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Pattern of succession in old-field vegetation at a regional scale

Sukcese na opuštěných polích v regionálním měřítku

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In contrast to the many detailed studies on succession conducted at local scales, there is still a lack of studies on succession at broad geographical scales. In this paper the following questions are addressed: Which of the components of seral old-field vegetation are associated with environmental factors at a broad geographical scale? To what extent do target (typical of natural and semi-natural vegetation), non-target (alien and synanthropic) and endangered species participate in the succession and on which factors is their participation dependent? Altogether 282 phytosociological relevés were recorded in old fields located in various parts of the country. The fields were from 1 to 91 years old. The following environmental characteristics were determined for each old field: altitude, phytogeographic region, soil moisture (dry, mesic, wet) and bedrock (basic, acidic). Species were classified based on the extent to which they are endangered, origin (natives, archaeophytes, neophytes) and affiliation with vegetation units. Vegetation data were analysed using multivariate statistics, generalized linear mixed models and regression trees. The results indicate that all the environmental characteristics had at least a slightly significant effect on the species composition of the different seral stages. Succession clearly differed in the three subseres and depended on soil moisture. The number of target species typical of deciduous woodland, dry grasslands and fringe communities increased during succession. In contrast, the number of archaeophytes, neophytes and synanthropic species decreased with field age. More endangered and target species and fewer archaeophytes, neophytes and synanthropic species occurred in warmer lowland than in colder upland areas. The number of endangered, target and the total number of species decreased with soil moisture, while the number of neophytes and synanthropic species increased. The number of target species typical of dry grasslands decreased with altitude while that of synanthropic species increased. The age of old fields and soil moisture appeared to be the most important drivers of succession at a broad geographical scale. In addition to local site factors, climate represented by altitude and reflected also in biogeographical regions modified the course of succession. Succession was clearly divergent.

Keywords: old fields, ordination, soil moisture, succession, target species, vegetation

Introduction

Secondary vegetation succession in old fields is the most frequently form of succession studied (Rejmánek & van Katwyk 2004). The great majority of these studies were carried out at a few sites with comparable environmental conditions using a space-for-time substitution approach or at sites where there are permanent plots (Pickett et al. 2001). Various ecological hypotheses have been tested using experimentally manipulated old-field successions (Cramer & Hobbs 2007).

However, there are not many studies of the patterns in old-field succession at broader landscape scales (but see Osbornová et al. 1990, Dovčiak et al. 2005, Otto et al. 2006, Ruprecht et al. 2007, Prévosto et al. 2011, Douma et al. 2012, Jírová et al. 2012) and this type of succession is very rarely studied at a country scale (Prach 1985, Szabo & Prach 2009). Whereas for the analysis of the effect of local environmental factors on the course of succession a detailed experimental approach is needed, the effects of geographically related factors such as altitude or climate are best revealed by using extensive data sets and a correlative approach. It is not easy, however, to gather data that is comparable in terms of the way the samples were collected, plot size and the estimates of cover of the different species. Such sampling is moreover time consuming and not easily and quickly conducted by one person. Because of the more than three-decade history of investigations on succession in old fields in the Czech Republic (see Osbornová et al. 1990, Prach et al. 2007a) and the recent effort of the first two authors, material has accumulated which we used to analyse some basic geographic patterns in old-field succession.

This study is based on phytosociological relevés recorded in a similar manner in differently aged old fields distributed over a rather large geographical area. Using this data we evaluated the role of altitude (reflecting climatic conditions such as temperature and precipitation), phytogeographical area and geological substratum in determining the course of succession. Because in previous studies site moisture was shown to have a decisive role (Osbornová et al. 1990, Prach et al. 2007a, Szabo & Prach 2009, Douma et al. 2012, Jírová et al. 2012) this factor was also included in the geographical analyses.

We addressed the following questions: (i) Which of the environmental factors is seral old-field vegetation associated with at a broad geographical scale? (ii) To what extent do target (i.e. typical of natural and seminatural vegetation), non-target (alien and synanthropic) and endangered species participate in the succession and on which factors is their participation dependent?

Methods

Study area and data collection

This study was conducted in the Czech Republic, mostly in the western part of the country, 48°45'–50°39'N, 12°04'–16°37'E. Altogether 282 differently aged relevés in 173 old-fields were recorded between 1975 and 2011. The altitude of the fields studied ranged from 170 to 756 m a.s.l and the age of the old fields varied from 1 to 91 years. In total 186 samples were collected in relatively warm and dry lowlands and 96 in relatively cold uplands, called Thermophyticum and Mesophyticum, respectively (Hejný & Slavík 1997, Kaplan 2012). The samples were phytosociological relevés previously analysed in Klaudisová (1976) and Jírová et al. (2012), completed with relevés collected for the purpose of this study by K. Prach and A. Jírová. Cover of all vascular plant species was estimated using the percentage scale (r, +, 1–100%), expect the relevés published in Klaudisová (1976) where the Domin cover-abundance scale (Kent & Coker 1992) was used. Samples, i.e. phytosociological relevés, were based on plots of from 16 m^2 (Klaudisová 1976, Jírová et al. 2012) to 25 m^2 (relevés made by K. Prach and A. Jírová), but there was no statistically significant (regression analysis) increase in the number of species with increasing plot size.

The soil moisture at each old field was estimated using three categories as in a previous study (Osbornová et al. 1990). It is possible to use this three degree scale in the field with a reasonable degree of accuracy (Osbornová et al. 1990, Prach et al. 2007a). There were 68 dry, 167 mesic and 47 wet samples, and based on geological maps 188 of them were collected from sites located on basic and 94 on acidic geological substrata (Cháb et al. 2007). For details see Table 1.

Table 1. – Total number of species in samples (Total no.), average number of species per sample (Average no.) and average cover (%) of species per sample (Cover) are displayed according to the following species characteristics: endangerment (Holub & Procházka 2000); origin (archaeophytes, neophytes; Pyšek et al. 2002); affiliation to phytosociological units: *Querco-Fagetea* (QercFag), *Festuco-Brometea*, incl. *Trifolio-Geranietea* (FestBro & TriGer), synanthropic species (Ellenberg et al. 1991), and groups of samples: phytogeographical area (Thermophyticum – Thermo; Mesophyticum – Meso; Hejný & Slavík 1997); soil moisture (dry, mesic, wet) and substratum (basic, acidic; Cháb et al. 2007).

		No. of samples		All species	Endangered	Archaeophytes	Neophytes	QuercFag	FestBro & TriGer	Synanthropic
All samples		282	Total no.	497	60	95	27	60	59	161
			Average no.	19	0.6	3.7	0.4	2.4	3.8	7.6
			Cover		1.0	11.0	1.4	23.4	20.5	32.2
Phytogeographical area	Thermo	186	Total no.	377	50	77	20	54	54	123
			Average no.	20	0.8	3.7	0.3	3.0	5.3	7.7
			Cover		1.2	9.5	1.2	29.5	29.0	24.6
	Meso	96	Total no.	308	22	63	14	29	21	104
			Average no.	18	0.4	3.9	0.7	1.3	1.0	7.3
			Cover		0.8	14.0	1.7	11.6	4.0	47.0
Soil moisture	Dry	68	Total no.	228	30	57	10	15	47	75
			Average no.	24	1.0	5.0	0.2	1.6	8.6	8.8
			Cover		1.7	9.3	0.1	13.5	54.0	21.8
	Mesic	167	Total no.	427	45	84	21	56	48	135
			Average no.	19	0.6	3.4	0.5	3.5	3.0	7.2
			Cover		1.1	10.6	1.6	34.0	12.6	30.4
	Wet	47	Total no.	151	5	41	6	6	3	70
			Average no.	14	0.2	3.3	0.4	0.2	0.1	7.2
			Cover		0.1	15.1	2.3	0.3	0.2	30.4
Substratum	Basic	188	Total no.	397	48	72	13	57	58	112
			Average no.	21	0.7	3.2	0.2	3.4	5.3	7.3
			Cover		1.4	7.6	1.0	34.0	29.6	21.4
	Acidic	94	Total no.	281	21	72	19	16	21	116
			Average no.	16	0.4	4.8	0.8	0.5	0.8	8.1
			Cover		0.6	17.9	2.1	2.1	2.1	53.8

The nomenclature follows Ellenberg et al. (1991) and Chytrý & Tichý (2003) for syntaxa and Kubát et al. (2002) for species.

Data analyses

All cover data were transformed into a percentage scale for easier comparison of data sets (van der Maarel 1979). A detrended corespondence analysis (DCA) of species and samples with log-transformed species data and downweighting of rare species was calculated. The significance of environmental variables (age, moisture, interaction of age and moisture, substratum, phytogeographical regions and altitude) was tested using CCA and the Monte Carlo permutation test with 499 permutations, with localities as covariables (latitude and longitude). Marginal (each variable separately) and conditional (= partial, the candidate variable as the only explanatory variable and others as covariables using forward selection) effects were tested using CCA (Lepš & Šmilauer 2003). All multivariate statistics were calculated using Canoco for Windows version 4.5 (ter Braak & Šmilauer 2002).

Species were classified in terms of their status of endangerment (CR – critically endangered, EN – endangered, VU – vulnerable and NT – near threatened; Holub & Procházka 2000), time of arrival in the country (indigenous, archaeophytes and neophytes; Pyšek et al. 2002) and their affiliation to the phytosociological units *Querco-Fagetea*, *Festuco-Brometea*, *Trifolio-Geranietea* and synantropic vegetation (*Artemisietea*, *Secalietea*, *Chenopodietea*, and *Agropyretea*) (Ellenberg et al. 1991, Chytrý & Tichý 2003). Species belonging to the *Festuco-Brometea* and *Trifolio-Geranietea* classes were considered as target species representative of xerotherm open communities, i.e. vegetation with a high nature conservation value (Chytrý 2007), which may develop in abandoned fields (Jírová et al. 2012). Species belonging to the *Querco-Fagetea* class were also considered as target, representative of the potential vegetation prevailing in the Czech Republic (Neuhäuslová 2001), which is likely to develop in the majority of old fields (Osbornová et al. 1990, Jírová et al. 2012). All alien species were considered as synantropic. All other species, which belonged to other syntaxa or are listed without any affiliation in Ellenberg et al. (1991) and Chytrý & Tichý (2003) were included in "rest".

The total number of species and the number and cover of species belonging to the above mentioned categories were calculated for all 282 samples. The effect of phytogeographical region (Thermophyticum, Mesophyticum), soil substratum (basic, acidic), soil moisture (wet, mesic, dry), successional age and altitude on relevé species richness and cover (of the individual species categories) were analysed using a generalized linear mixed model (GLMM), because the data represent a hierarchical split-plot design with both fixed and random effect factors. The linear predictor was related to the conditional mean of the response through the inverse link function defined in the GLM family. In the case of repeated sampling, a site was considered as a "main-plot" and this as a factor with a random effect. Phytogeographical region, substratum, and soil moisture were the categorical fixed effect factors, while successional age and altitude were the continuous fixed effect factors in the model. All tests were based on the restricted maximum likelihood (REML) approach. The statistical significance of the main effects was assessed by computing Bayesian highest probability (HPD) intervals using Markov chain Monte Carlo simulations (1000 permutations in each test), as this is preferred over normal confidence limits for GLMMs. Analyses were done using the lme4 (Bates & Maechler 2010) and language R packages (Baayen 2011) in R (R Development Core Team 2010). Statistica 10 (StatSoft Inc., Tulsa, www.statsoft.com) was used for post hoc tests to evaluate the direction of significant ($P \leq 0.05$) effects from the previous analyses.

Effects of phytogeographical region, substratum, soil moisture, successional age and altitude on species richness and plant cover were tested using conditional inference trees (Hothorn et al. 2006). This method is a non-parametric regression that produces a dichotomous tree that can be used as a predictive model and provide an insight into which environmental factors contribute to a high/low species richness and plant cover. At each split in the tree, all factors are tested and the predictor that best discriminates between high and low species richness plots is selected. The procedure continues until no environmental factors significantly discriminate between species richness or cover. The hierarchical structure of the P-values was adjusted for multiple testing using the Bonferroni correction. Analyses were performed with the party packages in R (Hothorn et al. 2006, R Development Core Team 2010).

Results

Results of the DCA ordination (Fig. 1) revealed that succession in the fields changed from a more or less common pool of weeds in three directions depending on soil moisture (in the CCA analysis one year old fields in the different moisture categories did not differ significantly in species composition). The subseres developed towards shrubby grassland on dry sites, closed woodland on mesic sites and marshes occasionally dominated by willows on wet sites, which is reflected in the species ordination (Fig. 1B). The first two axes explained 4.8% of the variability in species composition.

The CCA ordination indicates that the species composition of old fields is affected by the interaction between age and soil moisture, and separately by age of the field, soil moisture and conditionally also the substratum and altitude (Table 2).

Of the total number of 497 species six are critically endangered (CR), seven endangered (EN), 16 vulnerable (VU) and 31 near threatened (NT). Non-native species (122 taxa in total) included 95 archaeophytes and 27 neophytes; 60 species belonged to the class *Querco-Fagetea*, 35 to *Festuco-Brometea*, 24 to *Trifolio-Geranietea* and 161 were classified as synanthropic (for details see Electronic Appendix 1).

The GLMMs indicate (Table 3) that the cover and number of target species (classes *Querco-Fagetea*, *Festuco-Brometea* incl. *Trifolio-Geranietea*), and total number of species increased during succession. In contrast, the number and cover of archaeophytes and number of neophytes, synanthropic and endangered species decreased with field age. The cover of synanthropic species increased with altitude, while the number and cover of species belonging to the class *Festuco-Brometea* incl. *Trifolio-Geranietea*, decreased. Total number of species, the number of endangered species and both the number and cover of target species (*Querco-Fagetea*, *Festuco-Brometea* incl. *Trifolio-Geranietea*) were higher in Thermophyticum and in areas with a basic substratum.

On the other hand, there was a higher number and greater cover of synanthropic species, cover of archaeophytes and number of neophytes in Mesophyticum and on acidic substrata. The total number of species, and the number and cover of endangered species and species from *Festuco-Brometea* incl. *Trifolio-Geranietea* decreased with increase in soil moisture. The cover of neophytes and synanthropic species increased with soil moisture (Table 3).

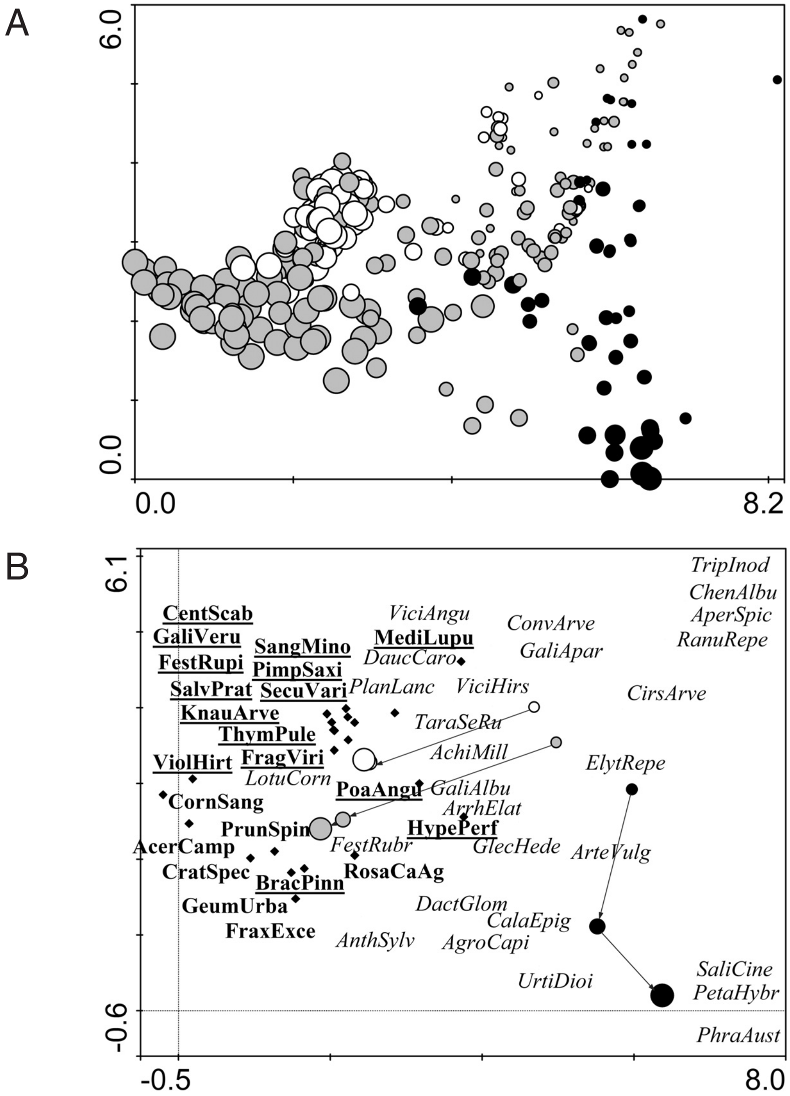

Fig. 1. – Ordinations (DCA) of samples (A) and species (B). White circles indicate samples from dry, grey mesic and black wet sites. Increasing size of the symbols indicates an increase in the age of the fields scored as: 1–2, 3–5, 6–10, 11–20, 21–30, 31–50 or more than 50 yrs. Centroids for the age groups 0–10, 11–20, and more than 20 yrs are used in (B). Only 50 species with the highest amount of variability explained by the first two ordination axes are shown. Abbreviations of species names are composed from the first four letters of the generic and specific names. All target species are in bold of which the species from the class *Festuco-Brometea* incl. *Trifolio-Geranietea* (*Brachypodium pinnatum*, *Centaurea scabiosa*, *Euphorbia cyparissias*, *Festuca rupicola*, *Fragaria viridis*, *Galium verum*, *Hypericum perforatum*, *Knautia arvensis*, *Medicago lupulina*, *Pimpinella saxifraga*, *Poa angustifolia*, *Sanguisorba minor*, *Securigera variegata*, *Salvia pratensis*, *Thymus pulegioides*, *Viola hirta*) are underlined and those from the class *Querco-Fagetea* (*Acer campestre*, *Cornus sanguinea*, *Crataegus* spp., *Fraxinus excelsior*, *Geum urbanum*, *Ligustrum vulgare*, *Prunus spinosa*, *Rosa canina* agg.) are in bold. Synanthropic species (*Apera spica-venti*, *Artemisia vulgaris*, *Cirsium arvense*, *Convolvulus arvensis*, *Daucus carota*, *Elytrigia repens*, *Galium aparine*, *Chenopodium album* agg., *Urtica dioica*, *Vicia hirsuta*) and remaining species (*Agrostis capillaris*, *Achillea millefolium* agg., *Anthriscus sylvestris*, *Arrhenatherum elatius*, *Calamagrostis epigejos*, *Dactylis glomerata*, *Festuca rubra*, *Galium album* agg., *Lotus corniculatus*, *Phragmites australis*, *Plantago lanceolata*, *Plantago media*, *Ranunculus repens*, *Salix cinerea*, *Taraxacum* sect. *Ruderalia*, *Tripleurospermum inodorum*, *Vicia angustifolia*) are in italics.

Table 2. – Results of the Monte Carlo permutation test (marginal effects) and forward selection (conditional effects) in an ordination (CCA) of 282 samples and 497 species. Variables selected explain 9.1% of the total explained variability in species composition. Only significant relationships (P < 0.01) between the variables and species composition are displayed.

CCA	Marginal	Conditional
Age × moisture	3.85	3.85
Age	3.68	1.01
Moisture	2.56	2.64
Substratum	n.s.	1.58
Altitude	n.s.	0.67

Table 3. – Relationships between the number (S) and cover (%) of all species, endangered species (CR, EN, VU, NT), target species (belonging to *Querco-Fagetea* and *Festuco-Brometea* & *Trifolio-Geranietea*), archaeophytes, neophytes and synanthropic species in the samples, and phytogeographical area (Thermophyticum – Thermo, Mesophyticum – Meso), substratum (basic and acidic), soil moisture (dry, mesic, wet), age of the fields and altitude were analysed using a generalized mixed effect model (with post hoc Tukey test for significant differences). Arrows pointing up indicate an increase and those pointing down a decrease in the respective characteristics.

		Preferred phyt. region	Preferred substratum	Moisture	Age	Altitude
Total	S	Thermo	basic	dry > mesic > wet	↑	n.s.
	%	n.s.	basic	n.s.	↑	n.s.
Endangered	S	Thermo	basic	dry > mesic > wet	↓	n.s.
	%	n.s.	n.s.	dry > mesic > wet	n.s.	n.s.
Querco-Fagetea	S	Thermo	basic	n.s.	↑	n.s.
	%	Thermo	basic	n.s.	↑	n.s.
Festuco-Brometea & Trifolio Geranietea	S	Thermo	basic	dry > mesic > wet	↑	↓
	%	Thermo	basic	dry > mesic > wet	↑	↓
Archeophytes	S	n.s.	acidic	n.s.	↓	n.s.
	%	Meso	acidic	n.s.	↓	n.s.
Neophytes	S	Meso	acidic	n.s.	↓	n.s.
	%	n.s.	n.s.	wet > mesic > dry	n.s.	n.s.
Synanthropic	S	Meso	acidic	n.s.	↓	n.s.
	%	Meso	acidic	wet > mesic > dry	n.s.	↑

The conditional inference tree analysis of total species richness indicated primarily a soil moisture effect, with dry old fields harbouring the highest number of coexisting species. Mesic sites were also species rich, particularly those in Mesophyticum on basic substrata and < 35-yr-old. The smallest number of species was recorded in wet old fields > 12-yr-old (Electronic Appendix 2). The analyses of endangered species also revealed a primary soil moisture effect, separating richer dry sites from less species rich mesic and wet fields, which were separated at the next node. The least number of endangered species occurred in wet fields in Mesophyticum (Electronic Appendix 3). Significantly more archaeophytes occurred in < 6-yr-old dry fields (Electronic Appendix 4). Soil reaction seems to be the important factor determining the presence of neophytes, with the highest number recorded in acidic, dry to mesic, young fields. On basic substrata, significantly more neophytes occurred in < 8-yr-old than older fields (Electronic Appendix 5). The conditional inference tree analysis of synanthropic vegetation mainly revealed an age effect, with > 8-yr-old fields harbouring significantly fewer synanthropic species than younger fields. Synanthropic species richness peaked at about 20 species per plot in < 8-yr-old dry fields (Electronic Appendix 6). Significantly more target species belonging to *Querco-Fagetea* were recorded in > 35-yr-old fields in Thermophyticum on mesic sites, while the lowest numbers occurred in < 10-yr-old fields on both dry and wet sites (Electronic Appendix 7). The target species of dry grasslands (*Festuco-Brometea*) and forest edges (*Trifolio-Geranietea*) were primarily associated with soil moisture that separated dry fields with about 10 target species per plot from mesic and wet fields with a much lower presence of those species. The highest number of target species typical of dry grasslands and forest-edge communities was recorded in > 10-yr-old dry fields. In the case of mesic and wet sites, a higher number of target species occurred on basic than acidic substrata (Electronic Appendix 8).

Discussion

The country-scale analysis revealed a divergence in succession, which in principle followed the same trajectories as revealed by previous analyses of datasets collected in a particular landscape (Prach et al. 2007a, Jírová et al. 2012). Osbornová et al. (1990) previously also report that succession diverges into three basic subseres, which reflect site moisture. Thus, site moisture seems to be a consistent factor determining succession (see also Douma et al. 2012) at least in central-European old fields and is second in importance after the generally accepted field age (Walker & del Moral 2003). The age of a succession, if studied, nearly always has a significant effect on the course of succession (see Prach & Řehounková 2006). Site moisture is reported as having a significant role in determining the course of succession in old fields in other large-scale studies (Ejrnaes et al. 2003, Otto et al. 2006). Site moisture is also the most important determinant of divergent succession in disused sand pits analysed at a country-scale (Řehounková & Prach, 2006). On the other hand, convergent succession is recorded as occurring at a country-scale in old-field succession in Finland (Prach 1985). This was probably a consequence of the uniform and rather humid environment in that country.

We are aware of the fact that site moisture was estimated approximately and subjectively and in particular cases could be biased, for example, by local weather conditions. A few outliers in Fig. 1A may indicate this, but they do not obviously influence the overall pattern. The estimates recorded in the three moisture categories were used in this study because they are supported by exact soil moisture measurements (Osbornová et al. 1990, Szabó & Prach 2009). Site moisture is generally influenced by local relief and climate (Ellenberg 1988), which is closely related to altitude (Box 1981). Thus, altitude can be used as a surrogate of the main macroclimate parameters, i.e. temperature and precipitation. The role of climate in the course of succession still remains rather speculative, but it is certainly important in determining the presence of woody species in semi-arid environments (Walker & del Moral 2003, Fridley & Wright 2012). Though central Europe is a rather humid region, local site factors, such as southern slopes and shallow soil, may create local semi-arid environments, which limit the establishment of woody species.

The development of shrubby grassland in our dry sere is evidence of such limitations (see also Prach et al. 2007a). The role of climatic conditions on the course of old-field succession was studied by Dovčiak et al. (2005) and Otto et al. (2006) who came to similar conclusions. Climate and soil pH are recognized as the most important environmental variables affecting the development of vegetation during the course of succession at human-made sites in central Europe (Prach et al. 2007b). Our substratum categories, i.e. basic and acidic, are a robust estimate of soil pH and had at least some significant effects on the course of succession in this study.

Because of evolutionary adaptations and the history of central-European vegetation, a higher number of plant species are confined to warmer regions with basic substrates (Chytrý et al. 2003, Ewald 2003), which was also confirmed by the positive significant relationships of total species number with Thermophyticum and basic substrates recorded in this study (the influence of increasing altitude was negative, although insignificant). The total number of species increased with decreasing site moisture (see also Osbornová et al. 1990, Prach et al. 2007a). Generally, this relationship is expected to be unimodal (Grime 1979). Because really dry and extremely wet land is not usually cultivated, we obviously observed only a part of the bell-shaped curve, which resulted in the pattern recorded.

The highest numbers of endangered species were recorded in young fields located in Thermophyticum and on basic substrates, which may be due to the higher presence of endangered weeds at these sites (Lososová et al. 2003). It is not surprising that species typical of dry grasslands are confined to dry and warmer sites in the deciduous woodland zone (Ellenberg 1988) and that both target groups of species typical of late or climax stages, i.e. either dry grasslands or woodlands, increased during the course of succession and that of synanthropic species decreased (Walker & del Moral 2003). Wetlands were not considered as target communities in the old fields studied because of eutrophication. Alien and all synanthropic species exhibited similar patterns being generally more numerous at wetter sites on acidic substrates in Mesophyticum. This is rather surprising, because aliens are especially more frequent in warmer and drier regions of the country (Pyšek et al. 2002, 2012a, b). This difference is possibly due to the fact that, in our data set, most of the dry old fields in Thermophyticum originated from less intensively used marginal areas of a protected landscape area or a military training zone, where there are fewer alien and synanthropic species than elsewhere. In addition, by coincidence, both these areas are on basic substrates. This biased our data set simply because arable land in other warmer and drier regions in the lowlands (Thermophyticum) in this country is only exceptionally abandoned, while fields in the wetter and colder uplands (Mesophyticum) are more frequently abandoned.

GLMM revealed the dominant role of the age of the succession and site moisture in determining the current pattern of vegetation. The methods used, i.e. ordination, GLMM and regression trees, provided complementary results: ordination illustrates the overall pattern, GLMM a detailed insight into the relationships between the particular characteristics of vegetation and environmental factors, and regression trees into the hierarchy of relationships. Thus, using all these methods improves the description and understanding of the course of succession.

In contrast to the many detailed studies on succession conducted at local scales, including those on old fields (Rejmánek & van Katwyk 2004, Cramer & Hobbs 2007), there is still a lack of studies on succession conducted at geographical scales. Undoubtedly, the results of such studies, in terms of the trends and variability in succession, can be better generalized than those obtained from studies of local sites. The results of this study can be used as a basis for predicting succession in old fields at a country scale.

See www.preslia.cz for Electronic Appendices 1–8

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Souhrn

Práce shrnuje sukcesní vývoj na základě analýzy 282 fytocenologických snímků ze 173 opuštěných polí, snímkovaných v letech 1975–2011 napříč Českou republikou. Sukcesní stáří snímkovaných ploch bylo v rozsahu 1–91 let. Pro každé opuštěné pole byly zjištěny nadmořská výška, fytogeografický region (termofytikum, mezofytikum) a geologický substrát (bazický či kyselý). Dále byla tříčlennou stupnicí odhadnuta půdní vlhkost (suché, mezické, vlhké pole). Druhy byly rozděleny na základě jejich ohrožení, původu (archeofyty, neofyty a původní) a příslušnosti k vegetačním jednotkám. Data byla analyzována ordinačními metodami, GLMM a regresními stromy. Výsledky ukazují, že všechny proměnné prostředí měly průkazný vliv na druhové složení sukcesních stádií. Sukcese se ubírala třemi směry podle půdní vlhkosti. Počet druhů lesů, suchých trávníků a bylinných lemů se během sukcese zvyšoval. Naopak počet archeofytů, neofytů a synantropních druhů se s časem od opuštění pole snižoval. V termofytiku bylo zaznamenáno více ohrožených a cílových druhů a méně archeofytů, neofytů a synantropních druhů než v mezofytiku. Stáří a půdní vlhkost se ukázaly být nejdůležitějšími faktory ovlivňujícími druhové složení opuštěných polí. Tato studie se může díky svému širokému geografickému záběru stát základem k předpovídání sukcesního vývoje na opuštěných polích na úrovni celé ČR.

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