Patterns of plant traits in annual vegetation of man-made habitats in central Europe

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Abstract

Man-made habitats in central Europe can be broadly divided into arable land with weed vegetation, and settlements and their surroundings, harbouring ruderal vegetation. The former is a predictable environment with frequent, regular and large-scale disturbances, while the latter is an unpredictable environment with irregular disturbances of varying spatial extent producing heterogeneous mosaics of different successional stages. We hypothesize that these differences in disturbance regimes select for different sets of biological and ecological plant traits in these two habitats. A data set of 2715 vegetation plots sampled in man-made habitats dominated by annual plants in the Czech Republic was combined with data on biological and ecological traits of vascular plants, mostly taken from the BiolFlor database. Differences due to temporal variation and location of plots in different climatic zones were partialled out using partial canonical correspondence analysis. Then the differences in traits of the plants growing on arable fields and in settlements were analysed using logistic and least-square regression models, both with and without phylogenetic correction. Plants growing on arable land were more often annuals, R-strategists, with overwintering green leaves, insect or self-pollinated, reproducing by seeds, with persistent seed banks and archaeophytes (i.e. those aliens that arrived prior to 1500). Plants growing in human settlements were more often biennials or perennials, C-strategists, wind-pollinated, flowering in mid summer, reproducing both by seeds and vegetatively, dispersed by wind or humans, neophytes (i.e. those aliens that arrived after 1500), species with high demands for light and nutrients and with more continental distribution ranges. Most associations between plant traits and habitats did not change after taking phylogenetic relationships into account. Traits strongly linked to phylogeny were especially modes of pollination and dispersal. By contrast, traits weakly linked to phylogeny included life strategy and alien status.

Keywords: Arable field; Disturbance; Phylogeny; Ruderal vegetation; Weeds

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Introduction

Man-made habitats have been a widespread component of the central European landscape for several millenia. Human activities influence vegetation by altering the environment, disturbance and facilitating the immigration of alien species (Gilbert, 1989). There are two broad types of annual vegetation growing in man-made habitats in central Europe: *weed vegetation* on arable land and *ruderal vegetation* in cities, towns, villages and industrial areas, on waste deposits, along roads and railways and in similar habitats (Holzner, 1982; Sukopp and Werner, 1983; Lososová, 2004; Lososová et al., 2004). Specific disturbance dynamics in each of these two habitat types provide a unique opportunity for the analysis of the link between large-scale disturbance regimes and the structure of plant communities.

Weed vegetation growing on arable land is subject to disturbances which are uniform over large areas and occur rather regularly, depending on the agricultural management of the crop. Instead of creating patchy mosaics consisting of successional communities of different ages, such disturbances tend to produce uniform landscapes, which provide few niches for the survival of species of later successional stages or species whose life cycles differ from those of the crop plants. This uniformity is further magnified by the large-scale homogenization of the competitive effects, which are imposed on weeds by the monodominant stands of crops. In contrast, ruderal vegetation growing in human settlements and similar habitats experiences irregular, unpredictable disturbances of varying extent, which create landscape mosaics of different successional stages (Pickett and White, 1985; Glenn-Lewin et al., 1992). We hypothesize that the disturbance regime in human settlements selects for plants with better ability of colonizing distant habitat patches and those adapted to survive in mid-successional stages. Macroecological comparison of a large number of species across a large number of sites on arable land and in human settlements may reveal the differences between predictable environments with regular large-scale disturbances and unpredictable environments with irregular small-scale disturbances.

Arable weed vegetation in central Europe is mainly composed of annual plants, which have the fastest post-disturbance regeneration, whereas ruderal habitats support vegetation types with predominance of either annuals (in the early successional stages) or perennials (in the mid-successional stages) (Ellenberg, 1988; Wittig, 2002). This paper does not include ruderal vegetation dominated by perennials, but focuses on the analysis of the vegetation types occurring in early successional stages dominated by annuals. It is likely that the structure of the highly dynamic annual vegetation mainly reflects current habitat qualities. Furthermore, the focus on the annual vegetation makes plant communities more comparable between the two habitats. An analysis based on annual-dominated vegetation is likely to reveal differences in plant traits attributable to the habitat distinctiveness, but not differences in successional age or large structural differences in vegetation.

Ecological distinctiveness of arable land and ruderal sites results in differences in the species composition of these two habitats, which are well documented in many phytosociological studies from central Europe (Mucina et al., 1993; Jarolímek et al., 1997; Wittig, 2002). Environmental filters imposed by different disturbance regimes and other abiotic or biotic factors are likely to select not only for specific groups of species, but also for specific plant traits or plant functional types (Sousa, 1980; McIntyre et al., 1995; Lavorel et al., 1997). However, such more general patterns of plant community structure in the man-made habitats are still insufficiently known.

Recent compilations of large databases of vegetation plot samples ('phytosociological relevés') (Ewald, 2001; Hennekens and Schaminée, 2001) and plant traits (e.g. Klotz et al., 2002) have facilitated analyses of plant trait patterns across different habitats (Ozinga et al., 2004b). In the present paper, large data sets of vegetation plots and plant traits are combined to assess the differences in plant traits between the two major types of man-made habitats in central Europe. This analysis is done by simultaneously using several traits, in order to reveal the association between different habitats, contrasting disturbance regimes and functional structure of plant communities.

Materials and methods

Vegetation plot data set

We compiled a data set of 4216 plot records of annual anthropogenic vegetation from the Czech Republic, taken from the Czech National Phytosociological Database (Chytrý and Rafajová, 2003). Plots were recorded between 1954 and 2003. They were selected on the basis of the assignment by the original authors to the vegetation classes Chenopodietea or Secalietea, which include anthropogenic vegetation of human settlements or arable land, dominated by annual weeds (Moravec et al., 1995). From this data set, we first eliminated plots lacking indication of accurate location and date of sampling. Then we deleted plots larger than $100\,m^2$, which may have been internally heterogeneous. By using the outlier analysis in the PC-ORD 4 program (McCune and Mefford, 1999), based on calculations of

the relative Euclidean (chord) distances between all pairs of plots, we detected and removed plots with deviating floristic composition. Plots deviating by more than two standard deviation units from the average were deleted. After these procedures, the data set consisted of 2715 plots (1009 plots from cereal fields, 889 from root-crop fields, 401 from villages, 416 from towns).

For each plot we compiled a set of variables supposed to affect species composition of plant communities. Altitude, mean annual rainfall and mean annual temperature were obtained by using overlays of plot locations using a digital elevation model and climatic maps, based on Vesecký et al. (1958), in the ArcGIS 8.3 program (www.esri.com). Crops were deleted from the species lists, classified into two simplified categories of cereals and root crops (see Lososová et al., 2004 for details) and used as explanatory variables. Records from human settlements were classified according to number of inhabitants as a village (less than 1000) or a town (more than 1000). In this way, we established the categorical variable habitat, with four categories: cereal field, root-crop field, village and town. Other explanatory variables were year of the record, accounting for vegetation change over the past decades, and season, accounting for phenological changes during the growing season. The time in the season was derived from the date of the record and defined on an ordinal scale as the number of periods of 2 weeks from the beginning of the year (see Lososová et al., 2004).

We deleted all records of bryophytes, because they were not consistently recorded in all plots. A few plants determined only at the genus level were not considered. All species only recorded once in the data set were deleted in order to eliminate noise. This procedure yielded a list of 487 species. Nomenclature of species follows Kubát et al. (2002). Species cover values, estimated at different ordinal scales, were converted to the mean percentage value for each degree of the scale and then transformed by taking the square root.

For the analysis we used both the entire data set of 2715 plots × 487 species and its two subsets, including plots from arable fields and human settlements.

Species traits

Species were characterized by their basic traits (e.g. modes of pollination or dispersal) as well as composite traits (such as CSR strategy) and other characteristics (e.g. Ellenberg indicator value or residence time of alien species in the invaded area). All of these categories are hereafter called 'traits' in this paper. Information on species traits was taken mainly from the BiolFlor database (Klotz et al., 2002). Data on the persistence of the seed bank were obtained from Thompson et al. (1997) and those on dispersal from Frank and Klotz

(1990). Alien species were classified according to Pyšek et al. (2002). Ellenberg indicator values (Ellenberg et al., 1992) were assigned to each species. Not all trait data were available for each species. Some species were assigned to more than one trait of a set of multistate categorical traits.

For each species, the following traits were used:

(a) Life span, with four categories: annual, biennial, monocarpic perennials (or pluriennial hapaxanthic plants, i.e. those with one seed set per life time) and polycarpic perennials (or pluriennial pollacanthic plants, i.e. those with several seed sets in their life time) (Krumbiegel in Klotz et al., 2002, pp. 93–118).

(b) 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).

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

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

(e) Pollen vector, with six categories: wind, insect, selfing, cleistogamy, pseudocleistogamy and geitonogamy (Durka in Klotz et al., 2002, pp. 133–175).

(f) Type of reproduction, with three categories: species reproducing only or mostly by seeds; species reproducing by seeds and vegetatively; species reproducing mostly or only vegetatively (Durka in Klotz et al., 2002, pp. 133–175).

(g) Seed bank type, with three categories (Thompson et al., 1997): transient seed bank with seeds that persist in the soil for less than one year; short-term persistent seed bank with seeds that persist in the soil for at least 1 year, but less than 5 years; persistent seed bank with seeds that persist in the soil for at least 5 years.

(h) Dispersal mode, with seven categories: anemochory (wind dispersal), myrmecochory (ant dispersal), epizoochory (external dispersal by animals), hydrochory (water dispersal), anthropochory (human dispersal), autochory (self dispersal) and endozoochory (dispersal via an animal's digestive system) (Frank and Klotz, 1990).

(i) Residence time of alien species, with two categories according to Pyšek et al. (2002): archaeophytes, which appeared in the study area before 1500, many of them as early as the advent of neolithic agriculture; neophytes, which appeared after 1500 (see Pyšek et al., 2004a for definitions).

(j) Indicator values (Ellenberg et al., 1992) for six environmental variables: light, temperature, continentality, moisture, soil reaction and nutrients, measured on a 9-degree (or 12-degree for moisture) ordinal scale.

Species ordinations

To characterize the general pattern of variation in species composition within the entire data set of vegetation plots we used an indirect ordination method, detrended correspondence analysis (DCA), from CA-NOCO 4.5 package (ter Braak and Šmilauer, 2002). As this analysis revealed a long gradient on the first axis (5.17 SD units), we used ordination methods based on the weighted averaging algorithm, which are more suitable for data showing predominantly a unimodal response of species to the environment, namely DCA and canonical correspondence analysis (CCA; ter Braak and Šmilauer, 2002). The effect of each variable on species composition was tested using a canonical correspondence analysis and Monte Carlo test with 999 permutations. To visualize the effects of explanatory variables, DCA was performed and explanatory variables, including categories of the habitat variable, were passively projected onto the ordination plot.

In order to rank species according to their affinity for individual habitats, unaffected by their correlations with other explanatory variables, we performed a partial CCA (pCCA; ter Braak and Šmilauer, 2002), with habitat as the single explanatory variable and all the other explanatory variables used as covariables. In this way, we partialled out the effects of the other explanatory variables on species composition. This analysis was performed, (1) for the entire data set, with settlement vs. arable field as the explanatory variable; (2) for the subset of plots from settlements, with village vs. town as the explanatory variable; (3) for the subset of plots from arable fields, with root crop vs. cereal as the explanatory variable.

Relating species traits to habitats

To identify the relationships between net effects of habitats and species traits, we used a method based on a combination of pCCA and logistic regression (Lososová et al., 2004). We used species scores on the first axis of the particular pCCA as the independent variable and presence/absence of a particular trait in each species as the dependent variable. To reduce noise, we used only species whose fit on the first pCCA axis was higher than the median. For each category of species traits and each data set or subset, we calculated a separate logistic regression. Relationships between Ellenberg indicator

values for species and their scores on the first pCCA axis were assessed using linear least-square regression. Ellenberg values are on an ordinal scale, but with a sample size of more than 100 species they tend to behave like continuous variables (ter Braak and Barendregt, 1986). Therefore, they are widely used in linear models as if continuous (Thompson et al., 1993; Ertsen et al., 1998; Schaffers and Sýkora, 2000; Prinzing et al., 2001, 2002; Ozinga et al., 2004a).

Phylogenetic corrections

Some of the relationships between species traits and habitats can result from the fact that phylogenetically related species often share the same traits and tend to be confined to the same habitats due to their common evolutionary history (Harvey and Pagel, 1991). Therefore, we used the method published by Desdevises et al. (2003) to separate the effect of habitat from that of phylogenetic relatedness among species on the patterns of species traits. This method enabled partialling out the effects of phylogeny and partitioning of the deviance in plant traits into components affected by either habitat or phylogeny. Species phylogeny available in the BiolFlor database (Durka in Klotz et al., 2002, pp. 75–91) was used to calculate patristic distances based on the number of nodes $+1$ (i.e. all branch lengths are set to unity) among all species, separately within the entire data set and the two subsets. These distance matrices were used in classical (metric) multi-dimensional scaling (cMDS) procedures. Due to the structure of the data, the last 5–7 dimensions in cMDS yielded negative eigenvalues, so we only calculated the dimensions with positive eigenvalues. These calculations were done in R (R Development Core Team, 2004). The function to calculate patristic distance was written by us in R and cMDS was calculated with the function cmdscale( ) in package 'stats'.

Separately for each species trait, we calculated a multiple logistic regression in which species scores on the cMDS dimensions were used as independent variables and presence/absence of the target trait in each species as the dependent variable. Only a few cMDS dimensions with the highest eigenvalues, which cumulatively accounted for 85% of the total variation, were used in these regressions. Subsets of cMDS dimensions which best explained variation in the dependent variable were determined using the Akaike Information Criterion (AIC) as a measure of fit. For several reasons, we did not use the complete set of eigenvectors: (i) Phylogenetic large-scale trends and medium-scale autocorrelations are only represented in the first few cMDS dimensions, whereas the many higher dimensions incorporate information on species-specific traits unrelated to phylogenetic trends, i.e. noise.

(ii) Variation explained tends to increase with the number of explanatory variables. Including too many eigenvectors as phylogenetic variables would therefore unduly bias the results. (iii) Too many explanatory variables may more easily corrupt model simplification procedures (e.g. stopping at local instead of global minima of AIC). Model simplification by using AIC instead of significance tests of the explanatory variables avoids the problem of multiple testing and hence inflated type I errors during model simplification. Where Ellenberg indicator values were used as independent variables instead of categorical plant traits, the same procedure was used but an ordinary least-square linear regression was applied instead of logistic regression.

We tested whether 47 traits differed significantly among the chosen habitat pairs. There is, therefore, a danger that these many tests will inflate the probability of type I errors, i.e. of reporting false significant results. Therefore, it is often recommended that one corrects for multiple testing, e.g. by using the sequential Bonferroni correction (Rice, 1989). However, it is not clear whether this correction is needed when (i) the same data set is analysed repeatedly, or (ii) the same hypothesis is analysed repeatedly, or (iii) in all the tests calculated in the same paper, or, as an extreme, (iv) for all tests performed in a scientist's life-time (Cabin and Mitchell, 2000; Moran, 2003). The boundaries between at least options (i) through (iii) can be uncertain and the choice is always subjective (Cabin and Mitchell, 2000). Furthermore, there are good reasons for rejecting the use of sequential Bonferroni correction in ecological studies for mathematical, logical and practical reasons (see Moran, 2003 for details). Therefore, we accept, present and discuss all significant results prior to correction. However, to allow the reader to compare the results, we additionally adjust P-values by the sequential Bonferroni corrections (Holm, 1979; Rice, 1989) and present them in the tables.

For each plant trait, species scores for a particular subset of cMDS dimensions, representing the effect of phylogeny, and species scores on the first pCCA axis, representing the effect of habitat, were used as independent variables in a multiple logistic regression (or multiple linear regression for Ellenberg indicator values). These regressions made it possible to test the net effect of habitat on the pattern of species traits, after subtracting the effect of phylogeny. The variation in each trait was partitioned into the components affected by habitat, phylogeny and the shared effect of both. For each plant trait we calculated, following Desdevises et al. (2003), the variation explained (A) by phylogeny inclusive of the overlap with habitat (based on the regression with the subset of cMDS dimensions only), (B) by habitat inclusive of the overlap with phylogeny (based on the regression with the first pCCA axis only), (C) jointly by phylogeny and habitat (based on the

regression with both cMDS dimensions and the first pCCA axis). Then we calculated the net effect of phylogeny as $C-B$, the net effect of habitat as $C-A$ and the shared effect of phylogeny and habitat as $A+B-C$. We used the log-likelihood in logistic regressions with categorical traits and R^2 in linear regressions with Ellenberg indicator values as measures of explained variation. Regression analyses were calculated in STATISTICA version 7 (www.statsoft.com) and SPSS version 8 (www.spss.com).

Results

Detrended correspondence analysis (Fig. 1) revealed the importance of macroclimatic variables, seasonal changes, year of record and habitat type (field or settlement) on the species composition of annual vegetation in man-made habitats. Mean annual temperature, annual rainfall, altitude and habitat type (arable field vs. settlement) correlated with the first DCA axis. The differences between cereal and root crop fields or between villages and towns, respectively, were less important.
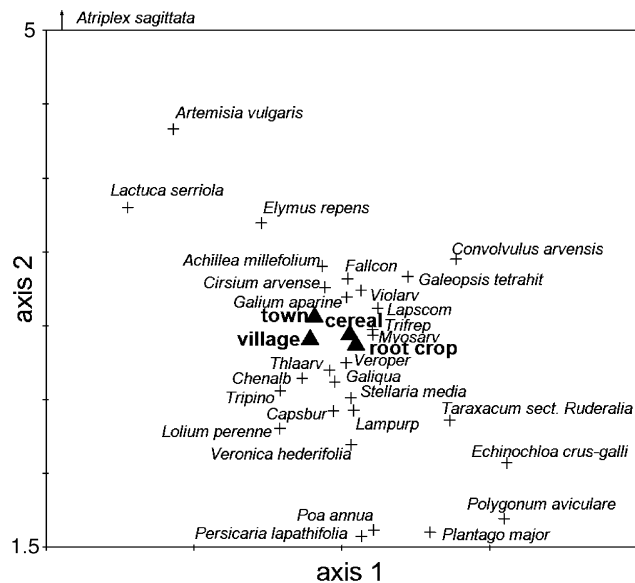
The difference between arable fields and settlements was the most important variable affecting species composition, based on the F statistic of Monte Carlo tests in canonical correspondence analysis. It was followed by mean annual rainfall, season, altitude, mean annual temperature and year. Climatic variables and altitude were strongly correlated with each other. The effects of each of these variables were significant at $P < 0.001$.
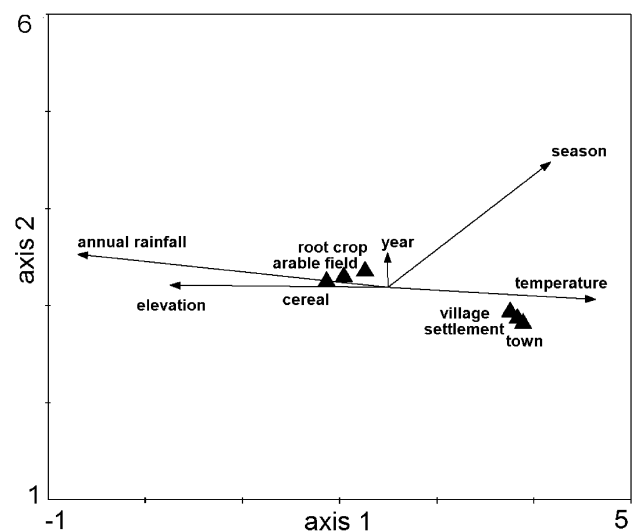
Fig. 1. Detrended correspondence analysis (DCA) diagram of annual vegetation of man-made habitats with passively projected explanatory variables. Eigenvalues: axis 1–0.533; axis 2–0.405.

Variation in species composition due to habitats, after subtracting the effects of the other variables, is shown in Fig. 2. The first axis represents the gradient between arable fields and settlements. Species typical of either arable fields or human settlements are shown in Table 1.

Differences in species traits between arable fields and settlements were significant for the majority of traits (Table 2). Comparing arable fields and settlements, plants with a negative value for the estimated regression coefficient are more common in fields and those with positive values in settlements. Plants growing in arable fields are often annuals, therophytes and R-strategists. Often they have overwintering green leaves. They are usually insect- or self-pollinated, reproduce by seeds and have a persistent soil seed bank. Species typical of settlements are more often biennials, polycarpic perennials or hemicryptophytes with a C-strategy. They are frequently pollinated by wind, reproduce by both seeds and vegetatively, and disperse by wind and man. They are heliophilous, nutrient-demanding and tend to have a more continental distribution than plants of arable fields. Archaeophytes are more common on arable land and neophytes in settlements. Proportions of variability explained by habitat type, phylogeny and the shared effect of both are shown in Table 2. Most of the results

Table 1. Twenty species with the highest fit in the partial CCA and their scores along the first ordination axis

Species	Ax 1 score	Fit
Hordeum murinum	1.281	0.029
Lepidium ruderale	1.277	0.035
Sisymbrium officinale	1.217	0.027
Atriplex sagittata	1.059	0.054
Ballota nigra	1.049	0.053
Urtica dioica	0.913	0.048
Poa pratensis	0.736	0.033
Artemisia vulgaris	0.647	0.055
Lolium perenne	0.577	0.049
Achillea millefolium agg.	0.306	0.031
Cirsium arvense	−0.303	0.043
Viola arvensis	−0.305	0.056
Fallopia convolvulus	−0.323	0.063
Sonchus arvensis	−0.414	0.034
Euphorbia helioscopia	−0.435	0.047
Anagallis arvensis	−0.565	0.107
Lamium amplexicaule	−0.624	0.034
Veronica polita	−0.733	0.043
Silene noctiflora	−0.744	0.053
Stachys annua	−1.081	0.035

The only explanatory variable is location of the plot either in a settlement or an arable field. Species with the highest positive and negative scores have the highest affinity to settlements and fields, respectively.

Fig. 2. Partial detrended correspondence analysis (pDCA) diagram of species with passively projected categorical variables indicating field or settlement habitats. Altitude, year, season, annual rainfall and mean annual temperature were used as covariables. Eigenvalues: axis 1—0.407, axis 2—0.379. Abbreviations: Capsbur, *Capsella bursa-pastoris*; Chenalb, *Chenopodium album*; Fallcon, *Fallopia convolvulus*; Galiqua, *Galinsoga quadriradiata*; Lampurp, *Lamium purpureum*; Lapscom, *Lapsana communis*; Myosarv, *Myosotis arvensis*; Thlaarv, *Thlaspi arvense*; Trifrep, *Trifolium repens*; Tripino, *Tripleurospermum inodorum*; Veroper, *Veronica persica*; Violarv, *Viola arvensis*.

remained remarkably constant after incorporating phylogenetic information. However, the positive association between hemicryptophytes and settlements was only significant after phylogenetic correction. By contrast, the positive relationship between insect pollination and settlements disappeared after phylogenetic correction. Some of the traits (e.g. types of pollination and dispersal mode) were strongly influenced by phylogeny. For example, phylogeny alone explained more than 50% of the variation in some pollination modes. Other traits (e.g. life strategy and residence time of alien species) were more related to habitat type than to phylogeny. However, the total variation in trait distribution explained by both habitat (arable land vs. settlement) and phylogeny did not exceed 22% except for insect pollination (60.6%), wind pollination (58.2%), anemochory (35.5%) and anthropochory (25.8%). The highest variations in plant traits explained by the pure effect of habitat were detected for life strategy and life span variables.

Differences in plant traits between cereal and root-crop fields were weak (Table 3). Most traits were not significantly associated with a particular crop type as defined in the present study. Species with a transient seed bank were more common in cereal fields, while species flowering in early spring, species with myrmecochorous dispersal (e.g. *Euphorbia peplus*, *Galinsoga quadriradiata*, *G. parviflora*, *Lamium purpureum*,

Table 2. Relationships between plant traits and settlement or arable field habitats, analysed by logistic regressions with categorical plant traits as dependent variables and linear least-square regressions with Ellenberg indicator values as dependent variables

Species traits	Settlement affinity			Settlement affinity corrected for phylogenetic relationships			Percentage variation explained by		
	Estimate	P	P adjusted	Estimate	P	P adjusted	Habitat only	phylogeny only	shared effect
Life span									
Annual (137)	−0.681	<0.001	0.002	−0.836	<0.001	<0.001	12.2	10.4	−2.3
Biennial (33)	0.666	0.005	n.s.	0.679	0.007	n.s.	5.3	13.4	1.1
Polycarpic perennials (86)	0.551	0.001	0.04	0.632	0.001	0.02	7.3	9.3	−0.8
Life form									
Hemicryptophyte (157)	—	n.s.	n.s.	0.385	0.03	n.s.	2.2	10.4	−0.2
Therophyte (131)	−0.636	<0.001	0.005	−0.707	<0.001	0.002	9.7	6.5	−0.9
Life strategy									
C (54)	0.861	<0.001	0.001	1.007	<0.001	<0.001	14.2	9.6	−1.9
CR (66)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
CSR (29)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
R (54)	−1.048	<0.001	<0.001	−0.981	<0.001	<0.001	13.8	1.3	3.2
Leaf persistence									
Summer green (127)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Overwintering green (60)	−0.488	0.008	n.s.	−0.478	0.009	n.s.	4.4	1.1	0.3
Persistent green (44)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Pollen vector									
Wind (51)	0.681	0.001	0.030	0.749	0.007	n.s.	3.2	50.2	4.8
Selfing (150)	−0.485	0.004	n.s.	−0.503	0.006	n.s.	4.1	13.5	1.0
Insect (173)	−0.481	0.01	n.s.	—	n.s.	n.s.	1.2	56.2	3.2
Reproduction									
Seed and vegetative (49)	0.592	0.003	n.s.	0.648	0.002	n.s.	6.6	6.6	−0.5
Seed (178)	−0.527	0.005	n.s.	−0.605	0.002	n.s.	5.8	10.0	−0.6
Seed bank type									
Transient (134)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Short-term persistent (135)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Persistent (124)	−0.659	0.02	n.s.	−0.686	0.01	n.s.	6.5	2.7	−0.1
Dispersal mode									
Anemochory (156)	0.611	<0.001	0.02	0.376	0.05	n.s.	1.9	22.8	5.8
Myrmecochory (50)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Epizoochory (113)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Hydrochory (29)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Anthropochory (20)	0.900	0.005	n.s.	0.759	0.003	n.s.	4.9	17	3.9
Autochory (54)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Alien status									
Archaeophyte (111)	−0.497	0.002	n.s.	−0.552	0.001	0.03	6.6	2.1	−0.9
Neophyte (23)	1.039	<0.001	0.030	1.047	<0.001	0.04	11.2	3.7	0.7
Ellenberg indicator value									
Light (225)	0.321	<0.001	0.002	0.289	<0.001	0.01	5.2	4.5	1.7
Temperature (192)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Continentality (189)	0.404	<0.001	0.03	0.357	0.003	n.s.	4.2	1.8	1.4
Moisture (209)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Soil reaction (154)	—	n.s.	n.s.	—	n.s.	n.s.	—	—	—
Nutrients (210)	0.764	<0.001	<0.001	0.744	<0.001	<0.001	10.7	8.4	1.0

Independent variables were (1) species scores on the first axis of pCCA, which increased with affinity for settlement habitats; (2) species scores on the first axis of pCCA and species phylogeny scores (scores on the dimensions from cMDS of patristic distances). Columns 'P adjusted' show significance values modified by sequential Bonferroni corrections. Explained variation is partitioned into the components due to net effect of habitat (settlement vs. field), net effect of phylogeny and shared effect of habitat and phylogeny. The following categorical traits that occurred in less than 20 species and were never significant are not shown: Life span: monocarpic perennial; Life forms: hydrophyte, chamaephyte, geophyte and phanerophyte; Life strategies: CS, SR and S; Leaf persistence: spring green; Pollen vector: cleistogamy, pseudocleistogamy and geitonogamy; Reproduction type: vegetative; Dispersal mode: endozoochory. Numbers of species that possess particular traits are given in parentheses after trait names. For Ellenberg indicator values, these indicate numbers of species for which the particular value was available.

Table 3. Relationships between plant traits and root-crop or cereal fields, analysed by logistic regressions with categorical plant traits as dependent variables and linear least-square regressions with Ellenberg indicator values as dependent variables

Species traits	Root crop affinity			Root crop affinity corrected for phylogenetic relationships			Percentage variation explained by		
	Estimate	P	P adjusted	Estimate	P	P adjusted	Habitat only	Phylogeny only	Shared effect
Flowering phase									
Pre-spring (20)	0.723	0.05	n.s.	—	n.s.	n.s.	8.6	15.6	0.4
Seed bank type									
Transient (130)	−1.281	0.02	n.s.	−1.285	0.02	n.s.	6.5	12.5	1.9
Dispersal mode									
Myrmecochory (22)	0.779	0.005	n.s.	0.813	0.02	n.s.	3.0	43.4	−3.4
Alien status									
Archaeophyte (77)	0.578	0.02	n.s.	0.562	0.03	n.s.	3.0	14.8	0.9
Ellenberg indicator value									
Light (194)	0.236	0.05	n.s.	—	n.s.	n.s.	1.7	6.8	0.3
Nutrients (158)	0.673	0.004	n.s.	0.609	0.006	n.s.	3.8	5.8	0.9

Independent variables were (1) species scores on the first axis of pCCA, which increased with affinity to root-crop habitats; (2) species scores on the first axis of pCCA and species phylogeny scores (scores on the dimensions from cMDS of patristic distances). Explained variation is partitioned into the components due to net effect of habitat (root crop vs. cereal), net effect of phylogeny and shared effect of habitat and phylogeny. The same set of traits was analysed as in Table 2, but the traits with non-significant relationships are not shown here. See Table 2 for further explanations.

Sonchus asper and *S. oleraceus*), archaeophytes, and heliophilous and nitrophilous species were more common in root crops. However, the relationship between crop type and pre-spring flowering phase and Ellenberg light value disappeared after applying a phylogenetic correction. In this comparison, phylogeny also explained more variation in plant traits than habitat (crop type in this case).

Differences between villages and towns were not significantly associated with any plant trait in spite of the fact that the ordination revealed differences in species composition between these two types of settlements. Species characteristic of villages include *Anthemis cotula*, *Papaver dubium* agg., *Urtica urens* and *Vicia sepium*, and of towns *Cerastium semidecandrum*, *Erysimum cheiranthoides*, *Poa pratensis* and *Tussilago farfara*.

Discussion

Despite the great variability and dynamics of annual vegetation in different man-made habitats, we found distinct patterns in species traits, which correspond to the dichotomy between arable weed and ruderal vegetation. We suggest that they also correspond to the dichotomy between the two disturbance regimes, the former with frequent and regular disturbances of large extent, and the latter with irregular and patchy disturbances. Patterns in some of the traits (e.g. alien status, life strategy, leaf persistence and seed bank type) are mainly explained by habitat properties rather than

phylogeny, suggesting that these traits evolved independently in several phylogenetic lineages. Some other traits (e.g. mode of pollination or dispersal) are more strongly related to phylogeny, i.e. their variation in man-made habitats can be explained to a large extent by niche conservatism (Prinzing et al., 2001). This means that the common ancestors of extant species already possessed particular traits and occupied similar habitats as their daughter species today (Harvey and Pagel, 1991; Harvey et al., 1995). It is evident that some traits are related to each other, even across different phylogenetic groups, which supports the concept of plant strategies (Grime, 2001) and plant functional classifications (Lavorel et al., 1997). For example, annual species are more often selfers, reproduce by seeds and form persistent seed banks. These plants are more often classified as R-strategists. By contrast, polycarpic perennials (usually hemicryptophytes) are usually characterized by a C, R or CRS strategy.

Life span, life form, leaf persistence and life strategy

Patterns in most traits related to life span and life form are roughly equally well explained by phylogenetic relatedness and habitat affinities independent of phylogeny. Annual species tend to be more represented in arable fields, while in human settlements their proportion is reduced at the expense of species with longer life spans – biennials and perennials. This pattern accords with the analysis of Hill et al. (2002), who found many perennials among the species with the highest affinity to

British urban habitats compared to non-urban sites. This trend was obvious in the current analysis in spite of the fact that the vegetation plot data set was selected to include vegetation dominated by annuals, both in arable fields and human settlements. Higher proportion of long-lived species in settlements reflects an existence of mosaics of successional stages of different age in ruderal habitats. While arable land is regularly disturbed at least twice every year due to agricultural management, human settlements contain both frequently disturbed sites and sites that are occasionally left undisturbed for several years. In the latter, vegetation has enough time to develop through early successional stages dominated by annuals to mid-successional stages with biennial and perennial herbs or even woody plants (Prach et al., 2001). Life strategies prevailing in weedy or ruderal vegetation are correlated with the pattern of life forms: settlement habitats, at least those with patches of older successional stages, favour competitors, i.e. mostly perennial plants, while arable fields support species with a ruderal strategy, i.e. mostly annuals (Grime, 2001; Booth et al., 2004). There is also some evidence that on a time scale of decades and centuries, increasing urbanization results in an increase in C-strategists in cities (Klotz and Gutte 1992; Chocholoušková and Pyšek, 2003), probably due to an increasing abundance of less frequently disturbed and nutrient-rich sites.

Overwintering green leaves were positively related to arable fields. They may be advantageous in this habitat due to the strongly decreased competition in winter, when the fields are either without crop plants or occupied by low and open stands of autumn-sown crops. This is similar to the observation of species with overwintering green leaves being more common in early successional vegetation where there is less competition (Ecke and Rydin, 2000).

Pollination mode

It is widely accepted that the proportion of different pollination modes in local floras and vegetation types forms distinct patterns (Regal, 1982; Culley et al., 2002; Kühn et al., 2006). The higher proportion of wind-pollinated species in settlements than in arable fields, revealed in our study, is strongly related to phylogeny. It correlates with a high proportion of Poaceae and Chenopodiaceae in settlement floras, but remains significant after partialling out the effect of phylogeny. Under-representation of wind-pollinated species in arable fields contrasts with the openness and windiness of agricultural landscapes. However, dense stands of crop plants may provide a more efficient wind protection for insect pollinators than open or fragmented stands of ruderal vegetation in human settlements. Besides the possible negative effects of wind on insect

pollinators, suitability of the habitats adjacent to arable land for insects and the resulting size of the pollinator species pool may also influence the pattern of pollination mode in man-made habitats. Arable fields are in more direct contact with grasslands, shrubberies or woodland edges and insects living there may serve as pollinators for arable weeds. By contrast, appropriate habitats for insect pollinators, in particular for the specialized ones, are largely missing in urban and polluted environments (Benvenuti, 2004), which means that wind-pollinated plant species are likely to be at a competitive advantage. This interpretation is consistent with succession studies. They document that newly created habitats are more easily colonized by plants that do not depend on mutualistic relationships with other organisms, such as insect pollinators (Whittaker et al., 1989; Prach and Pyšek, 1999; Ecke and Rydin, 2000; Culley et al., 2002). This pattern could result in an expectation that self-pollination will also be more favoured in settlements than in arable fields, but the opposite was true in the current analysis. This is probably due to the fact that selfers are generally over-represented among annual plants (Aarssen, 2000), and annuals are more frequent on arable land than in settlements.

Regeneration traits: reproduction type, seed bank and dispersal mode

Our analysis shows that species of arable land reproduce by seeds and form persistent seed banks more often than species of human settlements. Forming a persistent seed bank is a common strategy in predictable environments, including arable fields (Bakker et al., 1996; Baskin and Baskin, 1998; Thompson et al., 1998). By contrast, persistent seed banks provide fewer benefits in the less predictable ruderal habitats of human settlements. The high number of species with persistent seed banks occurring in arable fields may partly reflect recent changes in agricultural management. Modern seed cleaning techniques resulted in a decline in the number of weed species with the transient seed bank (e.g. *Agrostemma githago* or *Melampyrum arvense*), formerly sown along with crops (Firbank, 1990; Bakker et al., 1996). Also, a transient seed bank is typical of weed species of cereal fields but not of those that prefer root crops, as confirmed in our comparison of cereal and root-crop fields.

Two trends can be observed in ruderal habitats of human settlements. First, they harbour more species reproducing vegetatively, which is advantageous for long-term persistence in undisturbed or moderately disturbed sites (Noble and Slatyer, 1980; McIntyre et al., 1995). Such species are uncommon on arable land, where they are excluded by more frequent

disturbances. Second, ruderal habitats harbour more species adapted to dispersal by man and wind. The over-representation of anthropochory is not surprising, but the relationship between wind dispersal and human settlements is less straightforward, given that arable land is usually more exposed to wind. However, most weed species are usually overtopped by the canopy of planted crops, which can limit the efficiency of wind dispersal (Tackenberg et al., 2003; Ozinga et al., 2004a). Anemochory is considered to be an adaptation for the colonization of pioneer sites (Bakker et al., 1996; Prach and Pyšek, 1999). It enables dispersal over greater distances, which seems to be an advantage in the dynamic environment of human settlements, where some ruderal habitats rapidly vanish due to urbanization or spontaneous succession, while others appear after disturbances in other, often quite distant places.

Residence time of invasive plants and traits

The pattern we found, i.e. a higher proportion of archaeophytes on arable land and of neophytes in human settlements, is weakly affected by phylogenetic relationships and consistent with a number of previous studies from western and central Europe (Kowarik, 1995; Hill et al., 2002; Chocholoušková and Pyšek, 2003; Deutschewitz et al., 2003; Kühn et al., 2003; Chytrý et al., 2005; Wania et al., 2006). This pattern is, to some extent, correlated with the observed pattern of life span and life strategies. Pyšek et al. (2003) found that in the Czech flora, annuals make up 57.8% of archaeophytes, significantly more than among neophytes (39.4%). By contrast, perennials (38.2%) and woody plants (14.1%) are more frequent among neophytes than archaeophytes. R- and R-combined life strategies are more represented in archaeophytes, while the pure C-strategy is more frequent in neophytes. However, representation of archaeophytes and neophytes may considerably vary also within arable habitats or within human settlements. On central European arable land, neophytes are more represented in root crops than in cereals (Lososová et al., 2004; Pyšek et al., 2005). Comparing the whole floras of human settlements, neophytes are more common in larger cities while archaeophytes form a considerable proportion of the flora of smaller towns or villages (Pyšek, 1998a, b). However, this trend was not confirmed in the present study that focused on the annual vegetation of man-made habitats.

Environmental affinities

Our analysis partialled out the effects of temporal variation and of large-scale environmental variables that are known to affect the species composition of annual vegetation in central European man-made habitats (Lososová et al., 2004). After that, we focused on the variation in other environmental variables between the two habitats of interest: arable land and human settlements. We used Ellenberg indicator values, which were recently shown to give biased estimates in comparisons across different phytosociological classes (Wamelink et al., 2002). This limitation, however, could not affect the results of our study because it was based on data from two closely related phytosociological classes, which are considered as a single class in most recent phytosociological overviews (e.g. Mucina et al., 1993; Jarolímek et al., 1997).

Habitats of arable land appear to be more shaded, poorer in nutrients and contain fewer continental species. To some extent, these habitat affinities are phylogenetically related among species, indicating phylogenetic niche conservatism (Prinzing et al., 2001). However, a larger part of the variation is independent of phylogeny. Lower indicator values for light on arable land reflect shading of the weed community by crop plants, which is less important in root than cereal crops (Lososová et al., 2004).

The weed community, especially in cereals, also consists of species with lower nutrient requirements, probably because a large part of the available nutrients is taken up by crop plants and exported from the ecosystem with the harvested crop. By contrast, habitats in human settlements are not deliberately fertilized, but nutrient input is high and depletion low. The same trends were found in the flora of the Czech city of Plzeň when compared with that of the close surroundings (Chocholoušková and Pyšek, 2003). The higher nutrient requirements of root-crop weeds than cereal weeds probably reflect the fact that agricultural management of root crops involves more disturbances during a season. Root-crop weeds must therefore more frequently re-establish their populations, which requires more nutrients.

Interestingly, no difference in indicator values for temperature between arable land and human settlements was found in the current study, so the effect of urban heat islands (Gilbert, 1989; Wittig, 2002) was not confirmed. This may be due to the fact that the data set contained, besides those from larger cities, also plots from smaller towns and villages, where the heating effect is not so profound. However, no difference in temperature indicator values was found in the comparison of plots from towns and villages either. Instead of increased temperature, we recorded an increased indicator value for continentality in settlements. In the study of the ruderal vegetation of the city of Plzeň (Pyšek et al., 2004b), the continentality values of the annual vegetation were the highest of all the types of ruderal vegetation, but these values have decreased during the past three decades.

Conclusions

The present study combined partial canonical correspondence analysis with logistic and ordinary regression models to reveal the relationships between plant traits and habitats. Partial CCA made it possible to separate the net effects of habitat type (arable land or human settlement) from those of other variables. Inclusion of the matrix of patristic distances between species enabled the quantification of the relative magnitude of the effects of phylogenetic relatedness and habitat. The differences between arable land and ruderal habitats with annual vegetation seem to be caused by a set of environmental filters, which select for several biological and ecological plant traits. Patterns found in most of the traits related to life history, plant morphology and regeneration may be explained by the different disturbance dynamics existing in these two habitats, but patterns in some other traits require specific explanations, unrelated to the disturbance regime.

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