

# Alien flora of the Czech Republic, its composition, structure and history

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## Abstract

Comprehensive information on the alien flora of the Czech Republic is presented. The first complete list of non-native taxa reported from the country since the beginning of agriculture 7,300 year ago was developed from available knowledge. There are 1378 alien taxa, 33.4% of the total plant diversity of the country. The composition and structure of the alien flora is classified using the categories of Richardson *et al.* 2000 (there are 64.7% casuals, 28.8% naturalized, and 6.5% invasive taxa), by residence time (24.1% of archeophytes. i.e. introduced before 1500, and 75.9% neophytes introduced after then), by introduction mode (53.4% of accidental arrivals, 46.6% deliberate introductions), and by habitat type invaded (62.8% confined to human-made habitats, 11.0% recorded in seminatural and natural habitats, and 26.2% recorded in both). Archaeophytes differ from neophytes in the distribution of particular categories of invasive status, abundance in the landscape, vegetation type invaded, Grime's life strategies, and representation in families. Most "neophytic genera/families" contain very low number of species whereas in archaeophytes the distribution is shifted towards more species-rich genera/families. The available data suggest that the most intense immigration of archaeophytes occurred during Neolithic/Chalcolithic period, then proceeded at a steady pace until the Medieval when another peak of immigration occurred. Problems associated with acquiring reliable quantitative data on alien floras and with comparisons between regions are discussed.

## Introduction

Plant invasions have been receiving increasing attention since the 1980s worldwide and this interest has resulted in the publication of several books (e.g. Drake *et al.* 1989, Groves and di Castri 1991, di Castri *et al.* 1990, Stone *et al.* 1992, Pyšek *et al.* 1995, Williamson 1996, Carey *et al.* 1996). Studies on alien plants provide us with unique opportunities for research into ecological relationships, and the topic is perceived as having serious practical importance (Cronk and Fuller 1995, Luken and Thieret 1997). So far, the ecological approach to plant invasions has been mostly based on (a) biological and ecological features promoting the invasion success of particular species (e.g. Newsome and Noble 1989, Rejmánek 1995) and (b) the character and invasibility of invaded communities (Rejmánek 1989). Recently, both approaches are taken as complementary (Lodge 1993, Hobbs and Huenneke 1992).

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However, phytogeographical and floristic approaches, although not encouraged much by present scientometric criteria, are an integral part of research on plant invasions, and there is a growing awareness of the importance of taxonomy in studies dealing with alien plants (McNeely *et al.* 2001). Unfortunately, the distribution of available data over the globe is rather uneven. Comprehensive catalogues of alien floras have been produced and/or analysed for major “invasion hot spots” such as South Africa (Wells *et al.* 1986), Hawaii (Wester *et al.* 1992), California (Rejmánek *et al.* 1991), Australia (Groves 1998). In Central Europe, the lists of alien floras are mostly for big cities, as a result of the strong tradition of urban ecological research (e.g. Sukopp and Hejný 1990, Sukopp *et al.* 1995, Pyšek 1998a). Some excellent data sets have been produced, making it possible not only to record the present situation but also to infer the history of invasions and the development of alien floras in urban environments (Klotz 1984, Kowarik 1988, 1990, Gutte 1989, Sudnik-Wojcikowska 1987). However, the lists of urban aliens only relate to a specific habitat. Lists covering whole countries (i.e. the area of tens or hundreds of thousands of square kilometers) are of a greater importance as they include a wide range of habitats, thus providing a comprehensive overview of the alien flora of a given region. They can be used for comparative analyses, prediction and testing the ecological aspects of plant invasions (Thompson *et al.* 1995, Crawley *et al.* 1996, Kowarik 1990, Crawley 1987, Pyšek *et al.* 2002b, Williamson 2001). Also, these records serve as reference data sets for future comparisons.

Surprisingly, up to now solid data on the alien flora in Europe have been available only for the British Isles (Clements and Foster 1994, Ryves *et al.* 1995) although there is good knowledge of the overall situation with plant invasions in other European countries, too. For Germany, a database of the flora with information on alien status was published recently (Kühn and Klotz 2003), and there is very good information on aliens summarized in numerous specialized papers (Lohmeyer and Sukopp 1992, Kowarik 1995, 2003). In Poland, there is a list of archaeophytes available (Zajac 1979). Other countries tackle the problems of introduced plants to various degrees and precision in their local floras or checklists. However, it must be borne in mind that the influx of aliens into developed European countries has been increasing and standard floras can hardly be expected to cover alien species to a satisfactory degree of completeness (Sell and Murrell 1996).

There has also been no list of aliens of the Czech Republic until recently, there was only a list of archaeophytes available in the local literature (Oprávil 1980). However, the long-term floristic research conducted in the country has accumulated a body of information and gives a solid background for such a compilation. This paper gives information about the first complete catalogue of this group of plants in the country.

The Czech Republic is located in the centre of Europe, between 48°33' and 51°03' of latitude and 12°06' and 18°52' of longitude. It has diverse climatic and geographic conditions, covers an area of 78 864 square kilometers, and has 10.3 millions of inhabitants giving a human population density of 131 inhabitants per km<sup>2</sup>. The network of roads (0.71 km per km<sup>2</sup>) and railways (0.11 km per km<sup>2</sup>) is rather dense. These features certainly contribute to the richness of alien flora (Pyšek *et al.* 2002a, Pyšek and Prach 2003).

## Principles of compilation of the list

Published works on the flora of the Czech Republic, including the recent Flora of the Czech Republic (Hejný and Slavík 1988-1992, Slavík 1995-2000, six out of eight volumes have been published so far) and the Key to the flora of the Czech Republic (Kubát *et al.* 2002), was the basic information source. Earlier modern floral works from the second half of the 20th century were also critically evaluated (Dostál 1954, Dostál 1989), as was the list of archaeophytes, i.e. species introduced before the year 1500 (Opravil 1980). A database with biological and ecological attributes was compiled by using comprehensive floral works and specialized compendia (see Pyšek *et al.* 2002a). For other information not given in these sources, we searched the primary literature (see Pyšek *et al.* 2002a for references). We also used the herbaria of the National Museum Prague (PR), Charles University (PRC) and Institute of Botany Průhonice (PRA), unpublished information from colleagues, and the results of our own field research in 1999-2001.

Older floras and works related to plants non-native to the Czech Republic were considered when re-evaluating species status, whether it is native or alien (Webb 1985, Pyšek 1995, Richardson *et al.* 2000) and classifying taxa by their invasive status and residence time. For this, knowledge of a species' ecology and habitats occupied was used, as well as its historical dynamics and the role it plays in the landscape. The landscape history since the beginning of agriculture in the area was also considered (Ložek 1999).

An alien species (introduced, exotic, adventive) is understood as one which was introduced into the Czech Republic as a consequence of activities of Neolithic or post-Neolithic man or of his domestic animals (Webb 1985, Richardson *et al.* 2000). All alien species ever recorded in the country at least once in the wild were included. We did not take into account plants growing exclusively in cultivation but considered escapes. A plant escaped from cultivation was included if it reproduced on its own at least once outside the place where it was sown or planted (e.g. a flower bed or garden). In plants reproducing by seed, germination outside such a place was considered as an escape from cultivation. A plant reproducing clonally was considered as an escape from cultivation only if it survived the winter and persisted at a given site until the following growing season. A strictly geographical approach to plant invasions was therefore adopted (Rejmánek 1995). Only species alien to the whole country appear on the list, those that have predominantly a secondary distribution but also remnants of a natural distribution in the country have been known, be it a single site, were excluded. Doubtful records, which are sometimes listed without evidence from one flora to another, were not taken into account either. A conservative approach was adopted as it is easier to add taxa on the list in the future rather than remove erroneous records once included. "Historical aliens", i.e. species occurring at the territory in the past but not found recently, were also included not only in the name of scientific completeness but also since they may be present in neighbouring countries and re-introduced into the Czech Republic. Only taxa at the intraspecific level of subspecies or higher were distinguished, with a few exceptions (see Pyšek *et al.* 2002a).

Hybrids between natives and aliens were considered as aliens, even if they have arisen in the Czech Republic. They are non-indigenous species in the sense of not

having been at the territory before the onset of Neolithic agriculture (Williamson 2002). If a native species was taken into cultivation and cultivars produced which subsequently escaped into the wild (e.g. *Achillea ptarmica*), such a species was not included on the list because, at the taxonomic levels considered here, it is native.

Invasive status, i.e. the status which a species reached in the invasion process, was taken from the scheme proposed by Richardson *et al.* (2000), which is based on overcoming different kind of barriers an invading plant must face. Instead of using the rather complex Central European classification systems (Holub and Jirásek 1967, Schroeder 1969, see Pyšek *et al.* 2002a for comparison of these with the one used here) we distinguished three categories of invasion status. *Casuals* do not form self-replacing populations and rely on repeated introductions into the area, *naturalized plants* reproduce consistently without direct human intervention but do not necessarily invade local vegetation while *invasive plants* have the potential to create large populations and spread rather quickly over a considerable area (see Richardson *et al.* 2000 for precise and more detailed definitions). In a complete list of species, published by Pyšek *et al.* (2002), an attempt was also made to consider a species' "post-invasive" status. Taxa were labelled by using this term if they were thought to have been invasive in the past, so that their recent distribution is less and in many cases only a remnant of the past abundance and distribution. These are almost exclusively archaeophytes, there is no reason to believe that during the several millenia or centuries of their presence in the territory their abundance was the same as we observe nowadays.

With respect to the residence time, i.e. the time of a species' arrival to the territory, we distinguish archaeophytes (introduced before the discovery of America, approx. 1500 A. D.) and neophytes (introduced after that date). The original meaning of these terms as they were used by previous authors has slightly shifted since they were introduced (e.g. Holub and Jirásek 1967), namely the usage of the term "neophyte". Strictly speaking, deliberately introduced species are not neophytes (Holub and Jirásek 1967) and should be termed "xenophytes". For simplicity and compatibility with the prevailing recent usage of the term, we use it without regard to whether the species arrived accidentally or was brought in by humans deliberately. The term reflects only the residence time (species introduced after the year 1500) regardless of the mean of introduction.

Original information, evaluated for each species during the work on the project, also includes the type of abundance in the landscape. A special category termed "extinct" relates to the situation when no records have been known for a long period and it is highly improbable that the species would appear again. Quantitative estimate of the number of localities was made using the 5-degree scale which Clement and Foster (1994) applied to British aliens. The first record of the species in the country was noted for neophytes. This record crucially depends on the earliest floras available, and on their quality and completeness. Fortunately, these are regularly spread over the 19th century (Pohl 1809, Presl and Presl 1819, Opiz 1823, 1852, Čelakovský 1867-1881, Polívka 1900-1904) and provide us with solid information about the gradual enrichment of the flora by alien species. Types of habitat in which aliens are recorded was distinguished as follows: (i) natural (forested landscape and naturally treeless habitats), (ii) seminatural (cultural landscape excluding arable land, roads, railways and human settlements), and (iii) human-made habitats (Chytrý *et al.* 2001). The par-

ticular habitats in which the species is found were classified using Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (1992). The type of invaded vegetation was scored using the alliances of the Zürich-Montpellier phytosociological system (Chytrý *et al.* 2001). This system best reflects the vegetation diversity of the Central European landscape (Ellenberg 1988).

The database compiled also includes information on native distribution, mode of introduction into the Czech Republic (deliberate or accidental) and numerous biological and ecological attributes such as life form, Grime strategy, height, reproduction mode and breeding system, ploidy level, chromosome number, hybridization, flowering time, fruit/seed type and size, seed bank, dormancy, pollination and dispersal mode (see Pyšek *et al.* 2002a).

## Composition and structure of the alien flora of Czech Republic

The alien flora of the Czech Republic has 1378 taxa belonging to 542 genera and 99 families (see Pyšek *et al.* 2002a for the complete list), of the total number of taxa, 184 are hybrids. 24.1% are archaeophytes and 75.9% neophytes (Table 1). As to the invasive status, 64.7% are casuals, 28.8% were classified as naturalized, and 6.5% as invasive (Table 1). Four neophytes and 188 archaeophytes were regarded as post-invasive. Among 891 casual taxa, there are 91.7% neophytes and 8.3% archaeophytes, similarly, 76.7% of 90 invasive taxa are neophytes and 23.3% archaeophytes. The group of 397 naturalized taxa of the Czech alien flora consists of 59.7% archaeophytes and 40.3% neophytes (Table 1, Appendix 1).

*Table 1.* The number of taxa in particular categories of residence-time and invasion status, classified by the mode of introduction and the type of invaded habitat. Note that the sums in the latter two groups need not equal the total numbers because of missing data on a few species. Totals for basic categories are shown in bold letters. Delib = deliberate, Accid = accidental; Natur = natural and seminatural habitats (see text for explanation).

Residence time	Status	Total	Introduction mode			Invaded habitat		
			Delib	Both	Accid	Natur	Both	Man-made
Archaeophytes	Casual	<b>74</b>	30	4	40	7	16	51
	Naturalized	<b>237</b>	17	25	195	14	94	129
	Invasive	<b>21</b>	2	4	15	0	13	8
	Total	<b>332</b>	<b>49</b>	<b>33</b>	<b>250</b>	<b>21</b>	<b>123</b>	<b>188</b>
Neophytes	Casual	<b>817</b>	400	47	370	87	126	600
	Naturalized	<b>160</b>	94	18	48	35	66	59
	Invasive	<b>69</b>	45	4	20	9	45	15
	Total	<b>1046</b>	<b>539</b>	<b>69</b>	<b>438</b>	<b>131</b>	<b>237</b>	<b>674</b>
Aliens total	Casual	<b>891</b>	430	51	410	94	142	651
	Naturalized	<b>397</b>	111	43	243	49	160	188
	Invasive	<b>90</b>	47	8	35	9	58	23
	Total	<b>1378</b>	<b>588</b>	<b>102</b>	<b>688</b>	<b>152</b>	<b>360</b>	<b>862</b>

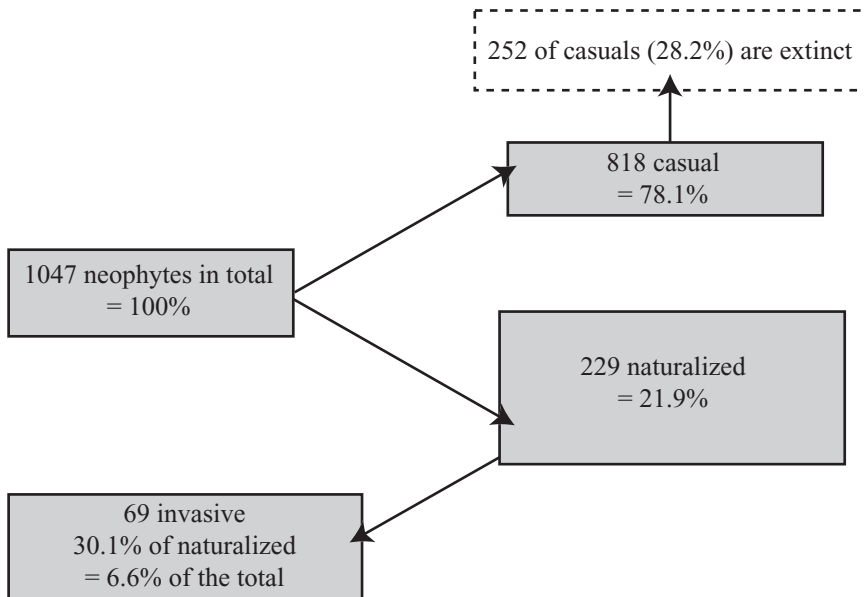


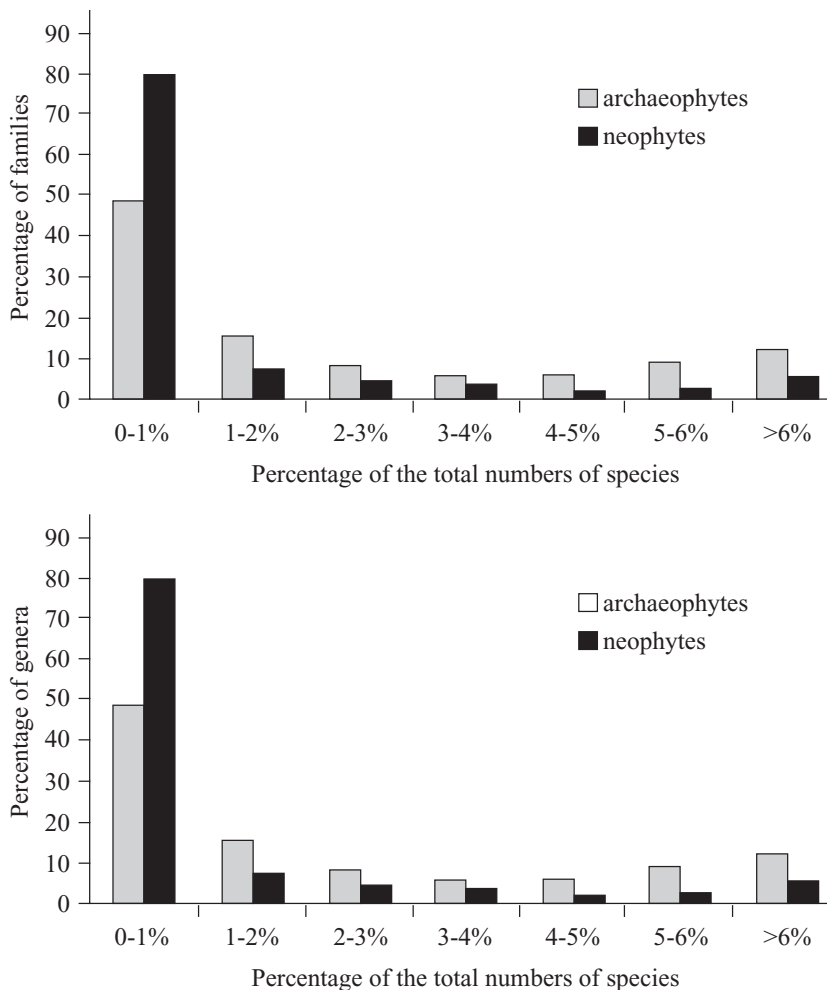
Fig. 1. Transition rates between particular categories of invasive status in Czech aliens introduced after 1500 (from Pyšek *et al.* 2002a; see text for explanation).

The proportion of introduced plants that were able to naturalize was only calculated for neophytes because in archaeophytes information on the initial stage, i.e. that of casuals, is missing. Of introduced neophytes, 21.9% are considered naturalized, while of the remaining 817 casuals, 230 species are considered extinct. Finally, 6.6% of introduced neophytes are invasive (Fig. 1), which figure is well within the range of theoretical rules of invasion biology (Williamson 1996).

The majority of archaeophytes came from the Mediterranean area, while neophytes have their origin in all continents, with other parts of Europe (39.8%), Asia (27.6%), and North America (15.1%) contributing most. Annuals are 57.8% of archaeophytes, significantly more than in neophytes (39.4%). Perennials (38.2%) and woody plants (14.1%) are more frequent among neophytes than among archaeophytes (Fig. 2). In total, the Czech alien flora consists of 44.0% annuals, 9.3% biennials, 34.4% perennials, 7.7% shrubs and 4.5% trees (Table 2).

Considering all aliens, 49.9% were introduced into the country accidentally, and 42.7% deliberately, the remaining 7.4% are thought to have been introduced by both means (Table 5). If the both-means group is not considered separately but included in both accidental and deliberate, accidental arrivals account for 53.4% of taxa and deliberate introductions for 46.6%. Since most archaeophytes reached the country as agricultural weeds, i.e. not introduced on purpose by humans, the ratio for total aliens is biased towards accidental introductions. Neophytes, on the contrary, include many taxa planted on purpose and escaping from cultivation (Kowarik 2003), hence their ratio is reversed: more were introduced deliberately (54.5%) than accidentally (45.5%). More than a half of the taxa are cultivated as ornamentals. Other frequent uses are food, medical, landscaping, and bee-keeping (Pyšek *et al.*

2002a). The majority of aliens (62.8%) are confined to human-made habitats, 11.0% were recorded exclusively in natural and/or seminatural habitats, and 26.2% occur in both types of habitat (Table 1).<sup>1</sup>



*Fig 2.* Frequency distribution of the number of species in families (a) and genera (b) present in the alien flora of the Czech Republic, compared for archaeophytes and neophytes. Because of a different total number of species in each group (archaeophytes = 332, neophytes = 1046), species richness of taxa was standardized and expressed as a percentage of the total number of species rather than the real number of species in respective genera and families.

1. For other details and analyses of the structure of alien flora, i.e. taxonomic structure, distribution of Raunkiaer's life forms and Grime's life strategies, frequency of planting purposes, number and structure of hybrids, distribution of ploidy levels, abundance, representation of taxa in phytosociological alliances see Pyšek *et al.* (2002).

The two basic groups of alien flora, distinguished by residence-time, differ in a number of characters (Table 3). The reverse ratio of casual and naturalized taxa (Table 1) reflects the fact that archaeophytes which did not become naturalized could usually not be recorded in our times, the 74 casuals in this group represent long cultivated, occasionally escaping species. In the same vein, 54.6% of neophytes have only 1-4 localities in the area (the corresponding figure for archaeophytes is 6.6%) but there are only 6.8% of them having more than 500 localities (compared to 51.8% of archaeophytes). Not surprisingly, R and R-combined life strategies are more represented in archaeophytes while a pure C-strategy is obviously more frequent in neophytes. As shown by Pyšek *et al.* (2002), the CSR strategy constitutes an advantage in terms of increasing a species' chance of becoming naturalized and invasive.

Differences in taxonomic structure between archaeophytes and neophytes are also obvious and statistically significant (Table 3). While Chenopodiaceae (6.6% of all archaeophytes), Apiaceae (5.1%) and Scrophulariaceae (4.5%) were more re-

*Table 2.* Composition of the alien flora by origin and life history. Species with more than one life form were included in each of them. Similarly, if a species distribution area covers more than one continent, it was considered as a representative of each of them. Percentages of total numbers are shown.

		Archaeophytes	Neophytes	All Aliens
Origin	Europe	51.6	39.8	43.1
	Asia	36.3	27.6	30.0
	Africa	12.2	6.8	8.3
	N America		15.1	10.9
	C America		3.7	2.7
	S America		5.6	4.1
	Australia		1.2	0.9
Life history	Annual herb	57.8	39.4	44.0
	Biennial herb	12.3	8.3	9.3
	Perennial herb	22.9	38.2	34.4
	Shrub	3.3	9.2	7.7
	Tree	3.6	4.9	4.5

*Table 3.* Summary of the differences between archaeophytes and neophytes in the distribution of selected characters (see Pyšek *et al.* 2002 for details). G-test for contingency tables was used. Number of localities was scored on the 5-degree scale of Clement and Foster (1994). Invaded vegetation was expressed as number of species occurring in phytosociological alliances.

	G	df	P
Invasive status	388.53	2	< 0.001
Representation of families	197.06	95	< 0.001
Life histories	56.91	4	< 0.001
Raunkiaer life forms	51.38	5	< 0.001
Life strategies	89.06	6	< 0.001
Ploidy levels	0.96	3	NS
Number of localities	476.92	4	< 0.001
Invaded vegetation	962.10	177	< 0.001



presented among archaeophytes, Fabaceae (7.3% of all neophytes), Onagraceae (3.6%), Solanaceae (3.2%), Polygonaceae (2.6%), and Amaranthaceae (2.2%) are typical of neophytes. Families most represented in both residence-time groups were Compositae, Gramineae, and Brassicaceae (see Pyšek et al. 2002a for complete data), i.e. those that are usually found to be most frequent in temperate alien floras all over the world (Daehler 1998, Pyšek 1998b). In total, there are 39 families and 162 genera containing archaeophytes and 98 families and 477 genera (including one nothogenus) with neophytes in the Czech alien flora. Distribution of the number of species within these higher taxonomic units is very different if archaeophytes and neophytes are compared (Fig. 2). As many as 93.1% of “neophytic genera” contain a very low number of species whereas in archaeophytes the distribution is shifted towards genera richer in species. The difference is even more striking when families are taken into account. The pattern observed reflects the higher variety of sources in neophytes in terms of geography (region of origin) and mode of introduction (transport vectors, commodities involved). Neophytes are a more random, often casual component of the alien flora. On the other hand, the distribution of species richness among higher taxonomic units in archaeophytes is more stable because of the long immigration history and the source area, i.e. mostly Mediterranean, is less distant from the target country and more homogeneous in terms of natural conditions.

## **History of alien introductions: 6000 years of immigration**

With the list of alien species available, it is possible to infer the course of human-induced plant invasions during the last 7,300 years, and reconstruct an approximate pattern of the enrichment of the native flora by alien species. The total number of native taxa in the flora of the Czech Republic is 2754 if hybrids are included, or 2256 without hybrids (Kubát et al. 2002). Since the beginning of Neolithic agriculture, this number has increased by 1378 (or 1194 excluding hybrids) to 4132 (3450).

The fact that Czech Republic is surrounded by large neighbouring continental landscapes of different natures (the Alps to the south, Carpathians to the east, Pannonian basin located southeast, a region of oceanic climatic on the west, and a northerly region of low habitat diversity resulting from the Quarternary glaciation) makes its landscape mosaic rather diverse, providing a number of different habitats and niches, as well as numerous migration routes, both natural and human-created. These are oriented mainly E-W and SE-NW.

The latter direction is reflected by many species reaching their northwestern distribution limits near the SE political boundaries of the Czech Republic (Slavík 1988). From the SE, there has been a continuous stream of plant invasions since the Neolithic agricultural colonization, this period was the first important one from the viewpoint of plant invasion. Landscape changes accompanied by immigration of new plant species continued during the Chalcolithic and as available data suggest (Table 4, Fig. 3b), this was the period during which a significant proportion of present-day archaeophytes (35% of the 137 species for which the data on time of immigration are available from palynological records) found their way to the Czech

Table 4. Number of archaeophytes reported for particular periods as dated from the territory of the Czech Republic (data from Opravil 1980, Lang 1994).

Period	Time range	Species	%
Neolite and Aeneolite	5300-2200 B.C	48	14.4
Bronze Age	2200-750 B.C.	24	7.2
Iron Age	750 B.C.-0	10	3.0
Roman Period and Migration Period	0-550	8	2.4
Prehistoric times	5300 B.C.-550	7	2.1
Medieval Period	550-500	40	12.0
no data available		196	58.9

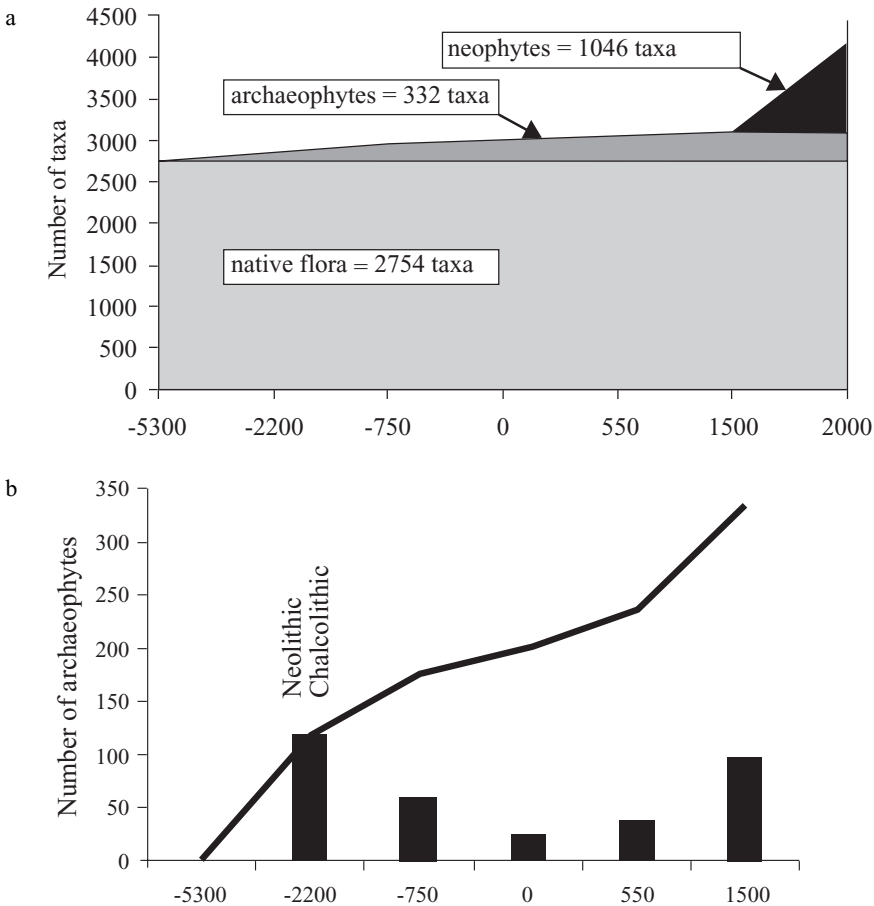


Fig. 3. Historical enrichment of the flora of Czech Republic by alien species over the last 7300 years (a). A detailed pattern is shown for archaeophytes (b) indicating the gradual acceleration of the cumulative curve in the Medieval. Note that the ordinate was re-calculated on basis of the 137 species for which the data were available and extrapolated to the total number of 332 species. See Table 4 for real numbers of archaeophytes and temporal delimitation of periods.

Republic and Central Europe in general. The invasion seems to have continued at a steady pace until Medieval times, another peak immigration period, the data suggest that it was responsible for 29.1% of the archaeophytic flora. These numbers are definitely conservative because we know almost nothing about extinctions in this group of immigrants. We may only guess from the data on neophytes where some information (although certainly under-estimated, too) is available, indicating that 230 species of 1046 (i.e. 22.1%) went extinct after their introduction. It may be supposed that the proportion of extinct immigrants was lower in archaeophytes than in neophytes because climatic conditions were more similar between the source and target areas, and due to a limited species pool in the former group. On the other hand, the period available to archaeophytes was much longer so the number of unsuccessful immigration attempts must have accumulated. The whole matter is very difficult to speculate about (more than anything else it illustrates how poor our data are), and probably the only safe conclusion that can be drawn is that there must have been at least 332 archaeophytes established during the 6,800 between the beginning of the Neolithic and the end of the Medieval period, and that the true number was certainly somewhat higher.

The immigration of archaeophytes was helped by the fact that as early as in the Chalcolithic, there was a rather high proportion of deforested landscape in the lowlands (Ložek 1999). The highest mountains were, however, colonized by people as late as the 17th to 19th century which means, given the high proportion of forested landscape in the Czech Republic, that until the Late Medieval, there were large portions of closed forests and these acted as barriers to migrations.

The Late Medieval brought about the building of towns and the large scale migration of people and goods (Le Gof 1982). The industrial revolution started in the Czech Republic in the 1850s and in the first half of the 20th century the Czech Republic was one of the best developed industrial countries in Europe. In 1945-1989 the country was characterized by special features of land-use, including so-called “collectivization” (concentration of agricultural production into large production units accompanied by excessive, ill-managed large-scale fertilization). At least 1046 taxa have entered the country since the end of the Medieval period. Many species of Asian and southeast-European arrived via one of the largest European railway stations in Čierna při Čope in the Slovak part of the former Czechoslovakia (Jehlík and Hejný 1974, Jehlík 1998). As well as railways and roads, traffic on the Elbe and Danube Rivers and their tributaries significantly contributed to the richness of present alien flora (Jehlík 1998).

A simple calculation shows that per-year rate of immigration for archaeophytes is 0.049, while neophytes increased at a rate of 2.09 species per year, i.e. 43 times faster. Although this very rough measure must be taken with caution because of the bias to the data discussed above, the numbers are nevertheless so strikingly different that they can be taken as a clear illustration of difference in the magnitude of alien species influx between the two periods.

## Alien flora of the Czech Republic in the European context

The alien flora of the Czech Republic consists of 1378 taxa of which 184 are hybrids. This number is probably the most reliable ever produced for the country. As noted by Pyšek *et al.* (2002a), the figures used to characterize the alien flora of the coun-

try up to now have been based mostly on the work of Dostál (1948-1950, 1954, 1958), i.e. a standard flora not paying any special attention to alien plants. The number of neophytes given in this source was 599 (compared to the present 1046) and the Jaccard coefficient of similarity between the two data sets is as low as 0.47. It seems therefore that with solid data at hand, a question may be asked: What is the proportion which alien species contribute to the total plant diversity of the territory?

However, such an estimate depends on several factors and it should be explicitly stated what data are used to produce the figure. As pointed out by Williamson (2002), not only are the numbers of aliens uncertain but those of native species are too, and they depend on whether or not microspecies and hybrids are included in the calculations. While hybrids are perfectly satisfactory taxa and there are approximately 400 of them in British Isles, counts of the British flora usually omit them. However, including hybrids and/or microspecies in the total of native species makes a huge difference to the comparison with other regions, in the case of relatively species-poor British flora the figure is about doubled (Williamson 2002).

The number of native taxa at species and subspecies level listed in the most recent account of the Czech flora (Kubát *et al.* 2002) is 2754. There is good reason to include microspecies in this count because there is good knowledge of most critical groups in the Czech Republic. Kubát *et al.* (2002) list more than 300 native species of *Hieracium*, *Rubus* and *Taraxacum* (excluding sect. *Ruderalia* which would add another 105 species currently known – Kirschner and Štěpánek 1992). The level of taxonomic knowledge of critical groups is reflected in the information on alien species: there are, for example, 14 alien *Rubus* species on the list (although not all of them are critical).

Using the totals of 1378 aliens and 2754 native species gives a 33.4% contribution of aliens to the total number of taxa reported from the country. If we exclude 498 crosses of native species listed by Kubát *et al.* (2002), the number of native taxa drops down to 2256. The corresponding figure for the alien flora, after excluding hybrids, is 1194. Without hybrids, the contribution of aliens to the total number of taxa is then 34.6%. The higher value obtained without hybrids reflects the fact that the hybridization rate is lower in aliens than in native species (Pyšek *et al.* 2002a). The reasons for less frequent hybrids in aliens may be (i) shorter common occurrence of potential parental species in the territory, (ii) their often limited distribution and smaller population sizes, and (iii) resulting lower chance to meet. Neophytes come from a diversity of geographical origins, hence biological barriers to hybridization may play a role as well. The native flora is also better known because of the tradition of floristic research and historical focus, and crosses of alien species might be under-recorded compared to those of the native flora (Pyšek *et al.* 2002a).

It can therefore be concluded that alien species constitute 33-35% of the flora of the Czech Republic, depending on criteria adopted for calculation.

There are several categories between which the distinction is sometimes difficult to make, i.e. whether a species is native or archaeophyte, archaeophyte or neophyte, casual or naturalized, and naturalized or invasive. The number of casuals is the “weakest link” in quantitative data on alien floras. Naturalized species, on the contrary, provide a rather reliable picture of the role alien species play in a given territory and their use for comparison between regions is more justified (Weber

1998). For this reason, the naturalized taxa of the Czech alien flora are listed in Appendix 1 to make them available to international readership.

Surprisingly, papers devoted specifically to critical inventories of aliens in a country, accompanied with species lists with some attributes, have only rarely been published, to our knowledge such data are only available for the UK (Clement and Foster 1994, Ryves *et al.* 1996) and the Czech Republic (Table 5). Although the British data set uses different criteria of invasive status, it can be roughly stated that their “casual” and “persistent” corresponds to “casual” used in the present paper (according to Richardson *et al.* 2000), and their “naturalised” roughly corresponds to “invasive” as used here. Other basic characteristics are available for both countries which makes the two datasets a convenient subject for comparison.

Since analyses of alien floras are rather frequent and have become a popular tool for searching for pattern and generating hypotheses in plant invasion research but specialized lists of aliens are almost missing for European countries, studies of that kind must rely on standard floras for comparisons. Such studies are best justified if they use the same source across the whole area considered, for example for the European continent Flora Europaea (Tutin *et al.* 1964-1980). Although Flora Europaea under-estimates the numbers of alien species, this bias concerns mostly casuals. For example, it gives 317 naturalized species for the former Czechoslovakia. It is impossible to separate this number between the two present countries, Czech Republic and Slovakia (see Pyšek *et al.* 2002a for discussion), but the fact that the current number of naturalized species is 397 for the Czech Republic only indicates that many species were not included (those that were introduced

Table 5. Comparison of the information published on alien flora of British Isles and Czech Republic.

	British Isles	Czech Republic
Source	Clement and Foster 1994, Ryves <i>et al.</i> 1996	Pyšek <i>et al.</i> 2002
Complete list of species	yes	yes
Doubtful species (“accepted with reservations as native”) mentioned	yes	no
Location of voucher specimens	yes	no
Residence time	pre/post-1930	pre/post 1500
First record	no	yes
Invasive status	casual, persistent, established, introduced, naturalized	casual, naturalized, invasive, post-invasive
Area of origin	yes	yes
Number of localities	1-4, 5-14, 15-49, 50-499, >500	1-4, 5-14, 15-49, 50-499, >500
Mode of introduction	yes: detailed system	deliberate/accidental
Life form	no	annual, biennial, perennial, (semi) shrub, tree
Type of invaded habitat	described in words	natural, seminatural, human- made
Type of invaded vegetation	no	phytosociological alliance
References	yes	yes

since the publication of *Flora Europaea* and became naturalized form a negligible part of the naturalized taxa). Nevertheless, the data contained in *Flora Europaea* have a comparative value and their careful analysis with respect to aliens yielded robust results (Weber 1998).

The picture of alien flora presented in this and previous papers (Pyšek et al. 2002a) would not be possible without a solid historical background and floristic tradition. Reliable, critical data on the flora and attention paid to alien species go back to the 19th century (Čelakovský 1867-1881, Polívka 1900-1904) and within a European context, probably only British Isles, Germany, Netherlands, Switzerland and the Nordic countries have a comparable wealth of floristic information and detailed botanical field research. After two centuries of focus on native species, such knowledge proved to be invaluable for research on alien plants as well.

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## Appendix 1

List of naturalized neophytes of the alien flora of the Czech Republic classified according to the families. Number of species in a given family is shown in parentheses. Families are written in bold, invasive species are followed by an asterisk. Criteria of invasiveness and naturalization follow Richardson et al. (2000). Names of families follow Mabberley (1999).

**Aceraceae (1):** *Acer negundo* L.\*; **Alliaceae (2):** *Allium paradoxum* (Bieb.) G. Don, *Allium tuberosum* Rottl. ex Spreng.; **Amaranthaceae (4):** *Amaranthus albus* L., *A. blitoides* S. Watson, *A. powellii* S. Watson\*, *A. retroflexus* L.\*; **Anacardiaceae (1):** *Rhus hirta* (L.) Sudw.\*; **Apiaceae (7):** *Angelica archangelica* L. subsp. *archangelica*\*, *Astrodaucus orientalis* (L.) Drude, *Cnidium silaifolium* (Jacq.) Simk., *Heracleum mantegazzianum* Sommier et Levier\*, *Imperatoria ostruthium* L.\*, *Myrrhis odorata* (L.) Scop.\*, *Smyrniium perfoliatum* L.; **Araceae (1):** *Acorus calamus* L.; **Asclepiadaceae (1):** *Asclepias syriaca* L.; **Balsaminaceae (2):** *Impatiens glandulifera* Royle\*, *Impatiens parviflora* DC.\*; **Berberidaceae (1):** *Mahonia aquifolium* (Pursh) Nutt.\*; **Betulaceae (1):** *Alnus rugosa* (Duroi) Sprengel; **Boraginaceae (1):** *Symphytum × upplandicum* Nyman; **Brassicaceae (15):** *Alyssum murale* W. et K., *Arabis alpina* L., *A. caucasica* Willd., *Bunias orientalis* L., *Cardamine chelidonia* L., *Erucastrum gallicum* (Willd.) O. E. Schulz, *E. nasturtifolium* (Poir.) O. E. Schulz, *Hesperis matronalis* L. subsp. *matronalis*, *Lepidium densiflorum* Schrad., *Leucosinapis alba* (L.) Spach, *Lunaria annua* L., *Sisymbrium altissimum* L., *S. loeselii* L.\*, *S. strictissimum* L., *S. volgense* Bieb. ex E. Fourn.; **Campanulaceae (1):** *Campanula rhomboidalis* L.; **Cannabaceae (1):** *Cannabis ruderalis* Janisch.\*; **Caprifoliaceae (2):** *Lonicera caprifolium* L., *Symphoricarpos albus* (L.) Blake\*; **Caryophyllaceae (2):** *Lychnis coronaria* (L.) Desr., *Silene dichotoma* Ehrh.; **Compositae (35):** *Ambrosia artemisiifolia* L.\*, *Artemisia annua* L., *A. tournefortiana* Rchb., *A. verlotiorum* Lamotte, *Aster × salignus* Willd.\*, *A. lanceolatus* Willd.\*, *A. novi-belgii* L.\*, *A. parviflorus* Nees, *A. versicolor* Willd.\*, *Bidens frondosa* L.\*, *Conyza canadensis* (L.) Cronq.\*, *Doronicum orientale* Hoffm., *D. pardalianches* L., *Echinops exaltatus* Schrad., *E. sphaerocephalus* L., *Erechtites hieracifolia* (L.) Rafin. ex DC., *Erigeron annuus* (L.) Pers. subsp. *septentrionalis* (Fern. et Wieg.) Wagenitz\*, *E. annuus* L. (Pers.) subsp. *annuus*, *E. strigosus* Muehl. ex Willd., *Galinsoga ciliata* (Rafin.) Blake\*, *G. parviflora* Cav.\*, *Helianthus × laetiflorus* Pers., *H. tuberosus* L.\*, *Inula helenium* L., *Iva xanthiifolia* Nutt., *Matricaria discoidea* DC.\*, *Pyrethrum macrophyllum* (W. et K.) Willd., *Rudbeckia hirta* L., *R. laciniata* L.\*, *Senecio vernalis* W. et K., *Solidago canadensis* L., *S. gigantea* Aiton\*, *Telekia speciosa* (Schreb.) Baumg.\*, *Xanthium album* (Widd.) H. Scholz, *X. spinosum* L.; **Convolvulaceae (2):** *Calystegia pulchra* Brummitt et Heywood, *Cuscuta campestris* Yuncker\*; **Cornaceae (1):** *Cornus sericea* L. emend. Murray; **Crassulaceae (6):** *Sedum anopetalum* DC., *S. hispanicum* L., *S. hybridum* L., *S. rupestre* L. subsp. *erectum* t'Hart, *S. spurium* M. Bieb., *Sempervivum tectorum* L.; **Cucurbitaceae (1):** *Echinocystis lobata* (Michx.) Torrev et A. Gray\*; **Dipsacaceae (1):** *Virga strigosa* (R. et Sch.) Holub\*; **Dryopteridaceae (2):** *Cystopteris bulbifera* (L.) Bernh., *Matteucia struthiopteris* (L.) Tod;

**Fabaceae (16):** *Amorpha fruticosa* L.\*, *Colutea arborescens* L., *Cytisus scoparius* (L.) Link subsp. *scoparius*\*, *Galega officinalis* L., *Genista sagittalis* L., *Glycyrrhiza glabra* L., *Laburnum anagyroides* Med., *Lupinus polyphyllus* Lindl.\*, *Medicago sativa* L. subsp. *sativa*, *M. × varia* Martyn, *Onobrychis viciifolia* Scop., *Robinia pseudacacia* L.\*, *Trifolium hybridum* L. subsp. *hybridum*, *T. pannonicum* Jacq., *Vicia grandiflora* Scop. subsp. *grandiflora*, *V. pannonica* Crantz subsp. *striata* (M. Bieb.) Nyman; **Fagaceae (1):** *Quercus rubra* L.\*; **Fumariaceae (1):** *Corydalis lutea* (L.) DC.; **Gentianaceae (1):** *Gentiana lutea* L.; **Geraniaceae (2):** *Geranium pyrenaicum* Burm. fil.\*, *G. sibiricum*; **Gramineae (9):** *Agrostis gigantea* Roth, *Arrhenatherum elatius* (L.) J. Presl et C. Presl subsp. *elatius*\*, *Glyceria striata* (Lamk.) A.S. Hitchc., *Hordeum jubatum* L., *Lolium multiflorum* Lamk., *Melica altissima* L., *Panicum capillare* L. subsp. *capillare*, *P. miliaceum* L. subsp. *ruderales* (Kitagawa) Tzvelev, *Setaria faberi* Herrmann; **Grossulariaceae (2):** *Ribes odoratum* Wendl. fil., *Ribes rubrum* L.; **Hyacinthaceae (3):** *Hyacinthella leucophaea* (C. Koch) Schur, *Puschkinia scilloides* Adams, *Scilla sibirica* Haw.; **Hydrocharitaceae (1):** *Elodea canadensis* Michx.\*; **Chenopodiaceae (4):** *Chenopodium pumilio* R. Br., *C. striatifforme* J. Murr, *C. strictum* Roth, *Kochia scoparia* (L.) Schrader subsp. *scoparia*\*; **Iridaceae (1):** *Sisyrinchium angustifolium* Mill.; **Juncaceae (2):** *Juncus tenuis* Willd.\*, *Luzula nivea* (Nath.) DC.; **Lamiaceae (8):** *Galeobdolon argentatum* Smejkal\*, *Leonurus intermedius* Holub, *L. villosus* Dum.-d'Urv., *Mentha × gracilis* Sole, *M. × rotundifolia* (L.) Huds., *M. spicata* L. subsp. *spicata*, *M. spicata* L. s.l., *Scutellaria altissima* L.; **Liliaceae (4):** *Erythronium dens-canis* L., *Iris germanica* L., *Ornithogalum nutans* L., *Polygonatum latifolium* (Jacq.) Desf.; **Malvaceae (1):** *Alcea rosea* L.; **Nyctaginaceae (1):** *Oxybaphus nyctagineus* (Michx) Sweet; **Oleaceae (3):** *Fraxinus ornus* L., *F. pennsylvanica* Marshall\*, *Syringa vulgaris* L.\*; **Onagraceae (8):** *Epilobium ciliatum* Rafin.\*, *E. dodonaei* Vill., *Oenothera biennis* L.\*, *O. depressa* Greene, *O. fallax* Renner emend. Rostanski, *O. glazioviana* M. Micheli, *O. pycnocarpa* Atkinson et Bartlett, *O. rubricaulis* Klebahn; **Orobanchaceae (3):** *Orobanche gracilis* Sm., *O. hederæ* Duby, *O. lucorum* A. Br.; **Oxalidaceae (3):** *Oxalis corniculata* L., *O. dillenii* Jacq., *O. fontana* Bunge; **Phytolaccaceae (1):** *Phytolacca esculenta* Van Houtte; **Pinaceae (3):** *Pinus nigra* Arnold, *P. strobus* L.\*, *Pseudotsuga menziesii* (Mirbel) Franco; **Polemoniaceae (1):** *Collomia grandiflora* Lindl.; **Polygonaceae (11):** *Fallopia aubertii* (L. Henry) Holub, *Persicaria polystachya* (Wall. ex Meisner) H. Gross\*, *Reynoutria × bohemica* Chrték et Chrtková, *R. japonica* Houtt. var. *japonica*\*, *R. sachalinensis* (F. Schmidt) Nakai\*, *Rumex alpinus* L.\*, *R. longifolius* DC.\*, *R. patientia* L. subsp. *patientia*, *R. scutatus* L., *R. thyrsoflorus* Fingerh.\*, *R. triangulivalvis* (Danser) Rech. fil.; **Portulacaceae (1):** *Claytonia alsinoides* Sims; **Primulaceae (2):** *Lysimachia punctata* L., *Primula vulgaris* Huds. subsp. *vulgaris*; **Ranunculaceae (5):** *Aconitum × cammarum* L., *Consolida orientalis* (Gay) Schrödinger, *Helleborus odoratus* W. et K., *H. viridis* L., *Pulsatilla slavica* Reuss; **Rosaceae (20):** *Duchesnea indica* (Andrew) Focke, *Physocarpus opulifolius* (L.) Maxim.\*, *Potentilla intermedia* L., *Prunus cerasifera* Ehrh., *P. serotina* Ehrh.\*, *Rosa rugosa* Thunb., *R. allegheniensis* Porter, *R. armeniacus* Focke, *R. canadensis* L., *R. laciniatus* Willd., *R. moschus* Juz., *R. odoratus* L., *R. parviflorus* Nutt., *R. silvaticus* Weihe et Nees, *R. tuberculatus* Bab., *R. xanthocarpus* Bureau et Franchet, *Sanguisorba minor* Scop. subsp. *polygamma* (W. et K.) Holub, *Sorbaria sorbifolia* (L.) A. Braun, *Spiraea crenata* L., *Waldsteinia trifolia* Rochel ex Koch; **Salicaceae (2):** *Populus × canadensis* Moench\*, *Salix acutifolia* Willd.; **Saxifragaceae (2):** *Saxifraga × geum* L., *Saxifraga hostii* Tausch subsp. *hostii*; **Scrophulariaceae (6):** *Antirrhinum majus* L., *Digitalis purpurea* L.\*, *Mimulus guttatus* DC.\*, *M. moschatus* Lindl., *Véronica filiformis* Sm.\*, *V. persica* Poir.\*; **Simaroubaceae (1):** *Ailanthus altissima* (Mill.) Swingle\*; **Solanaceae (5):** *Datura stramonium* L. var. *stramonium*, *D. stramonium* L. var. *tatula* (L.) Torrey, *Lycium barbarum* L.\*, *Scopolia carniolica* Jacq., *Solanum decipiens* Opiz; **Violaceae (2):** *Viola × haynaldii* Wiesb. in Baenitz, *V. suavis* Bieb.; **Vitaceae (2):** *Parthenocissus inserta* (Kerner) Fritsch\*, *P. quinquefolia* (L.) Planchon.