Journal of Biogeography (J. Biogeogr.) (2008) 35, 177–187

ORIGINAL ARTICLE

Plant attributes determining the regional abundance of weeds on central European arable land

Zdeňka Lososová[1,2], Milan Chytrý[1]* and Ingolf Kühn[3]

[1]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic,[2]Department of Biology, Faculty of Education, Masaryk University, Brno, Czech Republic and [3]Department of Community Ecology (BZF), UFZ - Helmholz Centre for Environmental Research, Halle, Germany

*Correspondence: Milan Chytrý, Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic.
E-mail: chytry@sci.muni.cz.

ABSTRACT

Aim Several recent studies have aimed to identify the biological, ecological and distributional attributes that determine the regional abundance of plant species. Here we aim to assess the relationships between regional abundance and species attributes in weeds on arable land.

Location Czech Republic, central Europe.

Methods The relationships between regional abundance and species attributes were studied with a data set of 381 weed species occurring on arable land in the Czech Republic. Regional species abundances were estimated from their occurrence frequency in vegetation plots distributed across the country. Using regression tree models, abundance was related to the biological traits, ecological indicator values, geographical distribution and habitat range of species. The models were calculated for the entire country and separately for weeds in cereals, root crops, lowlands and uplands. The effects of phylogenetic relatedness among species on their regional abundance were quantified and compared with the effects of species attributes.

Results The results were similar for the whole data set and its particular subsets. Phylogeny explained 11.2–14.9% and species attributes 16.1–56.9% of the variation in regional abundance of weed species. Removal of the phylogenetic signal did not result in important changes in the effects of particular attributes. The most abundant species were those flowering in pre-spring and early spring, adapted to low temperatures, relatively shade tolerant and with high nutrient requirements. The high regional abundance of these species positively correlated with their broad geographical (often circumpolar) distribution and broad habitat ranges.

Main conclusions The regional abundance of weeds can, to some extent, be explained by their attributes. The most important attributes are those that enable weeds to grow and reproduce in the cool season when there is limited competition with crop plants, and those that are adaptations to growth in dense vegetation stands and highly productive habitats.

Keywords
Commonness, Czech Republic, flowering time, geographical range size, habitat range, nutrient requirements, phylogeny, rarity, regression trees, species traits.

INTRODUCTION

Comparative analyses of multispecies assemblages over large areas have demonstrated that common and rare species differ in a number of biological traits and ecological characteristics (e.g. Kunin & Gaston, 1997). However, recently published studies cast doubt on the generality of any clear-cut distinctions in attributes between common and rare species (e.g. Murray *et al.*, 2002). Instead, it appears that relationships between species attributes and the regional abundances of

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd
www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2007.01778.x

species largely depend on the geographical and environmental context and the taxonomic or functional species assemblages studied (Lahti *et al.*, 1991; Kelly, 1996; Hegde & Ellstrand, 1999; Cadotte & Lovett-Doust, 2002; Murray *et al.*, 2002; Kolb *et al.*, 2006; Pocock *et al.*, 2006).

Little is known about the relationship between regional abundance and species attributes on temperate arable land, although several recent studies have analysed broad-scale patterns in species composition of weed vegetation and their underlying environmental variables (Dale *et al.*, 1992; Andersson & Milberg, 1998; Hallgren *et al.*, 1999; Lososová *et al.*, 2004). The weed flora of arable land provides an interesting model system for exploring the effect of species attributes on regional abundance because it is highly dynamic and experiences rapid changes in the abundance of individual species across large areas at a time-scale of decades. These dynamics include both the rapid spread of alien species (Holzner, 1978; di Castri, 1989; Pyšek *et al.*, 2005) and the decline of many weed species that used to be common but are now endangered or extinct over large areas (Hilbig, 1987; Andreasen *et al.*, 1996; Lososová, 2003). Consequently, common–rare differences in such a dynamic system are probably less affected by historical inertia than in other habitats, and more directly reflect the relationships between species attributes and the current environment.

Besides the direct causal effects of biological traits and ecological requirements, regional abundance can also be influenced by other distributional characteristics of species, e.g. range size or habitat range (Thompson *et al.*, 1998; Brändle *et al.*, 2003b; Pocock *et al.*, 2006). Although such distributional characteristics are themselves affected by biological traits and ecological requirements of species, they may influence the regional abundance of species, for example via source–sink effects. Knowledge of these properties is therefore important for a deeper understanding of common–rare differences.

In the present study we perform an exploratory analysis of the relationships between different attributes of weed species and their regional abundance on arable land in the Czech Republic. We aim to assess which biological traits, ecological characteristics and distributional characteristics are most closely related to the regional abundance of weed species on central European arable land.

MATERIALS AND METHODS

Estimation of the regional abundance of species

To estimate the regional abundance of weed species we used a large set of records of species composition in vegetation plots (relevés) selected from the Czech National Phytosociological Database (Chytrý & Rafajová, 2003). First, we selected 2696 plots that were between 12 and 100 m^2 in size and sampled on arable land. We then carried out stratified resampling of this data set in order to reduce possible oversampling of some habitats in some areas (Knollová *et al.*, 2005). For this purpose we divided the area of the Czech Republic into grid squares of 1.25 longitudinal minutes × 0.75 latitudinal minutes (*c.* 1.5 km × 1.4 km). If a grid square contained more than one plot belonging to the same phytosociological association (based on expert assignment by the surveyor), only the most recent plot was chosen and included in the final data set. The final data set contained 2033 plots from arable land distributed across the Czech Republic and originally inventoried by 32 authors. There were 278 plots from the period 1954–70, 628 from 1971–90 and 1127 from 1991–2004.

From this data set we deleted non-vascular plants, crop plants and species found in a single plot. This selection yielded 381 weed species that we considered to be representative of the weed flora of the country. We estimated the relative frequency (number of species occurrences in plots relative to the total number of plots) of each species within this data set and used this as a measure of the regional abundance of species on Czech arable land.

As it is known that some arable weeds have declined since the 1950s (Holzner, 1978; Hilbig, 1987; Kornaś, 1988; Andreasen *et al.*, 1996; Sutcliffe & Kay, 2000; Lososová, 2003; Pinke, 2004) and some alien weeds have spread during recent decades (Lososová *et al.*, 2004; Pyšek *et al.*, 2005), we correlated species abundances between the time periods 1954–70, 1971–90 and 1991–2004. Pearson's correlation coefficients were 0.95 and 0.92, respectively, between the two consecutive periods and 0.86 between the first and last mentioned period (all $P < 0.001$). Therefore, although several species tended to decline or increase, generally abundant species remained abundant and rare species remained rare. We could therefore safely use the data set from the entire period for the analysis.

Since Lososová *et al.* (2004) revealed that the main gradient in species composition of arable weed communities in the Czech Republic is related to altitude, we divided the vegetation plot data set into three subsets according to three altitudinal floristic regions of the Czech Republic (Skalický, 1988). The first subset contained 555 plots from the warm and dry, low-altitudinal floristic region (Thermophyticum) with 244 species, the second subset contained 1397 plots with 215 species from the mid-altitudinal floristic region (Mesophyticum) and the third subset contained only 81 plots with 178 species from the cool and wet, high-altitudinal floristic region (Oreophyticum). Because of its small number of plots, the subset from the last-mentioned region was not analysed. To show differences between the traits of weed species occurring in different crop types, we divided our data set into two categories – cereals and root crops (see Lososová *et al.*, 2004 for a detailed delimitation of these categories). The subset from cereal fields contained 1569 plots with 364 species and the subset from root-crop fields contained 464 plots with 291 species. We calculated the regional abundance of each weed species in the subsets of the low-altitudinal region, mid-altitudinal region, cereals and root crops.

The data sets were edited using the JUICE 6.3 program (Tichý, 2002). Taxonomic concepts and nomenclature of species follow Kubát *et al.* (2002).

© 2007 The Authors. Journal compilation © 2007 Blackwell Publishing Ltd

Species attributes

Information on biological traits and ecological and distributional characteristics of weed species was taken from different sources, but mainly from the BiolFlor data base (Klotz *et al.*, 2002). For each species, the following attributes were compiled:

1 Biological traits:

Plant height, maximum and mean (Kubát *et al.*, 2002).

Life span, with four categories: annual, biennial, monocarpic perennial (= pluriennial-hapaxanthic) and polycarpic perennial (= pluriennial-pollakanthic) (Krumbiegel in Klotz *et al.*, 2002, pp. 93–118).

Life-form, with five categories: chamaephyte, geophyte, hemicryptophyte, phanerophyte (including macrophanerophyte, nanophanerophyte, pseudophanerophyte and hemiphanerophyte) and therophyte (Krumbiegel in Klotz *et al.*, 2002, pp. 93–118).

Life strategy, with seven categories according to Grime (1979): competitors (C), competitors/ruderals (CR), competitors/stress-tolerators (CS), competitors/stress-tolerators/ruderals (CSR), ruderals (R), stress-tolerators (S) and stress-tolerators/ruderals (SR) (Klotz & Kühn in Klotz *et al.*, 2002, pp. 197–201).

Leaf persistence, with four categories: spring-green, summer-green, overwintering-green and persistent-green (Klotz & Kühn in Klotz *et al.*, 2002, pp. 119–126).

Reproduction type, with three categories: species reproducing only or mostly by seed, species reproducing by seed and vegetatively, and species reproducing mostly or only vegetatively (Durka in Klotz *et al.*, 2002, pp. 133–175).

Flowering phase, with three seasonal phases: pre-spring/early spring, mid-spring and summer, grouped from 10 phenological phases used in BiolFlor (Trefflich *et al.* in Klotz *et al.*, 2002, pp. 127–131).

Pollen vector, with three categories: wind, selfing and insect (Durka in Klotz *et al.*, 2002, pp. 133–175).

Dispersal mode, with five categories: anemochory, myrmecochory, epizoochory, autochory and endozoochory (Frank & Klotz, 1990).

2 Ecological characteristics:

Indicator values according to Ellenberg *et al.* (1992) for six environmental variables: light, temperature, continentality, moisture, soil reaction and nutrients, measured on a nine-degree ordinal scale (12 degrees for moisture).

3 Distributional characteristics:

Number of floristic zones, expressed on a nine-degree scale from one to nine of the world's floristic zones occupied by the species (Kühn & Klotz in Klotz *et al.*, 2002, pp. 227–239).

Floristic region, with five categories: circumpolar, Europe, Asia, America and Africa (Kühn & Klotz in Klotz *et al.*, 2002, pp. 227–239). In contrast to the previous characteristic, this is qualitative rather than quantitative information regarding species distribution.

Habitat range, quantified as the number of habitat types in which the species occurs in the Czech Republic. It was quantified on the basis of the geographically stratified data set of 20,468 vegetation plots distributed across the country and covering all major habitats. Each plot was assigned to one of 32 habitats based on the European Nature Information System (EUNIS) habitat classification (Davies & Moss, 2003). For each species, the number of habitat types was counted in which this species was recorded. For details of the data set and the list of habitats see Chytrý *et al.* (2005).

Species status as native or alien, with three categories according to Pyšek *et al.* (2002): native species, archaeophytes (species which appeared in the study area before 1500) and neophytes (species that arrived in the post-medieval period).

Handling phylogenetic information

Some of the relationships identified between the regional abundance of species and their attributes may result from the fact that some groups of phylogenetically related species are either common or rare due to their common evolutionary history (Harvey & Pagel, 1991). Therefore we incorporated phylogenetic information into our analyses. We used the species phylogeny available in the BiolFlor data base (Durka in Klotz *et al.*, 2002; pp. 75–91) and an eigenvector filtering approach proposed by Diniz-Filho *et al.* (1998): we calculated patristic distances among all pairs of species, i.e. the sum of branch lengths on a path along a phylogenetic tree between a pair of taxa. Since branch lengths are unavailable for the complete central European flora, we set all branch lengths as equal to one unit (see Prinzing *et al.*, 2001). Calculations were done separately within the country-wide data set and its four above-mentioned subsets. The matrices of patristic distances were subjected to principal coordinates analysis (PCoA), which is a generalization of principal components analysis (PCA) capable of using any kind of distance between objects. Each axis of the PCoA of the matrix of patristic distances represents a certain amount of phylogenetic variation proportional to the associated eigenvalue. We preferred this method to other more widely used ones since it is easy to use and has been proved to perform well under different evolutionary assumptions (Diniz-Filho *et al.*, 1998).

For the whole data set and each of its four subsets we calculated multiple regressions in which species scores on the PCoA axes were used as independent variables and species regional abundance was used as the dependent variable. Only the PCoA axes with the highest eigenvalues, cumulatively accounting for 95% of the total variation, were used in these regressions. The regressions identified the amount of the variation in species regional abundance attributable to phylogeny.

Relating species attributes to species abundance

First, we related the regional abundance of weed species (dependent variable) to the set of species attributes (independent variables) using regression trees (Breiman *et al.*, 1984; De'ath & Fabricius, 2000). Regression tree analysis is an exploratory statistical technique useful for the analysis of data

© 2007 The Authors. Journal compilation © 2007 Blackwell Publishing Ltd

sets with many independent variables, which may involve complex interactions. It provides hierarchical dichotomous classification of the data set into smaller groups in which the within-group variation in the response variable is minimized. At each node of the tree, cases (species in our case) are split dichotomously based on a certain value of a selected independent variable, later called the splitter variable.

Secondly, we investigated how regression trees change when the phylogenetic component of the variation in species abundance is removed. In this analysis, we calculated regression trees in which the dependent variables consisted of the residuals from the multiple regression of species abundance on the phylogenetic PCoA axes and the independent variables were the species attributes.

To select the optimal tree size, the 10-fold cross-validation method with the SE = 0 rule was used (Breiman *et al.*, 1984). The cross-validation procedure suggests the 'optimal' tree size, which is a compromise between maximizing the explained variation in the dependent variable and minimizing the risk of overfitting. At each node of the tree, we identified surrogate variables, i.e. variables that are able to separate cases in a similar way to the particular splitter variable. Only those variables having an associated value with respect to the splitter variable of > 0.5 were considered as surrogates. For each tree the explained variation in the dependent variable was calculated from their resubstitution relative errors, corresponding to the residual sums of squares. The relative importance of each independent variable in each regression tree was expressed by the importance value, which was computed by summing, over all nodes of the tree, the resubstitution error estimate and expressing these sums relative to the largest sum found over all independent variables. Thus the most important independent variable received a value of 100 and the others were scored relative to the best variable on a scale from 0 to 100. The importance value reflects the contribution of each variable stemming both from its role as a splitter and as a surrogate across all nodes of the tree.

Only those categorical attributes that occurred in ≥ 20 species were used for the analyses. Missing Ellenberg indicator values for some species were replaced by the mean values for particular factors.

All calculations were done in the programs STATISTICA 7.1 (http://www.statsoft.com/) and R 2.4.0 (R Development Core Team 2006, http://www.r-project.org/). The function for calculating patristic distances was written by us (see Appendix S1 in Supplementary Material). PCoA was calculated with the function cmdscale() in the R package 'stats'.

RESULTS

The most abundant species of the set of 381 weeds of arable land in the Czech Republic are listed in Table 1. The most abundant weed is *Viola arvensis*, which occurred in 73% of plots, followed by *Stellaria media*, *Capsella bursa-pastoris* and *Fallopia convolvulus*. The lists of the most abundant species are quite similar for cereal fields, low-altitudinal regions and mid-

Table 1 The most abundant weeds in the Czech Republic, in different crop types and in two altitudinal floristic regions. Numbers are relative measures of regional abundance, expressed as the percentage of vegetation plots from arable land in which the species was recorded.

Czech Republic		Cereals		Root crops		Low-altitudinal region		Mid-altitudinal region	
Viola arvensis	73	*Viola arvensis*	79	*Chenopodium album*	77	*Cirsium arvense*	69	*Viola arvensis*	74
Stellaria media	72	*Stellaria media*	71	*Stellaria media*	77	*Viola arvensis*	68	*Stellaria media*	74
Capsella bursa-pastoris	65	*Fallopia convolvulus*	67	*Capsella bursa-pastoris*	68	*Polygonum aviculare*	67	*Capsella bursa-pastoris*	65
Fallopia convolvulus	64	*Tripleurospermum inodorum*	65	*Cirsium arvense*	61	*Fallopia convolvulus*	66	*Myosotis arvensis*	64
Cirsium arvense	61	*Capsella bursa-pastoris*	64	*Taraxacum* sect. *Ruderalia*	58	*Stellaria media*	66	*Fallopia convolvulus*	64
Tripleurospermum inodorum	60	*Cirsium arvense*	61	*Fallopia convolvulus*	56	*Chenopodium album*	66	*Tripleurospermum inodorum*	63
Chenopodium album	58	*Myosotis arvensis*	58	*Elytrigia repens*	55	*Capsella bursa-pastoris*	63	*Cirsium arvense*	60
Myosotis arvensis	54	*Galium aparine*	57	*Veronica persica*	52	*Tripleurospermum inodorum*	57	*Galium aparine*	58
Thlaspi arvense	54	*Polygonum aviculare*	57	*Viola arvensis*	51	*Convolvulus arvensis*	57	*Thlaspi arvense*	56
Galium aparine	53	*Thlaspi arvense*	56	*Thlaspi arvense*	48	*Veronica persica*	57	*Chenopodium album*	55
Elytrigia repens	53	*Elytrigia repens*	52	*Convolvulus arvensis*	46	*Elytrigia repens*	55	*Elytrigia repens*	53
Polygonum aviculare	53	*Chenopodium album*	52	*Lamium purpureum*	46	*Thlaspi arvense*	54	*Veronica persica*	51
Veronica persica	51	*Veronica persica*	51	*Persicaria lapathifolia*	44	*Anagallis arvensis*	50	*Taraxacum* sect. *Ruderalia*	49

© 2007 The Authors. Journal compilation © 2007 Blackwell Publishing Ltd

altitudinal regions. The root-crop fields are slightly different – *Chenopodium album* is the most abundant species.

Regression trees were constructed separately for the whole data set, for weeds of cereal and root-crop fields and for weeds of two altitudinal floristic regions of the Czech Republic (Table 2). Optimal regression trees for the whole data set and for the weeds of cereal fields had the same topology with three terminal nodes and the same splitter variables at each node; therefore the tree graph is presented only for the latter (Fig. 1a). This tree explains 29% of the variation in the regional abundance of species. It shows that the regionally most abundant species are those with large geographical ranges, and particularly those flowering in pre-spring and early spring.

The optimal regression tree for root-crop weeds has four terminal nodes (Fig. 1b) and explains 56% of the variation in the regional abundance of species. The main split, based on Ellenberg indicator values, indicates that the most abundant weeds are demanding of nutrients and moisture. Among them, the most abundant species are again those flowering in pre-spring and early spring. Among the nutrient- and moisture-demanding species that flower later in the season, those with a broader geographical range (occurring in more than five floristic zones) are more abundant.

The optimal regression tree for weeds of the low-altitudinal region is divided into only two terminal nodes according to the flowering phase (not shown). This tree explains only 16% of the variation and indicates that species flowering in pre-spring and early spring are more abundant (mean percentage frequency $x = 24.6$, $n = 25$) than the others ($x = 9.3$, $n = 219$).

The optimal regression tree for weeds of the mid-altitudinal region has six terminal nodes and explains 49% of the variation in the regional abundance of species (Fig. 1c). In the mid-altitudinal region as well, the most abundant weed species are those flowering in pre-spring and early spring. Of these, species with a higher tolerance to low temperatures are more abundant. In the group of later-flowering species, those with higher nutrient requirements, annual life span and broader habitat range are the most abundant.

The most important attributes related to the regional abundance of species are similar in all analyses (Table 2) and remain stable when the phylogenetic component of variation is removed. Overall, phylogeny explains much less variation in species abundance than species attributes uncorrected for phylogeny (Table 3). For those attributes that did not appear as splitters or surrogates in regression trees but still had relatively high importance values (Table 2), the relationships identified by univariate Pearson correlations and *t*-tests for the whole data set are as follows: regional abundance of species decreases with mean plant height ($r = -0.59$; $P < 0.001$), is higher for therophytic life-form (*t*-test; $P < 0.001$) and CR strategy ($r = 0.32$; $P < 0.001$), decreases with Ellenberg indicator values for light and soil reaction ($r = -0.29$; $P < 0.001$ and $r = -0.04$; $P < 0.01$, respectively) and is higher for species with circumpolar distribution and lower for those with European distribution (*t*-test, both $P < 0.001$). The signs of the corresponding relationships are the same in particular subsets.

DISCUSSION

The most abundant weed species

Holzner (1982) recognized two contrasting tendencies in weed evolution. One tendency is the evolution of specialized weeds having a narrow adaptation to one crop. This specialization is advantageous if environmental conditions are stable. However, the profound changes in agricultural management during the last century caused a considerable decline in such species (Holzner, 1978; Hilbig, 1987; Kornaś, 1988; Andreasen *et al.*, 1996; Sutcliffe & Kay, 2000; Lososová, 2003; Pinke, 2004). The opposite tendency is the evolution of colonizers, which are adapted to different environments and possess effective dispersal strategies. Species reported to be among the most abundant weeds in our survey (Table 1) belong to the colonizers. Not all of the most abundant weeds, however, are confined to agricultural habitats. Most of them are widely distributed in different human-made habitats (Lososová *et al.*, 2006) and some are also found in mesic grasslands. Therefore they should be considered as ecological generalists occurring, among other habitats, on agricultural land.

The list of the most abundant weeds of the Czech Republic (Table 1) corresponds very well to similar lists from other countries of central and northern Europe, e.g. Finland (Hyvönen *et al.*, 2003), Denmark (Andreasen *et al.*, 1996), Poland (Trzcińska-Tacik, 1991) or Hungary (Glemnitz *et al.*, 2000). Glemnitz *et al.* (2000) reported *Polygonum aviculare*, *Fallopia convolvulus*, *Cirsium arvense* and *Chenopodium album* to be found on agricultural fields throughout Europe independently of climatic conditions. These species were among the most abundant weeds in the Czech Republic (Table 1). The most abundant weed of Czech arable land, *Viola arvensis*, has been reported as a recently expanding species not only in the Czech Republic but also in other countries (Hyvönen *et al.*, 2003; Tyšer & Holec, 2004). Consistency of the lists of the most common weeds from different countries indicates that our results are also valid beyond the Czech Republic, at least in central Europe and the southern Baltic region.

Biological traits and ecological characteristics of abundant weeds

Our data suggest that the most abundant weeds on central European arable land are species that flower in pre-spring or early spring, with requirements for low temperature and high nutrient uptake. They also have a certain, yet weaker, tendency to be an annual, therophyte, CR strategist with short stature, shade tolerance and adaptations to mesic and slightly acidic rather than dry and base-rich soils.

The ability to flower early in the growing season enables abundant weeds to use the period of low competition before

© 2007 The Authors. Journal compilation © 2007 Blackwell Publishing Ltd

Table 2 Importance of species attributes for explaining the regional abundance of weed species. Importance values (scaled from 0 to 100) relate to optimal regression trees, in which the regional abundance of species was used as the dependent variable and species attributes as independent variables.

Species attribute	Czech Republic 1	Czech Republic 2	Cereals 1	Cereals 2	Root crops 1	Root crops 2	Low-altitudinal region 1	Low-altitudinal region 2	Mid-altitudinal region 1	Mid-altitudinal region 2
Plant height										
Maximum	30	39	30	39	39	**52**	33	–	42	33
Mean	41	**55**	41	45	**54**	49	39	–	43	32
Life span										
Annual	**64**	49	**67**	25	**65**	19	39	–	**54**	37
Biennial	1	14	1	5	11	22	21	–	13	16
Polycarpic perennial	45	41	47	14	44	16	28	–	44	23
Life-form										
Geophyte	9	34	8	10	39	31	15	–	13	8
Hemicryptophyte	7	10	6	7	23	9	21	–	16	11
Therophyte	**62**	42	**65**	29	46	15	32	–	48	29
Life strategy										
C, competitors	16	10	16	2	25	1	9	–	18	8
R, ruderals	40	25	43	49	21	18	33	–	14	32
CR	20	28	19	10	**57**	43	33	–	**62**	32
CS	15	12	16	5	10	4	3	–	4	6
SR	22	22	21	48	5	36	40	–	21	47
CSR	7	6	8	7	12	12	13	–	14	6
Leaf persistence										
Summer-green	17	7	22	9	14	13	8	–	18	3
Overwintering-green	41	26	47	19	18	15	26	–	30	15
Persistent-green	1	7	1	3	14	7	7	–	7	11
Reproduction type										
Seed	16	22	17	12	27	28	17	–	22	19
Seed and vegetative	20	21	20	10	26	13	20	–	26	22
Flowering phase										
Pre-spring and early spring	**100**	**72**	**100**	**57**	**75**	38	**62**	–	48	**67**
Mid-spring	5	10	5	5	40	10	2	–	8	8
Summer	22	14	25	2	23	8	8	–	10	9
Pollen vector										
Wind	1	1	1	3	4	3	1	–	3	3
Insect	4	4	5	4	4	2	3	–	18	7
Selfing	5	6	7	3	9	3	8	–	4	2
Dispersal mode										
Anemochory	0	11	0	2	5	4	4	–	1	1
Myrmecochory	15	12	15	2	14	13	10	–	25	6
Epizoochory	16	17	18	9	27	14	24	–	36	27
Autochory	4	10	5	1	7	4	3	–	11	10
Ellenberg indicator values										
Light	**78**	**71**	**78**	**87**	**53**	**62**	**83**	–	**71**	**65**
Temperature	42	43	44	38	**50**	**76**	43	–	**78**	**100**
Continentality	32	38	29	34	45	41	35	–	46	34
Moisture	48	**56**	46	**62**	**64**	**72**	36	–	**66**	**57**
Soil reaction	44	**65**	39	22	36	40	33	–	**55**	38
Nutrients	**84**	**100**	**77**	**92**	**67**	**93**	**100**	–	**88**	**99**
Number of floristic zones	**72**	**71**	**66**	**100**	**100**	**100**	**88**	–	**100**	**81**
Floristic region										
Circumpolar	**53**	**84**	**50**	**91**	**62**	**78**	**71**	–	**78**	**69**
Europe	**55**	**81**	**52**	**91**	**56**	**79**	**81**	–	**77**	**77**
Asia	29	**51**	26	3	10	15	5	–	28	29
America	16	10	16	3	4	3	7	–	5	6
Habitat range	38	**71**	34	**55**	**84**	**72**	43	–	**96**	**52**

© 2007 The Authors. Journal compilation © 2007 Blackwell Publishing Ltd

Table 2 continued

	Czech Republic		Cereals		Root crops		Low-altitudinal region		Mid-altitudinal region	
Species attribute	1	2	1	2	1	2	1	2	1	2
Species status										
Native species	35	33	35	26	11	11	42	–	16	13
Archaeophytes	38	35	40	22	14	7	30	–	26	9
Neophytes	5	4	5	9	8	6	13	–	13	6

Column headings: 1, analysis not considering phylogenetic information; 2, analysis of net effects of species attributes after phylogenetic component of the variation in the regional abundance of species was removed.

Importance values ≥50 are in bold; values ≥75 are shaded. No optimal regression tree was found for the low-altitudinal region after the phylogenetic component of variation was removed.

The following categorical attributes that occurred in fewer than 20 species are not shown: monocarpic perennial (life span), chamaephyte and phanerophyte (life-forms), S (stress tolerators; life strategy), spring-green (leaf persistence), vegetative (reproduction type), endozoochory (dispersal mode) and Africa (floristic region).

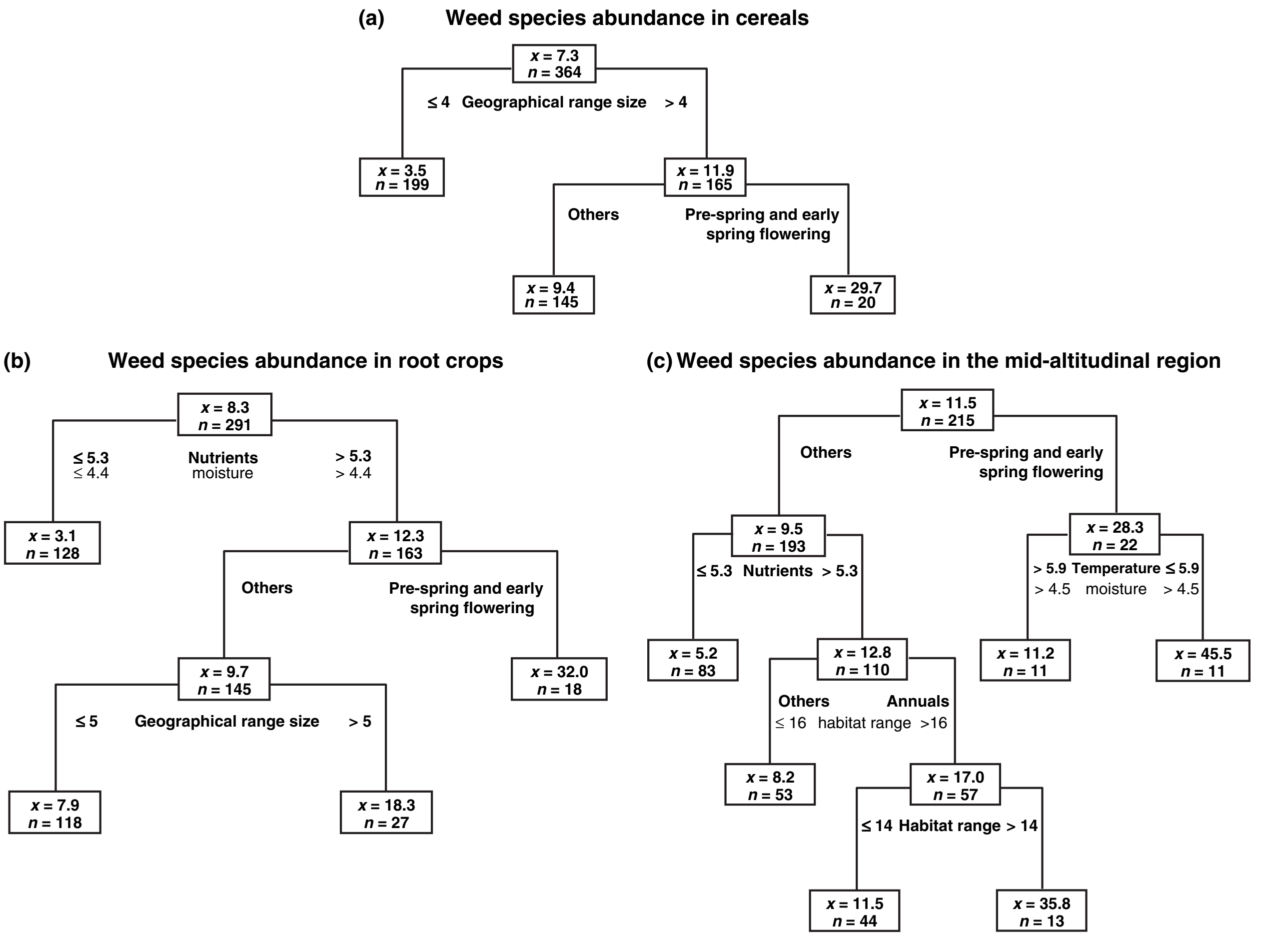

Figure 1 Regression trees explaining the regional abundance of weed species on arable land in the Czech Republic through species attributes. Boxes on the tree nodes contain information on the mean abundance of species in the particular node, i.e. percentage frequency of occurrence in vegetation plots (x) and the number of species occurring on that node (n). Splitter variables (and their split values for quantitative variables) are given in bold at each node. Surrogates, i.e. variables allocating most species to the same group as the primary splitter, are given in non-bold letters below the splitter variables.

© 2007 The Authors. Journal compilation © 2007 Blackwell Publishing Ltd

Table 3 Variation in the regional abundance of weed species explained by species attributes (including the embedded part of the phylogenetically structured variation) and by phylogenetic relatedness among species (including the embedded phylogenetically structured variation in species attributes).

	Variation explained	
	by attributes (%)	by phylogeny (%)
Czech Republic	30.8	11.3
Cereals	29.1	11.8
Root crops	56.3	11.2
Low-altitudinal region	16.1	14.9
Mid-altitudinal region	48.9	13.9

formation of dense stands of crop plants and before germination or vegetative growth of thermophilous, late-growing weed species. Most of these species do not only flower early, but extend their flowering period from early to late season. To mention a few examples from the list of the most abundant weed species on Czech arable land (Table 1), *Capsella bursa-pastoris, Stellaria media* and *Veronica persica* are able to flower and produce seeds throughout the year, *Polygonum aviculare* for up to 11 months, and *Anagallis arvensis* for up to 10 months (Trefflich *et al.* in Klotz *et al.*, 2002; pp. 127–131). The extended flowering period enables such species to increase the chance of cross-pollination and seed output, and probably thereby increase their regional abundance and extend their geographical range. Our observation of the importance of early flowering is consistent with the results of Brändle *et al.* (2003a), who demonstrated a correlation between the time span within a year during which a weedy species is able to germinate and the geographical range size. Lloret *et al.* (2005) also pointed out the importance of a long flowering period for the species of Mediterranean agricultural habitats. Similarly, Lahti *et al.* (1991) found that in the Finnish flora threatened taxa tend to start flowering later than their common relatives. The habit of early flowering in the regionally abundant weeds is consistent with the observation that these species are adapted to relatively cool environments. Ellenberg temperature values of the abundant species are mostly 5 or 6, while those of the less abundant species are usually 6 or 7. This adaptation enables weed species to extend their range to cooler areas and their growing period to the cooler seasons of the year. Tolerance to lower temperatures is probably associated with occurrence on mesic and slightly acidic rather than dry soils, because such soils prevail in cool areas of central Europe.

Abundant weeds also appear to be more demanding of nutrients than less abundant weeds, as suggested by the Ellenberg indicator values. It was shown in experimental studies that some of these species are supported by the addition of nutrients (e.g. *Fallopia convolvulus*, *Thlaspi arvense* and *Viola arvensis*, Pyšek & Lepš, 1991; *Elytrigia repens*, *Viola arvensis*, Hyvönen & Salonen, 2002). As predicted by theory (Grime, 1979; Tilman, 1988), their higher nutrient requirements appear to be related to lower light requirements: successful arable weeds seem to occupy nutrient-rich but more shaded habitats on the resource-ratio gradient *sensu* Tilman (1988). Ellenberg light values for abundant weed species are mostly 6 and 7, while those for less abundant species are mostly 7 and 8. Shade tolerance is especially important for short weed species in the period when they are overtopped by crop plants. Unlike the analyses of the British and Californian flora, where common species tended to be taller than rare species (Hegde & Ellstrand, 1999; Pilgrim *et al.*, 2004), our weed data exhibited the opposite tendency. The low-growing weeds were more abundant on arable land, probably because they more easily avoid the disturbances associated with crop harvest and agricultural management. If disturbed, short species may be able to regenerate more quickly than tall species. However, weeds with short stature growing in dense stands of crop plants must be shade tolerant.

Other important traits of regionally abundant weeds were their annual life span and therophytic life-form. Annuals and therophytes are a generally very common group of plants on arable land, because most agricultural crops are also annual, so the weeds follow the life cycle of the crop. Of the 381 weed species included in the present study, 51% were annuals, which is a considerably higher proportion than found in most other habitats of central Europe (Ellenberg, 1988).

Regional abundance related to geographical and habitat range

Besides biological traits and ecological characteristics, the regional abundance of weeds is also related to their large-scale distributional characteristics. Generally, regionally abundant weeds are those with larger, often circumpolar geographical ranges, which may extend across several latitudinal floristic zones. In contrast, less abundant weeds tend to have smaller, often European ranges. Abundant weeds also tend to be habitat generalists, occurring in several habitats beyond arable land. These patterns generally confirm the results of previous works, in which the local abundance of plant species was shown to be positively related to their regional range size (Thompson *et al.*, 1998; Brändle *et al.*, 2003b; Pocock *et al.*, 2006) or their habitat range (Thompson *et al.*, 1998; Kühn *et al.*, 2004). In such relationships, however, it is difficult to separate the cause and effect, because processes operating at the smaller scale can affect the patterns at the larger scale and vice versa.

Explanations of regional species abundance through the pattern of habitat utilization are usually based on either the 'resource availability hypothesis' or the 'niche breadth hypothesis' (Brown, 1984; Hanski *et al.*, 1993; Thompson *et al.*, 1998). The former suggests that species are abundant because the resources they use are common across the landscapes. The latter hypothesis, which is an alternative in some cases but often complementary to the former, suggests that some species are abundant because they are able to use a broader spectrum of resources than other species, i.e. to grow in a broader range of different habitats. Arable land is a rather uniform habitat that occurs over large areas, so it seems that most of its

© 2007 The Authors. Journal compilation © 2007 Blackwell Publishing Ltd

common species are those best adapted to it by their biological traits and ecological characteristics. This explanation would be consistent with the 'resource availability hypothesis'. At the same time, however, abundant species of arable land are those that are found in a broad range of other habitats, and this pattern is consistent with the 'niche breadth hypothesis'. Species pool effects (Taylor *et al.*, 1990; Zobel, 1992; Pärtel *et al.*, 1996) are likely to play a role here. Species occurring in more habitats are more common in the surrounding landscape, thus they may spread more easily to arable land. Gabriel *et al.* (2005) provided evidence for such processes, showing that weed communities can be more species-rich on those arable fields that are situated in a diverse landscape with more habitat types. However, the opposite process is also possible: abundant species of arable land may spread to the surrounding habitats. Since arable land is a widespread component of the central European landscape, this spread may affect many different habitats. Thus the broader habitat range of the common weed species may be a consequence rather than cause of their abundance within this single widespread habitat.

It is interesting that the history of the regional spread of species in the study area, expressed through their status as native, archaeophyte or neophyte, is only weakly related to the abundance of weed species on central European arable land. Although arable land contains most alien species of all central European habitats (Chytrý *et al.*, 2005), this pattern indicates that common and rare species are represented in similar proportions in the group of native plants and both groups of aliens. This suggests that frequent native and alien species probably share the same attributes (Thompson *et al.*, 1995).

CONCLUSIONS

Our analysis demonstrated that the regional abundance of weed species on central European arable land is related to some of their biological traits and ecological and distributional characteristics. Some of the attributes of abundant weeds identified in this study may differ from attributes identified in studies performed in other habitats or across different habitats, because abundant weeds of arable land should share, to some extent, the characteristics of an 'ideal weed' (Baker, 1965) rather than attributes of common species in general. However, habitat-specific studies of the determinants of species regional abundance, such as this one, are of considerable importance for the development of a deeper understanding of the patterns of commonness and rarity.

ACKNOWLEDGEMENTS

Our thanks are due to Jens-Christian Svenning and anonymous referees for their helpful comments on the previous version of the manuscript. This project was funded from grants MSM 0021622416 from the Ministry of Education of the Czech Republic, 206/05/0200 from the Czech Science Foundation, and Integrated Project 'ALARM: Assessing LArge scale environmental Risks with tested Methods' (GOCE-CT-2003-506675) from the European Commission within Framework Programme 6 (Settele *et al.*, 2005).

REFERENCES

Andersson, T.N. & Milberg, P. (1998) Weed flora and the relative importance of site, crop, crop rotation, and nitrogen. *Weed Science*, **46,** 30–38.

Andreasen, C., Stryhn, H. & Streibig, J.C. (1996) Decline of the flora in Danish arable fields. *Journal of Applied Ecology*, **33,** 619–626.

Baker, H.G. (1965) Characteristics and modes of origin of weeds. *The genetics of colonizing species* (ed. by H.G. Baker and G.L. Stebbins), pp. 147–172. Academic Press, New York.

Brändle, M., Stadler, J., Klotz, S. & Brandl, R. (2003a) Distributional range size of weedy plant species is correlated to germination patterns. *Ecology*, **84,** 136–144.

Brändle, M., Durka, W., Krug, H. & Brandl, R. (2003b) The assembly of local communities: plants and birds in non-reclaimed mining sites. *Ecography*, **26,** 652–660.

Breiman, L., Friedman, J.H., Olshen, R.A. & Stone, C.G. (1984) *Classification and regression trees*. Wadsworth International Group, Belmont, CA.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *The American Naturalist*, **124,** 255–279.

Cadotte, M.W. & Lovett-Doust, J. (2002) Ecological and taxonomic differences between rare and common plants of southwestern Ontario. *Ecoscience*, **9,** 397–406.

di Castri, F. (1989) History of biological invasions with special emphasis on the Old World. *Biological invasions: a global perspective* (ed. by J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson), pp. 1–30. John Wiley and Sons, Chichester.

Chytrý, M. & Rafajová, M. (2003) Czech National Phytosociological Database: basic statistics of the available vegetation-plot data. *Preslia*, **75,** 1–15.

Chytrý, M., Pyšek, P., Tichý, L., Knollová, I. & Danihelka, J. (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia*, **77,** 339–354.

Dale, M.R.T, Thomas, A.G. & John, E.A. (1992) Environmental factors including management practices as correlates of weed community composition in spring seeded crops. *Canadian Journal of Botany*, **70,** 1931–1939.

Davies, C.E. & Moss, D. (2003) *EUNIS habitat classification, August 2003*. European Topic Centre on Nature Protection and Biodiversity, Paris.

De'ath, G. & Fabricius, K.E. (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology*, **81,** 3178–3192.

Diniz-Filho, J.A.F., De Sant'ana, C.E.R. & Bini, L.M. (1998) An eigenvector method for estimating phylogenetic inertia. *Evolution*, **52,** 1247–1262.

Ellenberg, H. (1988) *Vegetation ecology of central Europe*, 4th edn. Cambridge University Press, Cambridge.

© 2007 The Authors. Journal compilation © 2007 Blackwell Publishing Ltd

Ellenberg, H., Weber, H.E., Düll, R., Wirth, W., Werner, W. & Paulißen, D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa, 2nd edn. *Scripta Geobotanica*, **18,** 1–258.

Frank, D. & Klotz, S. (1990) Biologisch-ökologische Daten zur Flora der DDR, 2nd edn. *Wissenschaftliche Beiträge der Martin-Luther-Universität Halle-Wittenberg*, **32,** 1–167.

Gabriel, D., Thies, C. & Tscharntke, T. (2005) Local diversity of arable weeds increases with landscape complexity. *Perspectives in Plant Ecology, Evolution and Systematics*, **7,** 85–93.

Glemnitz, M., Czimber, G., Radics, L. & Hoffmann, J. (2000) Weed flora composition along a north-south climate gradient in Europe. *Acta Agronómica Óváriensis*, **42,** 155–169.

Grime, J.P. (1979) *Plant strategies and vegetation processes*. John Wiley, Chichester.

Hallgren, E., Palmer, M.W. & Milberg, P. (1999) Data diving with cross-validation: an investigation of broad-scale gradients in Swedish weed communities. *Journal of Ecology*, **87,** 1037–1051.

Hanski, I., Kouki, J. & Halkka, A. (1993) Three explanations of the positive relationship between distribution and abundance of species. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R. Ricklefs and D. Schluter), pp. 108–116. University of Chicago Press, Chicago.

Harvey, P.H. & Pagel, M.D. (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

Hegde, S.G. & Ellstrand, N.C. (1999) Life history differences between rare and common flowering plant species of California and the British Isles. *International Journal of Plant Sciences*, **160,** 1083–1091.

Hilbig, W. (1987) Changes in segetal vegetation under conditions of industrialized agriculture. *Archiv für Naturschutz und Landschaftsforschung*, **27,** 229–249.

Holzner, W. (1978) Weed species and weed communities. *Vegetatio*, **38,** 13–20.

Holzner, W. (1982) Concepts, categories and characteristics of weeds. *Biology and ecology of weeds* (ed. by W. Holzner and N. Numata), pp. 3–20. Dr W. Junk Publishers, The Hague.

Hyvönen, T., Ketoja, E., Salonen, J., Jalli, H. & Tiainen, J. (2003) Weed species diversity and community composition in organic and conventional cropping of spring cereals. *Agriculture, Ecosystems and Environment*, **97,** 131–149.

Hyvönen, T. & Salonen, J. (2002) Weed species diversity and community composition in cropping practices at two intensity levels – a six-year experiment. *Plant Ecology*, **159,** 73–81.

Kelly, C.K. (1996) Identifying plant functional types using floristic data bases: Ecological correlates of plant range size. *Journal of Vegetation Science*, **7,** 417–424.

Klotz, S., Kühn, I. & Durka, W. (2002) BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde*, **38,** 1–334.

Knollová, I., Chytrý, M., Tichý, L. & Hájek, O. (2005) Stratified resampling of phytosociological databases: some strategies for obtaining more representative data sets for classification studies. *Journal of Vegetation Science*, **16,** 479–486.

Kolb, A., Barsch, F. & Diekmann, M. (2006) Determinants of local abundance and range size in forest vascular plants. *Global Ecology and Biogeography*, **15,** 237–247.

Kornaś, J. (1988) Speirochore Ackerwildkräuter: von ökologischer Spezialisierung zum Aussterben. *Flora*, **180,** 83–91.

Kubát, K., Hrouda, L., Chrtek, J. jun., Kaplan, Z., Kirschner, J. and Štěpánek, J. (eds) (2002) *Key to the flora of the Czech Republic*. Academia, Prague (in Czech).

Kühn, I., Brandenburg, M. & Klotz, S. (2004) Why do alien plant species that reproduce in natural habitats occur more frequently? *Diversity and Distributions*, **10,** 417–425.

Kunin, W.E. and Gaston, K.J. (eds) (1997) *The biology of rarity: causes and consequences of rare–common differences*. Chapman and Hall, London.

Lahti, T., Kemppainen, E., Kurtto, A. & Uotila, P. (1991) Distribution and biological characteristics of threatened vascular plants in Finland. *Biological Conservation*, **55,** 299–314.

Lloret, F., Médail, F., Brundu, G., Camarda, I., Moragues, E., Rita, J., Lambdon, P. & Hulme, P.E. (2005) Species attributes and invasion success by alien plants on Mediterranean islands. *Journal of Ecology*, **93,** 512–520.

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 in diversity and species composition. *Journal of Vegetation Science*, **15,** 415–422.

Lososová, Z., Chytrý, M., Kühn, I., Hájek, O., Horáková, V., Pyšek, P. & Tichý, L. (2006) Plant trait patterns in annual vegetation of Central European human-made habitats. *Perspectives in Plant Ecology, Evolution and Systematics*, **8,** 69–81.

Murray, B.R., Thrall, P.H. & Lepschi, B.J. (2002) Relating species rarity to life history in plants of eastern Australia. *Evolutionary Ecology Research*, **4,** 937–950.

Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, **75,** 111–117.

Pilgrim, E.S., Crawley, M.J. & Dolphin, K. (2004) Patterns of rarity in the native British flora. *Biological Conservation*, **120,** 165–174.

Pinke, G. (2004) Letzte Vorkommen von *Caucalidion*-Arten im Nordwesten Ungarns. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz, Sonderheft*, **19,** 73–82.

Pocock, M.J.O, Hartley, S., Telfer, M.G., Preston, C.D. & Kunin, W.E. (2006) Ecological correlates of range structure in rare and scarce British plants. *Journal of Ecology*, **94,** 581–596.

Prinzing, A., Klotz, S. & Brandl, R. (2001) The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society, Series B: Biological Sciences*, **268,** 2383–2389.

© 2007 The Authors. Journal compilation © 2007 Blackwell Publishing Ltd

Pyšek, P. & Lepš, J. (1991) Response of a weed community to nitrogen fertilization: a multivariate analysis. *Journal of Vegetation Science*, **2,** 237–244.

Pyšek, P., Sádlo, J. & Mandák, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74,** 97–186.

Pyšek, P., Jarošík, V., Chytrý, M., Kropáč, Z., Tichý, L. & Wild, J. (2005) Alien plants in temperate weed communities: prehistoric and recent invaders occupy different habitats. *Ecology*, **86,** 772–785.

R Development Core Team (2006) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Settele, J., Hammen, V., Hulme, P., Karlson, U., Klotz, S., Kotarac, M., Kunin, W., Marion, G., O'Connor, M., Petanidou, T., Peterson, K., Potts, S., Pritchard, H., Pyšek, P., Rounsevell, M., Spangenberg, J., Steffan-Dewenter, I., Sykes, M., Vighi, M., Zobel, M. & Kühn, I. (2005) ALARM – Assessing LArge-scale environmental Risks for biodiversity with tested Methods. *Gaia*, **14,** 69–72.

Skalický, V. (1988) Regional phytogeographical division. *Flora of the Czech Socialistic Republic*, Vol. 1 (ed. by S. Hejný and B. Slavík), pp. 103–121. Academia, Prague (in Czech).

Sutcliffe, O.L. & Kay, Q.O.N. (2000) Changes in the arable flora of central southern England since the 1960s. *Biological Conservation*, **93,** 1–8.

Taylor, D.R., Aarssen, L.W. & Loehle, C. (1990) On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos*, **58,** 239–250.

Thompson, K., Hodgson, J.G. & Rich, T.C.G. (1995) Native and alien invasive plants: more of the same? *Ecography*, **18,** 390–402.

Thompson, K., Hodgson, J.G. & Gaston, K.J. (1998) Abundance-range size relationships in the herbaceous flora of central England. *Journal of Ecology*, **86,** 439–448.

Tichý, L. (2002) JUICE, software for vegetation classification. *Journal of Vegetation Science*, **13,** 451–453.

Tilman, D. (1988) *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ.

Trzcińska-Tacik, H. (1991) Changes in the corn-weed communities in the Małopolska Upland (S. Poland) from 1947 to 1988. *Veröffentlichungen des Geobotanischen Institutes, Stiftung Rübel*, **106,** 232–256.

Tyšer, L. & Holec, J. (2004) Evaluation of the weed composition of agrophytocenoses in selected agricultural regions of the Czech Republic. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz, Sonderheft*, **19,** 209–214.

Zobel, M. (1992) Plant species coexistence – the role of historical, evolutionary and ecological factors. *Oikos*, **65,** 314–320.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Functions to transform species phylogenies into a patristic distance matrix, written for R (http://www.r-project.org/).

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01778.x

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

BIOSKETCHES

Zdeňka Lososová is a lecturer in botany at Masaryk University, Brno, Czech Republic. Her research focuses on the vegetation ecology of human-made habitats.

Milan Chytrý is an associate professor of botany at Masaryk University, Brno, Czech Republic. His research interests are in vegetation ecology, methods of vegetation analysis and macroecological patterns in multispecies assemblages of vascular plants.

Ingolf Kühn is a senior scientist at the UFZ - Helmholz Centre for Environmental Research, Halle, Germany. His research deals with plant invasions and plant traits and their relevance for patterns of diversity and distribution on a macroecological scale.

Editor: Jens-Christian Svenning

© 2007 The Authors. Journal compilation © 2007 Blackwell Publishing Ltd