The effect of land-use change on the distribution of *Gentianella austriaca* and *G. praecox* in Austria

Vliv změn ve využívání krajiny na rozšíření *Gentianella austriaca* a *G. praecox* v Rakousku

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Landscapes and their management in central Europe have dramatically changed during the last century, leading to an ongoing loss of biodiversity at all levels. To address the effect of these changes on the distribution of species and to better understand how changing proportions of different types of land-cover influence grassland taxa, we investigated the historical and present-day distribution of two *Gentianella* species (*G. praecox*, *G. austriaca*), considered to be indicators of oligotrophic grassland, in north-eastern Austria. The distribution data obtained from herbarium vouchers, literature and mapping projects was related to historical habitat data obtained from military maps dating back to the end of the 19th century and present-day data on habitat availability based on remote sensing methods. Areas of suitable and unsuitable habitats were obtained from historical and recent land-cover data for 133 sample plots of 78.5 h each, surrounding either extinct or extant *Gentianella* populations. Differences in percentages of habitat types between the extinct and the extant populations were investigated in the recent landscape data. Subsequently, the percentage changes between recent and historical landscape data were compared for extinct and extant populations. Results revealed regional and local hotspots of extinction and significant overall trends of gains in forest land-cover and losses in grassland and wetland land-cover, and deviating regional trends for arable field and settlement land-cover. There was a clear deteriorating effect of increased settlement and decreased wetland land-cover on the distribution of the species studied. Landscape heterogeneity indices, however, did not show significant differences between the extinct and extant populations sampled. Results are in line with well-documented trends in central Europe and indicate a need for rapid and effective conservation measures.

Keywords: biodiversity, *Gentianella austriaca*, *G. praecox*, habitat decline, herbaria, historical habitat maps, land use change, remote sensing habitat maps

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Introduction

Plant taxa depending on oligotrophic grasslands, such as *Gentianella austriaca* and *G. praecox*, are severely endangered, due to an ongoing, well documented loss of these habitats in central Europe (Pärtel et al. 2005, Krauss et al. 2010, Wesche et al. 2012, Fischer et al. 2018). The underlying spatial pattern in vascular plant diversity in cultivated landscapes is seen as the result of different land-use systems, which affect the natural conditions (Reiter et al. 2005, Wrbka et al. 2005a). In the case of north-eastern Austria, the correlation between land management, landscape structure and vascular plant diversity varies substantially. Whereas wilderness areas remain only in remote regions in the high Alps and along the Danube River, most of the forelands and valleys have been subjected to continuous human influence since the Neolithic period (Sauberer & Dullinger 2008). Today about one half of Austria can be described as open agricultural landscapes, shaped by different farming systems (Wrbka et al. 2005b). In the Alps traditional mountain peasantry based on dairy farming can be found, whereas crop-producing farms with large blocks of consolidated fields prevail in the lowlands in eastern Austria (Fink et al. 1989, Wrbka et al. 2002). In this respect, north-eastern Austria is a good example of central-European landscape gradients and is a region almost ideally suited for investigating the effect of changing agrarian land-use practices on biodiversity.

Before the industrial revolution, landscapes were characterized by grain crops and secondary grassland created by traditional land-use, especially by extensive livestock-grazing on land cleared of forest (Ellenberg & Leuschner 2010, Poschlod 2015). Anthropogenic habitats, such as secondary grasslands, were invaded by species formerly not native to the region and the biodiversity in the landscape created by extensive land-use was high (Pott 1996). Landscape patterns rapidly changed during the 19th century when population growth and technological development resulted in land-use intensification (Haber 2014, Poschlod 2015). Especially in eastern Austria, this development accelerated after World War II, when food production was increased by using fertilizers, pesticides and heavy machinery. From this period onwards, landscapes were subjected to more intensive disturbance, resulting in habitat fragmentation, eutrophication and degradation (Settele et al. 1996, Pykälä 2000, Steffan-Dewenter & Tscharntke 2002). In particular, grassland habitats in central-European lowlands were severely affected and almost completely transformed into arable land (Sauberer 1993, Sauberer et al. 1999). As a consequence, seminatural grassland is now of high priority for biodiversity conservation (Muller et al. 1998, Pykälä 2000, Willems 2001, Zechmeister et al. 2002, Wesche et al. 2012, Hülber et al. 2017).

This is true for the habitats of the *Gentianella* species considered here, which occur in oligotrophic grasslands with moderate disturbance such as pastures or meadows grazed for short periods after hay harvesting. These habitats depend on traditional management at low altitudes (Greimler & Dobeš 2000, Königer et al. 2012). Because of their niche characteristics *Gentianella* species have been used in conservation related research as indicators of biodiversity and habitat quality (Mitchley & Xofis 2005, Susan & Ziliotto 2006) and for evaluating different management approaches (Lennartsson & Oostermeijer 2001). Accordingly, *Gentianella* species as typical elements of seminatural grassland may be considered as indicators of habitats that have greatly declined in abundance over the past half-century.

Many *Gentianella* species are considered as endangered according to the national (e.g. Niklfeld & Schratt-Ehrendorfer 1999) and IUCN Red Lists (e.g. Bilz 2011). Understanding how this decline is connected with the obvious reduction in seminatural grassland (Essl et al. 2005) in the region investigated should provide a better estimate of long-term trends in the distribution of these taxa and result in the development of effective conservation measures. Comparisons of habitat distribution in the pre-industrial and present-day agrarian landscapes can help to identify those changes in land use (land cover) most significant for survival or extinction of species. To link the presence/absence of selected plant taxa with changes in habitat availability, present-day distribution and land-cover data should be jointly analysed with spatially explicit historical information.

Precise information on the recent distribution of indicator/flagship species such as *Gentianella* spp. can be retrieved from sources such as high resolution maps (Mann 1997), vegetation analyses (Greimler & Dirnböck 1996, Dirnböck & Greimler 1997), itineraries of mapping campaigns (unpublished data from the current scheme of "Mapping the Flora of Austria", coordination: H. Niklfeld and L. Schratt-Ehrendorfer, University of Vienna; later referred to as MFA) and monitoring programs (Engleder 2006, 2014). Historical floristic literature (as for north-eastern Austria, e.g. Neilreich 1846, 1851, 1859, Beck von Managetta 1893, Halácsy 1896) usually only provides low-resolution data. More precise information occasionally is given in floristic, taxonomic and biogeographic works (e.g. Kerner von Marilaun 1888, Wettstein 1892, 1896) and in the "Schedae ad floram exsiccatam Austro-Hungaricam" (e.g. Kerner von Marilaun 1882), which indicates herbaria as a major source of information. Besides their unquestioned role in plant systematics herbaria also provide valuable biogeographical and ecological information (Funk 2003, Lavoie & Lachance 2006, Lees et al. 2011, Everill et al. 2014). *Gentianella* species, due to a strong historical interest in their ecological/seasonal polymorphism (e.g. Wettstein 1892, 1896), are well represented in herbaria in eastern central Europe.

Finally, maps created for military and fiscal purposes during the times of the Austro-Hungarian monarchy, like the "Third Military Survey" (Franzisco-Josephinische Landesaufnahme or Dritte Landesaufnahme) conducted in the 1870s to 1880s (Hofstätter 1989) can provide information on historical land use and habitat distribution in the late 19th century. Extracting georeferenced habitat maps, however, is a complex task, especially the decoding of historical cartographic symbols. Present-day geodata on land cover on the other hand is easily available via remote sensing methods such as CORINE Land Cover 2012 (EEA 2016).

In this study we focus on the regional and local distribution history of two closely related taxa in north-eastern and northern Austria: *Gentianella austriaca*, and *G. praecox*. Both taxa have a mixed mating system (Greimler & Dobeš 2000, Plenk et al. 2016, Janečková et al. 2019) and are associated with extensively managed pastures and hay meadows. As biennials of low competitiveness they depend on a certain amount of disturbance to become established (Greimler & Dobeš 2000, Königer et al. 2012) and are sensitive to eutrophication (Greimler & Dobeš 2000, Engleder 2006). Both species have declined throughout their ranges (Greimler & Dobeš 2000, Berg 2001, Rösler 2001, Brabec 2005, Engleder 2006, Dolek et al. 2010), but there are regional differences. *Gentianella austriaca* seems to have declined only in the lowlands and low mountain ranges, whereas *G. praecox* was always rare at low altitudes.

Focusing on north-eastern Austria we want to (i) investigate sampling history and distribution of the two taxa over a period of nearly 200 years; (ii) identify hotspots of local decline and extinction; and (iii) relate distribution patterns to habitat change identified by comparing land-use data extracted from historical maps and recent land use revealed by remote-sensing methods.

Material and methods

The taxa studied

Both taxa are listed in the literature and deposited in herbaria under various names within *Gentianella* and *Gentiana*. We follow the taxonyms and systematics in Fischer et al. (2008) but due to the confusing nomenclature in the group and lack of citable common source give the authorities at the first citation of every taxon below. Here we do not separate the aestival variant of *Gentianella praecox* at the level of a subspecies, even though recent findings indicate strong reproductive isolation between early and late flowering variants (Plenk et al. 2016).

Gentianella austriaca (A. Kern. et Jos. Kern.) Holub is distributed in the mountains and plains in north-eastern Austria and northern Hungary (Bartha & Király 2015). Note that the specimens assigned to *G. austriaca* from the western part of Lower Austria include intermediate variants between this taxon and the adjacent *G. aspera* (Hegetschw. et Heer) Dostál ex Skalický, Chrtek et Gill. *Gentianella austriaca* grows in various types of oligotrophic calcareous grasslands, open forests, wetlands at low altitudes and grasslands up to the alpine zone.

Gentianella praecox (A. Kern. et Jos. Kern.) Dostál ex E. Mayer occurs in the Bohemian Massif in northern Austria, Bavaria/Bayrischer Wald, Germany (Zentralstelle für die floristische Kartierung Bayerns, Gefäßpflanzen 2019) and Bohemia, Czech Republic (Kaplan et al. 2018). In contrast to *G. austriaca*, a distinct seasonal dimorphism is documented (Kirschner & Kirschnerová 2000, Plenk et al. 2016) between the more common autumnal subsp. *bohemica* (Skalický) Holub and the aestival subsp. *praecox* of which only few populations exist in northern Austria. The Austrian populations of *G. praecox* grow in oligotrophic, acidophilous grasslands in the submontane to montane zone (Plenk et al. 2016). The most suitable habitats for both taxa, therefore, are oligotrophic grasslands at all altitudes and wetlands in colline to montane zones.

Data collection and data handling

All available Austrian vouchers of the two taxa in the herbaria BRNU, FBVA, IBF, LI, GJO, GZU, W and WU, selected accessions in M, NMG, WFBVA and WHB (abbreviations follow Thiers 2019) and in the private collections of G. Karrer (Langenzersdorf) and R. Stingl (Bad Vöslau) were evaluated regarding location and (if given) coordinates, habitat, altitude, collector and date. Vouchers housed in herbaria W and WU were databased and are available online via Virtual Herbaria JACQ (http://jacq.org). Additional data could be retrieved from the literature (Wettstein 1896, Greimler & Dirnböck 1996, Dirnböck & Greimler 1997, Mann 1997, Engleder 2014) and selected itineraries of field work for the MFA. Recent hitherto unpublished records by the authors and by

A. Mrkvicka (Vienna), W. Adler (Vienna) and K. Oswald (Lilienfeld) were included. The original dataset including duplicates contained 825 entries of different quality with respect to the localities. We used the Austrian Map Online (www.austrianmap.at/amap) to assign coordinates with error estimates for each and for the few records with only vague label information indicating small villages we used the church as a midpoint of the uncertainty circle to estimate the sampling site. Data on altitude and in few cases also on the habitat were completed using the same online resource.

For the analysis of the overall sampling history (in decades) we included all multiple entries (records from the same locality and year, n = 825). For further analyses, we removed multiple entries (resulting in n = 464, see Electronic Appendix 1). This dataset was used to generate a distribution map of the two species in eastern Austria in ArcMap 10.4.1. (ESRI, Redlands, California, USA).

To depict the entire sampling history investigated the numerous given habitats were standardized in four general classes: 1 – oligotrophic (dry) grassland including talus/bedrock; 2 – pastures and meadows; 3 – wetlands; 4 – open forests, clearings, forest edges, including roadsides. The given altitudes were transformed in altitudinal classes and the data was grouped according to the collecting date in age classes of 50 (final half decade 40) years with corresponding midpoints 1850, 1900, 1950 and 2000. Because of different land use history we divided the area investigated into six regions following Fischer et al. (2008) and Graßler (1984), however in both cases with modifications due to shared or different geology (Fig. 1): Wiener Becken (incl. Marchfeld east of Vienna), Kalk-Wienerwald (calcareous bedrock), Flysch-Wienerwald (Flysch bedrock), Kalk-Voralpen (Gutensteiner Alpen and Türnitzer Alpen), Nördliche Kalkalpen (Rax-Schneeberg-Gruppe, Mürzsteger Alpen, Ybbstaler Alpen including the northern part of Randgebirge östlich der Mur) and Waldviertel (incl. Dunkelsteiner Wald S of Danube).

To identify hotspots of decline and local extinction at local and regional scales the samples recorded during the past 55 years (1960–2014) were compared with those recorded before, the dataset was reduced to a subset (n = 133). Samples were randomly picked with the preconditions that all three plot categories (explained in the next paragraph) and all regions proportional to the entire data set were included and that all samples with assumed uncertainties in locality of more than 500 m were excluded. The time period was selected because it can be assumed, that agricultural intensification and urbanization have become effective during this past half of the century (Sauberer & Dullinger 2008).

To relate historical and recent distribution data with the gains/losses of habitat types in this period for the federal states of Lower Austria and Vienna (including a few sites in the adjacent areas of Burgenland and Styria), historical and actual land-use was compared. For this analysis we considered three classes of data (plot categories): (i) incidences of *G. austriaca*/*praecox* recorded after 1960, assuming a presence before 1960, below referred to as CON (confirmed); (ii) incidences of *G. austriaca*/*praecox* recorded only before 1960, below referred to as EXT (extinct); (iii) incidences of *G. austriaca*/*praecox* recorded only before 1960, however, later recorded as present in the vicinity, i.e. in the same grid cell [Quadrant] as defined by Niklfeld (1971) based on MFA data, below referred to as VIC (vicinity). The last category was implemented to see whether the empty plots with *Gentianella* presence in the vicinity show a different trend with the decline in suitable habitat.

Analyses of landscape change

Digitized map sheets of the Third Austro-Hungarian Military Survey (below referred to as TMS) (Fasching & Wawrik 1989, Hofstätter 1989) were georeferenced in ArcMap 10.4.1. (ESRI, Redlands, California, USA) using churches and other stable landmarks as control points. Sampling localities obtained from the above-described subset of 133 occurrences were buffered by including an area within a radius of 500 m in order to account for uncertainty especially in historical data, this resulted in 133 circular sample-landscapes of 78.5 ha each. To extract the spatial percentage of the different types of land cover each habitat patch was manually digitized for all sample landscapes in ArcMap 10.4.1. This resulted in a geodataset of historical land cover with high spatial accuracy (scale 1:12,500) and sufficient thematic resolution (17 habitat types, see Electronic Appendix 2) for the 133 sample landscapes.

In the next step the actual land cover was extracted from three different sources as no geodataset perfectly matching the thematic and spatial resolution of the historical land-cover data was available: we considered CORINE Land Cover, SINUS land-cover (Wrbka et al. 1999, Peterseil et al. 2004) and a so-called ecosystem map (Ökosystemkarte, thereafter called EUNIS) based on EUNIS level-2 categories (Umweltbundesamt 2014).

To make an informed decision on which of the three actual land-cover datasets is most appropriate for further analyses, an additional interpretation of current high-resolution aerial imagery (geoland.at 2019) was used for all 133 sample landscapes. The percentage coverage of six general and easily distinguishable habitat classes (Electronic Appendix 2) was estimated for each sample landscape using six cover classes (≤ 1%, > 1–5%, 6–25%, 26–50%, 51–75% and 76–100% coverage). Congruence between the latter dataset and the three actual land-cover datasets was evaluated: first the habitat classes were aligned, then the absolute values of coverage in the actual land-cover datasets were transformed into the six cover classes as described above and finally a pairwise comparison was done by counting cover-class mismatches. Minor differences in the two lowest cover classes were considered as matches due to the inherent error of this method. In this comparison CORINE Land Cover revealed the lowest congruence with the aerial imagery analysis (221 mismatches), while SINUS (164) and EUNIS (143) performed notably better. We decided, therefore, to use the EUNIS data for the subsequent analyses due to its highest congruence with the aerial imagery and the highest accuracy in the mapping of wetlands.

In order to compare the percentage distribution of different types of land cover in historical TMS data with the current situation as pictured by EUNIS an alignment of the discriminated habitat types in the two datasets was performed (Electronic Appendix 2). Gain and loss of area in those habitats between the historical and the recent landscape status was calculated for the dataset of 133 sample landscapes as well as for subsets.

Statistical analysis

First we examined the three plot categories CON, EXT, VIC, (i.e. the sampled areas surrounding collection sites of the *Gentianella* species) in the EUNIS maps using a Kruskall-Wallis test with Bonferroni corrections of significance estimates to test for differences in the percentages of suitable and unsuitable habitats, in which suitable habitats include grasslands and wetlands, unsuitable habitats arable fields, settlements and forest. This test was first done using the entire dataset of 133 sample landscapes and subsequently with two subsets (reg1: Alps and Prealps; reg2: Waldviertel, Wienerwald, and Wiener Becken) to account for different histories of land use.

Subsequently, the total changes (gains and losses) in the percentages (ha, %) of these habitat types between the TMS (1869–1887) and the EUNIS assessment (2013) were calculated across all regions for the three plot categories. For those habitats showing different tendencies the regions were combined into an increase and a decrease group, respectively. Mann-Whitney U-tests were employed in pairwise comparisons to test for identity of central tendencies (mean ranks) in the data.

Third, the changes (EUNIS/TMS) in habitat percentages between the three plot categories were compared in an additional design (similar to the comparison between the EUNIS plot categories) using a Kruskall-Wallis test with Bonferroni corrections of the significance estimates.

To assess the structure of sampled landscape plots we calculated landscape indices by employing V-LATE 2.0 beta extension (Lang & Tiede 2003) in ArcMap 10.4.1. Edge density (m/ha) and land-cover diversity as Shannon's diversity index (Wu 2013) were obtained for each plot and one-way ANOVA was used to test for differences in the trends between the three plot categories. For this and the above-mentioned statistics and graphs SPSS statistics 25.0 (IBM, Armonk, New York, USA) and Excel 2010 (Microsoft Corporation, Redmond, Washington, USA) were used.

Finally, to investigate the spatial continuity of suitable habitats we cross-tabulated areas of TMS and EUNIS data to calculate gross changes in habitat conditions (suitable/unsuitable) using ArcMap 10.4.1. (ESRI, Redlands, California, USA). The resulting percentage values of areas that assumedly remained suitable throughout the period of time investigated were tested for differences between the three categories CON, EXT, VIC within the entire sample as well as for the plots sampled in the different regions (Kruskall-Wallis tests with Bonferroni corrections). These analyses were done in R 3.6.3 (R Core Team 2020).

Results

Distribution patterns and hotspots of local extinction

The map (Fig. 1A) shows the entire distribution of the two taxa in Austria based on sampling over a period of nearly 200 years. Several hotspots of decline and local extinction at a small regional scale could be identified by comparing samples of the past 55 years (1960–2014) with those collected previously. During the past 55 years no plants of *G. austriaca* were recorded in the regions Marchfeld (northernmost Wiener Becken) and Flysch-Wienerwald and marked declines in abundance were recorded in the remaining Wiener Becken and foothills and lower mountains along the north-eastern margin of the Alps. Similarly, in the northernmost part of Waldviertel no plants of *G. praecox* were recorded and marked declines in abundance were recorded in the very southern part of its distribution and south of the Danube in Dunkelsteiner Wald.

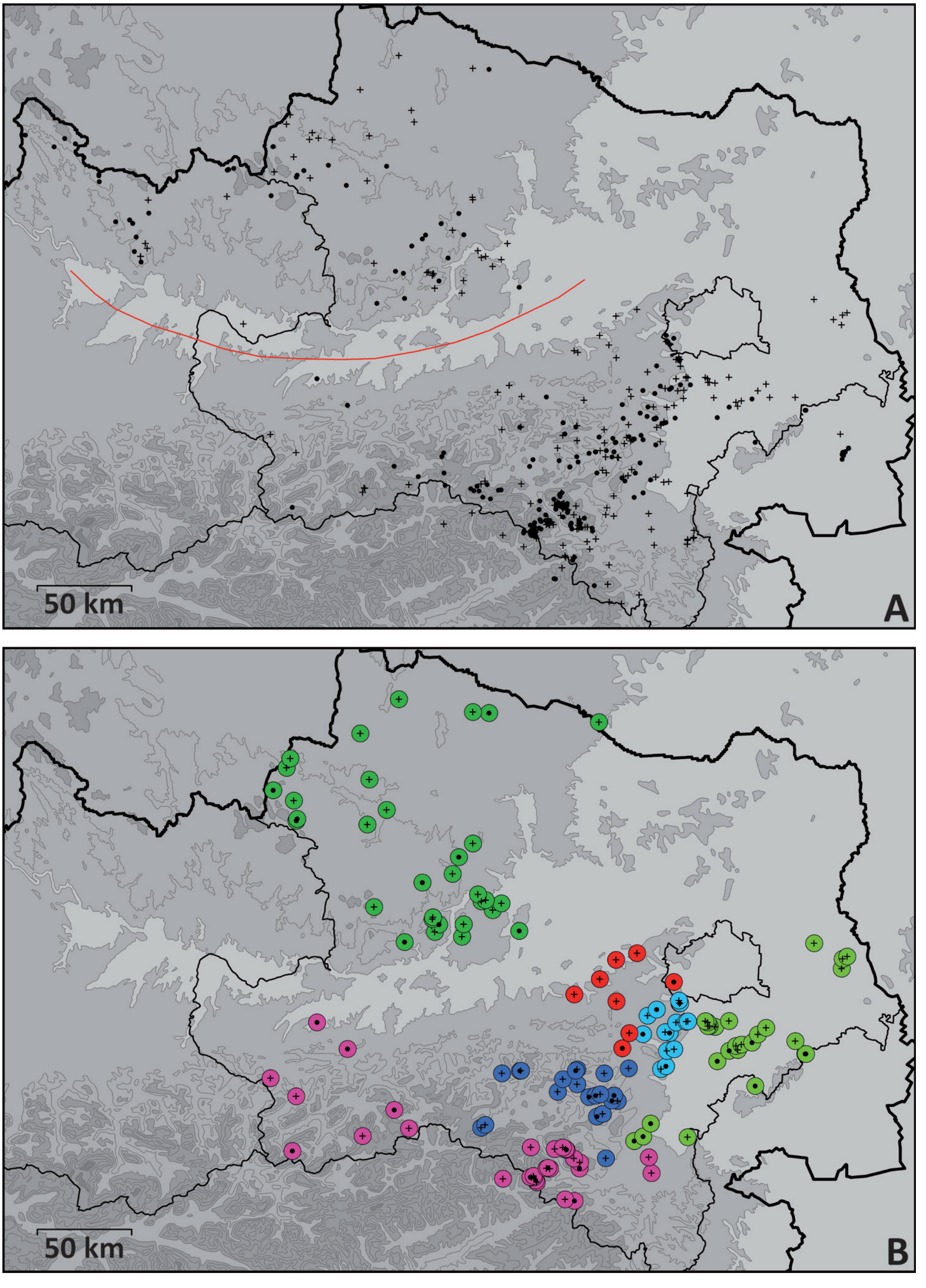

Fig. 1. – (A) Map depicting the distribution of *Gentianella austriaca* and *G. praecox* in Austria based on records spanning nearly 200 years. The points denote extant and crosses extinct (not found after 1960) populations, bold black lines indicate national, thin black lines federal borders and the red line separates the distribution of *G. austrica* in the south and *G. praecox* in the north. (B) Map of sampled plots, extant vs extinct populations and borders as in (A), regions are colour-coded: Wiener Becken light green, Kalk-Wienerwald light blue, Flysch-Wienerwald red, Kalk-Voralpen dark blue, Nördliche Kalkalpen purple, Waldviertel dark green.

Table 1. – Bonferroni corrected significances for the Kruskall-Wallis tests for differences in total and regional areas of habitat in plots of EUNIS maps for the three plot categories CON (incidences of *Gentianella austriaca/praecox* recorded after 1960 and assuming a presence before 1960), EXT (incidences of *G. austriaca/praecox* recorded only before 1960) and VIC (incidences of *G. austriaca/praecox* recorded only before 1960, however, currently present in the vicinity). Pairwise comparisons are given for cases where there is a significant difference (in bold) between groups: reg1 – Alps and Prealps; reg2 – remaining regions, na – not applied.

	n	CON/EXT/VIC	CON/EXT	CON/VIC	EXT/VIC
Suitable habitats	266	0.102	na	na	na
Grasslands	133	0.056	na	na	na
Grasslands reg1	51	0.992	na	na	na
Grasslands reg2	82	**0.012**	**0.009**	0.336	0.794
Wetlands	133	**0.016**	**0.014**	0.212	0.796
Unsuitable habitats	399	**0.010**	**0.049**	1.000	**0.013**
Arable fields	133	**0.000**	0.170	**0.022**	**0.000**
Arable fields reg1	51	**0.021**	0.113	1.000	**0.016**
Arable fields reg2	82	0.051	na	na	na
Settlements	133	**0.001**	**0.001**	0.454	0.068
Forest	133	0.063	na	na	na

Sampling history of Gentianella austriaca and G. praecox

The sampling history of the two taxa based on all the data evaluated including duplicates with coordinates and collecting year is given in Electronic Appendix 3. The sampling frequency of *G. austriaca* shows two peaks, one in the late 19th century and the other in the late 20th century. The general picture for *G. praecox* roughly resembles the pattern recorded for *G. austriaca* during the 19th and the early 20th century. During subsequent periods in the 20th century there was a more fluctuating pattern and a peak in *G. praecox* at the beginning of the 21st century.

Sampling frequencies in time-altitude-habitat space are shown in Fig. 2A for *G. austriaca* and Fig. 2B for *G. praecox*. These diagrams indicate that *G. austriaca* is confined to wetland habitats at the lowest altitudes, extending into less humid habitats at higher altitudes. At the highest altitudes pastures and various oligotrophic grasslands are the typical habitats of this species. *Gentianella praecox* was mainly found in various types of grassland at montane altitudes.

Comparison of plot categories in EUNIS maps

Results of tests for differences between the sample landscapes based on the EUNIS dataset and assigned to the three different plot categories are given in Table 1. Overall differences in the suitable habitats (grasslands and wetlands) are not significant. In detail, however, the lowest percentage of wetlands in the plots with extinct populations (EXT) differ significantly ($P < 0.05$) from those in plots with extant populations (CON). After splitting into two regional groups we found a significantly lower percentage ($P < 0.01$) of grassland in reg2 (Waldviertel, Wienerwald, and Wiener Becken) in plot category EXT. A significantly higher percentage of unsuitable habitats (arable fields, settlements, forest) was recorded in plot category EXT compared to CON and VIC (both $P < 0.05$). In detail, we found the high percentage of arable fields in the EXT plots was only significantly different from that in the VIC plots ($P < 0.001$). Splitting into two regions

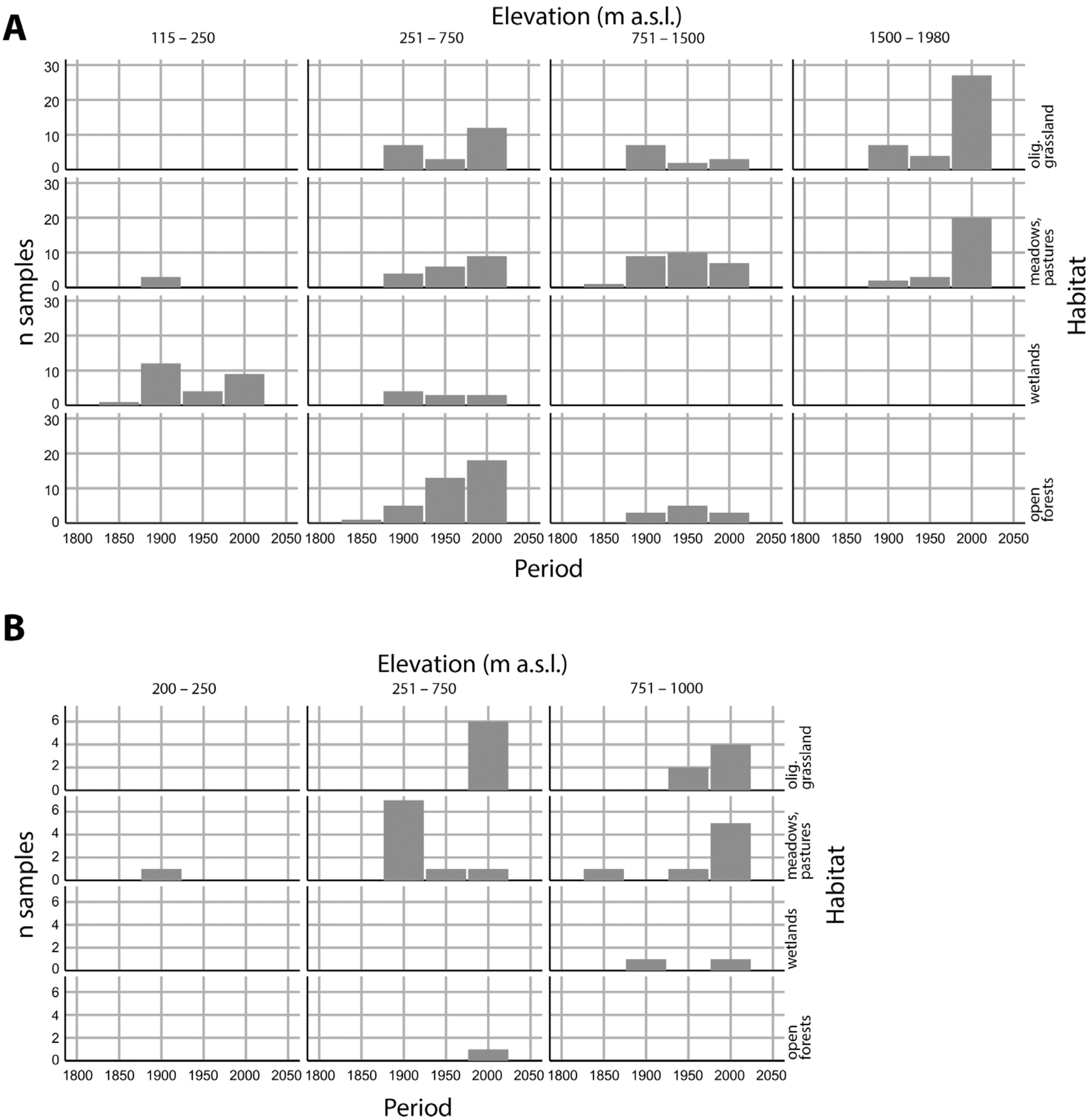

Fig. 2. – Bar charts of frequencies of occurrence excluding multiple entries in time-altitude-habitat space for (A) *Gentianella austriaca* and (B) *G. praecox.* Single records are aggregated for each 50 years starting in 1825 and placed according to their habitat. Habitat class: 1 – oligotrophic (dry) grassland including talus/bedrock; 2 – pastures and meadows; 3 – wetlands; 4 – open forests, clearings, forest edges (including roadsides) and altitude classes.

(as above) we found the same pattern only in reg1 (EXT/VIC: P < 0.05). The highest percentage of settlements in the plots with extinct populations differed significantly from that in plots with extant populations (CON/EXT: P < 0.01).

Table 2. – Differences in the percentages (ha, %) of suitable and unsuitable types of habitats in the TMS (1869–1887) and EUNIS assessment (2013) around collection sites of *Gentianella austriaca* and *G. praecox* for the three plot categories CON (incidences of *G. austriaca/praecox* recorded after 1960 and assuming a presence before 1960), EXT (incidences of *G. austriaca/praecox* recorded only before 1960) and VIC (incidences of *G. austriaca/praecox* recorded only before 1960, however, currently present in the vicinity); n – given for pairs; MR1 – mean rank TMS; MR2 – mean rank EUNIS; sig. – significance estimates based on nonparametric tests for identity of central tendencies (Mann-Whitney U-test), with significant values in bold.

Habitat	CON						EXT						VIC					
	n	ha	%	MR1	MR2	sig	n	ha	%	MR1	MR2	sig	n	ha	%	MR1	MR2	sig
Suitable	86	–468.5	–14	95.5	77.6	**0.015**	84	–629.5	–19	105.2	63.8	**0.000**	96	–654.4	–17	111.7	81.3	**0.000**
Grasslands	43	–276.4	–6	49.4	37.6	**0.028**	42	–340.0	–11	51.4	33.6	**0.001**	48	–509.1	–10	58.3	38.7	**0.001**
Wetlands	43	–192.1	–6	48.8	38.2	**0.013**	42	–289.5	–9	57.0	28.0	**0.000**	48	–145.3	–4	58.7	38.3	**0.000**
Unsuitable	129	574.1	17	129.8	129.2	0.943	126	853.1	26	118.7	134.3	0.088	144	864.8	23	147.2	141.8	0.574
Arable fields	43	51.2	2	43.9	43.1	0.876	42	147.3	6	41.8	43.2	0.788	48	–147.2	–4	55.3	41.7	**0.009**
Forest	43	504.3	15	37.1	49.9	**0.017**	42	330.5	11	36.9	48.1	**0.034**	48	732.8	20	40.3	56.7	**0.004**
Settlements	43	18.6	1	52.6	34.4	**0.000**	42	375.4	11	40.8	44.2	0.520	48	279.2	7	53.0	44.0	0.103

Comparison of historical TMS and recent EUNIS sampling plots

Both the plots around extinct and extant populations of the species of *Gentianella* studied exhibit similar trends in gain/loss in different types of habitats when comparing historical (TMS) and actual land use (EUNIS). The overall pattern (Table 2) for all regions for the combined suitable habitats (grasslands, wetlands) shows a significant reduction in the percentage of these habitats ($P < 0.05$) in all plot categories with the highest loss (–19%, $P < 0.001$) in EXT. There was a significant decrease in the percentage of grasslands in all plot categories with $P < 0.01$ in EXT and VIC and $P < 0.05$ in CON. A similar pattern was recorded for wetlands with $P < 0.001$ in EXT and VIC and $P < 0.05$ in CON. In contrast, we recorded a notably increased percentage of unsuitable habitats in all plot categories, with the highest increase in EXT of +26% approaching marginal significance ($P = 0.088$). In detail, there was a significant increase in the percentage of forest in all plot categories (CON, EXT: $P < 0.05$, VIC: $P < 0.01$), whereas for arable fields and settlements the pattern is complicated due to different and even conflicting trends in the regions (see details in Fig. 3). While there was a strong increase in arable fields in the region Wiener Becken in all plot categories (significant in EXT: $P < 0.05$) in the combined other regions there was a notable decline. The strong (although non-significant) increase in settlements (especially when the results for the regions Kalk-Wienerwald and Wiener Becken are combined) in plot categories EXT and VIC is in marked contrast with a low, however, significant ($P < 0.001$) increase in plot category CON, which is a consequence of the nonparametric analysis used due to an extreme positive skewness in one of the paired samples. All changes in habitat percentages in sampled plots are illustrated in the diagrams for each region and all types of habitats (arable fields, grasslands, forests, settlements, wetlands) with respect to the occurrence of *Gentianella* are shown in Electronic Appendices 4–9.

Tests for differences in the changes (TMS/EUNIS) between the three plot categories (Table 3) revealed significant differences in suitable habitats only for wetlands in the comparisons CON/EXT ($P < 0.01$) and EXT/VIC ($P < 0.05$). There was also no overall

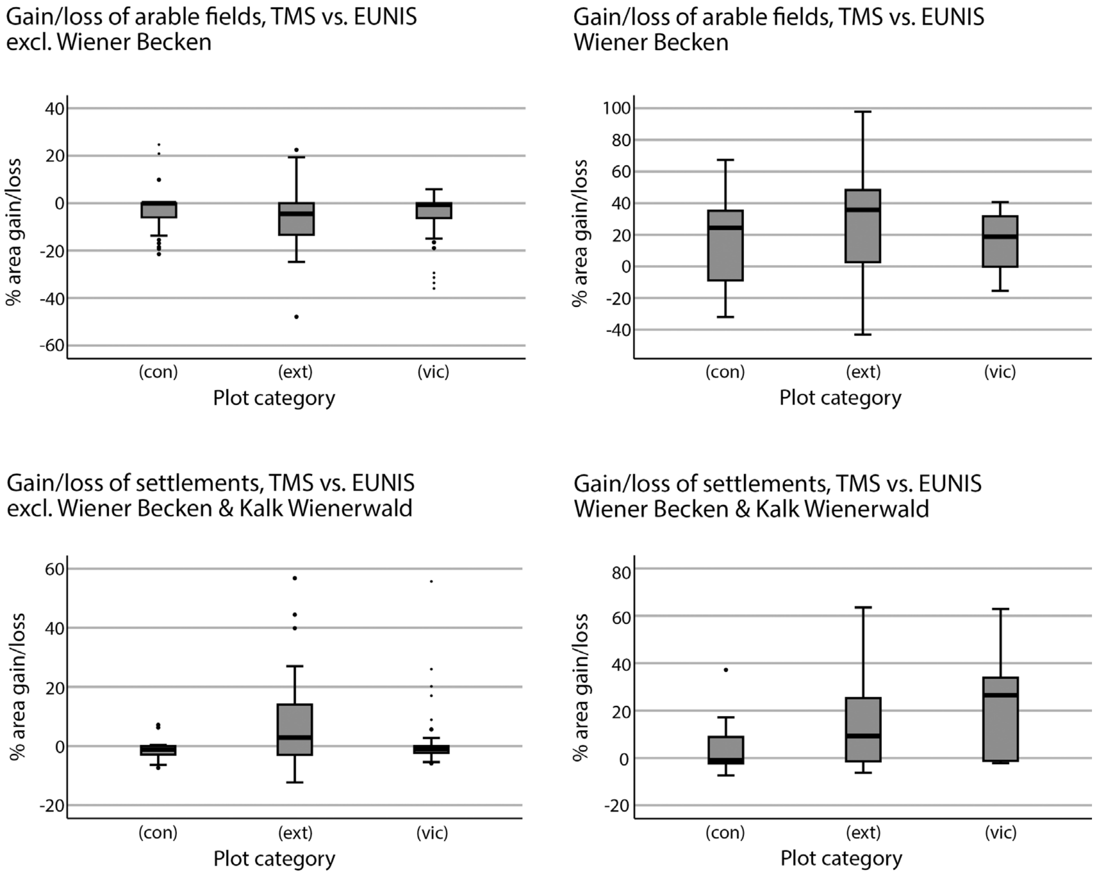

Fig. 3. – Box plots depicting the percentage changes in two types of habitats in the plot categories CON (incidences of *Gentianella austriaca/praecox* recorded after 1960 and assuming a presence before 1960), EXT (incidences of *G. austriaca/praecox* recorded only before 1960) and VIC (incidences of *G. austriaca/praecox* recorded only before 1960, however, currently present in the vicinity) between the TMS (Austrian Third Military Survey, 1869–1887) maps and the EUNIS assessment (2013), which show different regional trends.

significant difference in unsuitable habitats among the plot categories, however, investigating the habitat types separately revealed significant differences ($P < 0.05$) in settlements in the comparison CON/EXT. Edge density (m/ha) ranged from 45.3 to 727.5 and Shannon's diversity index from 0 to 1.975. The differences between the three categories, however, were not significant (edge density: $F = 0.129$; Shannon's diversity $F = 0.431$).

The mean percentage of continuously suitable habitats in all the plots sampled was 10.9%, with similar mean values of slightly above 13% for categories CON and VIC, whereas a significantly lower percentage ($P < 0.01$) of only 5.3% was recorded for category EXT, a pattern that was most pronounced in Wiener Becken (0.8%, $P < 0.01$). Habitat maps based on TMS and EUNIS data depicted in Figs 4 and 5 give a graphical representation of typical shifts in habitat percentages recorded in the plots sampled and show trends of landscape homogenization, decline in wetland habitats and increases in arable land and settlements.

Table 3. – Bonferroni corrected significance estimates for Kruskal-Wallis tests for differences between the three plot categories CON (incidences of *Gentianella austriaca/praecox* recorded after 1960 and assuming a presence before 1960), EXT (incidences of *G. austriaca/praecox* recorded only before 1960) and VIC (incidences of *G. austriaca/praecox* recorded only before 1960, however, currently present in the vicinity) regarding changes in suitable and unsuitable habitats between the TMS (1869–1887) and EUNIS assessment (2013). Pairwise comparisons are given when the among group differences are significant (in bold): reg1 – Alps and Prealps; reg2 – remaining regions, na – not applied.

Habitat	n	CON/EXT/VIC	CON/EXT	CON/VIC	EXT/VIC
Suitable habitats	266	0.162	na	na	na
Grasslands	133	0.750	na	na	na
Grasslands reg1	51	0.273	na	na	na
Grasslands reg2	82	0.778	na	na	na
Wetlands	133	**0.003**	**0.003**	1.000	**0.045**
Unsuitable habitats	399	0.265	na	na	na
Arable fields	133	0.754	na	na	na
Arable fields reg1	51	0.119	na	na	na
Arable fields reg2	82	0.500	na	na	na
Forest	133	0.186	na	na	na
Settlements	133	**0.043**	**0.043**	0.260	1.000

Discussion

Sampling history

Herbarium vouchers provide physical evidence of a taxon's presence at a specific site and at a specific moment, but are clearly imperfect indicators of the distribution history of the taxon. The largely artificial pattern in the sampling history is due to several reasons: (i) Multiple collections (duplicates) for commercially distributed series of exsicates (as the above mentioned Flora exsiccata Austro-Hungarica) and exchange between herbaria were common in the late 19th and early 20th century. This resulted in a high number of old records and over-representation of well-known and easily accessible sites in times when travelling was not as easy as today. Nonetheless, some of these sites obviously did support large populations as can be concluded from occasional remarks on herbarium labels. Evaluating floristic literature (e.g. Neilreich 1859, Wettstein 1892) one can conclude that these plants were common in the lowlands and lower mountain ranges, where currently they are rare or extinct (Niklfeld & Schratt-Ehrendorfer 1999, Greimler & Dobeš 2000, Engleder 2006, 2014). (ii) Collecting was especially affected by World War II and thereafter by paradigmatic-methodological shifts (new systematics, karyology etc.; Klemun & Fischer 2001). (iii) In Austria field activities increased again in the late decades of the 20th century due to a revival of floristics for compiling Red Lists (Niklfeld et al. 1986, Niklfeld & Schratt-Ehrendorfer 1999), the new Austrian flora (Adler et al. 1994), ongoing fieldwork for an atlas on the Austrian flora and mapping and conservation programs (Greimler & Dirnböck 1996, Dirnböck & Greimler 1997, Engleder 2006, 2014).

Examination of the spatial pattern of sampling revealed that some areas and places are over- or under-represented in the data in particular years or over long periods due to the above-mentioned activities. Additional noise in the data results from historical particularities such as opening formerly closed imperial hunting grounds in the western part of Vienna for the public only after World War I (Adler & Mrkvicka 2003).

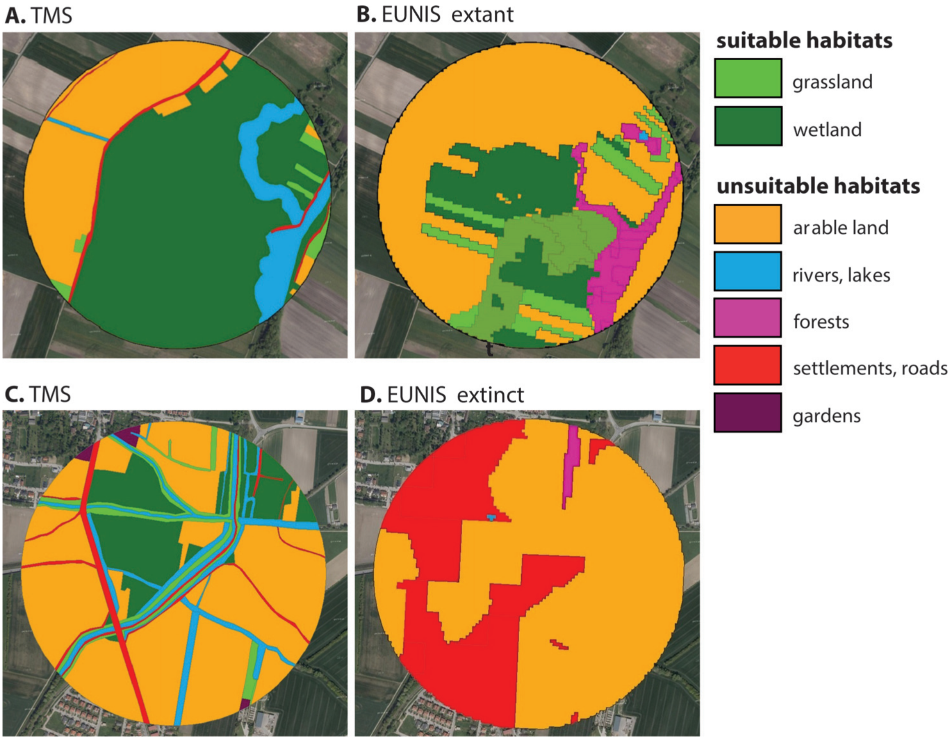

Fig. 4. – Maps showing the distribution and percentage of habitats in the sampled plots in the Wiener Becken region based on digitized TMS (Austrian Third Military Survey, 1869–1887) maps (A, C) and EUNIS data (B, D). The upper pair (A, B) represents a site (plot 291) with an extant population of *Gentianella austriaca*, the lower pair (C, D) a site (plot 336) where *G. austriaca* is extinct. Habitat types are colour-coded.

Changes in the frequency of occurrence of Gentianella austriaca and G. praecox

According to the information on herbarium labels, both *Gentianella* species occurred commonly in pastures, meadows and various oligotrophic grasslands of moderate to low humidity. However, neither of them were collected in dry grasslands at low altitudes (colline to submontane vegetation belt up to about 500 m). At these altitudes *G. austriaca* was usually confined to wetlands. At around medium altitudes (montane vegetation belt), it was more frequently found in less humid grassland habitats. At the highest altitudes (subalpine, alpine) it was found mainly in pastures and various oligotrophic grasslands of the *Seslerietalia caeruleae* alliance. Based on our data *Gentianella praecox* was never abundant at the lowest altitudes; it was collected mainly in pastures, meadows and other oligotrophic grasslands at altitudes of 500–1000 m.

According to the floristic literature *G. austriaca* was common around Vienna, in the plains south of Vienna and along the entire eastern margin of the Wienerwald (Neilreich 1846, 1851, 1859, Wettstein 1892, Beck von Managetta 1893, Halácsy 1896). More than half a century later Janchen (1977) still noted, that it is moderately common in the plains and in the lower mountain ranges in Lower Austria, although without reference to current field observations. Based on the available data, however, the situation must already have

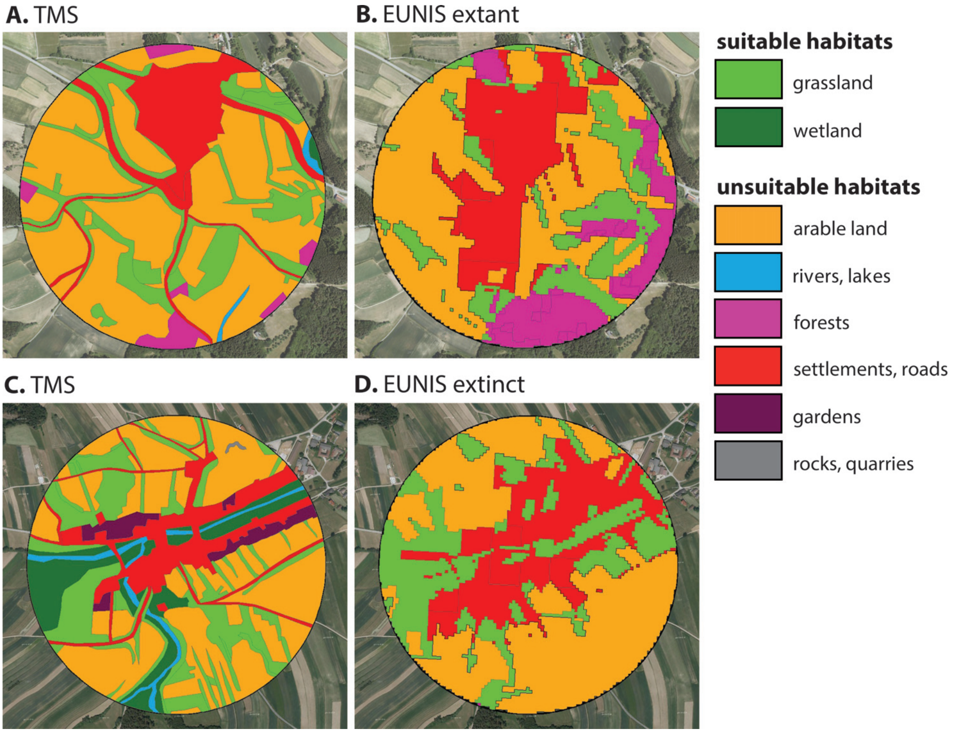

Fig. 5. – Maps showing the distribution and percentages of habitats in sampled plots in the Waldviertel region based on digitized TMS maps (A, C) and EUNIS data (B, D). The pair (A, B) represents a site (plot 420) with an extant population of *Gentianella praecox*, the pair (C, D) a site (plot 452) where *G. praecox* is extinct. Habitat types are colour-coded.

changed dramatically at this time. Many of the populations especially in the lowlands (Wiener Becken incl. Marchfeld) were extinct and the remainder often small and isolated (Greimler & Dobeš 2000; J. Greimler & D. Reich, personal observation).

Gentianella praecox was very common in the southern Waldviertel. It was originally described by Kerner von Marilaun (1888) based on material from this region, while earlier records from the Dunkelsteiner Wald and Waldviertel (Neilreich 1858) and from the Mühlviertel region (Duftschmid 1883) appear under a number of different names. However, precise data on its distribution are lacking in earlier literature and in Janchen (1977). More recently high-resolution spatial data became available from conservation programs (Engleder 2014) and studies on seasonal dimorphism (Plenk et al. 2016).

Decline in suitable habitats

Our analyses provide clear evidence of a marked loss of suitable habitats for both species in all three plot categories, not unexpectedly the trend was strongest in the EXT category and slightly less in the CON category. In category VIC, however, there were different trends due to the regional patterns differing markedly. The significantly smaller percentages of wetlands (overall) and grasslands at the lower altitudes of reg2 (Waldviertel, Wienerwald, and Wiener Becken) in the plot category EXT, which are extinct populations, point to habitat destruction as the most probable reason for local extinction. Including the historical map data, revealed a very clear and strong trend in the decline of suitable grassland-habitats for the investigated *Gentianella* species despite some methodological problems connected with interpreting historical TMS maps and the misclassifications and limits of the available medium resolution land-cover data. This decline was most severe in the Wiener Becken, which currently is a peri-urban area covered mainly by large-scale crop-fields, with virtually no remnants of formerly abundant wet meadows and semi-dry pastures (Bieringer & Grinschgl 2001). Large areas of grassland still exist in mountainous parts in north-eastern Austria, but there has been a shift from seminatural and oligotrophic meadows and pastures to unfavourable high-intensity grasslands especially in the montane zone (Zechmeister et al. 2002, Hülber et al. 2017). In addition, the landscape character has changed markedly from open grassland to closed forest as many of the less-productive grassland patches were reforested or abandoned and underwent secondary succession. Along with the general decline in wetlands, the marked spread of settlements, especially in peri-urban regions, is identified as another cause of habitat loss for *Gentianella*. Moreover, the latter changes differed significantly in the plots where *Gentianella* is currently present and those where it is extinct. This again indicates habitat destruction as a reason for local extinctions. In general, the changes in landscape structure documented in this study conform with the trends reported in large parts of central and eastern Europe (e.g. Skokanová et al. 2009, Lettner & Wrbka 2011, Balasz et al. 2016). The effect of spatial (dis)continuity in suitable habitats remains doubtful as a clear association was only recorded in Wiener Becken, whereas remaining populations in the other regions could either have survived in sometimes small though almost always present continuous suitable habitats or could have colonized newly created ones.

The rapidly advancing anthropogenic homogenization of central-European landscapes is well documented (e.g. Tscharntke et al. 2005) and its adverse effects on biodiversity have repeatedly been demonstrated in different areas and for organisms at various scales (e.g. Benton et al. 2003, Winqvist et al. 2011, Dorresteijn et al. 2015). However, comparing landscape plots with extinct and extant populations did not yield significant differences in landscape heterogeneity for neither of the investigated *Gentianella* species. In the past these species were often recorded in large, homogenous oligotrophic grassland habitats also in lowlands (Wettstein 1892). In fact, these habitats are virtually non-existent in the present-day agricultural landscape. *Gentianella* spp. and other taxa depending on nutrient-poor habitats were observed to retreat to small, often linear structures such as lynchets and embankments (Stadler et al. 2010). Lynchets and embankments are typically below the spatial resolution of the EUNIS data and thus are not reflected in landscape heterogeneity indices. On the other hand, many linear structures within agricultural landscapes suffered from severe eutrophication over the last few decades and nowadays are often colonized by species favoured by the high nutrient supply (Wood et al. 2017), therefore they do not necessarily represent suitable habitats for weak competitors.

Our landscape analyses depict general trends adversary to the survival of taxa depending on oligotrophic habitats, which is also partly reflected in significant differences between those plots where *Gentianella* is now extinct and those where it is still present. Other biotic and abiotic factors and underlying processes affecting species distributions such as restoration from the seed bank may not be important over a period of several decades for assessing presence/absence in *Gentianella* (Bucharová et al. 2012) although stochastic colonization may occur at any time. The trajectories of landscape changes are driven by general socioeconomic developments and may lead to an ongoing segregation between depleted lowland areas and abandoned mountain landscapes. Populations of species dependent on anthropogenic habitats maintained by low-input agriculture will therefore increasingly become isolated and threatened by local and regional extinction.

In conclusion, these results highlight the necessity of landscape-scale conservation, like establishing a network of seminatural grassland habitats, as is foreseen in the "green infrastructure" strategy (European Commission 2013). To achieve this, several strategic planning options and policy instruments should be used. Among others, agri-environmental schemes (AES), which are an element of EU Common Agricultural Policy (CAP, Pillar 2), seem to be promising. But as several authors point out (Concepción et al. 2008, Wrbka et al. 2008, Hülber et al. 2017), effective protection of biodiversity in agricultural landscapes calls for compulsory measures covering entire regions rather than single farms. Our data clearly highlights the necessity to supplement these requisite actions at a landscape level with intensified research and more specific measures for vulnerable taxa. In the case of the two investigated *Gentianella* species, but presumably also for many other endangered grassland species, the current distribution pattern is clearly shaped by general trends in landscape change, but the inherent/underlying reasons for the ongoing decline in the abundance of these taxa might not be resolved solely on basis of available landscape data. The necessity for conserving the lowland populations of *G. austriaca* was highlighted nearly 20 years ago (Greimler & Dobeš 2000), although without effect. For *Gentianella praecox*, listed as a species of priority concern in Annex II and V of the Habitats Directive (Council of the European Commission 1992), the local conservation efforts that endeavour to protect it (e.g. Königer et al. 2008, Dolek et al. 2010, Engleder 2014) should be accompanied by research on indicators of suitable habitats and integrated strategies.

See www.preslia.cz for Electronic Appendices 1–9

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Souhrn

Krajina střední Evropy a její management se během posledního století dramaticky změnily, což vede k pokračující ztrátě biologické rozmanitosti na všech úrovních. V článku jsme studovali dopad těchto změn na rozšíření druhů s cílem lépe porozumět, jak měnící se zastoupení různých typů krajinného pokryvu ovlivňuje výskyt taxonů travních porostů. Zkoumali jsme historické a současné rozšíření dvou druhů rodu *Gentianella*, považovaných v severovýchodním Rakousku za indikátory oligotrofních trávníků. Data o rozšíření získaná z herbářů, literatury a mapovacích projektů byla vztažena k historickými údajům o habitatech, získaným z vojenských map z konce 19. století, a k současnému zastoupení, zjištěnému metodami dálkového průzkumu. Rozšíření vhodných a nevhodných stanovišť pro výskyt *G. praecox* a *G. austriaca* bylo vymezeno podle historických a recentních údajů o krajinném pokryvu na 133 plochách o velikosti 78,5 ha, obklopujících buď zaniklé, nebo existující populace; následně byly pro vyhynulé a existující populace porovnány procentuální změny mezi historickým a současným stavem krajiny. Výsledky odhalily regionální a lokální ohniska, z nichž studované druhy vymizely, a statisticky významné celkové trendy nárůstu lesních porostů, úbytku travnatých a mokřadních porostů a kolísajících regionálních trendů pro zemědělské oblasti a sídla. Narůstající osídlení a ústup mokřadů měly negativní dopad na rozšíření sledovaných druhů, heterogenita krajiny se však na tom, zda populace zanikly nebo přežívají, nepodílela. Výsledky jsou v souladu s dokumentovanými středoevropskými trendy a poukazují na potřebu rychlých a účinných ochranářských opatření.

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