ALIEN PLANTS IN TEMPERATE WEED COMMUNITIES: PREHISTORIC AND RECENT INVADERS OCCUPY DIFFERENT HABITATS

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Abstract.   Variables determining the number of native and alien plants on arable land in Central Europe are identified. Species richness of 698 samples of weed floras recorded in the Czech Republic in plots of a standard size of 100 m² in 1955–2000 was studied in relation to altitudinally based floristic region, soil type, type of cultivated crop, climatic variables, altitude, year of the record, crop cover and height, and human population density in the region. Vascular plant species were classified into native and alien, the latter divided in archaeophytes, introduced before AD 1500, and neophytes, introduced after this date. The use of minimal adequate models in the analysis of covariance allowed determination of the net effects of mutually correlated environmental variables. Models for particular species groups explained 33–48% of variation in species numbers and 27–51% in proportions; however, explanatory variables affected native species, archaeophytes, and neophytes differently. The number and proportion of neophytes increased in 1955–2000, whereas the number of native species and archaeophytes declined (in archaeophytes more slowly in the warm than in the moderate to cool altitudinal floristic region). In warm and dry regions and on dry soils, where most archaeophytes find optimum conditions, fewer native species are able to persist in weed communities than in colder and wetter regions. Archaeophytes respond like neophytes to some variables (climate, seasonal development of crop) and alternatively like native species to other variables (increasing agricultural intensification through time, human population density). Archaeophytes are common in old crops introduced with the beginning of agriculture (cereals), but are poorly represented in relatively recently introduced crops (rape, maize), where neophytes are most numerous. These patterns reflect the history of plant invasions in Central Europe. Neolithic agriculture, introduced from the Near East in the sixth millenium BC, brought archaeophytes with crops and, by creating intense and continuous propagule pressure and imposing new agricultural management, facilitated their invasion. By contrast, the crops introduced during the past five centuries and their specific agrotechnical management have supported spreading of other weed species, mainly invaders from overseas.

Key words: agricultural management; archaeophytes; biological invasions; Central Europe; climate; crop characteristics; exotic species; invasion history; Neolithic agriculture; neophytes; soil type.

INTRODUCTION

Studies on plant invasions address several fundamental topics, one of them being the identification of features that make some habitats more invasible than others (Crawley 1987, Williamson 1996). It long has been recognized that human-made (anthropogenic) habitats, especially in settlements, are prone to invasion by alien species, which is attributable to habitat heterogeneity, frequent and diverse disturbances, and intensive propagule pressure typical of this environment (Gilbert 1989, Kowarik 2003). Arable land, a human-made habitat with a high representation of alien species, is an environment with specific disturbance regimes. Arable fields are not only disturbed with varying frequency, intensity, and predictability; they also have been directly created by disturbances associated with agriculture since the Neolithic Age (Ellenberg 1950, 1988, Holzner and Immonen 1982, di Castri 1989). Such disturbances can be described in terms of crop management but are difficult to quantify, as they often are hidden behind the overwhelming effect of site conditions (Pyšek and Lepš 1991, Dale et al. 1992, Salonen 1993, Erviö et al. 1994, Andersson and Milberg 1998, Hallgren et al. 1999). Studies analyzing the determinants of weed species richness are rare (Stevenson et al. 1997, Kleijn and Verbeek 2000, Hyvönen and Salonen 2002), and hardly any have focused on detecting general patterns of alien species invasions.

In another paper, using the same data set (Pyšek et al. 2005), we detected regional patterns of overall plant

species richness in temperate weed communities, and determined the net effects of environmental variables that are mutually correlated. Numbers of weed species were significantly affected by altitudinal floristic regions and by the year of sampling. The differences in diversity of the weed flora were mainly attributable to management, and partly to crop-specific agricultural practices, as well as to general intensification of management of arable fields during the past decades. However, the species pool of weeds on Central European arable land consists of two groups of species, distinct with respect to their origin status (sensu Pyšek et al. 2004a), specifically whether they are native or alien to the region. Among the latter, two groups are traditionally distinguished in Central Europe. Archaeophytes were introduced between the beginning of Neolithic agriculture and the European discovery of America, while species introduced after that date are termed neophytes (Thellung 1905, Holub and Jirásek 1967, Pyšek et al. 2002a). The separation between natives and archaeophytes is sometimes difficult and relies on a combination of palaeobotanical, archaeological, ecological, and historical evidence (Preston et al. 2002, Pyšek et al. 2004a). Given their different history in the target region and suite of traits in which archaeophytes differ from native taxa (Klotz et al. 2002, Pyšek et al. 2003c, 2004b) it can be expected that their occurrence in weed vegetation of present-day arable fields may not be driven by the same factors (Lososová et al. 2004). The aim of the present paper is to assess putative differences in the environmental affinities of native species, archaeophytes, and neophytes.

We employ a large data set of vegetation plots and statistical analysis to determine the net effect of particular explanatory variables. The present paper attempts to answer the following questions: (1) What are the principal variables determining the number and cover of native species, archaeophytes, and neophytes on Central European arable land, and do they differ among these groups? (2) What were the historical dynamics of native, archaeophyte, and neophyte species on arable land over the second half of the 20th century?

The Data

We used a data set of 712 vegetation plots from the Czech Republic, a country that represents a suitable model for studies of diversity at a landscape scale because of its variable geology and climate (Neuhäuslová et al. 2001). The survey was made by Z. Kropáč in 1955–2000, from March to October, in plots of a standard size of 100 m^2. In particular fields, the sample plot was usually located where weed vegetation was best developed, most diverse, and not affected by recent herbicide use. Therefore sample plots can be biased toward higher species richness than found in average weed vegetation existing in the landscape (Chytrý 2001). However, as they were all sampled by a single researcher who used the same sampling strategy over

the whole study period, direct comparison of weed species richness and cover is possible within our data set.

Species cover in the field was estimated using a Domin 10-degree scale, which was transformed to percentages to provide input data for analyses (Westhoff and van der Maarel 1978). The sample plots are stored in the Czech National Phytosociological Database (Chytrý and Rafajová 2003: No. 342001–342781). We deleted 14 randomly selected plots from those localities where more than one plot was sampled, in order to avoid oversampling of some areas (Pyšek et al. 2005). The remaining 698 sample plots, used in the analyses, were distributed throughout the country (Pyšek et al. 2005). Records of cultivated crop plants were deleted from the species data set and crop type was used as an environmental variable.

Vascular plant species were classified into native and alien, the latter group further divided in archaeophytes and neophytes. The status of these species was taken from Pyšek et al. (2002b).

For each sample plot, the following variables were recorded: (1) number of native species (range 1–31), archaeophytes (4–39), and neophytes (0–6); (2) percentage of native species (4.3–78.8%), archaeophytes (18.2–95.7%), and neophytes (0.0–24.0%); (3) relative cover of native species (3–89%), archaeophytes (11–97%), and neophytes (0–47%), determined as the sum of covers of all species in each group compared with the sum of covers of all species recorded in the sample plot; (4) crop cover (0–90%); (5) crop height (0–270 cm); (6) crop type, with the following eight categories, representing also a specific type of management: cereals 377 sample plots (following crops were distinguished within this category: wheat 174, rye 110, barley 65, oats 28), fodder 108 (legume–grass mixture 38, alfalfa 36, clover 29, other 5), root crops 90 (potato 64, beet 25, other 1), stubble (a field with remains of crop after harvest) 55, rape (canola) 24, vegetable 19, maize 18, and other crops 7 (flax, poppy, sunflower, millet); (7) year of the record (range 1955–2000); (8) season, derived from the date when the sample plot was taken (mid-March to early October) and coded as the number of half-month periods from the beginning of the year (e.g., 14 was a code for the second half of July [Lososová et al. 2004]); altitude (range 145–950 m above sea level); (9) soil type, classified into 9 categories, based on FAO-UNESCO (1988) classification: cambisol (brown soil) 347 plots (further divided into following subgroups: dystric 198, eutric 118, mollic 21, stagno-gleyic 10), luvisol 94, chernozem 80, calcaric regosol 78, planosol 43, fluvisol 21, podzol 13, rendzina 12, and phaeozem 10. Information on soil type was derived from Tomášek (2000).

Using overlays of sampling sites with digital maps in the ArcGIS geographic information system, the following five additional characteristics were obtained for each plot. First is altitudinal floristic region. Three basic regions are recognized in the Czech flora: Ther-

mophyticum, i.e., a region of thermophilous flora and vegetation; Mesophyticum with mesophilous flora and vegetation; and Oreophyticum with mountain flora and vegetation (Skalický 1988). Since there were only 22 records attributable to Oreophyticum, these were pooled with Mesophyticum. Consequently, only two regions, Thermophyticum ($n = 364$, termed as a warm altitudinal region), and Mesophyticum combined with Oreophyticum ($n = 334$, now designated as a moderate-to-cold altitudinal region), were used in the analyses. Second are climatic regions on a 12-degree ordinal scale representing a gradient from warm and dry to cold and wet (Quitt 1975). Third is mean annual temperature (range 4.5–9.5°C; 50-year averages taken from Vesecký et al. 1958). Fourth is annual precipitation sum (425–1300 mm; 50-year averages taken from Vesecký et al. 1958). Fifth is the density of human population (number of inhabitants per square kilometer) in the respective administrative district, which was taken as a measure of propagule pressure; the country consists of 77 districts of average size 1025 ± 394 km² (mean $\pm$ 1 SD).

In the literature on plant invasion, the term weed is usually used with the implication of negative impact, i.e., to designate invasive plant pests that are considered harmful, sometimes termed ''environmental weeds'' (Humphries et al. 1991, Randall 1997). In the United States, it is used for a subset of weedy taxa, those whose control/eradication is mandatory (Richardson et al. 2000b, Pyšek et al. 2004a). In the present paper, weeds are understood to be plants (not necessarily alien) that grow in sites where they are not wanted (Rejmánek 2000) without any implication of invasion status (in the sense of Pyšek et al. 2004a).

STATISTICAL ANALYSIS

The response variables were (a) species numbers, (b) species proportions, and (c) relative covers of native species, archaeophytes, and neophytes. Following Sokal and Rohlf (1995: 415–417), species numbers were square-root transformed to obtain an appropriate transformation for count data, and coded by adding 0.5 (because the numbers of neophytes included zeros). Data on proportions and relative covers were transformed into logits (e.g., Crawley 1993: 267–268). To prevent the logits that were estimated from small samples having undue influence, logits were weighted by the total number of species in each plot. The errors in the response variables were assumed to be binomially distributed (Cox and Snell 1990), and checked for overdispersion by examining whether the residual scaled deviances were not larger than the residual degrees of freedom (e.g., Crawley 1993: 278–279). For proportions, the overdispersion was small, and thus treated by McCullagh and Nelder's (1989) correction. For relative covers, the overdispersion was large, and the sample sizes were very unequal. Therefore, the overdispersion was treated by Williams' adjustment for un-

equal binomial denominators (Crawley 1993: 351–353, Pyšek et al. 2002a, 2003b). The appropriateness of the transformations was checked by plotting standardized residuals against fitted values, and by normal probability plots.

The explanatory variables included three categorical variables, further referred to as factors. They were altitudinal floristic region (two levels: warm, and moderate-to-cold), soil type (nine levels), and crop type (eight levels), and nine ordinal or continuous variables, hereafter referred to as covariates. These covariates were altitude, climatic regions, mean annual temperature, annual precipitation, crop height, crop cover, year of the record, season, and density of human population. To achieve a comparable influence, all the covariates, measured on different scales, were standardized to zero mean and unit variance.

Data were evaluated using analyses of covariance (ANCOVAs) in GLIM version 4 (Francis et al. 1994). The aim of each analysis was to determine (a) the minimal adequate model (Appendix A), and (b) net effect of each explanatory variable. This is an effect attributable only to a particular variable and unbiased by other explanatory variables (Appendix B). In the minimal adequate models, all explanatory variables (factors and covariates) were significantly different ($P < 0.05$) from zero and from one another, and all nonsignificant explanatory variables were removed. This was achieved by a stepwise process of model simplification, beginning with the maximal model, containing all factors, interactions, and covariates that might be of interest, then proceeding by the elimination of nonsignificant terms (using deletion tests from the maximal model), and retention of significant terms, following Lonsdale (1999) and Pyšek et al. (2002a, c, 2003a, 2005). To prevent biases to the model structures caused by correlation between variables, model simplifications were made by backward elimination from the maximal models by using stepwise analysis of deviance tables (Crawley 1993: 192–197). The results obtained thus were not affected by the order in which the explanatory variables were removed in the stepwise process of model simplification.

RESULTS

Representation of native species, archaeophytes, and neophytes in arable fields

The species pool of investigated plots in arable fields consisted of 186 native taxa, 149 archaeophytes, and 33 neophytes (368 taxa in total; Appendix C). This represents 6.8% of the total number of native taxa reported for the Czech flora ($n = 2754$; Kubát et al. 2002, Pyšek et al. 2002b), 45.2% of the country's archaeophytes ($n = 332$; Pyšek et al. 2002b) and 3.2% of its neophytes ($n = 1046$; Pyšek et al. 2002b). In sampling plots, archaeophytes were more represented than na-

TABLE 1. Representation of archaeophytes, neophytes, and native species in 698 sampling plots.

	No. species/plot		Species/plot (%)		Cover (%)		Species pool	
	Mean	1 SD	Mean	1 SD	Mean	1 SD	No.	%
Archaeophytes	20.0	6.4	60.0	12.4	59	16	149	40.5
Neophytes	1.3	1.2	3.8	3.7	4	6	33	9.0
Native	12.1	5.3	36.2	12.8	37	16	186	50.5

Notes: Mean species number per plot and the percentage contribution of the three groups based on species numbers and cover is shown. The species pool indicates the total number of species of each group in all the plots sampled and the percentage contribution to the total species pool.

tives both in species numbers and cover, and neophytes were again the fewest present (Table 1).

Overall models and percentage of explained variation

Minimal adequate models for particular species groups had a high predictive power. Explained variation ranged from 33 to 48% in species numbers and from 27 to 51% in proportions (Appendix D). The variables contributing to the explained variation were the year and season of the record, climate, crop type and its vigor, soil type, and human population density (Table 2).

Time of the record, represented by year and season, exhibited both direct effect, unbiased by relationship with other explanatory variables, and indirect effect, indicated by interactions with other variables. A highly significant interaction of year with altitudinal floristic region and of both year and season with crop type was found (Table 2).

The effect of climate was evaluated by using primary climatic variables (temperature, precipitation) and synthetic characteristics (altitudinal floristic regions, climatic regions, and altitude). Of the primary variables, only precipitation had a direct, significant effect. The effect of temperature, and climate in general, appeared best manifested indirectly, through synthetic variables. These variables exhibited both direct and indirect effect, the latter indicated by significant interactions of altitudinal floristic region with climatic regions, altitude, and crop cover (Table 2).

Crop type was the only variable that had a direct, significant effect on all variables investigated, that is, species number and proportion of native species, archaeophytes, and neophytes, respectively. In addition, an interaction of crop type with year, season, and crop height was found; in no case did crop height have a direct effect, and its influence was manifested only through this interaction. Similarly, crop cover only affected the investigated characteristics by an interaction with altitudinal floristic region. Soil type had an effect on all examined characteristics except for the proportion of neophytes. The effect of soil type was always direct, and this variable never interacted with others. The same was true for human population density (Table 2).

Relative covers of native species, archaeophytes, and neophytes were affected by none of the variables used, and maximum models with these characteristics as response variables were never significant. As indicated in Table 2, the effect of variables on the performance of particular species groups (native, archaeophytes, and neophytes) was not consistent, but affected their numbers and proportions in different ways. These particular effects are described below.

Effect of time: seasonal variation and changes over the last 45 years

The year of record had a significant effect on the number and proportion of neophytes and on the number of native species (Table 2), although each group responded to this variable in a different way (Table 3). Whereas the number and proportion of neophytes significantly increased from 1955 to 2000, the opposite was true for the number of native species.

Archaeophytes were not affected directly by the year of record, but by an interaction of this variable with altitudinal floristic region and with crop type (Table 3). Their number decreased both in warm and in moderate-to-cold altitudinal floristic regions, although the decrease was slower in the former. The interaction with crop type was manifested by the number of archaeophytes in fodder significantly increasing over the study period (Table 3).

The proportion of both neophytes and native species was directly affected by season (Table 2). While neophytes increased their proportion from spring to autumn, a reverse trend was true for native species (Table 3). Archaeophytes and the numbers of neophytes were not affected by the season directly, but through its interaction with crop type (Table 2). The number of neophytes in cereals, rape, vegetable, and other crops increased during the course of the season, and so did the number and proportion of archaeophytes in fodder, as well as the number of archaeophytes in stubble. In rape, however, there was a negative effect of season on the proportion of archaeophytes (Table 3).

Effect of climate

The proportion of neophytes decreased with increasing altitude (Table 3). This effect was direct and highly

Table 2. Test statistics and significance of explanatory variables in minimal adequate models.

| | Archaeophytes | | | | | |
| | Numbers | | | Proportional numbers | | |
Explanatory variable	F	df	P	F	df	P
Time of record						
Year of record	. . .	. . .	. . .	. . .	. . .	. . .
Season	. . .	. . .	. . .	. . .	. . .	. . .
(Altitudinal floristic region†) × (year)	24.46	2, 673	<0.0001	. . .	. . .	. . .
(Crop type†) × (year)	11.00	1, 672	0.001	. . .	. . .	. . .
(Crop type†) × (season)	24.21	3, 674	<0.0001	9.41	2, 679	<0.0001
Climate						
Annual precipitation	14.40	1, 672	0.0002	34.47	1, 678	<0.0001
Altitudinal floristic region†	. . .	. . .	. . .	23.01	1, 678	<0.0001
Climatic region	. . .	. . .	. . .	. . .	. . .	. . .
Altitude	. . .	. . .	. . .	. . .	. . .	. . .
(Altitudinal floristic region†) × (climatic region)	8.34	1, 672	0.004	. . .	. . .	. . .
(Altitudinal floristic region†) × (altitude)	. . .	. . .	. . .	22.45	1, 678	<0.0001
(Altitudinal floristic region†) × (crop cover)	10.59	1, 672	0.0012	. . .	. . .	. . .
Crop type						
Crop type†	2.99	6, 677	0.0069	3.59	7, 684	0.0008
(Crop type†) × (crop height)	12.78	2, 673	<0.0001	. . .	. . .	. . .
Soil type†	4.33	8, 679	<0.0001	5.15	8, 685	<0.0001
Human density	. . .	. . .	. . .	. . .	. . .	. . .

† Factors; other variables are covariates.

significant (Table 2). For proportions of archaeophytes and native species, there was an interaction of altitude with altitudinal floristic region (Table 2). Within the moderate-to-cold region, the proportion of archaeophytes decreased with increasing altitude. As a consequence of proportional decrease in archaeophytes and neophytes, the proportion of native species seemingly increased with altitude (Table 3). In fact, this decrease in proportional units was a consequence of the increase of the two remaining proportions. Unlike proportions, the numbers of species in particular groups were not affected by altitude.

Climatic regions, expressed on an ordinal scale increasing from warm and dry to cold and wet, had a direct effect on the number of native species, and an indirect effect, manifested by the interaction with altitudinal floristic region, on the number of archaeophytes (Table 2). Native species and archaeophytes responded to the effect of climatic regions in different ways. While the number of native species increased from warm and dry to cold and wet climatic conditions, the opposite trend was true for archaeophytes in moderate-to-cold floristic regions, where their numbers decreased towards cold and wet climatic regions (Table 3). No significant effect of climatic regions on the number of neophytes was found.

There was a direct, significant effect of annual precipitation on the number and proportion of archaeophytes and native species (Table 2), negative in the former and positive in the latter group (Table 3). Precipitation affected neither the number nor the proportion of neophytes.

Altitudinal floristic region had no effect on neophytes but significantly affected the performance of the other two groups. Besides its interaction with altitude and climatic regions described above, altitudinal floristic region had a direct effect on the number and proportion of native species and on the proportion of archaeophytes (Table 2). More native species were present in the moderate-to-cold than in the warm altitudinal floristic region. Similarly, in terms of proportions, native species were more represented in the moderate-to-cold rather than in the warm floristic region, whereas the warm altitudinal floristic region harbored proportionally more archaeophytes. In addition, there was a significant interaction between altitudinal floristic region and crop cover, influencing the number of archaeophytes and proportion of native species (Table 2). The number of archaeophytes in the moderate-to-cold region and the proportion of native species in the warm altitudinal floristic region both decreased with increasing crop cover (Table 3).

Effect of crop type

There was a direct and significant effect of crop type on number and proportion of species in all three groups (Table 2). The net effect of crop type on species numbers (Appendix E) and proportions (Appendix F) was fairly consistent. Archaeophytes were highly represented in cereals and root crops but little represented in rape. Neophytes were most represented in maize, and in terms of numbers also in root crops; by contrast native species performed best in fodder and stubble,

TABLE 2. Extended.

Neophytes						Native					
Numbers			Proportional numbers			Numbers			Proportional numbers		
F	df	P	χ^2	df	P	F	df	P	F	df	P
6.56	1, 677	0.0106	27.16	1	<0.0001	35.31	1, 677	<0.0001	. . .	. . .	. . .
. . .	. . .	. . .	25.34	1	<0.0001	. . .	. . .	. . .	13.14	1, 676	0.0003
. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
17.65	4, 680	<0.0001	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
. . .	. . .	. . .	. . .	. . .	. . .	14.93	1, 677	0.0001	41.37	1, 676	<0.0001
. . .	. . .	. . .	. . .	. . .	. . .	35.47	1, 677	<0.0001	30.00	1, 676	<0.0001
. . .	. . .	. . .	. . .	. . .	. . .	7.93	1, 677	0.005	. . .	. . .	. . .
. . .	. . .	. . .	30.16	1	<0.0001	. . .	. . .	. . .	. . .	. . .	. . .
. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	20.38	1, 676	<0.0001
. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	9.96	1, 676	0.0017
16.72	7, 683	<0.0001	43.07	7	<0.0001	9.26	7, 683	<0.0001	2.37	7, 682	0.0213
. . .	. . .	. . .	. . .	. . .	. . .	14.05	2, 678	<0.0001	12.68	2, 677	<0.0001
4.31	8, 684	<0.0001	. . .	. . .	. . .	3.35	8, 684	0.0009	6.59	8, 683	<0.0001
7.00	1, 677	0.0083	4.61	1	0.0318	. . .	. . .	. . .	. . .	. . .	. . .

and worst in vegetables, maize, and a miscellaneous group of other crops (Appendices E and F).

Besides the interaction of crop type with year and season, described above, there also was a significant interaction between crop type and its height, found for the number and proportion of native species and number of archaeophytes (Table 2). Number and proportion of native species increased with crop height in cereals, but decreased for fodder (Table 3).

Effect of soil type

The effect of soil type in minimal adequate models always was direct and significant, except the proportion of neophytes (Table 2). Net effects indicated that in terms of both species number and proportion, native species are poorly represented on chernozem and best on fluvisol soils. The occurrence of archaeophytes exhibited an opposite pattern, with the highest proportions on chernozem and rendzina and the lowest on fluvisol (Fig. 1).

Effect of human population density in the region

Human density had a significant and positive effect only on the number and proportion of neophytes and did not affect the occurrence of the other two groups (Table 2). Both number and proportional representation of neophytes increased with increasing human population density (Table 3).

DISCUSSION

Neither fish nor fowl: archaeophytes between native species and neophytes

Native species, archaeophytes, and neophytes respond to the variables affecting their performance on arable land in different ways (Table 4). On a half-century time scale (1955–2000), numbers of archaeophytes and native species have significantly decreased in sample plots on arable land in the Czech Republic. This corresponds to the repeatedly reported trend of a decrease over time in the richness of Central European weed flora (Tüxen 1962, Hilbig 1987, Kropáč 1988, Hilbig and Bachthaler 1992, Andreasen et al. 1996, Lososová 2003, Pyšek et al. 2005), which is usually attributed to the intensification of crop production and increasing use of herbicides and fertilizers. On the other hand, our study showed that neophytes are progressively more numerous in arable fields and their proportion also significantly increased during the second half of the 20th century. This accords well with the number of neophytes in the total flora of the Czech Republic steadily increasing over the study period: of the total number of neophytes with a known date for their first report, only 65% were present in 1955 (Pyšek et al. 2003d), and the remaining 35% were immigrants during the period addressed in the present paper. In addition, the naturalization process of some of the neophytes present in 1955 continued as they entered new habitats, including arable fields. The increasing performance of neophytes in arable fields is in accordance with their positive relationship to increased human population density, which supports a higher propagule pressure (Pyšek et al. 2002a, 2003a). Casual species, numerically the most abundant subgroup of neophytes, crucially depend on the repeated input of propagules for their continued existence (Richardson et al. 2000b). Human population density, on the other hand, had no effect on archaeophytes. Since these alien species have been present for millennia, a majority of them are nat-

TABLE 3. Regression slopes (±1 SE) in minimal adequate models.

	Archaeophytes	
Explanatory variable	Numbers	Proportional numbers
Time of record		
Year of record	. . .	. . .
Season	. . .	. . .
(Warm floristic region†) × (year)	−0.13 ± 0.033	. . .
(Moderate-to-cold floristic region†) × (year)	−0.24 ± 0.040	. . .
(Fodder†) × (year)	0.23 ± 0.070	. . .
(Cereal†) × (season)	0.37 ± 0.041	. . .
(Fodder†) × (season)	0.18 ± 0.057	0.14 ± 0.035
(Rape†) × (season)	. . .	−0.31 ± 0.120
(Stubble†) × (season)	0.25 ± 0.110	. . .
(Vegetable†) × (season)	. . .	. . .
(Other crop†) × (season)	. . .	. . .
Climate		
Annual precipitation	−0.13 ± 0.033	−0.12 ± 0.020
Climatic region	. . .	. . .
Altitude	. . .	. . .
(Moderate-to-cold floristic region†) × (climatic region)	−0.12 ± 0.043	. . .
(Moderate-to-cold floristic region†) × (altitude)	. . .	−0.13 ± 0.026
(Warm floristic region†) × (crop cover)	. . .	. . .
(Moderate-to-cold floristic region†) × (crop cover)	−0.13 ± 0.041	. . .
Crop type		
(Cereal†) × (crop height)	. . .	. . .
(Fodder†) × (crop height)	0.37 ± 0.090	. . .
(Other crop†) × (crop height)	1.36 ± 0.450	. . .
Human density	. . .	. . .

† Factors; other variables are covariates.

uralized (78% compared to 21% of neophytes [Pyšek et al. 2002b]) and widely distributed (52% are estimated to have >500 localities in the country compared to 7% of neophytes [Pyšek et al. 2003d]). These figures indicate that archaeophytes are present in the landscape in sufficient abundance, making them capable of persisting independently of human translocation of their diaspores.

With regard to a response to climate, both groups of aliens increase their representation under warm conditions (Table 4). This indicates the importance of a climatic match, a necessary condition for successful invasion (Chicoine et al. 1985, Panetta and Mitchell 1991, Scott and Panetta 1993, Richardson et al. 2000a). As most aliens of temperate zones were introduced from regions with warmer climate (Kowarik 1990, Sukopp 2002), they have to be able to flower early, which is the only effective mechanism to ensure proper seed set or storage of necessary embryonic food reserves (Reichard and Hamilton 1997, Pyšek et al. 2003d). The life cycle of many neophytes nevertheless is shifted toward warmer periods in late spring and summer (Crawley et al. 1996), which is reflected by an increase in their numbers and proportion as crop community develops (Table 4). The same increase over the season was found in archaeophytes, although the relationship was weaker than that for neophytes (for proportions: $P = 3 \times 10^{-3}$ and $P = 1 \times 10^{-7}$, respectively). At the same time, proportional representation of native species is decreasing. Although the differences in flow-

ering time between archaeophytes and native species are no longer detectable by comparison to the total country's flora (Pyšek et al. 2004a), the increase of archaeophyte representation with crop seasonal development indicates that after several millenia of adaptation, the effect of climatic conditions in the primary distribution range is still obvious. For archaeophytes climate still acts as a major constraint to their wider distribution, even in habitats to which they are otherwise perfectly suited (Lososová et al. 2004).

Archaeophytes respond like neophytes to some variables (climate, seasonal development of crop) and alternatively like native species to other variables (increasing agricultural intensification through time, propagule pressure). This can be explained by the history of alien plant invasions in Central Europe. With respect to invasions, arable land represents a special habitat. Neolithic agriculture was introduced into the study region from the Near East via the Mediterranean area; the process started in the sixth millenium BC and triggered a continuous stream of plant invasions from the southeast (Roberts 1998). Principal landscape changes accompanied by immigration of new plant species continued during the Late Neolithic/Copper Age, with improvements in agriculture such as introduction of ploughing implements. Based on palaeobotanical data, it is estimated that during the first thousand years after the advent of agriculture a significant proportion (35%, Pyšek et al. 2003c) of the presently known 332 archaeophytes found their way to the Czech Republic

TABLE 3. Extended.

Neophytes		Native	
Numbers	Proportional numbers	Numbers	Proportional numbers
0.036 ± 0.014	0.18 ± 0.034	-0.13 ± 0.021	$\cdots$
$\cdots$	0.24 ± 0.049	$\cdots$	-0.085 ± 0.022
$\cdots$	$\cdots$	$\cdots$	$\cdots$
$\cdots$	$\cdots$	$\cdots$	$\cdots$
0.18 ± 0.027	$\cdots$	$\cdots$	$\cdots$
$\cdots$	$\cdots$	$\cdots$	$\cdots$
0.38 ± 0.110	$\cdots$	$\cdots$	$\cdots$
$\cdots$	$\cdots$	$\cdots$	$\cdots$
0.31 ± 0.093	$\cdots$	$\cdots$	$\cdots$
0.73 ± 0.330	$\cdots$	$\cdots$	$\cdots$
$\cdots$	$\cdots$	0.12 ± 0.031	0.14 ± 0.020
$\cdots$	$\cdots$	0.10 ± 0.036	$\cdots$
$\cdots$	-0.22 ± 0.040	$\cdots$	$\cdots$
$\cdots$	$\cdots$	$\cdots$	$\cdots$
$\cdots$	$\cdots$	$\cdots$	0.12 ± 0.026
$\cdots$	$\cdots$	$\cdots$	-0.10 ± 0.030
$\cdots$	$\cdots$	$\cdots$	$\cdots$
$\cdots$	$\cdots$	0.15 ± 0.030	0.068 ± 0.023
$\cdots$	$\cdots$	-0.16 ± 0.079	-0.24 ± 0.057
$\cdots$	$\cdots$	$\cdots$	$\cdots$
0.037 ± 0.014	0.070 ± 0.032	$\cdots$	$\cdots$

and Central Europe (see also Lang 1994). Their immigration was facilitated by the fact that during the Copper Age, there already was a rather high proportion of deforested landscape in lowlands (Ložek 1973). Subsequently this invasion continued steadily until the Middle Ages (Pyšek et al. 2003c).

An important aspect of these historical processes is that many archaeophytic weeds were unintentionally but directly introduced by Neolithic farmers, namely as admixtures to crop seed. The diaspore pressure, a crucial condition for a successful invasion (Williamson 1996), must have been intense and continuous, and facilitated the early invasion of archaeophytes into local communities. During the Neolithic Age, crops and archaeophytes were sown into slightly disturbed native vegetation. Initially, fertilization was absent, and once the soil was depleted, cultivation shifted to other sites; individual landscape patches experienced periods of extensive management and abandonment (Ellenberg 1988). A primitive and rather ineffective tillage system came into use during the Copper Age and additionally contributed to the suppression of native species. This management, which supported archaeophytes, persisted for several millennia, until deep tillage was introduced in the 19th century. Until then, the persistence of perennial native species also was facilitated by rotational management systems in which fields were abandoned once every three years (Ellenberg 1988).

This places archaeophytes into an intermediate position between native and neophytic weeds. From an historical (residence time) and habitat viewpoint, archaeophytes are more similar to native weeds than to neophytes. However, their origin in climatically warmer regions makes them more similar to neophytes than to native species.

Effect of climate

The number of native weed species is lower in warmer and drier areas than in colder and wetter ones. This result is highly significant and consistent, whether it is tested by altitudinal floristic region or by climatic region. Such a consequence is rather surprising, since in temperate floras, native species richness generally increases towards regions with warmer climate (e.g., Pyšek et al. 2002c). An opposite pattern found here provides additional support for the above suggested scenario of archaeophytic species easily invading resident vegetation communities. In warm and dry regions with calcareous soils, the competition of naturalized archaeophytes with native species might have been sufficiently effective so that only a limited number of native weeds were able to persist on arable land. At higher altitudes with colder climate, under conditions less optimal for archaeophytes (Hügin 1999), more native species were able to successfully colonize the newly developing habitat. Additionally, higher altitudes of the study area were colonized as late as the Late Middle Ages and have contained arable fields for a much shorter time. Archaeophytes therefore had less time to become established in such landscapes, compared with warmer regions at lower altitudes with millennia of human colonization history.
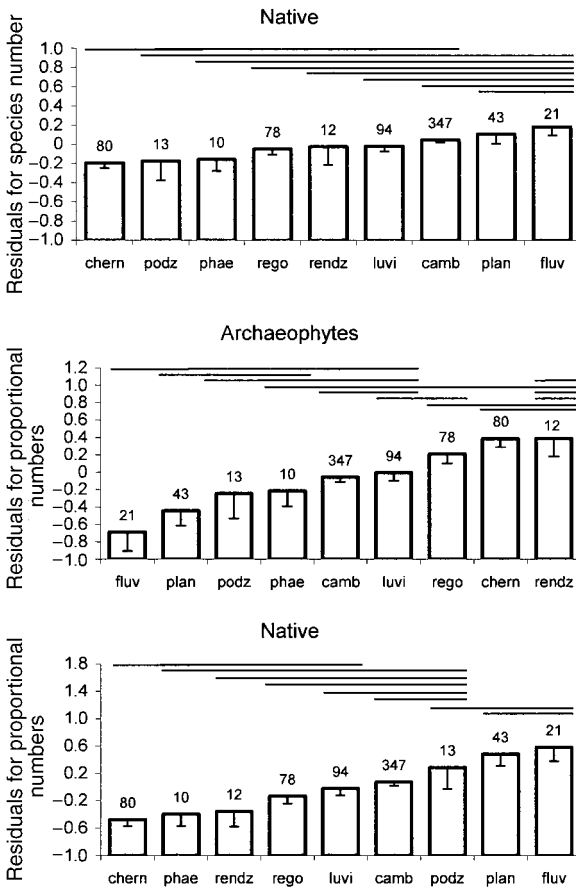
FIG. 1. Net effects of soil types on species numbers and proportions. The horizontal lines show soil type groups that are not significantly different by least significant differences (LSD). Histogram bars are means (-1 SE) with sample sizes displayed above. Key to abbreviations for soil types: chern, chernozem; podz, podzol; phae, phaeozem; rego, calcaric regosol; rendz, rendzina; luvi, luvisol; camb, cambisol; plan, planosol; fluv, fluvisol. For the number of native species, $F = 2.48$, df = 8, 689, $P < 0.05$, $R^2 = 2.8\%$; for the proportion of archaeophytes, $F = 4.72$, df = 8, 689, $P < 0.001$, $R^2 = 5.2\%$; for the proportion of native species $F = 5.37$, df = 8, 689, $P < 0.001$, $R^2 = 5.9\%$.

As in the companion study (Pyšek et al. 2005), the effect of climate was most obviously manifested indirectly, through altitude, climatic region, and altitudinal floristic region. In neophytes, altitude was the only climate-related predictor of their performance. However, the interaction of climate with temporal trends had a similar effect on the occurrence of archaeophytes as it did on native species; their numbers decreased over the study period, but less so in a warm altitudinal floristic region. We suggest that the more pronounced decrease in the number of archaeophytes over time in the moderate-to-cold altitudinal floristic region is caused by the fact that, at higher altitudes, intensification of crop production with increasing fertilization and increasing use of herbicides was temporally delayed, hence suppressing the weed flora progressively during the study period. In fertile lowland regions the intensification was already high at the beginning of the study period (Pyšek et al. 2005).

The effect of altitudinal floristic region on the performance of archaeophytes can be inspected in more detail by investigating the interaction of this variable with climatic regions (defined by a number of climatic variables [Quitt 1975]). The response of archaeophytes in moderate-to-cold altitudinal floristic regions was further differentiated based on climate, with their species number increasing towards warm and dry climatic regions. Obviously, archaeophytes find favorable environments across the entire warm altitudinal floristic region, but lack vigor under deteriorating conditions of a moderate or even cold region. These differences in climate affect their representation. Moreover, under suboptimal conditions experienced by most archaeophytes in the moderate-to-cold altitudinal floristic region and by native species under a warm regime, each group was negatively affected by crop cover. The number of archaeophytes decreased with increasing crop cover in the moderate-to-cold region, while the proportion of native species decreased with increasing crop cover in the warm region.

The present study also revealed a direct effect of a primary climatic variable, namely total annual precipitation. Archaeophytes are favored not only by a warm climate but also by a dry one, while native species are

TABLE 4. Summary of differences in the occurrence of weed species on Central European arable land, with respect to their origin and residence status.

Plant type	Time (1955–2000)	Season	Climate	Soils	Human density
Native species	decrease (N)	decrease (P)	more represented in cool and wet (N, P)	more represented on wet (N, P)	no effect
Archaeophytes	decrease (N)	increase (N, P)	more represented in warm and dry (N, P)	more represented on base-rich and dry (P)	no effect
Neophytes	increase (N, P)	increase (N, P)	more represented in warm (P)	no effect	increase (N, P)

Notes: Only general and unequivocal trends are outlined; some interactions with crop types that do not follow the general trends are omitted. Trends in numbers (N) and proportions (P) are indicated.

more numerous in weed communities from areas with higher precipitation. The effect of precipitation was found not only for proportional representation of both groups but also for the number of species. That neophytes were not affected by precipitation can be explained by the overwhelming effect of altitude, a variable in which the effect of precipitation is included. Neophytes in the flora of the Czech Republic are considerably more diverse in origin than archaeophytes that have been recruited almost exclusively from the Near East, Mediterranean, and adjacent regions (Pyšek et al. 2002*b*). The diverse origin of neophytes brought about a higher variation in requirements for moisture, manifested in regions to which they were introduced. Moreover, neophytes are present in the study region for a much shorter period of time; many of them have not yet occupied all climatically suitable areas and may not be so well adapted and finely tuned to the Central European climate. The response of neophytes to the climatic conditions is therefore best reflected by the coarser measure of altitude (Hügin 1999), while for the other two groups, present for a much longer time, it is more subtle and differentiated.

Effect of crop type

Crop type affected the representation of particular species groups not only directly but also by interactions with other variables. While in some crops archaeophytes proportionally increased during the course of a season, in others such as rape they were gradually decreasing. An increase of archaeophytes over the season is a common response and reflects the successional development of weed communities in the course of the growing season (Kropáč et al. 1971, Ellenberg 1988, Lososová et al. 2003, 2004). The negative relationship between weed performance and rape (*Brassica napus* L.) indicates an intense competition for nutrients and light, as increasing shading from the crop throughout the season leads to the suppression of weeds (Ellenberg 1988, Pyšek et al. 2005). Stands of rape are rather dense and the competitive effect on weeds may be quite strong. Of all crop types, rape harbors the lowest proportion of archaeophytes despite the fact that the total number of weed species is quite high (Pyšek et al. 2005). Rape initially was planted in the study territory rather late, during the 13th century, and modern cultivars came into massive use in the mid 20th century (Zelený 1992). The degree of coadaptation of archaeophytes to rape may therefore be lower than that to other crops.

Regarding long-term changes in weed vegetation, the only exception to the general decrease in the number of archaeophytes over the study period is fodder, where the trend was opposite. Many fodder crops in the study area are neophytes, especially alfalfa (*Medicago sativa* L.) and alsike clover (*Trifolium hybridum* L. subspecies *hybridum*). Although other frequently planted fodder crops are archaeophytes (garden pea, *Pisum sativum* L.) or native (red clover, *Trifolium pratense* L.), the contribution of neophytes to fodder is substantial. Alfalfa first was planted in France in the 16th century, and spread from there to Central Europe (Mansfeld 1986). Planting of alsike clover became popular in the Czech Republic late in the 19th century (Opiz 1852). The increase of archaeophytes within fodder over time therefore reflects a situation completely different from crops that are themselves archaeophytes. At the time alfalfa and alsike clover were introduced, archaeophytic weeds were already naturalized in the landscape and invaded new habitats formed by these crops. Our results indicate that this invasion is still in progress. That fodders with different residence times differ in the dynamics of their archaeophytes provides additional support for this conclusion. The number of archaeophytes increased over the study period in neophytic fodder crops, alfalfa and alsike clover (common regression slope (mean $\pm$ 1 SE) on the year of record = 0.21 $\pm$ 0.10; $n = 65$; $P < 0.05$). The situation in these crops thus is similar to invasions of all crops by neophytes, a group typified by an increasing trend of species numbers over the last 50 yr (Table 3). However, in the legume–grass mixture of native and archaeophyte fodder crops, the number of archaeophytes over the study period decreased (slope = -0.32 ± 0.11; $n = 38$; $P < 0.05$), as in other crops of archaeophytic origin.

Fodder also was exceptional in that the number and proportion of native species, otherwise quite high for this crop type, decreased with crop height. The opposite relationship, found in other crop types, indicates that weeds increase and cultivated crop species grow taller over time without any causal relationship (Pyšek et al. 2005). The pattern revealed in fodder may reflect the nitrogen-fixing capacity of legumes. As fodder crops grow, the soil is progressively more enriched by nitrogen (Gill and Fick 2001). This availability of nitrogen from symbiotic fixation to other plants is widely used in agriculture, where sequential cropping or intercropping systems with legumes increase yields of other crops (Bullied et al. 2002, Malhi et al. 2002). The nutrient-rich environment, however, is also becoming more favorable for nutrient-demanding weed species, and archaeophytes exhibit higher demands for nitrogen than native species (Pyšek et al. 2004*b*). Accordingly, some oligotrophic native species may be limited. This hypothesis is further supported by the fact that the negative effect on representation of native species was determined only by fodder height, not by seasonal development of this crop's stand. Both variables, season and height, are measures of change throughout the year, but the latter is more closely related to crop production and the associated increase in nitrogen contents of the soil.

Historical crop–weed associations are also reflected in the net effects exerted by particular crops on weed species with different origins and residence status, and act in concert with agricultural management. In our

study, these net effects are unbiased by the fact that particular crops are planted in specific climatic and soil conditions. This pattern is rather complex, but some trends can be discerned: occurrence of particular groups of weeds in relatively recently introduced crops (maize, rape, alfalfa, and alsike clover) is different from that in old traditional crops introduced with the beginning of agriculture. In terms of species numbers (Appendix E), archaeophytes are poorly represented in neophytic crops (rape, maize), where neophytes are most numerous. The pattern is reversed in cereals that are rich in archaeophytes but poor in neophytes. The pattern of native species richness in particular crops does not seem to depend on the length of cultivation.

An exception to the fact that more archaeophytes tend to occur in more ancient cultures and neophytes in modern ones are root crops, represented by potato and beet in our sample. Potato (*Solanum tuberosum* L.) was introduced to Europe during the 16th century, but its extensive planting at the study territory dates to the second half of the 18th century (Štěpánek and Tomšovic 2000). Beet (*Beta vulgaris* L.) has been planted extensively in the study area since the 18th century (Tomšovic 1990). Root crops are therefore neophytes, but harbor the highest number of archaeophytes of all crops. However, they are also rich in native weeds and neophytes. Root crops are managed by hoeing several times during the growing season, which decreases the competition from the crop and from already established weeds, and supports the establishment of many different weed species from propagule sources existing in the landscape.

Historical weed–crop associations and the crop-specific management also are reflected by proportions of species numbers, with archaeophytes best represented in cereals, and poorly represented in rape and fodder. Maize, another neophyte, harbored the highest proportion of neophytic weeds of all crop types. In general, it was the crop type poorest in weed species (Pyšek et al. 2005). Before maize germinates, the soil is treated with triazine herbicides, which suppress weeds but do not affect maize (Piutti et al. 2002). The limited number of species that are capable of coping with these herbicides are mostly recruits from the pool of neophytes.

Effect of soil type

Neolithic farmers brought the crops, management, and a substantial part of weed flora, but not the soils; these were local. The distribution of soil types at the study area is determined by climate and bedrock type. However, the net effects of soil types on the composition of weed communities identified here make it possible to infer the tentative scenario of development of weed communities on different soils. Archaeophytes are preferentially represented on calcareous and dry soils such as rendzina, chernozem, and regosol. By contrast, native species are under-represented on these soils, but over-represented on fluvisols, a productive soil type in river floodplains that is well supplied with nutrients, and water, and on planosols, that is, soils with a clay accumulation in the subsurface layer, which leads to seasonal waterlogging (Fig. 1). At the scale of local landscapes the gradient between dry and wet soils exerts similar effects on the performance of archaeophytes and native species, as does precipitation on a broader geographic scale (Table 3). While archaeophytes decrease and native species increase with precipitation, archaeophytes predominate on drier soils and native species on wetter soils if precipitation is held constant.

Identifying net effects: a tool to reveal hidden context

Minimal adequate models in this paper had a high predictive power, explaining ~40% of the variation in species numbers and proportions, and even 48–51% for native weeds alone. This is quite high compared to 29% explained by analyzing total species richness of weed flora not separated into native and alien species (Pyšek et al. 2005). This indicates that to obtain a closer insight, we need to separate native species from aliens, and classify the latter according to their residence status (Pyšek et al. 2003*b*). Dividing species into three groups (Table 4) not only made it possible to explain more variance, but also revealed some explanatory variables that appeared nonsignificant for the whole data set, because particular groups, namely archaeophytes and native species, responded to their action in an opposite and complementary way. Soil type can be used as an illustrative example of this phenomenon. A higher representation of archaeophytes on some soil types was compensated for by fewer native species present and vice versa, and as a result, this factor did not have a significant effect on the species richness of the weed community as a whole.

In previously published analyses, the effects of explanatory variables were often hidden by their covariance structure. The statistical approach used in this and earlier papers (Pyšek et al. 2002*a*, *b*, *c*, 2003*a*, 2005) allows us to evaluate the effects of particular variables, independent of other variables. The analysis thus gives a sound basis for unbiased discussion of regional patterns in performance of weeds on arable land and evaluation of underlying variables. It is possible to test previously suggested patterns of alien species richness in temperate plant communities, such as their affinity for warmer conditions (e.g., Mihulka 1998, Hügin 1999, Pyšek et al. 2002*a*), and the increase of neophytes over time (Kowarik 2003, Pyšek et al. 2003*b*), and separate the net effects from spurious results caused by mutual correlation of variables. Moreover, using this approach on a data set spanning several decades, and including a number of relevant variables, allowed considerable detail in the analysis of the observed pattern and revealed subtle and specific effects of particular variables.

LITERATURE CITED

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

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

Bullied, W. J., M. H. Entz, S. R. Smith, and K. C. Bamford. 2002. Grain yield and N benefits to sequential wheat and barley crops from single-year alfalfa, berseem and red clover, chickling vetch and lentil. Canadian Journal of Plant Science **82**:53–65.

Chicoine, T. K., P. K. Fay, and G. A. Nielsen. 1985. Predicting weed migration from soil and climate maps. Weed Science **34**:57–61.

Chytrý, M. 2001. Phytosociological data give biased estimates of species richness. Journal of Vegetation Science **12**:439–444.

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

Cox, D. R., and E. J. Snell. 1990. Analysis of binary data. Chapman and Hall, London, UK.

Crawley, M. J. 1987. What makes a community invasible? Pages 429–543 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, succession and stability. Blackwell Scientific, Oxford, UK.

Crawley, M. J. 1993. GLIM for ecologists. Blackwell Scientific, Oxford, UK.

Crawley, M. J., P. H. Harvey, and A. Purvis. 1996. Comparative ecology of the native and alien floras of the British Isles. Biological Transactions of the Royal Society B **351**: 1251–1259.

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

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

Ellenberg, H. 1950. Unkrautgemeinschaften als Zeiger für Klima und Boden. Landwirtschaftliche Pflanzensoziologie I. Verlag Eugen Ulmer, Stuttgart/Ludwigsburg, Germany.

Ellenberg, H. 1988. Vegetation ecology of central Europe. Cambridge University Press, Cambridge, UK.

Erviö, R., S. Hyvärinen, L.-R. Erviö, and J. Salonen. 1994. Soil properties affecting weed distribution in spring cereal and vegetable fields. Agricultural Science in Finland **3**: 497–504.

FAO-UNESCO. 1988. Soil map of the World. FAO, Rome, Italy.

Francis, B., M. Green, and C. Payne, editors. 1994. The GLIM System. Release 4 Manual. Clarendon Press, Oxford, UK.

Gilbert, O. L. 1989. The ecology of urban habitats. Chapman and Hall, London, UK.

Gill, J. L., and W. H. Fick. 2001. Soil nitrogen mineralization in mixtures of eastern gamagrass with alfalfa and red clover. Agronomy Journal **93**:902–910.

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

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

Hilbig, W., and G. Bachthaler. 1992. Wirtschaftsbedingte Veränderungen der Segetalvegetation in Deutschland in Zeitraum von 1950–1990. Angewandte Botanik **66**:192–209.

Holub, J., and V. Jirásek. 1967. Zur Vereinheitlichung der Terminologie in der Phytogeographie. Folia Geobotanica et Phytotaxonomica **2**:69–113.

Holzner, W., and R. Immonen. 1982. Europe: an overview. Pages 203–226 *in* W. Holzner and N. Numata, editors. Biology and ecology of weeds. Dr. W. Junk, The Hague, The Netherlands.

Hügin, G. 1999. Was sind Wärmezeiger? Untersuchungen zum Wärmebedürfnis von Ruderal- und Segetalpflanzen in Mitteleuropa. Tuexenia **19**:425–445.

Humphries, S. E., R. H. Groves, and D. S. Mitchell. 1991. Plant invasions of Australian ecosystems. Kowari **2**:1–134.

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

Kleijn, D., and M. Verbeek. 2000. Factors affecting the species composition of arable field boundary vegetation. Journal of Applied Ecology **37**:256–266.

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

Kowarik, I. 1990. Some responses of flora and vegetation to urbanization in Central Europe. Pages 45–74 *in* H. Sukopp, S. Hejný and I. Kowarik, editors. Urban ecology. SPB Academic Publishing, The Hague, The Netherlands.

Kowarik, I. 2003. Biologische Invasionen: Neophyten und Neozoen in Mitteleuropa. Verlag Eugen Ulmer, Stuttgart, Germany.

Kropáč, Z. 1988. Veränderungen der Unkrautgemeinschaften in der Tschechoslowakei und die Konsequenzen für die landwirtschaftliche Praxis. Wissenschaftlicher Zeitschrift der Universität Halle **37**:100–126.

Kropáč, Z., E. Hadač, and S. Hejný. 1971. Some remarks on the synecological and syntaxonomic problems of weed plant communities. Preslia **43**:139–153.

Kubát, K., L. Hrouda, J. Chrtek Jun, Z. Kaplan, J. Kirschner, J. Štěpánek, and J. Zázvorka, editors. 2002. Klíč ke květeně České republiky. Academia, Praha, Czech Republic.

Lang, G. 1994. Quartäre Vegetationsgeschichte Europas. Methoden und Ergebnisse. Gustav Fischer Verlag, Jena, Germany.

Lonsdale, M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**:1522–1536.

Lososová, Z. 2003. Estimating past distribution of vanishing weed vegetation in South Moravia. Preslia **75**:71–79.

Lososová, Z., M. Chytrý, Š. Cimalová, Z. Kropáč, Z. Otýpková, P. Pyšek, and L. Tichý. 2004. Weed vegetation of arable land in Central Europe: gradients of diversity and species composition. Journal of Vegetation Science **15**: 415–422.

Lososová, Z., J. Danihelka, and M. Chytrý. 2003. Seasonal dynamics and diversity of weed vegetation in tilled and mulched vineyards. Biologia **58**:49–57.

Ložek, V. 1973. Příroda ve čtvrtohorách. Academia, Praha, Czechoslovakia.

Malhi, S. S., R. P. Zentner, and K. Heier. 2002. Effectiveness of alfalfa in reducing fertilizer N input for optimum forage yield, protein concentration, returns and energy performance of bromegrass-alfalfa mixtures. Nutrient Cycling in Agroecosystems **62**:219–227.

Mansfeld, R. 1986. Verzeichnis landwirtschaftlicher und gärtnerischer Kulturpflanzen (ohne Zierpflanzen). Second edition. Volumes 1–4. Akademie-Verlag, Berlin, Germany.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. Chapman and Hall, London, UK.

Mihulka, S. 1998. The effect of altitude on the pattern of plant invasions: a field test. Pages 313–320 *in* U. Starfinger, K. Edwards, I. Kowarik, and M. Williamson, editors. Plant invasions: ecological mechanisms and human responses. Backhuys, Leiden, The Netherlands.

Neuhäuslová, Z., et al. 2001. Potential natural vegetation of the Czech Republic. Braun-Blanquetia **30**:1–80.

Opiz, F. M. 1852. Seznam rostlin květeny české. Spisů Musejních 44. V kommissí u Fr. Řivnáče, Praha, Austria.

Panetta, F. D., and N. D. Mitchell. 1991. Bioclimatic prediction of the potential distribution of some weed species prohibited entry to New Zealand. New Zealand Journal of Agricultural Research **34**:341–350.

Piutti, S., S. Hallet, S. Rousseaux, L. Philippot, G. Soulas, and F. Martin-Laurent. 2002. Accelerated mineralization of atrazine in maize rhizosphere soil. Biology and Fertility of Soils **36**:434–441.

Preston, C. D., D. A. Pearman, and T. D. Dines. 2002. New atlas of the British and Irish flora. Oxford University Press, Oxford, UK.

Pyšek, A., P. Pyšek, V. Jarošík, M. Hájek, and J. Wild. 2003*a*. Diversity of native and alien plant species on rubbish dumps: effects of dump age, environmental factors and toxicity. Diversity and Distributions **9**:177–189.

Pyšek, P., V. Jarošík, Z. Kropáč, M. Chytrý, J. Wild, and L. Tichý. 2005. Species richness and cover in Central-European weed communities: the effect of abiotic environment, crop and management over time. Agriculture, Ecosystems and Environment, *in press*.

Pyšek, P., V. Jarošík, and T. Kučera. 2002*a*. Patterns of invasion in temperate nature reserves. Biological Conservation **104**:13–24.

Pyšek, P., V. Jarošík, and T. Kučera. 2003*b*. Inclusion of native and alien species in temperate nature reserves: an historical study from Central Europe. Conservation Biology **17**:1414–1424.

Pyšek, P., T. Kučera, and V. Jarošík. 2002*c*. Plant species richness of nature reserves: the interplay of area, climate and habitat in a central European landscape. Global Ecology and Biogeography **11**:279–289.

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

Pyšek, P., D. M. Richardson, M. Rejmánek, G. Webster, M. Williamson, and J. Kirschner. 2004*a*. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon **53**:131–143.

Pyšek, P., D. M. Richardson, and M. Williamson. 2004*b*. Importance of residence status and source areas in analyses of alien floras. Diversity and Distributions **10**:179–187.

Pyšek, P., J. Sádlo, and B. Mandák. 2002*b*. Catalogue of alien plants of the Czech Republic. Preslia **74**:97–186.

Pyšek, P., J. Sádlo, and B. Mandák. 2003*c*. Alien flora of the Czech Republic, its composition, structure and history. Pages 113–130 *in* L. E. Child, J. H. Brock, G. Brundu, K. Prach, P. Pyšek, P. M. Wade, and M. Williamson, editors. Plant invasions: ecological threats and management solutions. Backhuys, Leiden, The Netherlands.

Pyšek, P., J. Sádlo, B. Mandák, and V. Jarošík. 2003*d*. Czech alien flora and a historical pattern of its formation: what came first to Central Europe? Oecologia **135**:122–130.

Quitt, E. 1975. Klimatické oblasti České socialistické republiky. Institute of Geography, Czechoslovak Academy of Sciences, Brno, Czechoslovakia.

Randall, J. M. 1997. Defining weeds of natural areas. Pages 18–25 *in* J. O. Luken and J. W. Thieret, editors. Assessment and management of plant invasions. Springer-Verlag, New York, New York, USA.

Reichard, S. H., and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. Conservation Biology **11**:193–203.

Rejmánek, M. 2000. Invasive plants: approaches and predictions. Austral Ecology **25**:497–506.

Richardson, D. M., W. J. Bond, W. R. J. Dean, S. I. Higgins, G. F. Midgley, S. J. Milton, L. Powrie, M. C. Rutherford, M. J. Samways, and R. E. Schulze. 2000*a*. Invasive alien species and global change: a South African perspective. Pages 303–349 *in* H. A. Mooney and R. J. Hobbs, editors. Invasive species in a changing world. Island Press, Washington, D. C., USA.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000*b*. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions **6**:93–107.

Roberts, N. 1998. The Holocene. An environmental history. Second edition. Blackwell, Oxford, UK.

Salonen, J. 1993. Weed infestation and factors affecting weed incidence in spring cereals in Finland—a multivariate approach. Agricultural Science in Finland **2**:525–536.

Scott, J. K., and F. D. Panetta. 1993. Predicting the Australian weed status of southern African plants. Journal of Biogeography **20**:87–93.

Skalický, V. 1988. Regionálně fytogeografické členění. Pages 103–121 *in* S. Hejný and B. Slavík, editors. Květena České socialistické republiky. Academia, Praha, Czechoslovakia.

Sokal, R., and F. J. Rohlf. 1995. Biometry. Third edition. W. H. Freeman, New York, New York, USA.

Štěpánek, J., and P. Tomšovic. 2000. 7. *Solanum* L.—lilek. Pages 260–280 *in* B. Slavík, J. Štěpánková, and J. Chrtek Jun, editors. Květena České republiky. Volume 6. Academia, Praha, Czech Republic.

Stevenson, F. C., A. Legere, R. R. Simard, D. A. Angers, D. Pageau, and J. Lafond. 1997. Weed species diversity in spring barley varies with crop rotation and tillage, but not with nutrient source. Weed Science **45**:798–806.

Sukopp, H. 2002. On the early history of urban ecology in Europe. Preslia **74**:373–393.

Thellung, A. 1905. Einteilung der Ruderal- und Adventivflora in genetische Gruppen. Die Flora des Kanton Zürich, 1. Teil. Die Ruderal- und Adventivflora des Kanton Zürich. Pages 232–236 *in* O. Naegeli and A. Thellung, editors. Vierteljahrschrift der Naturforschenden Gesellschaft in Zürich **50**.

Tomášek, M. 2000. Půdy České republiky. Czech Geological Institute, Praha, Czech Republic.

Tomšovic, P. 1990. 2. *Beta* L.—řepa. Pages 219–223 *in* S. Hejný, B. Slavík, L. Hrouda, and V. Skalický, editors. Květena České republiky. Volume 2. Academia, Praha, Czechoslovakia.

Tüxen, R. 1962. Gedanken zur Zerstörung der mitteleuropäischen Ackerbiozoenosen. Mitteilungen der Floristisch-Soziologischen Arbeitsgemeinschaft, N. F. **9**:60–61.

Vesecký, A., Š. Petrovič, V. Briedoň, and V. Karský. 1958. Climatic atlas of Czechoslovakia. Academia, Praha, Czechoslovakia.

Westhoff, V., and E. van der Maarel. 1978. The Braun-Blanquet approach. Pages 287–399 *in* R. H. Whittaker, editor.

Classification of plant communities. Dr. W. Junk, The Hague, The Netherlands.

Williamson, M. 1996. Biological invasions. Chapman and Hall, London, UK.

Zelený, V. 1992. 45. *Brassica* L.—brukev. Pages 215–218 *in* S. Hejný, B. Slavík, J. Kirschner, and J. Křísa, editors. Květena České republiky. Volume 3. Academia, Praha, Czechoslovakia.

APPENDIX A

A determination of minimal adequate models is available in ESA's Electronic Data Archive: *Ecological Archives* E086-040-A1.

APPENDIX B

A determination of net effects from minimal adequate models is available in ESA's Electronic Data Archive: *Ecological Archives* E086-040-A2.

APPENDIX C

Overview of species used in analyses with indication of their status and frequency of occurrence in sampled plots is available in ESA's Electronic Data Archive: *Ecological Archives* E086-040-A3.

APPENDIX D

Overall significance and variation explained by minimal adequate models is available in ESA's Electronic Data Archive: *Ecological Archives* E086-040-A4.

APPENDIX E

A comparison of the number of archaeophytes, neophytes, and native species in different crop types is available in ESA's Electronic Data Archive: *Ecological Archives* E086-040-A5.

APPENDIX F

A comparison of different crops in terms of the proportional numbers of archaeophytes, neophytes, and native species is available in ESA's Electronic Data Archive: *Ecological Archives* E086-040-A6.

Petr Pyšek, Vojtech Jarošík, Milan Chytrý, Zdenek Kropác, Lubomír Tichý, and Jan Wild. 2005. Alien plants in temperate weed communities: prehistoric and recent invaders. *Ecology* 86:772–785.

Appendix A. Determination of minimal adequate models.

In the maximal model, containing all factors, interactions and covariates that might be of interest, the interactions were fitted by regressing the response variable against each covariate within each level of each factor. In the first step of model simplification, the different slopes of response variable on each covariate within each factor level were in turn replaced by a common slope of the response variable on each covariate. The common slopes were regressed on the factors one after another, and the changes in residual deviance caused by removal of the different slopes for each covariate were assessed. After all covariates with a common slope were assessed, all non-significantly different slopes were deleted, and the reduced model was assessed. The analysis then continued on the reduced model. In this model, all remaining terms were deleted in turn from the reduced deviance table, and only those leading to a significant ($P < 0.05$) increase in residual deviance were retained. The deletion tests were repeated on the reduced models until, after removal from the last deviance table, the minimal adequate model that contained nothing but significant terms was determined.

When evaluating the proportional representations in all three categories of weeds, a care was taken when interpreting proportional representation of native species. An apparent reverse trend for native species was observed just as a consequence of the opposite trends in the proportions of archaeophytes and neophytes, that were analyzed before native species.

Petr Pyšek, Vojtech Jarošík, Milan Chytrý, Zdenek Kropác, Lubomír Tichý, and Jan Wild. 2005. Alien plants in temperate weed communities: prehistoric and recent invaders. *Ecology* 86:772–785.

Appendix B. Determination of net effects from minimal adequate models..

In the minimal adequate models, each response variable was significantly affected by several explanatory variables. To reveal a net effect of a particular explanatory variable, i.e., an effect attributable only to this variable and unbiased by other explanatory variables, all explanatory variables in the particular minimal adequate model, except that attributable to the particular net effect under consideration, were retained in the model, and the standardized residuals of the model were determined. To reveal the net effect, these residuals were then examined, using the residuals as the response variable, and the variable attributable to the particular net effect as the explanatory variable, assuming normal distribution of errors and identity link function (e.g., Lonsdale 1999; Pysek et al. 2002*a*,*c*; 2003*b*).

LITERATURE CITED

Lonsdale, M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**:1522–1536.

Pysek, P., V. Jarosík, and T. Kucera. 2002*a*. Patterns of invasion in temperate nature reserves. Biological Conservation **104**:13–24.

Pysek, P., T. Kucera, and V. Jarosík. 2002*c*. Plant species richness of nature reserves: the interplay of area, climate and habitat in a central European landscape. Global Ecology and Biogeography **11**:279–289.

Pysek, P., V. Jarosík, and T. Kucera. 2003*b*. Inclusion of native and alien species in temperate nature reserves: an historical study from Central Europe. Conservation Biology **17**:1414–1424.

Petr Pyšek, Vojtech Jarošík, Milan Chytrý, Zdenek Kropác, Lubomír Tichý, and Jan Wild. 2005. Alien plants in temperate weed communities: prehistoric and recent invaders. *Ecology* **86:772–785.**

Appendix C. Overview of species used in analyses with indication of their status (arch = archaeophyte; nat = native; neo = neophyte) and frequency of occurrence in sampled plots (*n* = 698). (j) = species present as juveniles. Nomenclature follows Ehrendorfer (1973). Species status follows Pyšek et al. (2002*b*).

Species	Status	Frequency (%)
Abutilon theophrasti	neo	0.1
Acer negundo (j)	neo	0.1
Acer pseudoplatanus (j)	nat	0.6
Acinos arvensis	nat	0.4
Adonis aestivalis	arch	13.5
Aegopodium podagraria	nat	0.9
Aethusa cynapium subsp. *agrestis*	arch	27.4
Agrimonia eupatoria subsp. *eupatoria*	nat	0.4
Agropyron repens	nat	65.9
Agrostemma githago	arch	1.3
Agrostis gigantea	neo	0.7
Agrostis stolonifera	nat	7.6
Agrostis tenuis	nat	2.1
Achillea millefolium agg.	nat	25.1
Achillea ptarmica	nat	0.1
Achillea setacea	nat	0.4
Ajuga chamaepitys	arch	2.0
Alchemilla vulgaris agg.	nat	3.6
Allium vineale	nat	0.1
Alopecurus myosuroides	arch	0.1
Alopecurus pratensis	nat	0.7
Alyssum alyssoides	nat	0.4
Amaranthus albus	neo	0.1
Amaranthus lividus	arch	0.4
Amaranthus powellii	neo	3.3
Amaranthus retroflexus	neo	8.5
Anagallis arvensis	arch	54.4
Anagallis foemina	arch	6.6
Androsace elongata	arch	0.3
Angelica sylvestris	nat	0.1
Anchusa arvensis	arch	12.5
Anthemis arvensis	arch	23.1
Anthemis austriaca	arch	8.9
Anthemis cotula	arch	2.6

Anthemis ruthenica	nat	0.3
Anthemis tinctoria	nat	0.1
Anthriscus sylvestris	nat	0.6
Apera spica-venti	arch	21.1
Aphanes arvensis	nat	16.9
Aphanes microcarpa	nat	0.3
Arabidopsis thaliana	nat	23.4
Arctium lappa	arch	0.4
Arctium tomentosum	arch	0.7
Arenaria serpyllifolia	nat	22.9
Armoracia rusticana	arch	0.6
Arnoseris minima	arch	0.6
Arrhenatherum elatius	neo	0.1
Artemisia vulgaris	nat	6.4
Asperugo procumbens	arch	0.1
Atriplex acuminata	arch	0.3
Atriplex patula	arch	32.1
Atriplex prostrata	nat	0.1
Avena fatua	arch	33.5
Avena sativa	arch	3.7
Beta vulgaris	arch	0.1
Bidens tripartita	nat	0.3
Bifora radians	arch	1.4
Brassica napus	arch	2.6
Bromus hordeaceus subsp. *hordeaceus*	arch	0.3
Buglossoides arvensis	nat	15.5
Bunias orientalis	neo	0.3
Bupleurum rotundifolium	arch	0.4
Camelina alyssum	arch	0.4
Camelina microcarpa	arch	3.3
Campanula patula	nat	0.1
Campanula rapunculoides	nat	23.4
Capsella bursa-pastoris	arch	73.4
Cardaria draba	arch	5.3
Carduus acanthoides	arch	1.9
Carduus nutans	nat	0.6
Caucalis platycarpos	arch	7.0
Centaurea cyanus	arch	28.8
Centaurea jacea	nat	0.1
Centaurea scabiosa	nat	0.9
Centaurium pulchellum	nat	0.1
Centunculus minimus	nat	0.1
Cerastium arvense	nat	0.1
Cerastium holosteoides	nat	17.2
Cerinthe minor	arch	1.0

Cichorium intybus	arch	2.1
Cirsium arvense	arch	73.9
Cirsium vulgare	arch	0.4
Conringia orientalis	arch	5.4
Consolida regalis	arch	30.1
Convolvulus arvensis	arch	47.3
Conyza canadensis	neo	8.2
Coronilla varia	nat	1.3
Coronopus squamatus	arch	0.1
Crepis biennis	arch	0.9
Crepis capillaris	arch	2.3
Cuscuta epithymum	arch	0.1
Dactylis glomerata	nat	1.0
Datura stramonium	neo	0.3
Daucus carota	nat	14.2
Descurainia sophia	arch	18.3
Deschampsia cespitosa	nat	0.3
Digitaria ischaemum	arch	1.1
Digitaria sanguinalis	arch	0.6
Diplotaxis muralis	arch	2.3
Echinochloa crus-galli	arch	8.7
Echium vulgare	arch	2.1
Epilobium adenocaulon	neo	1.3
Epilobium angustifolium	nat	0.1
Equisetum arvense	nat	18.1
Equisetum sylvaticum	nat	0.6
Eragrostis minor	arch	0.6
Erodium cicutarium	arch	29.1
Erophila verna	nat	8.7
Erucastrum gallicum	neo	0.6
Eryngium campestre	nat	0.3
Erysimum cheiranthoides	arch	8.5
Erysimum repandum	arch	0.4
Euphorbia cyparissias	nat	0.6
Euphorbia esula	nat	3.7
Euphorbia exigua	arch	23.2
Euphorbia falcata	arch	4.2
Euphorbia helioscopia	arch	36.4
Euphorbia peplus	arch	0.7
Euphorbia platyphyllos	nat	1.0
Euphorbia stricta	nat	0.1
Euphorbia virgata	nat	0.3
Falcaria vulgaris	nat	4.9
Fallopia convolvulus	arch	89.4
Festuca pratensis	nat	1.7

Festuca rubra	nat	0.1
Filago arvensis	nat	0.7
Filago minima	nat	0.1
Fumaria officinalis	arch	21.7
Fumaria rostellata	arch	2.6
Fumaria vaillantii	arch	5.7
Gagea pratensis	nat	1.0
Galeopsis angustifolia	nat	1.3
Galeopsis bifida	nat	9.0
Galeopsis ladanum	arch	1.6
Galeopsis pubescens	nat	2.3
Galeopsis tetrahit	nat	45.0
Galinsoga ciliata	neo	2.0
Galinsoga parviflora	neo	10.6
Galium album	nat	0.9
Galium aparine	nat	47.7
Galium spurium	arch	9.3
Galium tricornutum	arch	2.1
Geranium dissectum	arch	10.6
Geranium pusillum	arch	34.1
Glechoma hederacea	nat	2.1
Gnaphalium uliginosum	nat	17.0
Gypsophila muralis	nat	0.9
Heracleum mantegazzianum	neo	0.3
Heracleum sphondylium subsp. *sphondylium*	nat	0.4
Herniaria glabra	nat	0.3
Hibiscus trionum	arch	0.0
Holcus lanatus	nat	0.7
Holcus mollis	nat	9.6
Holosteum umbellatum	nat	2.0
Hordeum distichon	arch	3.4
Hyoscyamus niger	arch	1.0
Hypericum humifusum	nat	0.7
Hypericum maculatum	nat	1.7
Hypericum perforatum	nat	1.6
Hypochoeris glabra	nat	0.6
Hypochoeris radicata	nat	0.1
Chaenarrhinum minus	arch	9.3
Chaerophyllum aureum	nat	0.0
Chaerophyllum bulbosum	nat	0.1
Chenopodium album	nat	66.0
Chenopodium ficifolium	arch	3.2
Chenopodium glaucum	arch	1.7
Chenopodium hybridum	nat	7.2
Chenopodium polyspermum	arch	4.6

Chenopodium rubrum	nat	0.6
Chenopodium strictum	neo	0.1
Chenopodium suecicum	nat	0.3
Juncus bufonius	nat	6.2
Kickxia elatine	arch	0.6
Kickxia spuria	arch	2.7
Knautia arvensis subsp. *arvensis*	nat	3.7
Lactuca sativa	neo	0.1
Lactuca serriola	arch	2.9
Lamium amplexicaule	arch	41.8
Lamium purpureum	arch	28.9
Lapsana communis	arch	34.2
Lathyrus pratensis	nat	1.9
Lathyrus tuberosus	arch	17.3
Leontodon autumnalis	nat	0.4
Lepidium campestre	arch	0.3
Leucanthemum vulgare	nat	1.4
Linaria vulgaris	arch	11.6
Linum usitatissimum	arch	0.6
Lolium multiflorum	neo	3.9
Lolium perenne	nat	0.1
Lotus corniculatus	nat	0.7
Lupinus angustifolius	neo	0.1
Lupinus polyphyllus	neo	0.1
Luzula campestris	nat	0.1
Lycopodium annotinum	nat	0.1
Lychnis flos-cuculi	nat	0.1
Lysimachia nummularia	nat	0.3
Malva neglecta	arch	3.0
Malva pusilla	arch	1.0
Matricaria discoidea	neo	16.3
Matricaria chamomilla	nat	9.5
Medicago lupulina	arch	24.5
Medicago sativa	neo	0.6
Melampyrum arvense	arch	0.3
Melampyrum barbatum	neo	0.1
Melilotus alba	arch	0.4
Melilotus officinalis	arch	1.6
Mentha arvensis	arch	24.1
Mercurialis annua	arch	4.6
Misopates orontium	arch	0.3
Myosotis arvensis	arch	55.9
Myosotis discolor	nat	3.0
Myosotis ramosissima	nat	0.3
Myosotis stricta	nat	11.5

Myosoton aquaticum	nat	0.1
Myosurus minimus	nat	2.0
Neslia paniculata	arch	30.9
Nigella arvensis	arch	0.4
Nonea pulla	nat	1.6
Odontites verna	nat	1.3
Odontites vulgaris	nat	5.6
Onopordum acanthium	arch	0.1
Orobanche minor	arch	0.1
Oxalis fontana	neo	3.3
Panicum miliaceum subsp. *agricola*	neo	0.1
Panicum miliaceum subsp. *ruderale*	neo	0.1
Papaver argemone	arch	11.9
Papaver dubium	arch	6.7
Papaver rhoeas	arch	33.2
Pastinaca sativa subsp. *sativa*	arch	0.1
Persicaria lapathifolium subsp. *incanum*	nat	14.3
Persicaria lapathifolium subsp. *lapathifolium*	nat	17.8
Phleum pratense	nat	2.9
Phragmites australis	nat	0.1
Picris hieracioides	nat	0.7
Pimpinella major	nat	0.1
Pimpinella saxifraga	nat	0.1
Pinus sylvestris (j)	nat	0.3
Pisum sativum	arch	0.1
Plantago lanceolata	nat	12.9
Plantago major subsp. *intermedia*	nat	14.9
Plantago major subsp. *major*	arch	35.4
Plantago media	nat	1.0
Poa annua	nat	37.0
Poa compressa	nat	1.0
Poa palustris	nat	0.1
Poa pratensis	nat	1.0
Poa supina	nat	2.3
Poa trivialis	nat	5.3
Polycnemum arvense	arch	0.1
Polygonum amphibium	nat	1.7
Polygonum arenastrum	nat	23.9
Polygonum aviculare	arch	57.2
Polygonum bistorta	nat	0.1
Polygonum hydropiper	nat	12.8
Polygonum persicaria	nat	25.9
Polygonum rurivagum	nat	6.2
Portulaca oleracea	arch	0.9
Potentilla anserina	nat	8.3

Potentilla argentea	nat	0.4
Potentilla reptans	nat	2.7
Potentilla supina	neo	0.4
Prunella vulgaris	nat	3.0
Ranunculus acris	nat	0.6
Ranunculus arvensis	arch	7.0
Ranunculus auricomus agg.	nat	0.3
Ranunculus bulbosus	nat	0.3
Ranunculus ficaria subsp. *bulbifer*	nat	0.1
Ranunculus nemorosus	nat	0.1
Ranunculus repens	nat	17.6
Ranunculus sardous	nat	2.0
Raphanus raphanistrum	arch	49.9
Reseda lutea	arch	2.4
Rhinanthus alectorolophus	nat	1.3
Rhinanthus minor	nat	0.3
Rorippa sylvestris	nat	1.7
Rubus fruticosus agg.	nat	5.9
Rumex acetosa	nat	2.3
Rumex acetosella	nat	22.8
Rumex crispus	nat	39.0
Rumex obtusifolius	nat	11.0
Rumex tenuifolius	nat	0.3
Sagina procumbens	nat	5.7
Salix caprea (j)	nat	0.3
Salvia nemorosa	nat	0.1
Salvia verticillata	nat	1.7
Sambucus nigra (j)	nat	0.1
Sanguisorba minor	nat	0.4
Sanguisorba officinalis	nat	1.3
Scabiosa ochroleuca	nat	0.3
Scleranthus annuus	arch	37.5
Secale cereale	arch	2.3
Sedum maximum	nat	3.4
Senecio sylvaticus	nat	0.1
Senecio vernalis	neo	1.3
Senecio viscosus	nat	0.0
Senecio vulgaris	arch	4.6
Setaria glauca	arch	6.0
Setaria verticillata	arch	0.1
Setaria viridis	arch	7.4
Sherardia arvensis	arch	21.5
Silene alba subsp. *alba*	arch	16.3
Silene noctiflora	arch	37.4
Silene vulgaris subsp. *vulgaris*	nat	1.0

Sinapis alba	neo	0.3
Sinapis arvensis	arch	41.7
Sisymbrium officinale	arch	0.6
Solanum lycopersicum	neo	0.4
Solanum nigrum	arch	4.4
Solanum tuberosum	neo	2.1
Sonchus arvensis	arch	28.1
Sonchus asper	arch	36.2
Sonchus oleraceus	arch	11.7
Sorbus aucuparia (j)	nat	0.1
Spergula arvensis	arch	25.1
Spergularia rubra	nat	4.3
Stachys annua	arch	3.4
Stachys palustris	nat	17.5
Stellaria graminea	nat	2.4
Stellaria media	nat	80.4
Symphytum officinale	nat	1.1
Tanacetum vulgare	arch	1.7
Taraxacum sect. *Ruderalia*	nat	44.7
Teesdalia nudicaulis	nat	0.7
Thlaspi arvense	arch	66.0
Thlaspi perfoliatum	nat	2.0
Torilis japonica	nat	0.1
Trifolium arvense	nat	4.9
Trifolium aureum	nat	0.1
Trifolium campestre	nat	1.9
Trifolium dubium	nat	1.0
Trifolium hybridum	neo	4.3
Trifolium pratense	nat	6.9
Trifolium repens	nat	14.2
Tripleurospermum inodorum	arch	60.2
Triticum aestivum	arch	2.7
Tussilago farfara	nat	12.0
Urtica dioica	nat	0.1
Urtica urens	arch	1.9
Valerianella dentata	arch	15.3
Valerianella locusta	nat	1.9
Valerianella rimosa	arch	0.3
Veronica agrestis	arch	5.2
Veronica arvensis	arch	33.8
Veronica hederifolia	arch	13.3
Veronica chamaedrys	nat	0.7
Veronica opaca	arch	3.7
Veronica persica	neo	55.2
Veronica polita	arch	28.5

Veronica praecox	nat	2.3
Veronica prostrata	nat	0.1
Veronica serpyllifolia	nat	3.2
Veronica sublobata	nat	22.3
Veronica triloba	arch	5.3
Veronica triphyllos	arch	11.0
Veronica verna	nat	0.9
Vicia angustifolia	arch	34.0
Vicia cracca	nat	6.7
Vicia hirsuta	arch	34.7
Vicia pannonica subsp. *pannonica*	arch	0.4
Vicia sativa	arch	6.6
Vicia sepium	nat	0.3
Vicia tenuifolia	nat	1.0
Vicia tetrasperma	nat	23.8
Vicia villosa subsp. *varia*	nat	0.3
Vicia villosa subsp. *villosa*	arch	4.4
Viola arvensis	nat	86.4
Viola tricolor subsp. *tricolor*	arch	5.0

LITERATURE CITED

Ehrendorfer, F. Editor. 1973. Liste der Gefässpflanzen Mitteleuropas. Second edition, Gustav Fischer Verlag, Stuttgart, Germany.

Pyšek, P., J. Sádlo, and B. Mandák. 2002*b*. Catalogue of alien plants of the Czech Republic. Preslia **74**:97–186.

Petr Pyšek, Vojtech Jarošík, Milan Chytrý, Zdenek Kropác, Lubomír Tichý, and Jan Wild. 2005. Alien plants in temperate weed communities: prehistoric and recent invaders. *Ecology* **86:772–785.**

Appendix D. Overall significance (F, df, P) and variation (R^2) explained by minimal adequate models.

	Numbers				Proportional numbers			
	F	df	P	R^2 (%)	F	df	P	R^2 (%)
Archaeophytes	12.75	26, 671	<0.001	33.1	24.28	20, 677	<0.001	44.7
Neophytes	16.78	21, 676	<0.001	34.3	215.30[†]	11	<0.001	27.3
Native	29.86	21, 676	<0.001	48.1	29.05	22, 675	<0.001	51.2

[†] Chi-square test

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Appendix E. Comparison of the number of archaeophytes, neophytes and native species in different crop types. Ranks are given from 1 (richest crop) to 8 (poorest crop) for each group of weeds. Crop types significantly poorer and richer in LSD tests ($P < 0.05$) than the one displayed in a given row are indicated in columns. Root = root crops.

Crop type	n	Archaeophytes			Neophytes			Native species		
		Rank	Poorer crop types	Richer crop types	Rank	Poorer crop types	Richer crop types	Rank	Poorer crop types	Richer crop types
Cereal	377	3	–	root	7	–	stubble, rape, root, maize	5	–	stubble, root, fodder
Fodder	95	4	–	–	8	–	stubble, rape, root, maize	3	maize, cereal	stubble
Maize	18	6	–	–	1	fodder, cereal, other, vegetable, stubble, rape	–	7	–	stubble, root, fodder
Rape	24	7	–	root	3	fodder, cereal	maize	4	–	stubble
Root	90	1	cereal, rape	–	2	fodder, cereal, vegetable	–	2	maize, vegetable, cereal	–
Stubble	68	2	–	–	4	fodder, cereal	maize	1	maize, vegetable, cereal, rape, fodder	–
Vegetable	19	5	–	–	5	–	root, maize	6	–	stubble, root
Other	7	8	–	–	6	–	maize	8	–	–

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Appendix F. Comparison of different crops in terms of the proportional numbers of archaeophytes, neophytes, and native species. Otherwise as in [Appendix E](#).

Crop	n	Archaeophytes			Neophytes			Native species		
		Rank	Poorer crop types	Richer crop types	Rank	Poorer crop types	Richer crop types	Rank	Poorer crop types	Richer crop types
Cereal	377	1	stubble, fodder	-	7	-	root, rape, vegetable, other, maize	5	-	fodder
Fodder	95	6	-	root, cereal	6	-	root, rape, vegetable, maize	1	maize, cereal, root	-
Maize	18	3	-	-	1	stubble, cereal, fodder, root	-	7	-	fodder
Rape	24	8	-	-	4	stubble, cereal, fodder	-	2	-	-
Root	90	2	stubble, fodder	-	5	cereal, fodder	maize	4	-	fodder
Stubble	68	7	-	root, cereal	8	-	rape, vegetable, maize	3	-	-
Vegetable	19	4	-	-	3	stubble, cereal, fodder	-	8	-	-
Other	7	5	-	-	2	cereal	-	6	-	-