INVASIONS OF ALIEN PLANTS INTO HABITATS OF CENTRAL EUROPEAN LANDSCAPE: AN HISTORICAL PATTERN

Petr Pyšek[1], Karel Prach[2] and Bohumil Mandák[1]
[1]*Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic; e-mail: pysek@ibot.cas.cz;* [2]*Faculty of Biology, University of South Bohemia, Branišovská 31, CZ-370 01 České Budějovice, Czech Republic; e-mail: Karel.Prach@tix.bf.jcu.cz*

Abstract

The localities of 53 species alien to the flora of the Czech Republic were collated from their introduction to the present. The information on the distribution of particular species was obtained by using herbaria (contributing 37.4 % of the total number of localities), floristic periodicals (53.4 %) and unpublished data (9.1 %). In total, 32,277 localities were recorded. If given in the original source, information was recorded on the (i) the year of the record, and (ii) the type of the habitat. The classification of habitats yielded 14 types, divided into two main groups, (1) man-made, heavily disturbed habitats, and (2) less disturbed sites of a more natural origin. Aliens occur most frequently in cities and villages (25.6 % of the total number of localities), and riparian habitats (22.4 %). From the viewpoint of management, these habitats represent further potential sources for their spread into the landscape. The contribution of other habitat types never exceeds 10 %. The representation of forests is rather high (9.2 % including forest margins). The majority of "seminatural" habitats, namely scrub and grasslands, prove to be rather resistant. The representation of particular habitas has been changing remarkably in the course of the 20th century, the most conspicuous trend being a decrease in relative representation of urban habitats and an increasing role of habitats facilitating dispersal (including roads, railways and paths). These trends can be interpreted as a consequence of changes of intensity and type of disturbances affecting the landscape during this period. Every habitat, including forest interiors, has at least some well established invaders.

Introduction

In research on biological invasions, the importance of recipient habitat has been increasingly recognized (Lodge 1993). Although the species-view approach to predicting plant invasions has had some success recently (Rejmánek 1995, 1996) it is clear that attempts to predict the outcomes of invasions have a limited chance of succeeding if they do not take the characteristics of invaded habitats into account (Scott and Panetta 1993).

Nevertheless, scepticism concerning our predictive power with respect to plant invasiveness has its precedents. Recently, Williamson (1996) summarized available data on the role of habitat, carried out a critical assessment and came to similar conclusions to Crawley (1987) who compared the number of alien species in particular habitats in the British Isles, and Usher *et al.* (1988) who evaluated invasions into nature reserves at the global level. Studies yielding solid quantitative data are rather few and so the generalizations are not well established either (Williamson 1996):

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1. Each plant community is, in principle, invasible.
2. It is probable that some communities are more vulnerable to invasions than others.

In general the invasibility of communities and ecosystems depends much on (a) the position of invaded communities on environmental gradients (moisture, nutrients, disturbance, successional age), and (b) the biotic characteristics of invaded communities (Rejmánek 1989; Hobbs and Huenneke 1992; Hobbs and Humphries 1995; Tilman 1997). Disturbance is another important factor, particularly in man-made habitats where its intensity and frequency is usually high. Not only the intensity and frequency of disturbance but also the change in its regime can increase the vulnerability of plant communities to invasion (Hobbs and Humphries 1995).

Because of the lack of available data, our understanding of why some communities are more prone to invasions by alien plants than others remains, to a large extent, rather intuitive, and more carefully designed studies are needed to verify the hypotheses.

This chapter summarizes 250 years of history of plant invasions into the Czech flora by invaded habitat, and provides a large body of quantitative data to assess the invasibility of particular habitat types, broadly defined within the range of a landscape approach. It also evaluates the changes in the role of particular habitats on an historical time scale.

Data sources and methods

Species selection and collation of the data

Fifty three species alien to the flora of the Czech Republic (area of 78,854 km^2) were selected and information on their localities from the early days up to present was collated. The criteria for species selection were as follows:

(a) Alien status. The species considered were neophytes, i.e. introduced to the territory of the Czech Republic after 1500 A.D. The immigration status was obtained from Czech floras (Hejný and Slavík 1988–1992, Slavík 1995–1997), relevant papers on the topic (Opravil 1980) and databases covering neighbouring Central European countries (Frank and Klotz 1990; Ellenberg *et al.* 1991). The species were introduced between 1738 and 1963 (Pyšek *et al.*, unpublished data) and their area of origin is as follows: America 28, Europe or Eurasia 14, Asia 10, Australia 1.

(b) Degree of naturalization. The aim was to include all the major invaders in the Czech flora so as to get the most complete picture of habitats invaded. Naturalized, commonly occurring invaders were not considered only if taxonomically problematic, so not easily recognizable, and so the reliability of floristic records would be low (e.g. the species of *Aster*, *Stenactis, Oenothera*).

Species used in the analysis are listed in Appendix 1.

Information on the distribution of particular species was got from the following sources (only the occurrence in the wild was considered, i.e. records in cultivation were not included into the analysis):

(a) Major herbaria (Charles University Praha – PR, National Museum Praha – PRC, Masaryk University Brno – BRNU) as well as various local herbarium collections (CB, CHOM, HR, LIM, LIT, MJ, PL, ROZ, Příbram, Sokolov). In total, these herbaria comprise about 5,100,000 of specimens of vascular plants. Herbaria contributed 37.4 % to the total number of localities analysed in the present study.

(b) Botanical literature: All major floras, periodicals, floristic works and some manuscripts (dissertations, theses) were checked for the occurrence of the species. The proportion of published records was 53.4 % of the total number of localities.
(c) Unpublished data obtained by personal communications, including our own field research in the last few years. Unpublished data contributed 9.1 % to the total number of localities collated.

The work used the fact that in the Czech Republic there is a high density of floristic records going back a long time (Pyšek 1991; Pyšek and Prach 1993, 1995; Mandák and Pyšek, this volume).

Classification of habitats

If given in the original source, information was recorded on the (i) year of the record, and (ii) type of the habitat. Habitats were classified into 14 habitat types listed in Table 1. This classification might seem rather vague but seems to be the only possible one, considering the detail of habitat description normally given in floristic data.

Particular habitats differ in their abundance in the landscape and in the frequency and character of disturbances. On the basis of their origin and the intensity of disturbance, they were divided arbitrarily into two main groups: (1) man-made, heavily disturbed habitats (6 types), comprising urban sites, roads ditches and banks, railway areas, dumps of various materials, fields and old-fields, paths and their margins; (2) less disturbed sites of a more natural origin (8 types) including water courses and their shores, fishponds, scrub, grasslands, forests and their margins, and also large parks and the surroundings of solitary objects in relatively undisturbed landscape, such as chalets, gamekeeper's lodges etc. (Table 1). We are aware that this division is rather rough and arbitrary, but the data do not allow a more sophisticated delimitation to be used.

Results

The role of particular habitats

In total, 32,277 localities of the alien species considered were recorded, distributed rather unevenly among particular habitats (Table 2). Aliens occur most frequently in human settlements (including both large cities, towns and villages), which contribute 25.6 % to the total number of localities reported. Riparian habitats, i.e. surroundings of both running and still waters, are the second most important, together representing 22.4 %. The contribution of other habitat types never exceeds 10 %. However, the representation of forests, the relatively least disturbed habitats, is rather high (9.2 % if margins are included). The majority of "seminatural" habitats, mostly scrub and grassland, are rather resistant (Fig. 1).

Changes in the importance of habitats: temporal trends

The increase in the total number of localities at 50-years intervals is given in Table 2. The representation of particular habitats has changed remarkably in the course of the 20th century (Fig. 2, Table 2). There was a strong decrease in urban habitats, contrib-

Table 1. Classification of habitats given in floristic records. Particular habitats are arranged according to the level of disturbance, i.e. approximately from those disturbed and heavily affected by man to those with more "seminatural" character. The evaluation of the possibilities for the transport of diaspores is relative and based on observational experiences.

Habitat	Characteristics	Frequency in the landscape / Area	Intensity / type of disturbance	Possibilities for transport of diaspores	Status (seminatural vs. man-made
Urban	ruderal habitats and industrial sites in cities, towns and villlages	very frequent, large area	very high / various kinds	very high	man-made
Roads	road ditches and margins in settlements and open landscape	very frequent, small area	high / transport, trampling, salt treatments	very high	man-made
Railways	railway stations and tracks	frequent, small area	high / transport	very high	man-made
Arable land	managed fields, abandoned fields	very frequent, large area	high/agricultural management	moderate	man-made
Dumps	deposits of various character, i.e. dumps, rubbish tips, spoil heaps, dung heaps etc.	frequent, locally more represented, small area	low-high (depending on successional stage)	high (low after dumping)	man-made
Paths	paths in forests, meadows etc. and their margins (not affected by traffic)	very frequent, small area	moderate / various, e.g. trampling	moderate-high	man-made
Ponds	water bodies, mostly ponds and their shores and litoral, wetlands	locally frequent, small area	moderate / eutrofication, fishery	low-moderate	seminatural
Water courses	running waters, i.e. rivers, and brooks, and their shores	very frequent, small area	moderate / floods, eutrofication	high	seminatural
Scrubland	drier habitats dominated by shrubs, including dry xerotherm grasslands	frequent, small area	low	low	seminatural
Grasslands	fresh to moist grasslands subjected to regular management or abandoned	frequent, large area	moderate / mowing, agricultural management	low-moderate	seminatural
Forests	coniferous forests, deciduous woodlands, both seminatural and monocultural	very frequent, large area	low / forestry management practices	low	seminatural
Forest margins	transitions between forests and surrounding habitats	frequent, small area	moderate / various	low	seminatural
Parks	managed parks and gardens, public greenery, chateau gardens	less frequent, small area	low / gardening practices	low-moderate	seminatural
Solitary objects	chalets, gamekeeper's lodges and their surroundings etc.	rather rare, small area	low	low	seminatural

Table 2. Number of localities recorded in particular habitats (see Table 1 for habitat description and characteristics) during 50 year periods. Total number of localities does not correspond exactly to the figure obtained by summing up the numbers for particular periods because some of the records were not dated in the original sources. Similarly, the sum of total numbers in particular habitats exceeds the total of localities analysed (n = 32,277) as some localities were attributed to more than one habitat. Habitats are ranked by decreasing importance.

Habitat	-1850	1850-1900	1900-1950	1950-1995	Total	%
Urban	72	569	1754	5857	8331	25.61
Water courses	7	239	736	3162	4159	12.78
Ponds	5	173	556	2392	3136	9.64
Railways	0	78	389	2099	2581	7.93
Forests	1	44	374	1732	2155	6.62
Roads	2	33	220	1783	2045	6.29
Arable land	6	111	389	1419	1944	5.97
Paths	0	52	270	1582	1911	5.87
Deponies	3	32	249	1415	1716	5.27
Scrubland	2	39	322	1073	1440	4.43
Grasslands	7	72	262	1087	1432	4.40
Forest margins	0	15	163	666	848	2.61
Parks, gardens	11	74	151	349	569	1.75
Solitary objects	0	8	24	237	269	0.83
Total	116	1539	5859	24853	32536	

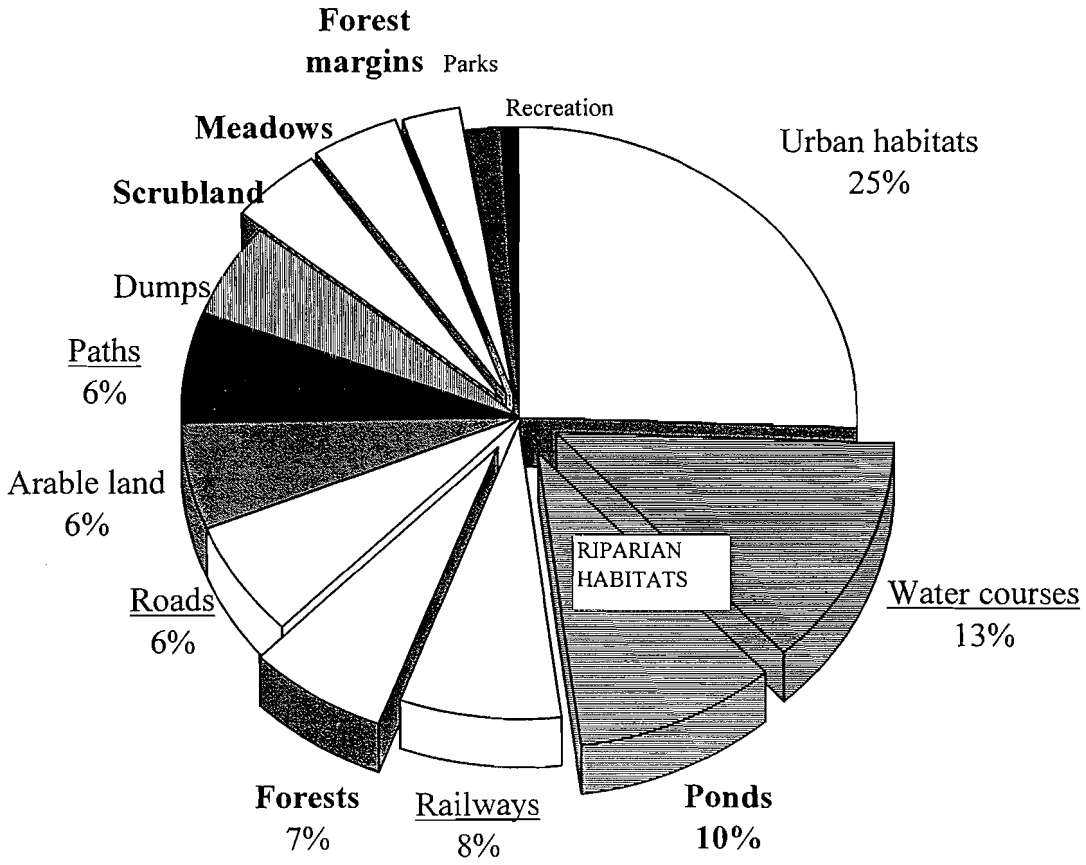

Fig. 1. Frequency of particular habitats in the whole data set from 32,277 localities of 53 major aliens to the Czech flora recorded between 1738–1995. Habitats considered as less heavily disturbed (i.e. "seminatural") are shown in bold letters, "transport" habitats are underlined. Approximate percentage representation is shown for more important habitats (exceeding 5 %).

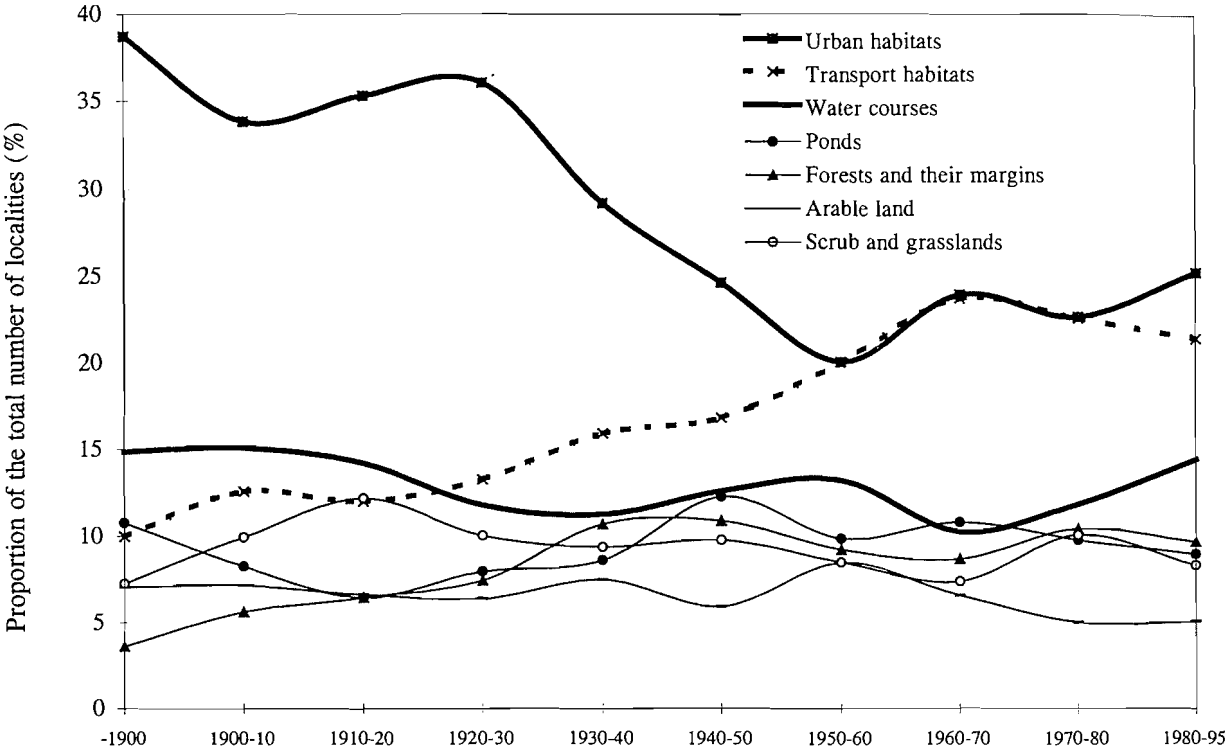

Fig. 2. Changes in representation of habitats of alien species during the 20th century. Proportional contributions to the total are displayed for particular decades. Some habitats were grouped to make the trends obvious, the values for each habitat can be found in Table 2. Transport habitats include road ditches and margins, railway areas and paths, but exclude water courses.

uting 38.7 % in 1900 but only 25.6 % in the last 15 years, and this trend was highly significant (slope of the regression of percentage representation in particular decades on time was significantly different from zero, $r = -0.85$, $F_{1,8} = 21.5$, $P < 0.01$). The most remarkable increase, on the other hand was found in "transport" habitats (including roads, railways and paths), representation of which started at 10 % in 1900 and between 1980–95 exceeded 20 %. This trend was also highly significant ($r = 0.94$, $F_{1,8} = 62.1$, $P < 0.0001$) and the same was true for dumps ($r = 0.81$, $F_{1,8} = 15.9$, $P < 0.01$). Forest habitats and their margins also enhanced their representation, reaching 3.6 % at the beginning of the century but fluctuating around 10 % in the last few decades ($r = 0.78$, $F_{1,8} = 12.4$, $P < 0.01$). Other habitat types do not exhibit interpretable trends in their representation over time ($P > 0.05$): $r = 0.26$, $F_{1,8} = 0.59$ for ponds, $r = 0.42$, $F_{1,8} = 1.8$ for water courses, $r = 0.51$, $F_{1,8} = 2.8$ for arable land, and $r = 0.09$, $F_{1,8} = 0.07$ for scrubland (Fig. 2).

The trends are not consistent between more disturbed (man-made) vs. less disturbed ("seminatural") habitats – e.g. the decrease in urban sites is compensated by an increase in "transport" habitats such as water courses, whereas the increase in forests is balanced by a decrease in parks, etc. so no change in the pattern of representation of both was found (regression slopes not significantly different from zero, $r = 0.09$, $F_{1,8} = 0.07$, $P = 0.79$).

Table 3. Major invaders in particular habitats. For each habitat, the proportional contribution of particular species to the total number of localities recorded in the habitat was calculated and three species with highest representation are listed. Total percentage contribution of these three species is shown in the last colums.

Habitat	Major invaders	Σ %
Urban	*Chamomilla suaveolens* 8.3, *Galinsoga parviflora* 6.5, *Amaranthus retroflexus* 6.0	20.8
Roads	*Cardaria draba* 7.7, *Chamomilla suaveolens* 6.2, *Epilobium ciliatum* 5.5	19.4
Railways	*Cardaria draba* 10.3, *Oenothera biennis* 7.5, *Conyza canadensis* 6.8	24.6
Arable land	*Veronica persica* 25.6, *Galinsoga parviflora* 20.4, *Amaranthus retroflexus* 7.6	53.6
Deponies	*Amaranthus retroflexus* 11.2, *Cardaria draba* 7.5, *Galinsoga parviflora* 6.5	25.2
Paths	*Juncus tenuis* 26.6, *Chamomilla suaveolens* 7.4, *Epilobium ciliatum* 5.8	39.8
Ponds	*Acorus calamus* 23.6, *Elodea canadensis* 18.7, *Potentilla norvegica* 8.5	50.8
Water courses	*Impatiens parviflora* 8.4, *Bidens frondosa* 7.4, *Impatiens glandulifera* 6.6	22.4
Scrubland	*Bryonia alba* 16.1, *Robinia pseudoacacia* 10.1, *Cardaria draba* 5.6	31.8
Meadows	*Trifolium hybridum* 29.9, *Juncus tenuis* 11.0, *Epilobium ciliatum* 7.8	48.7
Forests	*Juncus tenuis* 23.4, *Impatiens parviflora* 17.9, *Digitalis purpurea* 7.1	48.4
Forest margins	*Lupinus polyphyllus* 12.4, *Juncus tenuis* 10.8, *Digitalis purpurea* 10.0	33.2
Parks, gardens	*Geranium pyrenaicum* 16.6, *Impatiens parviflora* 11.7, *Galinsoga ciliata* 5.1	33.4
Recreation areas	*Impatiens parviflora* 8.5, *Juncus tenuis* 8.1, *Lupinus polyphyllus* 6.6	23.2

Species in particular habitats

Table 3 summarizes the major invaders of particular habitats. Some species occur in several habitats, e.g. *Chamomilla suaveolens, Impatiens parviflora, Juncus tenuis, Galinsoga parviflora, Epilobium ciliatum.* The joint contribution of the three most frequent species varies from 19.4 % to 53.6 % with respect to the habitats. Habitats with a high value for the three most frequently encountered invaders are those with rather specialized invasive aliens, notably arable fields, ponds, meadows, and forests. On the other hand, a less specialized alien flora is typical of urban habitats, roads, railways, water courses and recreational areas (Table 3).

Discussion

The data are remarkable for (a) the number of records included, (b) the historical timescale considered, and (c) the degree of completeness of the alien flora sampled. The pooled data representing more than 32 thousand localities of which 91.2 % were classified by habitat, are a very good measure of importance of particular habitats. The 53 species cover most major invasives of the Czech flora, a reasonably representative sample of the alien flora. This is the first quantitative data set in which it is possible to evaluate changes in the role that particular habitats played in the Central European landscape on the time scale of centuries.

We show that the major habitats of aliens in the Czech Republic are urban and riparian sites (Wittig 1991; de Waal *et al.* 1994; Kowarik 1995; Sukopp *et al.* 1995; Pyšek 1998). For management, these habitats are further potential sources of spread. This is confirmed by the increase in the importance of transport sites over time. Roads and railways are always connected with cities and villages and the steadily increasing rep-

Table 4. Comparison between the proportinal extent of land-use types in the Czech Republic (taken from statistical yearbook – Anonymous 1996) and their invasibility, expressed by the contribution to the total number of localities of alien species recorded in the present study.

Land-use category	Corresponding habitats in the present study	Area in the Czech Republic (%)	Contribution to the number of localities (%)
Arable land	Arable land	39.9	6.0
Meadows and pastures	Grassland, scrubland	14.4	8.8
Forests	Forests, forest margins	33.3	9.2
Surface waters	Ponds, water courses	2.0	22.4
Built-up area and other sites	Urban, railways, roads, paths, deponies, parks and gardens, solitary objects	10.4	53.6

resentation of these sites from the 1920s is an indication that alien species penetrate gradually more and more into the landscape, outside the limits of human settlements. However, almost every habitat has its own, well established invaders whose properties fit its characteristics (Crawley 1987). In quantitative terms, even forest interiors have some important invaders, *Impatiens parviflora* being a typical example (Trepl 1984).

Another limit to the data set is that it does not take into account the extent of the particular habitats in the landscape (Pyšek and Pyšek 1995); these are not known for the whole country. The only way to do this here was to group our habitat types into broader categories corresponding to administrative land use categories, whose area is regularly published for the whole country in statistical yearbooks (Anonymous 1996). The comparison between the proportion of particular land-use types and proportion of localities of alien plants in the corresponding habitat categories is given in Table 4. This is only tentative as some categories could not be related unambiguosly to the land-use types (e.g. paths can occur in many habitats). Scrubland was included into the category "meadows and pastures" as scrub usually develops on agricultural land, often in extensive or abandoned pastures, in abandoned meadows or as hedges between particular parcels. Also, the pattern of land-use has changed. Nevertheless, it still provides us with a rough picture of the importance of broadly defined land-use types.

A remarkable difference between the area of the habitat and its contribution to the abundance of aliens was found (χ^2 goodness-of-fit test with expected values derived from the area of the habitat: $\chi^2 = 85722.5$, df 4, $p < 10^{-9}$). The results indicate a higher invasibility of settlements and surface water areas and a low invasibility of less disturbed habitats, i.e forests, grassland and scrubland (Table 4). The low proportion of records from arable land could be explained by these habitat types harbouring archaeophytes which were not included in the present study.

The decrease in the proportion of urban habitats between 1920s and 1960s reflects changes of intensity and type of disturbance. Early in this century, cities were best places where the influx of aliens was concentrated, and where these species had the best chance of surviving or possibly establishing (Gilbert 1989; Wittig 1991). The surrounding open landscape was disturbed less and in a different way. From the 1930s on, the landscape has become gradually more disturbed which meant easier penetration of aliens. From the 1950s, the extent of urban habitats started to increase again as a consequence of remarkable building activity, e. g. large scale estates at the periphery

of big cities, leaving extensive wasteland to be colonized and providing for the initial successional stages of alien species (Mandák and Pyšek, this volume).

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Appendix 1. The species alien to the Czech flora which were used for the analysis of habitat preferences. Fifty-three species were considered. Nomenclature follows Tutin et al. (1964–1980).
Acer negundo, Acorus calamus, Ailanthus altissima, Amaranthus albus, Amaranthus powellii, Amaranthus retroflexus, Ambrosia artemisiifolia, Ambrosia trifida, Amorpha fruticosa, Bidens frondosa, Bryonia alba, Bunias orientalis, Cardaria draba[1], *Chamomilla suaveolens, Chenopodium botrys, Chenopodium foliosum, Chenopodium pumilio, Conyza canadensis, Corydalis lutea, Cymbalaria muralis, Digitalis purpurea, Echinocystis lobata, Elodea canadensis, Epilobium adenocaulon, Galinsoga ciliata, Galinsoga parviflora, Heracleum mantegazzianum, Hordeum jubatum, Impatiens glandulifera, Impatiens parviflora, Iva xanthiifolia, Juncus tenuis, Lupinus polyphyllus, Lycium barbarum, Mimulus guttatus, Oenothera biennis, Physocarpus opulifolia, Pinus nigra, Pinus strobus, Potentilla norvegica, Reynoutria japonica, Reynoutria sachalinensis, Robinia pseudoacacia, Rudbeckia laciniata, Sisyrinchium angustifolium, Solidago canadensis, Solidago gigantea, Telekia speciosa, Trifolium hybridum, Veronica filiformis, Veronica persica, Xanthium spinosum.*

[1] Some sources classify this species as an archaeophyte (Opravil 1980).