were considered diagnostic. Seven clusters were recognised as the appropriate level of division according to crispness classification method (BOTTA-DUKÁT et al. 2005). The final classification of the relevés was based on the TWINSpan results (Fig. 2).

The identification of associations was based on a supervised classification method using definitions created for syntaxonomical units from Slovakia (HEGEDŮŠOVÁ-VANTAROVÁ & ŠKODOVÁ 2014) and the Czech Republic (CHYTRÝ 2007). Plots, included in clusters 5 were collected almost exclusively in Poland. Thus, they did not fulfil the above mentioned definitions, and were recognized directly by



**Fig. 2.** Dendrogram illustrating the assignment of relevé groups identified by TWINSpan to particular syntaxonomical units. Cluster 1 – *Brachypodio pinnati-Molinietum arundinaceae*; Cluster 2 – *Carici albae-Brometum monocladi*; Cluster 3 – *Lilio bulbiferi-Arrhenatheretum elatioris*; Cluster 4 – *Campanulo glomeratae-Geranium sylvatici*; Cluster 5 – *Gladiolo-Agrostietum capillaris*; Cluster 6 – *Campanulo rotundifoliae-Dianthetum deltoidis*; Cluster 7 – *Meo athamantici-Festucetum rubrae*.

**Abb. 2.** Dendrogramm, das die durch TWINSpan für bestimmte syntaxonomische Einheiten identifizierte Zuordnung von Vegetationsaufnahmen-Gruppen illustriert. Syntaxonomische Einheiten der Cluster s. o.

comparison of the list of diagnostic species with Polish literature sources including phytosociological diagnoses of associations (PAWŁOWSKI & WALAS 1949, PAWŁOWSKI et al. 1960, GRODZIŃSKA 1961, MATUSZKIEWICZ 2001).

To identify the similarity of the distinguished vegetation units and the main environmental gradients exerting an impact on their species composition, a Detrended Correspondence Analysis (DCA) from the Canoco 4.5/Canodraw 4.1 software was used (TER BRAAK & ŠMILAUER 2002). Detrending by segments and a square-root transformation of species cover data were applied.

For most of the analysed plots, there were no direct measurements referring to light and edaphic conditions. Therefore, mean Ellenberg indicator values (EIVs) weighted by species cover and concerning light availability (L), continentality (C), temperature (T), moisture (F), soil reaction (R) and nutrients (N) were calculated for each vegetation plot. A correlation analysis using sample scores of the first four DCA axes was performed to determine the statistical relationship between the mean EIVs and the distribution of samples in an ordination space. In order to determine the statistical significance between variables, a modified permutation test with 499 unrestricted permutations was conducted using MoPeT\_v1.0.r script prepared in R software (R DEVELOPMENT TEAM 2008, ZELENÝ & SCHAFFERS 2012). The association between variables was expressed by Spearman's rank correlation coefficient. Finally, an analysis of variance (ANOVA) of mean EIVs among vegetation units (with 499 unrestricted permutations) was calculated using MoPeT\_v1.0.r script and R software as well (ZELENÝ & SCHAFFERS 2012).

Map illustrating the distribution of relevés was prepared using Alan Morton's DMAP version 7.5 software (<http://www.dmap.co.uk/index.htm>).

### 2.3 Syntaxonomical classification and nomenclature

The nomenclature of plant communities follows CHYTRÝ (2007), JAROLÍMEK et al. (2008) and HEGEDŮŠOVÁ-VANTAROVÁ & ŠKODOVÁ (2014), with special emphasis on the latter sources, because most of the analysed sites are located in Slovakia. Species nomenclature and aggregates in Supplements S1, S2 correspond to CHYTRÝ & TICHÝ (2003) and DŮBRAVKOVÁ et al. (2010).

### 3. Results

According to the obtained results, seven different clusters were distinguished (Fig. 2, Supplement S2).

#### 3.1 Description of the clusters

##### **Cluster 1 – *Brachypodio pinnati-Molinietum arundinaceae* Klika 1939 (all. *Bromion erecti* Koch 1926)**

Geographical distribution of relevés: Slovakia and the Czech Republic, mostly located in the White Carpathians (330–650 m a.s.l.).

All analysed relevés with the occurrence of *Lilium bulbiferum* subsp. *bulbiferum* are marked by high fidelity and frequency of species such as *Lathyrus latifolius*, *Betonica officinalis*, *Filipendula vulgaris*, *Potentilla alba*, *Brachypodium pinnatum*, *Cirsium pannonicum*, *Melampyrum cristatum*, *Koeleria pyramidata*, *Ranunculus polyanthemus*, *Trifolium rubens* and *Hypochaeris maculata*.

##### **Cluster 2 – *Carici albae-Brometum monocladi* Ujházy et al. 2007 (all. *Cirsio-Brachypodium pinnati* Hadač & Klika ex Klika 1951)**

Geographical distribution of relevés: mainly the Starohorské vrhy Mts in Slovakia; in this cluster two relevés from the Polish side of the Sudetes (Orlickie Mts) were also included. Altitude 560–960 m a.s.l.

It is a well-identifiable group with numerous diagnostic species (*Buphthalmum salicifolium*, *Hippocrepis comosa*, *Carex tomentosa*, *Phyteuma orbiculare*, *Globularia punctata*, *Bromus monocladus*, *Carex alba*) which achieve high frequency in this cluster. Currently, some plots have been abandoned and subjected to succession processes, as reflected in the presence of saplings of species such as *Acer pseudoplatanus*, *Tilia platyphyllos* and *Fraxinus excelsior*.

##### **Cluster 3 – *Lilio bulbiferi-Arrhenatheretum elatioris* Ružičková 2002 (all. *Arrhenatherion elatioris* Luquet 1926)**

This cluster also comprises relevés which are of a transitional character and refer to xerophilous grasslands or mountain hay meadows of the alliance *Polygono bistortae-Trisetion flavescens* Br.-Bl. & R. Tx. ex Marshall 1947.

Geographical distribution of relevés: Slovakia – the Starohorské vrhy Mts and the Veľká Fatra Mts (540–1025 m a.s.l.).

Species typical of lowland hay meadows, as well as these which prefer warm habitats, including taxa diagnostic for the *Festuco-Brometea* class, have strong participation and high fidelity in this cluster.

Among species diagnostic for *Lilio bulbiferi-Arrhenatheretum elatioris* with relatively high fidelity and constancy, among others, occur *Carduus glaucinus*, *Rhinanthus serotinus*, *Primula vulgaris*, *Aquilegia vulgaris*, *Campanula serrata* and *Silene vulgaris*; a large group is also created by species diagnostic for both *Lilio bulbiferi-Arrhenatheretum elatioris* and *Carici albae-Brometum monocladi* (*Buphthalmum salicifolium*, *Phyteuma orbiculare*, *Bromus monocladus*, *Silene vulgaris*). Moreover, species diagnostic in associations included in *Polygono bistortae-Trisetion flavescens*, such as *Trifolium montanum*, *Viola hirta* and *Arrhenatherum elatius* achieve high fidelity in this cluster.

**Cluster 4 – *Campanulo glomeratae-Geranium sylvatici* Ružičková 2002 (all. *Polygono bistortae-Trisetion flavescens* Br.-Bl. & R. Tx. ex Marshall 1947)**

Geographical distribution of relevés: Slovakia – the Starohorské vrhy Mts and the Veľká Fatra Mts (470–1025 m a.s.l.).

Among the diagnostic species of the association, except for *L. bulbiferum* subsp. *bulbiferum*, *Silene vulgaris* also achieves high fidelity in this cluster. The vast majority of species differentiating for the *Campanulo glomeratae-Geranium sylvatici*, which were recorded in the analysed relevés, show fidelity in *Lilio bulbiferi-Arrhenatheretum elatiori*, including species common to both communities (*Cirsium erisithales*, *Campanula glomerata*). Despite this, a share of constant species is typical of the *Campanulo glomeratae-Geranium sylvatici*, including the dominance of some of them (mostly *Geranium sylvaticum*). Phytocoenoses in cluster 4 differ from the mountain hay meadows known in the northern part of the Western Carpathians mainly in their higher share of both thermophilous species (*Plantago media*, *Origanum vulgare*) and those typical of *Arrhenatherion elatioris* (*Tragopogon orientalis*, *Arrhenatherum elatius*).

**Cluster 5 – *Gladiolo-Agrostietum capillaris* (Br.-Bl. 1930) Pawłowski & Walas 1949 (all. *Polygono bistortae-Trisetion flavescens* Br.-Bl. & R. Tx. ex Marshall 1947)**

Geographical distribution of relevés: the Spisko-Gubałowskie Foothills and Orawsko-Nowotarska Basin in the Polish part of the Western Carpathians (Fig. 1); single relevés originate from Slovakia and the Sudetes in the Czech Republic (700–1120 m a.s.l.).

In this cluster, there is a lack of species diagnostic for most associations included in *Arrhenatherion elatioris* (*Arrhenatherum elatius*, *Tragopogon orientalis*, etc.) as well as thermophilous species. However, a share of species diagnostic of hygrophilous meadows of the *Calthion* alliance (*Myosotis palustris*, *Lychnis flos-cuculi*, *Cirsium rivulare*, *Deschampsia caespitosa*) is clearly visible.

**Cluster 6 – *Campanulo rotundifoliae-Dianthetum deltoideis* Balátová-Tuláčková 1980 (all. *Violion caninae* Schwickerath 1944)**

Geographical distribution of relevés: Poland and the Czech Republic – mainly the Sudetes Mts (665–780 m a.s.l.). Isolated stands in the Slovak and Polish part of the Western Carpathians.

A distinctive feature of analysed relevés with *L. bulbiferum* subsp. *bulbiferum* is a slightly larger admixture of species such as *Arrhenatherum elatius*, *Stellaria graminea*, *Phleum pratense*, *Rhinanthus minor* than in typical plots of the association, indicating a transition to meadow communities. Some plots have been abandoned and subjected to succession, which is reflected in the presence of *Rubus idaeus*, *Urtica dioica*, *Calamagrostis epigejos*, *Senecio ovatus*, *Holcus mollis*, as well as saplings of *Betula pendula*, *Salix caprea* and *Picea abies*.

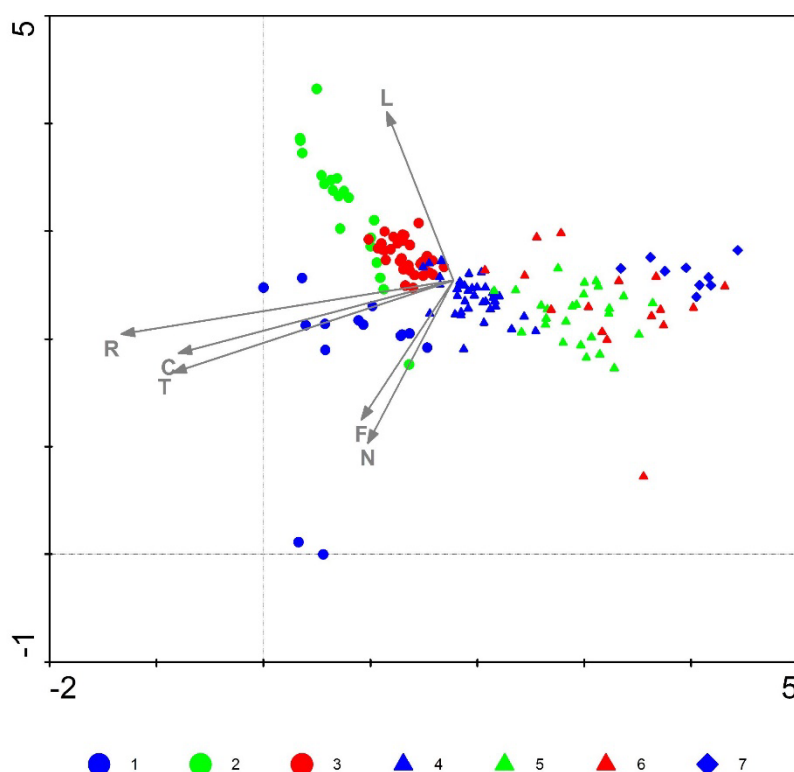
**Cluster 7 – *Meo athamantici-Festucetum rubrae* Bartsch & Bartsch 1940 (all. *Polygono bistortae-Trisetion flavescens* Br.-Bl. & R. Tx. ex Marshall 1947)**

Geographical distribution of relevés: Czech Republic (Ore Mts).

In this cluster, beyond the diagnostic species (*Cirsium heterophyllum*, *Galium saxatile*, *Meum athamanticum*, *Hypericum maculatum*, *Campanula rotundifolia*), a large share is also made up of species typical of degraded grasslands such as *Senecio ovatus*, *Holcus mollis*, *Epilobium angustifolium* and *Deschampsia flexuosa*. The abundance of *Sorbus aucuparia* indicates the lack of management measures as well.

### 3.2 Main environmental gradients

According to the DCA results, the first axis of the ordination diagram (length of gradient 4.434; eigenvalue 0.480) explained 32.3% species composition variability, whereas the second axis (length of gradient 4.322; eigenvalue 0.311) explained 6.9% of the variance. The arrangement of the studied samples along the first axis was correlated to the EIVs for temperature, continentality, soil reaction, moisture and nutrients (Table 1). The distribution of samples along the second axis was correlated to the EIVs for light, moisture and nutrients (Fig. 3, Table 1).



**Fig. 3.** DCA diagram of 157 relevés containing *Lilium bulbiferum* subsp. *bulbiferum*. Eigenvalues of the first and the second axes were 0.480 and 0.311, respectively. Passively projected environmental variables derived from Ellenberg indicator values are shown: L – Light; F – Moisture; N – Nutrients; R – Soil Reaction; C – Continentality; T – Temperature. Groups of relevés distinguished in the synoptic table (Supplement S2) and distribution map (Fig. 5) are marked by different symbols: 1 – *Brachypodio pinnati-Molinietum arundinaceae*; 2 – *Carici albae-Brometum monocladii*; 3 – *Lilium bulbiferi-Arrhenatheretum elatioris*; 4 – *Campanulo glomeratae-Geranium sylvatici*; 5 – *Gladiolo-Agrostietum capillaris*; 6 – *Campanulo rotundifoliae-Dianthetum deltoidis*; 7 – *Meo athamantici-Festucetum rubrae*.

**Abb. 3.** DCA-Diagramm von 157 Vegetationsaufnahmen mit *Lilium bulbiferum* subsp. *bulbiferum*. Die Eigenwerte der ersten und zweiten Achsen waren 0,480 bzw. 0,311. Passiv projizierte, von Ellenberg-Zeigerwerten abgeleitete Umweltvariablen sind gezeigt: L – Licht; F – Feuchte; N – Nährstoffe; R – Bodenreaktion; C – Kontinentalität; T – Temperatur. Gruppen von Vegetationsaufnahmen, die in der Übersichtstabelle (Supplement S2) und Verbreitungskarte (Abb. 5) unterschieden werden, sind durch unterschiedliche Symbole markiert (Syntaxonomische Einheiten s. o.).

**Table 1.** Significance of Spearman's rank correlation coefficient of Ellenberg indicator values with three main DCA axes using Zelený-Schaffers modified permutation test. Explanation: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; - - coefficient not significant.

**Tabelle 1.** Signifikanzen des Rangkorrelationskoeffizienten nach Spearman von Ellenberg-Zeigerwerten mit den drei DCA-Hauptachsen unter Verwendung des nach Zelený-Schaffers modifizierten Permutati-onstests. Erläuterung: \*  $p < 0,05$ ; \*\*  $p < 0,01$ ; - - Koeffizient nicht signifikant.

Ellenberg indicator value	Axis 1	Axis 2	Axis 3
Light	-	0.53*	0.45*
Temperature	-0.58*	-	-
Continentality	-0.64*	-	-
Moisture	0.87**	-0.64**	-
Soil reaction	-0.92**	-	-
Nutrients	0.59*	-0.63**	-

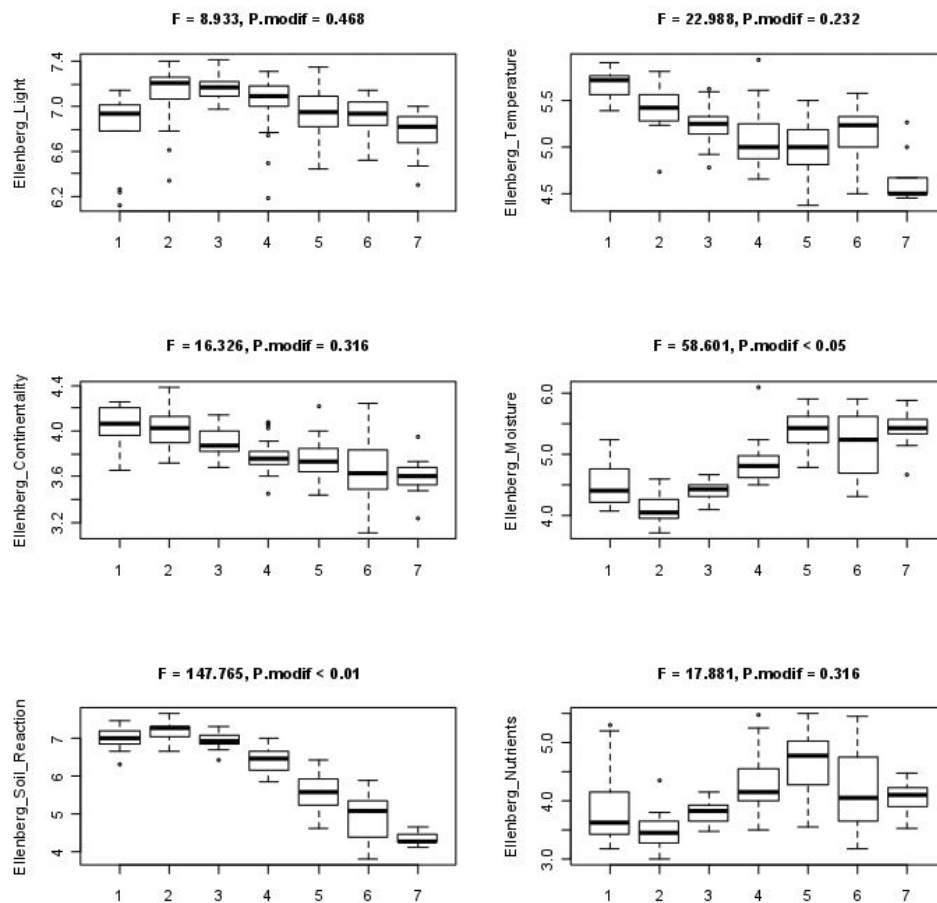
The samples which clearly differed from the others (outliers) due to floristic composition indicating the preferences of partial shading, as well as higher fertility and moisture (lower part of the diagram), were included in degraded, overgrown grasslands with an admixture of ruderal, forest or fringe species.

Distinguished clusters corresponding to particular plant communities differed to a greater or lesser extent from each other in the EIVs (Fig. 4). These communities were marked by similar values relating to light availability (median ranged from 6.8 to 7.2), continentality (3.6–4.1) and temperature (5.0–5.7). With respect to nutrients, the range was wider (3.5–4.8), but the diversity within individual clusters was greater than between them. The statistically significant differentiation between separate clusters (and at the same time the largest ranges) was observed for moisture (4.0–5.5,  $F = 58.6$ ,  $p < 0.05$ ) and soil reaction (4.4–7.3,  $F = 147.76$ ,  $p < 0.01$ ).

### 3.3 Relationship between the clusters

Clusters, which are shown in Figure 2, form three clearly distinct groups. In the first one there are plots marked by a high share of thermophilous species, including in the thermophilous grasslands of the *Festuco-Brometea* class or hay meadows of the *Lilio bulbiferi-Arrhenatheretum elatioris*. These communities occur almost exclusively in Slovakia, with isolated sites in the Czech Republic and Poland (Fig. 5). The second group consists of the communities of the mountain meadows of the alliance *Polygono bistortae-Trisetion flavescens*. Within this group, the *Campanulo glomeratae-Geranium sylvatici* is found only in Slovakia, while the *Gladiolo-Agrostietum capillaris* is observed north of the range of previous association with the centre of occurrence in the Polish part of the Western Carpathians. Therefore, the distribution of these communities suggests that they may be treated as geographical vicariants. The last group consists of phytocoenoses with a high proportion of acidophilous species included in both grasslands of the *Violion caninae* alliance and mountain meadows of the *Meo athamantici-Festucetum rubrae* association. Both types of phytocoenoses prefer habitats poor in nutrients, which results in numerous floristic similarities between them, despite of differences in the type of management and syntaxonomical position. Plots with the occurrence of *Lilium bulbiferum* subsp. *bulbiferum*, within this group, where found mainly in the Czech Republic and Poland (Fig. 5).



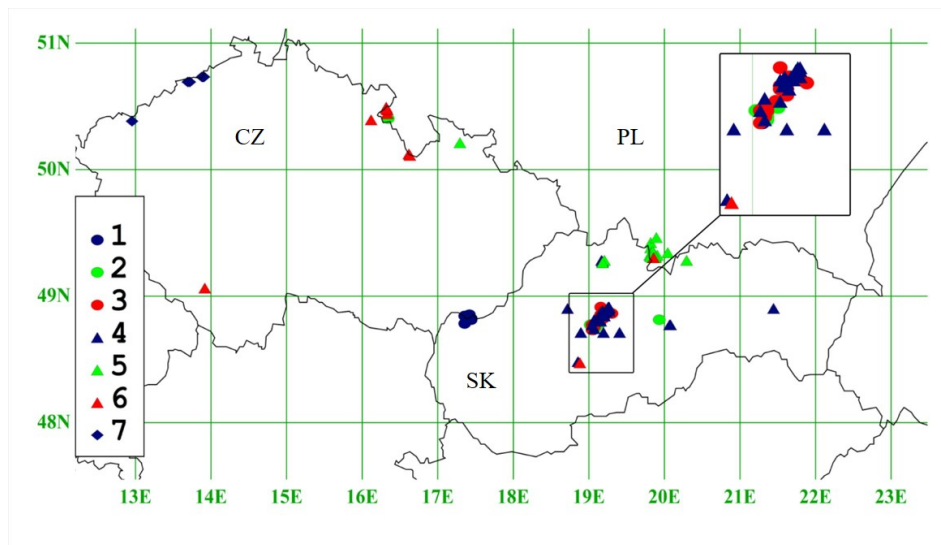


**Fig. 4.** The results of ANOVAs for Ellenberg indicator values tested by Zelený-Schaffers permutation test within plant communities with the occurrence of *Lilium bulbiferum* subsp. *bulbiferum* on the north-eastern border of its range in Central Europe. Explanation: 1 – *Brachypodio pinnati-Molinietum arundinaceae*; 2 – *Carici albae-Brometum monocladii*; 3 – *Lilio bulbiferi-Arrhenatheretum elatioris*; 4 – *Campanulo glomeratae-Geranietum sylvatici*; 5 – *Gladiolo-Agrostietum capillaris*; 6 – *Campanulo rotundifoliae-Dianthetum deltoidis*; 7 – *Meo athamantici-Festucetum rubrae*. ◻ – median; ◻ – 25–75%; I – non-outlier range, ○ – outliers, F – test statistics, *p. modif.* – result of Zelený-Schaffers permutation test.

**Abb. 4.** Ergebnisse von ANOVAs für Ellenberg-Zeigerwerte innerhalb von Pflanzengesellschaften mit dem Vorkommen von *Lilium bulbiferum* subsp. *bulbiferum* an der nordöstlichen Grenze seines Verbreitungsgebietes in Mitteleuropa, getestet mit dem nach Zelený-Schaffers modifizierten Permutationstest. Erläuterung: Syntaxonomische Einheiten s. o. ◻ – Median; ◻ – 25–75 %; I – Wertebereich ohne Ausreißer, ○ – Ausreißer, F – Teststatistik, *p. modif.* – Ergebnis des Zelený-Schaffers-Permutationstests.

#### 4. Discussion

Most of the previously published relevés with orange lily from Slovakia, the Czech Republic and Poland were traditionally assigned to *Festuco-Brometea* grasslands (KWIATKOWSKI & STRUK 2003) and *Molinio-Arrhenatheretea* meadows (GRODZIŃSKA 1961, KRAHULEC



**Fig. 5.** Distribution of the distinguished communities with occurrence of *Lilium bulbiferum* subsp. *bulbiferum* on the north-eastern border of its range.

Explanation: 1 – *Brachypodio pinnati-Molinietum arundinaceae*; 2 – *Carici albae-Brometum monocladii*; 3 – *Lilio bulbiferi-Arrhenatheretum elatioris*; 4 – *Campanulo glomeratae-Geranium sylvatici*; 5 – *Gladiolo-Agrostietum capillaris*; 6 – *Campanulo rotundifoliae-Dianthetum deltoides*; 7 – *Meo athamantici-Festucetum rubrae*.

**Abb. 5.** Verbreitung der unterschiedenen Gesellschaften mit Vorkommen von *Lilium bulbiferum* subsp. *bulbiferum* an der nordöstlichen Verbreitungsgrenze seines Vorkommens. Erläuterung der syntaxonomischen Einheiten s. o.

et al. 1997, BALÁTOVÁ-TULÁČKOVÁ 1985, SITAŠOVÁ 1998, RUŽIČKOVÁ 2002, KOCZUR 2012). However, in the literature sources and databases there were still relevés with the occurrence of *Lilium bulbiferum* whose syntaxonomical position had not been specified (HADINEC & LUSTYK 2006, ONDRÁČEK 2010) or they had been included in other types of communities belonging to the *Calluno-Ullicetea*, *Quercu-Fagetea* classes or the *Cynosurion* and *Caricion davallianae* alliances as well as *Aegopodio-Petasitetum* (BRAVENCOVÁ 2003).

All vegetation units distinguished in the present study are semi-natural communities which are maintained through extensive and traditional agricultural practices (PAWŁOWSKI et al. 1960, GRODZIŃSKA 1961, CHYTRÝ 2007, HEGEDUŠOVÁ-VANTAROVÁ & ŠKODOVÁ 2014). However, in other parts of the range, *L. bulbiferum* also occurs in communities which are of natural character. For instance, in the Alps it is observed in calcareous rocky grasslands of the alpine level, which represent the *Seslerion variaie* alliance, as well as in thermophilous fringes included in the *Origanetalia* order (BAUMGÄRTNER & HARTMANN 2001).

The Ellenberg Indicator Values (EIVs) proposed for the species (ELLENBERG et al. 1991) suggest that its optimal habitat is mainly connected with the sub-Atlantic climate of Central Europe (C 4), where it generally grows in well-lit places, but it tolerates semi-shade habitats (L 7); it prefers mesic soils with moderate moisture (F 5), neutral to alkaline (R 8), rather poor in nutrients (N 3). Regarding temperature the species is considered indifferent (T x).

The values of light and continentality calculated for the analysed groups of relevés oscillated around these given by ELLENBERG et al. (1991) as typical of *L. bulbiferum*, whereas the EIVs for soil reaction, moisture and nutrients considerably differed from them. On the north-

eastern edge of the range *L. bulbiferum* probably grows on soils with different moisture, which are richer in nutrients and also more acidic than in the southern part of Central Europe (BAUMGÄRTNER & HARTMANN 2001). However, comparable research conducted within the entire range of the species would be necessary to confirm this thesis.

A wide ecological tolerance of *L. bulbiferum*, with respect to different habitat conditions such as acidic to alkaline soils with various content of nutrients, determines the presence of orange lily in wide range of plant associations. The *Carici albae-Brometum monocladi* and *Lilio bulbiferi-Arrhenatheretum elatioris* develop on alkaline soils over dolomites and limestones (HEGEDŮŠOVÁ-VANTAROVÁ & ŠKODOVÁ 2014), whereas the *Brachypodio pinnati-Molinietum arundinaceae* also prefers alkaline soils but on calcareous flysch sandstones (CHYTRÝ 2007, HEGEDŮŠOVÁ-VANTAROVÁ & ŠKODOVÁ 2014). The other associations presented in this study occur on acidic soils which are derived from non-calcareous substrates – mainly sandstones and clays (PAWŁOWSKI et al. 1960, GRODZIŃSKA 1961, CHYTRÝ 2007, HEGEDŮŠOVÁ-VANTAROVÁ & ŠKODOVÁ 2014).

Despite such a diverse types of bedrock and different ranges of the EIVs for soil reaction within particular clusters, there were no significant differences in the fertility of habitats (EIV for N). The reason for this was a wide range of the EIVs for nutrients within most of the examined groups. It is possible that the extension of values of this factor was the consequence of changes in the habitat's richness caused by the lack of agricultural practices within the large number of studied plots. Since the content of nutrients usually increases in the absence of use (KORNAŠ & DUBIEL 1991, MOOG et al. 2002), we can conclude that within some of the examined vegetation plots there is a process of auto-eutrophication, which is supported by the accumulation of nitrogen under succession (LUKEN 1990).

A slight variation within the EIVs for light, continentality and temperature indicates a narrow ecological amplitude of *L. bulbiferum* and limits its occurrence to habitats which meet specific environmental conditions. Especially the range of the latter factor suggests that the sites of *L. bulbiferum*, on the north-eastern border of the range, concentrate mainly on moderately warm habitats. That is a much smaller range of tolerance than this suggested as typical of this species (ELLENBERG et al. 1991).

## 5. Conclusions

The results confirm our hypothesis that microclimatic conditions, which indicate a narrow ecological tolerance of the species to light availability and thermal conditions, may have a crucial effect on the distribution of *Lilium bulbiferum* subsp. *bulbiferum* on the north-eastern border of its range in Europe. These factors significantly reduce the possibility of penetration of orange lily into the sub-optimal habitats (tall herb, forest or scrub communities). On the other hand, owing to far wider ranges of tolerance to moisture conditions, nutrient availability and soil reaction than those considered characteristic for the species (ELLENBERG et al. 1991), orange lily can simultaneously occur in different communities such as moderately acidic pastures, moist mountain meadows or calcareous thermophilous grasslands. An almost exclusive presence of *L. bulbiferum* in semi-natural habitats suggests both that active management and active protection are essential to protect its full genetic variation on the European continent and in the north-eastern part of the range the species may be a naturalized archeophyte as it was supposed by ONDRÁČEK (2010), DANIHELKA et al. (2012) and PYŠEK et al. (2012). However, solution to the latter issue needs further study.

## Erweiterte deutsche Zusammenfassung

**Einleitung** – Die Feuer-Lilie *Lilium bulbiferum* L. kommt von Natur aus in den Gebirgen West- und Mitteleuropas, in den Alpen, dem Riesengebirge, dem Böhmerwald, den Sudeten, den Westkarpaten, dem Apennin und Korsika (MEUSEL et al. 1965) vor. *L. bulbiferum* gliedert sich in die beiden Unterarten subsp. *bulbiferum* (Abb. 1), welche im nordöstlichen Teil des Verbreitungsgebiets vorkommt (DOSTÁL 1989, DANIHELKA et al. 2012), und subsp. *croceum* (Chaix) Nyman, die vom Apennin und auf Korsika (CONTI et al. 2005) bis zur Elbe in Norddeutschland (<http://www.floraweb.de/webkarten/karte.html?taxnr=3401>) beobachtet wurde. Fast im gesamten Verbreitungsgebiet wird die Subspecies *bulbiferum* als selten und gefährdet eingestuft. Im nord-östlichen Gebietsteil, in den Westkarpaten und Sudeten, ist der Status der Art ungeklärt. Obwohl dortige Wuchsorte der Feuer-Lilie bislang als natürlich betrachtet wurden (MEUSEL et al. 1965), stellen dies neuere Untersuchungen in Frage und betrachten *L. bulbiferum* subsp. *bulbiferum* als eingebürgerten Archäophyten.

Hauptzweck der Arbeit ist es die Variabilität der Umweltbedingungen von Standorten im nordöstlichen Verbreitungsgebiet zu untersuchen, an denen *L. bulbiferum* subsp. *bulbiferum* vorkommt und als natürlich eingestuft wird. Darüber hinaus legt eine Revision der verfügbaren Literatur die Hypothese nahe, das Vorkommen des Taxons in der besagten Region sei durch Belichtung und Wärme limitiert, wohingegen Ansprüche an Nährstoffe, Bodenazidität und Wasserversorgung von untergeordneter Bedeutung sind.

**Methoden** – Untersucht wurden Pflanzengemeinschaften mit Vorkommen von *L. bulbiferum* subsp. *bulbiferum* in den Sudeten und Westkarpaten zwischen 2009 und 2013. Pflanzensoziologische Aufnahmen wurden nach der Braun-Blanquet-Methode aufgenommen (MUELLER-DOMBOIS & ELLENBERG 2002). Zusätzlich wurden Aufnahmen aus der Literatur und aus Vegetationsdatenbanken für Tschechien, die Slowakei und Polen ausgewertet. Insgesamt wurden 157 Aufnahmen verwendet.

Eine numerische Klassifikation der Aufnahmen wurde mit dem modifizierten TWINSPAN-Algorithmus vorgenommen (ROLEČEK et al. 2009), der in der JUICE Software implementiert ist (TICHÝ 2002). Mittlere deckungsgewichtete Ellenberg-Zeigerwerte (EIVs) für Licht (L), Kontinentalität (C), Temperatur (T), Feuchte (F), Bodenreaktion (R) und Nährstoffe (N) wurden pro Aufnahme berechnet (ELLENBERG et al. 1991). Diese wurden mit den ersten vier Achsen einer Entzerrten Korrespondenzanalyse (DCA) korreliert. Die mittleren Zeigerwerte zwischen den Clustern wurden mittels Varianzanalyse (ANOVA) mit nach Zelený-Schaffers modifiziertem Permutationstest verglichen.

**Ergebnisse** – Sieben Cluster mit der Feuer-Lilie wurden unterschieden (Abb. 2, Beilage S2). Sie repräsentieren folgende Assoziationen: *Brachypodio pinnati-Molinietum arundinaceae* Klika 1939 (Slowakei, Tschechien), *Carici albae-Brometum monocladii* Ujházy & al. 2007 (Starohorské vrhy-Gebirge in der Slowakei und Orlickie-Gebirge in Polen), *Lilio bulbiferi-Arrhenatheretum elatioris* Ružičková 2002 und *Campanulo glomeratae-Geranium sylvatici* Ružičková 2002 (Starohorské vrhy-Gebirge and Große Fatra in der Slowakei), *Gladiolo-Agrostietum capillaris* (Br.-Bl. 1930) Pawłowski & Walas 1949 (Polen, vereinzelt auch in der Slowakei und Tschechien), *Campanulo rotundifoliae-Dianthetum deltoides* Balátová-Tuláčková 1980 (Polen und Tschechien) and *Meo athamantici-Festucetum rubrae* Bartsch & Bartsch 1940 (tschechisches Erzgebirge). Die erste DCA-Achse vereinte 32,3 % der Varianz in der Artenzusammensetzung auf sich und war korreliert mit allen untersuchten Ellenberg-Zeigerwerten (Tabelle 1). Die zweite Achse repräsentierte 6,9 % der Varianz und war mit Licht, Feuchte- und Nährstoffzahl korreliert (Abb. 3, Tabelle 1). Die Cluster bzw. Assoziationen unterschieden sich hinsichtlich ihrer mittleren Ellenberg-Zeigerwerte m.o.w. stark (Abb. 3), jedoch ergaben sich nur für Feuchte- und Reaktionszahl signifikante Unterschiede (Abb. 4).

**Diskussion** – Die Mehrzahl der bislang publizierten Aufnahmen mit der Feuer-Lilie aus der Slowakei, Tschechien und Polen wurden den Klassen *Festuco-Brometea* und *Molinio-Arrhenatheretea* zugeordnet. Die numerische Analyse bestätigte, dass *L. bulbiferum* subsp. *bulbiferum* in ihrem nordöstlichen Verbreitungsgebiet vor allem im Grünland und nur sporadisch in Heiden der Klasse *Calluno-Ulicetea*

vorkommt. Vorkommen der Art in anderen Vegetationstypen (Wälder, Gebüsche, Hochstaudenfluren oder Niedermoore) hatten allenfalls zufälligen Charakter. Alle in dieser Studie unterschiedenen Vegetationseinheiten sind halbnatürlich und werden durch traditionelle extensive Landwirtschaft erhalten.

Die für die Vegetationseinheiten ermittelten Zeigerwerte für Licht und Kontinentalität bewegten sich in dem Bereich, den ELLENBERG et al. (1991) als typisch für *L. bulbiferum* definieren, während die Reaktions- und Nährstoffzahlen stärker abwichen. So wächst *L. bulbiferum* im Nordosten ihrer Verbreitung auf Böden, die feuchter, nährstoffreicher und saurer sind als die Zeigerwerte der Art nahelegen. Trotz der unterschiedlichen Böden und abweichender Bereiche der Bodenreaktion wurden keine signifikanten Unterschiede in der Nährstoffausstattung der Lebensräume nachgewiesen, da die Nährstoffzahlen innerhalb der Cluster eine starke Streuung aufwiesen. Möglicherweise war dies eine Folge von Lebensraumveränderungen in Folge des Erlöschens der landwirtschaftlichen Nutzung in einer erheblichen Anzahl von Aufnahmen. Die geringe Varianz von Licht- und Temperaturzahlen belegt eine enge ökologische Amplitude von *L. bulbiferum*, welche Vorkommen der Art auf spezifische Standortbedingungen einengt. Der enge Bereich von Temperaturzahlen belegt besonders deutlich, dass die Art am Nordostrand ihrer Verbreitung auf mäßig warme Lebensräume angewiesen ist und ihre Toleranz viel geringer ist als im südlichen Mitteleuropa (BAUMGÄRTNER & HARTMANN 2001).

**Schlussfolgerungen** – Die Untersuchung bestätigt die Hypothese, dass das Mikroklima (Licht und Temperatur) eine entscheidende Bedeutung für das Vorkommen von *L. bulbiferum* subsp. *bulbiferum* am Nordostrand ihrer Verbreitung hat. Beide Faktoren hindern die Feuer-Lilie daran in suboptimale Lebensräume (Hochstaudenfluren, Wald oder Gebüsche) vorzustoßen. Andererseits vermag die Art auf Grund ihrer großen Feuchte- und Reaktions-Amplitude ein bemerkenswert breites Spektrum an Vegetationstypen wie bodensaure Weiden, mäßig frische Bergwiesen und thermophile Kalkmagerrasen zu besiedeln. Die fast ausschließliche Bindung von *L. bulbiferum* an halbnatürliche Lebensräume legt nahe, dass aktive Pflege und Schutzmaßnahmen entscheidend für die Erhaltung der innerartlichen genetischen Vielfalt der Art auf dem europäischen Kontinent sind.

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### Supplements

**Supplement S1.** Phytosociological relevés of communities containing *Lilium bulbiferum* subsp. *bulbiferum* on the north-eastern border of its range in Europe.

**Beilage S1.** Vegetationsaufnahmen der Pflanzengesellschaften mit *Lilium bulbiferum* subsp. *bulbiferum* an seiner nordöstlichen Arealgrenze in Europa.

**Supplement S2.** Combined synoptic table of communities containing *Lilium bulbiferum* subsp. *bulbiferum* with percentage frequency and modified fidelity phi coefficient (superscript).

**Beilage S2.** Kombinierte Übersichtstabelle der Gesellschaften mit *Lilium bulbiferum* subsp. *bulbiferum* mit prozentualer Stetigkeit und modifiziertem Treue phi Koeffizient (Exponent).

**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.** Basic information about relevés.

**Anhang E1.** Basisinformationen zu den Vegetationsaufnahmen.

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