

Habitat preferences of the rare lizard-orchid *Himantoglossum adriaticum* H. Baumann

Habitatpräferenzen der seltenen Adria-Riemenzunge (*Himantoglossum adriaticum* H. Baumann)

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Abstract

Himantoglossum adriaticum is a rare and in many countries endangered orchid species. It grows on calcareous soils in natural and semi-natural, dry and mesophilic grasslands or open woodlands and is restricted to a small region along the Adriatic coast and within Central and Southeastern Europe. We compiled phytosociological relevés ($n = 84$) covering the whole distribution range to investigate its habitat preferences and collected soil samples from 41 relevés to determine various soil parameters. We then used a phytocoenological approach and ecological indicator values to characterize the vegetation.

Our study revealed that *H. adriaticum* is growing in two major habitat types, significantly differing in herb and shrub cover. Beside its preference for semi-natural grasslands, *H. adriaticum* occurs in man-made secondary habitats, such as the roadsides and temporary habitats during secondary succession after land-use abandonment. *Himantoglossum adriaticum* is most frequently growing in grasslands which can be characterized as the secondary succession state of the *Festuco-Brometea* vegetation class. Based on these findings, we developed mean indicator values for *H. adriaticum*, which were missing for its whole distribution range.

Keywords: coenosystematic elements, conservation, ecological indicator values, EU Habitats Directive, *Orchidaceae*

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

The Adriatic Lizard Orchid (*Himantoglossum adriaticum* H. Baumann) is a rare and in many countries endangered orchid species. It is one of the ten *Orchidaceae* species listed in the Annex II of the Habitats Directive 92/43/EEC of the European Commission. It is listed in the Red Data Books of most of the countries where it occurs (MAGLOCKY & FERÁKOVÁ

1993, CONTI et al. 1997, KIRÁLY 2007, GRULICH 2012). It is categorized as 'Critically Endangered (CE)' in the Czech Republic and in Slovakia, 'Endangered (EN)' in Austria and in Hungary, 'Vulnerable (VU)' in Slovenia and 'Near Threatened (NT)' in Croatia (DOSTALOVA et al. 2011). Globally, IUCN considers the species as not threatened (least concern). Compared to its congeners *H. jankae* and *H. hircinum*, the distribution range of *H. adriaticum* is restricted to a small region within Europe. According to the Global Biodiversity Information Facility (GBIF) database, it occurs in Italy, Slovenia, Austria, Slovakia and Montenegro. The Flora Croatica Database contains localities in Croatia, further populations are known from Bosnia-Herzegovina (MILANOVIĆ et al. 2015), Hungary (MOLNÁR V. 2011), the Czech Republic (RŮŽIČKA et al. 2004) and Albania (BARINA et al. 2005).

Because of the high conservation value of *H. adriaticum*, it is crucial to assess its habitat preferences and environmental attributes that affect its distribution range and abundance. A reliable assessment of these variables is particularly required for the effective conservation of species that are in risk of extinction (PRIMACK 2010).

In general, the distribution of terrestrial orchid species is predetermined by edaphic properties such as soil moisture, organic matter content, pH and nutrient levels. However, it is expected that these environmental parameters primarily limit the occurrence or the abundance of mycorrhizal fungi and only indirectly the orchids that rely upon them (BATTY et al. 2001, DIEZ 2007). At the same time, light availability seems to be an important environmental variable for many orchids (KULL & HUTCHINGS 2006).

In case of *H. adriaticum*, BAUMANN (1978) did not give information about its habitat preferences in his description, but later he reported that the species is a plant of calcareous dry grasslands and open woodlands (see BAUMANN & KÜNKELE 1982). In other publications, there are contrasting views about the habitat preferences of the species ranging from semi-natural habitats up to 1600 m a.s.l. like short poor grasslands, banks, thickets, woodland edges and open woodlands all over its distribution range (MRKVICKA 1990, KALIGARIČ et al. 2004, RYBKA et al. 2005, DELFORGE 2006, TRČAK et al. 2006, ČIČMIR et al. 2015, ŠEFFEROVÁ-STANOVÁ et al. 2015) to secondary habitats, such as traditional orchards, abandoned vineyards and mown grassy roadsides (KLAVER 2011, MOLNÁR V. 2011, GLASNOVIC et al. 2013, BÓDIS et al. 2014, MILANOVIĆ et al. 2015).

Until now, ecological indicator values for *H. adriaticum* were only given by LANDOLT et al. (2010) for populations in the Alps. It is unclear whether these would be different when considering the whole distribution range of the species. Indicator values describe the position of the realized niche of plant species. They range from 1 to 9 (ELLENBERG et al. 1991, BORHIDI 1995) or 1–5 (LANDOLT et al. 2010). By averaging them over all species per plot, these values yield information on the environmental conditions of the grasslands.

Our paper aims to summarize the habitat requirements of *H. adriaticum* based on published and newly collected data across its whole distribution range, and to develop indicator values for the species. We characterized the populated habitats using a phytocoenological approach in order to gain accurate information about the co-occurring species and the preferred types of vegetation units.

Additionally, we assessed its niche through ecological indicator values. We hypothesized, that *H. adriaticum* occurs in semi-natural and secondary habitats and that the occurrence and the abundance of the species is mostly correlated with light-related habitat variables.

2. Materials and Methods

2.1 Study species

The Adriatic Lizard Orchid is a terrestrial, tuberous photoautotrophic orchid with an overwintering rosette, which consists of 2–7 large, lanceolate, pale green basal leaves. These leaves are (6.6–)7.5–17.5(–24.7) cm long and (1.5–)2.5–4.5(–12.8) cm broad. The plant is growing 30–80 cm high, the inflorescence is elongated and lax, composed of 15–40 brownish red, typically malodorous flowers. The lip is deeply 3-lobed, the middle lobe is long, ribbon-like, curled and incised. The flower is deceptive, as no nectar is produced (DELFORGE 2006, MOLNÁR V. 2011).

2.2 Compilation of vegetation relevés

To characterize the plant communities harboring the target species, we conducted field surveys in Slovenia, Croatia, Austria, Hungary, Slovakia and Bosnia-Herzegovina in known localities of *H. adriaticum*. We set up 41 phytocoenological plots (2 m × 2 m) in different habitats, where the cover of vascular plants was recorded in percent. Additional cover-abundance data of 38 relevés were extracted from the European Vegetation Archive (EVA), from Italy, Austria, the Czech Republic and Slovakia (Fig. 1. and Table 1). Additional five relevés from Slovakia were also integrated (DUCHOŇ 2012).

Habitat variables [i.e., slope (°), cover of herb layer (%), cover of bryophyte layer (%), cover of litter (%), cover of tree layer (%), cover of bare soil (%)] and geographical information [latitude (°), longitude (°), altitude (m)] were available for all relevés. 41 soil samples were collected in different localities, near the *H. adriaticum* plants to analyze soil properties according to the Hungarian standard methods (BUZÁS 1993), such as pH in 1:2.5 soil to distilled water solution, salt content calculated from the electric conductivity of soil paste at plastic limit, calcium-carbonate content using the Scheibler equipment after reaction with hydrochloric acid, humus content by oxidation with potassium-dichromate, as well as nitrite and nitrate content with UV spectrometry. All environmental and soil variables are listed in Table 2.

Table 1. Phytocoenological relevés used for analyses. Notations: BrBl = original Braun-Blanquet scale; BrBlext = extended Braun-Blanquet scale (see WESTHOF & VAN DER MAAREL 1978; VAN DER MAAREL 2007); EVA = European Vegetation Archive; authors = field collected data by the authors.

Tabella 1. Für die Analysen benutzte Vegetationsaufnahmen. Anmerkungen: BrBl = originale Braun-Blanquet-Skala; BrBlext = erweiterte Braun-Blanquet-Skala (s. WESTHOF & VAN DER MAAREL 1978; VAN DER MAAREL 2007); EVA = European Vegetation Archive; authors = Felddaten der Autoren).

Country	<i>n</i>	Area (m ²)	Date	Reference	Data scale
Czech Republic	1	15–75	2008	EVA	BrBlext
Slovakia	9	16–30	2002–2005	EVA	BrBl, BrBlext
Slovakia	5	10–400	2009–2010	DUCHOŇ 2012	ordinal (1–9)
Slovakia	1	4	2016	authors	Cover (%)
Austria	25	6–400	1936–2012	EVA	BrBl, BrBlext
Austria	6	4	2016	authors	Cover (%)
Hungary	10	4	2016	authors	Cover (%)
Croatia	12	4	2016	authors	Cover (%)
Slovenia	7	4	2016	authors	Cover (%)
Bosnia-Herzegovina	5	4	2017	authors	Cover (%)
Italy	3	20–25	1986–2004	EVA	BrBl
Total	84				

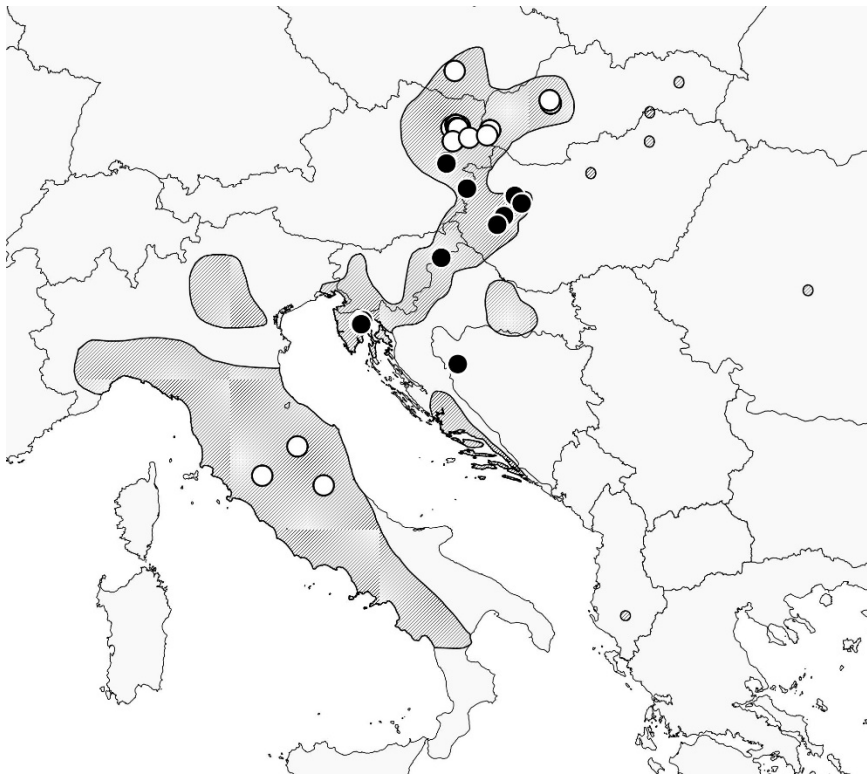


Fig. 1. Sampled plots across the distribution range of *Himantoglossum adriaticum*. Notations: area with grey colour = modified distribution range of *H. adriaticum* based on BAUMANN & KÜNKELE (1982); filled circles = plots from field survey made by the authors; open circles = plots from European Vegetation Archive (EVA) and published by DUCHOŇ (2012).

Abb. 1. Aufgenommene Plots im Verbreitungsgebiet von *Himantoglossum adriaticum*. Anmerkungen: Fläche mit grauer Farbe = modifiziertes Verbreitungsgebiet von *H. adriaticum* basierend auf BAUMANN & KÜNKELE (1982); ausgefüllte Kreise = Plots von Geländeaufnahmen der Autoren; offener Kreis = Plots aus dem European Vegetation Archive (EVA) und publiziert von DUCHOŇ (2012).

2.3 Data analyses

The compiled relevés contained data on different scales (original Braun-Blanquet scale, extended Braun-Blanquet scale, ordinal (1–9) scale). Accordingly, the data was transformed into ordinal values (ord%) following VAN DER MAAREL (2007).

To determine *H. adriaticum* habitat and ecological requirements, we summarized the ecological indicator values and coenosystematic categories of all species in the relevés following BORHIDI (1995). We used (i) nitrogen supply (NB) ranging from 1 (soils extremely poor) to 9 (hyperfertile soils); (ii) degree of continentality of the general climate (CB) ranging from 1 (euoceanic) to 9 (eucontinental); (iii) relative light intensity (LB) ranging from 1 (full shadow) to 9 (full light); and (iv) heat supply (TB) ranging from 1 (subnival and subboreal belt) to 9 (eumediterranean evergreen belt). For the indicator value and coenosystematic analyses we calculated the distribution of species frequency among the categories (DIEKMANN 2003).

The correlation between species composition of vegetation and environmental parameters (habitat, geographical information, soil) was displayed by non-metric multidimensional scaling (NMDS) calculated using the Canoco5 package (TER BRAAK & ŠMILAUER 2012). Canoco5 maximizes the variation of

Table 2. Variability of the environmental parameters in the relevés.**Tabelle 2.** Variabilität der Umweltparameter in den Vegetationsaufnahmen.

Environmental variable	Mean	Min.	Max.
<i>Geography</i>			
Altitude	336.83	62.00	950.00
Longitude	16.06	11.89	18.39
Latitude	47.07	42.63	49.14
Slope	15.14	0	80.00
<i>Vegetation</i>			
Cover of herbs	73.78	10	100
Cover of shrubs	27.72	0	100
Cover of trees	26.15	0	90
Cover of bryophytes	18.32	0	80
Cover of litter	24.42	2	70
Cover of bare soil	4.50	0	20
<i>Soil</i>			
pH _{dw}	7.07	6.30	7.50
Salt content	0.03	0.02	0.10
CaCO ₃ content	18.18	0.05	64.10
Humus content	7.54	1.50	26.92
NO ₂ and NO ₃ content	24.21	2.00	148.00
<i>Diversity</i>			
Number of species	34.6	7	63
Shannon diversity	12.42	2.22	28.73
Simpson diversity	7.08	1.41	26.44

case scores along NMDS axes by applying a principal component rotation. NMDS was applied to the ordinal transformed value data set. To compare environmental and habitat variables between the groups of plots obtained by NMDS, we applied a t-test.

We calculated α -diversity for the relevés and we considered three diversity indices: (i) the number of species; (ii) Shannon diversity (dominant and rare species are weighted equally) and (iii) Simpson diversity (weighted towards the frequent species) for the diversity analyses. We transformed the α -diversity components into their number of equivalents to let the α -diversity component vary independently of each other (JOST 2007). Therefore, we applied an expH and 1/D transformation to the Shannon and Simpson diversity values.

To analyze the relationship between habitat types, diversity values, environmental variables and the cover of *H. adriaticum*, Spearman rank-correlations were calculated (ZAR 1999).

To determine the relative indicator values of *H. adriaticum*, we calculated the mean and the median of the relative indicator values of the accompanying plant species. During the calculation we excluded rare and occasionally appearing species, and only included species having a frequency of > 41% among the relevés. All statistical analyses were conducted with Statistica (STATSOFT 2006).

2.4 Nomenclature used

Nomenclature of vascular plants follows KIRÁLY (2009), the one of the *Orchidaceae* species follows MOLNÁR (2011) and THE PLANT LIST (2013). Nomenclature of vegetation types follows BORHIDI (1995) and MUCINA et al. (2016).

3. Results

3.1 Phytocoenological description of the habitats

Altogether, 523 species were recorded (65 tree and shrub species, 458 herbaceous species) in 84 relevés (34.6 species on average). Mean cover of herbaceous species across all relevés was 0.22% (0.003% to 15.05%). Trees and/or shrubs occurred in 85.7% of the relevés and the mean cover of the species across all relevés was 0.38% (0.003% to 4.08%). The mean total cover of the herbaceous layer, shrub layer and canopy layer was 74.71%, 27.79% and 28.89%, respectively. Only *Bromus erectus* was close to reach a moderately high frequency value (60–80%). Nine species had intermediate (40–60%) and 26 had low (20–40%) frequencies (Table 3). We found 485 (92.7%) species that were recorded in only 0.1–20% of the relevés, 190 species were found only in one relevé.

The *Orchidaceae* family was widely represented (11 genera, 18 species) in the relevés, but the frequency of the occurring species across all relevés was generally below 0.1%. The most frequent orchid species were *Anacamptis morio* and *Ophrys fuciflora* (frequency of both species = 7.14%) as well as *A. pyramidalis* (frequency = 4.76%).

Most of the species were hemicryptophytes (H = 55.4%), and the second most frequent life-form were phanerophytes (M+MM+Ch+N = 16.9%). Also therophytes (Th = 12.5%), cryptophytes (G = 11.3%) and hemitherophytes (TH = 4.4%) occurred.

Species in the relevés belonged to 19 phytosociological groups according to BORHIDI (1995; Hungarian plant communities; Fig. 2). Species of the *Trifolio-Geranietea*, *Rhamno-Prunetea*, *Festuco-Brometea* and *Molinio-Arrhenatheretea* vegetation classes had the highest relative frequencies among the relevés (Fig. 2).

Himantoglossum adriaticum occurred in 10 phytocoenological classes according to the classification of MUCINA et al. (2016). These classes belong to the vegetation of the nemoral forest zone, the steppe zone and the Mediterranean zone. Five of these units are grasslands, three of them forests and two shrub dominated communities. Thirteen habitats have a high conservational value as they are listed in the Annex I of the Habitats Directive 92/43/EEC of the European Commission (Supplement E2).

3.2 Species indicator values

According to the median and mean ecological indicator values of the accompanying species, we obtained the following median values for *H. adriaticum*: heat supply (TB = 6), soil moisture (WB = 3), soil nitrogen (NB = 3) and continentality (CB = 4). The analyses obtained extreme values for soil reaction (RB = 8), light intensity (LB = 7) and soil salt concentration (SB = 0).

With respect to continentality, we found a balanced distribution of frequencies between suboceanic species (CB = 4) and subcontinental species (CB = 6) (Fig. 3).

According to indicator values of nitrogen supply, species of oligotrophic (NB = 2–3, i.e., *Galium boreale*, *Stipa joannis*, *Inula salicina*, *Trifolium montanum*, *Chrysopogon gryllus*, *Bromus erectus*, *Carex humilis*, *Geranium sanguineum*) and submesotrophic habitats (NB = 4, i.e., *Cornus sanguinea*, *Plantago lanceolata*) were the most frequent among the relevés.

Moreover, we found species that are mostly living in light conditions to be most frequent (LB = 7–8, i.e., *Teucrium chamaedrys*, *Dactylis glomerata*, *Centaurea scabiosa*, *Bromus erectus*, *Euphorbia cyparissias*, *Salvia pratensis*).

Table 3. Frequency and constancy values of species, which frequency value were larger than 20%. See Table 1 for details of the relevés.

Tabelle 3. Frequenz und Stetigkeitsklasse der Arten, deren Frequenz größer als 20 % war. Für Details der Vegetationsaufnahmen s. Tabelle. 1.

Taxon	Frequency [%]	Constancy	Cover mean	Cover median
<i>Himantoglossum adriaticum</i>	100.00	V	0.7	0.6
<i>Bromus erectus</i>	60.71	IV	15.1	4.5
<i>Teucrium chamaedrys</i>	52.38	III	1.5	0.3
<i>Festuca rupicola</i>	51.19	III	2.8	0.3
<i>Dactylis glomerata</i>	50.00	III	1.4	0.3
<i>Sanguisorba minor</i>	47.62	III	1.0	0.0
<i>Euphorbia cyparissias</i>	47.62	III	0.5	0.0
<i>Brachypodium pinnatum</i>	46.43	III	6.4	0.0
<i>Lotus corniculatus</i>	45.24	III	0.7	0.0
<i>Salvia pratensis</i>	44.05	III	2.0	0.0
<i>Medicago falcata</i>	42.86	III	1.3	0.0
<i>Centaurea scabiosa</i>	40.48	II	1.5	0.0
<i>Arrhenatherum elatius</i>	32.14	II	1.7	0.0
<i>Dorycnium germanicum</i>	32.14	II	1.1	0.0
<i>Crataegus monogyna</i>	30.95	II	1.2	0.0
<i>Peucedanum cervaria</i>	29.76	II	1.5	0.0
<i>Viola hirta</i>	28.57	II	0.4	0.0
<i>Plantago lanceolata</i>	28.57	II	0.6	0.0
<i>Carex flacca</i>	27.38	II	1.7	0.0
<i>Briza media</i>	27.38	II	0.7	0.0
<i>Asperula cynanchica</i>	27.38	II	0.3	0.0
<i>Geranium sanguineum</i>	26.19	II	3.3	0.0
<i>Pimpinella saxifraga</i>	26.19	II	0.3	0.0
<i>Acer campestre</i>	25.00	II	0.4	0.0
<i>Cornus sanguinea</i>	25.00	II	4.1	0.0
<i>Medicago lupulina</i>	25.00	II	0.2	0.0
<i>Inula ensifolia</i>	25.00	II	2.5	0.0
<i>Achillea collina</i>	25.00	II	0.2	0.0
<i>Vincetoxicum hirundinaria</i>	23.81	II	0.8	0.0
<i>Bupleurum falcatum</i>	23.81	II	0.2	0.0
<i>Anthyllis vulneraria</i>	23.81	II	1.1	0.0
<i>Picris hieracioides</i>	23.81	II	0.3	0.0
<i>Ligustrum vulgare</i>	22.62	II	0.9	0.0
<i>Coronilla varia</i>	22.62	II	0.7	0.0
<i>Knautia arvensis</i>	22.62	II	0.4	0.0
<i>Plantago media</i>	22.62	II	0.3	0.0
<i>Achillea millefolium</i>	22.62	II	0.3	0.0
<i>Prunus spinosa</i>	21.43	II	0.8	0.0

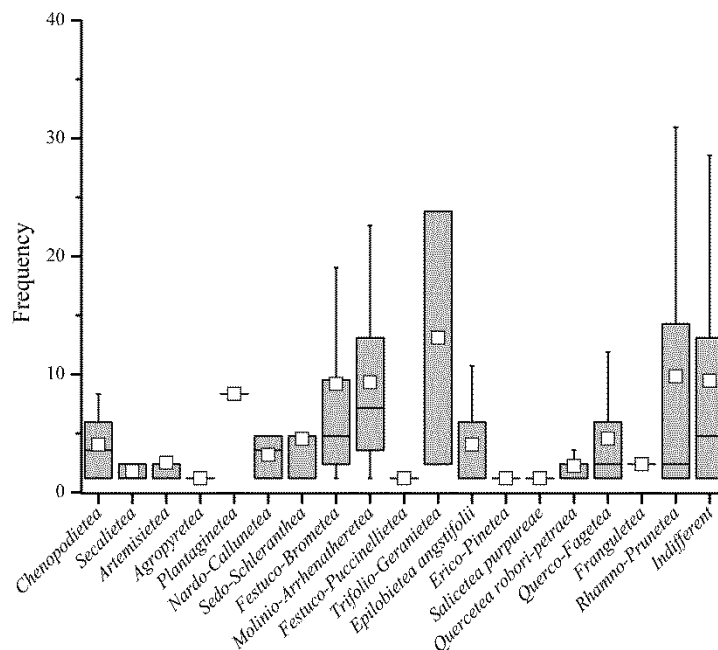


Fig. 2. Distribution of species frequency between plant phytosociological units (BORHIDI 1995). Boxes are 25% – 75% percentiles, whiskers are outliers, horizontal lines are median values, open squares are mean values.

Abb. 2. Verteilung der Artfrequenzen zwischen pflanzensoziologischen Einheiten (BORHIDI 1995). Kästchen sind 25 % – 75 % Perzentile, Whisker sind Ausreißer, horizontale Linien Medianwerte, offene Quadrate Mittelwerte.

According to the heat supply values, we found the highest frequencies of species growing in montane-submontane habitats (TB = 5–6, i.e., *Dactylis glomerata*, *Euphorbia cyparissias*, *Brachypodium pinnatum*, *Teucrium chamaedrys*, *Sanguisorba minor*, *Medicago falcata*).

3.3 Environmental variables and vegetation composition

According to the soil analyses, *H. adriaticum* prefers neutral to basiphilous soils with a medium to high carbonate content, a low salt concentration, a relatively high humus content and a low nutrient concentration (see Table 2).

According to their species composition, the NMDS analyses separated the relevés into two distinct groups of habitat types (Fig. 4). The first two axes explained 40.6% and 33.7% of the total variance of species-environment relationships, respectively (Fig. 5). The obtained two habitat types significantly differed in the cover of herb, shrub and tree layers (*t-test*, $p < 0.05$) and showed a tendency to differ in pH (*t-test*, $p = 0.07$).

We found that a higher inclination significantly decreased the number of species, the Simpson and the Shannon diversity ($R = -0.25$, $p = 0.029$; $R = -0.29$, $p = 0.01$; $R = -0.34$, $p = 0.0028$; respectively). Soil, habitat and geographical variables did not correlate significantly with the diversity values.

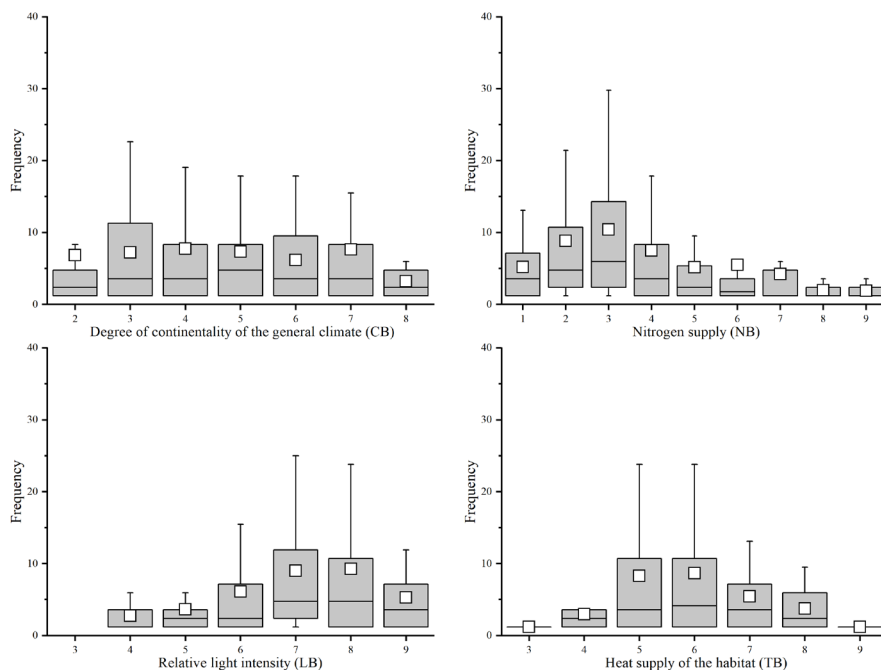


Fig. 3. Distribution of species frequency (mean cover \pm S.E.) between the indicator values of continentality (CB), nitrogen supply (NB), light intensity (LB) and heat supply of the habitat (TB). Boxes are 25% – 75% percentiles, whiskers are outliers, horizontal lines are median values, open squares are mean values.

Abb 3. Verbreitung der Artfrequenzen (Mittelwert \pm Standardfehler) zwischen den Zeigerwerten der Kontinentalität (CB), Stickstoffversorgung (NB), Lichtintensität (LB) und Wärmeversorgung des Habitats (TB). Kästchen sind 25% – 75% Perzentile, Whisker sind Ausreißer, horizontale Linien Medianwerte, offene Quadrate Mittelwerte.

Species number and Shannon diversity were negatively related with the cover of *H. adriaticum* ($R = -0.25$, $p = 0.02$; $R = -0.28$, $p = 0.009$; respectively). In addition, inclination and bryophyte cover were negatively related with the cover of *H. adriaticum* ($R = -0.26$, $p = 0.02$; $R = -0.39$, $p = 0.04$; respectively).

4. Discussion

In our study we investigated the habitat preferences of *H. adriaticum* across its distribution range. The negative correlation of species diversity and *H. adriaticum* abundance may indicate the position of the species in rather species poor transitional ecotone habitats. According our findings, *H. adriaticum* prefers several habitat types, because the relevés were separated by their cover of herbs, trees and shrubs in our ordination analysis (see Fig. 4). This is also mirrored by the mean indicator values and the coenosystematical composition of the relevés. On the one hand, we found a high number of accompanying species with relatively low frequencies and these species distributed equally between the indicator value categories. On the other hand, species from the *Trifolio-Geranietea* phytocoenological unit

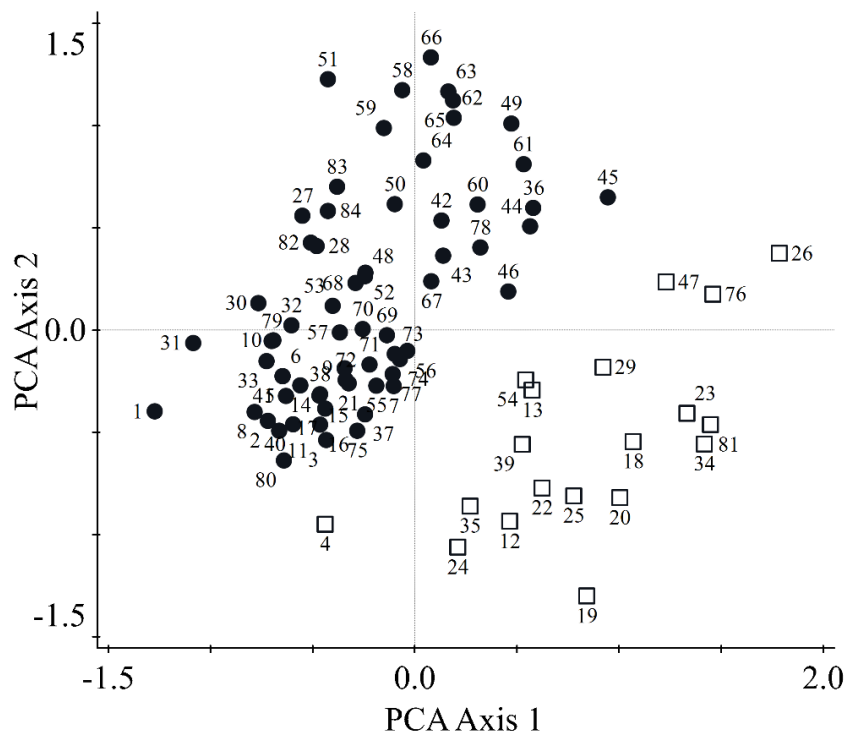


Fig. 4. Ordination of plots containing *Himatoglossum adriaticum*. Ordination plot was based on percentage cover of species in the sampled plots using principal component rotation of NMDS axes. Notations: open square = plots with high cover of trees and shrubs; filled circle = plots with low cover of trees and shrubs.

Abb. 4. Ordination von Plots mit *Himatoglossum adriaticum*. Der Ordinationsplot basierte auf prozentualen Deckungswerten der Arten in den aufgenommenen Plots unter Verwendung der Hauptkomponentenrotation der NMDS-Achsen. Anmerkungen: offenes Quadrat = Plots mit hoher Deckung von Bäumen und Sträuchern; ausgefüllter Kreis = Plots mit geringer Deckung von Bäumen und Sträuchern.

were the most frequent amongst the relevés. This coenosystematic unit includes sub-mediterranean and sub-continental thermophilous vegetation and is positioned in the transition of mesic grasslands and dry woodlands (KLAVER 2011, FEKETE et al. 2017).

The transitional (i.e., ecotone) position of the habitats of *H. adriaticum* is also confirmed by the high frequency of species of semi-dry (*Festuco-Brometea*) and mesic grasslands (*Molinio-Arrhenatheretea*) as well as dry scrublands (*Rhamno-Prunetea*). In addition, our indicator value analysis that this species prefers submesotrophic habitats characterized by mainly light loving, montane-submontane plant species.

Our newly calculated indicator values for the whole distribution range of *H. adriaticum* largely correspond to the ones given in LANDOLT et al. (2010; 1–5 scale: heat supply - 4.5, soil moisture - 1.5, soil nitrogen - 2, continentality - 3, soil reaction - 4, light intensity - 4, soil salt concentration - 0). Our results further corroborate the findings of DELFORGE (2006) who characterized *H. adriaticum* as a species occurring in woodland edges and open woodlands, preferring habitats from full sun to mid-shade conditions. In addition, at the northern

and suppress *H. adriaticum* in abandoned grasslands. However, under dense shrub and tree layers, he found individuals to produce exceptionally long stems (up to 100 cm) and dense inflorescences. The authors also mentioned that in such habitats, where pollinators are largely missing, the elongated (etiolated) inflorescences are only rarely pollinated. After spending many years under dense scrub or tree layers, the plants even produce only vegetative shoots. We made similar observations of the retrogression of the *H. adriaticum* individuals in meadows, abandoned vineyards and traditional orchards in Hungary and Slovenia (Bódis et al. unpublished data). Albeit our results indicate that *H. adriaticum* tolerates shading by trees and shrubs to a certain degree, we did not find a significant correlation between the abundance of *H. adriaticum* and the cover of the tree and shrub layer.

According to the ecological indicator values of the accompanying species we could set up values for *H. adriaticum* that indicate a rather generalistic but light-loving behaviour of the species.

5. Conclusions

Overall, we can conclude that *H. adriaticum* can persist in a wide range of habitats from mesic grasslands to dry scrublands from medium to high elevations. The primary habitats of *H. adriaticum* are open forests, with a mosaic of full sunny and shaded patches, where the species grows in small groups. Large, extended populations can be found in secondary habitats, which offer similar ecological conditions (Supplement E1). The relatively high frequency of scrubland species indicates that *H. adriaticum* prefers the ecotone position, edges of man-made secondary habitats (e.g., roadsides), or temporary habitats during secondary succession (e.g., on abandoned vineyards or grasslands).

The most characteristic habitats of *H. adriaticum* are grasslands dominated by *Bromus erectus* and *Brachypodium pinnatum*. These habitats belong to the submediterranean group of the class *Festuco-Brometea*, reported from Italy, Slovenia, Croatia, Bosnia and Herzegovina, Hungary, Austria and Slovakia (MUCINA et al. 2016). These grasslands are amongst the most species-rich plant communities in Europe (e.g., WILSON et al. 2012), containing a large number of rare and endangered species and are defined as important orchid sites in the EU Habitats Directive.

6. Conservational outlook

The decline of orchid populations is often associated with a change of anthropogenic influences, usually caused by environmental and habitat changes. Among the anthropogenic processes, abandonment is one of the greatest threats to grassland biodiversity due to scrub encroachment (ENYEDI et al. 2008, DENGLER et al. 2014, VALKÓ et al. 2018), as well as the intensification of land use (KULL & HUTCHINGS 2006, GILHAUS et al. 2017). KULL & HUTCHINGS (2006) found that species growing in dry grasslands and woodlands suffer from greater range contractions than wet grassland species, and that species requiring open conditions decline more than those that can tolerate at least some shade. The decline of dry grasslands is a serious threat to *H. adriaticum*. However, we showed that *H. adriaticum* has an ability to expand to secondary habitats such as roadsides, dikes along channels and old grass quarries, which allow the survival in a rapidly changing environment. Such secondary man-made habitats have been shown to be important for the conservation of endangered species and to preserve diverse grasslands (e.g., DEÁK, et al. 2016, MOLNÁR et al. 2018). According to our

own field experiences, the main threatening factor is scrub encroachment in these habitats. Hence, maintaining semi-shaded and open vegetation patches by regular cuttings is important for *H. adriaticum* and could be also favourable for other orchids (e.g., FARRELL 1991).

Erweiterte deutsche Zusammenfassung

Einleitung – Die Adria-Riemenzunge (*Himantoglossum adriaticum* H. Baumann) ist eine bis 80 cm große terrestrische Orchidee mit einer überwinternden Rosette, die aus 2–7 lanzettlichen Blättern besteht. Der Blütenstand ist länglich und locker aus 15–40 bräunlich-roten, typischerweise übelriechenden Blüten zusammengesetzt. Die Einzelblüten besitzen eine tief 3-lappige Lippe, mit einem langen, bandförmigen, schraubenartig gedrehten und geschlitzten Mittellappen (DELFORGE 2006, MOLNÁR 2011). *Himantoglossum adriaticum* ist eine seltene und gefährdete Art. Sie ist eine der zehn Orchideenarten, die im Anhang II der FFH-Richtlinie der Europäischen Kommission aufgeführt sind. Die Art ist zudem in den nationalen Roten Listen der Länder aufgeführt, in denen sie vorkommt (MAGLOCKY & FERÁKOVÁ 1993, CONTI et al. 1997, KIRÁLY 2007, GRULICH 2012). Das Verbreitungsgebiet von *H. adriaticum* umfasst Italien, Slowenien, Österreich, die Slowakei, Montenegro, Kroatien, Bosnien-Herzegowina, Ungarn, die Tschechische Republik und Albanien, und ist verglichen mit jenem der verwandten Arten *H. jankae* und *H. hircinum* deutlich kleiner.

Das Vorkommen von terrestrischen Orchideenarten ist unter anderem von verschiedenen Bodenfaktoren, wie Bodenfeuchte, Gehalt an organischer Substanz, pH und Nährstoffgehalt abhängig. Diese Faktoren beeinflussen auch das Vorkommen von Mykorrhizapilzen, die essentiell für die meisten Orchideenarten sind, da sie die Pflanzen besonders während der Keimung mit Nährstoffen versorgen (BATTY et al. 2001, DIEZ 2007). Auch die Lichtintensität ist eine wichtige, die Lebensraumpräferenz von Orchideenarten beeinflussende Umweltvariable (KULL & HUTCHINGS 2006).

Für *H. adriaticum* sind die Habitatpräferenzen nur unzureichend beschrieben und es finden sich in der Literatur unterschiedlichste Angaben, von halbnatürlichen Grünländern über Waldsäume und -lichtungen bis hin zu Sekundärhabitaten wie Straßenrändern (BAUMANN 1978, BAUMANN & KÜNKELE 1982, MRKVICKA 1990, KALIGARIČ et al. 2004, RYBKA et al. 2005, DELFORGE 2006, TRČAK et al. 2006, KLAVER 2011, MOLNÁR V. 2011, GLASNOVIC et al. 2013, BÓDIS et al. 2014, ČIČMIR et al. 2015, MILANOVIĆ et al. 2015, ŠEFFEROVÁ-STANOVÁ et al. 2015). Zeigerwerte für diese Art waren bislang nur für die Populationen im Alpenraum verfügbar (LANDOLT et al. 2010).

Für eine effektive Erhaltung von bedrohten Arten ist es erforderlich, deren Habitatpräferenzen zu kennen und Umwelteigenschaften zu bewerten, die potentiell die Verbreitung und die Häufigkeit einer Art beeinflussen (PRIMACK 2010). Wegen des hohen Erhaltungswertes von *H. adriaticum* ist es daher wichtig, diese Variablen zu definieren.

Unsere Studie hat deshalb das Ziel, die Habitatanforderungen von *H. adriaticum* auf der Basis von publizierten und neu erhobenen Daten in ihrem Verbreitungsgebiet zusammenzufassen und Zeigerwerte für das gesamte Verbreitungsgebiet der Art vorzuschlagen. Wir charakterisieren im Folgenden die besiedelten Lebensräume anhand der vorkommenden Arten sowie der Diversität und geben Auskunft zu den bevorzugten abiotischen Lebensraumbedingungen von *H. adriaticum* anhand mittlerer Zeigerwerte.

Methoden – Zur Charakterisierung der von *H. adriaticum* besiedelten Pflanzengemeinschaften erstellten wir insgesamt 41 Vegetationsaufnahmen mit einer Flächengröße von 2 m × 2 m in Slowenien, Kroatien, Österreich, Ungarn, der Slowakei und Bosnien-Herzegowina. Wir erfassten alle vorkommenden Gefäßpflanzenarten, schätzten ihre prozentuale Deckung und nahmen Bodenproben (Tab. 2). Achtunddreißig Vegetationsaufnahmen, die wir in unseren Analysen verwendeten, stammen aus dem Europäischen Vegetationsarchiv (EVA) und umfassen Standorte in Italien, Österreich, Tschechien und der Slowakei (Abb. 1 und Tab. 1), weitere fünf Aufnahmen aus der Slowakei extrahierten wir aus DUCHOŇ (2012). Im Feld erfassten wir ausserdem verschiedene Vegetationsparameter und integrierten geographische Informationen. Die Bodenproben untersuchten wir anschließend im Labor (s. Tab. 2).

Für jede Vegetationsaufnahme errechneten wir zunächst die mittleren ökologischen Zeigerwerte für Stickstoffversorgung, Kontinentalität, Lichtintensität und Temperatur nach BORHIDI (1995; 1–9 Skala), sowie die Artenzahl, die Shannon-Diversität und die Simpson-Diversität.

Wir verwendeten multivariate Analysen (NMDS) zur Darstellung der Korrelationen der Artenzusammensetzung mit den Umweltparametern. Danach errechneten wir den Zusammenhang zwischen Lebensraumtypen, der Diversität und Umweltvariablen mit dem Deckungsgrad von *H. adriaticum* unter Verwendung von Spearman Rangkorrelationen (ZAR 1999). Um die relativen Indikatorwerte von *H. adriaticum* zu bestimmen, berechneten wir den Median der relativen Zeigerwerte aus den Vegetationsaufnahmen, wobei wir seltene und vereinzelt vorkommende Arten ausschlossen.

Ergebnisse – Die Vegetationsaufnahmen ließen sich unterschiedlichen Vegetationsklassen zuordnen (nach MUCINA et al. 2016), darunter Wald-, Gebüsch- und Offenlandgesellschaften. Dreizehn Lebensräume sind aufgrund ihres hohen Erhaltungswertes im Anhang II der FFH-Richtlinie der Europäischen Kommission aufgeführt (Anhang E2).

Anhand der mittleren Zeigerwerte der Begleitarten errechneten wir folgende Zeigerwerte für *H. adriaticum*: Temperaturzahl - 6, Bodenfeuchtezahl - 3, Stickstoffzahl - 3, Kontinentalitätszahl - 4, Reaktionszahl - 8, Lichtzahl - 7 und Salztoleranzzahl - 0. Die Art bevorzugt demnach neutrale bis basiphile Böden mit mittlerem bis hohem Kalkgehalt, einer geringen Salzkonzentration, einem relativ hohen Humusgehalt und einer niedrigen Nährstoffversorgung (s. Tab. 2).

Die multivariaten Analysen trennten die Aufnahmen nach ihrer Artenzusammensetzung in zwei Gruppen von Lebensraumtypen (Abb. 4), die sich in der Deckung von Kraut-, Strauch- und Baumschichten unterscheiden, sprich Offenland und Gehölz-dominierte Einheiten. Interessanterweise korrelierte die Deckung von *H. adriaticum* negativ mit der Anzahl der Arten, der Hangneigung und der Moosdeckung.

Diskussion – Die von uns neu für das gesamte Verbreitungsgebiet errechneten ökologischen Zeigerwerte für *H. adriaticum* entsprechen weitgehend den für die Art in LANDOLT et al. (2010) angegebenen. Die negative Korrelation zwischen der Artenvielfalt und der Deckung von *H. adriaticum* könnte auf eine schlechte Konkurrenzfähigkeit der Art hindeuten. Sie kommt in verschiedenen Lebensraumtypen vor, oft jedoch in Ökotonen, also Übergängen zwischen Ökosystemen, wie Offenland und Wald. Dies spiegelt sich auch in den vorwiegend intermediären Zeigerwerten und der Artenzusammensetzung der Aufnahmen wider, da zahlreiche Begleitarten mit relativ niedriger Frequenz und relativ heterogenen Zeigerwerten in den Aufnahmen vorkamen. Mit hoher Stetigkeit traten jedoch Arten der Klassen *Trifolio-Geranietea*, *Festuco-Brometea*, *Molinio-Arrhenatheretea* und *Rhamno-Prunetea* auf. Diese Arten charakterisieren sub-mediterrane und subkontinentale thermophile Vegetationstypen und zeigen einen Übergang von mesischem Grünland zu trockenen Wäldern an (KLAVER 2011, FEKETE et al. 2017). Unsere Ergebnisse bestätigen frühere Studien, welche diese Übergangslbensräume als bevorzugte Habitate von *H. adriaticum* anführten (z. B. RYBKA et al. 2005, DELFORGE 2006). Ebendiese Vegetationstypen sind jedoch keine Klimaxstadien und entstanden oft aus verbuschten Trockenrasen nach Aufgabe der Nutzung.

Der Rückgang von Orchideenpopulationen ist oft mit Umwelt- und Habitatveränderungen verbunden; zum Beispiel durch die Aufgabe der Bewirtschaftung aber auch die Landnutzungsintensivierung – zwei der größten Gefährdungen der Grünlanddiversität (z. B. KULL & HUTCHINGS 2006, GILHAUS et al. 2017, VALKÓ et al. 2018). Auch für *H. adriaticum* sind zu intensiv genutzte Wiesen oder zu dichte Gehölzbestände ungeeignet als Lebensraum. Die Art ist somit auf eine moderate Nutzung angewiesen oder muss sich stetig ausbreiten und neue Satellitenpopulationen bilden. Der Rückgang von Trockenrasen stellt somit eine ernsthafte Bedrohung dar. *Himantoglossum adriaticum* ist jedoch in der Lage, Populationen in sekundären Lebensräumen wie Straßenrändern und Deichen entlang von Kanälen aufzubauen. Nach unseren eigenen Erfahrungen ist die Verbuschung der Lebensräume der größte Gefährdungsfaktor für die Art. Es ist somit essentiell, für ihre Erhaltung halbschattige und offene Trockenrasen durch regelmäßiges Entbuschen zu bewahren, was sich zudem positiv auf andere Arten auswirken könnte.

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Supplements

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. Exemplary habitats of *Himantoglossum adriaticum*.

Anhang E1. Beispiele für Habitats von *Himantoglossum adriaticum*.

Supplement E2. The list of vegetation types where *Himantoglossum adriaticum* occurred.

Anhang E2. Liste der Vegetationstypen mit *Himantoglossum adriaticum*.

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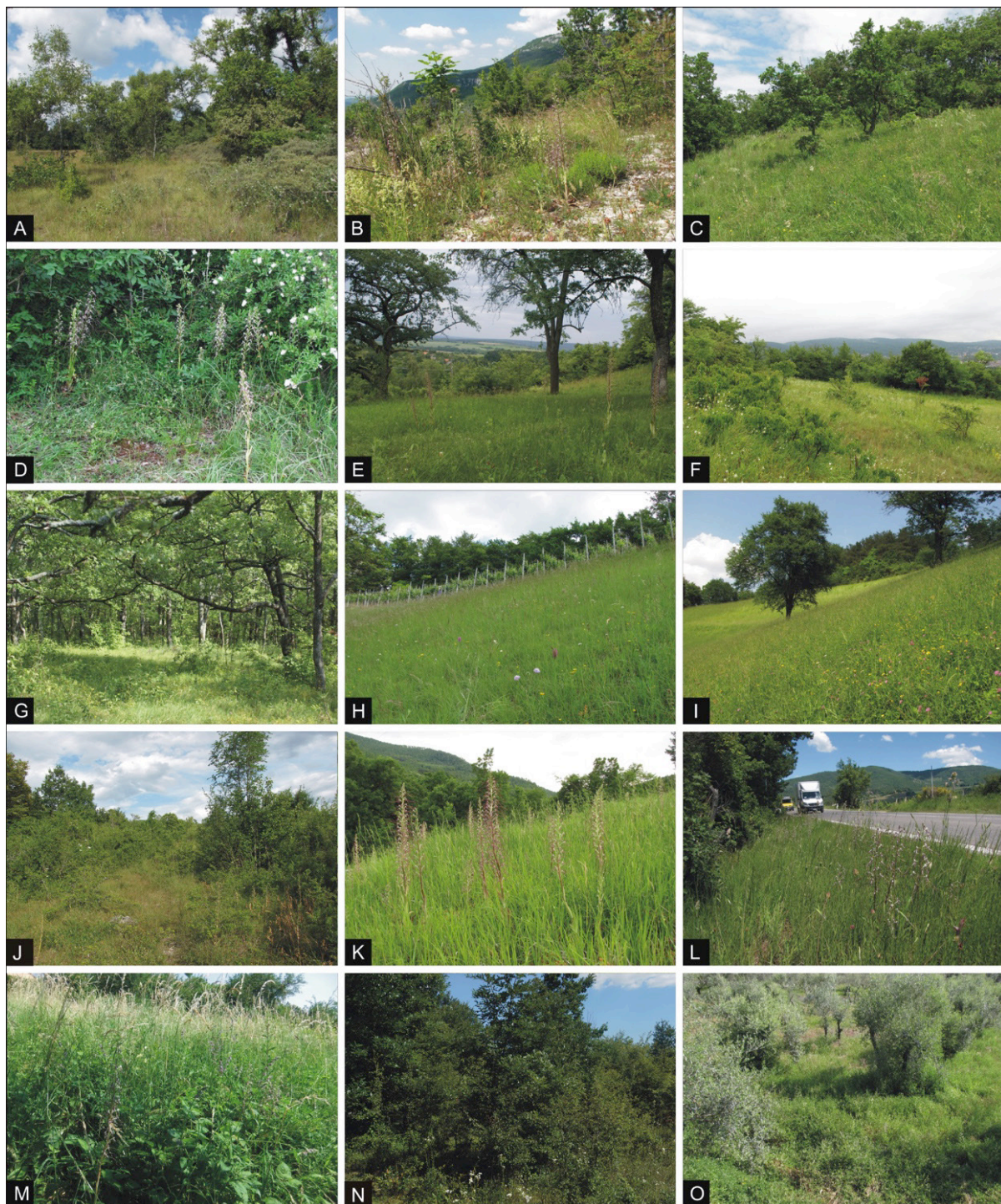
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Supplement E1. Exemplary habitats of *H. adriaticum*. A – grassland-scrub mosaic in riverside sand pit (Lobau, Vienna; Austria). B – calcareous open rocky grassland (Ucka, Istrian peninsula; Croatia). C – forest steppe meadow (Keszthely; Hungary). D – edge of thermophilous forest (Keszthely; Hungary). E – mown traditional orchard (Kőszeg; Hungary). F – abandoned vineyard with semi-dry grassland (Stupava; Slovakia). G – thermophilous *Quercus pubescens* forest (Uhrovec, Slovakia). H, I – *Bromus erectus* hay meadows (Mala Varnica; Slovenia). J – grassland-scrub mosaic of abandoned pasture (Suvaja, Bosnia & Herzegovina). K – *Brachypodium pinnatum* semi-dry grassland in abandoned vineyard (Appechio, Italy). L – mown roadside (Greve in Chianti; Italy). M – *Arrhenatherum elatius* hay meadow (Kőszeg, Hungary). N – scrubland (Herend, Hungary). O – Olive grove (Radda in Chianti, Italy). Photographs: A–D, F, H–L, O by J. Bódis, E, G, N by A Molnár V., M by É. Biró; all taken between 2012 and 2016.

Anhang E1. Beispiele für von Habitate von *H. adriaticum*. A – Grasland-Busch-Mosaik in Flussauen-Sandgrube (Lobau, Wien; Österreich). B – offener felsiger Kalkmagerrasen (Ucka, istrische Halbinsel; Kroatien). C – Waldsteppenwiese (Keszthely; Ungarn). D – thermophiler Waldsaum (Keszthely; Ungarn). E – gemähte traditionelle Obstwiese (Kőszeg; Ungarn). F – aufgelassener Weinberg mit Halbtrockenrasen (Stupava; Slowakei). G – thermophiler *Quercus pubescens*-Wald (Uhrovec, Slowakei). H, I – *Bromus erectus*-Heuwiesen (Mala Varnica; Slowenien). J – Grasland-Busch-Mosaik einer aufgelassenen Weide (Suvaja, Bosnien & Herzegowina). K – *Brachypodium pinnatum* –Halbtrockenrasen in aufgelassenem Weinberg (Appechio, Italien). L – gemähter Straßenrand (Greve in Chianti; Italien). M – *Arrhenatherum elatius*-Heuwiese (Kőszeg, Ungarn). N – Buschland (Herend, Ungarn). O – Olivenhain (Radda in Chianti, Italien). Fotos: A–D, F, H–L, O: J. Bódis, E, G, N: A Molnár V., M: É. Biró; alle 2012–2016.



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Supplement E2. The list of vegetation types where *H. adriaticum* occurred. Names of coenotaxa, which were mentioned in the references or relevés as habitats of this species are underlined. The list was made according to the ‘Hierarchical floristic classification system of plant communities of Europe’ (MUCINA et al. 2016) Abbreviations: A: Austria, BIH: Bosnia-Herzegovina, I: Italy, H: Hungary, HR: Croatia, SLO: Slovenia, SK: Slovakia. * marks vegetation types listed in Annex I of Council Directive 92/43/EEC (the ‘Habitats Directive’) of the European Commission.

Anhang E2. Liste der Vegetationstypen mit *Himantoglossum adriaticum*. Namen von Syntaxa, die in den Referenzen oder in Vegetationsaufnahmen als Habitate der Art genannt wurden, sind unterstrichen. Die Liste wurde gemäß dem hierarchischen floristischen Klassifikationssystem von Pflanzengesellschaften in Europa (MUCINA et al. 2016) erstellt. Abkürzungen: A: Österreich, BIH: Bosnia-Herzegowina, I: Italien, H: Ungarn, HR: Kroatien, SLO: Slowenien, SK: Slowakei. * markiert Vegetationstypen, die im Annex I der Richtlinie 92/43/EEC (FFH-Richtlinie) des Rates der Europäischen Kommission gelistet sind.

VEGETATION OF THE NEMORAL FOREST ZONE

ZONAL TEMPERATE BROAD-LEAVED FORESTS

Class: FAG *Carpinio-Fagetea sylvaticae*

Order: FAG-03 *Carpinetalia betuli*

SUBMEDITERRANEAN GROUP OF ALLIANCES

Alliance: FAG-03C *Erythronio dentis canis-Carpinion betuli* (I, HR)

*91L0 Illyrian oak – hornbeam forests (*Erythronio-Carpinion*)

Class: PUB *Quercetea pubescentis*

Order: PUB-01 *Quercetalia pubescenti-petraeae*

GROUP OF COOL-TEMPERATE ALLIANCES

Alliance: PUB-01-B *Quercion pubescenti-petraeae*

*91H0 Pannonian woods with *Quercus pubescens* (H)

*91M0 Pannonian-Balkan turkey oak- sessile oak forests (H)

GROUP OF SUBMEDITERRANEAN ALLIANCES ON CALCAREOUS SUBSTRATES

Alliance: PUB-01F *Fraxino orni-Ostryion* (= *Ostryo-Carpinion orientalis*) (HR)

*8140 Eastern Mediterranean screes

Ass.: *Quercus pubescenti-Ostryetum carpinifoliae* (I)

GROUP OF SUBMEDITERRANEAN ALLIANCES ON SILICEOUS SUBSTRATES

Alliance: PUB-01L *Crataego laevigatae-Quercion cerridis*

Ass.: *Listero ovatae-Quercetum cerridis* (I)

INTRAZONAL SCRUB AND WOODLANDS OF THE NEMORAL ZONE

Class: RHA *Crataego-Prunetea*

GROUP OF COOL TEMPERATE ORDERS

Order: RHA-01 *Prunetalia spinosae*

Group of Eastern European alliances (forest-steppe and steppe zones)

Alliance: RHA-01J *Prunion fruticosae* (SK)

*40A0 Subcontinental peri-Pannonic scrub (SK)

GROUP OF WARM-TEMPERATE ORDERS

Order: RHA-02 *Paliuretalia*

GROUP OF EASTERN SUBMEDITERRANEAN ALLIANCES

Alliance: RHA-02E *Paliuro-Petterion* (*Rhamno-Paliurion*) (HR)

INTRAZONAL BOREO-TEMPERATE GRASSLANDS AND HEATH

Class: SED *Sedo-Scleranthetea*

Order: SED-04 *Alysso-Sedetalia*

COOL-TEMPERATE GROUP OF ALLIANCES ON ROCKY SUBSTRATES

Alliance: SED-04A *Alysso alyssoidis-Sedion* (*Alysso-Sedion*) (BIH)

*6110 Rupicolous calcareous or basophilic grasslands of the *Alysso-Sedion*

Class: GER *Trifolio-Geranietea sanguinei*

Order: GER-02 *Antherico ramosi-Geranietalia sanguinei*

GROUP OF COOL-TEMPERATE ALLIANCES

Alliance: GER-02A *Geranion sanguinei* (SK, A)

Class: MOL *Molinio-Arrhenatheretea*

GROUP OF ORDERS OF TEMPERATE WET MEADOWS AND TALL-HERB MEADOWS FRINGES

Order: MOL-05 *Molinetalia caeruleae*

EASTERN EUROPEAN GROUP OF ALLIANCES

Alliance: MOL-05D *Deschampsion caespitosae*

*6510 Lowland hay meadows (*Alopecurus pratensis*, *Sanguisorba officinalis*) (SLO)

VEGETATION OF THE STEPPE ZONE

ZONAL STEPPE GRASSLAND

Class: FES *Festuco-Brometea* (A, HR)

GROUP OF ORDERS OF SUB-XERIC STEPPIC GRASSLAND

Order: FES-01 *Brachypodietalia pinnati*

Alliance: FES-01A *Bromion erecti* (BIH)

Alliance: FES-01B *Cirsio-Brachypodion pinnati* (SK, A)

Ass.: *Polygalo majoris-Brachypodietum* (A)

GROUP OF ORDERS OF CLOSED TUSSOCK STEPPES

Order: FES-02 *Festucetalia valesiaceae*

POST GLACIAL GROUP OF STEPPE ALLIANCES

Alliance: FES-02 *Festucion valesiaceae* (SK, A, H)

*6240 *Sub-pannonic steppic grasslands* (H)

GROUP OF ORDERS OF ROCKY STEPPIC GRASSLANDS

Order: FES-5 *Stipo pulcherrimae-Festucetalia pallentis*

*6190 *Rupicolous pannonic grasslands* (*Stipo-Festucetalia pallentis*) (H)

SILICICOLOUS GROUP OF ALLIANCES

Alliance: FES-05B *Asplenio-Festucion pallentis* (*Asplenio septentrionalis-Festucion pallentis*) (SK)

CALCAREOUS GROUP OF ALLIANCES

Alliance: FES-05C *Bromo pannonici-Festucion csikhegyensis* (*Bromo pannonici-Festucion pallentis*) (SK)

GROUP OF SUBMEDITERRANEAN ORDERS

Order: FES-08 *Artemisio albae-Brometalia erecti*

Alliance: FES-08B *Festuco-Bromion*

*6210 *Semi-natural dry grasslands and scrubland facies on calcareous substrates – important orchid sites* (*Festuco-Brometalia*) (SK, H, SLO, HR, I)

Ass.: *Centaureo bracteatae-Brometum erecti* (I)

Ass.: *Filipendulo-Mesobrometum* (A)

Order: FES-09 *Scorzoneretalia villosae* (HR)

*62A0 *Eastern sub-mediterranean dry grasslands* (*Scorzoneretalia villosae*) (HR)

VEGETATION OF THE MEDITERRANEAN ZONE

ZONAL MEDITERRANEAN FORESTS AND SCRUB

Class: QUI *Quercetea ilicis*

*9340 *Quercus ilex* and *Quercus rotundifolia* forests

Order: QUI-01 *Quercetalia ilicis*

GROUP OF CENTRAL AND EASTERN MEDITERRANEAN ALLIANCES

Alliance: *Fraxino ornii-Quercion ilicis* (*Quercion ilicis*) (HR)

INTRAZONAL MEDITERRANEAN SCRUB

Class: CYT *Cytisetia scopario-striati*

Order: CYT-03 *Spartio juncei-Cytisetalia scoparii* (stands of *Spartium junceum*) (HR)

INTRAZONAL MEDITERRANEAN GRASSLANDS AND HERBLANDS

Class: LYG *Lygeo sparti-Stipetea tenacissimae* (*Thero-Brachypodietea*)

*6220 Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*

Order: LYG-01 *Cymbopogono-Brachypodietalia ramosi*

WESTERN MEDITERRANEAN GROUP OF ALLIANCES

Alliance: LYG-01A *Phlomidio lychniditis-Brachypodion retusi* (*Thero-Brachypodion*) (I)