

Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats

Rostlinné invaze v České republice: současný stav, dynamika zavlékání, invazní druhy a invadovaná stanoviště

Dedicated to the centenary of the Czech Botanical Society (1912–2012)

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Pyšek P., Chytrý M., Pergl J., Sádlo J. & Wild J. (2012): Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. – *Preslia* 84: 575–629.

The Czech Republic has a strong tradition of research on synanthropic and alien plants, both historically and recently, which results in a good knowledge of alien flora and invasion patterns. In this paper the current situation of plant invasions in the country is reviewed from the viewpoint of the composition of the country's alien flora (based on a recently published checklist of alien taxa) and that of the level of habitat invasions, expressed as the proportion of alien species among all species recorded, and large-scale patterns of invasions in landscapes. At present there are 1454 alien taxa recorded in the national flora, consisting of 350 archaeophytes, introduced since the beginning of Neolithic agriculture until the end of the Medieval Period, and 1104 neophytes, introduced in the Modern Period. In the last two centuries there was a steady increase in the number of alien taxa without a decelerating trend. Arrivals of neophytes from the Mediterranean region and extra-Mediterranean Europe proceeded at the same speed until ca the 1870s; thereafter the Mediterranean region started to be the main donor of the country's alien flora. Most species native to more distant areas such as extra-Mediterranean Asia and North America were arriving later. Of the total number of alien taxa, 985 (67.7%) are classified as casual, 408 (28.1%) as naturalized but non-invasive, and 61 (4.2%) as invasive. Alien taxa contribute 33.3% to the total plant diversity ever recorded in the country, or 14.6% to the permanently present flora (excluding extinct natives and including only naturalized alien taxa). These figures are within the range reported from other European countries. Currently there are 11 archaeophytes and 50 neophytes with invasive populations in the Czech Republic. Factsheets of the invasive neophytes are provided with information on their invasion history, ecology, habitat affinities and impact, and the map of current distribution. The highest invasive species densities (illustrated by a map) as well as the highest levels of invasion in plant communities are found in cities and villages and their surroundings, floodplains of large rivers, disturbed regions in the north, and agricultural landscapes and forestry plantations in warm lowlands, especially in southern Moravia, and central and eastern Bohemia. The level of invasion in the country decreases with altitude, with neophytes responding to this factor more strongly than archaeophytes. A new quantification of the level of invasion for all phytosociological alliances of the Czech Republic is presented. The habitats and vegetation types harbouring the highest proportions of alien species in the Czech Republic are generally either those with a high level of disturbance or with fluctuating input of resources, especially nutrients, in some cases also water or light. Habitats with limited fluctuation of resource availability such as dry, wet and saline grasslands, base-rich fens, and broad-leaved deciduous woodlands appear to be rather resistant to invasion. Future spread of alien species will mainly depend on changing land use and climate.

Key words: alien flora, altitude, archaeophytes, casual species, Czech Republic, distribution maps, exotic, habitat invasions, historical dynamics, invasive species, level of invasion, naturalized species, neophytes, non-native, plant communities

Introduction

The Czech Republic, a central-European country with an area of 78,867 km² and 10.3 million inhabitants, exhibits several features that make it prone to invasions by alien plants. Historical and biogeographic factors include its location on the cross-roads of the continent, many natural or human-created migration routes opening possibilities for colonization, and long-lasting human influence that further diversified the naturally diverse and heterogeneous landscape mosaic (see Pyšek et al. 2002b, Chytrý 2012 for details). Studies on plant invasions considerably benefit from a strong botanical tradition and in-depth knowledge of the country's flora (Kubát et al. 2002, Danihelka et al. 2012, Kaplan 2012) and plant communities (Chytrý 2007, 2009, 2011).

Stemming from a solid background created by a systematic study of plants in human-made habitats since the 1970s (e.g. Hejný et al. 1973, 1979, Jehlík & Hejný 1974, Jehlík 1998; see Pyšek & Prach 2003 for a review of the history of research), a thorough research into the biogeography and ecology of alien plants in the Czech Republic was triggered by the publication of the Catalogue of alien plants of the Czech Republic by Pyšek et al. (2002b; recently updated, Pyšek et al. 2012a). In the last decade, a wide array of issues were addressed at the regional scale, such as the role of species traits in determining species invasiveness (e.g. Pyšek et al. 2009, 2011a, Štajerová et al. 2009, Kubešová et al. 2010, Moravcová et al. 2010), patterns of habitat invasibility (Chytrý et al. 2005, 2008a, 2009b, Pyšek et al. 2005, Simonová & Lososová 2008, Láníková & Lososová 2009, Lososová & Cimalová 2009, Lososová & Grulich 2009), including invasions in nature reserves (Pyšek et al. 2002b, 2003b), as well as topics related to impact and risk assessment (Křivánek & Pyšek 2006, Hejda et al. 2009a, Pyšek et al. 2011b), and case studies of individual invasive species (see Appendix 1 and references therein). Summarized information on invasive species was made available to the national scientific community (e.g. Křivánek 2006, Pyšek et al. 2008a), but also to the broader public including state authorities, NGO's and managers (e.g. Nielsen et al. 2005, Vačkář 2005, Mlíkovský & Stýblo 2006, Pergl & Pyšek 2010).

The above research has been mostly centered around the Institute of Botany of the Academy of Sciences of the Czech Republic, Department of Ecology of Charles University in Prague, and Department of Botany and Zoology, Masaryk University, Brno, and recently pursued within the European projects addressing biological invasions such as DAISIE (DAISIE 2009) and ALARM (Settele et al. 2005). The data on alien flora of the Czech Republic became part of the pan-European database (DAISIE 2008) and contributed to analyses of invasion patterns at the continental and global levels (e.g. Chytrý et al. 2008b, 2009a, 2012, Hulme et al. 2009, Winter et al. 2009, Pyšek et al. 2010a, b, 2012b, Vilà et al. 2010, Essl et al. 2011; see Pyšek & Hulme 2011 for a review).

In the present paper we (i) review the diversity patterns in the alien flora of the Czech Republic and historical dynamics of introductions on the time scale of centuries; (ii) provide fact sheets of invasive neophytes in the Czech Republic including information on their impact and distribution maps; and (iii) summarize available information on the patterns of invasion across landscapes and habitats in the country. A comprehensive analysis of the structure and composition of the Czech alien flora, including other characteristics not reported here such as taxonomic patterns, life histories, cover in plant communities, habitat niche, and pathways of introduction, can be found in the two editions of the Catalogue

of alien plants of the Czech Republic (Pyšek et al. 2002b, 2012a), as well as other summary papers addressing plant invasions in this country (Chytrý et al. 2005, 2009b).

Patterns in the diversity of alien flora

Based on a recent update, the complete alien flora of the Czech Republic in terms of plants that have ever been recorded in the country consists of 1454 taxa (see Pyšek et al. 2012a; their Appendix 2 for the complete list of taxa). This represents an increase by 76 taxa, compared to the 1378 reported a decade ago (Pyšek et al. 2002b). Such an increase is not only due to the influx of newly arriving taxa recorded during the last decade but also due to a thorough exploration and taxonomic re-evaluation of literature, herbaria and other sources (Pyšek et al. 2012a). Currently, the 1454 taxa consist of 350 archaeophytes (plants introduced since the beginning of Neolithic agriculture until the end of Medieval Period; see Holub & Jirásek 1967, Pyšek et al. 2002b, 2004b for definitions) and 1104 neophytes (plants introduced in the Modern Period). The two groups markedly differ in the numbers of taxa in particular categories along the introduction–naturalization–invasion continuum (INIC; following the concept of Richardson et al. 2000, Blackburn et al. 2011; Fig. 1) as well as in percentages (Table 1). While the numbers of naturalized but non-invasive archaeophytes and neophytes are similar (201 vs 207), there are more invasive taxa among neophytes (50 vs 11). However, the markedly higher total taxonomic diversity of neophytes is due to the much higher number of casual taxa (847 vs 138; Fig. 1). Consequently, expressed in relative terms, the ratio of naturalized and casual species is reversed in both groups: the majority of archaeophytes are naturalized (60.6% vs 39.4% of casuals) but only a minority of neophytes (23.3% vs 76.7%; Table 1). The percentage of naturalized taxa among all aliens increases, particularly for neophytes, if only plants assumed to be currently present are taken into account. If taxa that are considered vanished (i.e. those recorded only once or a few times in the past and not observed for a long time; for the vast majority of vanished species it means not observed since 1987, i.e. in the last 25 years; see Pyšek et al. 2012a) are excluded, the reversed pattern remains the same (Table 1).

This difference in species richness of the two historical groups of alien species results from the fact that the number of archaeophytes is by definition (introduced up to 1500 A.D.) no longer increasing (Pyšek & Jarošík 2005). Even more relevant for the species richness issue is that the archaeophytes we observe today are winners in the invasion process lasting for millennia and we have no information on the frequency of their failures in the past (Pyšek et al. 2012a). It needs to be, however, borne in mind that to some extent invasions by neophytes tell a story of the archaeophytes' past (Pyšek et al. 2011a). There is no reason to believe that invasions by archaeophytes were in principle different from modern invasions of neophytes in terms of introductions-and-failures, and booms-and-busts (*sensu* Williamson 1996, Blackburn et al. 2011) of similar dynamics as we observe for neophytes; although the intensity and frequency of these phenomena was probably lower than today due to different pathways, lower propagule pressure and absence of overseas invaders. The assumption of similar dynamics in the past is reflected in some archaeophytes being labelled as post-invasive, inferring from their ecology and population dynamics (see e.g. Pyšek et al. 2002b, Medvecká et al. 2012).

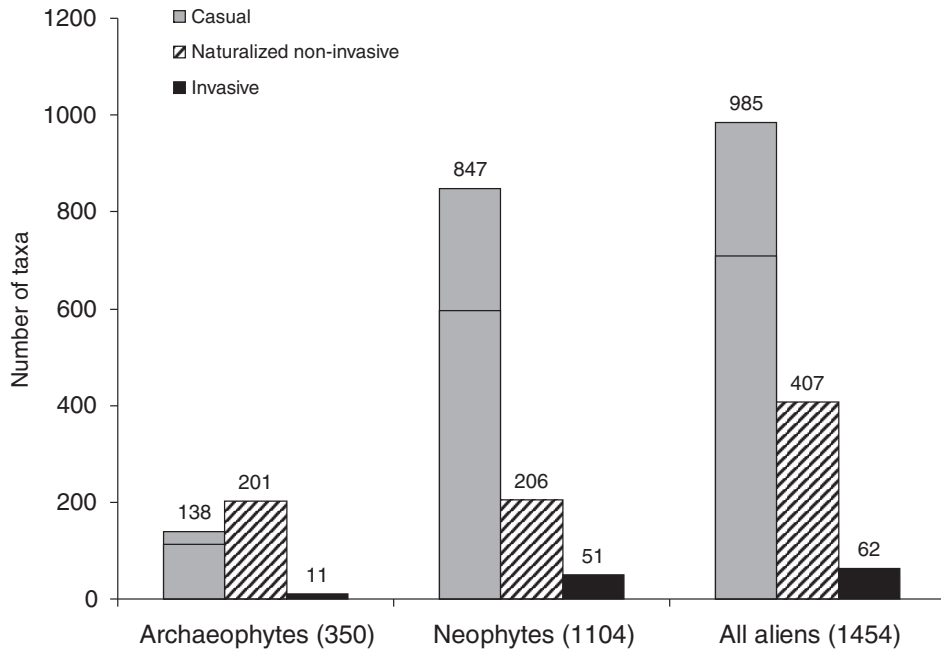


Fig. 1. – Numbers of alien taxa in the Czech flora, shown separately for all aliens and the two subgroups distinguished with respect to the residence time status, archaeophytes and neophytes. Taxa are classified according to the stage they reached along the introduction–naturalization–invasion continuum (INIC), which describes how species proceed in the invasion process by overcoming geographical, environmental and biotic barriers (Richardson et al. 2000, 2011, Richardson & Pyšek 2006, Blackburn et al. 2011). For each group, taxa are divided into casual, naturalized but non-invasive and invasive; the upper part of the bar representing casuals indicates the proportion of vanished taxa.

Table 1. – Representation of the groups of alien taxa, classified according to residence-time status and invasion status, in the alien flora of the Czech Republic. Percentages of taxa in particular groups are shown for (A) complete alien flora with every taxon ever recorded being considered, and (B) taxa that may be assumed to occur at present (i.e. excluding the 277 vanished taxa from the complete flora). Note that 'invasive' is a subgroup of 'naturalized', therefore the total number of naturalized taxa is the sum of naturalized but non-invasive, and invasive.

	A. All taxa (%)				B. Currently present taxa (%)			
	Casual	Naturalized non-invasive	Invasive	Naturalized total	Casual	Naturalized non-invasive	Invasive	Naturalized total
Archaeophytes	39.4	57.5	3.1	60.6	34.6	62.0	3.4	65.4
Neophytes	76.7	18.7	4.6	23.3	69.9	24.1	6.0	30.1
All aliens	67.7	28.0	4.3	32.3	60.1	34.6	5.3	39.9

If archaeophytes and neophytes are merged into a single group of aliens, 67.7% of taxa in the total Czech alien flora (985) are classified as casual and 32.3% (469) as naturalized. Separating the latter group according to the more advanced stages of the INIC indicates that 408 taxa (28.1% of the total alien flora) are currently naturalized but non-invasive, and 61 taxa (4.2%) are invasive (Fig. 1, Appendix 1).

These figures correspond reasonably well with results from other European countries that compiled complete checklists of their alien plants (see e.g. Pyšek & Richardson 2006, Lambdon et al. 2008 for overviews). However, including a complete record of all casual taxa on the national or regional lists is still an exception rather than rule. The comparability is also limited by varying approaches to national checklists that may differ mainly in how criteria for naturalized or invasive taxa are applied, and whether only neophytes or also archaeophytes are included. Considering only neophytes (to express the losses along the INIC for archaeophytes is not possible due to missing information on unsuccessful casuals during invasion history), the naturalization rate of 23.3% (i.e. the percentage of taxa of the total pool of introduced aliens that became naturalized) in the Czech flora corresponds well to that found in other European countries such as 22.7% reported for Belgium (Verloove 2006), 20.5% for Hungary (Balogh et al. 2004), 25.4% for Austria (Essl & Rabitsch 2002) and 26.8% for Slovakia (Medvecká et al. 2012).

The recently published comprehensive account of the alien flora of Slovakia (Medvecká et al. 2012) provides an excellent opportunity to compare the patterns of plant invasions in two neighbouring countries with shared culture and history, which were part of the same state until 20 years ago, and yet differ in geography, and hence in opportunities for invasion. A brief comparison of the two recent catalogues (Pyšek et al. 2012a vs Medvecká et al. 2012) indicates that overall, disproportionately less taxa are considered naturalized in the Czech Republic (28.1% of all aliens) than in Slovakia (39.1%), the difference being mainly due to a higher number of casual neophytes recorded in the former country (985 vs 457). The representation of taxa among casual, naturalized, and invasive neophytes in the Czech Republic and Slovakia is very similar (75.7% vs 73.2%, 18.7% vs 22.8% and 4.5% vs 4.0%, respectively), indicating that in both checklists the transitions along the INIC are reasonably well captured.

Regional distribution of invasive plants

Data on the distribution of invasive plants in the Czech Republic can be used to express the difference among the country's regions in the intensity of plant invasions (Fig. 2). Using the occurrence of invasive taxa mapped in Appendix 1 as a measure of the level of invasion at the landscape scale indicates that the most invaded areas are the surroundings of big cities, floodplains of large rivers, regions with post-mining disturbed landscapes in the northern parts of the country, and warm lowlands in east-central Bohemia and southern Moravia (see Chytrý 2012, Kaplan 2012 for the description of climatic and geographical characteristics and their distribution within the country). This pattern corresponds reasonably well with previously published maps based on the proportional representation of all neophytes in habitats of the Czech Republic (Chytrý et al. 2009b).

Contribution of aliens to the plant diversity of the Czech Republic

The data recently updated for both native (Daníhelka et al. 2012) and alien flora (Pyšek et al. 2012a) of the Czech Republic make it possible to precisely estimate enrichment of the national flora by alien species (Pyšek et al. 2003c). Considering all taxa ever recorded in the national flora, i.e. including extinct natives and vanished aliens, gives the totals of 1454 alien

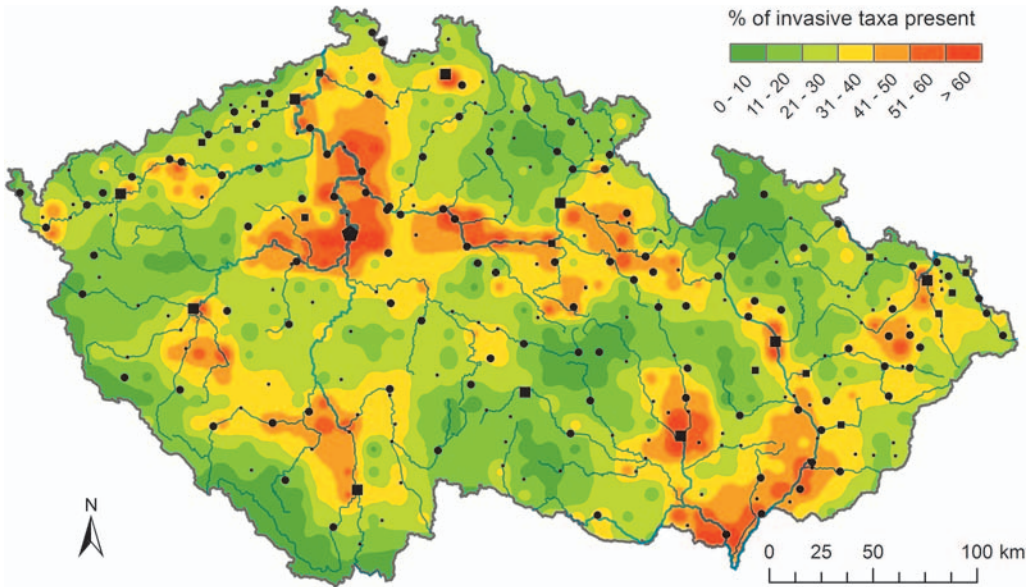


Fig. 2. – Intensity of plant invasions in the Czech Republic based on the occurrence of the 40 invasive neophytes mapped in Appendix 1. Percentage of invasive taxa present in each CEBA grid cell (6×10 minutes) was interpolated using inverse distance weighted interpolator applied to 12 neighbouring points (power parameter = 2). The location of rivers and that of towns and cities is indicated, with symbol size corresponding to the city size.

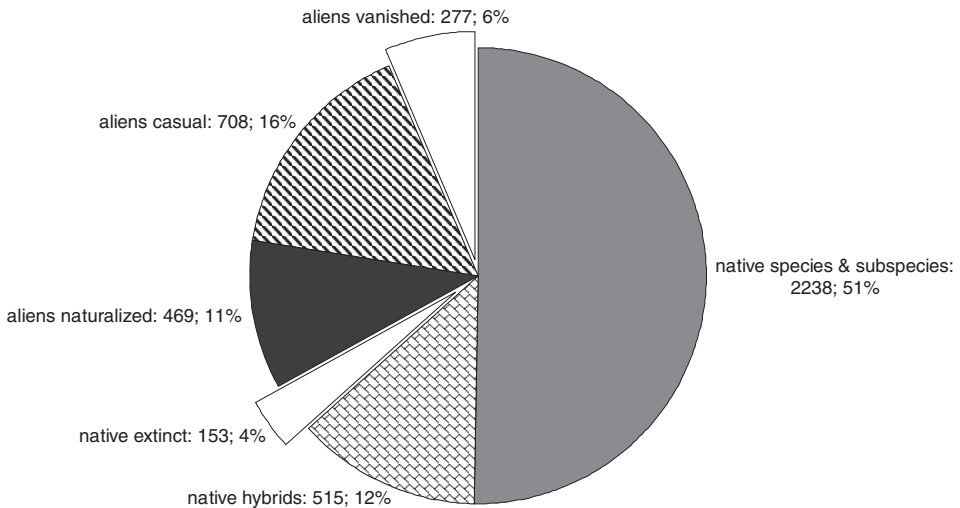


Fig. 3. – Composition of the flora of the Czech Republic with respect to native and alien status, categories of aliens, and historical and current presence of taxa in the country. Data on numbers in native flora are from Kaplan (2012) and Danihelka et al. (2012), those on alien flora from Pyšek et al. 2012a.

and 2906¹ native taxa and indicates that the former contribute 33.3% (Fig. 3). Of this value, 8.0% are attributed to archaeophytes and 25.1% to neophytes. The total proportion in the flora is the figure usually reported in the plant invasion literature. For European countries where complete lists of casual species are available, the proportion of all aliens among the total flora ranges widely from rather low values in the southern countries, such as 13% in Italy (Celesti-Grappo et al. 2009) or 12% in Spain (Sanz-Elorza 2004 cited by Celesti-Grappo et al. 2009), to those comparable with the Czech Republic found in central-European countries. These include e.g. Austria (27.0%, Essl & Rabitsch 2002), Hungary (26.6%, Balogh et al. 2004, number of native taxa from Winter et al. 2009) and Poland (27.3%, Tokarska-Guzik 2005, number of native taxa from Winter et al. 2009). The highest percentages of alien taxa are reported from more northerly and westerly located regions of Europe, e.g. 35.3% in Estonia (Oöpik et al. 2008), 41.0% in Belgium (Verloove 2006, number of native taxa from Winter et al. 2009) or 53.4% in the UK (Lambdon et al. 2008), where relatively species-poor native floras are a factor increasing proportional contribution of aliens.

Estimates given in the literature, however, depend on which taxa are included in the assessment of total plant diversity (e.g. subspecies, hybrids), how thorough and long-term is the recording of casual aliens, whether or not archaeophytes are included, etc. (see Pyšek et al. 2002b, Williamson 2002, Lambdon et al. 2008 for discussion). This can be demonstrated using the Czech flora; excluding hybrids and/or taxa no longer present (extinct natives and vanished aliens) shifts the proportional representation of aliens to 36.3% or 29.9%, respectively. This is because hybridization among native species is more frequent (17.7%) than hybridization with alien species involved (6.6%), hence the proportion increases; but the opposite is true for extinct and vanished taxa – extinctions account for 5.3% of the total native flora, but vanished taxa for 19.1% of the alien flora.

As the variation in the reported figures results not only from the composition of floras but also from other factors that introduce biases, invasion histories and regions can only be rigorously compared with these potentially biasing factors in mind. Again, one country for which such comparison is possible (because there is a recent checklist of alien species built by using similar criteria) is the neighbouring Slovakia. In this country alien taxa make up 21.5% of the total number ever recorded in its territory, of which 6.6% are attributed to archaeophytes and 14.9% to neophytes (Medvecká et al. 2012). The overall contribution of alien taxa is therefore markedly lower than the above estimate for the Czech Republic. Another possible comparison is of the taxa that are permanently present in the two countries, i.e. excluding extinct natives and including only naturalized alien taxa (Fig. 3). This measure yields a figure of 14.6% alien contribution to the permanent plant diversity in the Czech Republic, 6.6% and 8.0% attributed to archaeophytes and neophytes, respectively. To obtain a comparable value, 73 taxa classified as extinct in the Red List of Slovak flora (Feráková et al. 2001) need to be subtracted from the number of native species in the flora of Slovakia, 3337 taxa reported by Medvecká et al. (2012), and compare the resulting figure with 373 alien taxa permanently present in this country (206 naturalized archaeophytes and 167 naturalized neophytes; Medvecká et al. 2012). This gives 10.3% contribution of alien plants to the total plant diversity in Slovakia, again a lower figure than the corresponding 14.6% for the Czech Republic (Pyšek et al. 2012a).

¹ Note that this figure differs from the preliminary estimate of 2945 used for calculating the percentages of alien taxa in Pyšek et al. (2012a), which results in slightly different proportions reported here.

Since both countries have similar size, climate, demography, current macroeconomic parameters (The World Bank Group 2007), i.e. factors that are known to determine alien species richness on a large scale (e.g. Vilà & Pujadas 2001, Taylor & Irwin 2004, Pyšek et al. 2010b, Essl et al. 2011), and comparable intensity of floristic research, the explanation of these differences needs to be sought mainly in topography, land cover and history. First, Slovak native flora is richer, reflecting the heterogeneity of habitats between the Pannonian lowlands and high mountain ranges of the Carpathians. Second, large parts of Slovakia are covered by mountainous areas of the Western Carpathians, which are less invaded because of the general tendency of mountainous areas to be less invaded than lower altitudes (Becker et al. 2005, Alexander et al. 2011, McDougall et al. 2011). Third, Czech Lands became industrialized already in the second half of the 19th century (in 1918 they inherited about 70% of the industry of the former Austro-Hungarian Monarchy), while Slovakia was industrialized only after World War II. This earlier start of industry in the Czech Republic undoubtedly intensified transportation and introduction of alien species.

Dynamics of invasions over time

Pyšek et al. (2012a) give the year of the first record for 771 neophytes (i.e. 70% of the total number recorded) and show that there is a rather steady increase of four alien arrivals per year since the beginning of the 19th century without any distinct decelerating trend. If the dynamics based on taxa with known year of the first record are projected to the total neophyte flora, the total number of neophytes would reach 1264 by 2050 should the current trend persist (see Pyšek et al. 2012a for details). These trends indicate that the number of alien species recorded in the Czech Republic will be increasing at a similar rate in the near future, corresponding to the trend reported for Europe (Lambdon et al. 2008, Hulme et al. 2009).

Displaying the dynamics of arrivals of alien neophytes separately by invasion status reveals that the rate of increase in the cumulative number of naturalized taxa somewhat decelerated in the 20th century, while casuals exhibit an opposite trend, with a steep increase since the 1950s (Fig. 4A). This acceleration is due to landscapes becoming more suitable to invasions after dramatic changes in land-use that occurred after World War II (Williamson et al. 2005) but also, to some extent, reflects increased interest in alien plant research since the 1970s (Pyšek et al. 2002b, 2011b). However, the rapidly increasing numbers of neophytes are a warning because naturalized or even invasive species recruit from casuals with a delay of decades, due to the lag phenomena and invasion debt (Kowarik 1995, Aikio et al. 2010, Essl et al. 2011).

The dynamics of arrivals also convincingly demonstrate the role of residence time in invasions; this is evident if naturalized species are split into naturalized but not (yet) invasive, and invasive. Not only is the current distribution of neophytes positively related to minimum residence time, with those present for longer time being more widely distributed or more abundant (Pyšek & Jarošík 2005, Rejmánek et al. 2005), but also residence time affects the invasion status of alien species. Figure 3B shows that of the neophytes currently classified as invasive in the Czech Republic (Pyšek et al. 2012a; Appendix 1), 50% were introduced up to 1872, i.e. earlier than naturalized but non-invasive (1886) and much earlier than casual neophytes (1956). Taking the presence of 90% of taxa as another measure reveals even more marked differences; this percentage of invasive, naturalized but non-invasive, and casual taxa were introduced before 1901, 1968 and 2001, respectively (Fig. 4B).

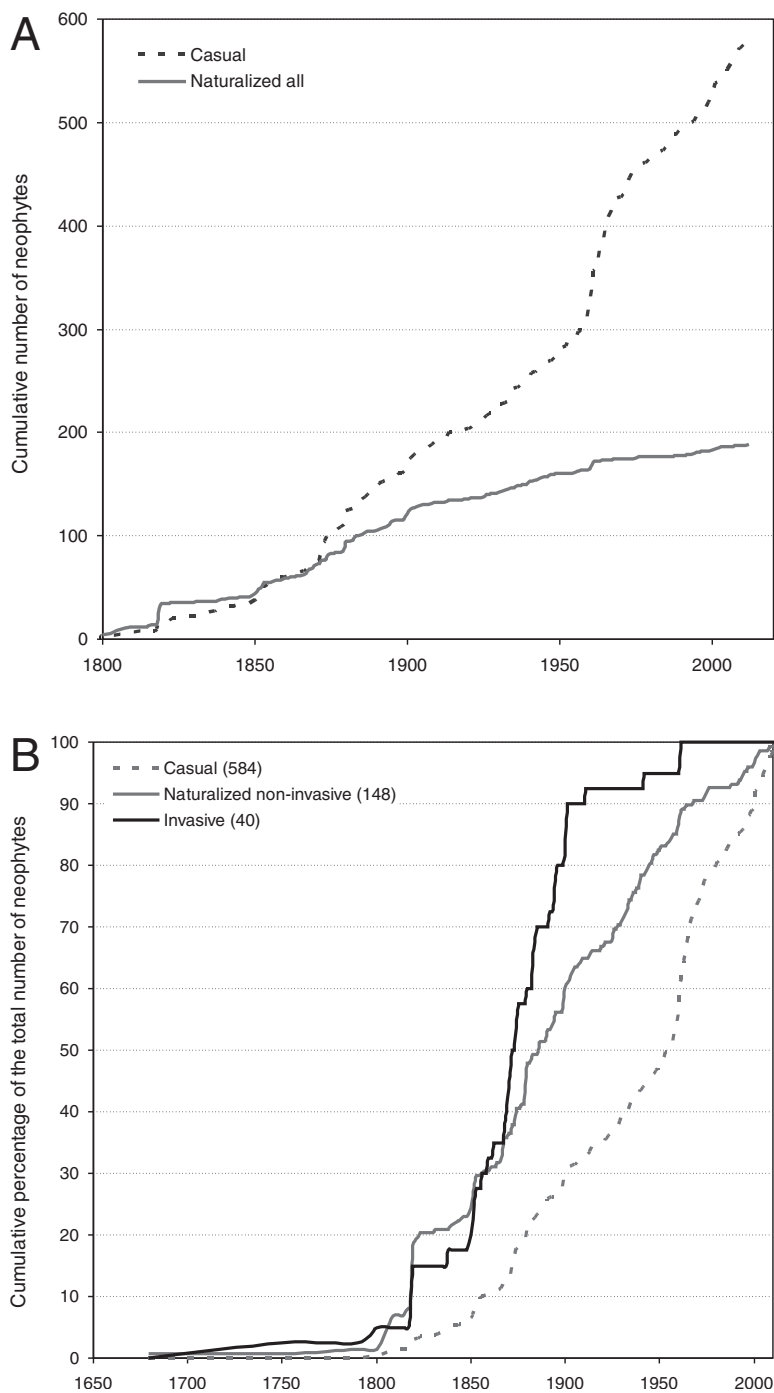


Fig. 4. – Increase in the cumulative number of alien neophytes reported up to the given year shown separately for casual and naturalized (A), and as cumulative percentage of the currently known numbers, displayed for casual, naturalized non-invasive, and invasive neophytes (B). Based on taxa for which the year of the first record is available ($n = 772$). Data from Pyšek et al. 2012a.

The rates of species introductions differed not only by invasion status but also by origin. The classification of the geographic regions of origin of alien taxa in the Czech flora adopted by Pyšek et al. (2012a) differed from the previous account (Pyšek et al. 2002b) in separating the Mediterranean region as one of the donor areas (covering respective parts of southern Europe, northern Africa and western Asia from Turkey and Israel to Afghanistan). This revealed that this region is the main donor not only of archaeophytes (e.g. Preston et al. 2004, Pyšek et al. 2004c, Pyšek & Jarošík 2005), 52.7% of which arrived from there, but also of neophytes (28.7%; Fig. 5). For neophytes, the other most represented regions of origin are parts of Europe and Asia other than the Mediterranean region, contributing 19.9% and 14.2% of taxa, respectively, and North America (16.7%; Fig. 5). The dynamics of introduction of neophytes from these main donor regions indicate that the arrivals from the Mediterranean region and extra-Mediterranean Europe proceeded at the same speed until ca the 1870s, whereas afterwards the introductions from the Mediterranean region became more frequent. In general, species native to more distant areas such as Asia and North America were arriving later (Fig. 6A). In relative terms, however, the introductions of the European species were the fastest; 50% of all currently known taxa from this region were in place by 1895, compared to 1926 for the Mediterranean species, 1935 for North American species and 1958 for Asian species (Fig. 6B).

The estimation of long-term introduction dynamics of archaeophytes revealed that 35.2% of presently known taxa were introduced in the Neolithic/Chalcolithic period (5500–2200 years BC) and more than half (52.7%) are thought to have been present by the end of the Bronze Age, ca 750 years BC (Pyšek et al. 2003c, based on data in Pyšek et al. 2002b). The temporal dynamics of archaeophytes in the Czech flora also reflects a clear effect of the residence time, detectable after centuries to millenia since the start of their invasions. Taxa that are most widespread at present were introduced earlier than those currently less widely distributed (Pyšek & Jarošík 2005).

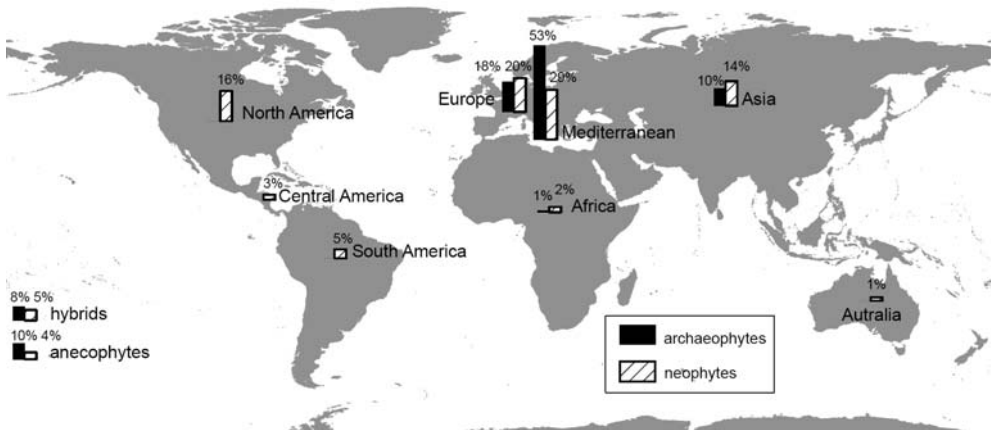


Fig. 5. – Donor regions of alien plants in the Czech Republic. The height of the bar reflects the percentage of the total number of taxa that are alien in the Czech Republic and native to the respective region (shown on top of the bar). Note that the Mediterranean region is distinguished as a separate one, covering respective parts of southern Europe, northern Africa and western Asia from Turkey and Israel to Afghanistan. Europe, Asia and Africa refer to their parts other than the Mediterranean region in this delimitation (Pyšek et al. 2012a). Hybrids and anecophytes, i.e. taxa whose native distribution ranges are unknown or highly uncertain (Kühn & Klotz 2002, 2003; 199 taxa in total) are included in the calculation of the percentage contributions of donor regions. Based on data from Pyšek et al. (2012a).

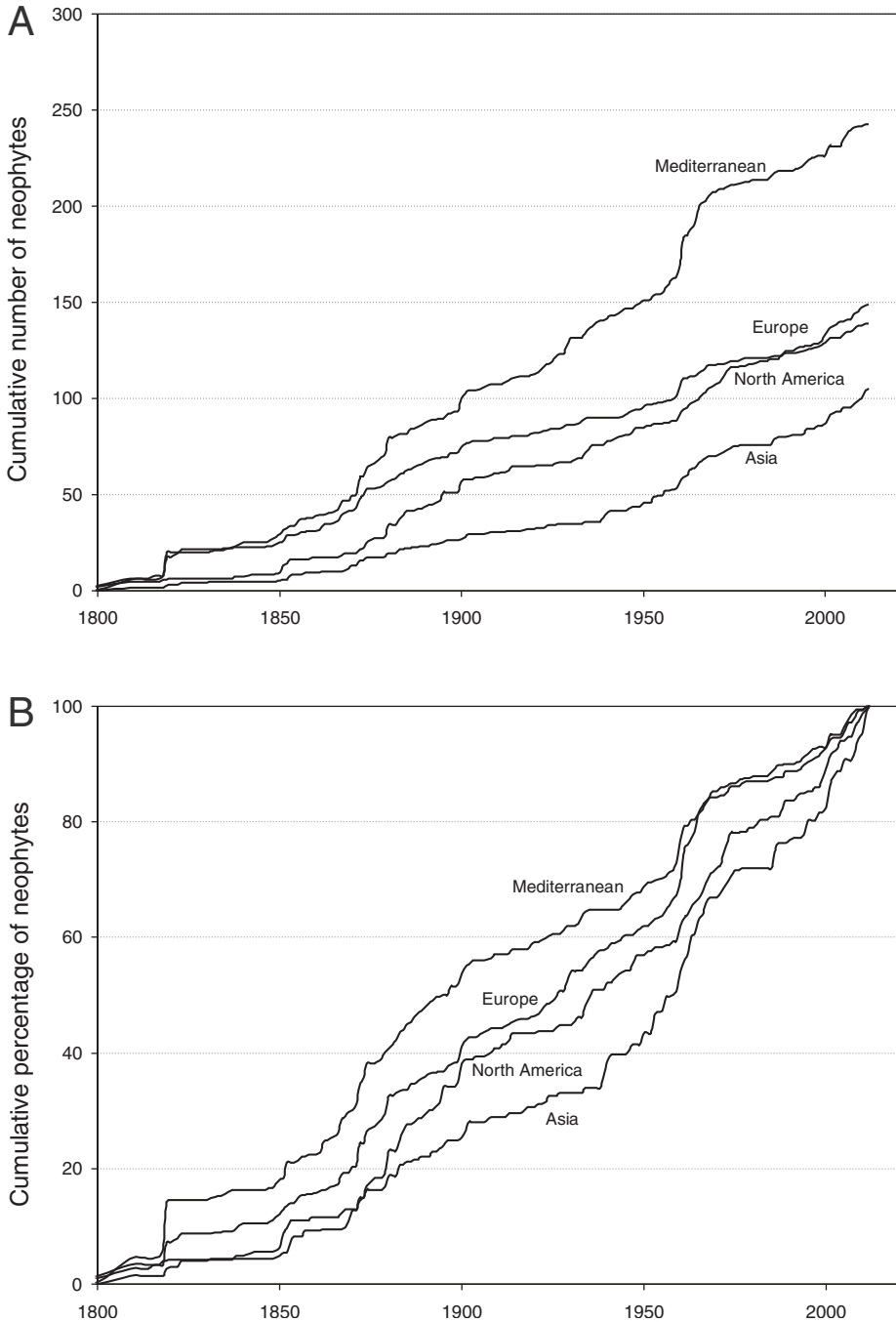


Fig. 6. – Arrivals of alien neophytes in the flora of the Czech Republic from four main donor regions, shown as increase in (A) the cumulative number of taxa originating from the given region, and (B) cumulative percentage of the currently known numbers. If a taxon originated from more than one region, only the respective fraction was considered for each (i.e. 1/2 for a taxon originating in two regions). See Fig. 2 for delimitation of regions.

Invasive taxa in the Czech Republic

The recent update of the alien plant checklist of the Czech Republic labelled 61 taxa as invasive (Pyšek et al. 2012a). This work followed the definition of an ‘invasive species’ as one that forms self-replacing populations over many life cycles, produces reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of introduction, and has the potential to spread over long distances (Richardson et al. 2000, Pyšek et al. 2004b, Blackburn et al. 2011). In addition to this definition, Pyšek et al. (2012a) introduced the metapopulation criterion to separate invasive species from naturalized, to account for the historical population dynamics of the respective taxa, and classified the invasion status based on the population history viewed from the current perspective, i.e. the state in which the populations of a given species exist at present. Therefore, some taxa previously considered invasive are now classified as naturalized, reflecting the ‘boom-and-bust phenomenon’ (sensu Williamson 1996, Blackburn et al. 2011). Another principle adopted was that of the highest stage achieved at the population level, reflecting that individual populations of an alien species may occur in a region in different stages of the INIC (e.g. Essl et al. 2009, Meyerson et al. 2010a, b, Saltonstall et al. 2010). Therefore, if some populations of a species reached the invasion stage, the species is classified as invasive (see Pyšek et al. 2012a for details on the approach).

Among the taxa currently considered as invasive there are 11 archaeophytes (*Angelica archangelica* subsp. *archangelica*, *Arrhenatherum elatius*, *Atriplex sagittata*, *Cirsium arvense*, *Conium maculatum*, *Digitaria ischaemum*, *Echinochloa crus-galli*, *Eragrostis minor*, *Portulaca oleracea* subsp. *oleracea*, *Prunus cerasifera* and *Stellaria pallida*) and 50 neophytes. Invasive neophytes occur in a wide range of habitats (Table 2) and are addressed in detail in Appendix 1, where information on their ecology, invasion history, current distribution, trends and impact is summarized based on available information. Some of them were subject to intensive research in the Czech Republic, such as *Heracleum mantegazzianum*, *Reynoutria* spp., *Impatiens* spp. and *Pinus strobus* (see Appendix 1 for references).

Table 2. – Occurrence of invasive taxa in habitats in the Czech Republic (ar – archaeophytes, neo – neophytes). The classification of habitats follows that used in Sádlo et al. (2007; n = 88). Affinity to a habitat is indicated using the following scale: 1 – occurrence (the taxon does not have an ecological optimum there, and often is rare); 2 – optimum (the taxon has an ecological optimum in the habitat or in a part of it); 3 – dominant (the taxon has an ecological optimum in the habitat, and at the same time it frequently attains a cover above 25% in areas > 10 m² or > 100 m² in herbaceous or woody vegetation, respectively); 4 – constant dominant (same as for the previous category but the taxon also determines the general appearance of the habitat, occurring in > 40% of the localities of the habitat; see Sádlo et al. 2007 for details). The following habitats are not listed as no invasive taxa were recorded there: 2A – Alpine grasslands on siliceous bedrock, 3A – macrophyte vegetation of eutrophic and mesotrophic still waters, 3B – macrophyte vegetation of water streams, 5F – transitional mires, 5G – raised bogs, 5H – wet peat soils and bog hollow, 10H – inland vegetation of succulent halophytes, 10J – inland saline steppes, 12P – peatland pine forests, 12R – acidophilous spruce forests, and 12S – basiphilous spruce and fir forests. Data taken from Sádlo et al. (2007) except *Beta vulgaris* Altissima Group, *Reynoutria xbohemica* and *Symphotrichum xsalignum* that are newly assigned here, and updated for the purpose of the present paper. See Appendix 1 for neophyte factsheets.

Taxon	Residence time status	1A	1B	1C	1D	2B	3C	4A	4B	4C	4D	4E	4F	4G	4H	4I	4J	4K	4L
		Calcareous cliffs	Siliceous cliffs and block fields	Walls	Mobile calcareous screes	Subalpine tall-forb and tall-grass vegetation	Vegetation of oligotrophic lakes and pools	Reed-beds of eutrophic still waters	Halophilous reed and sedge beds	Eutrophic vegetation of muddy substrata	Riverine reed vegetation	Reed vegetation of brooks	Mesotrophic vegetation of muddy substrata	Tall-sedge beds	Vegetation of low annual hygrophilous herbs	Vegetation of nitrophilous annual hygrophilous herbs	River gravel banks	<i>Petasites</i> fringes of montane brooks	Nitrophilous herbaceous fringes of lowland rivers
<i>Acer negundo</i>	neo	1	.	1
<i>Ailanthus altissima</i>	neo	.	.	1
<i>Amaranthus powellii</i>	neo	1	.	.	.
<i>Amaranthus retroflexus</i>	neo	1	.	.	1
<i>Ambrosia artemisiifolia</i>	neo
<i>Asclepias syriaca</i>	neo
<i>Bassia scoparia</i>	neo
<i>Beta vulgaris</i> Altissima Group	neo
<i>Bidens frondosus</i>	neo	1	1	1	2	2	1	1	1	2	3	.	.	2
<i>Bunias orientalis</i>	neo
<i>Cannabis sativa</i> var. <i>spontanea</i>	neo
<i>Conyza canadensis</i>	neo	1	1	2	1	1	1	1	.	.	1
<i>Cuscuta campestris</i>	neo
<i>Echinocystis lobata</i>	neo	1	.	.	1	.	.	.	1	.	.	.	2
<i>Echinops sphaerocephalus</i> subsp. <i>sphaerocephalus</i>	neo	1
<i>Erigeron annuus</i>	neo	.	1	2
<i>Fraxinus pennsylvanica</i>	neo
<i>Galinsoga parviflora</i>	neo	.	.	1	1	1	.	.	1
<i>Galinsoga quadriradiata</i>	neo	.	1	1	2	.	.	1
<i>Helianthus tuberosus</i>	neo	3
<i>Heracleum mantegazzianum</i>	neo	1	1	.
<i>Impatiens glandulifera</i>	neo	1	2	1	.	.	1	1	1	1	3
<i>Impatiens parviflora</i>	neo	1	1	1	2	1	.	1	.	.	1	1	.	1	1	1	1	1	2
<i>Lupinus polyphyllus</i>	neo	1	.	.
<i>Lycium barbarum</i>	neo	.	1
<i>Oxalis corniculata</i> var. <i>corniculata</i>	neo	.	1	1
<i>Oxalis dillenii</i>	neo	.	1	1
<i>Parthenocissus inserta</i>	neo
<i>Pinus strobus</i>	neo
<i>Populus ×canadensis</i>	neo	.	.	.	1	1	1	1	.	1
<i>Prunus serotina</i>	neo
<i>Quercus rubra</i>	neo
<i>Reynoutria japonica</i> var. <i>japonica</i>	neo	1	1	.	.	.	1	2	1	2	.
<i>Reynoutria sachalinensis</i>	neo	1	1	.	.	.	1	2	1	2	.
<i>Reynoutria ×bohemica</i>	neo	1	1	.	.	.	1	2	1	2	.
<i>Robinia pseudoacacia</i>	neo	1	1	1	1
<i>Rudbeckia laciniata</i>	neo	1	1	1	1
<i>Rumex alpinus</i>	neo	.	.	.	1	2	2	.	.
<i>Rumex longifolius</i> subsp. <i>sourekii</i>	neo	.	.	.	1	1	.
<i>Sisymbrium loeselii</i>	neo	.	1	1	1	.	.	.	1
<i>Solidago canadensis</i>	neo	.	1	1	1	1	1
<i>Solidago gigantea</i>	neo	1	.	.	.	1	.	.	1	.	.	.	1	2	.
<i>Symphoricarpos albus</i>	neo	1	1	.
<i>Symphyotrichum lanceolatum</i>	neo	2	1	.	1	1	1	.	2	1	1	.	.	.	3
<i>Symphyotrichum novi-belgii</i>	neo	1
<i>Symphyotrichum ×salignum</i>	neo	1
<i>Symphyotrichum ×versicolor</i>	neo	1
<i>Telekia speciosa</i>	neo
<i>Angelica archangelica</i> subsp. <i>archangelica</i>	ar	.	.	.	1	.	1	.	.	2	1	.	1	.	1	1	1	.	.
<i>Arrhenatherum elatius</i>	ar	1	1	1	2	.	1	1	1	1	1	1	1	1	1	1	1	1	2
<i>Atriplex sagittata</i>	ar	1	.	.	1	1	.	.	.	2
<i>Cirsium arvense</i>	ar	.	1	.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Conium maculatum</i>	ar	1	1
<i>Digitaria ischaemum</i>	ar	1	1
<i>Echinochloa crus-galli</i>	ar	.	.	.	1	1	1	1	1	1	1	.	.	2	3	.	.	.	1
<i>Eragrostis minor</i>	ar
<i>Portulaca oleracea</i> subsp. <i>oleracea</i>	ar
<i>Prunus cerasifera</i>	ar
<i>Stellaria pallida</i>	ar
Number of neophytes	.	3	5	12	4	3	1	5	2	2	15	8	1	4	5	18	9	13	21
Number of archaeophytes	.	1	1	2	1	2	1	5	3	1	6	4	0	3	4	6	3	3	5

Taxon	5A	5B	5C	5D	5E	6A	6B	6C	6D	6E	6F	6G	7A	7B	8A	8B	8C	8D	8E	8F	
	Hard-water springs with tufa formation	Lowland and montane soft-water springs	Alpine and subalpine soft-water springs	Calcareous fens	Acidic moss-rich fens and peatland meadows	Mesic <i>Arrhenatherum</i> meadows	Montane mesic meadows	Pastures and park grasslands	Alluvial meadows of lowland rivers	Wet <i>Cirsium</i> meadows	Intermittently wet <i>Molinia</i> meadows	Vegetation of wet disturbed soils	Subalpine and montane acidophilous grasslands	Submontane <i>Nardus</i> grasslands	Hercynian dry grasslands on rock outcrops	Submediterranean dry grasslands on rock outcrops	Narrow-leaved sub-continental steppes	Broad-leaved dry grasslands	Acidophilous dry grasslands	Thermophilous forest fringe vegetation	
<i>Acer negundo</i>
<i>Ailanthus altissima</i>
<i>Amaranthus powellii</i>
<i>Amaranthus retroflexus</i>
<i>Ambrosia artemisiifolia</i>
<i>Asclepias syriaca</i>
<i>Bassia scoparia</i>
<i>Beta vulgaris</i> Altissima Group
<i>Bidens frondosus</i>
<i>Bunias orientalis</i>
<i>Cannabis sativa</i> var. <i>spontanea</i>
<i>Conyza canadensis</i>
<i>Cuscuta campestris</i>
<i>Echinocystis lobata</i>
<i>Echinops sphaerocephalus</i> subsp. <i>sphaerocephalus</i>
<i>Erigeron annuus</i>
<i>Fraxinus pennsylvanica</i>
<i>Galinsoga parviflora</i>
<i>Galinsoga quadriradiata</i>
<i>Helianthus tuberosus</i>
<i>Heracleum mantegazzianum</i>
<i>Impatiens glandulifera</i>
<i>Impatiens parviflora</i>	1	1
<i>Lupinus polyphyllus</i>
<i>Lycium barbarum</i>
<i>Oxalis corniculata</i> var. <i>corniculata</i>
<i>Oxalis dillenii</i>
<i>Parthenocissus inserta</i>
<i>Pinus strobus</i>
<i>Populus</i> × <i>canadensis</i>
<i>Prunus serotina</i>
<i>Quercus rubra</i>
<i>Reynoutria japonica</i> var. <i>japonica</i>	.	1
<i>Reynoutria sachalinensis</i>	.	1
<i>Reynoutria</i> × <i>bohemica</i>	.	1
<i>Robinia pseudoacacia</i>
<i>Rudbeckia laciniata</i>
<i>Rumex alpinus</i>	.	.	1
<i>Rumex longifolius</i> subsp. <i>sourekii</i>
<i>Sisymbrium loeselii</i>
<i>Solidago canadensis</i>
<i>Solidago gigantea</i>
<i>Symphoricarpos albus</i>
<i>Symphyotrichum lanceolatum</i>
<i>Symphyotrichum novi-belgii</i>
<i>Symphyotrichum</i> × <i>salignum</i>
<i>Symphyotrichum</i> × <i>versicolor</i>
<i>Telekia speciosa</i>
<i>Angelica archangelica</i> subsp. <i>archangelica</i>
<i>Arrhenatherum elatius</i>
<i>Atriplex sagittata</i>
<i>Cirsium arvense</i>
<i>Conium maculatum</i>
<i>Digitaria ischaemum</i>
<i>Echinochloa crus-galli</i>
<i>Eragrostis minor</i>
<i>Portulaca oleracea</i> subsp. <i>oleracea</i>
<i>Prunus cerasifera</i>
<i>Stellaria pallida</i>
Number of neophytes	1	4	1	0	1	15	5	7	8	7	4	11	1	2	3	3	3	4	2	4	
Number of archaeophytes	0	0	0	1	1	3	2	4	2	2	2	3	0	1	1	1	1	1	1	3	

Taxon	9B	9C	9D	9E	9F	10G	10I	11A	11D	11H	11I	11J	11L	11N	11R	12A	12B	12C	12D	12E
	Open vegetation of acidic sands	<i>Festuca</i> grasslands on acidic sands	Pannonian sand steppes	Acidophilous vegetation of spring therophytes and succulents	Basiphilous vegetation of spring therophytes and succulents	Continental vegetation of annual hatophilous grasses	Inland saline meadows	Dry lowland to subalpine heathlands	Subalpine acidophilous <i>Pinus mugo</i> scrub	Subalpine deciduous scrub	Willow carrs	Willow galleries of loamy and sandy river banks	Tall mesic and xeric shrub	Low xeric scrub	Scrub and pioneer woodland of forests clearings	Alder carrs	Alluvial forests	Oak-hornbeam forests	Ravine forests	Herb-rich beech forests
<i>Acer negundo</i>	2	.	.	2	.	.	2	.	.	.
<i>Ailanthus altissima</i>	1
<i>Amaranthus powellii</i>	1
<i>Amaranthus retroflexus</i>	1
<i>Ambrosia artemisiifolia</i>	1	1	1
<i>Asclepias syriaca</i>	1
<i>Bassia scoparia</i>
<i>Beta vulgaris</i> Altissima Group
<i>Bidens frondosus</i>	1	.	.	.	1	2	.	1	.	1
<i>Bunias orientalis</i>	1	1
<i>Cannabis sativa</i> var. <i>spontanea</i>
<i>Conyza canadensis</i>	2	1	2	1	1	.	1	1	1	1	1
<i>Cuscuta campestris</i>
<i>Echinocystis lobata</i>	2	1	.	.	.
<i>Echinops sphaerocephalus</i> subsp. <i>sphaerocephalus</i>	1	1
<i>Erigeron annuus</i>	.	1	1	.	2
<i>Fraxinus pennsylvanica</i>	1	.	2
<i>Galinsoga parviflora</i>	1	2	1	1	1
<i>Galinsoga quadriradiata</i>	1	1
<i>Helianthus tuberosus</i>	1
<i>Heracleum mantegazzianum</i>	2	.	1
<i>Impatiens glandulifera</i>	2	1	.	1	.	1
<i>Impatiens parviflora</i>	1	1	1	1	2	1	3	3	3	2	.
<i>Lupinus polyphyllus</i>	1	.	2
<i>Lycium barbarum</i>	1	.	3
<i>Oxalis corniculata</i> var. <i>corniculata</i>
<i>Oxalis dillenii</i>
<i>Parthenocissus inserta</i>	2	.	1
<i>Pinus strobus</i>	1
<i>Populus ×canadensis</i>	1	2	.	.	1	.	2
<i>Prunus serotina</i>	1	.	1	2	.	.	.
<i>Quercus rubra</i>	.	1	1	.	.	.	1	.	1	.	1
<i>Reynoutria japonica</i> var. <i>japonica</i>	2	.	.	1	.	2
<i>Reynoutria sachalinensis</i>	2	.	.	1	.	2
<i>Reynoutria ×bohemica</i>	2	.	.	1	.	2
<i>Robinia pseudoacacia</i>	1	1	2	.	1	1	2	.	.
<i>Rudbeckia laciniata</i>	1	.	1	1	1
<i>Rumex alpinus</i>	1	1	1
<i>Rumex longifolius</i> subsp. <i>sourekii</i>	1	1
<i>Sisymbrium loeselii</i>	1	.	1	1	.
<i>Solidago canadensis</i>	1	.	.	.	2	.	.	1	.	1
<i>Solidago gigantea</i>	1	.	.	.	2	.	.	1	.	1
<i>Symphoricarpos albus</i>	1	.	.	3	.	1	1	.	.	.
<i>Symphyotrichum lanceolatum</i>	1	.	.	.	1	.	.	1	.	1
<i>Symphyotrichum novi-belgii</i>	1	.	.	.	1	1	.	2	.	1
<i>Symphyotrichum ×salignum</i>	1	.	.	.	1	.	.	2	.	1
<i>Symphyotrichum ×versicolor</i>	1	.	.	1	.	1
<i>Telekia speciosa</i>	1	.	1
<i>Angelica archangelica</i> subsp. <i>archangelica</i>	1	1
<i>Arrhenatherum elatius</i>	1	2	1	1	1	.	1	1	.	.	.	1	2	2	1	.	1	1	1	1
<i>Atriplex sagittata</i>	1
<i>Cirsium arvense</i>	1	1	.	1	.	.	2	.	.	1	1	1	1	1	1	1
<i>Conium maculatum</i>	1	.	.	1
<i>Digitaria ischaemum</i>	2	1
<i>Echinochloa crus-galli</i>	.	.	.	1	.	1	1	1
<i>Eragrostis minor</i>	1	1	.	1	1
<i>Portulaca oleracea</i> subsp. <i>oleracea</i>	1
<i>Prunus cerasifera</i>	2	.	2	.	.	1	1	.
<i>Stellaria pallida</i>	.	1	.	1	1
Number of neophytes	5	4	2	1	1	0	8	1	1	2	2	19	12	4	38	2	23	5	3	1
Number of archaeophytes	5	4	1	5	3	1	3	1	0	1	1	4	4	2	7	1	2	2	2	1

Taxon	12F Limestone beech forests	12G Acidophilous beech forests	12H Peri-Alpidic basiphilous thermophilous oak forests	12I Sub-continental thermophilous oak forests	12J Acidophilous thermophilous oak forests	12K Acidophilous oak forests	12L Boreo-continental pine forests	12O Peri-Alpidic pine forests	12Q Peatland birch forests	12T <i>Robinia pseudoacacia</i> plantations	12U Plantations of broad-leaved non-native trees	12V <i>Picea</i> plantations	12W <i>Pinus</i> and <i>Larix</i> plantations	13A Annual vegetation of ruderal habitats	13B Annual vegetation of arable land	13C Annual vegetation of trampled habitats	13D Perennial thermophilous ruderal vegetation	13E Perennial nitrophilous herbaceous vegetation of mesic sites	13F Herbaceous vegetation of forests clearings and <i>Rubus</i> scrub	Habitats occupied
<i>Acer negundo</i>	3	.	.	1	.	.	1	1	1	9	
<i>Ailanthus altissima</i>	3	.	.	1	1	1	1	1	1	11	
<i>Amaranthus powellii</i>	1	2	1	1	1	8	
<i>Amaranthus retroflexus</i>	1	.	.	.	2	2	1	1	1	10	
<i>Ambrosia artemisiifolia</i>	2	1	.	1	.	6	
<i>Asclepias syriaca</i>	1	.	.	.	1	.	2	1	.	8	
<i>Bassia scoparia</i>	2	1	.	1	.	3	
<i>Beta vulgaris</i> Altissima Group	1	2	.	.	.	2	
<i>Bidens frondosus</i>	1	.	.	1	1	22	
<i>Bunias orientalis</i>	1	.	.	.	1	1	1	2	1	9	
<i>Cannabis sativa</i> var. <i>spontanea</i>	2	1	.	.	.	2	
<i>Conyza canadensis</i>	1	1	.	1	3	2	2	2	1	1	34	
<i>Cuscuta campestris</i>	2	1	.	2	.	4	
<i>Echinocystis lobata</i>	2	.	7	
<i>Echinops sphaerocephalus</i> subsp. <i>sphaerocephalus</i>	1	.	2	1	.	9	
<i>Erigeron annuus</i>	1	1	2	1	2	13	
<i>Fraxinus pennsylvanica</i>	3	1	1	.	5	
<i>Galinsoga parviflora</i>	1	1	.	2	2	1	1	1	1	13	
<i>Galinsoga quadriradiata</i>	1	1	.	2	2	1	1	1	1	13	
<i>Helianthus tuberosus</i>	1	.	.	.	1	1	.	2	2	.	7	
<i>Heracleum mantegazzianum</i>	1	3	1	14	
<i>Impatiens glandulifera</i>	1	1	2	1	16	
<i>Impatiens parviflora</i>	1	1	2	1	1	2	1	.	4	2	2	1	1	.	.	1	3	2	45	
<i>Lupinus polyphyllus</i>	3	2	2	14	
<i>Lycium barbarum</i>	2	2	.	.	1	.	.	1	1	.	11	
<i>Oxalis corniculata</i> var. <i>corniculata</i>	1	2	2	1	.	.	8	
<i>Oxalis dillenii</i>	1	2	1	1	.	.	9	
<i>Parthenocissus inserta</i>	1	1	1	.	5	
<i>Pinus strobus</i>	.	1	.	.	.	2	2	1	.	.	.	1	3	7	
<i>Populus ×canadensis</i>	2	3	2	1	1	15	
<i>Prunus serotina</i>	2	1	1	6	
<i>Quercus rubra</i>	.	1	.	1	.	2	1	.	.	3	.	2	1	14	
<i>Reynoutria japonica</i> var. <i>japonica</i>	1	3	.	12	
<i>Reynoutria sachalinensis</i>	1	3	.	12	
<i>Reynoutria ×bohemica</i>	1	3	.	12	
<i>Robinia pseudoacacia</i>	.	.	2	2	2	1	.	.	4	2	.	1	1	.	.	1	1	1	24	
<i>Rudbeckia laciniata</i>	2	1	10	
<i>Rumex alpinus</i>	2	1	12	
<i>Rumex longifolius</i> subsp. <i>sourekii</i>	2	1	.	7	
<i>Sisymbrium loeselii</i>	.	.	1	.	1	.	.	.	2	1	.	3	.	1	2	1	.	16		
<i>Solidago canadensis</i>	1	1	.	1	.	.	3	.	1	14		
<i>Solidago gigantea</i>	1	.	1	.	.	1	3	1	14		
<i>Symphoricarpos albus</i>	1	1	2	.	9	
<i>Symphyotrichum lanceolatum</i>	1	3	.	19	
<i>Symphyotrichum novi-belgii</i>	2	3	1	13	
<i>Symphyotrichum ×salignum</i>	1	2	1	11	
<i>Symphyotrichum ×versicolor</i>	2	2	.	7	
<i>Telekia speciosa</i>	1	2	.	7	
<i>Angelica archangelica</i> subsp. <i>archangelica</i>	1	.	11	
<i>Arrhenatherum elatius</i>	1	.	1	1	1	1	1	1	2	2	1	1	2	1	1	2	2	1	62	
<i>Atriplex sagittata</i>	1	1	.	.	3	1	1	2	1	.	12	
<i>Cirsium arvense</i>	.	.	1	1	1	1	1	1	3	2	1	3	2	3	44	
<i>Conium maculatum</i>	1	1	.	2	1	.	8	
<i>Digitaria ischaemum</i>	2	1	2	1	.	1	10	
<i>Echinochloa crus-galli</i>	2	2	1	1	.	1	19	
<i>Eragrostis minor</i>	2	.	2	1	.	.	7	
<i>Portulaca oleracea</i> subsp. <i>oleracea</i>	2	1	2	1	.	.	5	
<i>Prunus cerasifera</i>	1	1	1	1	.	9	
<i>Stellaria pallida</i>	1	1	.	1	2	.	2	1	.	11	
Number of neophytes	1	3	3	3	3	5	4	0	1	14	20	5	6	25	14	9	34	37	20	.
Number of archaeophytes	1	0	2	2	1	1	1	1	0	5	5	2	3	9	7	8	10	6	4	.

Patterns of plant invasions across landscapes and habitats in the Czech Republic

Important insights into patterns of invasion in different habitats and plant communities have been gained by combining the knowledge of alien flora with approaches of vegetation ecology. Plant invasion patterns across landscapes, habitats or vegetation types can be quantified as the level of invasion, measured as the number of alien species, or the proportion of aliens to all species, per unit area. The level of invasion is influenced by habitat invasibility (i.e. its vulnerability to invasion; Rejmánek 1989) and propagule pressure of alien species (Lonsdale 1999, Chytrý et al. 2008a). The latter can be understood either as the number of propagules arriving to a given location (propagule pressure *sensu stricto*) or the number of arriving species (colonization pressure; Lockwood et al. 2009). Technically, habitat invasibility can be quantified by separating the effect of propagule pressure from the level of invasion measured at sampled sites (Lonsdale 1999, Chytrý et al. 2008a), however, exact measurement of propagule pressure is very difficult. Therefore studies of invasibility are limited to the use of proxy variables such as land-use types in the surroundings of the sampled sites. In the Czech Republic such a study indicated a rather strong relationship between the level of invasion and habitat invasibility: generally, invulnerable habitats tend to be invaded to a high level and vice versa, although there are exceptions (Chytrý et al. 2008a). Unfortunately, for habitats restricted to areas with limited propagule pressure, it cannot be assessed from observational data whether they are invulnerable or resistant to invasions.

Level of invasion and altitude

A decrease in the level of plant invasion towards high altitudes is a globally consistent pattern. Generally, alien floras of the mountain areas are subsets of alien floras of the surrounding lowlands, the former consisting of species with the broadest climatic tolerance which continuously spread from the foothill regions (Alexander et al. 2011, McDougall et al. 2011). For example, Pyšek et al. (2011c) demonstrated that neophytes in the Czech Republic were most often introduced to the areas located at about 250–400 m a.s.l. and they subsequently spread to higher altitudes. This is supported by the fact that species with earlier first records (thus, presumably introduced earlier) tend to have a broader altitudinal range. The altitudinal pattern of invasion is explained by the low-altitude filter effect, limited landscape connectivity in the mountains and limited gene flow from lowland populations to peripheral populations at high altitudes, which hinders development of adaptations to high-altitude environments (Becker et al. 2005). In addition, the available total land area decreases with altitude, which may further contribute to lower levels of invasion, e.g. by reducing the diversity and extent of available habitats, and thereby reducing the frequency of invasion foci for further spread.

Although the altitudinal range of the Czech Republic (115–1602 m a.s.l.) is not very broad, the decrease in the level of invasion with altitude is distinct and well documented (Fig. 7). It has been demonstrated in comparative studies of landscape segments, e.g. using a landscape transect that encompassed an altitudinal gradient in southern Bohemia (Mihulka 1998), Czech nature reserves (Pyšek et al. 2002a), and grid cells of flora mapping in the Bílé Karpaty Mts of south-eastern Moravia (Otýpková et al. 2011). A possible explanation of such patterns might be that higher altitudes generally contain less invulnerable habitats. However, analyses performed within individual habitats, using vegetation plots, also detected a decreasing trend in the level of invasion toward higher altitudes, e.g. for

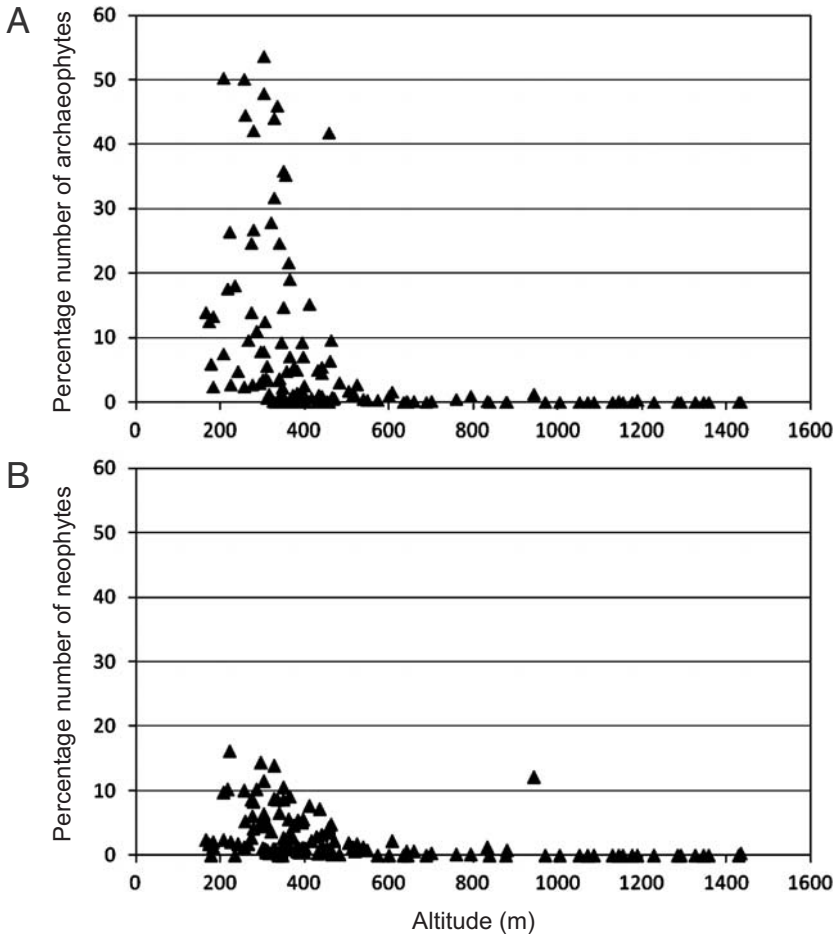


Fig. 7. Percentage of (A) archaeophytes and (B) neophytes, relative to the number of all species occurring in phytosociological relevés, plotted against altitude. Values are means for phytosociological alliances of the Czech Republic. Data for percentages of alien species are from Table 3 and altitudes were taken from the relevés used as the data source for Table 3. Note that the altitudinal range of the Czech Republic is 115–1602 m a.s.l. The outlier in the right part of graph (B) represents the alliance *Rumicion alpini*.

weed communities of arable land (Lososová et al. 2004, Pyšek et al. 2005), ruderal vegetation (Simonová & Lososová 2008) and most other habitat types of the Czech Republic except those with narrow altitudinal range (Chytrý et al. 2009b). In most contexts, neophytes respond to altitude more strongly than archaeophytes, the former being more distinctly concentrated in the lowlands.

Level of invasion across habitat types

An analysis based on a data set of 20,468 vegetation plots, classified into 32 habitat types of the EUNIS classification (Chytrý et al. 2005), revealed that the plots contained on average 9.0% of archaeophyte species, 2.3% neophytes, and the rest were native species. Arable land

and anthropogenic ruderal vegetation were shown as the habitat types harbouring the highest proportions of both archaeophytes and neophytes, while deciduous broad-leaved forestry plantations (of e.g. *Populus ×canadensis*, *Quercus rubra* and *Robinia pseudoacacia*) were highly invaded, especially by neophytes. These habitats not only have the largest proportion of alien species in small plots but also the largest regional pools of alien species, i.e. species occurring in the Czech Republic and adapted to these habitats (Sádlo et al. 2007). Levels of invasion for more finely divided vegetation types, basically on the level of phytosociological alliances, were quantified for ruderal vegetation (Simonová & Lososová 2008), weed vegetation (Lososová & Grulich 2009) and forests (Chytrý et al. 2009b).

A new quantification of the level of invasion for all phytosociological alliances of the Czech Republic, following the classification system accepted in the monograph Vegetation of the Czech Republic (Volumes 1–3: Chytrý 2007, 2009, 2011, and manuscript of Volume 4, see also Chytrý 2012) and the new catalogue of alien species (Pyšek et al. 2012a), is presented in Table 3. It is based on a stratified-random selection of 20,830 relevés from the Czech National Phytosociological Database (Chytrý & Rafajová 2003, code EU-CZ-001 according to Dengler et al. 2011) and prepared using the same methods as the previous quantification (Chytrý et al. 2005), but it uses more finely defined vegetation units and newer relevés made since 1980. Compared to the previous quantifications (Chytrý et al. 2005, 2009b, Simonová & Lososová 2008, Lososová & Grulich 2009), the new results indicate lower numbers of archaeophytes and higher numbers of native species in some cases, which is mainly due to reclassification of 41 species considered as archaeophytes by Pyšek et al. (2002b) to native in Pyšek et al. (2012a). However, the general trend remains the same as reported in the previous studies.

The most invaded habitats and vegetation types of the Czech Republic, in terms of the proportions of alien species they harbour, are generally either disturbed or have fluctuating inputs of resources, especially nutrients, and in some cases water or light. A comparison with corresponding habitats in other European countries showed that such habitats are also among the most invaded elsewhere, although the composition of alien floras is very different among European regions (Chytrý et al. 2008b). In contrast, habitats with limited fluctuation of resource availability such as dry, wet and saline grasslands, base-rich fens, and broad-leaved deciduous woodlands appear to be rather resistant to invasion, although they can be invaded to some extent in areas with high propagule pressure (Chytrý et al. 2008a). This supports the theory of fluctuating resource availability as the main cause of plant invasions (Davis et al. 2000).

Sites, areas or habitats with a high proportion of neophytes usually also have a high proportion of archaeophytes, as shown in the data from Czech nature reserves (Pyšek et al. 2002a), regional grid mapping of flora (Otýpková et al. 2011) or vegetation plots over the whole Czech Republic (Chytrý et al. 2005). However, there is some variation around this general trend. Archaeophytes are often more numerous in treeless vegetation on dry to mesic soils, while neophytes are more common in disturbed woody vegetation, wetlands or aquatic habitats (Chytrý et al. 2005, 2008b). On arable land in the Czech Republic, archaeophytes are more represented in areas with less precipitation and on drier soils, such as chernozem or rendzina, although neophytes are also common there (Pyšek et al. 2005). This pattern obviously results from the fact that most archaeophytes originate from the dry areas of the Mediterranean region, including the Middle East (Pyšek et al. 2012a), and are therefore pre-adapted to dry open habitats (di Castri 1989, Pyšek & Jarošík 2005).

The incidence of alien species (their number, proportion of all species, or cover) is generally higher in early successional stages and it decreases with successional age (Rejmánek 1989). This pattern was observed in different successional seres in the Czech Republic, for example in abandoned fields in dry areas of the Bohemian Karst (central Bohemia; Rejmánek 1989) or southern Moravia (Sojneková 2011), southern-Bohemian peat bogs disturbed by peat extraction (Bastl et al. 1997), disused sand or gravel pits across the country (Bastl et al. 1997, Řehouňková & Prach 2008) and some other early-successional habitats (Prach et al. 2008). However, the course of succession can be changed if strongly competitive alien species occur near the successional site. For example, Řehouňková & Prach (2008) observed that the occurrence of mature *Robinia pseudoacacia* trees within 100 m from a disused sand or gravel pit resulted in formation of *Robinia* groves during spontaneous succession in the pit.

The most invaded areas in the Czech Republic are agricultural landscapes with predominating arable fields, cities and villages, and lowland woods with extensive forestry plantations. River floodplains, especially in the lowlands, are also highly invaded (Vymyslický 2001, Matějček 2008, Kalusová 2009, Kalníková 2012). Mid- and high-altitudinal landscapes are less invaded, especially if they are forested (Chytrý et al. 2009b). In the European context, the Czech Republic belongs to a highly invaded area of western and central Europe, which is characterized by on average higher levels of invasion than the boreal zone of northern Europe or the Mediterranean and sub-Mediterranean zones of southern Europe (Chytrý et al. 2009a).

Habitat type is the most important determinant of the level of plant invasion in the Czech Republic, followed by altitude (and associated effects of climate) and variation in propagule pressure (Chytrý et al. 2008a). However, the patterns of invasion across habitats also depend on the composition of alien flora introduced to the target area, in terms of its species' habitats in their native ranges. Hejda et al. (2009b) showed that most neophytes occurring in the Czech Republic originate from various types of ruderal vegetation, dry grasslands, broad-leaved deciduous woodlands, moist and wet grasslands including tall-forb vegetation, cliffs and rock outcrops, arable land and mesic grasslands. Especially those neophytes that originate from riverine habitats, eroded slopes and avalanche tracks are most likely to become invasive, once they are introduced to central Europe (Hejda et al. 2009b).

Table 3. – Mean proportional numbers of native species, archaeophytes (arch) and neophytes (neo), relative to all species occurring in phytosociological relevés, and mean summed covers of each of these groups in relevés calculated for phytosociological alliances of the Czech Republic. Relevés of all vegetation types from the Czech National Phytosociological Database were used, but excluded were relevés made before 1980 and those made in plots $< 50 \text{ m}^2$ or $> 500 \text{ m}^2$ in forest vegetation, $< 10 \text{ m}^2$ or $> 500 \text{ m}^2$ in shrub vegetation, and $< 10 \text{ m}^2$ or $> 100 \text{ m}^2$ in shrub vegetation. These relevés were classified to phytosociological associations using an expert system for automatic classification developed as a part of the project Vegetation of the Czech Republic. Relevés assigned to each association were resampled in order to reduce oversampling of some areas: the relevés were assigned to cells of a geographical grid of 1.25 longitudinal \times 0.75 latitudinal minutes; from each grid cell, only one relevé was selected at random. The selected relevés were grouped into phytosociological alliances according to the hierarchical structure of associations and alliances published in Vegetation of the Czech Republic (Chytrý 2007, 2009, 2011). Relevés of vegetation dominated by non-vascular plants (class *Charetea* and stands of pleustophytic liverworts) were removed from the data set. The resulting data set, used for the analyses, included 20,830 relevés. Non-vascular plants, taxa identified to the genus level only and hybrids were excluded. Crops were excluded from the relevés of weed vegetation (alliances XBA-XBF). Summed covers of all species within each group (native, archaeophyte and neophyte) were quantified according to the formula given in Chytrý et al. (2005: 343); n = number of relevés used for the calculation.

	n	Proportion of species (%; mean±SD)			Summed cover (%; mean±SD)		
		native	arch	neo	native	arch	neo
Forests							
LAA. <i>Alnion glutinosae</i> – alder carrs	77	98.8±1.9	0.1±0.5	1.1±1.8	89±6	0±0	1±2
LAB. <i>Salicion cinereae</i> – willow carrs	33	98.8±2.3	0.1±0.6	1.1±2.3	84±7	0±0	1±1
LBA. <i>Alnion incanae</i> – ash-alder alluvial forests	252	97.2±3.5	0.7±1.4	2.2±2.8	91±7	1±3	4±10
LBB. <i>Carpinion betuli</i> – oak-hornbeam forests	300	98.7±2.1	0.4±1.2	0.9±1.7	89±7	0±1	1±5
LBC. <i>Fagion sylvaticae</i> – eutrophic beech forests	568	98.9±2.2	0.3±1.2	0.8±1.8	90±7	0±1	1±5
LBD. <i>Sorbo torminalis-Fagion sylvaticae</i> – calcicole beech forests	31	98.6±2.6	1.1±2.5	0.2±1.0	89±6	1±1	0±0
LBE. <i>Luzulo-Fagion sylvaticae</i> – acidophilous beech forests	274	99.4±2.0	0.1±0.7	0.5±1.8	87±7	0±0	0±1
LBF. <i>Tilio platyphylli-Acerion</i> – ravine forests	295	97.5±3.9	0.9±2.3	1.6±2.5	87±10	1±2	3±9
LCA. <i>Quercion pubescenti-petraeae</i> – peri-alpide basiphilous thermophilous oak forests	31	97.8±2.3	0.9±1.8	1.2±1.6	88±9	1±3	3±7
LCB. <i>Aceri tatarici-Quercion</i> – subcontinental forest-steppe oak forests	8	96.4±3.7	2.3±2.3	1.3±1.7	87±11	3±2	1±2
LCC. <i>Quercion petraeae</i> – acidophilous thermophilous oak forests	147	98.0±2.6	1.4±2.1	0.6±1.3	86±9	1±2	1±2
LDA. <i>Quercion roboris</i> – acidophilous oak forests	104	98.3±3.2	0.7±1.9	1.0±2.4	85±10	0±1	1±1
LEA. <i>Erico carnea-Pinion</i> – basiphilous montane pine forests of Central and South-eastern Europe	8	98.7±1.7	0.4±1.1	0.9±1.6	92±5	0±0	2±5
LFA. <i>Festuco-Pinion sylvestris</i> – basiphilous continental pine forests	11	98.7±1.9	0.6±1.4	0.7±1.7	76±12	0±1	1±1
LFB. <i>Dicrano-Pinion sylvestris</i> – acidophilous boreo-continental pine forests	195	99.5±2.1	0.2±1.1	0.3±1.7	74±17	0±0	0±0
LFC. <i>Piceion abietis</i> – central European acidophilous spruce forests	55	100.0±0.0	0.0±0.0	0.0±0.0	80±10	0±0	0±0
LFD. <i>Vaccinio uliginosi-Pinion sylvestris</i> – bog woodlands	51	100.0±0.0	0.0±0.0	0.0±0.0	78±12	0±0	0±0
Scrub							
KAA. <i>Salicion triandrae</i> – willow scrub of loamy and sandy river banks	28	92.4±8.9	2.9±4.2	4.8±6.7	90±9	2±4	4±10
KAB. <i>Salicion elaeagno-daphnoidis</i> – willow scrub of river gravel accumulations	11	84.0±11.7	6.9±7.7	9.1±5.0	68±15	3±3	5±4
KAC. <i>Salicion albae</i> – willow poplar-forests of lowland rivers	79	91.2±9.3	2.8±5.5	6.1±7.5	91±6	1±3	10±19
KBA. <i>Prunion fruticosae</i> – low xeric scrub	18	88.6±15.8	9.6±12.1	1.8±4.4	84±8	5±6	1±3
KBB. <i>Berberidion vulgaris</i> – tall mesic and xeric scrub	157	93.1±7.8	4.7±6.0	2.1±4.3	85±9	4±8	2±5
KBC. <i>Sambuco-Salicion capreae</i> – mesic scrub of forest clearings, canopy openings and disturbed sites	95	95.6±6.2	2.7±5.3	1.7±3.1	87±10	1±2	1±5
KBD. <i>Aegopodio podagrariae-Sambucion nigrae</i> – nitrophilous scrub of ruderal habitats	74	66.8±16.2	24.6±14.8	8.7±9.0	68±30	16±15	29±34
KBE. <i>Chelidonio majoris-Robinion pseudoacaciae</i> – black locust groves with nitrophilous species	189	78.7±9.6	11.1±8.0	10.2±5.7	71±17	16±20	60±14
KBF. <i>Balloto nigrae-Robinion pseudoacaciae</i> – black locust groves on dry sandy soils	31	72.2±9.3	17.6±11.4	10.2±5.7	50±24	31±22	50±16
KBG. <i>Euphorbio cyparissiae-Robinion pseudoacaciae</i> – low black locust groves and scrub at dry and warm sites with shallow soil	9	85.8±5.5	7.9±5.4	6.3±4.0	72±12	6±5	64±19
KCA. <i>Pinion mugo</i> – subalpine dwarf pine scrub	18	100.0±0.0	0.0±0.0	0.0±0.0	87±8	0±0	0±0
Alpine and subalpine vegetation							
AAA. <i>Loiseleurio procumbentis-Vaccinion</i> – arcto-alpine dwarf-shrub vegetation	16	100.0±0.0	0.0±0.0	0.0±0.0	76±14	0±0	0±0
ABA. <i>Juncion trifidi</i> – wind-swept alpine grasslands on base-poor soil	13	99.8±0.9	0.0±0.0	0.2±0.9	65±15	0±0	0±1
ABB. <i>Nardo strictae-Caricion bigelowii</i> – closed alpine grasslands on base-poor soil	8	100.0±0.0	0.0±0.0	0.0±0.0	80±11	0±0	0±0
ACA. <i>Agrostion alpinae</i> – species-rich rock-outcrop grasslands in the Sudetes cirques	9	100.0±0.0	0.0±0.0	0.0±0.0	49±23	0±0	0±0
ADA. <i>Calamagrostion villosae</i> – subalpine tall grasslands	21	100.0±0.0	0.0±0.0	0.0±0.0	85±7	0±0	0±0
ADB. <i>Calamagrostion arundinaceae</i> – subalpine grasslands with <i>Calamagrostis arundinacea</i>	8	99.7±1.0	0.3±1.0	0.0±0.0	75±21	0±1	0±0
ADC. <i>Salicion silesiacae</i> – subalpine deciduous scrub and woodland	8	100.0±0.0	0.0±0.0	0.0±0.0	86±5	0±0	0±0
ADD. <i>Adenostylin alliariae</i> – subalpine tall-forb vegetation	37	99.9±0.5	0.1±0.5	0.0±0.0	80±11	0±0	0±0
ADE. <i>Dryopterido filicis-maris-Athyrium distentifolii</i> – subalpine tall-fern vegetation	14	100.0±0.0	0.0±0.0	0.0±0.0	80±11	0±0	0±0

	n	Proportion of species (%; mean±SD)			Summed cover (%; mean±SD)		
		native	arch	neo	native	arch	neo
Rock and scree vegetation							
SAA. <i>Cystopteridion</i> – vegetation of calcareous rock outcrops and walls	105	85.5±16.4	9.3±12.5	5.2±10.3	27±14	2±3	1±4
SAB. <i>Asplenion cuneifolii</i> – vegetation of serpentine outcrops	20	99.6±1.6	0.4±1.6	0.0±0.0	34±22	0±0	0±0
SAC. <i>Asplenion septentrionalis</i> – vegetation of siliceous rock outcrops and talus slopes	52	98.3±3.5	1.2±3.1	0.5±1.9	41±17	0±1	0±1
SAD. <i>Androsacion alpinae</i> – vegetation of siliceous talus slopes in subalpine and alpine belts	2	100.0±0.0	0.0±0.0	0.0±0.0	22±5	0±0	0±0
SBA. <i>Cymbalaria muralis-Asplenion</i> – wall vegetation with neophytes of Mediterranean origin	63	54.3±23.4	31.7±21.9	14.0±16.1	10±12	21±20	9±16
SCA. <i>Stipion calamagrostis</i> – vegetation of calcareous screes	32	83.5±13.0	13.9±12.3	2.6±7.3	44±19	6±6	1±1
SCB. <i>Galeopsion</i> – vegetation of siliceous screes	8	87.4±10.5	7.0±4.9	5.6±11.9	38±13	5±5	4±11
Aquatic vegetation							
VAA. <i>Lemnion minoris</i> – vegetation of lemniids and free-floating aquatic ferns and liverworts	689	98.7±8.5	0.0±0.0	1.3±8.5	83±13	0±0	1±9
VAB. <i>Utricularion vulgaris</i> – vegetation of bladderworts in mesotrophic to eutrophic water bodies	84	98.9±4.8	0.0±0.0	1.1±4.8	76±18	0±0	0±2
VAC. <i>Hydrocharition morsus-ranae</i> – vegetation of large free-floating vascular plants	222	98.9±5.2	0.0±0.0	1.1±5.2	86±10	0±0	0±1
VBA. <i>Nymphaeion albae</i> – vegetation of aquatic plants rooting in the bottom with leaves floating on the water surface	313	99.0±4.7	0.1±0.9	0.9±4.5	71±19	0±1	1±5
VBB. <i>Potamion</i> – vegetation of aquatic plants rooting in the bottom	1000	92.9±19.2	0.0±0.0	7.1±19.2	70±28	0±0	11±28
VBC. <i>Batrachion fluitantis</i> – vegetation of aquatic plants in streams	119	99.4±3.7	0.0±0.0	0.6±3.7	69±19	0±0	0±0
VBD. <i>Ranunculion aquatilis</i> – vegetation of aquatic plants in shallow water bodies with fluctuating water table	154	99.1±4.0	0.0±0.0	0.9±4.0	73±18	0±0	0±1
VDA. <i>Littorellion uniflorae</i> – submerged vegetation of oligotrophic water bodies	2	100.0±0.0	0.0±0.0	0.0±0.0	20±5	0±0	0±0
VDB. <i>Eleocharition acicularis</i> – vegetation of amphibious plants in shallow, oligotrophic to mesotrophic water bodies	119	97.6±6.3	1.1±3.6	1.3±4.4	78±14	0±1	0±1
VDC. <i>Sphagno-Utricularion</i> – vegetation of oligotrophic pools with bladderworts	27	98.9±4.1	0.0±0.0	1.1±4.1	68±17	0±0	0±1
Wetland vegetation							
MAA. <i>Eleocharition ovatae</i> – vegetation of short-growing annual herbs on exposed bottoms of fisponds	259	92.3±7.9	4.5±5.5	3.2±4.6	61±20	2±4	2±4
MAB. <i>Radiolion linoidis</i> – vegetation of short-growing annual herbs on wet sand	5	84.6±10.6	6.9±8.1	8.5±8.6	40±14	6±9	15±18
MAC. <i>Verbenion supinae</i> – vegetation of annual herbs on base-rich exposed bottoms in warm areas	8	83.7±9.3	13.9±10.0	2.4±3.4	59±14	12±14	1±1
MBA. <i>Bidenion tripartitae</i> – nitrophilous vegetation of exposed bottoms and wet ruderal habitats	248	90.0±10.6	5.4±7.4	4.6±6.7	75±19	2±5	8±21
MBB. <i>Chenopodium rubri</i> – nitrophilous vegetation with <i>Chenopodium</i> and <i>Atriplex</i> in wet habitats	63	72.8±18.8	21.6±15.4	5.6±7.5	68±17	7±11	2±7
MCA. <i>Phragmition australis</i> – fresh-water reed vegetation	1974	94.0±15.4	0.5±2.7	5.4±15.2	73±24	0±1	7±22
MCB. <i>Melilotto dentati-Bolboschoenion maritimi</i> – continental brackish marsh vegetation	38	95.3±7.8	2.6±5.5	2.1±5.2	73±17	1±2	1±2
MCC. <i>Eleocharito palustris-Sagittarion sagittifoliae</i> – vegetation of large wetland herbs in habitats with periodical changes of water level	812	96.2±8.3	1.1±4.4	2.7±6.8	75±17	0±2	1±4
MCD. <i>Phalaridion arundinaceae</i> – reed and tall-sedge vegetation on river banks	143	89.5±11.2	5.6±7.7	4.9±7.9	82±12	2±4	2±4
MCE. <i>Glycerio-Sparganion</i> – medium-tall reed stands along brooks and on floating islands	564	97.3±6.9	0.6±2.8	2.2±6.0	80±15	0±2	1±2
MCF. <i>Carici-Rumicion hydrolopathi</i> – vegetation of wetland herbs on organic muddy sediments	81	97.1±7.1	0.0±0.4	2.8±7.0	81±15	0±0	0±1
MCG. <i>Magno-Caricion elatae</i> – tall-sedge vegetation in littoral zones of oligotrophic and mesotrophic water bodies	260	98.3±6.1	0.4±2.6	1.3±5.5	80±13	0±1	0±1
MCH. <i>Magno-Caricion gracilis</i> – tall-sedge vegetation in littoral zones of eutrophic water bodies	780	96.4±8.1	0.8±3.7	2.7±7.0	84±9	0±1	1±2
Spring and mire vegetation							
RAA. <i>Caricion remotae</i> – vegetation of non-calcareous forest springs	207	99.3±2.3	0.1±0.9	0.6±2.0	68±18	0±0	1±4
RAB. <i>Lycopodo europaei-Cratoneurion commutati</i> – vegetation of calcareous forest springs with tufa formation	20	98.5±4.8	0.5±2.0	1.0±4.5	27±25	0±0	0±0

	n	Proportion of species (%; mean±SD)			Summed cover (%; mean±SD)		
		native	arch	neo	native	arch	neo
RAC. <i>Epilobio nutantis-Montion fontanae</i> – vegetation of subatlantic, submontane springs in open habitats	19	98.6±4.8	0.2±0.8	1.2±4.6	59±18	0±1	0±1
RAD. <i>Swertio perennis-Dichodontion palustris</i> – vegetation of non-calcareous alpine and subalpine springs	27	100.0±0.0	0.0±0.0	0.0±0.0	52±25	0±0	0±0
RBA. <i>Caricion davallianae</i> – calcareous fens	91	99.5±1.4	0.4±1.1	0.2±0.8	73±18	0±1	0±0
RBB. <i>Sphagno warnstorffii-Tomentypnion nitentis</i> – fens with calcicolous species and calcitolerant peat mosses	60	100.0±0.0	0.0±0.0	0.0±0.0	70±11	0±0	0±0
RBC. <i>Caricion canescenti-nigrae</i> – slightly acidic fens	112	99.9±0.5	0.0±0.4	0.0±0.4	69±15	0±0	0±0
RBD. <i>Sphagno-Caricion canescentis</i> – acidic fens (transitional mires)	181	100.0±0.4	0.0±0.0	0.0±0.4	55±19	0±0	0±0
RBE. <i>Sphagnion cuspidati</i> – vegetation of bog hollows	29	100.0±0.0	0.0±0.0	0.0±0.0	25±20	0±0	0±0
RCA. <i>Sphagnion magellanici</i> – continental and subcontinental bogs	99	100.0±0.0	0.0±0.0	0.0±0.0	57±20	0±0	0±0
RCB. <i>Oxycocco palustris-Ericion tetralicis</i> – oceanic and suboceanic bogs	9	100.0±0.0	0.0±0.0	0.0±0.0	61±23	0±0	0±0
RCC. <i>Oxycocco microcarpi-Empetrium hermaphroditum</i> – boreal bogs	10	100.0±0.0	0.0±0.0	0.0±0.0	49±17	0±0	0±0
Grassland and heathland vegetation							
TAA. <i>Cypero-Spergularion salinae</i> – inland salt marshes with annual halophilous grasses	8	85.7±10.3	12.5±7.7	1.8±3.3	68±16	2±2	1±1
TCA. <i>Puccinellion limosae</i> – intermittently dry saline grasslands	8	94.1±7.9	5.9±7.9	0.0±0.0	63±16	2±3	0±0
TCB. <i>Juncion gerardii</i> – mesic and wet saline grasslands	48	90.2±7.9	7.4±6.3	2.4±3.4	64±16	4±4	5±11
TDA. <i>Arrhenatherion elatioris</i> – lowland to submontane mesic meadows	778	94.1±5.1	5.4±4.7	0.5±1.5	73±14	14±18	1±4
TDB. <i>Polygono bistortae-Trisetion flavescens</i> – montane mesic meadows	66	99.0±1.6	0.9±1.5	0.1±0.6	89±10	1±3	0±0
TDC. <i>Cynosurion cristati</i> – mesic pastures and perennial grasslands of trampled habitats	330	85.7±14.9	9.5±12.6	4.8±6.2	71±18	6±13	6±14
TDD. <i>Molinion caeruleae</i> – intermittently wet, nutrient-poor meadows	116	99.2±1.5	0.8±1.5	0.1±0.5	81±9	1±3	0±0
TDE. <i>Deschampsion cespitosae</i> – lowland floodplain meadows	190	95.5±4.8	3.5±3.9	1.0±2.2	82±11	3±7	1±2
TDF. <i>Calthion palustris</i> – wet tall-herb meadows	913	98.5±3.5	0.9±2.5	0.7±2.0	84±11	1±3	1±2
TEA. <i>Nardion strictae</i> – subalpine <i>Nardus</i> grasslands	23	100.0±0.0	0.0±0.0	0.0±0.0	82±9	0±0	0±0
TEB. <i>Nardo strictae-Agrostion tenuis</i> – montane <i>Nardus</i> grasslands with alpine species	22	100.0±0.0	0.0±0.0	0.0±0.0	86±8	0±0	0±0
TEC. <i>Violion caninae</i> – submontane and montane <i>Nardus</i> grasslands	83	99.0±1.8	1.0±1.7	0.0±0.3	83±8	1±3	0±0
TED. <i>Nardo strictae-Juncion squarrosi</i> – wet <i>Nardus</i> grasslands	8	99.3±2.1	0.0±0.0	0.7±2.1	65±15	0±0	0±1
TEE. <i>Euphorbio cyparissiae-Callunion vulgaris</i> – dry lowland and colline heathlands	16	97.5±4.9	1.4±2.6	1.1±4.5	76±10	1±1	0±1
TEF. <i>Genisto pilosae-Vaccinion</i> – submontane to subalpine <i>Vaccinium</i> heathlands	144	99.4±1.9	0.4±1.5	0.2±0.9	74±13	0±1	0±0
TFA. <i>Corynephorion canescentis</i> – open sand grasslands	45	93.4±7.8	4.8±6.5	1.8±3.4	49±20	1±2	1±1
TFB. <i>Thero-Airion</i> – vegetation of annual grasses on sandy soils	24	86.6±19.3	12.4±18.8	0.9±2.7	33±16	16±23	0±1
TFC. <i>Armerion elongatae</i> – closed sand grasslands	62	93.8±6.7	4.9±5.5	1.3±2.5	68±13	3±4	1±1
TFD. <i>Hyperico perforati-Scleranthion perennis</i> – submontane acidophilous vegetation of shallow soils	116	97.1±4.3	2.5±4.0	0.4±1.6	55±17	1±3	1±4
TFE. <i>Arabidopsion thalianae</i> – acidophilous vegetation of vernal therophytes and succulents	55	95.9±5.5	3.6±4.8	0.5±1.5	49±18	2±3	1±5
TFF. <i>Alysso alyssoidis-Sedion</i> – basiphilous vegetation of vernal therophytes and succulents	35	90.2±10.6	9.2±9.9	0.5±2.3	57±16	6±12	0±1
TGA. <i>Festucion vaginatae</i> – Pannonian sand steppe grasslands	8	84.6±10.6	13.3±10.2	2.1±2.3	51±21	7±7	1±1
THA. <i>Alysso-Festucion pallentis</i> – Hercynian rock-outcrop vegetation with <i>Festuca pallens</i>	50	97.7±3.2	2.2±3.1	0.0±0.3	52±21	1±2	0±2
THB. <i>Bromo pannonici-Festucion pallentis</i> – Pannonian vegetation of limestone outcrops	8	99.5±1.4	0.5±1.4	0.0±0.0	55±10	0±0	0±0
THC. <i>Diantho lummitzeri-Seslerion</i> – <i>Sesleria caerulea</i> grasslands	34	98.4±2.5	1.3±2.4	0.3±1.1	64±16	1±1	1±7
THD. <i>Festucion valesiacae</i> – narrow-leaved dry grasslands and short-grass steppes	112	95.9±4.9	3.7±4.4	0.4±1.4	78±9	2±6	0±2
THE. <i>Cirsio-Brachypodion pinnati</i> – subcontinental broad-leaved semi-dry grasslands and tall-grass steppes	218	96.4±3.5	2.3±2.8	1.3±2.0	77±10	2±5	1±4

	n	Proportion of species (%; mean±SD)			Summed cover (%; mean±SD)		
		native	arch	neo	native	arch	neo
THF. <i>Bromion erecti</i> – suboceanic broad-leaved semi-dry grasslands	92	96.8±2.5	3.0±2.4	0.2±0.8	80±11	4±7	0±1
THG. <i>Koelerio-Phleio phleoidis</i> – acidophilous dry grasslands	86	96.6±3.4	3.3±3.4	0.1±0.6	71±11	5±13	1±7
THH. <i>Geranion sanguinei</i> – dry herbaceous fringe vegetation	90	96.1±5.9	3.3±5.2	0.6±1.6	80±8	3±8	0±1
THI. <i>Trifolion medii</i> – mesic herbaceous fringe vegetation	108	94.8±4.2	4.9±4.1	0.3±1.2	79±10	4±6	0±1
Ruderal and weed vegetation							
XAA. <i>Coronopodo-Polygonion arenastris</i> – annual vegetation of dry trampled habitats	188	65.0±19.8	26.6±17.6	8.3±8.7	60±29	16±18	2±6
XAB. <i>Saginion procumbentis</i> – annual vegetation of mesic trampled habitats	192	77.2±16.3	15.2±13.4	7.6±6.7	57±22	6±11	8±16
XBA. <i>Caucalidion</i> – thermophilous weed vegetation of cereal fields on base-rich soils	350	41.9±12.6	53.7±12.0	4.4±3.9	27±16	31±18	4±10
XBB. <i>Veronico-Euphorbion</i> – basiphilous weed vegetation in root-crop fields	346	40.7±13.7	47.9±13.4	11.5±7.7	27±18	30±18	14±19
XBC. <i>Scleranthion annui</i> – weed vegetation of cereal fields on acidic soils	358	53.9±12.0	41.8±11.8	4.3±3.6	39±19	35±20	6±12
XBD. <i>Arnoserdion minimae</i> – weed vegetation of cereal fields on nutrient-poor acidic soils	2	68.8±6.4	24.0±3.7	7.1±10.1	31±11	21±10	3±4
XBE. <i>Oxalidion fontanae</i> – weed vegetation of cereal and root-crop field in cool areas	207	53.7±12.9	35.8±12.4	10.6±6.1	38±20	25±17	15±21
XBF. <i>Spergulo arvensis-Erodion cicutariae</i> – weed vegetation of dry sandy soils	87	39.8±17.9	50.2±18.3	10.0±6.6	22±20	32±22	11±18
XBG. <i>Atriplicion</i> – ruderal vegetation of tall annual herbs	362	47.1±16.8	44.0±16.4	8.8±9.4	34±29	45±32	13±24
XBH. <i>Sisymbriion officinalis</i> – ruderal vegetation of winter-annual grasses	74	50.1±18.5	44.6±16.5	5.3±6.5	19±14	63±17	2±5
XBI. <i>Malvion neglectae</i> – ruderal vegetation of prostrate annual herbs on nutrient-rich soils	57	45.5±14.3	45.9±15.6	8.6±7.3	24±18	59±21	4±7
XBJ. <i>Salsolion ruthenicae</i> – annual ruderal vegetation of disturbed gravelly and sandy soils	24	57.5±18.2	26.4±12.0	16.1±11.4	33±20	25±22	8±9
XBK. <i>Eragrostion cilianensi-minori</i> – late-summer thermophilous ruderal and weed vegetation of sandy soils	39	40.0±17.6	50.3±18.0	9.7±9.8	11±10	49±27	3±5
XCA. <i>Onopordion acanthii</i> – thermophilous archaeophyte-rich ruderal vegetation with biennial and perennial herbs	45	53.8±16.2	42.0±14.7	4.2±5.4	39±21	49±17	4±10
XCB. <i>Dauco carotae-Melilition</i> – ruderal vegetation with biennial and perennial herbs on stony and gravelly soils	621	68.8±17.3	24.7±15.7	6.6±7.0	53±25	23±26	20±29
XCC. <i>Convolvulo arvensis-Elytrigion repentis</i> – ruderal vegetation with perennial herbs on dry or intermittently dry soils	205	68.6±19.1	27.8±17.9	3.6±7.2	71±26	21±26	3±10
XCD. <i>Artemisio-Kochion prostratae</i> – relict vegetation of the Pleistocene loess steppes	3	81.9±1.2	18.1±1.2	0.0±0.0	59±17	7±5	0±0
XCE. <i>Arction lappae</i> – nitrophilous ruderal vegetation with biennial and perennial species in man-made habitats	142	62.4±17.9	35.1±17.2	2.4±4.5	35±22	65±22	1±4
XDA. <i>Senecionion fluviatilis</i> – nitrophilous herbaceous fringes of floodplain forests	118	77.9±11.0	7.7±8.2	14.4±8.6	43±24	3±4	62±28
XDB. <i>Petasition hybridi</i> – vegetation of montane and submontane floodplains with <i>Petasites</i>	127	96.4±5.4	1.7±4.4	1.9±3.8	85±11	1±2	1±2
XDC. <i>Impatienti noli-tangere-Stachyion sylvaticae</i> – nitrophilous vegetation of forest fringes, canopy openings and clearings with perennial herbs	126	90.0±12.7	6.4±9.4	3.6±5.4	59±23	5±12	6±15
XDD. <i>Geo urbani-Alliarion petiolatae</i> – nitrophilous vegetation of disturbed forest fringes with annual and biennial herbs	64	77.6±16.5	19.0±15.1	3.3±4.5	61±23	16±18	3±7
XDE. <i>Aegopodion podagrariae</i> – nitrophilous ruderal vegetation with broad-leaved perennial herbs	521	76.7±18.1	14.7±13.4	8.6±13.1	59±31	7±11	30±39
XDF. <i>Rumicion alpini</i> – montane nitrophilous vegetation of broad-leaved herbs	8	86.6±7.7	1.3±3.5	12.2±4.9	26±17	1±2	78±16
XEA. <i>Fragarion vescae</i> – herbaceous vegetation at sites of disturbed forest	276	96.3±5.4	1.5±3.9	2.2±3.4	75±17	1±5	3±9

Changes in the level of invasion over time

There are distinct temporal trends in the representation of alien species in Czech vegetation, however, they are opposite between archaeophytes and neophytes. Lososová & Simonová (2008) compared data on ruderal and weed flora in Moravia between the early 20th century and the turn of the 21st century, showing a decrease in archaeophytes and increase in neophytes. The same trends for these two groups of aliens were confirmed in the analyses of data spanning over a few decades in the second half of the 20th century, e.g. for weed vegetation across the Czech Republic (Lososová et al. 2004, Pyšek et al. 2005) or ruderal vegetation in the city of Plzeň (Pyšek et al. 2004a; here the increase in neophytes was non-significant). These trends will probably continue in the future, although the future spread of alien species in vegetation will mainly depend on changing land use. European scenarios of future changes in the level of invasion project smaller increases in central Europe than in north-western Europe (Chytrý et al. 2012). The mean level of invasion across landscapes may even slightly decrease in the regions where large areas of arable land are abandoned, leading to a subsequent decrease in alien species during succession.

Management and legislation

Various approaches are used to manage introduced species, which differ with respect to the stage of invasion and the pathway of introduction (Hulme et al. 2008). The most effective and cheapest approach is prevention of introductions or early detection followed by rapid response to control potential invasive species (Brooks & Klinger 2009, Pyšek & Richardson 2010). It has been shown several times that eradications are possible only for relatively small infestations before the species starts to spread (Rejmánek & Pitcairn 2002, Simberloff 2003, Genovesi 2007, Pluess et al. 2012). As available time and financial resources are always limited for monitoring and management of introduced species, proper prioritization based on (i) the relative impact of alien species, (ii) their potential to spread and establish in new locations, and (iii) feasibility of their control should be made (Brooks & Klinger 2009).

Unfortunately in Europe, including the Czech Republic, the legislation regarding alien species and implementation of early warning systems is still rather inconsistent, with the only exception being economically important pests and weeds or species directly affecting human health (Šíma 2008). Although there is an ongoing effort towards developing the EU information system for alien species (Genovesi et al. 2010, Shine et al. 2010), the issue remains unsolved in many countries. In the Czech Republic, the key legislative instrument for biodiversity conservation is the Act no. 114/1992, which restricts deliberate introductions of non-native species into the wild. A second important legislative tool is the Act no. 326/2004 on phytosanitary care, which focuses on weeds and sets the obligation to minimize the impact of alien species on nature (Šíma 2008).

The Czech Republic is still lacking a systematic assessment of the ecological and economic impacts of alien plants. Papers rigorously testing ecological impacts are only starting to appear (Hejda et al. 2009a). Information on costs incurred by invasions of alien species is only available at local scales and for specific eradication events and management efforts, mostly from protected areas. These data relate to individual invasive species, such as *Pinus strobus*, for which a management cost of 4.5 million CZK was estimated for populations in the České Švýcarsko National Park from 2000–2003 (including costs associated with

management of the locally non-native *Larix decidua*). Another example is the management of six major invasive taxa subjected to control in the Český ráj Landscape Protected Area in 2003, where the costs reached 450,000 CZK (Křivánek 2006). A study of *Heracleum mantegazzianum* estimated the total annual economic impact of this species in the Czech Republic reaching up to 2.5 million CZK (Linc 2012). Therefore, a thorough nationwide assessment of ecological and economic impacts of alien plants in the Czech Republic stands out as one of the main future challenges for both researchers and practitioners.

Acknowledgements

We thank Laura Celesti-Grapow and Franz Essl for helpful comments on the manuscript. The work was supported by grant no. P504/11/1028 (Czech Science Foundation), long-term research development project no. RVO 67985939 (Academy of Sciences of the Czech Republic) and institutional resources of Ministry of Education, Youth and Sports of the Czech Republic. P.P. acknowledges the support by the Praemium Academiae award from the Academy of Sciences of the Czech Republic.

Souhrn

Díky silné tradici výzkumu synantropních a potažmo nepůvodních rostlin se v České republice nahromadila data, která poskytují dobrou představu o nepůvodní flóře a rostlinných invazích. Práce shrnuje současný stav z hlediska složení nepůvodní flóry (na základě nedávno publikovaného nového přehledu nepůvodních taxonů) a invadovanosti krajiny a jednotlivých biotopů. Dosud bylo u nás zaznamenáno 1454 nepůvodních taxonů, z nichž 350 jsou archeofyty a 1104 neofyty. V posledních dvou stoletích přibývaly zavlečené druhy stálým tempem a dynamika zavlékání nejeví známky zpomalení. Přibližně do 70. let 19. století přibývaly zhruba stejně rychle taxony mediteránní a taxony zavlečené z ostatních částí Evropy, poté se však Středomoří stalo hlavním zdrojem české zavlečené flóry. Druhy ze vzdálenějších oblastí, jako je Asie a Severní Amerika, se začaly ve velkém objevovat s určitým zpožděním. Z celkového počtu zavlečených taxonů je 985 (67,7 %) klasifikováno jako přechodně zavlečené, 408 (28,1 %) jako naturalizované avšak neinvazní a 61 (4,2 %) jako invazní. Nepůvodní druhy tvoří 33,3 % z celkového počtu taxonů, které byly kdy zaznamenány v české flóře; pokud ze srovnání vyloučíme původní vyhynulé taxony a z nepůvodních zahrneme pouze trvale přítomné, tedy naturalizované taxony, podíl zavlečených klesne na 14,6 %. Tato zastoupení odpovídají hodnotám známým z jiných středoevropských zemí. V České republice je v současné době evidováno 11 archeofytů a 50 neofytů, které tvoří invazní populace. Appendix 1 přináší přehled těchto taxonů s informacemi o historii invaze, ekologii, vazbě na stanoviště, případných důsledcích invaze a rozšíření taxonu, které je doplněno mapkou. Oblastmi s největší hustotou invazních druhů v krajině, jakož i nejvyšší invadovaností rostlinných společenstev a jejich stanovišť jsou města nebo vesnice a jejich okolí, nivy velkých řek, oblasti s krajinou narušenou po těžbě uhlí na severu Čech a Moravy, zemědělská krajina a výsadby dřevin v teplých nížinách, zejména na jižní Moravě a ve středních a východních Čechách. Invadovanost klesá s nadmořskou výškou, a to zřetelněji pro neofyty, jejichž výskyt je silněji koncentrován v nížinách. Práce nově přináší kvantitativní přehled invadovanosti všech fytoecologických svazů české vegetace; narušovaná stanoviště a stanoviště, na kterých kolísá množství dostupných zdrojů (zejména živin, ale i vody nebo světla), a na ně vázané vegetační typy jsou nejvíce invadovány. Další šíření nepůvodních druhů do vegetace bude záviset hlavně na tom, jak se bude měnit obhospodařování krajiny.

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Received 2 July 2012

Revision received 18 July 2012

Accepted 20 July 2012

Appendix 1. – Factsheets of invasive neophytes in the Czech Republic. The list of taxa is taken from Pyšek et al. (2012a). Distribution maps are shown in grid cells of CEBA mapping system (Niklfeld 1999), based on data taken from the Database of the flora of the Czech Republic (www.florabase.cz, accessed in June 2012), with permission of the original data providers (Institute of Botany AS CR, Masaryk University Brno and Czech Botanical Society), and other sources specified below. Only occurrences outside cultivation are considered in the maps. Maps are not shown for taxa where sufficient information on distribution is not available, mostly due to low reliability of records in taxonomically difficult taxa that are easy to be misidentified in the field. Note that the distribution maps are generally somewhat underestimated since they are not the result of systematic mapping of invasive species, but for the taxa presented they reflect the patterns of geographic distribution reasonably well. Habitat affinities of invasive taxa, including archaeophytes, are summarized in Table 2.

Acer negundo L. (*Sapindaceae*) is a dioecious tree reaching a height up to 20 m; in the Czech Republic it grows shorter, up to 10 m in height. It is native to eastern and central parts of North America (Koblížek in Slavík et al. 1997). Its moderate resistance to flooding combined with tolerance to water deficits enable it to occur in a wide range of habitats ranging from wetlands and floodplain forests to relatively dry forests and grasslands (Médrzycki 2011). The introduced range covers Europe, part of Asia and Australia (DAISIE 2009). The species was imported to Europe as an ornamental tree in the 17th century, with its first record in the UK dating from 1688 (Kowarik 1992). It became a popular garden tree due to its fast growth in the first years. In the second half of the 19th century it was planted in parks, along roads, in wind-breaks and shelter belts (Tutin et al. 1968). The first record of spontaneous occurrence in the wild in the Czech Republic is probably from the Elbe riverbank near Neratovice in 1875 (Pyšek et al. 2002b). It is commonly planted in the country, with a variety of cultivars on the market. It spreads by seed and easily resprouts from stumps. It prefers moist open habitats with sufficient supply of organic nutrients on clayey or sandy soils. The species is planted in urban areas, industrial zones and wind-breaks, where the planted trees give rise to populations originating through mostly vegetative growth. Above 350 m a.s.l. seed reproduction is only occasional. It also forms spontaneous invasive populations along large rivers, where it invades disturbed floodplain forests (especially along the Morava and lower Dyje river; Hrázský 2005), and in areas recultivated after coal mining. Except in these plantations, it rarely occurs as a strong dominant with a high cover, and often occurs together with many other neophytes such as *Aster* spp., *Fraxinus pennsylvanica*, *Helianthus tuberosus*, *Robinia pseudoacacia* and *Solidago* spp. It is recorded from 7 habitat types (Table 2). The invasion is most pronounced in warm regions in the Czech Republic, namely in southern and central Moravia (Fig. 8), where it is common, builds extensive monodominant stands and spreads rapidly. *Acer negundo* is ranked among the 40 most invasive woody species of the world (Rejmánek & Richardson 1996). It has negative impacts due to pollen causing allergenic reactions in humans (Esch et al. 2001) and through competition with other species at invaded sites.

Ailanthus altissima (Mill.) Swingle (*Simaroubaceae*) is a fast-growing deciduous tree, ~20 m tall, reproducing both vegetatively by root suckers, and by seed (up to 325,000 seeds per year are produced by a single tree; Bory & Clair-Maczulajtys 1980, Kowarik & Säumel 2007, DAISIE 2009). It is native to eastern Asia (China and Korea) and introduced worldwide, including Australia and the Pacific Islands. The species was introduced to Europe in 1784 or earlier (some sources suggest an introduction time of ca 1750 to the UK) as an ornamental tree (Koblížek in Slavík et al. 1997). In the Czech Republic the first record of planting comes from 1813 (Svoboda & Svobodová 1969) and in the wild from a forest near Veltrusy, central Bohemia (Čelakovský 1868–1883, Pyšek et al. 2012a). The species is highly tolerant of polluted air and poor soils, and is markedly resistant to varying temperatures, humidity, light and moisture levels, and is thus able to grow in stressful habitats (Kavka 1969). At present it spreads in large cities and their suburbs and industrial zones where it forms large stands independent of original plantings. Beside urban habitats, it occurs in shrub and grassland vegetation, especially in warmer areas; it is recorded from 10 habitat types (Table 2). It is spread by wind and water (Kowarik & Säumel 2008). As a rather weak competitor it is only able to establish in sparse vegetation, although after establishment it intensively spreads by root suckers. Typical habitats in the Czech Republic are railway corridors where invasion is supported by cutting vegetation, which enables *Ailanthus* to form dense thickets by clonal growth. It often grows combined with *Robinia pseudoacacia* stands and together with other neophytes such as *Lycium barbarum*, *Parthenocissus quinquefolia*, *Acer negundo* and *Syringa vulgaris*. It has been occasionally planted in dry grasslands on steep slopes where it forms clonal scrub or short woodland with thermophilous species, vegetation similar to that found in southeastern Europe (Sirbu & Oprea 2011). The invasive populations in the Czech Republic are concentrated in southern Moravia (Fig. 8). The impact of *A. altissima* on native vegetation is through its formation of dense thickets and allelopathic effects inhibiting growth and germination of native species (Heisey 1990, Lawrence et al. 1991). The plant sap can induce dermatitis in humans. Another important aspect is that the root system of the tree often damages pavements, walls, and buildings (Celesti-Grapow & Blasi 2004, DAISIE 2009).

Amaranthus powellii S. Watson (*Amaranthaceae*) is an annual herb native to tropical and subtropical South and Central America. Its invaded range includes colder regions of North America, Europe, Asia, Africa and Australia, where it grows in open ruderal vegetation in urban areas and as a weed in fields and gardens. The first record in the Czech Republic is from a potato field near Mnichovo Hradiště, northeastern Bohemia, where it was observed in 1853 (Sekera 1854). The oldest herbarium specimen is from 1931. Introduced to the Czech Republic as contaminant of grain, oil seed, ore, cotton and wool, it is common in warm lowland regions (Fig. 8) and tends to spread to colder areas and higher altitudes (Jehlík in Hejný et al. 1990). Until the 1960s it occurred only in ruderal habitats in villages and along roads (Deyl 1964). It started to spread rapidly in the 1980s supported by frequent planting of maize and beet (Hejný et al. 1973). In the 1990s it became common as a weed in agricultural fields (Jehlík in Hejný et al. 1990). It is resistant to some herbicides (Salava & Chodová 2007) and in the last decade its invasion has been supported by their regular application in agriculture, railway transport and in urban areas. Compared to the congeneric *A. retroflexus*, it is less widely distributed, confined to warmer areas, less drought-resistant and more nutrient-demanding, which is reflected in it being currently more invasive in agricultural fields and vegetable gardens than in ruderal habitats (Table 2).

Amaranthus retroflexus L. (*Amaranthaceae*) is an annual herb native to North America, introduced to regions with temperate and warm climate on all continents except for Antarctica. In the native range it is a component of pioneer riverine vegetation. The oldest records in the Czech Republic, to where it was introduced as a contaminant in grain, oil seed, cotton and wool, are from 1818 in Prague and 1822 in Uherské Hradiště, southern Moravia (Jehlík in Hejný et al. 1990). Seed contamination of soils and commodities is linked to its extreme fecundity, with a single plant producing up to 500,000 seeds, which remain viable in the soil for up to 5 years (Deyl 1964). It grows in relatively dry and nutrient-rich urban and agricultural habitats such as rubbish dumps, soil heaps after mining along roads, rivers and railroads, and as a weed in fields; it is recorded from 10 habitat types (Table 2). Its invasion has been supported by an increase in maize and beet planting, although currently it benefits mostly from its tolerance of herbicides, high salinity levels, polluted soil (Jehlík in Hejný et al. 1990, Mikulka & Chodová 1998) and eutrophication of the landscape. Further massive spread in currently occupied habitats is unlikely since the species is widespread and common (Fig. 8) and appears to have colonized most available habitats. However, further spread of herbicide-resistant populations to less suitable habitats as well as into higher altitudes cannot be excluded. The major impact of this species is due to its reduction of agricultural yield.

Ambrosia artemisiifolia L. (*Asteraceae*) is an annual herb with a native range in North America, including the central and eastern USA, where it grows as a pioneer species of open semi-arid habitats. In its invaded range, which includes all continents as well as some islands (New Zealand, Hawaii, Madagascar, Mauritius; Slavík in Slavík et al. 2004, Brandes & Nitzsche 2007), it is known from a wide range of open and nutrient-rich, disturbed ruderal habitats and arable land (Chauvel et al. 2006, Essl et al. 2009, Pinke et al. 2011). The species was introduced to Europe in the second half of the 19th century as a contaminant of agricultural products, bird seed and with agricultural machinery (Chauvel et al. 2006). Several independent introductions have been documented (Genton et al. 2005). Early introductions in Europe mostly resulted in short-lived casual occurrences. Established populations only developed in the first decades of the 20th century, and commonly after the World War II. Within the last few decades *A. artemisiifolia* has significantly increased its range and abundance in many European countries (DAISIE 2009), and spread into a number of habitats (Essl et al. 2009). The invasion is supported by a high amount of produced seed (1200–2500 seeds per plant, Fumanal et al. 2007, Moravcová et al. 2010), which form a long-term persistent soil-seed bank, with seeds remaining viable for up to 40 years (Baskin & Baskin 1980). The first record in the Czech Republic is from 1883, in a clover field near Třeboň, southern Bohemia, and from a field near Doudlevice near Plzeň, western Bohemia (Čelakovský 1885, Polívka 1900–1904). These individuals were probably introduced with clover seed from North America. The next wave of introductions occurred in the second half of the 20th century from two different sources: with grain from Canada and soya beans from North America, and with Ukrainian grain and Soviet ore (Slavík in Slavík et al. 2004). The species is confined to warm regions in the Czech Republic (Fig. 8) and prefers open dry habitats on sandy or gravel substrata and low vegetation cover. After rapid spread in the 1980s–1990s, the invasion decelerated recently. The species is limited by requiring well-aerated soils and being a weak competitor. It rarely spreads in urban spaces, along railways, in sand pits, coal mining heaps or into semi-natural grasslands. In southern Moravia, however, it has started to occur as a weed of maize fields recently (Mikulka 2011). It occurs mostly in ruderal habitats (Table 2), in particular along railways where it is supported by the use of herbicides, to which some populations are resistant. It also partly avoids herbicides, because they are applied at the end of spring when *Ambrosia* populations are only starting to germinate, having phenological optimum in the autumn. It is scattered and locally abundant, especially at railways but does not form monodominant stands yet. The pollen of *A. artemisiifolia* is the most allergenic of all plant species occurring in

Europe (Jäger 2000). Its pollen curve peaks in August–September in the Czech Republic, especially in southern Moravia (Rybníček 2000). It is spreading with easterly winds, most probably from the Hungarian lowlands (Obstová 2012). Due to its so far rare occurrence in the Czech Republic it does not present any strong threat for the allergic population in this country, but its importance as an allergen can increase in the future (Rybníček 2000). The economic costs of ragweed invasion in Germany are estimated at 32 million euros annually, nearly entirely incurred within the health sector (Reinhardt et al. 2003). Additionally, annual costs of human ragweed allergy in France and Italy amount to 2 million euros (Buttenschøn et al. 2009). Furthermore, in other countries *A. artemisiifolia* significantly reduces crop yields, especially in spring-sown crops like sunflower, soybean, maize and vegetables (Weber & Gut 2005, Sheppard et al. 2006). However, in most of Europe, the infestation of agricultural fields is a relatively recent phenomenon; thus impacts on crop yield are still minor.

Asclepias syriaca L. (*Apocynaceae*) is a rhizomatous perennial native to the eastern North America, with a distribution ranging from Canada to North Carolina. In its native range the species grows in prairies, along roads and railways, and at disturbed sites. It was introduced to many regions of the world, and to Europe in 1629. The first record of planting in the Czech Republic is from the Lány chateau park, central Bohemia, in 1786 (Slavík in Slavík et al. 2000), and that of escape from cultivation is from 1901 (Polívka 1900–1904). It was planted for multiple purposes in the past, including medicinal, textile, oil and bee keeping. It is currently kept in cultivation mostly as an ornamental (Slavík in Slavík et al. 2000). In the Czech Republic, it is abundant and invasive only in warm lowlands, especially in southern Moravia (Fig. 8) where it spreads over long distances by seed. However, the spread by rhizomes is a more important vector, such as with contaminated soil during railway construction. In Bohemia, it forms rather large but isolated stands, and long-distance dispersal is limited. The populations colonize open habitats along roads, railways, in vineyards and shrub margins, abandoned places in settlements and dry banks of streams (Table 2). The stands have an appearance of tall grassland, persist for decades and are relatively species-rich (Lániková in Chytrý 2009). The species is toxic to humans and herbivores. Some impact of *Asclepias* on species diversity is reported from southern Europe where it colonizes nutrient-poor soils and sand dunes (Wittenberg 2005).

Bassia scoparia (*Amaranthaceae*) occurs in two subspecies in the Czech Republic, **subsp. scoparia** and **subsp. densiflora** (B. D. Jacks.) Ciruja et Velayos. It is an annual plant up to 2 m tall, native in a large area from south-eastern Europe to eastern Asia, where it grows in dry open steppe habitats and as a weed in fields. It was introduced, as a contaminant of seed for agriculture as well as an ornamental plant, to warmer parts of Europe, South Africa, Americas and Australia (Jehlík 1998). The first report of cultivation of the subspecies *scoparia* in the Czech Republic is from 1811, that of escape from 1819 (Opiz 1823); subspecies *densiflora* was introduced with commodities from the former Soviet Union and was first collected in Moravia in Popice (1901, A. Schierl, OLM) and in Bohemia in Prague-Zlíchov (1930 Rohlena, PRC). The rapid spread in warm regions (Fig. 8) only started at the beginning of the 1990s. The species prefers sandy and gravelly soil with low nutrient content, and occurs in open dry habitats; it grows well on salty and polluted soils (Lososová in Chytrý 2009). It colonizes ruderal habitats, namely along railways, but also grows along roads, in sand pits and on sand heaps (Table 2), and forms dense closed stands persisting for several years. It is wind-pollinated, thus maintaining a genetic link with populations in cultivation. In southern Moravia it is reported to occur as a weed in maize fields (Mikulka 2011). Populations are herbicide-resistant and have the development peak in the autumn, therefore benefiting from the spring application of herbicides (Mikulka & Chodová 1998). Both subspecies grow together in invaded localities, with the subspecies *scoparia* being more common.

***Beta vulgaris* Altissima Group** (*Brassicaceae*) covers the annual weedy types that started to occur in the 1980s in the Czech Republic. The plants have been introduced with beet seed from southern and southwestern Europe, mainly Italy and France (Skalický & Pulkrábek 2006), where they originated through the pollination of cultivated sugar beet (*Beta vulgaris* Altissima Group) with the pollen of the wild *B. vulgaris* subsp. *maritima* or of weedy annual plants derived from some cultivars of the Altissima Group (Pyšek et al. 2012a). The first records of this “weedy beet” come from the 1970s in the UK (Soukup & Holec 2004). It started to spread massively rather recently. A survey from 2006 revealed that weedy beet occurred on 70% of farms over the Czech Republic growing sugar beet and on 4% of those its density exceeded 1000 plants/ha (Landová et al. 2010). Plants of weedy *Beta vulgaris* occur in a variety of growth forms, from large to small root bodies and differing in root branching, total plant weight or number of produced seeds. They germinate early in the season before the cultivated sugar beet. The seeds form a long-term persistent seed bank which makes eradication difficult. Occurrence of weedy beet in fields is a serious economic problem as it competes with the sugar beet, and represents an obstacle to the harvest and processing of the sugar beet. The chemical control of weedy beet is prevented by the impossibility of using

herbicides in sugar beet fields. Alternative (mechanical) methods can partly reduce the seed set, but high regeneration capacity makes it necessary to repeat the cutting of flowering stems several times in season. Hybridization with native species in the Czech Republic has not been observed, but transfer of genes from GMO sugar beet to weedy species is reported (Bartsch et al. 1999).

Bidens frondosus L. (*Asteraceae*) is an annual plant native to large areas of North America, from southern Canada to the southern USA, where it grows in riparian habitats, at lake shores, as well as along roads and railways. The invaded range covers Europe, Asia and New Zealand (Štěpánková in Slavík et al. 2004). It was introduced to Europe, possibly as a wool contaminant, at the end of the 18th century, with the first record from 1777 in Poland (Lhotská 1966). In the Czech Republic it was first reported in 1894 (Pyšek et al. 2002b) and became naturalized in the first half of the 20th century (Hejný 1948). At present it occurs in most regions of the country (Fig. 8) and colonizes a wide range of moist habitats with sufficient nutrient supply. It was recorded in 21 habitat types, and is among dominant species in vegetation of nitrophilous annual hygrophilous herbs (Table 2). Its competitiveness, compared to native congeners, is enhanced by markedly higher drought resistance. The populations occur on riverbanks, shores of water bodies, and in road ditches and waste places with sufficient soil moisture. The species is common in urban areas, industrial zones and mining areas. It forms dense but small populations, usually up to several m². *Bidens frondosus* has little impact on diversity of invaded communities; early germination and tall stature enable it to suppress native species that, nevertheless, coexist following invasion. It appears to have colonized the majority of suitable habitats, and further spread thus depends on the frequency of available sites.

Bunias orientalis L. (*Brassicaceae*) is a biennial or perennial herb up to 1.7 m tall, reproducing by seed and root fragments. The native range is in Siberia and eastern and southeastern Europe, although according to some authors it is restricted to Armenia (Smejkal in Hejný et al. 1992). It grows at forest edges and on riverbanks (Clapham et al. 1962). It was introduced to North America and most of Europe, where it has been known since the 17th century. The first record in the Czech Republic is from 1856. It was introduced namely as a contaminant in maize, and with horse fodder imported from Russia (Smejkal in Hejný et al. 1992, Jehlík 1998). Until the 1920s there were only a few occurrences reported in Europe, but it started to be more common in the Czech Republic after World War II (Jehlík & Slavík 1968, Hejný et al. 1973). Contemporary spread is often due to unintentional transport of soil material. It has spread massively in the last two decades, mainly in ruderal grassland along roads, in abandoned fields, on recultivated mining areas in lowlands and moderately warm mid-altitudinal regions (Fig. 9). Only recently it started to extend its altitudinal range, and it was also reported to spread by floods (Křivánek 2004). It occurs in a range of ruderal, but also semi-natural habitats, classified into nine habitat types (Table 2). Optimum conditions include perennial thermophilous ruderal vegetation on deeper and drier clayey soil rich in mineral nutrients. The species invades mostly secondary human-made habitats, where the impact on native diversity is relatively low; however, it may become a troublesome weed in some agricultural ecosystems. It can reduce species diversity of grasslands where it has developed large and dense populations in the last 20 years. There is no record of impact of *B. orientalis* on human health or documented hybridization with native species (Mandák in Mlíkovský & Stýblo 2006).

Cannabis sativa var. *spontanea* Vavilov (syn. *Cannabis ruderalis* Janitsch.; *Cannabaceae*), an annual herb up to 1.3 m tall, is native to dry steppe areas in central Asia, where it also grows at disturbed sites along roads and railways, and in cities and villages, i.e. in habitats similar to where it grows in its invaded range in Europe and North America (Chrték in Hejný et al. 1988, Jehlík 1998). The taxon was introduced to Europe for use as bird seed and as an agricultural crop used for fibre, and was also unintentionally introduced as a crop contaminant. In the Czech Republic it was first recorded growing in the wild in 1868, in Hustopeče, southern Moravia (Wesely, BRNM). Its distribution in the Czech Republic is confined to the warm and dry areas of southern Moravia, where it spreads in agricultural landscapes and in the surroundings of villages on deep, dry soils rich in nitrogen and mineral nutrients. It invades annual vegetation of ruderal habitats and arable land (Table 2), and builds dense stands on rubbish dumps, in waste places, along roads and paths, and at the margins of vineyards, maize and other fields. Hybridization between *C. sativa* var. *spontanea* and cultivated forms is reported (Chrték in Hejný et al. 1988).

Conyza canadensis (L.) Cronquist (*Asteraceae*) is an annual species native to North America where it grows at disturbed open sites in meadows or fields. A single plant produces up to 100,000 achenes (Deyl 1964). The species was unintentionally introduced to all other continents except Antarctica. It is common especially in regions with temperate and subtropical climates. Typical habitats in the invaded range are dumps, ruderal and urban sites, road and railway verges or semi-natural grasslands. The first record in the Czech Republic is from 1750. It is reported as naturalized and common in early floras from the beginning of the 19th century (Presl & Presl 1819),

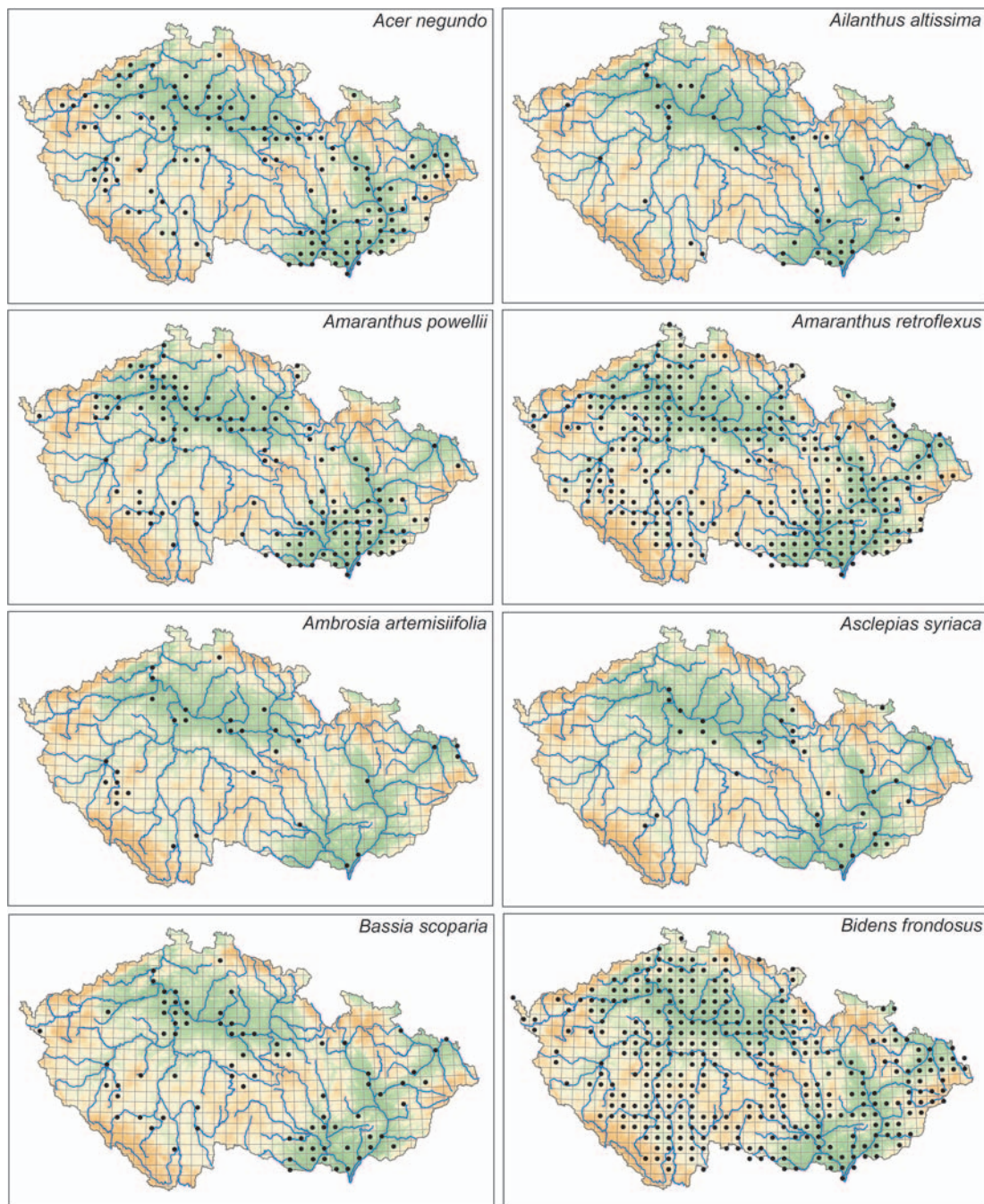


Fig. 8. – Distribution of *Acer negundo*, *Ailanthus altissima*, *Amaranthus powellii*, *A. retroflexus*, *Ambrosia artemisiifolia*, *Asclepias syriaca*, *Bassia scoparia* subsp. *scoparia* et *densiflora* and *Bidens frondosus* in the Czech Republic. Unless indicated otherwise, distribution maps in Figs 8–12 are based on data stored in the Database of the flora of the Czech Republic (www.florabase.cz), with permission of the original data providers (Institute of Botany AS CR, Masaryk University, Brno, and Czech Botanical Society). Note that these databases still contain many gaps, therefore maps in Figs 8–12 should be understood as indications of general distribution pattern rather than accurate distribution maps. For the distribution of *Ambrosia artemisiifolia* and *Bassia scoparia*, data from Mikulka (2011) were used as an additional source.

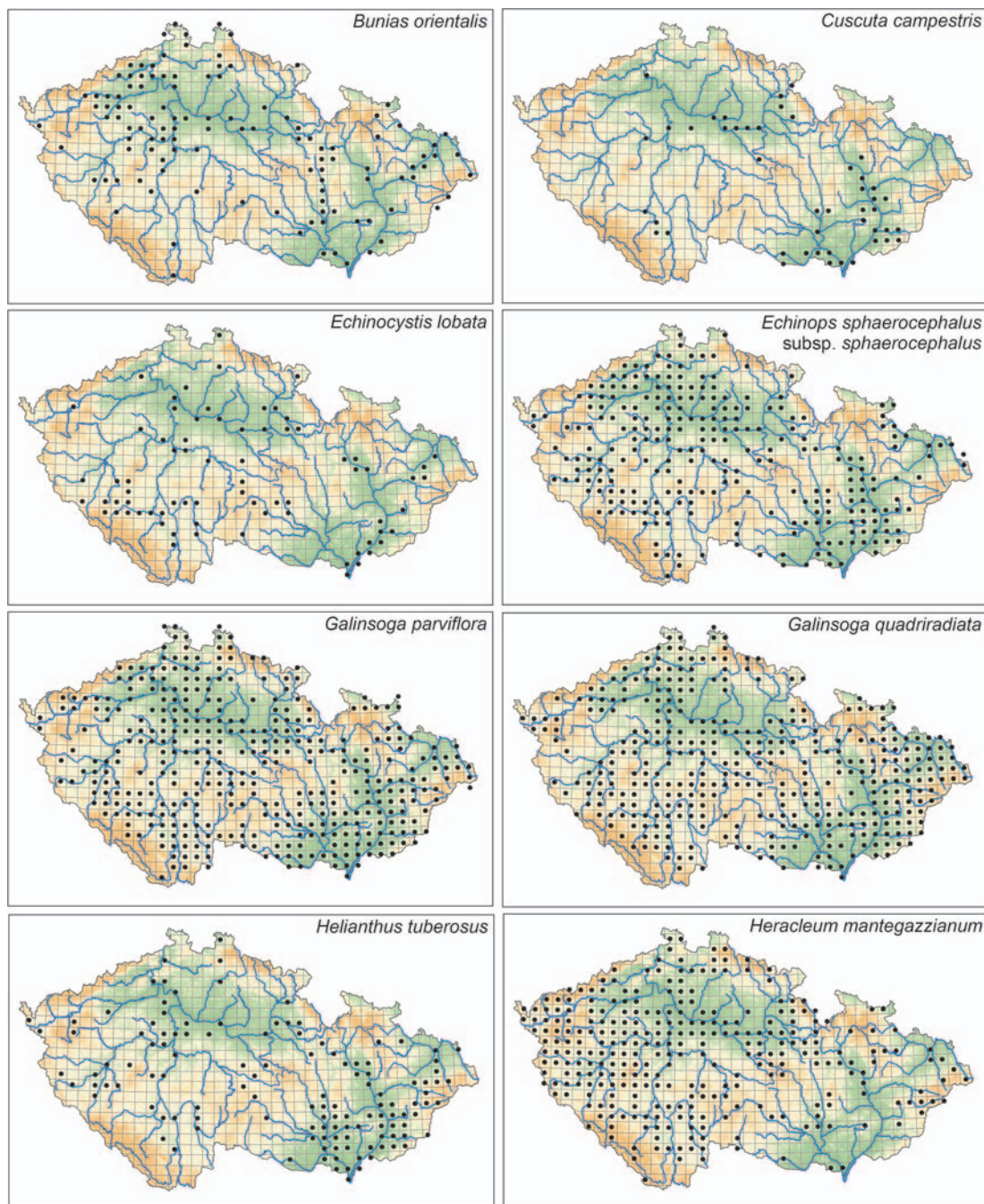


Fig. 9. – Distribution of *Bunias orientalis*, *Cuscuta campestris*, *Echinocystis lobata*, *Echinops sphaerocephalus* subsp. *sphaerocephalus*, *Galinsoga parviflora*, *G. quadriradiata*, *Helianthus tuberosus* and *Heracleum mantegazzianum* in the Czech Republic. The map of *Heracleum mantegazzianum* is based on www.florabase.cz and Pergl et al. (2012).

and numerous records from the beginning of the 18th century exist from neighbouring Germany (Šída in Slavík et al. 2004). It is widely distributed in the Czech Republic, and occurs in 33 habitat types; it is a dominant in annual ruderal vegetation and finds an ecological optimum in many other habitats (Table 2). Although it was introduced long ago, it is still spreading into higher altitudes and into semi-natural vegetation, forest clearings and other habitats. Its invasion is supported by its resistance to triazine-based herbicides, which is reported to have developed in the 1970s (Jursík et al. 2008), and which allows populations to spread in urban areas or industrial zones. It grows as a weed in vineyards, hop fields, orchards and vegetable fields. In Europe, it is a significant weed in warmer areas and in fields where it may reach high densities and therefore negatively affect the yield of agricultural crops (Moragues & Rita 2005, Wittenberg 2005).

Cuscuta campestris Yunck. (*Cuscutaceae*) is an annual parasitic plant native to western North America where it grows in open grasslands and fields. It was introduced to most of the world, often as seed contaminant. The first record in Europe comes probably from the Czech Republic and is from 1883 in Prague (Jehlík 1998, Chrtek sen. in Slavík et al. 2000). The distribution of the species in the Czech Republic is scattered. It is common only in warm lowlands such as those of the Elbe river, and in southern Moravia (Fig. 9), where it occurs as a weed in clover and alfalfa fields and in gardens, or in southern Bohemia, where it grows on exposed fishpond bottoms. It only occurs in four habitat types, with optimum in annual and perennial nitrophilous ruderal vegetation (Table 2). Chrtek in Slavík et al. (2000) attribute this species' recent spread to its high tolerance of salinity, a feature that allows it to spread along roads. Where it occurs in high densities, it is reported to exert a major impact on agriculture, reducing yield (Jehlík 1998). It was considered as rare in the 1960s (Deyl 1964), but at present it is starting to extend its altitudinal range.

Echinocystis lobata (Michx.) Torr. et A. Gray (*Cucurbitaceae*) is an annual vine native to North America where it grows at open sunny sites in floodplains and on forest fringes. The species was introduced to temperate and continental Europe at the beginning of the 20th century (1906, Slovakia) and to the Czech Republic in 1911 (DAISIE 2009). The pathways of its introduction to Europe are linked to botanical gardens, from where it spread across the continent. Currently it is commonly planted as a fast-growing garden ornamental for covering fences and walls (Chrtková in Hejný et al. 1990). The frequency of planting has increased in the last 20 years and has contributed to the species starting to spread. Its invasion in the Czech Republic has been supported by seed transported by water, especially during floods (Slavík & Lhotská 1967). This mode of dispersal is reflected by its distribution in the Czech Republic, where it is confined to large rivers (Fig. 9). It invades semi-natural habitats, being assigned to seven habitat types, finding its ecological optimum in lowland nitrophilous herbaceous fringes, willow galleries of riverbanks, and perennial nitrophilous vegetation of mesic to wet sites (Table 2). The species is demanding of light, nutrients and moisture, which limits its invasion outside stream corridors. The impact of the species is through its ability to cover large areas and overgrow native vegetation. Furthermore the whole plant contains substances that are toxic to humans and animals (DAISIE 2009).

Echinops sphaerocephalus L. **subsp. sphaerocephalus** (*Asteraceae*) is a herbaceous perennial plant native to Europe, with the area of native distribution ranging from southern Europe to southern Siberia. It occurs as introduced in the rest of Europe and North America. In both distribution ranges it grows at disturbed sites along roads and rivers, in urban areas and dry grasslands, preferring nutrient-rich soils and sunny places. In the Czech Republic it is grown as a garden ornamental species and is still sown into the wild by bee keepers, e.g. on railway banks (Slavík in Slavík et al. 2004). The first record from the territory of the Czech Republic is from 1871 (Pyšek et al. 2002b). The taxon is relatively widely distributed, being more abundant in warm regions (Fig. 9) and found in nine habitat types, with optimum in perennial thermophilous ruderal vegetation (Table 2). It has recently spread in dry, disturbed ruderal grasslands. In the past its occurrence was restricted to the surroundings of villages and stone quarries, although currently it is common in suburban areas and spreads in the landscape along roads, extending its altitudinal range. It also invades mesic habitats such as road ditches. No clear impact on biodiversity or human health has been reported in the literature.

Erigeron annuus (L.) Desf. (*Asteraceae*) occurs in two subspecies in the Czech Republic: **subsp. annuus** is annual, and **subsp. septentrionalis** (Fernald et Wiegand) Wagenitz is annual or biennial. The species is native to North America (northern and eastern USA and southeastern Canada) where it grows in dry forests, forest clearings, open rocky sites, grasslands, along roads and railways, and as a weed in gardens and fields. Its introduced range covers Europe, and parts of Asia and New Zealand (Šída in Slavík et al. 2004). Introduced to Europe as an ornamental at the beginning of the 18th century (Jehlík 1998), its later spread across the continent was mostly due to unintentional introductions as a seed and soil contaminant. The earliest record of the species in the Czech Republic is from 1884

(Pyšek et al. 2012a). The two subspecies differ in their distribution in the Czech Republic; subsp. *septentrionalis* is more common, while subsp. *annuus* is scattered (Šída in Slavík et al. 2004). However, the precise distribution and invasion history is difficult to outline as both subspecies are easy to confuse, making literature reports less reliable. It grows in 12 habitat types, with an ecological optimum in herbaceous fringes of lowland rivers, forest clearings and perennial thermophilous ruderal vegetation (Table 2). It prefers light and dry habitats, with its recent spread supported by large-scale disturbances, eutrophication, and extension of suburban areas. In the second half of the 20th century it was mostly an urban weed limited to waste places but at present it penetrates into open landscape, where it occurs not only at disturbed sites but also in semi-natural grassland. Its invasion is supported by occasional moving. The impact of the species is as a weed on agricultural land (Jehlík 1998).

Fraxinus pennsylvanica Marshall (*Oleaceae*) is a large deciduous tree up to 25 m tall, native in the eastern part of North America where it grows as a light-demanding and early successional species in a wide range of environmental conditions, although it is mostly found on moist and nutrient-rich soils along rivers. The first record of its planting in Europe is from 1783, and in the Czech Republic from 1835. The species is planted in parks and occasionally also in forest plantations (Koblížek in Slavík et al. 1997). It spreads into natural and semi-natural alluvial forests where it has its ecological optimum. It also occurs in scrub and pioneer woodlands on forest clearings (Table 2) and spreads in suburbs and coal-mining areas, where it is planted for habitat reclamation. As a fast-growing and early-reproducing woody plant, it establishes in ruderal vegetation of waste places early in succession, and later invades grassland, scrub and forest margins. Its distribution is scattered, confined to large river floodplains. At present it is spreading fast but its invasion is in the initial phase. It is reported to exert impact through commonly hybridizing with its introduced congeners used in forest plantations (Walter et al. 2005)

Galinsoga parviflora Cav. (*Asteraceae*) is an annual species native to the Andes of South America, with secondary synantropic distribution in temperate and subtropical regions of the whole world. It has been recorded growing from lowlands up to 3600 m a.s.l. As for its congener *G. quadriradiata*, its natural habitats in the native range are floodplains. In the invaded range it occurs as a weed of agricultural fields and gardens as well as in disturbed urban habitats. A single plant can produce up to 6000 highly germinable achenes. The first record of *G. parviflora* is from 1785 at a botanical garden in Paris, France. In the Czech Republic it was first recorded in 1880 and new localities started to be reported rapidly; the strongest invasion occurred from the 1920s to 1940s, when the species became widespread (Slavík in Slavík et al. 2004). Following initial introduction to botanical gardens and subsequent escape, the main pathway of further spread was as a contaminant of soil and agricultural seed. The species occurs in a wide range of habitats in the Czech Republic (13; Table 2), however, in most of them only occasionally. It requires well-aerated, moist and nitrogen-rich soil, but cannot tolerate a high cover of other species and is sensitive to frost (Deyl 1964); these factors limit its spread into higher altitudes in the country. It is abundant in gardens, rubbish heaps, compost heaps, along walls in cities and in cultures of root crops such as vegetables, beet and potatoes. In the Czech Republic it is common (Fig. 9) and has colonized the majority of sites with suitable habitats. Recently, for example, it has started to appear at road margins. The species spreads both by seed and clonally by adventitious roots at the stem base; if weeded manually, rooting bases of stems remain in the soil and ripening of achenes continues for a few days after removal. These features make it a serious weed in crops. It is a host plant of some agriculturally important viruses, insects and nematodes (Slavík in Slavík et al. 2004).

Galinsoga quadriradiata Ruiz et Pav. (*Asteraceae*) is an annual plant native to the Andes and Central America, where it occurs in periodically flooded sites along rivers. As its previously described congener, it was introduced to other continents where it occurs in similar human-made habitats. It was introduced to Europe in the 19th century. The earliest record of planting in the Czech Republic is from 1823 and that of escaped plants from Prague in 1890 (Slavík in Slavík et al. 2004). Both species are very similar in terms of pathways of introduction and dispersal, ecological requirements and habitat affinities (Table 2). Massive invasion of this species occurred later than that of its congener, during the second half of the 20th century. Currently it is slightly less common than *G. parviflora* but also occurs across most of country's territory (Fig. 9). It exhibits high salt and heavy-metal tolerance (Reinhardt et al. 2003). Its impact is that of a serious weed in agricultural crops and in being a host plant of some agriculturally important viruses, insects and nematodes (Slavík in Slavík et al. 2004).

Helianthus tuberosus L. (*Asteraceae*) is a perennial herb up to 3 m tall, reproducing by seeds or tubers. This species is native to the central and eastern portions of the USA and southeastern Canada, where it grows on wet meadows and in abandoned fields. In its invaded range (parts of North and South America, northern Africa, Australasia, temperate Asia and Europe) it occupies sunny ruderal sites along roads and rivers as well as field edges and urban habitats with nutrient-rich soils (Kirschner & Šída in Slavík et al. 2004). The species was intro-

duced to Europe probably during the 17th century. The first record in the wild in the Czech Republic is from 1885. *Helianthus tuberosus* is planted for ornamental purposes and as food for wild animals, namely boar (Kirschner & Šída in Slavík et al. 2004). Recently, the tubers started to be used as a dietetic food. The species prefers clayey, humid, nutrient-rich soils and spreads locally near plantings, such as in villages and forest openings. It is, however, most invasive in floodplains where tubers are spread by floods; on fluvial sediments even small fragments of tubers can sprout from a depth of up to 1 m. It is invasive particularly along large rivers in Moravia (Fig. 9) and in the surroundings of lowland settlements. *Helianthus tuberosus* occurs in seven habitat types, acting as a dominant of nitrophilous herbaceous fringes of lowland rivers, but also finding optimum conditions in perennial ruderal vegetation of warm and mesic sites (Table 2). Primary (F1) hybrids with other species of the genus were not recorded (Kirschner & Šída in Slavík et al. 2004). The probability of their occurrence is low due to late flowering of *H. tuberosus*, which prevents the seed from ripening in local conditions. Impact on species diversity of invaded communities is reported from the Czech Republic: stands reaching 50–100% cover reduce species richness by ~30% (Hejda et al. 2009a).

Heracleum mantegazzianum Sommier et Levier (*Apiaceae*) is usually a monocarpic, short-lived perennial species that can live up to 13 years (Pergl et al. 2006), reproducing exclusively by seed (Moravcová et al. 2006), forming a short-term persistent seed bank up to at least five years (Krinke et al. 2005, Moravcová et al. 2007) and persisting in some localities for decades (Pergl et al. 2012). A single plant produces on average 20,000 seeds that germinate up to 90% (Moravcová et al. 2006, Perglová et al. 2006). Its native distribution is in the Western Greater Caucasus, where it grows in tall-forb vegetation below the timberline, forest clearings and along forest margins (Ochsmann 1996). In 1817 it was introduced to Europe as a garden ornamental, but multiple introductions followed (Jahodová et al. 2007), and it is now considered as invasive or naturalized in many European countries and North America (Page et al. 2006, Pyšek et al. 2008b). The invasion of *H. mantegazzianum* in the Czech Republic has been described in detail. The first record comes from 1862, when it was introduced into the park of the Kynžvart chateau, western Bohemia (Pyšek 1991, Pyšek et al. 2008b). Fifteen years later it was found escaped and became naturalized in the close vicinity of the garden. The duration of the lag phase, or the time between its introduction and the start of its exponential spread, was estimated to last ~60 to 70 years, with rapid invasion starting in the 1940s (Pyšek & Prach 1993). Rapid spread and increase in abundance of *H. mantegazzianum* was promoted by a radical change in land use and anthropogenic disturbances after World War II, especially in the western part of the Czech Republic, where the species was originally introduced (Müllerová et al. 2005). *Heracleum mantegazzianum* invades nutrient-rich sites in semi-natural grasslands, forest edges and anthropogenic habitats (Pyšek & Pyšek 1995, Thiele et al. 2007). However, it is also able to establish in nutrient-poor habitats such as peaty meadows or acidic soils in forest clearings. It produces a large amount of litter in which seed can germinate and seedlings establish. Based on local conditions, it can form large populations harbouring thousands of individuals; however, more often it is found in smaller populations of few individuals along linear landscape features such as roadsides and streams (Thiele & Otte 2006). In the Czech Republic, the distribution is concentrated in western Bohemia, from where it spread eastward (Pyšek 1991). In other parts of the country it forms mostly small local stands and rarely occurs in dry and warm lowlands (Fig. 9). *Heracleum mantegazzianum* has been reported to reduce species diversity of invaded communities; stands with 70–100% cover reduce species richness by 50–60% depending on scale (Hejda et al. 2009a). The species is harmful to humans due to its phytotoxic sap causing blisters on the skin (Nielsen et al. 2005). It is difficult to eradicate due to the existence of a seed bank and high regeneration ability (Nielsen et al. 2005, Pyšek et al. 2007b). The species was the subject of a European framework programme project GIANT ALIEN (www.giant-alien.dk, Pyšek et al. 2007a).

Impatiens glandulifera Royle (*Balsaminaceae*) is an annual species native to the Himalayas, reaching up to 2.5 m height and belonging to the most invasive species in Europe (Perrins et al. 1993, DAISIE 2009). It was introduced as a garden ornamental to Europe (UK) in 1839 and first recorded as escaped in 1855 (Beerling & Perrins 1993). Now it is recorded from 35 European countries (Lambdon et al. 2008). It was also introduced to North America. In both distribution ranges it grows on riverbanks, in roadside ditches and at forest margins. In the Czech Republic, the first record of planting as a garden ornamental comes from 1846 and that of occurrence outside cultivation from 1896 (Slavík 1996, Slavík in Slavík et al. 1997); however, rapid invasion only started in the mid-20th century (Pyšek & Prach 1993) and currently the species is common in the country (Fig. 10). *Impatiens glandulifera* is a dominant species of nitrophilous herbaceous fringes of rivers. It also finds optimum conditions in willow galleries of loamy and sandy riverbanks and in riverine reed vegetation, but it occurs in 16 habitat types. It also invades fresh soil heaps, forest clearings, margins of forests outside floodplains and forest road verges. Until recently its invasion in the Czech Republic has been restricted to floodplains and surroundings of villages with nutrient-rich humus and permanently moist soils. However, in the last decades the species has started to widen its habitat niche by spreading outside floodplains, such as in forest clearings and abandoned meadows

(Malíková & Prach 2010). At present, a new wave of spread is observed into drier sites, in some cases less rich in nutrients, and shaded by tree canopy. The species produces higher biomass than its congeners and is plastic in terms of response to nutrient availability and shading, but it also exhibits some genetically based population differentiation (Skálová et al. 2012). Its competitive ability in the Czech Republic may be reduced by late frosts to which seedlings are sensitive (Skálová et al. 2011). It regenerates well after disturbances using adventitious roots from stem nodes. Due to its massive spread and extensive populations in riparian habitats, it is considered a conservation problem (DAISIE 2009). However, despite forming populations with a high cover of up to 90%, it does not markedly reduce the numbers of species co-occurring in invaded stands, although invasion does alter species composition (Hejda & Pyšek 2006, Hejda et al. 2009a; but see Bremner & Hulme 2006 for the more substantial effects reported from the UK). *Impatiens glandulifera* was also shown to reduce the availability of pollinators for co-occurring native species (Chittka & Schürkens 2001).

Impatiens parviflora DC. (*Balsaminaceae*) is an annual herb assumed to be native in the mountains of Central Asia (including the southern part of western Siberia, western Mongolia, the adjacent Turanian region and the western Himalayas; Slavík in Slavík et al. 1997). Its habitats in native range include shaded streambeds and stony mountain slopes. In the introduced range, it is widely distributed in Europe, Africa, North America and Asia; the first record in Europe is from 1831 from a botanical garden in Geneva (Coombe 1956). In the Czech Republic it was first recorded in 1844 in a botanical garden in Prague, and in the wild ca 1870 (Slavík in Slavík et al. 1997). Its widespread distribution in the Czech Republic was reached after World War II, with the period of its most massive invasion spanning the 1970s and 1980s, when it dominated forest floors in both natural and cultivated forests. After this time, its invasion was slowed by an introduced monophagous aphid, *Impatiens asiaticum* (Starý 1970). At present, *I. parviflora* is common over the whole area of the Czech Republic (Fig. 10) except treeless landscapes or nutrient-poor coniferous forests. It is, however, less dominant than three decades ago and it appears to have already colonized the majority of suitable habitats. *Impatiens parviflora* is strongly confined to sites shaded by tree canopy, preferring humus, loose, moist and nutrient-rich soils, and invading both disturbed ruderal habitats in and around settlements and more natural forest habitats. It is recorded from 45 habitat types, as a dominant species in a number of them (perennial nitrophilous herbaceous vegetation of mesic sites, and herb layers of alluvial forests, oak-hornbeam forests, and ravine forests), and as a constant dominant in *Robinia pseudoacacia* plantations (Table 2). In the Czech Republic, *I. parviflora* is reported to be less plastic in terms of response to nutrients and shading than its congener *I. glandulifera*, but exhibits stronger genetically based population differentiation (Skálová et al. 2012). It is also highly sensitive to frosts (Skálová et al. 2011). Its impact on native biodiversity in the invaded range is probably weak because of its poor competitive ability (Hejda 2012).

Lupinus polyphyllus Lindl. (*Fabaceae*) is a rhizomatous perennial up to 1.6 m tall, native to western North America, where it grows in wet mountain grasslands and along streams. It was introduced and became naturalized in the eastern parts of North America as well as in Europe, including its northern part. In Europe it was first recorded in the UK in 1826, and in the Czech Republic in 1895. It has been planted as a garden ornamental, but the invasion was more promoted by it being sown in the wild. Since the end of 19th century it was sown, as a nitrogen-fixing plant, in forests for enrichment and amelioration of acidic soils and as a pasture crop for animals. It is still used for soil stabilization at road and railway banks (Tomšovic & Bělohávková in Slavík et al. 1995). It differs from most other invasive herb species in the Czech Republic in being confined to non-calcareous, slightly moist and nutrient-poor soils in cold hilly landscapes and foothills. A genetic link with ornamentals cultivated as *L. ×hybridus* is probable though not proven. The species is common in the Czech Republic, especially in its western part (Fig. 10). It is recorded in 14 habitat types, becoming dominant in perennial thermophilous ruderal vegetation (Table 2). Invaded habitats reflect the locations of plantings. It invades along rivers, in unmanaged grasslands, along roads and railways, on ruderal and disturbed sites, in meadows and forest margins, or on sandy soils. However, at present *Lupinus polyphyllus* exerts its main impact through dominating vegetation in military areas, game preserves and on heaps from mining. However, despite forming stands with a high cover of 60–95% in invaded vegetation, its effect on native species richness is rather moderate. Hejda et al. (2009a) report ~20% reduction in species richness.

Lycium barbarum L. (*Solanaceae*) is a shrub up to 3 m tall. Some authors consider it native to southeastern Europe and Asian parts of the Mediterranean region (Skalická in Slavík et al. 2000), but it is more likely native to China. It is introduced in other parts of Europe and Asia, northern Africa and North America. The first record of planting in the Czech Republic is from 1785 (Křivánek in Mlíkovský & Stýblo 2006), and that of its occurrence in the wild is from 1870 (Pyšek et al. 2012a). The species is rather common, being more abundant in warm regions (Fig. 10). Its distribution still to a large extent corresponds to plantings along railway corridors from the 19th and

early 20th century. In warm and dry regions it was also planted in hedgerows, as an ornamental shrub and for soil stabilization; currently it is only rarely used. It is a deep-rooting, light-demanding species, colonizing deep, relatively dry, light, nutrient-rich basic soils at disturbed sites (Skalická in Slavík et al. 2000). Most stands originate from planted shrubs that spread by vigorous clonal growth; it does not reproduce by seed in the Czech Republic as it rarely bears fruit and seedlings do not establish. Long-distance dispersal is by root fragments and rooting branches that get dispersed following disturbance, e.g. during the remodelling of railway corridors. Populations last for a long time and are supported by cutting, which reduces competition from co-occurring trees and initiates new growth. It occurs as a dense stout shrub, a climber in tree stands, or a short shrub on extremely dry substrates. It grows in 11 habitat types (Table 2). The invasion in the Czech Republic seems to have reached its peak – the populations persist and increase in size, but new stands do not appear too often. The ability of *L. barbarum* to rapidly occupy new sites and exert strong impact on native diversity is documented from other parts of Europe (Křivánek in Mlíkovský & Stýblo 2006).

Oxalis corniculata* L. var. *corniculata (*Oxalidaceae*) is an annual, biennial or short-lived creeping perennial herb with a native distribution range in the tropical and subtropical belts of Asia and Africa, including the Mediterranean region. It was introduced to temperate regions of the Northern Hemisphere (Europe, North America, Asia) where it became naturalized in open disturbed sites along roads, in the edges of fields and urban gardens. It occurs as a serious weed in gardens, fields, lawns and glasshouses (Holub in Slavík et al. 1997). In the Czech Republic it was first reported in 1852, and it is most likely still being introduced with contaminated soil. It occurs in nine habitat types, with an ecological optimum in annual vegetation of arable land and annual vegetation of trampled habitats (Table 2). At present its occurrence is still mostly confined to cities and villages, the invasion being supported by spread of suburban areas with garden allotments. It has been slowly increasing in abundance in the last 30 years but the range of habitats is not widening (Deyl 1964). It spreads, both by seed and stem fragments, on loose well-aerated soils such as garden beds, glasshouses or heaps of garden substrata. Its ability to grow fast makes it a noxious garden weed, especially early in the season when it profits from competitive superiority over seedlings of other species. It also occurs in pavement crevices, railway areas and along walls, but only rarely as a weed of agricultural crops.

***Oxalis dillenii* Jacq.** (*Oxalidaceae*) is an annual, biennial or short-lived creeping perennial herb native to eastern and central North America, where it grows in prairies and broad-leaved forests, but also in a variety of disturbed habitats. It was likely introduced to Europe during the first half of 19th century as a garden ornamental. It became naturalized starting in the second half of 19th century, but its spread was recorded only after World War II (Holub in Slavík et al. 1997). The likely pathway of introduction to the Czech Republic is via contaminated soil. It is confined to warm lowland regions (Fig. 10) and started to spread in the last decades, now occurring in nine habitat types (Table 2). Its occurrence is concentrated at low altitudes, mostly in settlements and suburban areas. The invasion started in the last decade when the species began to spread in a wide range of habitats such as waste places, rubbish dumps, along paths and railways, field margins, open grassland, root crops and fodder crops. Its future spread can be expected, but because of it being a weak competitor which does not dominate vegetation, it is unlikely to become an invader with serious impact.

Parthenocissus inserta (A. Kern.) Fritsch (*Vitaceae*) is a woody vine native to North America. It was introduced to Europe at about 1800, and the first record of an escaped population in the Czech Republic is from 1900 (Pyšek et al. 2012a). Planted as an ornamental species in parks and gardens, it escapes and spreads in villages and their surroundings, from where it invades alluvial forests in warmer parts of the country (southern Moravia, central Bohemia; Koblížek in Slavík et al. 1997; Fig. 10). The species requires moist, nutrient-rich soils and spreads slowly, supported by succession of ruderal scrub towards tree-dominated stands. It is able to propagate clonally, which enhances its invasive potential and impact on invaded vegetation.

***Pinus strobus* L.** (*Pinaceae*) is a coniferous tree with a native distribution range in eastern North America. In its native range it is an important forestry species planted in extensive, often monodominant, forests. *Pinus strobus* was introduced to Europe in 1705 (Skalická in Hejný et al. 1988). The introduction to the Czech Republic for forestry purposes, with the first record in 1784 (Nožička 1965), preceded that for ornamental purposes (1812, Skalická in Hejný et al. 1988). In the Czech Republic the species is locally invasive on sandy acidic soils in sandstone areas, especially Labské pískovce (Fig. 10), where it gradually outcompetes the native *Pinus sylvestris*. It was first cultivated there in 1798 and started to spread in the 1950s in planted mixed forests, but also in other habitat types (Table 2), including open rock-outcrop vegetation. Its invasion and impact is restricted to extremely poor soils; the native pine poorly regenerates in *P. strobus*-dominated stands. The invasion in this sandstone area has

accelerated since the 1990s and still goes on. The species exerts strong impacts on invaded communities through developing dense stands and changing the dynamics of litter decomposition. Its invasion in Labské pískovce has been subject to ongoing research (Hadincová et al. 1997, 2008, Hanzélyová 1998, Münzbergová et al. 2010).

Populus ×canadensis Moench (*Salicaceae*) is a fast-growing tree up to 40 m tall. It originated as a product of both intentional and spontaneous hybridization of the European *P. nigra* with North American *P. deltoides* around 1750. The hybrid has been widely planted in wind-breaks and as an ornamental species in parks and gardens (Koblížek in Hejný et al. 1990). The first record of cultivation of *P. ×canadensis* in the Czech Republic is from 1852 (Svoboda 1981). In this country it reproduces both by seed and root suckers and spreads to a great distance from plantings. *Populus ×canadensis* invades disturbed habitats along streams, which is reflected in its distribution in the Czech Republic being concentrated in floodplains (Fig. 10), however, it is often found also in urban and suburban areas and sand pits. It is often planted at sites of former hardwood floodplain forests, but it also spontaneously occurs in more natural alluvial forests, willow galleries of loamy and sandy riverbanks, and other habitats (14 habitat types, Table 2). The recorded impact of the hybrid is through further hybridization with the native *P. nigra* and is at present exacerbated by utilization of *P. ×canadensis* as a biofuel plant (Křivánek in Mlíkovský & Stýblo 2006).

Prunus serotina Ehrh. (*Rosaceae*) is native to large areas in eastern North America and Central America, where it grows as a tree up to 35 m tall. It reproduces by seed dispersed by birds and small vertebrates, as well as vegetatively through the formation of dense polycorms (Mulligan & Munro 1981, Starfinger 1997). Its habitat in the native range is deciduous and pine forests. The species was introduced to Europe and Asia. The first record of European introduction is from 1623 in France (Chrtěk in Hejný et al. 1992). *Prunus serotina* was planted as a forest and park tree, and since it is tolerant to air pollution and poor soil it was also widely used in urban areas, for soil amelioration and for restoration of mining areas (Reinhardt et al. 2003). Following introduction the species was released from the effect of a parasitic fungus that has been shown to control its populations in the native range; this might have contributed to its invasiveness (Reinhart et al. 2010). In the Czech Republic, the species was introduced to cultivation in 1811 (Chrtěk in Hejný et al. 1992). In this country it grows as a short tree or shrub reaching 3–6 m in height. It occurs on various soils but prefers moist, acidic, well-drained soils (Křivánek in Mlíkovský & Stýblo 2006). Its habitat niche in the Czech Republic is still rather narrow. It occurs in six habitat types, with an ecological optimum in alluvial forests and acidophilous oak forests (Table 2). It also spreads in forest clearings and along forest paths and roads, reducing density and richness of understorey species. It was also observed to establish on abandoned fields on sandy soils and in sand pits. Invasion in the Czech Republic is markedly accelerating at the moment, especially in the lowlands, being supported by ongoing eutrophication of nutrient-poor forests, and exhibiting first signs of colonization of treeless landscapes. The distribution in the country is still rather localized (Fig. 11). *Prunus serotina* exerts an impact on native species by being a strong competitor that forms dense thickets. Impact on humans can be through bark and seeds that are toxic (Starfinger 2010).

Quercus rubra L. (*Fagaceae*) is a tree up to 40 m tall, native to a large area in eastern North America where it is an important source of hardwood. It grows on a wide range of dry-mesic to mesic sites and occurs in various habitats ranging from nutrient-rich soils to sandy plains and rock outcrops. Currently the species is widely cultivated in temperate regions of Europe and Asia as a popular forestry and ornamental tree. It was introduced to Europe in 1691, and is known to have been planted in the Czech Republic since 1799 (Koblížek in Hejný et al. 1990). In this country, its use was mostly as a garden and park ornamental until several decades ago when it started to be introduced into forest plantations, often in monocultures; in the 2000s it was planted on more than 4000 ha (Křivánek et al. 2006). It is also used for reclaiming post-mining areas and for reforestation of arable land. It is now widespread, invading mainly in central and eastern Bohemia in the Elbe river lowland (Fig. 11). It is recorded from 14 habitat types (Table 2). *Quercus rubra* has a short juvenile period and spreads into surrounding vegetation because it is more shade-tolerant than native oaks. It prefers open forest on light, nutrient-poor soils. So far it does not spread outside forests. As a fast- and well-growing, shade-tolerant tree, it has an impact on forest understorey, exacerbated by slowly decomposing leaf litter inhibiting succession (Dobrylovska 2001). Economic evaluation of impact of *Quercus rubra* has been done for Germany and estimated that removal of invasive populations and restoration of invaded sites would cost 716,000 euros annually (Reinhardt et al. 2003).

Reynoutria japonica Houtt. var. *japonica* and *R. sachalinensis* (F. Schmidt) Nakai (*Polygonaceae*) are rhizomatous perennials native to East Asia, from where they were introduced to Europe as garden ornamentals and fodder plants in the 19th century (Conolly 1977, see Bailey & Conolly 2000 for review of the history of early introduction to Europe). In the Czech Republic the genus *Reynoutria* (syn. *Fallopia*) is represented also by the invasive

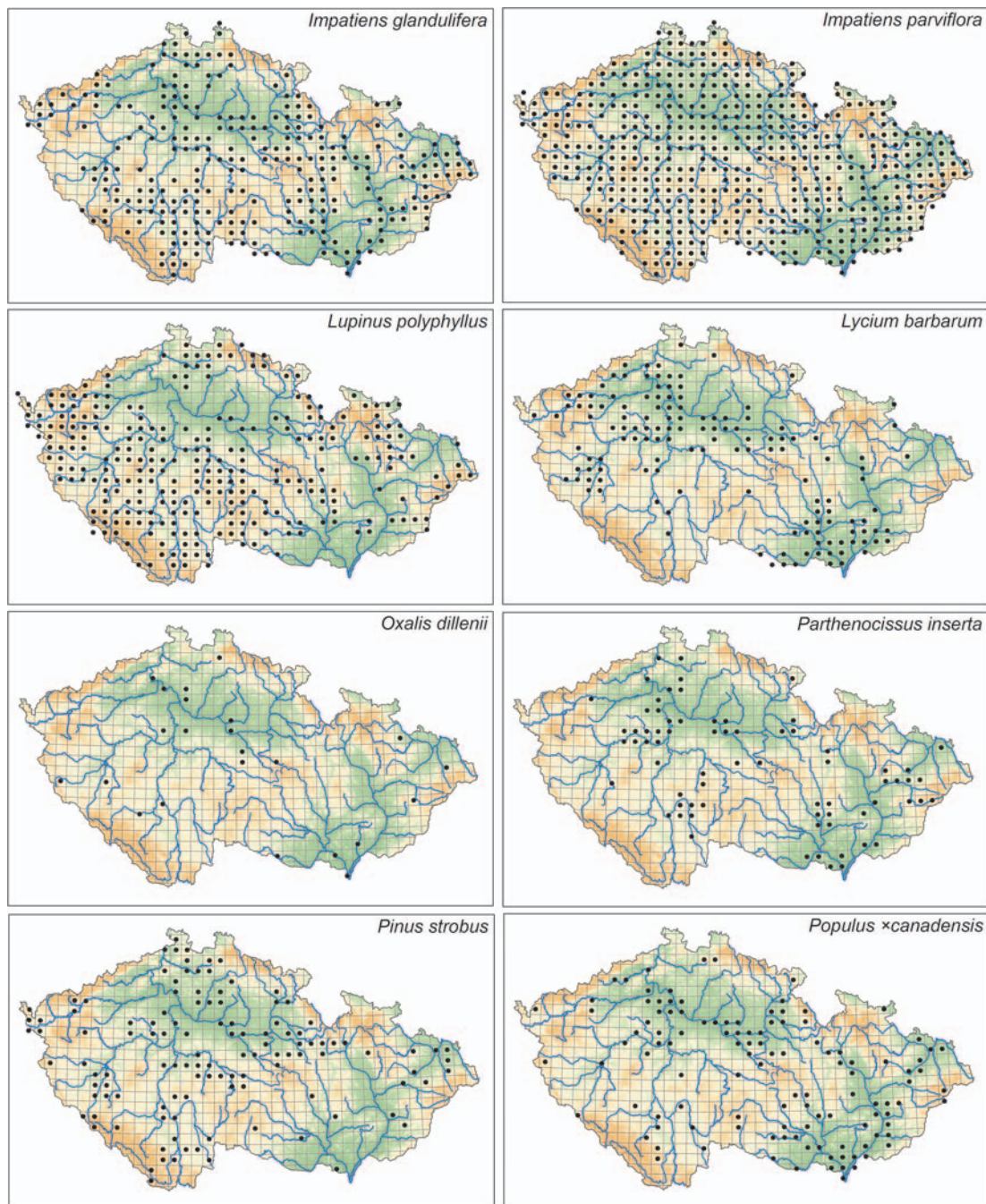


Fig. 10. – Distribution of *Impatiens glandulifera*, *I. parviflora*, *Lupinus polyphyllus*, *Lycium barbarum*, *Oxalis dillenii*, *Parthenocissus inserta*, *Pinus strobus* and *Populus x canadensis* in the Czech Republic. Note that the distributions of *Populus x canadensis* and *Oxalis dillenii* are rather underestimated; the latter species may be under-recorded because its invasion is a relatively recent phenomenon, the former because it is difficult to determine with certainty.

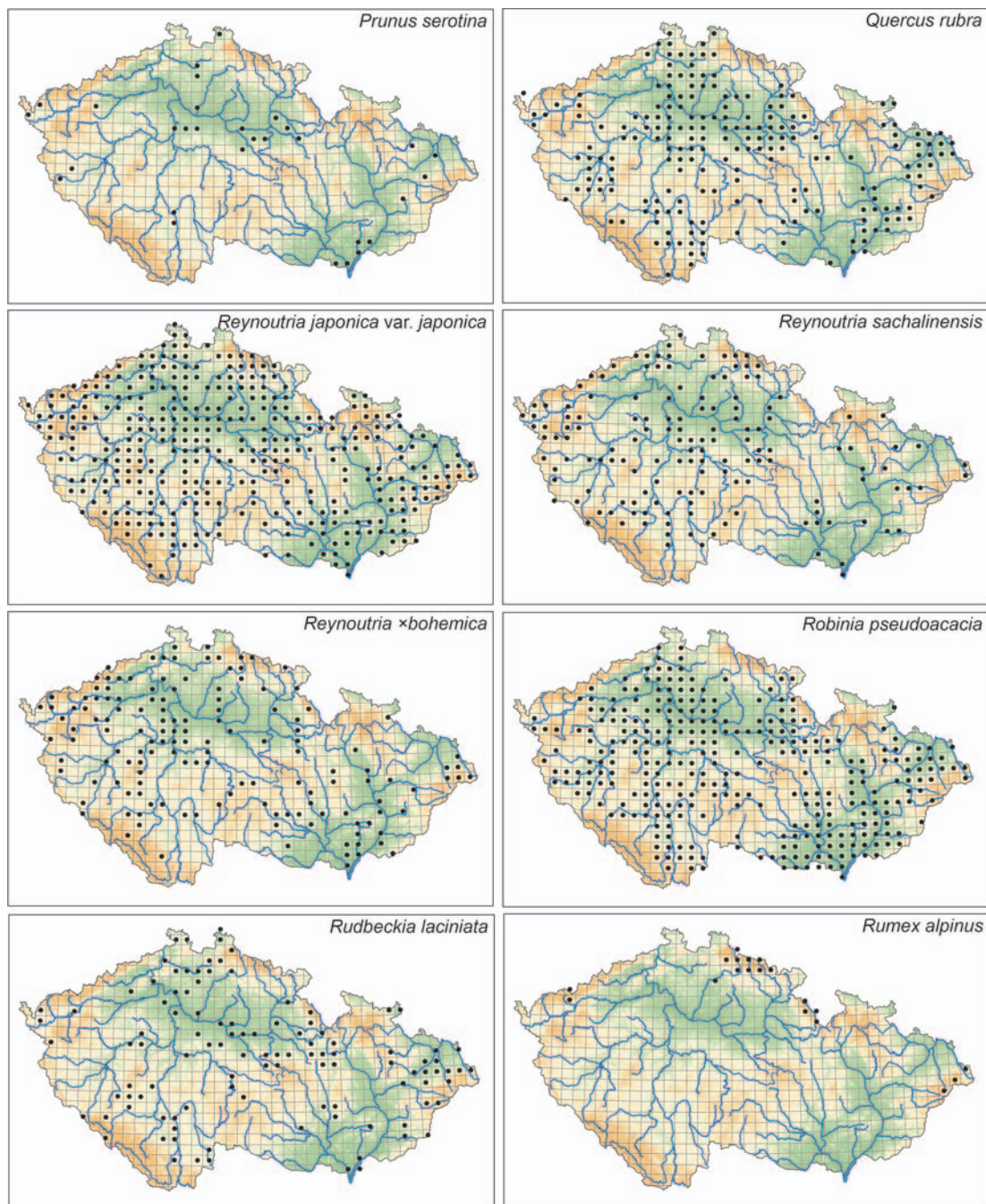


Fig. 11. – Distribution of *Prunus serotina*, *Quercus rubra*, *Reynoutria japonica* var. *japonica*, *R. sachalinensis*, *R. xbohemica*, *Robinia pseudoacacia*, *Rudbeckia laciniata* and *Rumex alpinus* in the Czech Republic. Distribution of *Reynoutria* taxa is based on maps published in Mandák et al. (2004), used with permission from the Czech Botanical Society.

hybrid *R. xbohemica* Chrtek et Chrtková. The hybrid, first grown in gardens in the UK in 1872, is likely to have arisen on this continent several times independently and is also known from the native range of the parental species (Bailey & Conolly 2000). In their native range, *Reynoutria* taxa grow along rivers and in disturbed open habitats and forest edges. *R. japonica* var. *japonica* is also known to colonize volcanic slopes and bare lava fields (Beerling et al. 1994). The invaded range covers Europe, North America and Australasia. All three taxa were introduced to the Czech Republic as garden ornamentals; the first record of *R. japonica* var. *japonica* in cultivation is from 1883, outside cultivation from 1902. *R. sachalinensis* was first collected in 1921, and the earliest record of the hybrid *R. xbohemica* is from 1950. The invasion occurred in the second half of the 20th century when the species spread over the territory of the country. That of the hybrid lagged behind the two parental species but proceeded faster (see Mandák et al. 2004 for the detailed history of introduction) due to its competitive superiority over the parents (Bímová et al. 2001, Pyšek et al. 2003a). In the early 2000s, *R. japonica* var. *japonica* was recorded from 1335 localities, *R. sachalinensis* from 261 and the hybrid from 382 (Mandák et al. 2004). Typical for the *Reynoutria* complex of taxa is large intraspecific ploidy variation in both the native and invaded ranges (Mandák et al. 2003), and interspecific hybridization that is a common phenomenon especially in invaded regions (see te Beest et al. 2012 for review of the role of ploidy in their invasion). In the Czech Republic, all three taxa are still planted as garden ornamentals. Their dispersal is mainly vegetative through regeneration from rhizome and stem segments transported with contaminated soil and water (Bímová et al. 2003, Pyšek et al. 2003a). Sexual reproduction rarely occurs, being constrained by the lack of pollen grains in some taxa or inefficient seedling establishment (Bailey et al. 1995). *Reynoutria japonica* var. *japonica* was introduced to Europe as a single female clone which spread across the continent (Bailey & Conolly 2000). *Reynoutria* taxa became widely naturalized and now represent some of the worst invasive plants in the Czech Republic in terms of their impact. They occur in a number of habitat types (12), forming dominants in perennial nitrophilous herbaceous vegetation of mesic to wet sites (Table 2). They are demanding of moisture and nitrogen and invade in settlements, often in abandoned garden centres, and in floodplains where the invasion is supported by periodical large-scale disturbances such as floods, during which rhizomes are spread and new habitats suitable for colonization created. The strongest impact is recorded in river floodplains in northeastern Moravia or northern Bohemia (Fig. 11). Due to their high competitive ability, high biomass production and efficient vegetative reproduction (Horn & Prach 1995, Brabec & Pyšek 2000, Bímová et al. 2003), knotweeds are classified as transformer species (sensu Richardson et al. 2000) that cause alterations in hydrological processes and displacement of native plant species. The invasion by *Reynoutria* taxa exhibits the most severe impact on species richness and diversity among central-European alien plants, reducing the number of species present prior to invasion by 66–86%, depending on the taxon (Hejda et al. 2009a). *Reynoutria* taxa are not reported to affect human health, but exert impacts on infrastructure by damaging roads and flood-prevention structures, and increasing the erosion potential of rivers (Beerling 1991, Reinhardt et al. 2003). For *R. japonica*, a biological control agent, the psyllid *Aphalara itadori*, has been released in the UK recently (Shaw et al. 2009).

Robinia pseudoacacia L. (*Fabaceae*) is a deciduous tree up to 30 m tall. In its native range in central and eastern North America it grows as an early successional species in open and disturbed habitats. The tree has a good regeneration capacity, resprouting well from roots and stumps. The invaded range covers temperate areas of the world. *Robinia pseudoacacia* was introduced to Europe in 1601 as an ornamental species. Later it was used for timber production and erosion control. It has been cultivated in the Czech Republic since 1710, after which time it became widely used in parks (Chrtková in Slavík et al. 1995). The first record of its spontaneous occurrence in the wild is from 1874 (Pyšek et al. 2012a). Since the 1760s it has been planted for timber, erosion control, to support soil eutrophication and as a bee plant (Kolbek et al. 2004). It grows up to ~500 m a.s.l., mostly in central Bohemia and southern Moravia, locally in extensive groves (Vítková & Kolbek 2010; Fig. 11). It is tolerant of drought and air pollution, and grows on sandy, poorly drained and saline substrates. It is resistant to fire and trimming and does not suffer from attacks of pests and diseases (Musil 2005). It reproduces by seed, but seedlings only establish following disturbances at warm sites. Spread is due to root suckers, and root fragments contribute to dispersal. This is why most populations are found close to original plantings, whereas long-distance dispersal happens only occasionally, and is mostly linked to transport of material from mines, quarries and sand pits. The species is recorded in 24 habitats (Table 2). The whole plant is toxic for humans and cattle, and produces allelopathic substances that inhibit germination and growth of native species (DAISIE 2009). However, stands of *R. pseudoacacia* harbour some rare native species, especially vernal geophytes (e.g. from the genera *Allium* and *Gagea*), that are able to tolerate the effects of allelopathic compounds. Low ability of long-distance spread and difficult eradication are probably the reasons why old populations of *R. pseudoacacia* are often tolerated by nature conservation authorities, except when they invade in steppe vegetation with a conservation value.

***Rudbeckia laciniata* L. (Asteraceae)** is a stout perennial species reproducing both by seeds and rhizome fragments. Its native range is in northeastern Canada and the eastern and central USA, where it grows along streams and in wet habitats from lowlands to mountains. The invaded range covers Europe, spanning central Russia and the Caucasus, China, Japan and New Zealand. It has been planted in Europe since the early 17th century, in the Czech Republic since the 19th century. At present a number of cultivated forms as well as hybrids with *R. nitida* are frequently planted in gardens (Bělohávková in Slavík et al. 2004), but only the one with the oldest history of planting escapes. The first record in the wild from the Czech Republic is from 1895 (Pyšek et al. 2012a). Currently the species is common in the country, namely in its eastern, northern and southwestern parts (Fig. 11). *Rudbeckia laciniata* efficiently spreads by rhizome fragments dispersed by water in riparian habitats and wet meadows, and along roads and railways (Francírková 2001). It occurs in nine habitat types (Table 2). About 80% of populations persist at invaded sites for many decades, with a recorded maximum of 135 years for one clone (Pyšek et al. 2001). The species forms stands that may reach cover values of up to 80–100% and reduces species diversity compared to uninvaded stands by ~30%, depending on the measure used (Hejda et al. 2009a).

***Rumex alpinus* L. (Polygonaceae)** is a clonal herbaceous perennial up to 1.5 m tall, native to the mountains of central and southern Europe, the Caucasus and northern Turkey. The species was introduced to the mountains elsewhere in Europe including Great Britain, in North America and southeastern Asia (Kubát in Hejný et al. 1990). The first literature record from the Czech Republic is from 1819, but the species might have been introduced already in the second half of the 16th or the beginning of the 17th century by woodcutters coming from the Alps to the Krkonoše and Orlické hory Mts (Hendrych 2001). The species occurs in mountain ranges in the northern part of the country (Fig. 11), with invasive populations concentrated in the Krkonoše Mts where the invasion rapidly started after World War II, supported by abandonment of mountain grasslands (Červenková & Münzbergová 2009). Plants spread by rhizomes (Klímeš et al. 1993) and invade abandoned nutrient-rich meadows or cattle pastures. It also occurs in a variety of habitat types including some semi-natural habitats, e.g. gravel riverbanks and along montane brooks (Table 2). Current spread is supported by ruderalization of mountain landscapes. Invasive populations may reach a cover up to 75–100% and reduce species richness of invaded communities by ~50% (Hejda et al. 2009a).

***Rumex longifolius* subsp. *sourekii* Kubát (Polygonaceae)** is a rhizomatous perennial up to 1.8 m tall. This subspecies was described from the Czech Republic. The species *R. longifolius* is native to the Pyrenees and mountains of Scotland, Ireland and Scandinavia where it grows in moist grasslands and along streams (Kubát in Hejný et al. 1990). The first record of invasive populations in the Czech Republic comes from 1961, and rapid invasion followed towards the end of the 20th century (Kubínová & Krahulec 1997, 1999). The populations are restricted to mountain areas where they occur at disturbed sites along water courses, ruderalized or abandoned meadows and pastures, road margins and in human settlements, finding their ecological optimum in perennial nitrophilous herbaceous vegetation (Table 2). The subspecies *sourekii* is more widespread than the rarely occurring subsp. *longifolius*. The invasion started in the 1980s, and in the 1990s *R. longifolius* subsp. *sourekii* was already locally common in the Krkonoše, Krušné hory and Jizerské hory Mts (Fig. 12), and it is still spreading (Kubát et al. 2002). At present, it also colonizes suitable habitats at lower altitudes. It is sensitive to mowing (Kubínová & Krahulec 1997). Potential impact of this invasion results from the fact that species in the genus *Rumex* easily hybridize; this taxon is involved in three hybrids with native species in the Czech Republic (Kubát et al. 2002, Pyšek et al. 2012a).

***Sisymbrium loeselii* L. (Brassicaceae)** is an annual plant with native distribution ranging from southern Europe, including the Mediterranean region, to Central Asia (Dvořák in Hejný et al. 1992), where it grows on mountain slopes and in disturbed habitats of road verges and field edges (Košínková in Mlíkovský & Stýblo 2006). The invaded range includes the rest of Europe and North America. The first record in the Czech Republic is from 1819. It is more common in warm regions (Fig. 12) and occurs in a wide range of habitat types (16), forming a dominant component of the annual vegetation of ruderal habitats (Table 2). In the past populations were restricted to urban areas, but started to spread to open landscapes in the last 30 years. At present it occurs in villages, quarries and mining areas, reclaimed spoil heaps and abandoned fields, and also colonizes disturbed steppe vegetation. It is a competitively weak, early successional thermophilous species colonizing newly created habitats and easily establishing following disturbance in grassland; it rarely occurs on arable land.

***Solidago canadensis* L. (Asteraceae)** is a rhizomatous herbaceous plant reproducing vegetatively and by seeds. The native range includes almost the whole of North America, from Alaska and Labrador in the north to Mexico and Florida in the south (Hegi 1979, Slavík in Slavík et al. 2004). The species is naturalized in temperate and southern Europe, eastern Asia, Australia and New Zealand (Weber 2003, Slavík in Slavík et al. 2004). In its native

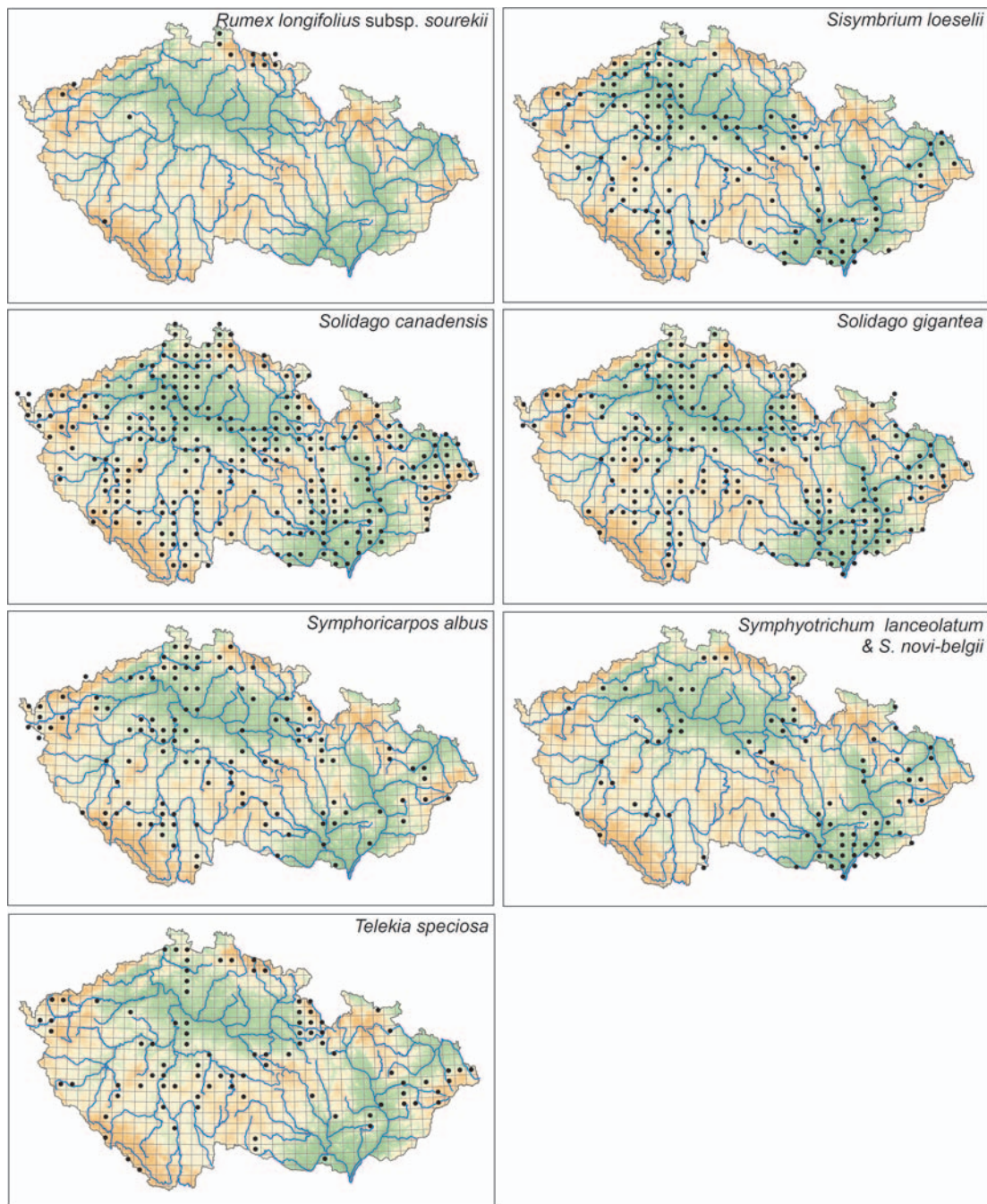


Fig. 12. – Distribution of *Rumex longifolius* subsp. *sourekii*, *Sisymbrium loeselii*, *Solidago canadensis*, *S. gigantea*, *Symphoricarpos albus*, *Symphyotrichum lanceolatum* & *S. novi-belgii* and *Telekia speciosa* in the Czech Republic. The distributions of the two *Symphyotrichum* species reflect the overall pattern but are strongly under-recorded; merged distribution is presented because of determination difficulties.

range it is found at forest edges, along rivers and in a variety of disturbed habitats such as abandoned pastures, roadsides, abandoned fields, grasslands and urban areas (Walck et al. 1999). It occupies similar habitats in the invaded range (Weber 2003). *Solidago canadensis* was introduced to botanical gardens in Europe as an ornamental plant (Weber 1998), with the first record in this continent being from 1645 (DAISIE 2009). It was introduced to the Czech Republic as a bee plant and a garden ornamental and first recorded in the wild in 1838. The invasion started as early as the first half of the 19th century (Slavík in Slavík et al. 2004). It is now common in most regions of the country (Fig. 12) and occurs in 13 habitat types, becoming a dominant in perennial thermophilous ruderal vegetation (Table 2). Seeds and rhizomes are often dispersed as soil contaminants (CABI 2004). It has been suggested that the species suppresses co-occurring species by allelopathic compounds released to the soil (Abhilasha et al. 2008). A negative impact on human health due to pollen allergies has been suggested, albeit without supporting data (Slavík in Slavík et al. 2004).

Solidago gigantea Aiton (*Asteraceae*) is a rhizomatous perennial plant reproducing both by seeds and vigorous clonal growth of rhizomes. It is native to southern Canada and eastern USA, and occurs as introduced in temperate and southern Europe, eastern Asia and New Zealand (Slavík in Slavík et al. 2004). The species was introduced to Europe as an ornamental plant in botanical gardens. The first record is from 1758 in London. In its native range it is found in grasslands and open forests, while in the invaded range it grows mainly in disturbed habitats along roads and railways (Weber 1998). Introduced as a garden ornamental and important bee plant, it was first reported to occur in the wild in the Czech Republic in 1851. The invasion started in the second half of the 19th century, supported by seeds and rhizomes dispersed with contaminated soil. By the 1930s it formed stands along rivers and also started to spread to disturbed sites such as heaps from coal mining in northeastern Moravia (Slavík in Slavík et al. 2004). Compared to its congener *S. canadensis*, this species forms denser stands, prefers moister and more nutrient-rich soils and is less common. It is more confined to riverbanks and floodplains of large rivers (Fig. 12). It occurs in 13 habitat types, growing as a dominant in perennial nitrophilous herbaceous vegetation of mesic and wet sites (Table 2). Impact of the species on native vegetation is similar to that of *S. canadensis*. It was observed to reduce the species richness and diversity of invaded plant communities by ~25–30% (Hejda et al. 2009a).

Symphoricarpos albus (L.) S. F. Blake (*Caprifoliaceae*) is a shrub with a height of up to 2 m, native to the western part of North America. The species was introduced outside its native range, including the Czech Republic, as an ornamental that is commonly planted in parks and gardens and along fences and roads (Chrték in Slavík et al. 1997). Its introduced range is almost cosmopolitan. The first record from Europe is probably from 1879. In the Czech Republic, it only occasionally reproduces by seed, and occurs scattered in the whole country, most frequently being planted and subsequently escaping in colline to submontane areas (Křivánek in Mlíkovský & Stýblo 2006; Fig. 12). Besides scrub vegetation it also occurs in perennial nitrophilous herbaceous vegetation of mesic sites. However, it occurs in nine habitat types altogether, including semi-natural vegetation such as riverine reed stands, fringes of montane brooks, willow galleries of riverbanks and alluvial forests (Table 2). Populations persist in once invaded sites for a long time and, to some extent, are resistant to the establishment of trees; very few other species occur in the understorey.

*Symphotrichum*² *lanceolatum* (Willd.) G. L. Nesom (syn. *Aster lanceolatus* Willd.; *Asteraceae*) is a perennial herbaceous species native to eastern North America. It was introduced to Europe in 1837 and became naturalized across most of the continent, from southwestern France to southernmost Scandinavia, up to central Russia and with isolated occurrences in the Iberian Peninsula (Kovanda & Kubát in Slavík et al. 2004). It is frequently planted in the Czech Republic, escaping from cultivation and invading in a wide range of habitat types (19 in total), including semi-natural riparian habitats. It occurs as a dominant in perennial nitrophilous herbaceous vegetation of mesic sites and in nitrophilous herbaceous fringes of lowland rivers, and is often found thriving in reed- and tall-sedge beds (Table 2). The invasion is ongoing, particularly on riverbanks in southern Moravia, but also

² Taxonomy of this group of species is extremely difficult because European populations include plants that are products of artificial breeding in cultivation and spontaneous hybridization following escape. The reported taxa may be affected by other taxa of the genus *Symphotrichum* and at present, the breeding also involves intergeneric hybrids artificially synthesized between species of other genera of the *Astereae* tribe, with effort to break genetic barriers becoming increasingly intensive (Nesom 1994). The invasion potential of invasive taxa of the genus *Symphotrichum* results from vigorous clonal growth, efficient dispersal by seed, robust stature and tolerance to a wide range of moisture conditions. They are limited by light and nutrient availability. Their current spread is supported by large-scale disturbances, especially in suburban landscapes and floodplains. This, together with the genetic basis of invasion due to hybridization, makes this group of taxa potentially dangerous future invaders.

along rivers in northern Bohemia (Fig. 12; Kovanda & Kubát in Slavík et al. 2004). It is reported to exert significant impacts on invaded communities (Hejda et al. 2009a).

Symphotrichum novi-belgii (L.) G. L. Nesom (syn. *Aster novi-belgii* L.; *Asteraceae*) is a perennial species with a native distribution range covering an ~150-km-wide belt along the Atlantic coast of North America, from the Appalachian Mts to southern Canada. As for the previous species, natural habitats include riparian communities along rivers and lakes. It is naturalized in Europe, from northern Italy to southern Scandinavia, in the UK and France, with isolated occurrences in Romania and the central part of European Russia (Kovanda in Slavík et al. 2004). It was introduced to Europe in 1710. The first record from the Czech Republic is from 1850 (Pyšek et al. 2012a). Planted as an ornamental, the species is less invasive than *S. lanceolatum*, occurring in 12 habitat types, but it also invades semi-natural habitats such as alluvial meadows of lowland rivers (Fig. 12). It occurs as a dominant of perennial nitrophilous herbaceous vegetation of mesic and wet sites (Table 2). It has been reported to reduce the species diversity of invaded communities by ~30–40%, depending on the measure and scale (Hejda et al. 2009a).

Symphotrichum xsalignum (Willd.) G. L. Nesom (syn. *Aster xsalignus* Willd.; *Asteraceae*) is an anecophyte resulting from hybridization of the previous two North American species, *S. lanceolatus* and *S. novi-belgii*, which most likely happened in European gardens (Kovanda in Slavík et al. 2004). It is reported to be almost sterile, with less than 0.1% of achenes ripening. At present it is cultivated and naturalized all over Europe, having been first collected in the wild in 1872. The distribution in the Czech Republic is scattered. It invades namely riparian scrub.

Symphotrichum xversicolor (Willd.) G. L. Nesom (syn. *Aster xversicolor* Willd.; *Asteraceae*) is considered a product of artificial breeding between *S. laevis* and *S. novi-belgii*, which probably happened in Europe. It is planted as an ornamental in most countries of central and western Europe where it escapes from cultivation and has become naturalized (Kovanda in Slavík et al. 2004). In the Czech Republic, it occurs in six habitat types, invading mainly in perennial thermophilous ruderal vegetation and perennial nitrophilous herbaceous vegetation of mesic and wet sites (Table 2).

Telekia speciosa (Schreb.) Baumg. (*Asteraceae*) is a rhizomatous perennial up to 2 m tall, native to the mountains of southern and eastern Europe, northern Anatolia and the Caucasus. *Telekia speciosa* grows at mountain forest edges, disturbed habitats, and along roads and rivers. It is naturalized in areas outside its native distribution in Europe including the European part of Russia, in similar habitats as in the native range (Kaplan in Slavík et al. 2004). This nitrophilous, shade-tolerant species, requiring moist clayey soils, was introduced as a garden ornamental to the Czech Republic, with the first record in the wild dated around 1820 (Pyšek et al. 2012a). It is still commonly planted and escapes along streams, in the surroundings of parks and gardens where it is planted, as well as in other habitat types such as forest margins, old forest clearings or unmown road ditches. Its ecological optimum is in perennial nitrophilous herbaceous vegetation of mesic and wet sites (Table 2). It is most commonly distributed at middle altitudes, especially in northeastern Bohemia (Fig. 12). The species causes pollen allergies and allergic reaction of skin (Šádlo & Mandák in Mlíkovský & Stýblo 2006).