

Weeds shift from generalist to specialist: narrowing of ecological niches along a north-south gradient

Polní plevele se mění z generalistů na specialisty – zužování ekologických nik podél severojižního gradientu

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There are changes in the realized niches of species along environmental gradients, especially at the edge of their distribution where they become more specialized. A classical case is weeds of the *Caucalidion* alliance that spread with agriculture from the Fertile Crescent and thrive in a wide range of climates that differ from that prevailing in their native area. We used large data sets of vegetation collected in central Europe (3383 plots) and north-western Balkans (4505 plots) and used a co-occurrence species algorithm to calculate the specialist/generalist status of weed species. The change in the width of the ecological niches was tested using target species. Our assumptions were confirmed as the same characteristic species of *Caucalidion* weed vegetation in the north-western Balkans are more specialized in central Europe, where they occupy more basic habitats that vary less in terms of soil reaction. Testing niche theory using real data is especially important for nature conservation because specialists are more prone to decline in abundance or to go extinct.

Key words: Balkan, *Caucalidion*, central Europe, niche width, species co-occurrence, weed vegetation

Introduction

Ecological behaviour of plants has been of interest to community ecologists for a long time. It is well understood that ecological behaviour changes along ecological gradients (Hájková et al. 2008). Traditionally the term ‘ecological behaviour’ in central Europe has the same meaning as ‘ecological niche’. Niche breadth varies depending on the environmental gradient and according to Diekmann & Lawesson (1999) there are three possible reasons for this: (i) The physiological demands of a species can differ as is the case for ecotypes in different regions; (ii) constant habitat rule of Walter & Walter (1953) that describes the change in the habitat of a species due to changes in environmental conditions and compensation of one ecological parameter by another; (iii) presence or absence of potential competitors and change in the competitive relationships between species.

Hutchinson (1957) defines species niche in terms of a combination of environmental characteristics of the hypervolume. Some species have wider niches (realized) than others, which results in the distributions of species in space and their presence in different habitats. It is

expensive to measure niche width using manipulative experiments (Pearman et al. 2008), therefore other approaches are needed. Fridley et al. (2007) propose an algorithm that calculates species co-occurrences and using this pattern we can describe the width of the niches plant species. This algorithm is based on the assumption that in a large data set, habitat specialization of an individual species corresponds to the β -diversity of vegetation plots in which the target species is present. They assume that generalists co-occur with many species within a given plot and therefore have wide ecological niches. Therefore, habitat generalists co-occur with many different species across their range while habitat specialists co-occur with relatively few different species. This approach is especially useful for analyzing large databases of vegetation plots.

Zelený (2009) and Manthey & Fridley (2009) further improved this approach using other β -diversity measures to avoid bias due to the effect of the species pool. Manthey et al. (2011) use modified approaches to assess habitat specialists and generalists in two regions with species pool of different sizes. Recently Botta-Dukát (2012) modified this approach by using species pool instead of raw data and excluding outliers. This gives robust and unbiased estimates of the co-occurrence-based niche width measurements, which are independent of the size of the species pool.

To detect variation in species niche breadth along a north-south gradient in Europe, we focused on weed vegetation. The majority of cereal weeds in Europe originate from the Mediterranean region and Near East and were transported with cultural plants as cultivation of crops spread into the Old World (di Castri 1989). These species are termed archaeophytes if they arrived in ancient times (Pyšek et al. 2012) and most arrived in central Europe approximately 7500 cal. yr BP (Chytrý 2012). Although they adapted to some degree to new ecological conditions (e.g. cultivation and climate) they are far from their old centre of distribution. Populations of species at the limits of their range usually have narrower niche widths and are more specialized, which results in the evolution of habitat specialists. Weeds of the alliance *Caucalidion* prefer basic and warm (calcareous) fields in the north but are widespread and indifferent to this type of soil in the south of central Europe (Holzner 1978). Compared to other weeds *Caucalidion* species are sensitive to temperature and moisture conditions (Lososová et al. 2006, 2009). This is the main reason why these species prevail in the lowlands in the Czech Republic, areas where the temperature is higher and most soils are base rich. In the Balkans *Caucalidion* alliance is the most widespread type of vegetation in cereals and is found also at high altitudes (Šilc et al. 2008).

The alliance *Caucalidion* includes the annual thermophilous weed vegetation of cereal crops in central and south-eastern Europe. It is a northward spread of Mediterranean cereal weeds that started with the spread of agriculture (Lososová & Grulich 2009). It is distributed from the Mediterranean to southern Scandinavia, Great Britain, the Iberian Peninsula and southern Urals, but with a clear centre in central Europe and the Balkans (Ferro 1990, Lososová et al. 2009). Five associations are known from the Czech Republic. They are *Caucalido platycarpi-Conringietum orientalis*, *Lathyro tuberosi-Adonidetum aestivalis*, *Euphorbio exiguae-Melandrietum noctiflori*, *Stachyo annuae-Setarietum pumilae* and *Veronicetum hederifolio-triphylli* (Lososová et al. 2009). In Balkan national surveys the latter two are classified differently. Delimitation of the alliance in the north-western Balkans at the association level is very variable: *Kickxietum spuriae* (Slovenia and Croatia), *Galio tricornuti-Ranunculetum arvensis* (Slovenia), *Consolido-Polygonetum avicularis*,

Consolido-Vicietum striatae, *Sinapi-Biforietum radians*, *Stachyeto-Ajugetum chamaepitys*, *Vulpio-Holcetum lanatis* (Serbia), *Caucalido daucooidis-Scandicetum pecten-veneris* (Macedonia) (Kojić et al. 1998, Hulina 2002, Kratovalieva 2002, Šilc & Čarni 2007, Trinajstić 2008).

Populations of some species of weeds are becoming ecologically very specialized in the new area and therefore *Caucalidion* species have experienced a profound decline in recent decades due to changes in agricultural management (Lososová 2003, Pinke 2004, Lososová & Simonová 2008). At the edge of a species distribution individuals are more sensitive and less vigorous (Holzner 1978). Also specialists are more prone to decline in abundance and become extinct than generalists (Rooney et al. 2004, Clavel et al. 2011) and a key trait in predicting the response of a population to environmental change is its degree of ecological specialization (Boulangeat et al. 2012).

Habitat generalists are those species that co-occur with many different species throughout their range while habitat specialists co-occur with relatively few different species. We hypothesize that populations of *Caucalidion* species are generalists in the south and specialists in central Europe and that populations of the same *Caucalidion* species perform differently in each region along a north-south gradient.

Material and methods

Species data

Two data sets of arable field weed vegetation were used; one collected in the Czech Republic (central Europe) and the other in the north-western Balkans, which here includes Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Montenegro and Macedonia. The first data set comprised 3383 relevés and the second 4505 relevés, with a total of 1149 species (Table 1). The Czech data set contains samples mostly collected from the second half of last century until present. The plot sizes vary from 2 m² to 100 m², the majority being 20 m². The north-western Balkans data set includes plots from 1938 till present, varying in area from 2 to 400 m², but mostly 50 m². Vegetation samples were stored in the TURBOVEG database (Hennekens & Schaminée 2001). The species nomenclature follows the Flora Europaea (Tutin et al. 1968–1980, 1993) except for the species *Oxalis dillenii* Jacq. Information about the planted crops and juveniles of trees and shrubs was not included in the analyses because such data were not recorded by all researchers. Finally taxa that were only determined to genus were deleted. We aggregated all subspecies to the species level and some critical taxa to a higher level.

Selection of species diagnostic of *Caucalidion* in central Europe was made based on Vegetation of the Czech Republic (Lososová et al. 2009) and for north-western Balkans according to Šilc et al. (2009). Both lists of diagnostic species of the *Caucalidion* alliance in the Czech Republic and Balkans were merged together and this total list of diagnostic species was used in subsequent analyses. Only species present in both data sets were used for comparison.

Table. 1 – Basic data in the data sets (weed vegetation and *Caucalidion*). Crop and woody species are not included.

Dataset	Number of relevés	Species/plot	Species pool
North-western Balkan	4505	18.86 ± 8.13	797
<i>Caucalidion</i>	403	18.26 ± 6.49	380
Central Europe	3383	23.89 ± 9.97	615
<i>Caucalidion</i>	708	25.56 ± 10.32	498

Statistical analyses

To detect specialist and generalist *Caucalidion* species in both European regions we calculated theta (θ) values using the modified version of the procedure proposed by Mantley & Fridley (2009), using the statistical environment R (R Development Core Team 2008). Species with at least 10 occurrences were used and we selected 100 random samples for each species. Among five alternative measures of theta, which results average turnover, we used Whittaker's beta, as proposed by Zelený (2009). Low theta-value means that a species is a specialist and vice versa.

For comparison of niche breadth changes between data sets we divided the theta value for a particular species by the maximum theta in both data sets and compared their relative values. A difference in the ratios for the central-European and north-western Balkans data sets is taken to represent a change in the width of the ecological niche, with a negative difference indicating a decrease in width.

For each species we determined its ecological indicator value for soil reaction according to Pignatti (2005). Only soil reaction was used as an ecologically important factor for *Caucalidion* species, because the hypothesis predicts a shift in soil preference (Holzner 1978). We calculated mean ecological indicator values for each plot weighted by species cover using the Juice program (Tichý 2002). For each *Caucalidion* species we expressed amplitude of ecological values (Max-Min) for plots in which particular species were found in both data sets.

Results

Different species were indicated as specialists and generalists in weed vegetation of both regions (Table 2). Beside species that are considered typical weeds (e.g. *Lathyrus aphaca*, *Bifora radians*) there were other common species among the specialists (*Agrostis gigantea*, *Solanum dulcamara*) and generalists (*Ballota nigra*, *Festuca pratensis*); the latter species are more characteristic of other habitats like grassland or ruderal sites.

Most frequent species are very similar in both data sets (11 species out of 20 are the same), with weeds that thrive in all types of crops prevailing. Fifty one species were selected that are characteristic of the *Caucalidion* alliance and with at least 10 occurrences in the central-European and north-western Balkans data sets (Table 3). Species characteristic of the *Caucalidion* alliance have statistically significant different ratios of theta values in the central-European and north-western Balkans data sets (Wilcoxon paired test, $z = 6.205$, $P < 0.01$). In central Europe all species except *Reseda lutea* show shifts towards specialization. The highest niche width change was detected for *Bifora radians*, *Galium tricornutum* and *Lathyrus aphaca*.

Table 2. – Twenty most specialist and generalist species in the central-European and north-western Balkans data sets of arable field weed vegetation. Theta values according to Zelený (2009) are presented. Low theta value means that the species is a specialist and vice versa for generalist.

Central Europe		North-western Balkan	
Specialist species	Theta	Specialist species	Theta
<i>Lathyrus aphaca</i>	2.710	<i>Rhinanthus minor</i>	2.408
<i>Veronica praecox</i>	2.809	<i>Cyperus rotundus</i>	2.423
<i>Crepis capillaris</i>	2.849	<i>Juncus bufonius</i>	2.847
<i>Myosotis discolor</i>	2.902	<i>Erysimum repandum</i>	2.902
<i>Ranunculus sardous</i>	2.978	<i>Solanum dulcamara</i>	2.968
<i>Conringia orientalis</i>	2.982	<i>Ornithogalum narbonense</i>	2.981
<i>Sagina procumbens</i>	3.028	<i>Tribulus terrestris</i>	2.985
<i>Galeopsis ladanum</i>	3.141	<i>Symphytum tuberosum</i>	3.014
<i>Kickxia spuria</i>	3.142	<i>Eragrostis pilosa</i>	3.023
<i>Bifora radians</i>	3.145	<i>Plantago crassifolia</i>	3.063
<i>Bidens tripartita</i>	3.161	<i>Panicum miliaceum</i>	3.077
<i>Spergularia rubra</i>	3.170	<i>Amaranthus powellii</i>	3.105
<i>Galium tricorutum</i>	3.195	<i>Valerianella locusta</i>	3.208
<i>Juncus bufonius</i>	3.224	<i>Oxalis dillenii</i>	3.319
<i>Veronica opaca</i>	3.226	<i>Veronica triphyllos</i>	3.324
<i>Agrostis gigantea</i>	3.235	<i>Chamomilla suaveolens</i>	3.341
<i>Trifolium hybridum</i>	3.240	<i>Stellaria nemorum</i>	3.395
<i>Filaginella uliginosa</i>	3.267	<i>Galinsoga ciliata</i>	3.414
<i>Chenopodium glaucum</i>	3.278	<i>Amaranthus cruentus</i>	3.430
<i>Papaver dubium</i>	3.283	<i>Oxalis acetosella</i>	3.446
Generalist species	Theta	Generalist species	Theta
<i>Artemisia vulgaris</i>	4.366	<i>Trifolium arvense</i>	5.293
<i>Galium album</i>	4.404	<i>Sanguisorba minor</i>	5.300
<i>Arrhenatherum elatius</i>	4.440	<i>Veronica hederifolia</i>	5.310
<i>Lolium perenne</i>	4.454	<i>Bromus sterilis</i>	5.313
<i>Carduus acanthoides</i>	4.468	<i>Melilotus officinalis</i>	5.319
<i>Bromus japonicus</i>	4.493	<i>Viola tricolor</i>	5.324
<i>Lamium album</i>	4.500	<i>Raphanus raphanistrum</i>	5.334
<i>Echium vulgare</i>	4.516	<i>Bromus arvensis</i>	5.340
<i>Cirsium vulgare</i>	4.524	<i>Coronilla varia</i>	5.343
<i>Conyza canadensis</i>	4.533	<i>Hypericum perforatum</i>	5.350
<i>Setaria verticillata</i>	4.543	<i>Festuca pratensis</i>	5.355
<i>Portulaca oleracea</i>	4.624	<i>Lotus corniculatus</i>	5.382
<i>Eragrostis minor</i>	4.648	<i>Plantago lanceolata</i>	5.384
<i>Cerastium arvense</i>	4.662	<i>Filago arvensis</i>	5.405
<i>Euphorbia cyparissias</i>	4.770	<i>Tripleurospermum inodorum</i>	5.409
<i>Agrostis capillaris</i>	4.775	<i>Trifolium campestre</i>	5.453
<i>Poa angustifolia</i>	4.786	<i>Anthemis arvensis</i>	5.468
<i>Digitaria sanguinalis</i>	4.827	<i>Asperula arvensis</i>	5.584
<i>Ballota nigra</i>	4.913	<i>Medicago sativa</i>	5.633
<i>Pimpinella saxifraga</i>	5.015	<i>Anthemis cotula</i>	5.865
20 most frequent species	Frequency	20 most frequent species	Frequency
<i>Viola arvensis</i>	2225	<i>Convolvulus arvensis</i>	3081
<i>Stellaria media</i>	2216	<i>Chenopodium album</i> agg.	2663
<i>Capsella bursa-pastoris</i>	2021	<i>Cirsium arvense</i>	2612
<i>Matricaria perforata</i>	2010	<i>Setaria pumila</i>	1709
<i>Cirsium arvense</i>	1998	<i>Echinochloa crus-galli</i>	1678
<i>Bilderdykia convolvulus</i>	1944	<i>Stellaria media</i>	1677
<i>Chenopodium album</i> agg.	1889	<i>Amaranthus retroflexus</i>	1676

<i>Galium aparine</i> agg.	1843	<i>Polygonum aviculare</i> agg.	1634
<i>Veronica persica</i>	1756	<i>Bilderdykia convolvulus</i>	1458
<i>Polygonum aviculare</i> agg.	1724	<i>Capsella bursa-pastoris</i>	1438
<i>Elymus repens</i>	1694	<i>Veronica persica</i>	1176
<i>Taraxacum officinale</i> agg.	1570	<i>Elymus repens</i>	1164
<i>Thlaspi arvense</i>	1548	<i>Digitaria sanguinalis</i>	1036
<i>Myosotis arvensis</i>	1527	<i>Taraxacum officinale</i> agg.	1035
<i>Lamium purpureum</i>	1350	<i>Cynodon dactylon</i>	1027
<i>Convolvulus arvensis</i>	1296	<i>Sonchus arvensis</i>	982
<i>Anagallis arvensis</i>	1219	<i>Polygonum lapathifolium</i>	979
<i>Euphorbia helioscopia</i>	1041	<i>Galium aparine</i> agg.	961
<i>Lapsana communis</i>	1012	<i>Galinsoga parviflora</i>	950
<i>Veronica arvensis</i>	965	<i>Sinapis arvensis</i>	943

A shift of particular target species from habitat generalism to specialism is evident. There is also a clear difference in the number of species indicated as *Caucalidion* characteristic that are recorded in only one data set (eight in north vs 23 in south). In addition to the lower number of typical *Caucalidion* species (*Agrostemma githago*, *Turgenia latifolia*, *Scandix pecten-veneris*) in the central-European data set, there are also fewer widespread species (*Vicia narbonensis*, *Vicia pannonica*) with southern distributions. Other species that occur in weed communities in the north are widespread weeds (*Myosotis arvensis*, *Viola arvensis*) or ruderal species (*Arctium tomentosum*, *Lapsana communis*).

Based on the theta ratios there are two distinct groups of *Caucalidion* species. In the central-European data set the amplitudes of the soil reaction ecological indicator for specialist species is also narrower (statistically significant) but not in the north-western Balkans data set (Figs 1, 2). Differences in the amplitudes in ecological values for soil reaction between data sets are statistically significant (Wilcoxon test, $z = 2.179$, $P < 0.05$).

Discussion

Our analysis of co-occurrence of species and incidence of specialists clearly support the hypothesis of an ecological shift in the strategies of *Caucalidion* species in the north as proposed by Holzner (1978). Species of weeds that are evolutionary adapted to disturbed and warm sites in the south have narrower ecological niches but are found in similar sites in northern areas. A warm climate is the most important factor determining a high species richness and abundance (Hyvönen et al. 2011).

Specialist species are generally declining and experiencing a high risk of extinction and global changes are responsible for their decrease in abundance (Devictor et al. 2010, Clavel et al. 2011). In the case of *Caucalidion* the specialization is a response of the species being “artificially” moved from their home range and not being adapted to the lower temperatures and higher precipitation in the new region. Therefore, in the new region they occupy calcareous substrates that are warmer and drier.

Compared to other types of vegetation, weed vegetation has one of the largest species pools in central Europe (Sádlo et al. 2007). Whereas the total species pool of weeds is higher in the north-western Balkans data set there is for *Caucalidion* vegetation a high species richness per plot in the Czech Republic (Table 1), which indicates a low level of competitive exclusion as is also documented by Lososová et al. (2009).

Table 3. – Ratio of theta values for *Caucalidion* species occurring in both data sets. A negative difference in the ratio in the two data sets indicates a narrowing of the species niche.

Species	Central Europe		North-western Balkan		Δ
	Whittaker	Ratio	Whittaker	Ratio	
<i>Adonis aestivalis</i>	3.486	0.597	4.128	0.707	–0.110
<i>Aethusa cynapium</i>	3.907	0.669	4.292	0.735	–0.066
<i>Ajuga chamaepitys</i>	3.480	0.596	4.474	0.766	–0.170
<i>Anagallis arvensis</i>	3.939	0.674	5.022	0.860	–0.185
<i>Anagallis foemina</i>	3.656	0.626	4.659	0.797	–0.172
<i>Anthemis austriaca</i>	3.774	0.646	4.339	0.743	–0.097
<i>Atriplex patula</i>	3.765	0.644	4.648	0.796	–0.151
<i>Avena fatua</i>	3.792	0.649	4.593	0.786	–0.137
<i>Bifora radians</i>	3.163	0.541	4.965	0.850	–0.308
<i>Buglossoides arvensis</i>	3.623	0.620	5.188	0.888	–0.268
<i>Camelina microcarpa</i>	3.689	0.631	4.050	0.693	–0.062
<i>Capsella bursa-pastoris</i>	4.175	0.715	4.956	0.848	–0.134
<i>Caucalis platycarpus</i>	3.776	0.646	4.755	0.814	–0.168
<i>Centaurea cyanus</i>	3.621	0.620	5.263	0.901	–0.281
<i>Cerintho minor</i>	3.636	0.622	5.125	0.877	–0.255
<i>Chenopodium album</i> agg.	4.235	0.725	4.925	0.843	–0.118
<i>Cirsium arvense</i>	4.205	0.720	5.186	0.888	–0.168
<i>Consolida regalis</i>	3.927	0.672	5.085	0.870	–0.198
<i>Convolvulus arvensis</i>	4.286	0.734	5.266	0.901	–0.168
<i>Descurainia sophia</i>	4.033	0.690	4.166	0.713	–0.023
<i>Euphorbia falcata</i>	3.516	0.602	4.626	0.792	–0.190
<i>Euphorbia helioscopia</i>	4.034	0.690	4.617	0.790	–0.100
<i>Fumaria officinalis</i>	3.718	0.636	5.114	0.875	–0.239
<i>Fumaria vaillantii</i>	3.374	0.578	4.641	0.794	–0.217
<i>Galium tricoratum</i>	3.269	0.559	5.020	0.859	–0.300
<i>Geranium pusillum</i>	4.149	0.710	4.248	0.727	–0.017
<i>Lamium amplexicaule</i>	4.046	0.693	4.986	0.853	–0.161
<i>Lamium purpureum</i>	4.071	0.697	4.632	0.793	–0.096
<i>Lathyrus aphaca</i>	2.715	0.465	4.896	0.838	–0.373
<i>Lathyrus tuberosus</i>	3.835	0.656	5.089	0.871	–0.215
<i>Matricaria perforata</i>	4.165	0.713	5.379	0.921	–0.208
<i>Medicago lupulina</i>	3.763	0.644	5.295	0.906	–0.262
<i>Neslia paniculata</i>	3.545	0.607	5.135	0.879	–0.272
<i>Papaver rhoeas</i>	4.057	0.694	4.977	0.852	–0.157
<i>Polygonum aviculare</i> agg.	4.125	0.706	5.235	0.896	–0.190
<i>Ranunculus arvensis</i>	3.558	0.609	5.119	0.876	–0.267
<i>Reseda lutea</i>	4.196	0.718	4.191	0.717	0.001
<i>Setaria viridis</i>	4.244	0.726	4.324	0.740	–0.014
<i>Sherardia arvensis</i>	3.489	0.597	4.364	0.747	–0.150
<i>Sonchus arvensis</i>	3.891	0.666	4.750	0.813	–0.147
<i>Sonchus asper</i>	3.798	0.650	4.722	0.808	–0.158
<i>Stachys annua</i>	3.880	0.664	4.737	0.811	–0.147
<i>Stellaria media</i>	4.194	0.718	4.822	0.825	–0.108
<i>Thlaspi arvense</i>	4.070	0.697	5.173	0.885	–0.189
<i>Valerianella dentata</i>	3.481	0.596	3.993	0.683	–0.088
<i>Veronica hederifolia</i>	3.975	0.680	5.258	0.900	–0.220
<i>Veronica persica</i>	4.123	0.706	4.812	0.824	–0.118
<i>Veronica polita</i>	4.039	0.691	4.453	0.762	–0.071
<i>Vicia sativa</i>	3.727	0.638	5.196	0.889	–0.251
<i>Viola arvensis</i>	4.153	0.711	4.703	0.805	–0.094
<i>Viola tricolor</i>	3.762	0.644	5.216	0.893	–0.249

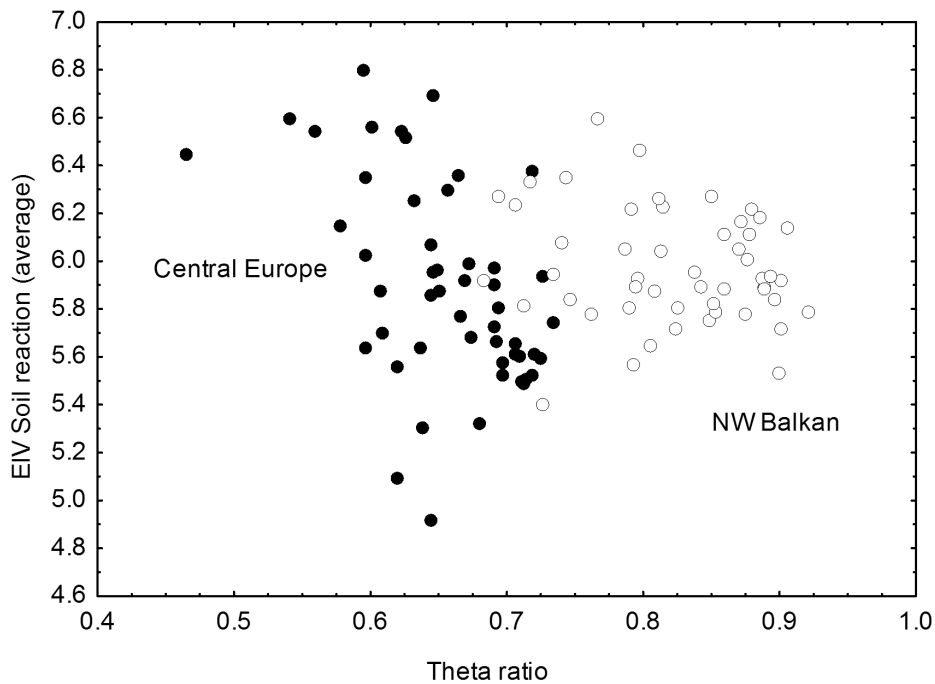


Fig. 1. – Scatter diagram of the relationship between the average ecological value for reaction of *Caucalidion* species in both data sets and the theta ratio.

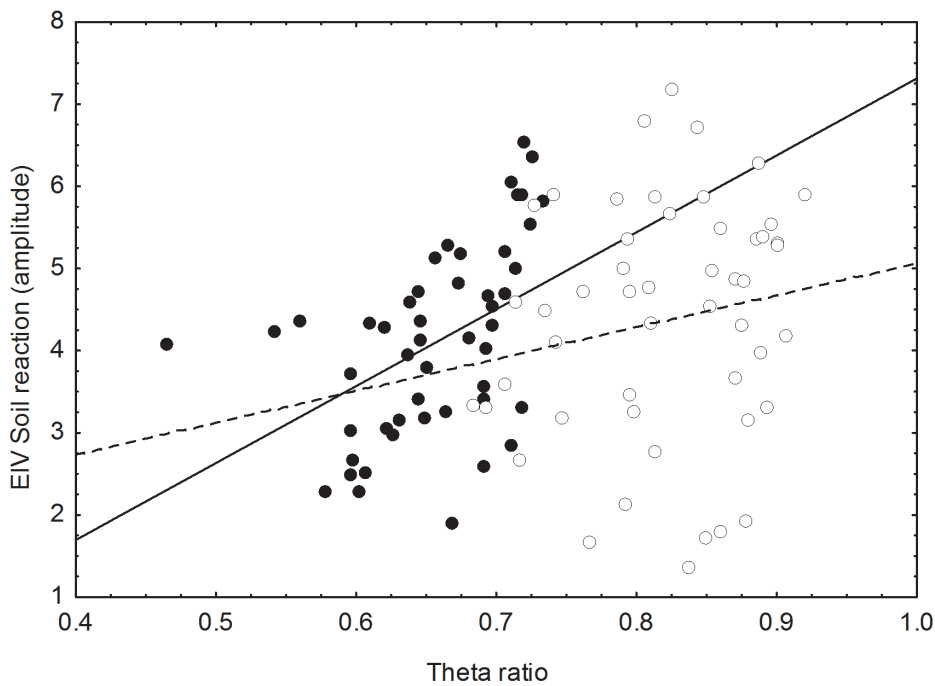


Fig. 2. – Scatter diagram of the relationship between the amplitude of the ecological reaction value for *Caucalidion* species in both data sets and the theta ratio.

Certainly, the results are affected by the differences in bedrock and soil conditions in central Europe and north-western Balkans. In central Europe base-rich habitats are restricted to a relatively small area compared to the Balkan Peninsula where such habitats prevail. Spatial isolation of suitable habitats results in greater specialization. Level of specialization would even increase if there were greater limitations to dispersal such as barriers to migration, which would result in different local communities becoming isolated. An example of this is the geographically isolated *Caucalidion* vegetation with *Lathyrus aphaca*, which occurs in only a few small arable fields in the Bílé Karpaty Mts (eastern part of the Czech Republic; Otýpková 2001).

Generalists are favoured in heterogeneous and disturbed environments, while specialists occur in more stable environments (Clavel et al. 2011). It is striking that *Caucalidion* species are generalists in their native range (if we assume the Balkans form part of their native range as these species were spread there earlier) and specialists in areas into which they spread more recently. The level of agricultural disturbance along the gradient is similar but the abiotic parameters, e.g. climate, change dramatically.

Archaeobotanical evidence of species composition of weed vegetation in Neolithic times indicates a gradual decrease in apophytes and increase of immigrants from the south and east (Rösch 1998). At that time *Caucalidion* species were newcomers and possibly invasive and analogous situations are currently occurring. Recent comparative analyses of introduced species show that generalists are more likely to become established than specialists (Clavel et al. 2011). They indicate that generalists are more abundant and therefore more likely to be introduced (number of introduced events and individuals are important). Since Neolithic times the climate in south-eastern Europe has not changed dramatically but previously may have been cooler and wetter (Kreuz et al. 2005), so we can assume that *Caucalidion* weeds were also specialists in this area at that time. Their successful establishment contradicts recent hypotheses that generalists are better invaders. In our case generalists became successful invaders by becoming specialists in these novel ecosystems. Possible explanation of this successful invasion by specialists could be a high number of introduced events in combination with the introduction of agriculture.

Changes in the ecology of the area could be blurred by the changes that have occurred in agricultural methods over the last few decades, most of all seed-cleaning. One could argue that *Caucalidion* species and most specialists in general are particularly endangered when at the limits of their distribution (Holzner 1978, Lososová et al. 2004). Specialists occupy a narrow ecological niche and a small change in ecological conditions can result in them becoming extinct.

Although intensive farming can cause a decline in *Caucalidion* weed vegetation (Hilbig & Bachthaler 1992, Lososová 2003, Pinke 2004, Kropáč 2006, Lososová & Simonová 2008, Címalová & Lososová 2009), the data set analysed comprised vegetation plots from regions along the whole gradient with similar agricultural practices. Therefore, agriculture affects the weed vegetation similarly along the whole gradient. Currently, the same widespread species of weeds dominate the weed vegetation in both regions (Table 1). Nevertheless political changes in both regions after 1990 and changes in farming systems in recent years have endangered the weed vegetation, which adds another reason for the conservation of *Caucalidion* species (Hotze & van Elsen 2006). The expectation is that with climatic change and increase in temperature there will be more fields that are suitable for *Caucalidion* weed vegetation, but whether seeds of these species will continue to be present in the species pool (seed bank) is questionable.

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Souhrn

Šířka ekologické niky druhů se mění se změnou environmentálních podmínek. Zvláště na okraji svého areálu se druhy stávají specializovanějšími. Cílem práce je srovnání šířky ekologických nik diagnostických druhů plevelové vegetace svazu *Caucalidion* ve dvou oblastech střední Evropy, lišících se svými klimatickými podmínkami, České republice a zemích severozápadního Balkánu. Polní plevely svazu *Caucalidion* byly do Evropy zavlečeny s počátkem zemědělství. Pocházejí zpravidla z jihovýchodní Evropy a Eurasie, přesto tyto rostliny přežívají ve střední Evropě v klimatických podmínkách, které se liší od jejich původního areálu. Pracovali jsme s databází fytoecologických snímků plevelové vegetace České republiky, zahrnující 3383 snímků, a databází snímků severovýchodního Balkánu, zahrnující 4505 snímků. Stanovili jsme diagnostické druhy svazu, které jsou společné pro oba regiony, a testovali jsme míru specializace těchto diagnostických druhů svazu v obou regionech. Jako míru specializace jsme použili algoritmus výpočtu společných výskytů druhů. Prokázali jsme, že všechny diagnostické druhy svazu jsou specializovanější v České republice než na Balkáně, tedy že se na svých stanovištích setkávají s méně druhy a mají zde užší ekologickou niku. Stanoviště, která v České republice osídluje, jsou bazičtější než na Balkáně. Vedle toho, že jsme potvrdili dosavadní předpoklady, které však nebyly dosud nikdy doloženy na reálných datech, jsou naše výsledky významné pro aplikaci v ochranářské praxi.

References

- Botta-Dukát Z. (2012): Co-occurrence-based measure of species' habitat specialization: robust, unbiased estimation in saturated communities. – *J. Veg. Sci.* 23: 201–207.
- Boulangeat L., Lavergne S., Van Es J., Garraud L. & Thuiller W. (2012): Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. – *J. Biogeogr.* 39: 204–214.
- Chytrý M. (2012): Vegetation of the Czech Republic: diversity, ecology, history and dynamics. – *Preslia* 84: 427–504.
- Cimalová Š. & Lososová Z. (2009): Arable weed vegetation of the northeastern part of the Czech Republic: effects of environmental factors on species composition. – *Plant Ecol.* 203: 45–57.
- Clavel J., Julliard R. & Devictor V. (2011): Worldwide decline of specialist species: toward a global functional homogenization? – *Front. Ecol. Env.* 9: 222–228.
- Devictor V., Clavel J., Julliard R., Lavergne S., Mouillot D., Thuiller W., Venail P., Villegger S. & Mouquet N. (2010): Defining and measuring ecological specialization. – *J. Appl. Ecol.* 47: 15–25.
- di Castri F. (1989): History of biological invasions with special emphasis on the Old World. – In: Drake J. A., Mooney H. A., di Castri F., Groves R. H., Kruger F. J., Rejmánek M. & Williamson M. (eds), *Biological invasions: a global perspective*, p. 1–30, John Wiley and sons, Chichester.
- Diekmann M. & Lawesson J. E. (1999): Shifts in ecological behaviour of herbaceous forest species along a transect from northern Central to North Europe. – *Folia Geobot.* 34: 127–141.
- Ferro G. (1990): Revisione della vegetazione segetale Mediterranea ed Europea dell'ordine *Secalietalia* [Revision of the segetal vegetation of the order *Secalietalia* in the European Mediterranean]. – *Braun-Blanquetia* 6: 1–59.
- Fridley J. D., Vandermaast D. B., Kuppinger D. M., Manthey M. & Peet R. K. (2007): Co-occurrence based assessment of habitat generalists and specialists: a new approach for the measurement of niche width. – *J. Ecol.* 95: 707–722.
- Hájková P., Hájek M., Apostolova I., Zelený D. & Dítě D. (2008): Shifts in the ecological behaviour of plant species between two distant regions: evidence from the base richness gradient in mires. – *J. Biogeogr.* 35: 282–294.
- Hennekens S. M. & Schaminée J. H. J. (2001): TURBOVEG, a comprehensive data base management system for vegetation data. – *J. Veg. Sci.* 12: 589–591.
- Hilbig W. & Bachthaler G. (1992): Wirtschaftsbedingte Veränderung der Segetalvegetation in Deutschland im Zeitraum von 1950–1990. 2. Zunahme herbizidverträglicher Arten, nitrophiler Arten, von Ungräsern, vermehrtes Auftreten von Rhizom- und Wurzelunkräutern, Auftreten von Neophyten, Förderung gefährdeter Ackerunkrautarten, integrierter Pflanzenbau. – *Angew. Bot.* 66: 201–209.

- Holzner W. (1978): Weed species and weed communities. – *Vegetatio* 38: 13–20.
- Hotze C. & van Elsen T. (2006): Arable field species on organically and conventionally worked farmland at the Eastern base of the Meissner Developments throughout the last 30 years. – *J. Plant Dis. Protect.* 20: 547–555.
- Hulina N. (2002): Contribution to the knowledge of segetal vegetation of Croatia. – *Hacquetia* 1: 205–208.
- Hutchinson G. E. (1957): Concluding remarks. – *Cold Spring Harb. Sym.* 22: 415–442.
- Hyvönen T., Glemnitz M., Radics L. & Hoffmann J. (2011): Impact of climate and land use type on the distribution of Finnish casual arable weeds in Europe. – *Weed Res.* 51: 201–208.
- Kojić M., Popović R. & Karadžić B. (1998): Sintaksonomski pregled vegetacije Srbije [Syntaxonomical overview of vegetation of Serbia]. – *Inst. Biol. Istraž. "Siniša Stanković"*, Beograd.
- Kratovalieva S. (2002): Ass. *Caucalido daucoidis-Scandicetum pectinis-veneris* Tx. 37 in weed vegetation on Skopje valley territory. – *Acta Herbologica* 12: 49–58.
- Kreuz A., Marinova E., Schafer E. & Wiethold J. (2005): A comparison of early Neolithic crop and weed assemblages from the Linearbandkeramik and the Bulgarian Neolithic cultures: differences and similarities. – *Veg. Hist. Archaeobot.* 14: 237–258.
- Kropáč Z. (2006): Segetal vegetation in the Czech Republic: synthesis and syntaxonomical revision. – *Preslia* 78: 123–209.
- Lososová Z. (2003): Estimating past distribution of vanishing weed vegetation in South Moravia. – *Preslia* 75: 71–79.
- Lososová Z., Chytrý M., Cimalová Š., Kropáč Z., Otýpková Z., Pyšek P. & Tichý L. (2004): Weed vegetation of arable land in Central Europe: gradients of diversity and species composition. – *J. Veg. Sci.* 15: 415–422.
- Lososová Z., Chytrý M., Cimalová Š., Otýpková Z., Pyšek P. & Tichý L. (2006): Classification of weed vegetation of arable land in the Czech Republic and Slovakia. – *Folia Geobot.* 41: 259–273.
- Lososová Z. & Grulich V. (2009): Chorological spectra of arable weed vegetation types in the Czech Republic. – *Phytocoenologia* 39: 235–252.
- Lososová Z., Otýpková Z., Sádlo J. & Láníková D. (2009): Jednoletá vegetace polních plevelů a rudérálních stanovišť (*Stellarietea mediae*) [Annual vegetation of arable land and ruderal habitats (*Stellarietea mediae*)]. – In: Chytrý M. (ed), *Vegetace České republiky 2. Plevelová, rudérální, skalní a suťová vegetace* [Vegetation of the Czech Republic 2. Weed, ruderal, rock and scree vegetation], p. 73–205, Academia, Praha.
- Lososová Z. & Simonová D. (2008): Changes during the 20th century in species composition of synanthropic vegetation in Moravia (Czech Republic). – *Preslia* 80: 291–305.
- Manthey M. & Fridley J. D. (2009): Beta diversity metrics and the estimation of niche width via species co-occurrence data: reply to Zelený. – *J. Ecol.* 97: 18–22.
- Manthey M., Fridley J. D. & Peet R. K. (2011): Niche expansion after competitor extinction? A comparative assessment of habitat generalists and specialists in the tree floras of south-eastern North America and south-eastern Europe. – *J. Biogeogr.* 38: 840–853.
- Otýpková Z. (2001): Plevelová vegetace Bílých Karpat [Weed vegetation of the White Carpathians]. – Thesis, Masarykova univerzita v Brně, Brno.
- Pearman P. B., Guisan A., Broennimann O. & Randin C. F. (2008): Niche dynamics in space and time. – *Trends Ecol. Evol.* 23: 149–158.
- Pignatti S. (2005): Valori di Bioindicazione delle Piante Vascolari della Flora d'Italia [Indicator values of vascular plants of Italian flora]. – *Braun-Blanquetia* 39: 1–97.
- Pinke G. (2004): Last occurrence of *Caucalio* species in north-western Hungary. – *J. Plant Dis. Protect.* 19: 73–82.
- Pyšek P., Danihelka J., Sádlo J., Chrtek J. Jr., Chytrý M., Jarošík V., Kaplan Z., Krahulec F., Moravcová L., Pergl J., Štajerová K. & Tichý L. (2012): Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. – *Preslia* 84: 155–255.
- R Development Core Team (2008): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria, URL: <http://www.R-project.org>.
- Rooney T. P., Wiegmann S. M., Rogers D. A. & Waller D. M. (2004): Biotic impoverishment and homogenization in unfragmented forest understory communities. – *Conserv. Biol.* 18: 787–798.
- Rösch M. (1998): The history of crops and crop weeds in south-western Germany from the Neolithic period to modern times, as shown by archaeobotanical evidence. – *Veg. Hist. Archaeobot.* 7: 109–125.
- Sádlo J., Chytrý M. & Pyšek P. (2007): Regional species pools of vascular plants in habitats of the Czech Republic. – *Preslia* 79: 303–321.
- Šilc U. & Čarni A. (2007): Formalized classification of the weed vegetation of arable land in Slovenia. – *Preslia* 79: 283–302.

- Šilc U., Vrbničanin S., Božić D., Čarni A. & Dajić Stevanović Z. (2008): Phytosociological alliances in the vegetation of arable fields in the northwestern Balkan Peninsula. – *Phytocoenologia* 38: 241–254.
- Šilc U., Vrbničanin S., Božić D., Čarni A. & Dajić Stevanović Z. (2009): Weed vegetation in the north-western Balkans: diversity and species composition. – *Weed Res.* 49: 602–612.
- Tichý L. (2002): JUICE, software for vegetation classification. – *J. Veg. Sci.* 13: 451–453.
- Trinajstić I. (2008): Biljne zajednice Republike Hrvatske [Plant communities of the Republic of Croatia]. – Akademija šumarskih znanosti, Zagreb.
- Tutin T. G., Burges N. A., Chater A. O., Edmondson J. R., Heywood Y. H., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. (eds) (1993): *Flora Europaea*. Vol. 1., Ed. 2. – Cambridge University Press, Cambridge.
- Tutin T. G., Heywood Y. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. (eds) (1968–1980): *Flora Europaea*. Vol. 2-5. – Cambridge University Press, Cambridge.
- Walther H. & Walther E. (1953): Einige allgemeine Ergebnisse unserer Forschungsreise nach Südwestafrika 1952/53: das Gesetz der relativen Standorts Konstanz; das Wesen der Pflanzengemeinschaften. – *Ber. Deutsch. Bot. Ges.* 66: 227–235.
- Zelený D. (2009): Co-occurrence based assessment of species habitat specialization is affected by the size of species pool: reply to Fridley et al. (2007). – *J. Ecol.* 97: 10–17.

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