Forestry and horticulture as pathways of plant invasions: a database of alien woody plants in the Czech Republic

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Abstract

Recent checklists, overviews and databases of alien floras for European countries do not pay special attention to woody plants. The majority of the checklists cover only taxa that occur in the wild. Woody plants are suitable subjects of studies on plant invasions because detailed records of introduction for forestry and horticultural purposes are available. This paper provides information on the database of alien woody species in the Czech Republic. Trees, shrubs and woody vines with mean height exceeding 0.5 m are included. In total, 126 characteristics covering taxonomy, geography, invasion, history of planting, biology and ecology, horticulture, and use were collected for each species. Although some characteristics in the database are specific for the Czech Republic, most information is applicable to the whole of Central Europe and potentially also to other temperate climate regions. The basic information on the structure of cultivated woody plants is presented.

Introduction

Woody species are a specific group of aliens, because they make up a substantial proportion of the most noxious alien species worldwide (Weber 2003). Many exotic trees introduced for commercial exploitation, wind protection or ornamental purposes subsequently became invaders (Reichard & Hamilton 1997, Zalba & Villamil 2002), and some change the character, condition, form or nature of invaded ecosystems (transformers *sensu* Richardson *et al.* 2000, Rejmánek *et al.* 2005). Impacts of invasive tree species are diverse (Versfeld & van Wilgen 1986, Simberloff *et al.* 2003) and include suppression of native plants (Richardson *et al.* 1989), reduction of wildlife habitat and increased water loss (Zavaleta 2000), increased fuel loads and altered fire regimes (Brooks *et al.* 2004), and nutrient enrichment (Vitousek & Walker 1989, Richardson & Higgins 1998). Invasions by alien woody plants have serious economic consequences (Zavaleta 2000, van Wilgen *et al.* 2001, Taylor & Irwin 2004) that can negate advantages gained from their commercial use (Richardson *et al.* 2004).

Recently, detailed checklists, overviews and databases of alien floras have been produced for a number of European countries (British Isles: Clement & Foster

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1994, Ryves *et al.* 1996; Czech Republic: Pyšek *et al.* 2002; Germany: Klotz *et al.* 2002; Austria: Essl & Rabitsch 2002; Hungary: Mihály & Botta-Dukát 2004; Switzerland: Wittenberg 2005). These works focus on vascular plants as a whole, hence they do not pay special attention to woody plants, and the majority of them only cover taxa that occur in the wild; cultivated plants are included only if they escape from cultivation or, if they become naturalized in a given country. Nevertheless, woody plants provide us with an excellent opportunity to study plant invasions from a known source pool of species (Prinzing *et al.* 2004, Pyšek *et al.* 2004, Křivánek *et al.* 2006), because detailed records of introduction for forestry and horticultural purposes are available. In addition, detailed data on residence time (*sensu* Rejmánek 2000, Pyšek & Jarošík 2005) and the history and extent of planting improve our ability to follow and predict invasions (Frenot *et al.* 2001, Rouget & Richardson 2003, Barton *et al.* 2004, Křivánek *et al.* 2006) and woody plants were successfully used in risk-assessment screening schemes in various regions of the world (Pheloung *et al.* 1999, Daehler & Carino 2000, Daehler *et al.* 2004, Weber & Gut 2004, Křivánek & Pyšek 2006).

However, there is no specialized database of alien woody species for a temperate area. This paper provides information on the Database of Alien Woody species with special regard to alien Invasive woody Species in the Czech Republic (DAWIS). DAWIS includes data on alien woody species that are distributed by garden centres and commonly planted in the Czech Republic. Although some characteristics covered by the database are specific for the Czech Republic, most information is applicable to the whole of Central Europe and potentially to other regions with temperate climates. In this paper, we present basic information on the structure of cultivated woody plants and how that is reflected in the structure of woody species recorded in the wild of the Czech Republic.

Methods

Species selection

The species included in the database were selected on the basis of frequency of planting in the Czech Republic. This was assessed according to the information included in national floras and atlases (Kavka 1968, 1969, 1974, Hieke 1984, 1985, Hejný & Slavík 1988, 1990-1992, Slavík 1995-2000, Koblížek 2000, Pyšek *et al.* 2002) and to how frequently a species appeared in catalogues of seed and living plants of 121 garden centres and botanical gardens, covering the period from 1852 to present.

Trees, shrubs and woody vines with a mean height of over 0.5 m are included. The database includes neither monocotyledons nor any semi-shrubs nor dwarf shrubs. Monocots were excluded because of their different ecology and very low number of species planted in Central Europe.

The species were divided into two groups according to whether they only occur in cultivation or have escaped into the wild. The former group is represented by species not escaping from cultivation, that are further classified on the basis of the purpose and frequency of planting into: (1) Species planted only in specialized collections or requiring special planting treatment; those offered by garden centres and botanical gardens were included in this category. (2) Species frequently planted in parks and gardens, based on the list by Koblížek (2000). (3) Species frequently planted in parks and gardens as well as in forests, based on data from UHUL (2000).

The second group consists of species that are known to have escaped from cultivation in the Czech Republic. It was divided into three classes: (4) casual, (5) naturalized and (6) invasive, following the approach and terminology of Richardson *et al.* (2000) and Pyšek *et al.* (2004). The main source of data was the Catalogue of alien plants of the Czech Republic (Pyšek *et al.* 2002).

Characteristics included in the database

In total, when available, 126 characteristics were collected for each species. They are divided into eight groups termed as follows (for details see also Appendix 1):

1. **Taxonomy** (4 characteristics) includes valid name of species and its synonyms, family and information on whether it belongs to a monotypic genus. The nomenclature used in the database follows the compendium of woody species planted in parks and gardens in the Czech Republic (Koblížek 2000). The nomenclature of rarely planted taxa not included in the previous source follows Rehder (1940, 1949).
2. **Geography** (3) includes data on the origin and distribution of the species in its native range and on the distribution in the Czech Republic. Main data sources: Rehder (1940, 1949), Kavka (1968, 1969, 1974), Hejný and Slavík (1988, 1990-1992), Slavík (1995-2000) and Koblížek (2000).
3. **Invasion** (8) covers the date of escape from cultivation, habitats occupied and number of localities in the wild in the Czech Republic. This information was extracted from the Catalogue of alien plants of the Czech Republic (Pyšek *et al.* 2002) and the related database (P. Pyšek & K. Prach, unpublished) and from the database of floristic records FLDOK held by the Institute of Botany Průhonice. Where relevant, information on invasive behaviour of the species in other parts of the world is included. Main data sources: Reichard (1997), Bingelli *et al.* (1998), Pyšek *et al.* (2002), Randall (2002), Haysom and Murphy (2003) and Weber (2003).
4. **History** (4) includes data on the first known introduction to Europe and to the Czech Republic and the location where the species was first planted in the Czech Republic. Main data sources: Svoboda (1976, 1981), Pyšek *et al.* (2002).
5. **Biology and ecology** (43) refer to morphology, reproduction and toxicity, and summarize requirements for planting in terms of soils, water regime, precipitation and temperature. Main data sources: Rehder (1940), Kavka (1968, 1969, 1974), Hejný and Slavík (1988, 1990-1992), Burns and Honkala (1990), Slavík (1995-2000), Koblížek (2000), Bruns (2004) and internet sources (CABI 2003, NCSU 2004).
6. **Horticulture** (54) summarizes how often the species appears in catalogues of seed and living plants of botanical gardens and arboreta. The data include 14 historical catalogues from 1852-1940, 93 recent catalogues from 2000 and seed catalogues of 14 botanical gardens and arboreta from 1992-2004. This information was completed from the distribution of species in 823 chateau parks in the

country and 13 city parks in Prague. Other data sources: Hieke (1984, 1985), Kavka (1968, 1969, 1974), Sortiment (2000) and internet sources (Okrasné dřeviny 2005). In some cases, imprecise nomenclature in older catalogues made it impossible to verify the identity of some offered species (for example, the name *Pinus nigra* in older catalogues often related not only to *Pinus nigra* Arnold, but also to *Picea mariana* Britt., Sterns & Poggenb.).

7. **Use** (6) relates to six categories: agro-forestry; soil conservation and erosion control; ornamental; land reclamation; windbreaks and hedges; and collections only. Main data sources: Kavka (1968, 1969, 1974), Hieke (1984, 1985), UHUL (2000), Koblížek (2000), Bruns (2004) and internet sources (CABI 2003, NCSU 2004, Okrasné dřeviny 2005).
8. **Special characteristics** (4) refer to the alien-native species relationships, i.e. whether a species has a native congener in the Czech Republic or planted congener that does not escape from cultivation. Main sources: Rehder (1940, 1949), Koblížek (2000) and Pyšek *et al.* (2002).

Results

Numbers of species, their taxonomic affiliation and origin

Based on above criteria, 1,691 alien woody species planted in the Czech Republic are included in the DAWIS database. Of these, 127 species are known to have escaped from cultivation. The remaining 1,564 aliens do not escape from cultivation in the Czech Republic; among them, 333 species are present only in specialized collections and 1,231 are commonly planted in parks and gardens. Twenty-eight species planted in gardens are also used in forestry, and 14 of those have already escaped from cultivation (Křivánek *et al.* 2006; Table 1).

Table 1. Number and distribution of alien woody species in the Czech Republic. See text for data sources. Pest species encompass aliens whose introduction and/or spread threaten biological diversity ("invasive alien species" in terms of the definition used by the Convention on Biological Diversity (2002).

Category	**Number of species**
Predicted number of woody species introduced into the Czech Republic	4,360
Native species	278
Species hardy in the temperate climate	5,700
Alien species included in the DAWIS database	1,691
Species escaped from cultivation	127
Casual	73
Naturalized	37
Invasive	17
Pest species	11
Species not escaped from cultivation	1,564
Planted only in collections	333
Planted commonly in parks and gardens	1,217
Planted in forestry but not escaping	14

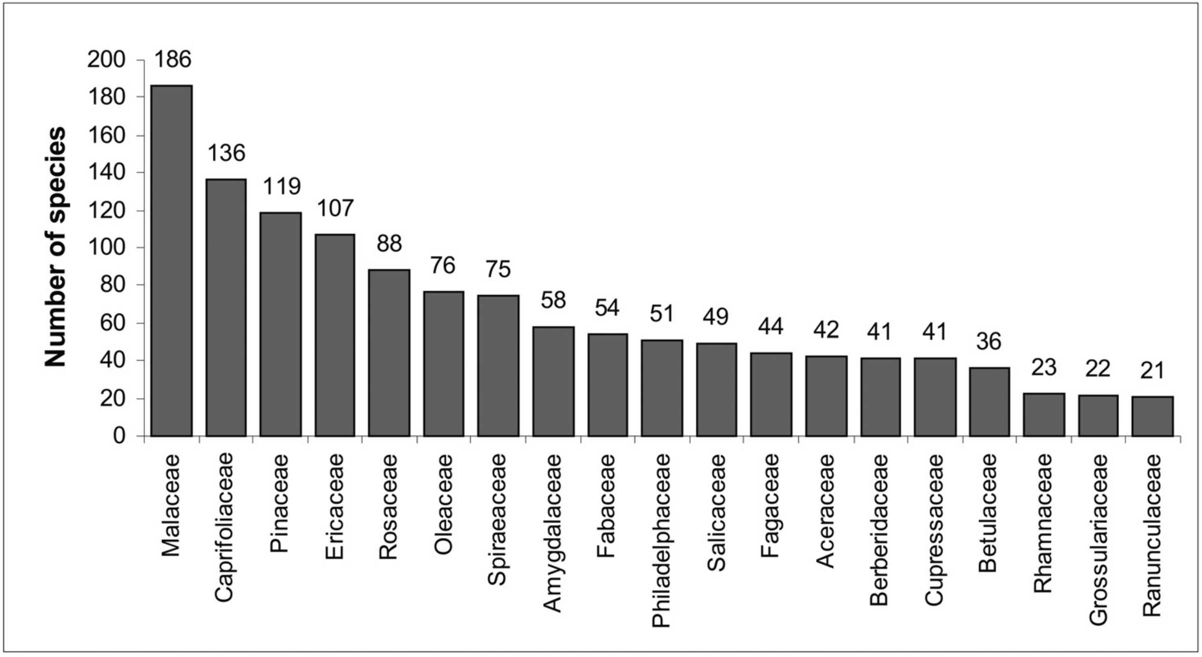

Fig. 1. Distribution in families of alien woody species planted in the Czech Republic (n = 1,691). Families with more than 20 alien species are shown.

Species from 90 families are included. Nineteen families are represented by more than 20 alien species (Fig. 1): Malaceae (186 species; with *Cotoneaster*, *Crataegus* and *Sorbus* being the genera richest in species), Caprifoliaceae (136 species; *Lonicera*) and Pinaceae (119) provide the highest numbers of species. Some families include important ornamental taxa with many cultivars although the botanical species is rarely kept in cultivation (e.g. Cupressaceae or Ericaceae).

Most species were introduced from Asia (922) and North America (439). Only few species come from very distant or/and climatically different areas like Africa or Australia (Fig. 2).

Invasion

Of the 127 woody species escaping from cultivation, at present only 73 occur in the wild as casuals, and 54 species are naturalized. Of naturalized species, 17 are considered invasive (Pyšek *et al.* 2002). Eleven invasive woody species are considered pests in the Czech Republic (Křivánek *et al.* 2004, Křivánek *et al*. 2006, Křivánek & Pyšek 2006): *Acer negundo* L., *Ailanthus altissima* (Mill.) Swingle, *Laburnum anagyroides* Med., *Lycium halimifolium* Mill., *Mahonia aquifolium* (Pursh) Nutt., *Padus serotina* (Ehrh.) Borkh., *Pinus strobus* L., *Populus* × *canadensis* Moench, *Quercus rubra* L., *Robinia pseudoacacia* L. and *Sarothamnus scoparius* (L.) Koch. Pest species are aliens whose introduction and/or spread threaten biological diversity, i.e. "invasive alien species" according to the definition of the Convention on Biological Diversity (2002).

In general, woody species escaping from cultivation are not frequent in the wild. Only *Robinia pseudoacacia* and *Sarothamnus scoparius* are common, having 615 and 754 reported localities, respectively. Sixty-eight species are rare (with only 1-50 localities) and 13 are locally abundant (50 localities and more) (Pyšek *et al*. 2002).

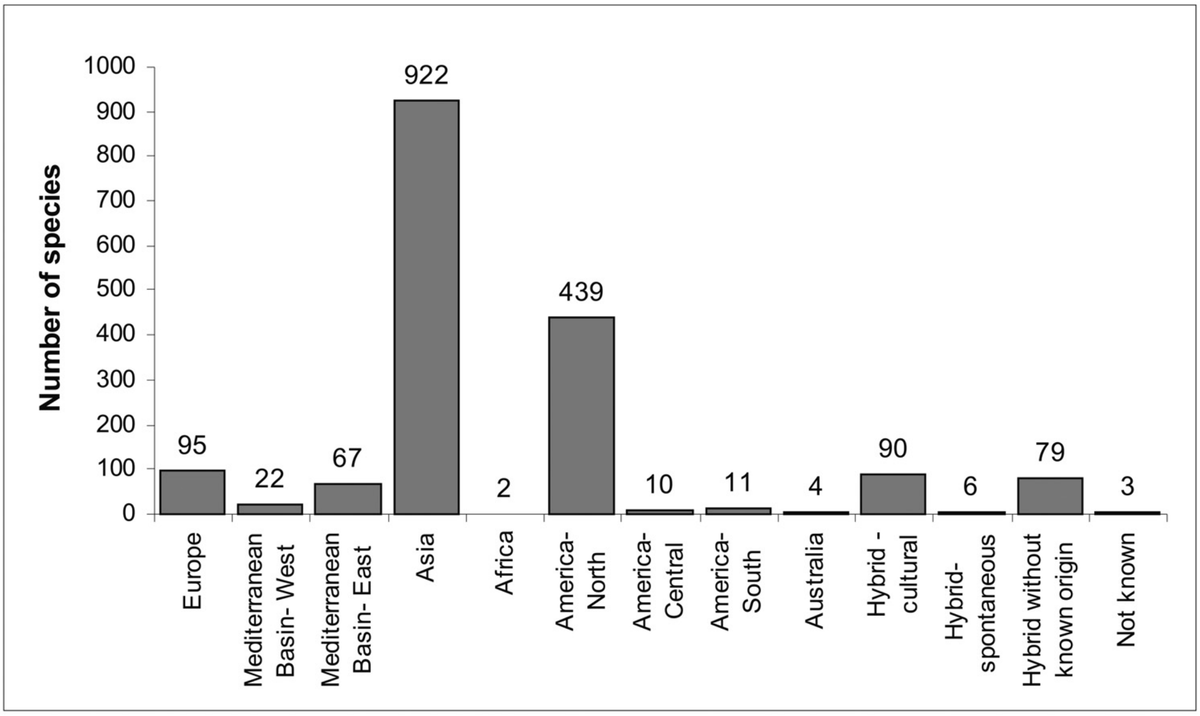

Fig. 2. Distribution of alien woody species planted in the Czech Republic (n = 1,691) according to the region of origin. The Mediterranean Basin was divided into the western part, including Europe and northern Africa, and eastern part, including Europe and western Asia. Cultural hybrids are those produced in the culture, spontaneous are products of hybridization in the wild. For 79 hybrid species the origin is unknown. Species with origin in more than one region are considered in each of them.

Casual species are most abundant in human-made habitats (in the sense of Chytrý *et al.* 2001). This type of habitat harbours 53 of the 73 casual species. Fifteen casual species are relics of former cultivation (Pyšek *et al*. 2002). The 37 naturalized species are fairly evenly distributed among human-made (22 species), semi-natural (defined as a managed landscape except settlements, communications and arable land: 31 species) and natural habitats (i.e. natural forests and naturally treeless habitats: 23 species). The same holds true for the 17 invasive species: 14 occur in natural, 15 semi-natural and 13 human-made habitats (Pyšek *et al.* 2002).

Of the woody species invasive in the Czech Republic, 41.2% (7 species) are reported as invasive elsewhere. However, 68.6% (81) of species reported as invasive elsewhere have not escaped from cultivation in the Czech Republic (Fig. 3).

History of introduction and residence time

The oldest data on introductions to the Czech Republic come from the second half of the 16th century. The year of first introduction into the Czech Republic is known for 674 species, however the year of first introduction into other parts of Europe is available only for 414 species. The country lagged in the rate of introductions to Europe until approximately the 1750s. Most species were introduced to Europe between 1650-1900 (85.3%), while in the Czech Republic between 1800-1950, 88.6% of the introduced plants arrived. The abrupt change in the pattern of intro-

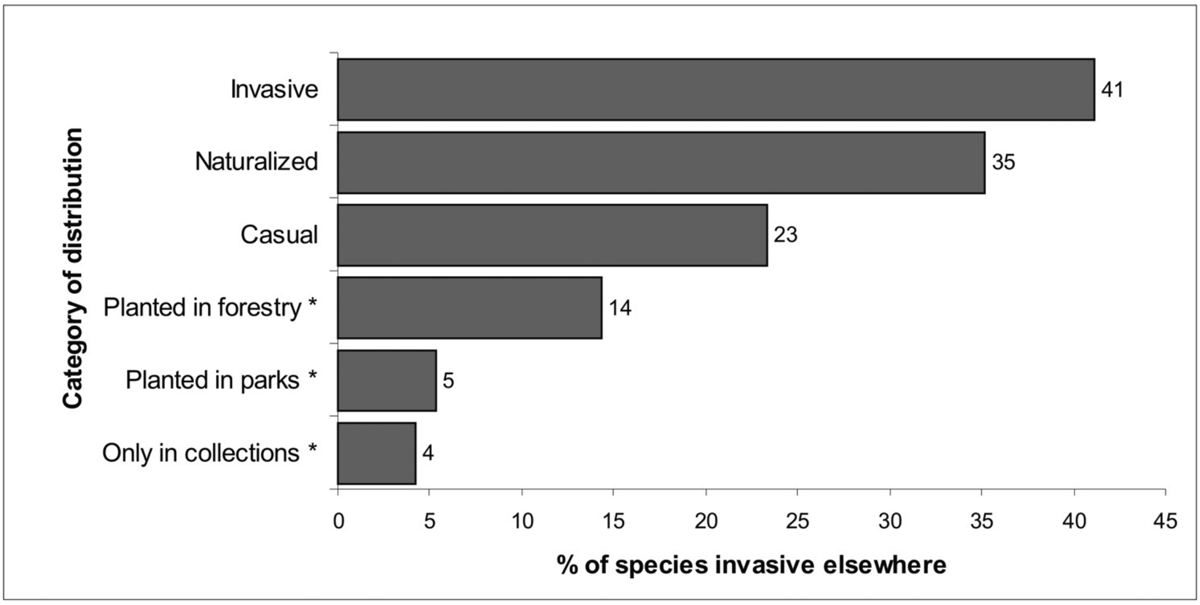

Fig. 3. Percentage of alien woody species in the Czech Republic, classified according to the planting purpose and invasion status, that are reported as invasive in other parts of the world. Categories marked * include species not escaping from cultivation.

duction of plants since the second half of the 18th century is obvious; introductions peaked between 1850 and 1900 (Fig. 4). The mean lag of introduction to the Czech Republic, behind that into Europe is 65.7 years (n = 375; S.D. = 59.7). However, 25 species were introduced to the Czech Republic earlier than to other parts of Europe.

The relationship between the time of introduction and current abundance of the species is obvious. Species that are invasive were introduced on average earlier (mean = 1789; S.D. = 50.8; n = 15) while those planted only in collections and not escaping from cultivation were introduced later (mean = 1867; S.D. = 42.4; n = 584). Species widely used in landscape planning, urban areas and forestry were introduced over the whole period, mostly from 1550 to 1900. On the other hand, species used only as ornamentals have been introduced mainly since the end of the 19th century (Fig. 5).

The lag phase, in the sense of Kowarik (1995), defined as the time between the first introduction and first escape from cultivation, is known for 44 species. The mean lag phase was 112 years (S.D. = 54.9; n = 44), 110 years for shrubs (S.D. = 57.7; n = 26) and 116 years for tree species (S.D. = 52.1; n = 18). The shortest lag phase (20 years) was recorded for the naturalized shrub *Alnus rugosa* (Duroi) Sprengel, the longest in the casual shrub *Philadelphus coronarius* L. (257 years). The mean lag for invasive species was 100 years (S.D. = 43.1; n = 9), for naturalized and casual species 101 (S.D. = 45.8; n = 6) and 122 (S.D. = 58.2; n = 28) years, respectively. The lag phase was the shortest for species of hybrid origin (mean = 75 years; S.D. = 53.0; n = 3) and for those from North America (mean = 89; S.D. = 45.5; n = 16). On the other hand, Eurasian and eastern Mediterranean species had lag times of 122 (S.D. = 46.2; n = 16) and 149 (S.D. = 65.8; n = 9) years, respectively.

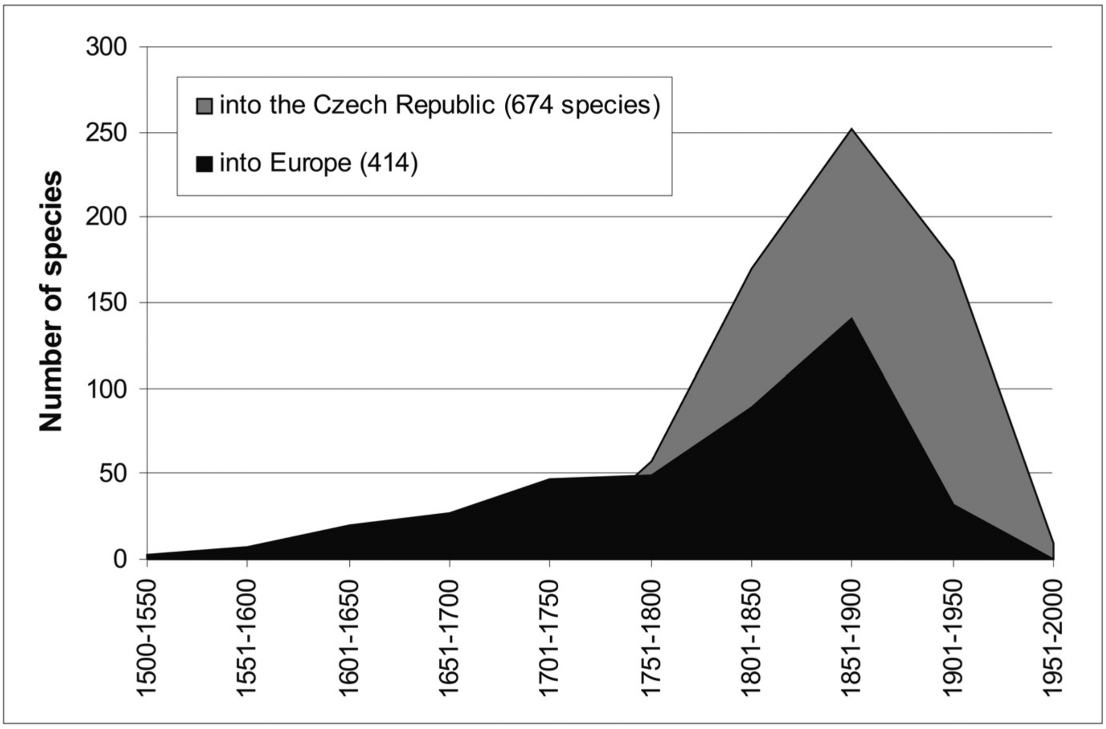

Fig. 4. Distribution of the dates of introduction of woody species to Europe and the Czech Republic.

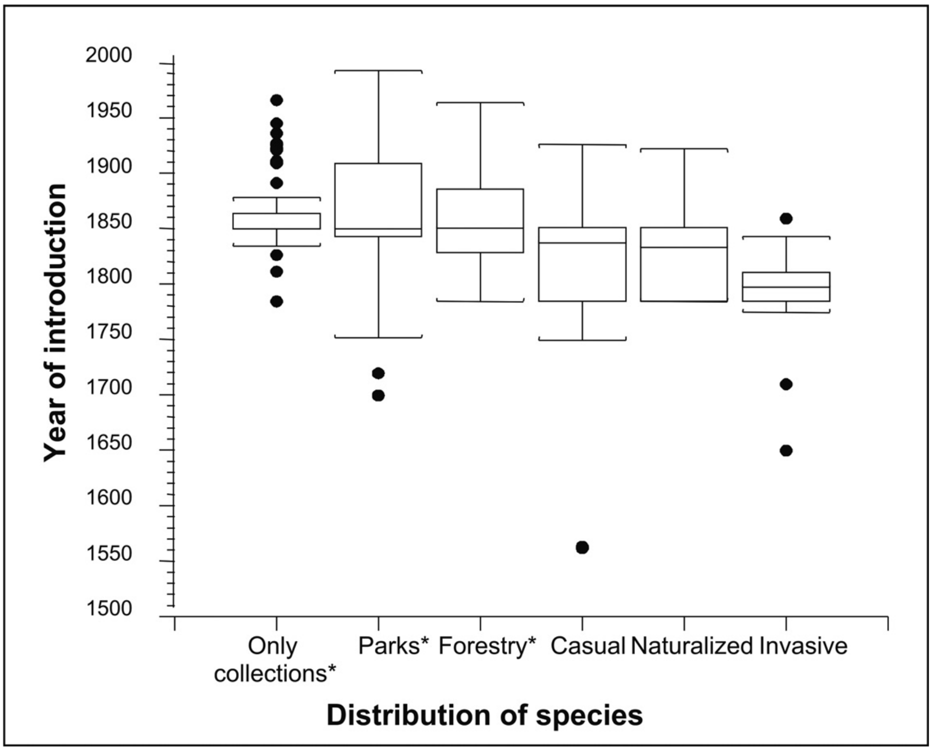

Fig. 5. Mean residence time of alien woody species in the Czech Republic classified according to the planting purpose and invasion status (n = 674). Categories marked * include species not escaping from cultivation (see text for details).

Biology and ecology

Life forms of 56% of the species (947 species) are shrubs, 26% (444) are trees and 4% (65) are woody vines; with 14% (235) of species having an intermediate life form between tree and shrub, i.e. both growth forms occur with similar frequency (e.g. *Acer ginnala* Maxim., *Cotinus coggygria* Scop., *Laurocerasus officinalis* Roem., *Laburnum anagyroides*, *Rhus typhina* L., *Syringa vulgaris* L.).

Most tree species have a juvenile period of 20-40 years. For 1,563 species (92%), generative reproduction is the main mode, 36% (603 species) also reproduce vegetatively by runners and 57% (964) by cuttings. Among the generatively reproducing species, 70% are hermaphrodites, 21% monoecious and only 9% dioecious. Insect pollination prevails for 76% of the species, 21% of species are pollinated by wind and the remaining 3% have both modes reported. The distribution of pollination modes reflects preferences for ornamental species with attractive flowers.

In the Czech Republic, mean annual temperature is 7.3ºC (min. 0.4ºC, max. 10.1ºC), mean annual precipitation is 672.6 mm (min. 384.6, max. 1497.8) (CHMI 2005). Most species included in the database persist successfully in areas with a mean annual temperature of 5ºC (31.7% of 442 species for which this information is available); only 10.6% require temperatures higher than 7ºC. On the other hand, 57 (12.9%) species grow well in areas with a mean annual temperature of 0ºC. In terms of annual precipitation, 81% (324 species of 399 for which this information is available) of the species require only 400 mm, which is considerably less than the country average.

Horticulture

Of the 1,252 taxa offered by garden catalogues, 37% are included only as recent offers (as of 2000) but are absent from the historical catalogues (1852-1940). On the other hand, 41% of species that were covered by the historical catalogues are no longer offered (Table 2). This pattern perhaps reflects an absence in the Czech Republic of former institutions such as the Dendrological Society in Průhonice. This society was very active in the beginning of the 20th century and introduced a number of species; its activities ceased after World War II. Only 22% of species were included in both historical and recent catalogues.

Many species have a large number of ornamental cultivars (Okrasné dřeviny 2005), only a small fraction of which are distributed by garden centers. As many as 1,651 species are offered in five ornamental cultivars. More than 30 cultivars are only offered for *Thuja occidentalis* L. (60 cultivars), *Chaenomeles speciosa* (Sweet) Nakai (57 cultivars) and *Chamaecyparis obtusa* S. & Z. (49 cultivars).

In total, 523 species are planted in chateau and city parks (Table 1, 2), but only a few are widely distributed. The most abundant woody plants in the 823 chateau parks and 13 city parks in Prague are *Thuja occidentalis* (present in 99% of parks), *Picea pungens* Engelm. (84%), *Syringa vulgaris* (83%) and *Aesculus hippocastanum* L. (75%).

The extent of planting, which is a convenient proxy for propagule pressure resulting from human activities (Křivánek *et al*. 2006) is related to the frequency of species in the wild and to their invasion success (Table 2). All species considered invasive, at

Table 2. Distribution of species in garden catalogues, parks and as monumental trees, related to their invasion status (sensu Pyšek *et al.* 2004). Monumental trees are those that are considered important aesthetically or biologically and protected by the national legislation. Historical catalogues are those from 1852-1940, recent catalogues relate to 2000.

	Species number	**Historical catalogues**	**Recent catalo gues**	**Total catalogues**	**Chateau parks**	**Prague parks**	**Monumental trees**
Total number of sources	-	14	107	121	823	13	53
Not-escaped	1,564	819	732	410	429	80	34
Casual	73	57	55	47	48	15	11
Naturalized	37	25	24	20	17	8	4
Invasive	17	17	15	15	15	9	4

present, were included in historical catalogues, and 88% of them are in recent catalogues. In addition, 88% and 53% are planted in chateau and city parks, respectively. On the other hand, 78% of casual species can be found in historical catalogues and 75% in recent ones, with 66% planted in parks. Of species not escaping from cultivation, only 47% and 52% are found in historical and recent catalogues, respectively, and only 27% and 5% are planted in chateau and city parks, respectively (Table 2).

In total, 53 alien species are among officially declared monumental trees. Monumental trees are related to aesthetically or biologically remarkable individuals that are protected by national legislation (the law for landscape protection and natural conservation; Table 2). The most often protected species among aliens is the casual *Platanus* × *hispanica* Mill. with 87 individuals country wide.

Use of species

Invasive species are widely used, and unfortunately, often also recommended for use (Table 3). Most invasive species are used as ornamentals, in agro-forestry and for soil conservation purposes. Averaged across categories of use, invasive species account for 53% of all species.

Species that are used only for horticultural collections rarely escape, but two naturalized species, *Fallopia aubertii* (L. Henry) Holub and *Alnus rugosa*, recruit from this group (Table 3). Both species are relatively common, but only little used as ornamentals and/or in landscape planning.

Table 3. The use of species and their invasion status (sensu Pyšek *et al.* 2004). Multiple uses are considered in each category.

Use	**Not-escaped**	**Casual**	**Naturalized**	**Invasive**	**Total**
Agro-forestry	64	6	3	10	83
Soil conservation and erosion control	191	18	10	10	229
Ornamental	1,492	73	35	17	1,617
Land reclamation	86	4	3	6	99
Windbreaks and hedges	63	1	1	2	67
Only in collections	72	0	2	0	74

Discussion

The total number of alien woody species introduced to the Czech Republic is unknown. However, based on the number of species known to have escaped from cultivation and number of pests in the Czech Republic, probabilities predicted by Tens Rule (Williamson 1996, Williamson & Fitter 1996) and the number of species hardy in temperate climate (Úradníček & Maděra 2001), the number of alien woody species that were introduced into the Czech Republic can be estimated to 4,360 species (Křivánek *et al.* 2006, Křivánek & Pyšek 2006; Table 1). The presented DAWIS database includes species commonly planted in the country and distributed by garden centres for at least the last 150 years. In the light of this, the 1,691 species included are a highly representative sample, making the information on the structure of alien woody flora rather robust.

Species with colourful hermaphroditic flowers fertilized by insects prevail among cultivated woody plants. This pattern reflects the predominant purpose of planting, which is ornamental use. Hermaphroditic species are also easier to reproduce than monoecious or dioecious taxa. The primary ornamental use has a context with the history of introduction and actual use of species (Fig. 5). Most species with a wide use were primarily introduced as ornamentals, and only later was it found out that they can also be used in forestry, land reclamation or windbreaks.

Fairly precise data are available for the distribution and ecology of species escaped from the cultivation (Pyšek *et al.* 2002). However, the number of species and their status, especially that of casuals, change over time and few other taxa could presently be evaluated as casual additions to that list.

The number of introduced species varies largely among genera and families (Fig. 1). Although many invasive woody species belong to genera containing a single invasive species, membership to a large genus becomes a sort of "mark of Cain", for all its representatives in risk assessment screening schemes. The probability that a large genus includes an invasive species is greater than for small genera (Křivánek & Pyšek 2006), hence the presence of an invasive representative in the genus should not be taken as a strict indication of the potential danger imposed to the other species of the same genus.

Many invasive species in the Czech Republic are also reported as invasive in other parts of the world. However this criterion needs to be applied with species' climatic requirements in mind, because many species invasive in areas with a different climate cannot grow in Central Europe without special care provided by gardeners. Such species only occur as casuals or have not yet escaped from cultivation.

Although for most species, the introduction to the Czech Republic was later than to Europe as a whole, at least for 25 species, it seems that the Czech Republic was the country of the first introduction to Europe. The mean lag phase of alien woody species in Brandenburg, Germany was 147 years (Kowarik 1995), i.e. 35 years longer than in the Czech Republic. Similarly the lag phase for trees was 54 years greater (170 years in Brandenburg) and for shrubs 21 years longer (131) in Brandenburg. The two regions are, however, difficult to compare in terms of lag phases because of different sizes. Evaluated for the whole area of the Czech Republic, the probability that an earlier escape from cultivation is recorded is higher than for the geographically limited area of Brandenburg in Germany.

There are two possible explanations for the close relationship between the invasion success of a woody plant and its residence time. Species introduced earlier can be better adapted due to their longer residence time (Rejmánek 2000, Pyšek & Jarošík 2005), and/or species with pre-adaptation to the temperate climate of Central Europe were selected first for planting by gardeners. The former concept is documented in Fig. 5: most invasive species were introduced earlier than naturalized and casual species, or those that have not yet escaped from cultivation. Even if the introduction of new taxa ceased, it is likely that the number of escaping and invasive taxa would increase because of the lag phase (Kowarik 1995).

Although some characteristics covered by the DAWIS database are specific for the Czech Republic, most information is applicable to the whole Central Europe and potentially also to other regions with temperate climates. The information on ecology, geography and use of species has been used for testing the efficiency of risk assessment screening systems developed in other parts of the world (Křivánek & Pyšek 2006).

The DAWIS database was developed with MS Access software. The application allows researchers to both visit fact sheets of species and search species according to their specific characteristics. The database is freely available at the web pages of the Institute of Botany, Academy of Sciences of the Czech Republic (http://www.ibot.cas.cz/invasions).

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Appendix 1: List of characteristics included in the DAWIS database:

Trait	Comments
	TAXONOMY
Species	Scientific name of the species.
Family	Scientific name of the family.
Monotype genus	In total 32 species are the only representative of the genus.
Synonyms	Taxonomic synonyms for the valid name of the species.
	GEOGRAPHY
Origin	Geographical location of the origin of the species.
Native region	Detailed characteristics of the geographical area of origin.
Vegetation type	Vegetation types in the Czech Republic, where the species grows well or where its planting is recommended.
	INVASION
First escape	Year of the first known escape from cultivation (only given for neophytes).
Lag phase	Time between the first known introduction into cultivation and the first known escape from cultivation.
Landscape type	Natural/seminatural/human made habitats.
Syntaxa	Alliances of the Zürich-Montpellier phytosociological system.
Abundance	Abundance categories in the wild in the Czech Republic.
Number of localities	Number of localities of the species in the wild (excluding parks, gardens and urban landscapes).
Invasiveness elsewhere	Information on the invasion outside Central Europe.
Invasiveness in the world	Number of regions (32 in total, following classification of Weber 2003) where the species is considered invasive.
	HISTORY
Introduction mode	Deliberately/accidentally/both ways.
First in EU	Year of the first known introduction into Europe.
First in the CR	Year of the first known introduction into the Czech Republic.
Period of introduction	Archaeophyte (introduced before 1500 A.D.) or neophyte (after 1500 A.D.).
First place	Location of the first cultivation in the Czech Republic.
	ECOLOGY
Life form	Life form in Central Europe: shrub, tree, vine.
Leaf persistence	Deciduous/semi-deciduous/evergreen.
Roots	Quality of roots and stability: deep/flat root system.
Height	Mean height under the conditions of Central Europe.
Crown average	Diameter of tree crown or of the whole shrub in Central Europe.
Juvenile period	Age at first flowering.
Flowering period	Length of flowering period (only for dicotyledonous species; I-XII).
Breeding system	Type of spatial separation of generative organs (hermaphroditic, monoecious, dioecious).
Pollination	Pollination syndrome: wind, insects or both.
Flower colour	
First fruit	Age at first fruiting.
Fruit character	Dry or fleshy fruits.
Fruit type	Morphological type of fruit: achene, berry, capsule, cone, drupe, follicle, nut, or pome.
Seed weight	Mean weight of one seed (mg)
Fruit maturity	Period of fruit maturity (I-XII).
Germination (%)	Mean germination (%).

Appendix 1: *Continued.*

Reproduction	Three types of reproduction are included: generative, vegetative by runners and vegetative by cuttings.
Calcium	Relationship to the calcium contents in the soil: growth favoured on Ca-rich soils/neutral/growth restrained on Ca-rich soils.
Ecological tolerance	Six characteristics describing the tolerance to exhalations, frost, shade, drought, water-logging and wind.
Quick regeneration	Regeneration after disturbance (quick-good/medium/slow-poor).
Damage by animals	High/medium/low.
Nitrogen fixation	Capability to fix aerial nitrogen.
Soil requirements	Eight characteristics describing the relationship (positive/neutral / negative) to sandy, loamy, clay, permeable, staunch, very acid, acid and neutral soils.
Optimum temperature	Expressed as mean annual temperate (ºC).
Minimum temperature	Minimum mean annual temperature necessary for good growth (ºC).
Optimum precipitation	Expressed as mm/year.
Minimum precipitation	Minimal mean annual precipitations necessary for good growth (mm/year).
Toxicity	Toxicity of species organs: extremely toxic/very toxic/toxic/slightly toxic.
Toxic parts	All parts/fruits (fruit and seed)/seeds (only seeds).

HORTICULTURE

Historical garden catalogues	List of historical garden catalogues that contain the species (n = 14 catalogues).
Catalogues of botanical gardens and arboreta	List of seed catalogues of botanical gardens and arboreta including the species (n = 14).
Distribution: Sortiment 2000	Number of garden centres distributing the species in 2000 (programme Sortiment 2000). In total 93 garden centres.
Distribution: no. of cultivars	Number of actually distributed ornamental cultivars of the species.
Actual distribution: total	Total number of garden centres and botanical gardens currently distributing the species (1992-2004).
Distribution: total	Three categories are distinguished: distributed only at present (1992-2004) / only in the past (1852-1940) / in both periods.
Important horticultural species	Horticulturally important, i.e. of a high ornamental quality, often used and planted.
Chateau parks in CR	Number of chateau parks where the species is planted in the Czech Republic (n = 823 parks).
Prague city parks	List of city parks in Prague where it is planted in (n = 13 parks).
Parks in CR: total	Total number of parks in the Czech Republic, where the species is planted (n = 836).
Monumental trees	Number of individuals declared as monumental trees and protected by law in the Czech Republic.

USE

Use	Recommended for use in forestry, landscape architecture, urban greenery or only planted in specialized collections.
Use: categories	Five categories: (i) agro-forestry; (ii) soil conservation and erosion control; (iii) ornamental; (iv) land reclamation, (v) windbreaks and hedges.

SPECIAL CHARACTERISTICS

Congeneric species	Congener escaping from cultivation is present / absent in CR.
Number of congeners	Number of alien congeners included in the DAWIS database.
Native genus in the CR	Presence / absence of a native congener.
Distribution level	(A) not escaping from cultivation: 1 - planted only in specialized collections, 2 - frequently planted in gardens and parks, 3 - planted in gardens and parks as well as in the forestry. (B) escaping from cultivation: 4 - casual, 5 - naturalized, 6 - invasive.

Pseudotsuga menziesii (Mirbel) Franco, naturalized north American species. The oldest individual in the Czech Republic introduced in 1843 from Flottbeck, Germany. Protected area American garden near Chudenice, south-west Bohemia. Photo: M. Křivánek, 2004.

Chapter 2 ~ Forestry and its role in naturalization

Křivánek, M., Pyšek, P., Jarošík, V. 2006: Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conservation Biology 20 (5): 1487-1498.

Planting History and Propagule Pressure as Predictors of Invasion by Woody Species in a Temperate Region

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Abstract: *We studied 28 alien tree species currently planted for forestry purposes in the Czech Republic to determine the probability of their escape from cultivation and naturalization. Indicators of propagule pressure (number of administrative units in which a species is planted and total planting area) and time of introduction into cultivation were used as explanatory variables in multiple regression models. Fourteen species escaped from cultivation, and 39% of the variance was explained by the number of planting units and the time of introduction, the latter being more important. Species introduced early had a higher probability of escape than those introduced later, with more than 95% probability of escape for those introduced before 1801 and <5% for those introduced after 1892. Probability of naturalization was more difficult to predict, and eight species were misclassified. A model omitting two species with the largest influence on the model yielded similar predictors of naturalization as did the probability of escape. Both phases of invasion therefore appear to be driven by planting and introduction history in a similar way. Our results demonstrate the importance of forestry for recruitment of invasive trees. Six alien forestry trees, classified as invasive in the Czech Republic, are currently reported in nature reserves. In addition, forestry authorities want to increase the diversity of alien species and planting area in the country.*

Keywords: alien forestry trees, Czech Republic, invasive trees, species naturalization

Historia de Siembra y Presión de Propágulos como Predictores de la Invasión de Especies Leñosas en una Región Templada

Resumen: *Estudiamos 28 especies de árboles no nativos que actualmente están sembrados con fines forestales en la República Checa para determinar la probabilidad de su escape del cultivo y naturalización. Utilizamos indicadores de la presión de propágulos (número de unidades administrativas en que una especie está sembrada y área total de siembra) y del tiempo de introducción al cultivo como variables explicativas en modelos de regresión múltiple. Catorce especies escaparon del cultivo, y 39% de la varianza fue explicada por el número de unidades de siembra y del tiempo de introducción, con mayor importancia del último. Las especies introducidas temprano tuvieron una mayor probabilidad de de escapar que las introducidas posteriormente, con más de 95% de probabilidad de escapar las introducidas antes de 1801 y < 5% las introducidas después de 1892. La probabilidad de naturalización fue más difícil de pronosticar, y 8 especies fueron clasificadas erróneamente. Un modelo sin las 2 especies de mayor influencia sobre el modelo produjo predictores similares de la naturalización y de la probabilidad de escapar. Por lo tanto, ambas fases de la invasión parecen ser dirigidas de manera similar. por la historia de siembra y de introducción. Nuestros resultados demuestran la importancia de la silvicultura en el reclutamiento de árboles invasores. Actualmente, seis árboles forestales no nativos, clasificados como invasores en la República Checa, son reportados en reservas naturales.*

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Adicionalmente, las autoridades forestales desean incrementar la diversidad de especies no nativas y el área de siembra en el país.

Palabras Clave: árboles forestales no nativos, árboles invasores, naturalización de especies, República Checa

Introduction

Invasions of alien tree species resulting from commercial planting began on a large scale in the twentieth century (Richardson 1998), but these invasions represent a serious problem in many areas (Richardson & Rejmánek 2004). Alien woody species represent a substantial proportion of the most noxious alien species worldwide (Weber 2003), and even intact forests are not resistant to invasion (Rejmánek 1996). Many exotic trees introduced for commercial exploitation, wind protection, or ornamental purposes subsequently became invaders (Zalba & Villamil 2002), and some change the character, condition, form, or nature of ecosystems (transformers sensu Richardson et al. 2000). Impacts of invasive tree species are diverse (Versfeld & van Wilgen 1986; Simberloff et al. 2003) and include suppression of native plants (Richardson et al. 1989), reduction of wildlife habitat (Zavaleta 2000), increased water loss (Zavaleta 2000), increased fuel loads and altered fire regimes (Brooks et al. 2004), and nutrient enrichment (Vitousek & Walker 1989; Richardson & Higgins 1998). The phenomenon of alien tree invasions has serious economic consequences (Zavaleta 2000; van Wilgen et al. 2001; Taylor & Irwin 2004) that can negate advantages gained from their commercial use (Richardson et al. 2004).

Among invasive alien plants, the most severe effects result from those intentionally introduced and cultivated to serve human needs (Kowarik 2005). This is especially so in the case of woody plants because under certain conditions any widely planted alien tree species may become naturalized and invade natural ecosystems (Richardson 1998). Forestry is an important pathway of introduction of alien tree species into new areas: 443 tree species are planted in forests around the world and 282 of them are invasive (sensu Richardson et al. 2000). In Europe, 12 species are naturalized and another 12 are invasive (Haysom & Murphy 2003).

Predicting which species will invade is a fundamental challenge in invasion ecology (Daehler et al. 2004). Studies of woody plants based on natural experiments created by centuries of deliberate planting in various parts of the world (Rouget & Richardson 2003; Richardson & Rejmánek 2004) have to date provided the best predictive framework (Rejmánek & Richardson 1996; Rejmánek et al. 2005). Information not only on species traits but also on environmental determinants and propagule pressure substantially improves predictions of the outcome of invasions (Rouget & Richardson 2003). Human-induced propagule pressure in particular is a crucial factor in plant invasions (Lonsdale 1999; Leung et al. 2004, Chytrý et al. 2005).

We explored the role of forestry in tree species invasions in the temperate zone of Europe. We considered the following questions: What is the relative importance of spatial (extent of planting) and temporal (history of planting) factors in determining the probability of naturalization? Do these factors affect the probability of escape from cultivation and of subsequent naturalization in the same way?

Methods

Study Area

The Czech Republic is at the geographical center of Europe, and the intensive movement of people and goods through this area since early times has contributed to the introduction of many alien species (Pyšek et al. 2002*b*; Mandák et al. 2004). The landscape is intensively used and rather fragmented due to the long-term effect of human activities, and large undisturbed areas of landscape are virtually nonexistent (Pyšek & Prach 2003).

Planting aimed at forest recovery in the Czech Republic started in the second half of the eighteenth century (Blaščák 2003). Since the second half of the nineteenth century, many alien trees, previously only grown for horticultural purposes, have been in experimental forest plantations (Beran & Šindelář 1996). Now approximately 90% of forests in the country consist of nonindigenous trees, either of foreign provenances of native species or of alien species (Hynek & Dorňák 2003). Up to now, 127 alien woody species have been reported from the wild (occurring outside cultivation), 37 of which are naturalized and 17 are invasive (Pyšek et al. 2002*b*). Eleven species affect ecosystems and are considered transformers (Křivánek et al. 2004).

Data

We collated data for all 28 tree species alien (non-native, exotic) to the Czech Republic that are planted currently for forestry purposes (Table 1). Based on Pyšek et al. (2002*b*) and following the terminology of Richardson et al. (2000), we classified the species into (1) not escaping from cultivation, (2) escaping from cultivation but only occurring as casuals, and (3) naturalized. Casual species

Table 1. Alien tree species planted in the Czech Republic for forestry purposes and included in the study.

Species	*Origin*[a]	*Status*[b]	*Year of introduction*	*Planting area (ha)*	*Number of planting units*	*Number of localities outside cultivation*
Abies concolor (Gord.) Engelm.	Nam	no	1910	0.89	5	1
Abies grandis Lindl.	Nam	no	1879	733.32	39	5
Abies nordmanniana (Stev.) Spach.	As	no	1845	1.80	8	0
Abies procera Rehd.	Nam	no	1865	0.04	1	0
Acer negundo L.	Nam	nat[c,e]	1835	337.06	21	133
Aesculus hippocastanum L.	Eu As	cas[e]	1576	551.87	38	181
Ailanthus altissima (Mill.) Swingle	As	nat[c,e]	1813	12.79	6	17
Castanea sativa Mill.	Eu Af As	cas	1562	24.64	11	21
Fraxinus americana L.	Nam	no	1835	53.35	4	6
Juglans nigra L.	Nam	cas	1835	679.08	9	20
Juglans regia L.	As	nat[e]	1852	84.13	18	48
Padus serotina	Nam	nat[c,e]	1852	12.36	18	22
Picea engelmanni (Parry) Engelm.	Nam	no	1879	10.77	7	0
Picea glauca (Moench) Voss	Nam	no	1835	584.86	20	0
Picea mariana (Mill.) Britt., Sterns et Poggenb.	Nam	no	1835	18.27	10	0
Picea omorika (Pančic) Purkyně	Eu	no	1906	200.25	25	1
Picea pungens Engelm.	Nam	no	1910	9885.50	40	33
Pinus banksiana Lamb.	Nam	no	1912	257.99	31	22
Pinus cembra L.	Eu	no	1852	2.23	6	5
Pinus contorta Dougl.ex Loud.	Nam	no	1965	89.51	6	2
Pinus nigra Arnold	Eu	nat[e]	1824	3688.56	39	175
Pinus strobus L.	Nam	nat[c,e]	1812	3089.89	41	114
Platanus × *hispanica* Mill.	h	cas	1835	3.48	11	1
Populus cult.[d]	h	nat[c,e]	1852	1933.97	24	58
Pseudotsuga menziesii (Mirbel) Franco	Nam	nat[e]	1842	4369.83	41	96
Quercus palustris Muenchh.	Nam	no	1835	5.98	7	3
Quercus rubra L.	Nam	nat[c,e]	1852	4379.97	40	194
Robinia pseudoacacia L.	Nam	nat[c,e]	1835	14190.12	36	615

[a] *Abbreviations: Af, Africa; As, Asia; Eu, Europe; Nam, North America; h, hybrid (taken from Rehder 1940; Koblížek 2000; Pyšek et al. 2002*b*).*

[b] *Abbreviations: no, not escaped; cas, casual; nat, naturalized (see text for definitions).*

[c] *Classified as invasive (Pyšek et al. 2002*b*).*

[d] *Various cultivars of the hybrid* Populus ×canadensis *Moench (* = P. nigra × P. deltoides*) are used in forestry.*

[e] *Recorded in nature reserves (based on Pyšek et al. 2002*a*).*

are defined as alien plants that do not form self-replacing populations and rely on repeated introductions for their persistence. Naturalized plants reproduce consistently and sustain populations over many life cycles without direct intervention by humans. Invasive plants are a subset of naturalized plants that have the potential to spread over a considerable area (Richardson et al. 2000; Pyšek et al. 2004).

For species escaping from cultivation, the total number of localities reported from the Czech Republic (i.e., frequency) was determined based on the national database of published floristic records (FLDOK) deposited at the Institute of Botany, Průhonice.

For each species, year of the first report of cultivation in the country was considered ("time of introduction") (Svoboda 1976, 1981). Information on the extent of planting was obtained from the Forest Management Institute, Brandýs nad Labem (Czech Republic), which is based on the administrative system of 41 so-called natural forest areas. These areas are administrative units defined on the basis of geography, geomorphology, and climate, which are the main determinants of the identity of planted tree species (Plíva & Žlábek 1986). They vary in size (range 1,453–256,378 ha), with an average of 59,008 ha. Based on the data in 2000, we used the following measures of the extent of planting: (1) total area (termed "planting area") and (2) number of areas (termed "planting units") in which the species was planted (Table 1). The planting area was obtained as a sum of the sizes of planting units in which a species was planted.

Statistical Analysis

We analyzed the data with multiplicative regression models that included interactions between explanatory variables (Quinn & Keough 2002). The response variables were the probability of escape, the probability of naturalization, and frequency, and explanatory variables were planting area ($\log_{10}$ transformed), time of introduction, and number of units (ln transformed).

Because the explanatory variables were measured on different scales, they were standardized to zero mean and unit variance to achieve comparable influence for all. The standardization enabled direct comparisons of variable effects because steeper regression slopes directly indicated larger effects. Using the standardized values, we checked collinearity with a matrix of correlation coefficients and by calculating tolerance values. To achieve the latter, we compared the regression of the explanatory variable in question against all the remaining explanatory variables in the model. The tolerance values for each explanatory variable were considered unacceptably low if their values in the expression $1 - r^2$ (where r^2 is the variance explained by the remaining explanatory variables) were <0.1 (Quinn & Keough 2002). These low tolerance values, indicating a high correlation, can negatively affect the estimates of model parameters.

Through our analysis we sought to determine the minimal adequate model in which all explanatory variables and their interactions were significantly ($p < 0.05$) different from zero and from one another and all nonsignificant terms were removed. This was achieved by a stepwise process of model simplification, beginning with the maximal model (containing all explanatory variables and their interactions) and then proceeding with elimination of nonsignificant terms (through deletion tests from the maximal model) and retention of significant terms (e.g., Pyšek et al. 2002*a*). To prevent biases to model structures caused by correlation between variables, we applied a backward elimination from the maximal models with stepwise analysis of deviance tables (Crawley 1993). Thus the results were not affected by the order in which the explanatory variables were removed in the stepwise process of model simplification. We checked appropriateness of the models by plotting standardized residuals against fitted values and by normal probability plots (e.g., Crawley 1993).

Following Quinn and Keough (2002), we analyzed interactions among the explanatory variables by using centered variables (i.e., variables rescaled by subtracting their mean from each observation). Significant interaction between two explanatory variables was examined with simple slopes of the multiplicative models at varying values of the interacted variables. We used simple slopes of one variable on another to arrive at three specific values of the changing variable: mean and mean plus and minus its sample standard deviation (Quinn & Keough 2002).

Successful escape and naturalization events were modeled in logistic regressions by specifying binomial error distributions and logit link functions, with escape and naturalization outcomes (success or failure) as response variables. We evaluated overall significance of the logistic regressions by a G^2 test on likelihood ratio chi-square statistic (i.e., as the deviance of the maximum likelihood model). First we evaluated the individual parameters of logistic regressions and their interactions by deletion tests based on the G^2 statistic, and then we evaluated the same parameters by a maximum likelihood version of a t test. This test (Wald statistic) is based on asymptotic standard errors (ASEs) of the parameter estimates. Odds and their confidence intervals (CI) were used as a measure of how the odds change with the one-unit change of the parameters and to predict the >95% and the <5% probability of escape or naturalization (see e.g., Crawley 1993). An overall goodness of fit of the models to the data was assessed with the Hosmer and Lemeshow (1989) test. Frequency was square-root transformed and modeled with the ordinary least square regression (OLS) with a normal distribution of errors and identity link function.

To determine which species had the largest influence on the established minimal adequate models, we assessed points with the largest influence on the statistics with either the distribution of Cook's distances (Cook 1977) (in OLS regression) or $\Delta\beta$ (the analog of Cook's statistic in logistic regression [Hosmer & Lemeshow 1989]). Data points with the largest Cook's distances or $\Delta\beta$ were sorted in descending order and weighted out of the analysis one after another (Gilchrist & Green 1994; Jarošík et al. 2002). We refitted parameter values after weighting out each data point and assessed the significance of changes in their parameters through deletion (logistic regressions) or t (OLS regression) tests. If the refitted parameters changed significantly, the points weighted out were assumed to have caused this change. Standardized residuals (i.e., the standardized differences between the observed and fitted values for each species) were also inspected. However, the inspection of the residuals themselves is not enough to reveal significant changes in parameter estimates, because extreme values often have the smallest residuals (Crawley 1993). Therefore, the use of Cook's distances or $\Delta\beta$, combining leverage and residuals in a single statistic of absolute values of weighted standardized deletion residuals, appeared to be a more appropriate method for examining influential data points than the residuals themselves.

For logistic models, we compared the original (with all species included) and refitted (with some species omitted one after another based on $\Delta\beta$) minimal adequate models. We made this comparison by calculating the number of misclassified species and by comparing G^2, Wald statistics, odds and their CI, and the values of Hosmer and Lemeshow tests of these models. In addition, we assessed the value of r^2_L (i.e., the explained variance for logistic models suggested by Menard [2000]) and the value of the Akaike information criterion (AIC) for the best model (i.e., one that provides the maximum fit of the logistic model for the fewest number of explanatory variables [Quinn & Keough 2002]). We considered the refitted models better than the original ones if they explained more variance and had lower values of AIC (because a low value of AIC suggests a better fit for the lower number of parameters). We performed calculations in software packages GLIM (version 4, Francis et al. 1994) and SPSS (version 12, SPSS, Chicago, Illinois).

Results

Probability of Escape

Of the 28 species analyzed, 14 escaped from cultivation (Table 1). The probability of escape was significantly affected by the time of introduction and by the number of units (Fig. 1; Table 2). This minimal adequate model was highly significant ($G^2 = 23.53$; df = 2; $p < 0.0001$) and explained 39% of variance ($r^2{}_L = 0.39$). This model also had a high information value (AIC = 209.66), with no evidence of a lack of fit (Hosmer and Lemeshow test: $\chi^2 = 5.59$; df = 7; $p = 0.59$) (Table 3).

Species that were introduced early had a higher probability of escape than those that were introduced later. The odds ratio for each year of introduction was estimated as 0.885, with 95% CI from 0.997 to 0.785 (Table 2). That is, holding the ln of the number of units constant and starting with the first record of introduction in 1562, each species in each year had a 0.885 chance of escaping, with >95% probability of escape in 1801 and <5% probability in 1892 (Fig. 1).

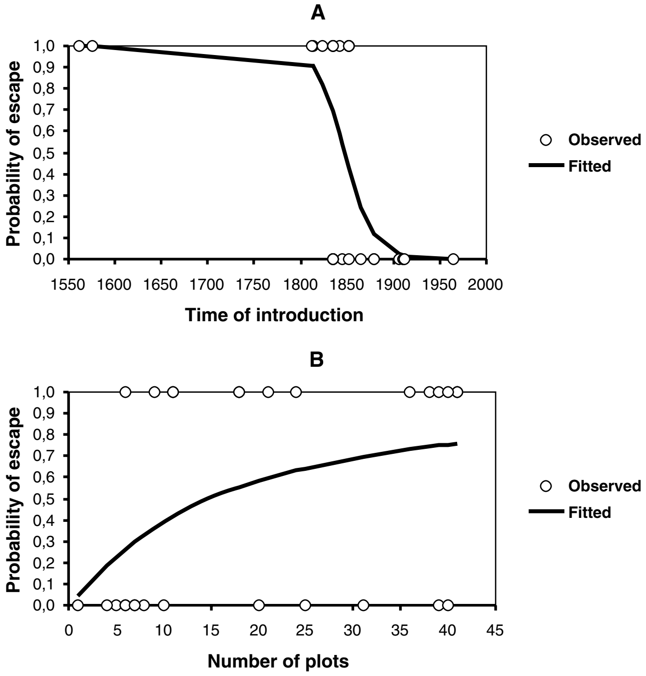

Figure 1. The probability that an alien tree species will escape from cultivation in the Czech Republic based on (A) the time of introduction for cultivation and (B) number of units (plots) in which it is planted. The figure is based on simple logistic regressions. Parameters of this model, based on multiple logistic regression, are given in Table 2, statistics are given in Table 3.

Table 2. Parameters in logistic regression of the minimal adequate model of the probability of escape of the introduced woody species.

Parameter	*Estimate*	*ASE*[a]	G[2b]	*df*	p	*Odds ratio*[c]	*95% CI of odds ratio*	*Standardized estimate*	*ASE*[a]	*Tolerance values*[d]	*Wald statistic*[e]	*df*	p
Intercept	218.2	108.5						1.214	0.8084		2.239	1	0.135
Time of introduction	−0.1227	0.06055	17.92	1	<0.0001	0.885	0.785–0.997	−10.24	5.054	0.98	4.050	1	0.044
Ln (number of units)	3.155	1.595	9.591	1	0.0019	23.466	1.010–545.014	2.950	1.492	0.98	3.867	1	0.049

[a] *Asymptotic standard errors.*

[b] *G^2 test on likelihood ratio χ^2 statistic (i.e., the deviance of the maximum-likelihood model).*

[c] *Odds and their confidence intervals (CI) measure how the odds change with the one unit change of the parameters.*

[d] *Tolerance values measure collinearity of the parameters (i.e., the impact of correlation of the parameters on their estimates).*

[e] *Wald statistic is a maximum likelihood version of a* t *test.*

Table 3. Statistics of the minimal adequate models for the probability of escape and the probability of naturalization of alien forestry species in the Czech Republic.

							Hosmer and Lemeshow test^d		
Event	*Omitted species*	G^{2a}	*df*	p	$r^2{}_L{}^b$	*AIC*^{c}	χ^2	*df*	p
Escaped	none	23.53	2	<0.0001	0.39	209.66	5.59	7	0.59
Naturalized	none	11.48	5	0.043	0.31	603.10	4.64	7	0.70
	Castanea sativa	14.54	5	0.012	0.41	426.10	6.25	7	0.511
	Castanea sativa and *Aesculus hippocastanum*	20.23	2	<0.0001	0.58	185.94	2.883	6	0.823

[a] *G^2 test on likelihood ratio χ^2 statistic (i.e., the deviance of the maximum likelihood model).*
[b] *Explained variance for logistic models as suggested by Menard (2000)*
[c] *Akaike information criterion for the best model (i.e., one that provides the maximum fit of the logistic model for the least number of predictors).*
[d] *Describes an overall goodness of fit of the models to the data.*

The model also predicted an increase in the probability of escape with increasing number of units. Holding the time of introduction constant, the odds ratio per the ln of one unit was 23.466 (95% CI: 1.010–545.014) (Table 3). This corresponded to <5% probability of escape for one unit and, approximating beyond the range of the number of units under the study, to >95% probability for 200 units (Fig. 1).

The minimal adequate model misclassified 3 of the 28 species. *Picea glauca* and *P. omorica* are not escaped but were classified as escaped, and the escaped *Juglans nigra* was classified as not escaped. These three species also had the largest differences between the observed and fitted values (the largest standardized residuals) and caused the largest changes in the parameters of the model after being deleted from the model (they had the largest values of $\Delta\beta$). Results did not change, however, if *Picea glauca*, the species with the largest $\Delta\beta$, was omitted. That is, the misclassified species did not cause significant changes in the structure or the explanatory power of the minimal adequate model.

The estimates of the parameters were highly significant when evaluated by G^2 test (time of introduction: $G^2 = 17.92$, df = 1, $p < 0.0001$; ln of the number of units: $G^2 = 9.591$, df = 1, $p = 0.0019$) and still significant when evaluated by the Wald statistic (time of introduction: $G^2 = 4.050$, df = 1, $p = 0.044$; ln of the number of units: $G^2 = 3.867$, df = 1, $p = 0.049$). Because the parameters were not correlated, there was no negative impact on their estimates due to collinearity (tolerance values = 0.98) (Table 2).

Probability of Naturalization

Of the 28 species analyzed, 10 were considered naturalized (Table 1). The original minimal adequate model for all species indicated a significant interaction between the time of introduction and the ln of the number of units ($G^2 = 4.007$, df = 1, $p = 0.045$) and between the time of introduction and the log of planting area ($G^2 = 4.057$, df = 1, $p = 0.044$) (Table 4). This suggests that the time of introduction alone cannot be used for the prediction of the probability of naturalization, because it is differentially affected by low and high number of planting units and by small and large extent of planting area. This model was significant ($G^2 = 11.48$, df = 5, $p = 0.043$, $r^2{}_L = 0.31$) and gave no evidence for a lack of fit (Hosmer and Lemeshow test: $\chi^2 = 5.59$, df = 7, $p = 0.59$); however, it had a low information value (AIC = 603.10) (Table 3). Moreover, the confidence intervals of the odds ratio of all parameters included one, indicating that changes in these parameters do not allow prediction of the probability of a species being naturalized. The tolerance value for the standardized log of area was unacceptably low, indicating a possibility of detrimental effects on the estimated regression parameters (Table 4). Eight of the 28 species were misclassified, and when the species with the largest $\Delta\beta$, *Castanea sativa*, was omitted, the parameters of the model changed significantly (Tables 3 & 4).

The refitted minimal adequate model without *Castanea sativa* explained more variance ($r^2{}_L = 0.41$) and had larger information value (AIC = 426.10) than the original one with all species included (Table 3). Most importantly, the confidence interval of the odds ratio of the interaction between time of introduction and ln of the number of units did not include one (Table 4), which enabled prediction of the probability of naturalization against time of introduction for different values of the ln of the number of units. With a low number of units (mean + 1 SD of the ln of the number of units), regression of the number of years since introduction did not change the probability of naturalization ($G^2 = 0.125$, df = 1, $p = 0.72$). However, with a high number of units (mean – 1 SD), the regressed years marginally decreased the probability of naturalization ($G^2 = 3.698$, df = 1, $p = 0.054$). This indicates that, similar to the probability of escape (Table 2), but only for a high number of units, the probability of naturalization increases for species introduced early. However, 6 of the 27 species remained misclassified, and when the species with the largest $\Delta\beta$, *Aesculus hippocastanum*,

Table 4. Parameters of the minimal adequate models of the probability of naturalization of alien forestry species in the Czech Republic

Omitted species	*Parameter*	*Estimate*	*ASE*[a]	G^{2b}	*df*	p	*Odds ratio*[c]	*95% CI of odds ratio*	*Standardized estimate*	*ASE*	*Tolerance values*[d]	*Wald statistic*[e]	*df*	p
None	intercept	166.137	128.588						−0.8484	0.5440		2.424	1	0.428
	log(planting area)	111.557	79.585	1.812	1	0.18	2.81E+48	0.000–1.55E+116	1.449	1.102	0.096	1.727	1	0.189
	time of introduction	−0.093	0.07	1.694	1	0.19	0.911	0.794–1.046	−1.511	1.296	0.711	1.334	1	0.248
	ln (number of units)	−132.657	94.497	0.228	1	0.63	0.000	0.000–6.7E+22	0.4946	1.054	0.218	0.220	1	0.639
	(time of introduction) × (ln[number of units])	0.073	0.051	4.007	1	0.045	1.075	0.972–1.189	5.292	3.6792	0.194	2.030	1	0.154
	(time of introduction) × (log[area])	−0.060	0.043	4.057	1	0.044	0.942	0.865–1.025	−6.615	4.629	0.198	2.001	1	0.157
Castanea sativa	intercept	654.637	358.437						−0.7191	0.6178		1.346	1	0.246
	log(planting area)	119.029	83.055	0.341	1	0.56	4.94E+51	0.000–2.46E+122	0.699	1.193	0.199	0.342	1	0.559
	time of introduction	−0.360	0.196	5.638	1	0.017	0.698	0.475–1.025	−7.499	4.188	0.525	3.161	1	0.075
	ln (number of units)	−273.507	134.622	1.388	1	0.24	0.000	0.000–0.000	1.451	1.339	0.217	1.168	1	0.280
	(time of introduction) × (ln[number of units])	0.150	0.074	7.63	1	0.0057	1.162	1.006–1.342	11.68	5.715	0.207	4.141	1	0.42
	(time of introduction) × (log[area])	−0.065	0.045	4.36	1	0.037	0.938	0.858–1.024	−7.482	5.225	0.190	2.047	1	0.152
Castanea sativa and *Aesculus hippocastanum*	intercept	204.0	108.3						0.3707	0.7362		0.251	1	0.616
	time of introduction	−0.1163	0.06085	12.64	1	0.00038	0.89	0.789–1.005	−9.710	5.079	0.99	3.561	1	0.059
	ln (number of units)	3.792	1.809	12.54	1	0.00040	44.361	1.223–1609.011	3.545	1.692	0.99	4.286	1	0.038

[a] *Asymptotic standard errors.*

[b] *G^2 test on likelihood ratio χ^2 statistic (i.e., the deviance of the maximum likelihood model).*

[c] *Odds and their confidence intervals (CI) measure how the odds change with the one unit change of the parameters.*

[d] *Tolerance values measure collinearity of the parameters (i.e., the impact of a correlation of the parameters on their estimates).*

[e] *Wald statistic is a maximum likelihood version of a* t *test.*

was omitted from this refitted model, the parameter estimates again changed dramatically (Tables 3 & 4).

The refitted minimal adequate model with both *Castanea sativa* and *Aesculus hippocastanum* omitted was highly significant ($G^2 = 20.23$, df = 2, $p < 0.0001$), explained most variance ($r^2_L = 0.58$), had the largest information value (AIC = 185.94), and gave the largest overall goodness of fit to the data (Hosmer and Lemeshow test: $\chi^2 = 2.88$, df = 6, $p = 0.82$) (Table 3). Only 4 of the remaining 26 species were misclassified: *Picea glauca* as naturalized and *Ailanthus altissima*, *Juglans regia*, and *Padus serotina* as not naturalized. These species had the largest standardized residuals and $\Delta\beta$, but when these species were deleted from this refitted minimal adequate model, the model's parameters did not change significantly.

Predicting the probability of naturalization based on the refitted minimal adequate model with two omitted species (Fig. 2) yielded results very similar to the model predicting the probability of escape (Fig. 1). Both models differed only by inclusion of *Castanea sativa* and *Aesculus hippocastanum* in the original minimal adequate model for escape. These two species were missing from the refitted model for naturalization. Similar to the model predicting the probability of escape, the probability of naturalization in the refitted model was significantly affected by the time of introduction ($G^2 = 12.64$, df = 1, $p = 0.00038$) and by the ln of the number of units ($G^2 = 12.54$, df = 1, $p = 0.00040$). As before, the estimates were not negatively affected by collinearity (tolerance values = 0.99) (Table 4), suggesting that both the temporal (time of introduction) and the spatial (the number of units) factors were estimated reliably.

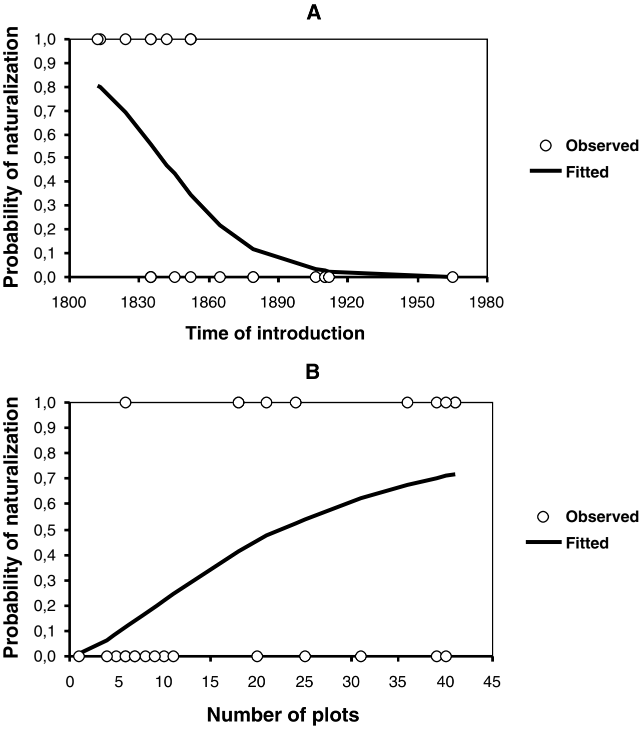

Figure 2. The probability of naturalization of alien tree species planted in the Czech Republic based on (A) the time of introduction for cultivation and (B) the number of units (plots) in which they are planted. The figure is based on simple logistic regressions. Parameters for this model, based on multiple logistic regression, are given in Table 4, statistics are given in Table 3. Castanea sativa *and* Aesculus hippocastanum *were omitted (see text for details).*

With the two species omitted and mutually comparable standardized values of the parameters, the estimates for escape (Table 1) and naturalization (Table 4) overlapped widely in their asymptotic standard errors (ASE, Tables 2 and 4). However, the ASEs for the time of introduction in the naturalization model were only marginally significant (Wald statistic = 3.561, df = 1, $p = 0.059$). Consequently, the prediction of naturalization based on the odds ratio of the time of introduction included zero (Table 4); hence, only the ln of the number of occupied units could be used to predict the probability of naturalization. Species planted at four units had >5% probability of naturalization and, approximating beyond the range of the number of occupied units under study, those planted at 200 units would have >95% probability of naturalization (Fig. 2). However, species planted at one unit had >5% probability of escape. That is, this refitted minimal adequate model predicted the 5% probability of naturalization for more units than the minimal adequate model for escape, but the same 95% probability of escape and naturalization was predicted for species planted at 200 units.

The planting area had no significant effect on either the probability of naturalization or the probability of escape.

Frequency of Species Escaped from Cultivation

Planting area had a significant effect on the number of localities recorded in natural and seminatural vegetation (Fig. 3). For the 14 species escaped from cultivation (Table 1), the minimal adequate model indicated a significant effect of the log of planting area ($\sqrt{\text{number of localities}} = -1.169 + 4.096 \log(\text{planting area})$, df = 1, 12, $F = 19.68$, $p = 0.00081$, $r^2 = 0.62$). Neither the time of introduction nor the number of units appeared significant. *Robinia pseudoaccacia* (Fig. 3) caused the largest change in the regression slope of the number of localities on planting area after deleting this species from the minimal adequate model (Cook's distance = 0.94). However, the decrease in the regression slope was not significant ($t = 1.12$, df = 12, $p = 0.14$), suggesting that inclusion of this species did not cause significant changes in the structure and explanatory power of the model.

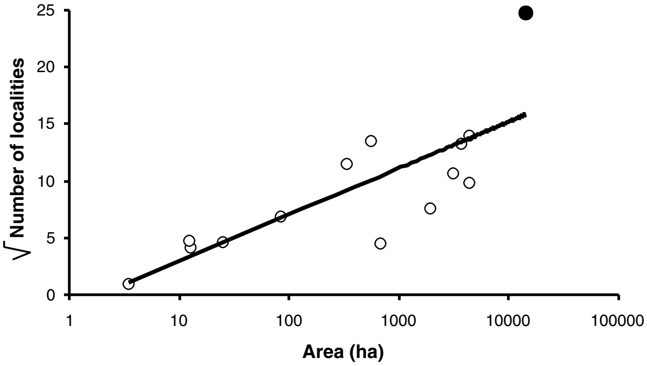

Figure 3. Relationship between the number of localities of alien tree species reported from natural and seminatural habitats in the Czech Republic and the planting area. Fitted values are given in the text. The black point is Robinia pseudoaccacia.

Discussion

Extent of Planting as a Surrogate for Propagule Pressure

Propagule pressure is a crucial determinant of invasion success (Lonsdale 1999; Rejmánek et al. 2005). It can fundamentally influence the probability of invasions by alien species in both space (widespread dissemination, abundant plantings) and time (long history of cultivation) (e.g., Kowarik 1995; Richardson 1996; Rouget & Richardson 2003). Unfortunately, it is difficult to measure and express quantitatively, particularly on a large scale (Rouget & Richardson 2003). Quantitative surrogates for propagule pressure such as number of visitors to nature reserves (Lonsdale 1999), human population size (McKinney 2002), or economic activity (Taylor & Irwin 2004) have been used.

In studies of tree invasions, information on the extent and character of planting can be used as a surrogate for propagule pressure. Forestry records often provide reliable estimates of planting area and time of introduction. In addition, longevity of trees and their easy mapping allow for determining dispersal foci, the distance from which can be used as another surrogate for propagule pressure (Rouget & Richardson 2003).

The data we used on planting are recent and may have varied over several centuries of species invasions, thus exerting different effects during the analyzed period. Nevertheless, historical data available for individual species (Blaščák 2003) indicate that changes over time in the relative extent of their planting were not so dramatic as to affect the robust results of our models.

Planting History and Propagule Pressure as Triggers of Invasion

The probability of escape increased with the time since introduction and the number of planting areas, with the former predictor being more important than the latter. A rather high proportion of explained variation indicates that these predictors determined to a large extent whether the invasion started or not. Unexplained variation may be attributable to species-specific traits and habitat conditions.

For species introduced to cultivation before the beginning of the nineteenth century, there was a 95% probability that they had escaped from cultivation, whereas those introduced after the end of the nineteenth century had the same probability that they had not escaped up to now. Such predictions must be interpreted in the present context: time acts as an important driver of invasion and species not escaped yet may start to invade in the future (Kowarik 1995). Effects of global warming (e.g., Bengtsson 1997) may play an important role in this respect because invasions of many alien species in Central Europe are constrained by low temperatures (Pyšek et al. 2003).

Interpreting the other significant predictor of the probability of escape, number of planting units, is more difficult. With 41 planting units recognized by the forestry classification system in the Czech Republic, a linear approximation beyond the range of data does not account for a possible threshold number of units between 42 and 200, above which the character of the relationship may change unpredictably. Nevertheless, it indicates that the number of available units is too low to ensure that a species will escape from cultivation just because it is widely planted, regardless of planting history.

Unlike the number of units, the total planting area did not affect the probability of a species escaping from cultivation. It is likely that the high number of units exposed the species to a wide range of geographical conditions and increased the chance that a species would encounter conditions suitable for escape from cultivation or for naturalization. That a large area itself did not contribute to the invasion success possibly reflects that planting of a species, however extensive, may be concentrated to a limited region where the escape from cultivation may be prevented by factors beyond propagule pressure, such as climate constraints, lack of dispersal vectors, or lack of disturbance.

Planting area was the only significant predictor of the frequency of occurrence of casual and naturalized tree species outside cultivation. Neither the number of units nor time since introduction played a role in frequency of occurrence. This indicates that factors affecting the dynamics of spread of these species in the landscape are different from those that determine whether the process of invasion starts or not. It appears that the amount of propagules supplied by planted stands has an overwhelming effect on species frequency in the landscape, regardless of how these propagules are distributed over a wide range of geographical conditions. In addition, once a species becomes naturalized (10 of the 14 escaping species in the data set are naturalized), it creates additional propagule pressure from wild, reproducing populations. The effect of these propagules on the species' population dynamics may be more important than what would correspond to their proportional amount because they increased the propagule pressure under the conditions that were sampled and proved suitable by maternal populations (i.e., where the species became naturalized).

Are Naturalization and Escape Driven by the Same Forces?

The minimal adequate model for escape provided better results than that for naturalization. That the prediction for the latter, more advanced stage of invasion was less reliable than that for the beginning of invasion is not surprising because naturalization is driven by a more complex array of factors than mere escape from cultivation (Kowarik 1995; Rejmánek et al. 2005). To become naturalized, a species must overcome reproductive barriers in the area of introduction (Richardson et al. 2000). Once this has happened, its occurrence is less dependent on short-lasting opportunities, including chance (Crawley 1989). Variation in species traits and the effect they have on the probability of naturalization thus makes predicting naturalization more difficult than predicting escape. The number of species planted for forestry purposes was too low to allow for the statistical analysis of species traits. Nevertheless, some insight can be gained by exploring species that were misclassified by the predictive models, whether they have some specific features responsible for them not fitting the statistical patterns.

The two species that caused the difference between the minimal adequate models of escape and naturalization with all species included (*Castanea sativa* and *Aesculus hippocastanum*) are reported as first introduced in 1562 and 1576, respectively. The introduction of the remaining species did not start before 1812. Both these species were introduced early, have escaped from cultivation, but are not naturalized. That is why their inclusion changed the prediction of naturalization but not that of escape. Omitting the earliest introduced species (*Castanea sativa*) yielded results similar to those of the escape model and indicated the increasing probability of naturalization for species introduced early, although only when they were planted at a high number of units. With both species omitted, the probability of naturalization depended on the same predictors as that of escape. The only difference was that the 5% probability of naturalization was predicted for a higher number of units than the probability of escape. That more planting units are needed for a species to naturalize than to escape from cultivation results from the character of the invasion process, with progressively fewer species overcoming subsequent barriers (Richardson et al. 2000).

Forestry as a Pathway for Alien Tree Species

Some alien woody species potentially represent a significant threat to biodiversity worldwide because of their high invasiveness and impact on invaded vegetation (Binggeli 1998; Haysom & Murphy 2003; Richardson & Rejmánek 2004). Forestry introduces individuals from provenances suitable for a particular climate and implements large-scale planting, creating massive propagule pressure (Rouget & Richardson 2003). This makes forestry a very efficient pathway for invasions (Richardson 1998; Haysom & Murphy 2003). Compared with horticulture, fewer species are introduced via forestry but proportionally more naturalize or invade. Of 4360 alien woody species introduced into the Czech Republic for horticultural purposes and 1358 alien species frequently planted in parks and gardens (M. K., unpublished), only 127 are thought to have escaped from cultivation (Pyšek et al. 2002*b*). The effect of forestry, however, acts on a large scale. In 2000 the 28 tree species we analyzed in this study were planted on 45203 ha, representing 1.77% of the total forest area in the country (available from http://www.uhul.cz/slhp3/defaultA.htm). Knowledge of factors determining the probability of alien trees escaping from cultivation or becoming naturalized is therefore crucial for minimizing impacts of future invasions associated with forestry and conserving biodiversity. In addition, the number of invaders in the future will likely increase due to the lengthy lag phases in invasions of woody species even if new introductions ceased (Kowarik 1995), which is improbable because more species are planted over larger areas (Richardson & Rejmánek 2004). In the Czech Republic, the threat is enhanced by forestry practices. The area used for plantations of alien trees could increase up to 7% of the total forest area and currently there are 24 other tree species being planted and tested as potential candidates for future introductions into the landscape (ÚHÚL 1994; Beran & Šindelář 1996).

The data documenting a link between forestry-mediated invasions and nature conservation are also available. Of the 28 species planted for forestry purposes, 6 that are classified as invasive in the Czech Republic (Table 1) occur in nature reserves. Although they do not currently invade massively in the reserves studied in a previous paper (Pyšek et al. 2002*a*), their occurrence represents a potential threat to the biodiversity of protected areas in this country.

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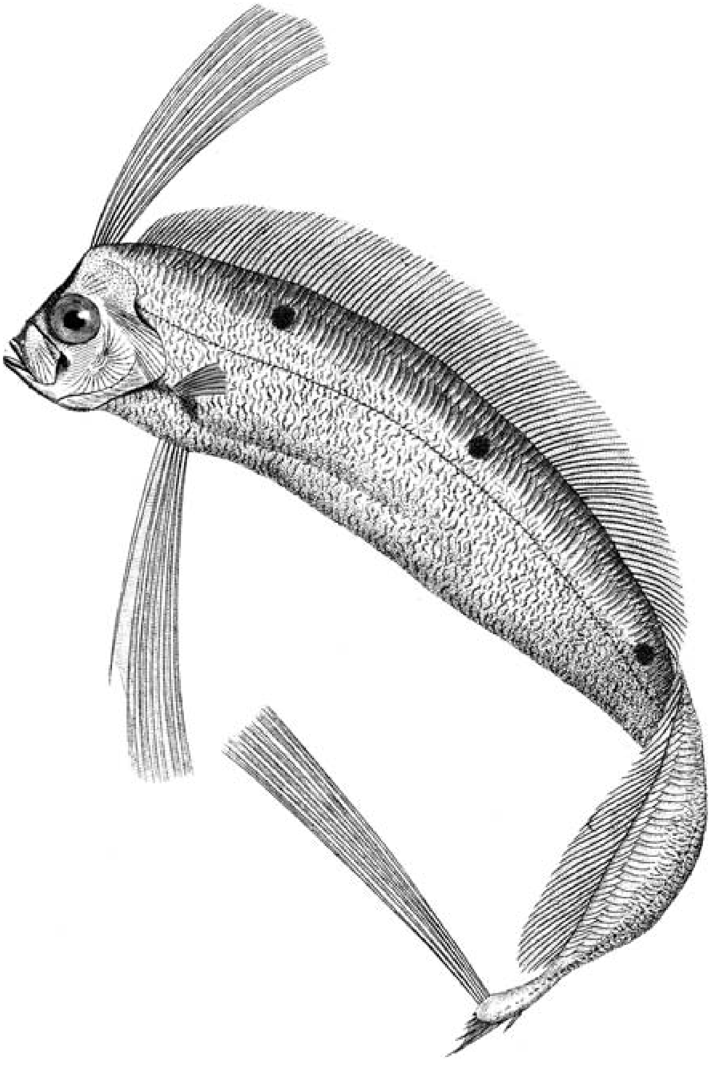

Chapter 3 ~ Propagule pressure vs. biological traits; Aliens vs. natives

Pyšek, P., Křivánek, M., Jarošík, V. Propagule pressure, residence time, climatic match, species traits and similarity to native species discriminate naturalized woody aliens from those that fail. (Submitted)

Propagule pressure, residence time, climatic match, species traits and similarity to native species discriminate naturalized woody aliens from those that fail

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Abstract

We studied the probability of escape from cultivation and naturalization of woody plants cultivated for ca 150 years in the Czech Republic, Central Europe. Using regression trees, we analysed 109 escaped–not escaped congeneric pairs, 44 naturalized–not naturalized congeneric pairs, and 53 triads each consisting of escaped–not escaped–native congeners. The predictors of the above probabilities we used allowed us to explores the complex effects of the following factors: residence time in the target region; propagule pressure expressed as the intensity of planting in the target area; evolutionary adaptation to climate in the region of native distribution reflected by the area of origin; and 21 species biological and ecological traits. The low misclassification rate of the naturalization model, 19.3%, indicates that the variables used included major determinants of invasion. Residence times were significantly longer and propagule pressure significantly higher for species that escape from cultivation and naturalize than for their congeners that do not. The probability of escape increased with early introduction to the Czech Republic, while that of naturalization with the introduction into Europe. This indicates that some species may have been already adapted to European conditions when introduced to the Czech Republic. Importantly, the probability of escape from cultivation depends exclusively on propagule pressure; none of the biological traits had a significant effect. The probability of naturalization depends not only on propagule pressure, but also on the area of origin. Species originating in Asia are less likely to naturalize in Central Europe than those from North America or other parts of Europe. The only biological trait affecting the probability of naturalization is fruit size; within species of European origin with a low propagule pressure, species with fruits smaller than 1.1 cm are less likely to naturalize than those with bigger fruits. The results indicate that the relative role of biological traits and other factors is stage-dependent and that the traits only play a role in later, more advanced stages of invasion. If the propagule pressure from planting is strong enough, woody species eventually escape from cultivation no matter what biological traits they possess. Alien species escaping from cultivation were more similar to their native congeners in the majority of traits than were non-escaping congeners, which indicates that species that are functionally similar to native woody plants are more likely to invade. This does not support the functional interpretation of Darwin's naturalization hypotheses and limiting similarity theory.

Keywords: alien, biological traits, climate match, Darwin's naturalization hypothesis, invasion, niche, limiting similarity, naturalization, propagule pressure, woody species

Introduction

One of the fundamental questions of invasion biology – which traits predispose a species to become invasive in the region to which is introduced – has been the focus of invasion biology since it has become established as a distinct branch of contemporary ecology (Baker 1965, Roy 1990, Rejmánek 1996, 2000). Many studies have attempted to profile successful invaders (see Pyšek et al. 2006, and Pyšek & Richardson 2007 for reviews). In the last decade, however, it has been recognized that the traits are only part of any explanation for invasion success, and that other factors such as residence time (Crawley et al. 1996, Pyšek & Jarošík 2005, Křivánek et al. 2006), propagule pressure (Rejmánek 2000, Brown & Peet 2003, Rouget & Richardson 2003, Foxcroft et al. 2004, Kühn et al. 2004, Daehler 2006, Křivánek et al. 2006) and climate match (Thuiller et al. 2005) co-determine whether and when a species will invade. This recognition has led to the application of models that analyze several groups of factors at the same time; some studies recently addressed the role of traits in plant invasions in relation to other potentially confounding factors that co-determine invasiveness (Hamilton et al. 2005, Thuiller et al. 2006, Wilson et al. 2007). It follows that because of this context-dependence, the role of traits in plant invasions can only be assessed properly when the main confounding factors are controlled for.

In addition, it has been suggested that the factors important at each stage of invasion, such as introduction vs. naturalization, are different, with socio-economic factors being generally important initially, with biogeographical, ecological and evolutionary factors increasing in importance in later stages (Williamson 2006). This implies that different traits are important at different stages of the invasion process (Kolar & Lodge 2001, Pyšek et al. 2003), but this has not been rigorously tested so far by using real data.

Studies on woody species has contributed substantially to our understanding of the invasion process (Rejmánek & Richardson 1996, Richardson & Rejmánek 2004, Richardson 2006, Křivánek & Pyšek 2006, Křivánek et al. 2006, Herron et al. 2007). Very good availability of trait data as well as detailed information about planting history in many parts of the world (Richardson et al. 2004) makes woody plants a suitable model for testing the role of factors determining naturalization success, and for separating the influence of biological traits from that of confounding factors. In addition, many woody plants are among the most important invasive species with serious impact on ecosystems invaded (transformers *sensu* Richardson et al. 2000; Carmen & Brotherson 1982, Richardson & Higgins 1998, Richardson et al. 1989, Vitousek & Walker 1989, Zavaleta 2000, Lowe et al. 2001). On the other hand they are the most important group in terms of forestry, ornamental gardening and landscape architecture. The need for a compromise between commercial use and nature protection made them a subject of risk-assessment schemes aimed at separating species with a high likelihood of post-introduction naturalization and spread from those that can be safely introduced (Reichard & Hamilton 1997, Pheloung et al. 1999, Křivánek & Pyšek 2006).

The approach used in this paper allowed us to reduce some of the biases that constrain analyses of the determinants of invasiveness in plants. We use woody plants cultivated in the Czech Republic, Central Europe, to address the above issues in a complex model including major factors known to co-determine naturalization success: (i) evolutionary adaptation to climate in the native distribution region, (ii) propagule pressure and (iii) residence time in the target region, i.e. for how long the species has been present in (Central) Europe, and (iv) a wide range of species biological traits. By explicitly considering the above factors, as well as traits, we aim to reveal the direct effects of biological traits unbiased by climatic match, propagule pressure and residence time. By using the congeneric approach (Pyšek & Richardson 2007), we eliminated the role of phylogenetic relatedness which has been shown to bias the effect of traits on invasion (Crawley et al. 1996, Pyšek 1997, Hamilton et al. 2005. Lloret et al. 2005, Cadotte et al. 2006). Further, the stage-dependence of the role of traits and other factors (Williamson 2006) is addressed by comparing two stages of the invasion process (Richardson et al. 2000). Finally, by using a set of native congeners, we explored whether the traits of alien woody species escaping from cultivation are more similar to traits of those that do not escape or to those of native species, which question is related to the limiting similarity theory (Tilman 1982, Silvertown 2004) and to functional aspects of the Darwin naturalization hypothesis, validity of which is a subject of an ongoing debate (e.g. Daehler 2001, Duncan & Williams 2002, Procheş et al. 2007).

Material and methods

Species data and variables

Alien woody plants escaping from cultivation in the Czech Republic were used as the data set. Only neophytes (introduced to Europe after the discovery of America, see Pyšek et al. 2004 for definition) were considered. Species were classified according to their invasion status into (i) escaping from cultivation but only occurring as casuals in the wild (further referred to as "escaped"), and (ii) naturalized, i.e. forming self-reproducing populations in the wild. The categories of invasion status were as defined in Richardson et al. (2000) and Pyšek et al. (2004) and classification of species followed that in Pyšek et al. (2002b).

Using the DAWIS database held at the Institute of Botany, Průhonice, Academy of Sciences of the Czech Republic (Křivánek & Pyšek 2007, http://www.ibot.cas.cz/invasions/projects.htm#dawis), which contains information on 1691 alien trees, shrubs and woody vines with a mean height of over 0.5 m grown in garden centres and commonly cultivated in this country, each alien species occurring in the wild (escaped or naturalized) was amended with (a) an alien congener not escaping from cultivation (termed "not escaped") or escaping but not naturalized, and (b) native congener, if such species is present in the country flora (Kubát et al. 2002). Congeners were chosen so as to be phylogenetically as close as possible, based on the most recent taxonomical treatments. Where an alien congener was not cultivated or a native congener was not present in the native flora of the country, it was substituted by the phylogenetically closest relative (Electronic Appendix 1). This approach was adopted to eliminate phylogenetic bias in the data set. Second, since the primary focus of the study was to identify species traits associated with the two stages of invasion (escape from cultivation and naturalization) an effort was made to select non-escaping congeners that were introduced at similar times and planted at comparable intensity to those escaped and occurring in the wild, in order to reduce the effect of residence time and propagule pressure, respectively, on the invasion process.

This screening yielded (i) 109 escaped–not escaped congeneric pairs, (ii) 44 naturalized–not naturalized congeneric pairs and (iii) 53 triads each consisting of escaped–not escaped–native congener (Electronic Appendix 1). The former two data sets were used to analyse the probability of escape from cultivation (Model I) and naturalization (Model II), respectively, the latter to explore, whether alien woody plants escaping from cultivation are more similar in their traits to native species than are those that do not escape (Model III).

The information obtained for each species from the DAWIS database (Křivánek & Pyšek 2007) can be divided into (i) introduction variables, and (ii) trait variables (see Electronic Appendix 2 for details). The introduction variables were only applicable to Models I and II and included: (1) Time of introduction into cultivation in the Czech Republic and Europe, a measure of minimum residence time; (2) intensity of planting in the Czech Republic expressed as the number of garden centres and botanical gardens selling the species; (3) type of use: ornamental, landscaping, forestry; (4) area of origin: Asia, Europe, Mediterranean, North America, hybrid.

Trait variables were used in all analyses and included: (5) life form: tree, shrub, vine; (6) leaf persistence: deciduous, conifers; (7) height (m); (8) duration of the juvenile period, expressed as the age at first flowering (years); (9) beginning and (10) duration of the flowering period in the Czech Republic (months); (11) breeding system: hermaphrodite, monoecy, dioecy; (12) fruit type: dry, fleshy; (13) seed weight (mg); (14) fruit size (cm); (15) beginning and (16) duration of fruit maturity (months); (17) germination (%); (18) type of reproduction: only generative, also vegetative; (19) nitrogen fixation: yes/no; (20) minimum mean annual temperature at which the species is planted in the Czech Republic, a measure of the tolerance to frost; (21) minimum mean annual precipitation at which the species is planted in the CR, a measure of the drought tolerance.

Statistical analysis

For each trait described as a continuous variable (Table 1), paired comparisons of the congeners were made separately on the probability of escape from cultivation (Model I) and naturalization (Model II). Because the normal distribution of all the data was not achieved by transformation, the tests were made by first calculating the difference in each pair, and then by using the non-parametric one-sample Wilcoxon's signed rank test, which compares the mean of the differences among the congeners with the null hypothesis that this difference is equal to zero (Crawley 2002, p. 178-179). Because this procedure involved repeated tests of different traits of the same set of species and since it was necessary to adjust the values of the type I error α at the 5% level, sequential Bonferroni tests with the associated experimentwise error rate α based on the Dunn-Šidák method were applied (Sokal & Rohlf 1995, p. 241–242).

The relationship between residence time in the Czech Republic and Europe was examined by regressing residence time for the Czech Republic on that in Europe. To check for outliers in this least-square regression, which could suggest that the delay in the introduction to the Czech Republic comparing to Europe does not remain the same during the whole range of the introduction period (cf. Křivánek et al. 2006), species points with the largest influence on the regression were assessed by Cook's (1977) distances, sorted in descending order, weighted out of the analysis one after another, and the model re-fitted after weighting out each of the data points. Whether a point could be considered outlier was assessed by t-test, as a significant change of the regression line when the point deleted from the analysis (Gilchrist & Green 1994; Jarošík et al. 2002). Because both the residence times might be estimated with error, the effect of the possible errors on the estimate of the regression slope was assessed by fitting major axis regression (Sokal & Rohlf 1995) and then comparing 95% confidence interval of the major axis slope with that of the least square slope.

The effects of species traits on the probability of escape/naturalization (Model I/II), and the analysis of similarity of species traits of escaped and non-escaped aliens with those of native species (Model III) were assessed by classification trees (Breiman et al. 1984; De'ath & Fabricius 2000). The invasion status (Model I: escaped vs. not-escaped; Model II: naturalized vs. not-naturalized; Model III: escaped vs. not escaped vs. native congener) were the response variables, other variables, including the identity of congeners, were explanatory. Classification trees are an appropriate statistical method, since many explanatory variables had missing values and some had non-normal distributions. These features of the data precluded two alternative methods, i.e. binary logistic regression (e.g. Grotkopp et al. 2002) which could be used for all the explanatory variables, and discrimination analysis (Rejmánek & Richardson 1996, Muth & Pigliucci 2006) which could be used for the continuous variables. The trees were constructed by binary recursive partitioning in CART v. 6.0 (Breiman et al. 1984, Steinberg & Colla 1995), which uses the most reliable pruning strategy of over-growing trees, ensuring that any important tree structure is not overlooked. To find the optimal tree, a sequence of nested trees of decreasing size, each of them being the best of all trees of its size, were constructed, and their resubstitution relative errors were estimated. A random subset of the data (a test subset), comprising approximately 20% of all the data, was used to obtain estimates of cross-validated relative errors of these trees. These estimates were then plotted against tree size, and the minimum cost tree was selected as the optimal tree (Steinberg & Colla 1995). Following De'ath & Fabricius (2000), a series of 50 cross-validations were run, and the modal (most likely) single tree was chosen for description. The quality of the best single classification tree was evaluated by its misclassification rate, i.e. by comparing the misclassification rate of this best model with misclassification rate of the null model (De'ath & Fabricius 2000).

The best trees were represented graphically, with the root Node 1 standing for undivided data at the top, and the terminal nodes, describing the homogeneous groups of data, at the bottom of the hierarchy. The quality of each split was expressed by improvement, corresponding to misclassification rate at each node. Surrogates of each split, describing splitting rules that closely mimicked the action of the primary split, were assessed and ranked according to their association values, with the highest possible value 1.0 corresponding to the surrogate producing exactly the same split as the primary split. To prevent missing explanatory variables to have an advantage as splitters, the explanatory variables were penalized in proportion to the degree to which they were missing, and treated by back-up rules that closely mimicked the action of the primary splitters. To reduce the splitting power of high categorical variables (the identity of congeners with 109, 44 and 53 categories in Model I, II, and III, respectively), these were also adjusted to have no inherent advantage over continuous variables, following penalization rules described by Steingerg & Colla (1995).

Results

Elimination of biases

Time of introduction to the Czech Republic and Europe was significantly earlier for species that escape from cultivation and naturalize than for their congeners that do not, and the propagule pressure was higher in the former group (Table 1). Residence times in the Czech Republic and Europe are significantly correlated (Fig. 1), which suggests that the time of introduction to cultivation in the Czech Republic (mean±S.D. = 1835±69.5) depends on the previous introduction of the species to Europe (1774±95.8). The delay in introduction to the country, compared to Europe, was the same over the whole period examined, because although the species with the largest influence on the residence times are concentrated in the early times of introductions, they do not cause a significant change in the regression line. Moreover, the relationship is not biased by possible errors in the estimates of the residence times, as indicated by the 95% confidence interval of the major axis regression slope of the residence times overlapping with that of the least square regression (Fig. 1).

The results thus indicate that species that escape from cultivation or become naturalized are characterized by a longer residence time and higher propagule pressure than their congeners which do not escape. Consequently, the bias to the effect of traits, resulting from propagule pressure and residence time, could not be eliminated in the present data set, and these two factors were therefore included, as explanatory variables, in further analyses.

Effect of traits on the probability of escape from cultivation and of naturalization

Paired comparisons of congeners for all traits described as continuous variables showed that the probabilities of both escape and naturalization significantly ($P < 0.05$) increased with increasing propagule pressure. The probability of escape increased with early introduction into the Czech Republic, while that of naturalization with the introduction into Europe. No other trait had a significant effect in pair-wise comparisons (Table 1).

The classification tree, which incorporated all traits including categorical, revealed that the probability of escape (Model I) depends exclusively on propagule pressure; none of the biological traits had a significant effect. A higher probability of escape from cultivation was predicted if the species was planted in at least three garden centers. The misclassification rate of the best model was 34.4%, compared to 50% for the null model (Fig. 2).

Unlike the probability of escape, the probability of naturalization (Model II) depends not only on propagule pressure, but also on other variables including biological traits. The best classification tree had misclassification rate of 19.3%, lower than that for escape. Species originating in Asia are less likely to naturalize in Central Europe than those from North America or other parts of Europe, including the Mediterranean. Within the latter group, the probability of naturalization depends on propagule pressure. If it is low, as for species planted in less than three garden centers, it depends on fruit size whether or not a species becomes naturalized. Those with fruits smaller than 1.1 cm are less likely to naturalize than those with fruit size exceeding this threshold (Fig. 3).

Importantly, the identity of congeners significantly affected none of the resulting trees. It only appeared as a surrogate, with the highest association value of 0.89 at node 3 of the probability of naturalization tree (Fig. 3), but its improvement value was only 6% of that of the primary splitter, i.e. fruit size. This indicates that the traits identified as important in analyses are generally valid for the data set used, unbiased by species phylogenetic relatedness.

Trait similarity of native species with those of escaped and not-escaped aliens

Differences in biological traits among native species, aliens escaped from cultivation and cultivated aliens that do not escape are summarized in Fig. 4 (Model III, with the misclassification rate of 47.2% compared to 66.7% of the null model). The three groups differ in the duration of flowering period, fruit size and minimum tolerated temperature. Inspection of the relative frequencies at the four splitting nodes indicates that the numbers of native species are always closer to those of escaped than to those of not escaped aliens, with the only exception of minimum temperature range 2.5–5.5 °C (Fig. 4). Alternative classification tree with 15 terminal nodes (not shown) had the misclassification rate 34.6% and identified the length of juvenile period and beginning of fruit maturity as additional traits discriminating between the three groups, in which escaped species were again more similar to native than were those that do not escape. The duration of fruit maturity and height also appeared in the tree, but without a consistent pattern discriminating between the three species groups.

The identity of congeners only appeared as a surrogate in the tree with 15 terminal nodes, with surrogate improvement value only 1% of the primary splitter, beginning of fruit maturity. This again indicates negligible bias imposed on the results by phylogenetic relatedness.

Discussion

Determinants of invasion act in concert and are context-dependent

Despite increasing awareness of factors that determine species naturalization success and invasiveness, invasion biology is still at the phase of developing robust generalizations (Richardson & Pyšek 2006). This is because many biological, environmental, and anthropogenic factors interact to determine the distribution of invasive species and because many analyses of invasiveness have been flawed by not considering fundamental issues of residence time, e.g. how much time a species has had to spread, availability of suitable habitats, and propagule pressure (Sol et al. 2008). However, including residence time and potential range always significantly increases the explanatory power of the models and whether or not they are taken into account can also affect which factors emerge as significant determinants of invasiveness (Pyšek & Jarošík 2005, Wilson et al. 2007). These issues were recently addressed in several studies. Thuiller et al. (2006) used environmental factors, land use, life-history traits of the invaders, residence time, origin, and human to examine the spatial pattern of invasive alien plant species in South Africa, and showed that after accounting for environmental factors, the pattern of invasions was driven by human uses, life forms, and reproductive traits. Hamilton et al. (2005) compared life-history correlates of invasion success between regional and continental spatial scales among non-native plants of eastern Australia. After controlling for residence time and cross-correlation with other life-history traits, small seed mass and high specific leaf area were correlated with invasion success, but the results varied with scale (Hamilton et al. 2005). The outcome of such studies always depends on which factors are included as explanatory variables but overall their results indicate that major determinants of invasion success are complex and need to be investigated in concert.

The approach used in this paper allowed us to assess, for woody plants cultivated in Central Europe for ca 150 years, a complex effect of crucial determinants of naturalization, i.e., (i) residence time in the target region, (ii) propagule pressure expressed as the intensity of planting in the target area, (iii) evolutionary adaptation to climate in the native distribution region reflected by the area of origin, and (iv) a wide range of species biological traits.

The low misclassification rate of the naturalization model, 19.3%, indicates that the variables used included major determinants of invasion.

Further, by analyzing the probability of escape from cultivation and that of naturalization as two separate stages of the invasion process (Richardson et al. 2000, Richardson & Pyšek 2006, Williamson 2006), we showed that the relative role of biological traits and other factors is stage-dependent and that the traits only play a role in later, more advanced stages of invasion. More importantly, biological species traits and climatic adaptation manifested via the region of origin had no effect on the probability that a species would escape from cultivation. If the propagule pressure from planting is strong enough, woody species eventually escape from cultivation no matter what are their biological traits.

Residence time matters

In our analysis, the effect of phylogenies was eliminated by congeneric approach (Pyšek & Richardson 2007), but the original intention of eliminating confounding effects of propagule pressure and residence time in analyses of traits, by selecting congeneric pairs with comparable levels of these characteristics, was constrained by the availability of data. For that reason, residence time and propagule pressure were included as explanatory variables in the models.

Time of introduction into cultivation in the Czech Republic significantly influenced the likelihood of both escape from cultivation and that of naturalization in pair-wise comparisons of congeners, the effect being more pronounced in the former stage (Table 1). The results further indicate that the effect of residence time interacts with scale; whereas the probability of escape is associated with the time of introduction to the Czech Republic, that of naturalization depends on the time of introduction to a wider area of Europe. This can be interpreted in terms of interaction between residence time and propagule pressure. Residence time integrates aspects of propagule pressure: the longer the species is present in the region, the greater the size of the propagule bank, and the greater the probability of dispersal, establishment, and the founding of new populations (Rejmánek et al. 2005). The first stage of invasion, which is, in planted woody species, represented by an escape from cultivation, is sooner or later reached if there is a strong enough propagule pressure but many of the escapees fail to naturalize (Křivánek & Pyšek 2007, Křivánek et al. 2006). A long history of cultivation in a wider geographical region at the continental scale of Europe, however, reflects that some species may have been already adapted to European conditions when introduced to the Czech Republic. Comparing all species in the data set, including those for which information is available only on date of introduction to either Czech Republic or Europe, they were introduced to this country with an average delay of almost 80 years (average time of introduction to the Czech Republic: 1828±71, n = 158; to Europe: 1752±105, n = 138), which means several generations later, depending on the length of juvenile period. This points out to the importance of studying the naturalization process independently of state borders as national data may have a limited potential.

Climatic match and propagule pressure matter

The pair-wise analyses revealed that propagule pressure played a crucial role and that this was more important than residence time. Furthermore, residence time was no longer significant in complex models when the region of origin was introduced as a variable. It is, however, likely that the effect of residence time in our data was partly manifested via the area of origin since species from different continents were introduced to Central Europe at different times (Pyšek et al. 2003). Indeed, the area of origin had a significant effect on residence time and when both predictors were included together in a model, the effect of residence time became non-significant.

The effect of the origin is more complex than that of the time of introduction alone, because the origin primarily reflects climatic match. Upon introduction, species from various continents were differently predisposed to Central European climate, these differences resulting from evolutionary adaptations to local climatic conditions in their native distribution areas. Species originating in climatically similar regions such as other parts of Europe, including the Mediterranean Basin, and North America are more likely to naturalize than those from Asia. Like the effect of traits and residence time, the effect of origin was also stage-dependent; the region of native distribution only becomes important when it comes to naturalization (compare Figs 2 and 3).

In our study, propagule pressure was the most important determinant of escape from cultivation and second most important of naturalization. In general, studies that explicitly filter out confounding effects of propagule pressure have the potential to reveal inherent trait-related determinants of invasibility (Pyšek & Richardson 2007). That propagule pressure, both in space (by widespread dissemination, abundant plantings) and/or time (by long history of cultivation), fundamentally influences the probability of invasions by alien species has been convincingly demonstrated (Rejmánek 2000, Brown & Peet 2003, Rouget & Richardson 2003, Richardson 2006). A previous paper based on woody species data in the Czech Republic (Křivánek et al. 2006) showed that as far as propagule pressure is concerned, not only overall planting intensity is important, but also its spatial distribution: species planted over a wider geographic range, hence sampling a more diverse suite of environmental conditions, were more likely to naturalize (see also Wilson et al. 2007).

The role of biological traits overestimated?

Within the scientific community, opinions on whether or not it is possible to link invasiveness to plant traits range from “relative agnosticism to sanguine confidence” (Cadotte et al. 2006). Nevertheless, a recent review of literature revealed that there is a strong support for height, vigorous vegetative growth, early and extended flowering, and reproductive characteristics as traits universally associated with invasiveness in vascular plants (Pyšek & Richardson 2007). Studies reporting these findings are fairly robust, as they were tested in different regions of the world and based on different floras (Crawley et al. 1996, Cadotte et al. 2006, Richardson 2006). Nevertheless, the direct effect of biological traits on invasion success of woody species in the Czech Republic is minor once we control for confounding factors, and is only detectable for the second stage of the invasion process, i.e. naturalization. This is somewhat surprising, considering that some traits have been repeatedly identified as determining invasion success (see Pyšek & Richardson 2007 for a review) and there are several papers demonstrating the role of traits specifically for woody plants. The well-established theory of determinants of invasiveness in woody plants posits that invasiveness is associated with early flowering and fruit maturity, small seed weight, short period between mast years and capacity for dispersal of fruits/seeds by vertebrates (Rejmánek & Richardson 1996, Richardson & Rejmánek 2004).

We suggest several explanations for this result: (i) Our data set included representatives of a single life form, which reduces overall variation in traits, and also, life form itself has been often identified as important trait associated with invasiveness (Crawley et al. 1996, Herron et al. 2007, see Pyšek & Richardson 2007 for a review). (ii) Classical studies on invasiveness of woody plants (Rejmánek & Richardson 1996) did not explore the role of species traits in relation to that of confounding factors, which can result in over-estimating of the importance of traits (Richardson et al. 1994, Pyšek & Jarošík 2005, Wilson et al. 2007). Also, these studies focus explicitly on invasion, a more advanced stage of the invasion process than the stage of naturalization addressed in our study. This is an important difference since the role of biological traits increases as particular stages of invasion are overcome by invading species, and for the final stage of invasion it is more pronounced than earlier stages (P. Pyšek et al., unpublished). (iii) The information on planting history is very detailed for woody species, hence the planting intensity used in our study is probably a more precise surrogate of propagule pressure than human population density or economic parameters usually used for his purpose (e.g. McKinney 2001, Pyšek et al. 2002a, Taylor & Irwin 2004, Thuiller et al. 2005). Therefore, its crucial effect may be more obvious and explain larger proportion of variation in our study than was the case in other studies. (iv) Finally, which traits turn out to be significant depends on what data are available and which traits can be included in models. However, this does not seem to constrain our results since the variables analyzed in our study included all major traits identified as important in previous papers, i.e. height, flowering time, duration of juvenile period and fruit/seed characteristics related to dispersal (Richardson & Rejmánek 2004, Pyšek & Richardson 2007).

Fruit size was the only important biological trait that appeared marginally significant in pair-wise comparisons and significant in models accounting for the effect of confounding factors. Most studies exploring the correlation between seed/fruit size and invasion success also yielded non-significant results (Pyšek & Jarošík 2005, Lloret et al. 2005, Cadotte et al. 2006, but see Hamilton et al. 2005). This may be partly because there are two contrasting groups of aliens, short-lived herbs and woody species, having on average small and large seeds, respectively, each of them successful in different environments. Another reason may be that having both small and large seeds brings about potential pros and cons for an alien plant. Small seed mass is correlated with increased seed output, small seeds are easily dispersed by wind and persist longer in soil than large seeds, while large seeds are generally thought to be better for establishment and more attractive to vertebrate dispersers (Pyšek & Richardson 2007).

We found that under low propagule pressure, species with fruits smaller than 1.1 cm are significantly less likely to naturalize than those with fruit size exceeding this threshold. This indicates that advantages of having large fruits prevail over limited seed output associated with large fruits. The size of the propagule seems to be more important than its character, i.e. whether the fruit is dry or fleshy – this trait was also included in the analysis but was not significant. However, the type of fruit is closely associated with its size, fleshy fruits being significantly larger than dry fruits (one-way factorial ANOVA on log fruit size: $F = 21.30$; $df = 1, 198$; $P < 0.001$) which indirectly supports previous results that in woody species, vertebrate and human-mediated dispersal associated with large fleshy fruits is an important factor contributing to invasiveness (Rejmánek 1995, Richardson & Rejmánek 2004).

Better not be different: New insights on Darwin's Naturalization Hypothesis

By employing a set of native congeners, we explored whether the traits of alien woody species escaping from cultivation are more similar to traits of those that do not escape or to those of native species. The rationale behind this comparison was that if escaping species had traits different from native species invasions would predominantly occur in empty niches or at marginal parts of niche space (Crawley et al. 1996, Strauss et al. 2006). This assumption would support the niche complementarity concept and limiting similarity theory (Tilman 1982, Silvertown 2004, Emery 2007), predicting that species already present in the community should suppress invasion by functionally similar species with similar resource requirements (Lodge 1993, Fargione et al. 2003, Tilman 2004, Von Holle & Simberloff 2004). As this was not the case and escaping species were more similar to their native congeners than were non-escaping species, we suggest that alien woody plants invade in the same niches and compete with native species.

Such an approach provides a different insight into an ongoing debate on the validity of the Darwin's naturalization hypothesis (Procheş et al. 2007), which posits that naturalization is easier for species from non-allied genera, because they are less similar to native flora; this is assumed to lead to a less intense competition and exploitation of different resources than are those utilized by native species. Darwin's naturalization hypothesis has been subjected to frequent testing in the last decade, but the tests were based on species numbers, i.e. are there significantly more or less alien species in a region with congeners in its native flora (e.g. Rejmánek 1996, Daehler 2001, Duncan & Williams 2002)? None of the studies focused on trait spectra of native and alien congeners. However, the phylogenetic pattern changes with the spatial and phylogenetic scales considered; at the spatial scale relevant to competitive interactions, closely related species are spatially separated, whereas at the regional scale, species in the same genera or families tend to co-occur more often than by chance (Procheş et al. 2007).

Our data provide indirect insights on the issue; the approach we used is not taxonomic since phylogenetic relatedness was controlled by using congeneric approach. It rather relates to a more general issue of similarity of aliens and native – Darwin himself used taxonomy as a proxy for ecological similarity, which makes this attitude to his hypothesis justified. Our results do not support Darwin's hypothesis and accord with previous analyses of alien floras of Hawai'i (Daehler

2001) and New Zealand (Duncan & Williams 2002). The naturalization success of temperate woody plants depends on the ability of species to utilize available resources and/respond to stress or disturbances in the occupied habitat. Successful alien woody plants are successful despite of being similar to native woody plants species, because they are able to compete with them in their niches.

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Table 1. Effect of traits described as continuous variables on the probability that an alien woody species cultivated in the Czech Republic escapes from cultivation or becomes naturalized. The differences in traits between escaped vs. not-escaped and naturalized vs. not-naturalized, respectively, were tested by non-parametric paired comparisons of congeners, with significance assessed at 5% level using sequential Bonferroni tests with the associated experimentwise error rate α based on Dunn-Šidák method. P of individual traits are non-adjusted values of type I error in the paired comparisons, arranged in descending order of significance. Only P's of traits in **bold**, which are smaller than their sequentially increasing associated α's, are significant at 5% level of significance.

Trait	Probability of escape		Trait	Probability of naturalization	
	P	Associated α = 0.05		P	Associated α = 0.05
High propagule pressure	0.0000312	0.003938	**High propagule pressure**	0.00150	0.003938
Early introduction to CR	0.000864	0.00423	**Early introduction to Europe**	0.00200	0.00423
Heavy seed	0.0219	0.00465	Early introduction to CR	0.0392	0.00465
Early introduction to Europe	0.0236	0.00512	Large fruit	0.0442	0.00512
Extended flowering	0.0271	0.00568	Early fruit maturity	0.185	0.00568
Large fruit	0.0656	0.00639	Minimum precipitation	0.208	0.00639
Early flowering	0.0967	0.00730	Extended flowering	0.246	0.00730
Minimum precipitation	0.179	0.00851	Height	0.342	0.00851
Height	0.267	0.0102	Minimum temperature	0.383	0.0102
Short juvenile period	0.293	0.0127	Early flowering	0.404	0.0127
Minimum temperature	0.362	0.0170	Short juvenile period	0.473	0.0170
Early fruit maturity	0.574	0.025	Seed weight	0.671	0.025
Extended fruit maturity	0.643	0.050	Extended fruit maturity	0.712	0.050

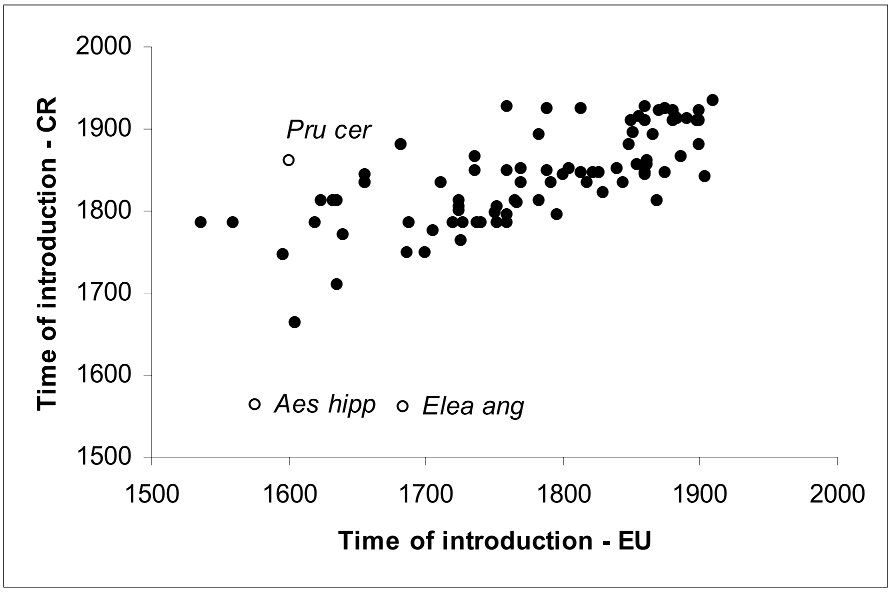

Fig. 1. Relationship between the time of introduction to the Czech Republic (CR) of cultivated alien woody plants and the time of their introduction to Europe (EU). Regression equation: CR = 954 + 0.50 EU; 95% CI of the regression slope = 0.39 – 0.61; F = 50.99; df = 1, 86; R^2 = 0.47. Empty symbols indicate species with largest Cook distances, having the highest influence on the slope of the least square regression. Aes hipp – *Aesculus hippocastanum*, Elea ang – *Eleagnus angustifolia*, Pru cer – *Prunus cerasifera*. Omitting *Aesculus hippocastanum*, the species with the largest Cook distance, does not yield a different value of the slope (t = -0.80; df = 86, NS). Taking into account errors in estimates of the time of introduction on both axes and using major axis regression results in the equation: CR = 716 + 0.63 EU, with 95% CI for regression slope of the major axis 0.49 – 0.79.

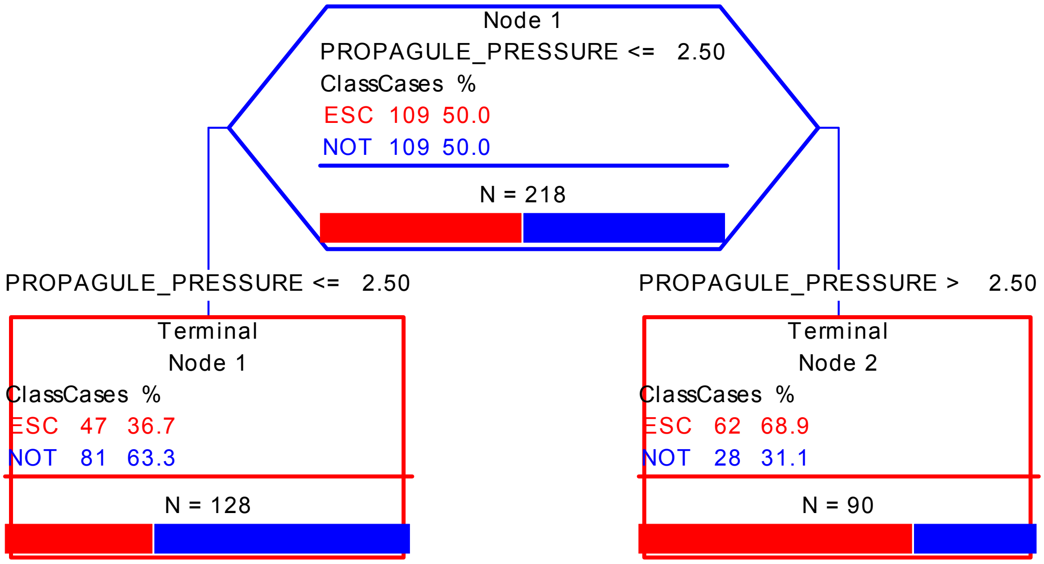

Fig. 2. Classification tree analysis of the probability of escape from cultivation of alien woody plants grown in the Czech Republic, based on the comparison of 109 escaping and not-escaping congeneric pairs (see text for details). Each node (polygonal table) and terminal node (rectangular table) shows node number, splitting variable name, split criterion and number of cases of escaped (ESC) and not-escaped (NOT) species. The misclassification rate of the model is 34.4%, compared to 50% for the null model (guessing the probability of ESC and NOT being equal, i.e. 50%).

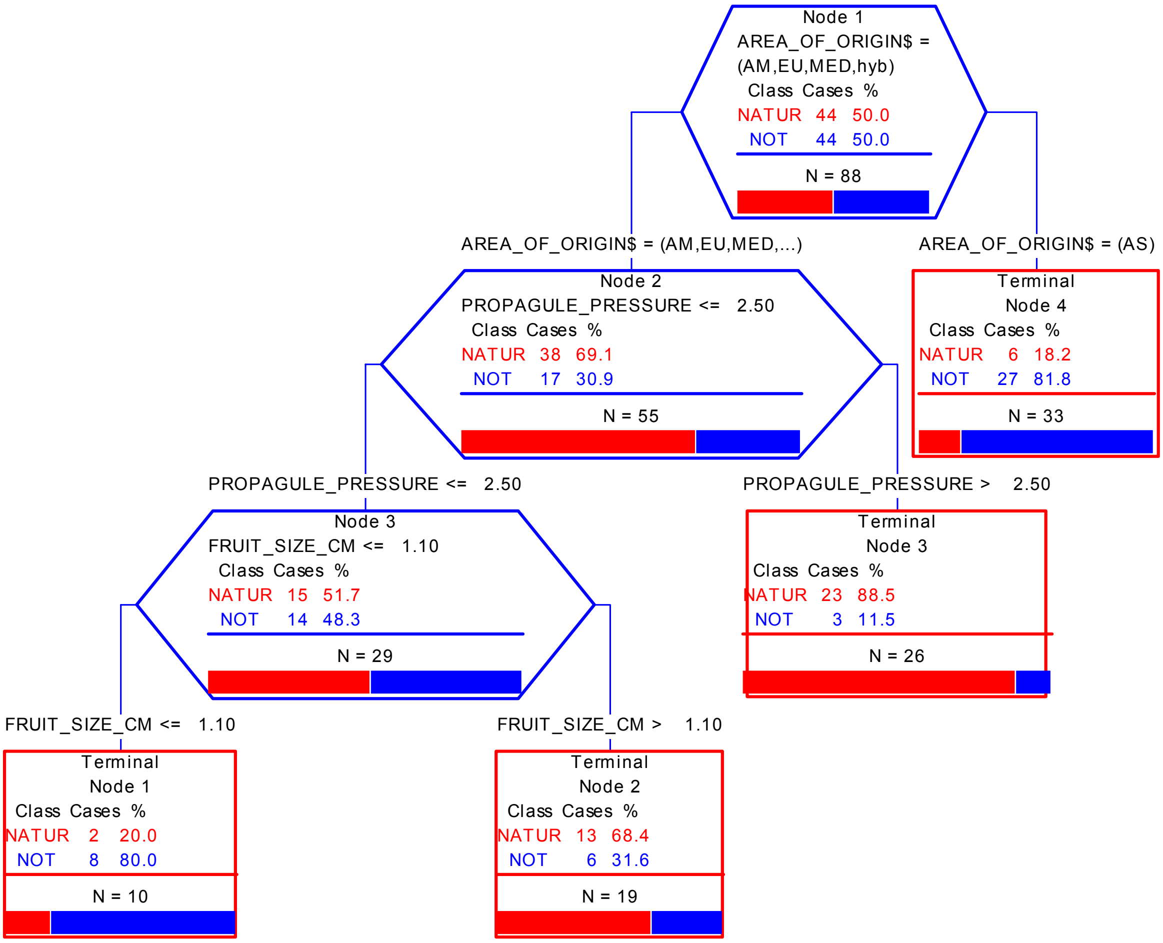

Fig 3. Classification tree analysis of the probability that an alien woody plant species cultivated in the Czech Republic becomes naturalized, based on the comparison of 44 naturalized and not-naturalized congeneric pairs (see text for details). Each node (polygonal table) and terminal node (rectangular table) shows node number, splitting variable name, split criterion and number of cases of naturalized (NAT) and not-naturalized (NOT) species. The misclassification rate of the model is 19.3%, compared to 50% for the null model (guessing the probability of ESC and NOT being equal, i.e. 50%).

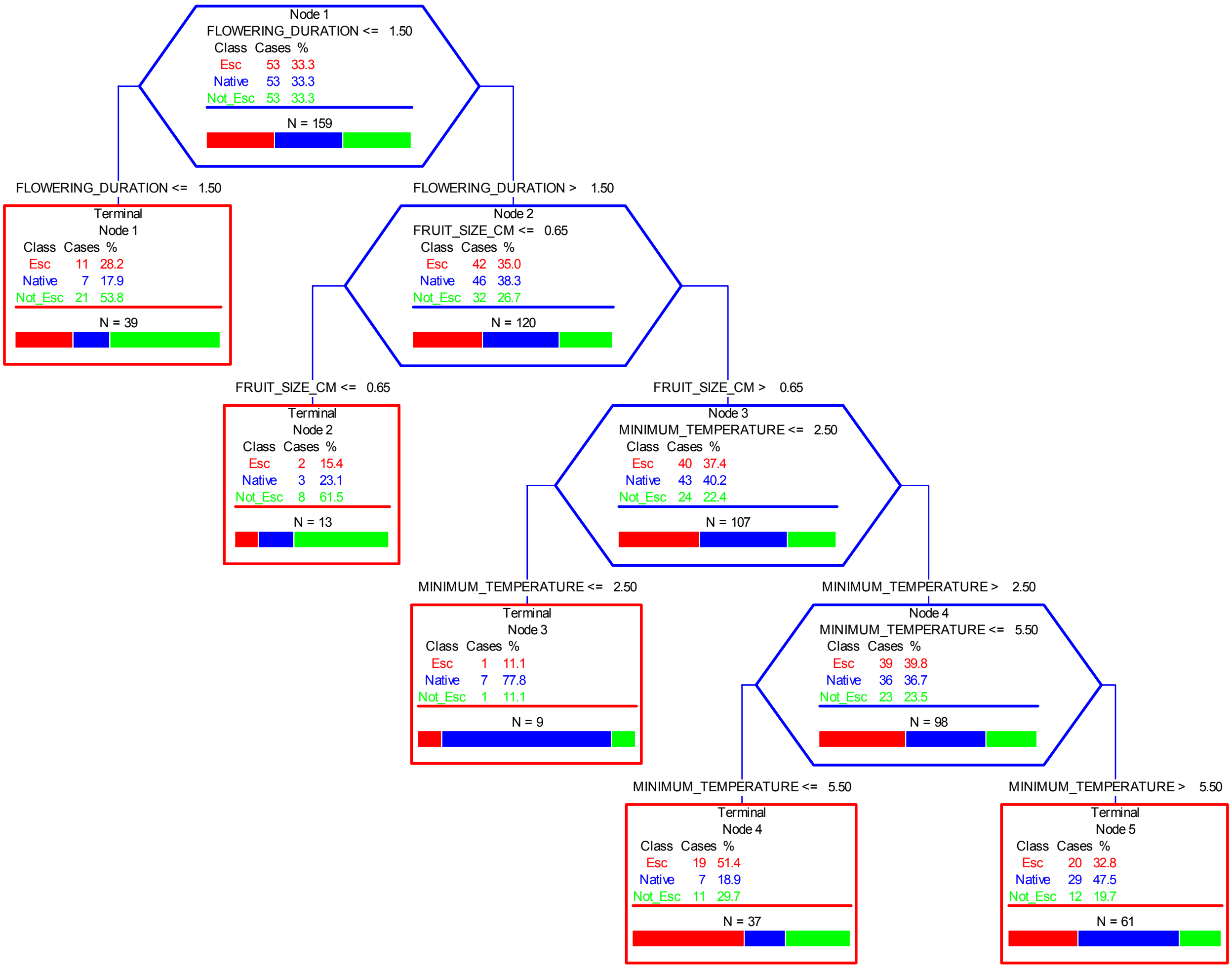

Fig. 4. Classification tree analysis comparing the traits of native woody species in the Czech Republic with those cultivated woody aliens that escaped (ESC) and did not escape (NOT ESC) from cultivation, based on 53 congeneric triads. Each node (polygonal table) and terminal node (rectangular table) shows node number, splitting variable name, split criterion and number of cases of the three groups. The misclassification rate of the model is 47.2%, compared to 66.7% for the null model (guessing with the initial class assignment ESC).

Appendix 1

List of tested species: 109 pairs of escaped/not-escaped species; 44 pairs of naturalized/not-naturalized species and 53 triads of escaped/not-escaped/native species. Family codes: Ace-Aceraceae; Ana-Anacardiaceae; Ber-Berberidaceae; Bet-Betulaceae; Big-Bignoniaceae; Bud-Buddlejaceae; Cap-Caprifoliaceae; Cel-Celastraceae; Cor-Corylaceae; Crn-Cornaceae; Cup-Cupressaceae; Ele-Cupressaceae; Fab-Fabaceae; Fag-Fagaceae; Gro-Grossulariaceae; Hip-Hippocastanaceae; Jug-Juglandaceae; Ole-Oleaceae; Phi-Philadelphaceae; Pin-Pinaceae; Pla-Platanaceae; Pol-Polygonaceae; Ran-Ranunculaceae; Ros-Rosaceae; Sal-Salicaceae; Scr-Scrophulariaceae; Sol-Solanaceae; Til-Tiliaceae; Ulm-Ulmaceae; Vit-Vitaceae. Area of origin: AM-North America; As-Asia; EU-Europe; MED-Mediterranean; H-Hybrid. Naturalization status: Cas-Casual; Nat-Naturalized. In the CR – time of the first known introduction in the Czech Republic. Nomenclature follows Koblížek (2000).

Species	**Family**	**Origin**	**Naturalization**	**In the CR**	**Not escaped alien congener**	**Native congener**
Acer ginnala Maxim.	*Ace*	AS	CAS	1845	*Acer tataricum* L.	*Acer campestre* L.
Acer monspessulanum L.	*Ace*	EU	CAS	1835	*Acer palmatum* Thunb.	-
Acer negundo L.	*Ace*	AM	NAT	1785	*Acer nikoense* Maxim.	*Acer platanoides* L.
Acer saccharinum L.	*Ace*	AM	CAS	1811	*Acer rubrum* L.	*Acer pseudoplatanus* L.
Aesculus ×carnea Hayne	*Hip*	H	CAS	1835	*Aesculus pavia* L.	-
Aesculus hippocastanum L.	*Hip*	MED	CAS	1563	*Aesculus flava* Soland.	-
Ailanthus altissima (Mill.) Swingle	*Scr*	AS	NAT	1799	*Ailanthus vilmoriniana* Dode	-
Alnus rugosa (Duroi) Sprengel	*Bet*	AM	NAT	1852	*Alnus japonica* (Thunb.) Steud.	*Alnus glutinosa* (L.) Gaertn.
Amelanchier lamarckii Schroeder	*Ros*	AM	NAT	1785	*Amelanchier laevis* Wieg.	-
Amelanchier ovalis Med.	*Ros*	MED	CAS	1835	*Amelanchier florida* Lindl.	-
Amorpha fruticosa L.	*Fab*	AM	NAT	1811	*Amorpha glabra* Poir.	-
Buddleja davidii Franchet	*Bud*	AS	CAS	1911	*Buddleja alternifolia* Maxim.	-
Castanea sativa Mill.	*Fag*	MED	CAS	1562	*Castanea dentata* (Marsh.) Borkh.	-
Catalpa bignonioides Walter	*Big*	AM	CAS	1763	*Catalpa ovata* G. Don	-
Celastrus orbiculatus Thunb.	*Cel*	AS	CAS	1910	*Celastrus scandens* L.	-
Celtis occidentalis L.	*Ulm*	AM	CAS	1811	*Celtis australis* L.	-
Chaenomeles japonica (Thunb.) Spach	*Ros*	AS	CAS	1847	*Chaenomeles speciosa* (Sweet) Nakai	-
Chamaecyparis lawsoniana (A. Murray) Parl.	*Cup*	AM	CAS	1855	*Chamaecyparis pisifera* S. et Z.	-
Chamaecytisus elongatus (W.et K.) Link	*Cup*	EU	CAS	1852	*Coronilla emerus* L.	*Chamaecytisus supinus* (L.) Link
Clematis flammula L.	*Ran*	MED	CAS		*Clematis montana* Buch.-Ham.ex DC.	-
Clematis tangutica (Maxim.) Korshinsky	*Ran*	AS	CAS		*Clematis orientalis* L.	*Clematis vitalba* L.
Clematis viticella L.	*Ran*	MED	CAS	1852	*Clematis alpina* (L.) Mill.	-
Colutea arborescens L.	*Fab*	EU	NAT	1835	*Colutea orientalis* Mill.	-
Corylus colurna L.	*Cor*	MED	CAS	1847	*Corylus chinensis* Franch	-

Corylus maxima Mill.	*Cor*	MED	CAS	1927	*Corylus americana* Marsh.	*Corylus avellana* L.
Cotinus coggygria Scop.	*Ana*	MED	CAS	1785	*Cotinus obovatus* Raf.	-
Cotoneaster bullatus Boiss.	*Ros*	AS	CAS	1910	*Cotoneaster dielsianus* Pritz	*Cotoneaster integerrimus* Med.
Cotoneaster horizontalis Decne	*Ros*	AS	CAS	1910	*Cotoneaster praecox* Vilm.	-
Cotoneaster lucidus Schlecht.	*Ros*	AS	CAS		*Cotoneaster divaricatus* Rehd. et Wils	*Cotoneaster melanocarpus* Fisch. ex Blytt
Crataegus crus-galli L.	*Ros*	AM	CAS	1811	*Crataegus pinnatifida* Bunge	*Crataegus monogyna* Jacq.
Crataegus flabellata (Bosc ex Spach) K.Koch	*Ros*	AM	CAS		*Crataegus orientalis* Palla ex Bieb.	*Crataegus ×media* Bechst.
Crataegus mollis Torrey et A. Gray	*Ros*	AM	CAS	1925	*Crataegus pentagyna* W. et K. ex Willd	*Crataegus laevigata* (Poiret) DC.
Crataegus pedicellata Sarg	*Ros*	AM	CAS	1785	*Crataegus intricata* Lange	*Crataegus praemonticola* Holub
Crataegus persimilis Sarg.	*Ros*	AM	CAS		*Crataegus azarolus* L.	*Crataegus ×macrocarpa* Hegetschw.
Dasiphora fruticosa (L.) Rydb.	*Ros*	EU, AS	CAS	1785	*Dasiphora parviflora* (Lehm.) Juz.	-
Deutzia scabra Thunb.	*Phi*	AS	CAS	1847	*Deutzia gracilis* S. et Z.	-
Diervilla lonicera Mill.	*Cap*	AM	CAS	1785	*Diervilla sessilifolia* Buckl.	-
Eleagnus angustifolia L.	*Ele*	MED	CAS	1562	*Eleagnus commutata* Bernh. ex Rydb.	-
Fallopia aubertii (L. Henry) Holub	*Pol*	AS	NAT	1910	*Fallopia baldschuanica* (Regel) Holub	-
Forsythia suspensa (Thunb.) Vahl	*Ole*	AS	CAS	1860	*Forsythia viridissima* Lindl.	-
Fraxinus ornus L.	*Ole*	MED	NAT	1785	*Fraxinus nigra* Marsh.	*Fraxinus angustifolia* Vahl.
Fraxinus pennsylvanica Marshall	*Ole*	AM	NAT	1811	*Fraxinus americana* L.	*Fraxinus excelsior* L.
Hippophaë rhamnoides L.	*Ele*	EU, AS	CAS	1785	*Hippophaë salicifolia* D. Don.	-
Juglans nigra L.	*Jug*	AM	CAS	1750	*Juglans cinerea* L.	-
Laburnum anagyroides Med.	*Fab*	EU	NAT	1785	*Laburnum alpinum* (Mill.) J.Presl	-
Laurocerasus officinalis Roem.	*Ros*	MED	CAS	1811	*Laurocerasus lusitanica* (L.) Roem	-
Lonicera caprifolium L.	*Cap*	MED	NAT	1852	*Lonicera periclymenum* L.	*Lonicera xylosteum* L.
Lonicera tatarica L.	*Cap*	AS	CAS	1785	*Lonicera maackii* (Rupr.) Maxim.	*Lonicera nigra* L.
Lycium halimifolium Mill.	*Sol*	MED	NAT	1785	*Lycium ruthenicum* Murray	-
Lycium chinense Mill.	*Sol*	AS	CAS	1841	*Lycium pallidum* Miers.	-
Mahonia aquifolium (Pursh) Nutt.	*Ber*	AM	NAT	1844	*Mahonia bealei* (Fort.) Carr.	-
Padus serotina (Ehrh.) Borkh.	*Ros*	AM	NAT	1811	*Padus maackii* (Rupr.) Kom.	*Padus avium* Mill.
Padus virginiana (L.) Mill.	*Ros*	AM	CAS	1811	*Padus cornuta* (Royle) Carr.	*Padus petraea* Tausch
Parthenocissus inserta (Kerner) Fritsch	*Vit*	AM	NAT	1663	*Parthenocissus tricuspidata* (S et Z.) Planch.	-
Parthenocissus quinquefolia (L.) Planchon	*Vit*	AM	NAT	1835	*Parthenocissus himalayana* (Royle) Planchon	-
Paulownia tomentosa (Thunb.) Steudel	*Scr*	AS	CAS	1844	*Paulownia fortunei* (Seem) Hemsl.	-
Philadelphus coronarius L.	*Phi*	MED	CAS	1562	*Philadelphus floridus* Beadle	-
Physocarpus opulifolius (L.) Maxim.	*Ros*	AM	NAT	1785	*Physocarpus amurensis* (Maxim.) Maxim.	-
Pinus nigra Arnold	*Pin*	MED	NAT	1796	*Pinus banksiana* Lamb.	*Pinus rotundata* Link.

Pinus strobus L.	*Pin*	AM	NAT	1775	*Pinus flexilis* James	*Pinus sylvestris* L.
Platanus ×hispanica Mill.	*Pla*	H	CAS	1750	*Platanus occidentalis* L.	-
Platycladus orientalis (L.) Franco	*Ele*	AS	CAS	1785	*Thuja occidentalis* L.	-
Populus ×canadensis Moench	*Sal*	H	NAT	1798	*Populus simonii* Carr.	*Populus ×canescens* (Aiton) J. E. Smith
Populus balsamifera L.	*Sal*	AM	CAS	1811	*Populus lasiocarpa* Oliv.	*Populus nigra* L.
Prunus cerasifera Ehrh.	*Ros*	MED	NAT	1860	*Cerasus serrulata* (Lindl.) G. Don	*Prunus spinosa* L.
Pseudotsuga menziesii (Mirbel) Franco	*Pin*	AM	NAT	1830	*Pseudotsuga japonica* (Shiras.) Beissn	-
Quercus rubra L.	*Fag*	AM	NAT	1799	*Quercus palustris* Muenchh.	*Quercus robur* L.
Rhus typhina L.	*Ana*	AM	NAT	1811	*Rhus glabra* L.	-
Ribes aureum Pursh	*Gro*	AM	CAS	1844	*Ribes americanum* Mill.	*Ribes alpinum* L.
Ribes odoratum Wendl. fil.	*Gro*	AM	NAT	1852	*Ribes sanguineum* Pursh.	*Ribes petraeum* Wulf.
Ribes rubrum L.	*Gro*	EU	NAT	1852	*Ribes diacanthum* Pall.	*Ribes nigrum* L.
Ribes spicatum Robson	*Gro*	EU, AS	CAS		*Ribes multiflorum* Kit. ex Roem et Schult.	*Ribes uva-crispa* (L.) Mill
Robinia pseudoacacia L.	*Fab*	AM	NAT	1710	*Robinia viscosa* Vent.	-
Rosa ×alba L.	*Ros*	H	CAS	1852	*Rosa moschata* J. Herrmann	*Rosa dumalis* Bechst.
Rosa foetida J. Herrmann	*Ros*	AS	CAS	1663	*Rosa sericea* Lindl.	*Rosa tomentosa* Sm.
Rosa glauca Pourr.	*Ros*	EU	CAS	1822	*Rosa multiflora* Thunb.	*Rosa inodora* Fries.
Rosa rugosa Thunb.	*Ros*	AS	NAT	1841	*Rosa hugonis* Hemsl.	*Rosa canina* L.
Rubus allegheniensis Porter	*Ros*	AM	NAT	1777	*Rubus thibetanus* Franch.	*Rubus sulcatus* Vest
Rubus armeniacus Focke	*Ros*	AS	NAT	1850	*Rubus loganobaccus* Bailey	*Rubus praecox* Bertol
Rubus canadensis L.	*Ros*	AM	NAT		*Rubus cockburnianus* Hemsl.	*Rubus nessensis* W. Hall
Rubus laciniatus Willd.	*Ros*	EU, AM, AS	NAT	1808	*Rubus crataegifolius* Bunge	*Rubus nemoralis* Ph. J. Mueller
Rubus moschus Juz.	*Ros*	AS	NAT		*Rubus adenophorus* Rolfe	*Rubus pedemontanus* Pikwart
Rubus occidentalis L.	*Ros*	AM	CAS		*Rubus leucodermis* Torr. et A. Gray.	*Rubus idaeus* L.
Rubus odoratus L.	*Ros*	AM	NAT	1785	*Rubus deliciosus* Torr.	*Rubus constrictus* Ph. J. Mueller et Lefévre
Rubus parviflorus Nutt.	*Ros*	AM	NAT	1923	*Rubus flosculosus* Focke	*Rubus angustipaniculatus* Holub
Rubus phoenicolasius Maxim.	*Ros*	AS	CAS	1883	*Rubus spectabilis* Pursh.	*Rubus koehleri* Weihe
Rubus sylvaticus Weihe et Nees	*Ros*	EU	NAT		*Rubus illecebrosus* Focke	*Rubus macrophyllus* Weihe et Ness
Rubus tuberculatus Bab.	*Ros*	EU	NAT		*Rubus setchuenensis* Burreau et Franchet	*Rubus dollnensis* Spribille
Rubus ulmifolius Schott	*Ros*	EU	CAS		*Rubus lasiostylus* Focke	*Rubus elatior* Gremli
Salix ×sepulcralis Simk.	*Sal*	H	CAS	1927	*Salix ×blanda* Anderss.	*Salix alba* L.
Salix acutifolia Willd.	*Sal*	EU, AS	NAT	1863	*Salix irrorata* Anderss.	*Salix caprea* L.
Sarothamnus scoparius (L.) Koch	*Fab*	EU	NAT		*Caragana frutex* (L.) K. Koch	-
Sorbaria sorbifolia (L.) A. Braun	*Ros*	AS	NAT	1811	*Sorbaria aitchisonii* (Hemsl.) Rehd.	-
Sorbus domestica L.	*Ros*	MED	CAS	1562	*Sorbus intermedia* (Ehrh.) Pers.	*Sorbus aucuparia* L.

Spiraea ×billardii Dippel	*Ros*	H	CAS	1910	*Spiraea ×fontenaysii* Lebas.	-
Spiraea ×macrothyrsa Dippel	*Ros*	H	CAS	1923	*Spiraea ×brachybotrys* Lange	-
Spiraea alba Duroi	*Ros*	AM	CAS	1850	*Spiraea latifolia* (Ait.) Borkh.	*Spiraea salicifolia* L.
Spiraea crenata L.	*Ros*	MED	NAT	1844	*Spiraea nipponica* Maxim.	-
Spiraea douglasii Hooker	*Ros*	AM	CAS	1846	*Spiraea tomentosa* L.	-
Spiraea chamaedryfolia L.	*Ros*	EU, AS	CAS	1924	*Spiraea henryi* Hemsl.	-
Swida sericea (L. emend. Muray) Holub	*Crn*	AM	NAT	1835	*Swida alba* (L.) Opiz	*Swida sanguinea* (L.) Opiz
Symphoricarpos albus (L.) Blake	*Cap*	AM	NAT	1860	*Symphoricarpos occidentalis* Hook.	-
Symphoricarpos orbiculatus Moench	*Cap*	AM	CAS	1785	*Symphoricarpos ×chenaultii* Rehd.	-
Syringa vulgaris L.	*Ole*	MED	NAT	1650	*Syringa josikaea* Jacq. fil. ex Reichenb.	-
Tilia tomentosa Moench	*Til*	MED	CAS	1810	*Tilia americana* L.	*Tilia cordata* Mill.
Toxicodendron quercifolium (Michx.) Greene	*Ana*	AM	CAS	1852	*Toxicodendron verniciflua* (Stokes) Barkl.	-
Ulex europaeus L.	*Fab*	EU	CAS	1785	*Ulex minor* Roth.	-
Vitis riparia Michx.	*Vit*	AM	CAS	1844	*Vitis coignetiae* Pulliat ex Planch.	*Vitis vinifera* L. ssp. *sylvestris* (C. C. Gmelin) Hegi
Zelkova serrata (Thunb.) Mak.	*Ulm*	AS	CAS	1927	*Zelkova carpinifolia* (Pall.) K. Koch	-

Appendix 2

List of tested variables. The introduction variables were only applicable to models I. and II. (see text for details). Available for means the number of alien species the data are available for (in total 218 species).

Variable	Comments	Available for
Introduction variables		
Time of introduction in EU	Year of first known introduction into Europe. For European species means year of introduction out of the natural range. Introduction range from 1536 to 1910.	138
Time of introduction in the Czech Republic	Year of first known introduction into the Czech Republic. Range from 1562 to 1933.	158
Propagule pressure	Number of historical garden catalogues (1852-1940; 14 catalogues), actual garden catalogues (2000; 93 catalogues) and botanical gardens and arboreta (1992-2004; 14 centres) distributed the species. In total 121 catalogues. Species included in 0-12 historical (53 species not included), 0-19 (136 not) actual garden catalogues and in 0-9 (82 not) botanical gardens.	218
Type of use	Actual and/or recommended use of species in horticulture (ornamental; 212 species), landscaping (155) and/or forestry (16).	218
Area of origin	Origin of the species. Tested species come from: North America (AM; 77 species), Asia (AS; 77), Europe (EU; 18), Mediterranean (MED; 28) or are hybrids (H; 12). 1 species comes from EU+AM+AS and 5 from EU+AS. The Mediterranean Basin includes Europe, West Asia and North Africa.	218
Trait variables		
Life form	Life form of the species in Central Europe: shrub (136 species), tree (69) or vine (13).	218
Leaf persistence	Persistence of leaves in temperate climate: deciduous (208 species) / conifers (10).	218
Height	Mean height of species in conditions of Central Europe (in metres: from 0.5 to 50 m).	218
Juvenile period	Age at first flowering (years) - from 10 to 40 years.	46
Beginning of the flowering period	Month of beginning of flowering period (1-12).	218
Duration of the flowering period	Length of flowering period (number of months). Duration from 1 to 6 months; nearly 59% of species flowering for 2 months.	218
Breeding system	Type of spatial separation of generative organs: hermaphrodite (164 species), monoecy (33), dioecy (21).	218
Fruit type	Type of fruits of the species: dry (118 species) / fleshy fruits (100).	218
Seed weight	Mean weigh of one seed (mg): from 0.2 mg to 11 g.	133
Fruit size	Mean size (length) of fruits (cm): from 0,2 to 30 cm.	200
Beginning of the fruit maturity	Month of beginning of fruit maturity (1-12), most of the fruits mature in September.	218
Duration of the fruit maturity	Length of period of maturation of the fruits (number of months). Mostly 1 or 2 months.	218
Germination (%)	Mean germination of seeds (%): from 2 to 100%.	75
Type of reproduction	Reproduction only generative (from seeds; 216 species) or also vegetative (runners, layers, cuttings; 91 species).	218
Nitrogen fixation	Species can fix air nitrogen - only 17 species can.	218
Minimum mean annual temperature	Minimal mean annual temperature necessary for good growth (°C): from 0 to 9°C.	204
Minimum mean annual precipitation	Minimal mean annual precipitation necessary for good growth (mm): for most species 400 mm.	204

Chapter 4 ~ Risk assessment

Křivánek, M., Pyšek, P. 2006: Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe). Diversity & Distributions 12: 319-327.

Diversity and Distributions, (Diversity Distrib.) (2006) **12**, 319–327

BIODIVERSITY RESEARCH

Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe)

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ABSTRACT

To assess the validity of previously developed risk assessment schemes in the conditions of Central Europe, we tested (1) Australian weed risk assessment scheme (WRA; Pheloung *et al.* 1999); (2) WRA with additional analysis by Daehler *et al.* (2004); and (3) decision tree scheme of Reichard and Hamilton (1997) developed in North America, on a data set of 180 alien woody species commonly planted in the Czech Republic. This list included 17 invasive species, 9 naturalized but non-invasive, 31 casual aliens, and 123 species not reported to escape from cultivation. The WRA model with additional analysis provided best results, rejecting 100% of invasive species, accepting 83.8% of non-invasive, and recommending further 13.0% for additional analysis. Overall accuracy of the WRA model with additional analysis was 85.5%, higher than that of the basic WRA scheme (67.9%) and the Reichard–Hamilton model (61.6%). Only the Reichard–Hamilton scheme accepted some invaders. The probability that an accepted species will become an invader was zero for both WRA models and 3.2% for the Reichard–Hamilton model. The probability that a rejected species would have been an invader was 77.3% for both WRA models and 24.0% for the Reichard–Hamilton model. It is concluded that the WRA model, especially with additional analysis, appears to be a promising template for building a widely applicable system for screening out invasive plant introductions.

Keywords

Alien plants, biological invasions, Central Europe, forestry, invasive species, prediction, weed risk assessment.

INTRODUCTION

The search for characteristics of invasive species (Crawley *et al.*, 1996; Rejmánek, 1996) is a central issue in invasion biology, as it determines our ability to predict the invasion success of alien plants in new regions (Richardson & Pyšek, 2006). Over the last 30 years, attempts to identify traits of successful invasive species shifted from studies focused on all vascular plants (Baker, 1974; Pyšek *et al.*, 1995; Crawley *et al.*, 1996) to those dealing with restricted taxonomic and/or life-form groups (Rejmánek & Richardson, 1996; Grotkopp *et al.*, 2002; Richardson & Rejmánek, 2004; Rejmánek *et al.*, 2005b), often in geographically and ecologically specified areas (Kowarik, 1995; Tucker & Richardson, 1995). Predicting which species will invade has been a long-standing goal of ecologists (Kolar & Lodge, 2001); this knowledge is translated into risk assessment schemes that attempt to predict the behaviour of alien species in secondary areas (Daehler & Carino, 2000). Only a small proportion of introduced alien species becomes naturalized and invasive (di Castri, 1989; Williamson, 1996). It has been proposed that about one of 10 introduced species becomes casual, one of 10 casuals naturalized, and one of 10 naturalized aliens becomes a pest (Tens Rule: Williamson & Fitter, 1996; Williamson, 1996). In the same vein, about 1% of introduced plants are estimated to invade natural vegetation (Kowarik, 1995). The risk assessment schemes attempt to identify this small fraction of species that can be potentially harmful to natural vegetation and invade large areas.

Two groups of risk assessment models can be recognized, based on the methods used and the phase of the invasion process they target. (1) Pre-introduction models predict the potential behaviour of a species prior to its introduction (Scott & Panetta, 1993; Pheloung, 1995; Tucker & Richardson, 1995; Rejmánek & Richardson, 1996; Reichard & Hamilton, 1997; Pheloung *et al.*, 1999; Daehler & Carino, 2000; Reichard, 2001; Daehler *et al.*, 2004; Weber & Gut, 2004). Such approaches often use statistical discrimination analysis and classification and regression trees

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(CARTs). These schemes are often based on rating systems (e.g. Pheloung, 1995) or on hierarchical decision trees (e.g. Reichard & Hamilton, 1997); the only screening procedure based on biological plant attributes and some ecological interactions of woody plants is in Rejmánek & Richardson (1996; see also Richardson & Rejmánek, 2004). (2) Post-introduction models focus on predicting the future behaviour of species that have already become naturalized or invasive in the new area. Such schemes typically rely on geographical information systems (Higgins *et al.*, 1999; Sax, 2001; Windrlechner, 2001; Windrlechner & Iles, 2002; Rouget & Richardson, 2003; Dark, 2004; Marais *et al.*, 2004; Rouget *et al.*, 2004; Windrlechner *et al.*, 2004). In addition, empirical schemes based on investigators' experience have been used (Hejný *et al.*, 1973), but the predictive power of such attempts was rather limited compared to sophisticated statistical and geographical approaches (Pyšek, 2001).

Rapid development of computing facilities and increasing availability of databases allowed for increasing generality of recently developed screening models (Daehler & Carino, 2000). The Weed Risk Assessment (WRA) scheme developed for Australia and New Zealand (Pheloung, 1995; Pheloung *et al.*, 1999) and successfully tested in Hawaii and other Pacific islands (Daehler & Carino, 2000; Daehler *et al.*, 2004) is a promising tool for assessing the risks from plant invasions. This study explores predictive potential of WRA in a biogeographical zone that has not been subject to testing so far and compares it with other schemes. We used alien woody species commonly planted in the Czech Republic, Central Europe, a country prone to invasions by alien species (Pyšek *et al.*, 2002; Mandák *et al.*, 2004; Chytrý *et al.*, 2005). Invasions by woody species often alter the functioning of invaded ecosystems (Williamson, 1999; Richardson *et al.*, 2000). On the other hand, there is a strong requirement for finding non-harmful woody species for commercial use (Richardson, 1998; Richardson *et al.*, 2004a). These two contradicting aspects make the need for reliable weed risk assessment schemes for woody plants particularly urgent. Moreover, woody plants are a frequently used test group (Rejmánek & Richardson, 1996; Reichard & Hamilton, 1997; Reichard, 2001; Windrlechner, 2001; Windrlechner & Iles, 2002; Windrlechner *et al.*, 2004; Rejmánek *et al.*, 2005a) because of detailed records of introduction history and plentiful data on biology, ecology, and adaptation to climate of target areas (Richardson *et al.*, 2004b). This study aims at exploring the extent to which risk assessment schemes developed in other parts of the world and for different ecological and climatic conditions are useful under the temperate conditions of Central Europe.

METHODS

Risk assessment schemes tested

Three models were chosen for testing: (1) weed risk assessment scheme (WRA) (Pheloung, 1995; Pheloung *et al.*, 1999); (2) WRA with additional decision tree analysis of species recommended for further evaluation (Daehler *et al.*, 2004; fact sheets available at http://www.botany.hawaii.edu/faculty/daehler/WRA); and (3) Reichard and Hamilton's decision tree (Reichard & Hamilton, 1997; Reichard, 2001). The former two models were selected because they have already been tested in a number of regions around the world (Pheloung *et al.*, 1999; Daehler & Carino, 2000; Daehler *et al.*, 2004). Proving them successful under temperate conditions of Central Europe would be a further step to their wider applicability. Reichard and Hamilton's scheme was used because it was primarily designed for woody species in the temperate zone (i.e. for conditions applicable to our study region).

(1) The WRA model (Pheloung *et al.*, 1999) was developed for Australian and New Zealand alien plants. It consists of 49 questions divided into sections on biogeography, biology/ecology, and traits potentially contributing to the invasiveness. Answers are scored from −3 to +5 and the species is accepted for introduction (score < 1), rejected (> 6), or recommended for further analysis (1–6). A minimum of 10 answers are needed for a species to be evaluated: at least two in the biogeography section, two in traits section and six in biology/ecology. However, for proper evaluation it is recommended that at least one-third of questions are answered.

(2) WRA with additional decision tree analysis (further referred to as 'WRA+Daehler') resulted from testing the WRA in Hawaii (Daehler & Carino, 2000) and other Pacific islands (Daehler *et al.*, 2004). Species qualified by the WRA for further analysis are subjected to an additional questionnaire, built as a binary decision tree and resulting in the same classification as the WRA scheme, i.e. accept, reject or recommended for further analysis.

(3) Reichard and Hamilton's decision tree was built for woody species in North America (Reichard & Hamilton, 1997) and Hawaii (Reichard, 2001). It consists of seven questions in a binary (yes/no) tree. Similarly to the WRA analysis, a species is recommended for acceptation, rejection, or further analysis and monitoring.

In our study, questions related to geography and climate were modified to reflect the conditions of the target area. In WRA, suitability of species to Australian climate was changed to suitability to Central European climate (question 2.01) and origin or naturalization in regions with extended dry periods was changed to origin or naturalization in regions with temperate climate (question 2.04). In the Czech Republic, the mean annual temperature is 7.3 °C (min. 0.4 °C, max. 10.1 °C), and the mean annual precipitation is 672.6 mm (min. 384.6, max. 1497.8) (Czech Hydrometeorological Institute, http://www.chmu.cz). The presence of effective natural enemies in Australia was changed to the presence of effective natural enemies in the Central Europe (question 8.05). In the Reichard–Hamilton scheme, North America was changed to Central Europe in questions related to invasiveness of the species outside the target region and to its membership in a genus or family with another strongly invasive representative. The question about origin in parts of North America other than the region of the proposed introduction was changed to origin of the species in other parts of Europe.

Following present trends in taxonomy and nomenclature, a taxonomic concept of broader genera was adopted, i.e. *Prunus* s.l. (including *Cerasus, Padus,* and *Laurocerasus*), *Acer* (*Acer*, *Negundo*), and *Cornus* (*Cornus*, *Swida*). This approach allows for better reflection of evolutionary relationships than concept of narrow genera, when evaluating invasiveness of closely related taxa. Status of hybrids followed the approach of Pyšek *et al.* (2004), i.e. they were considered native to Europe only if both parent species originated from this continent.

Species tested

The data set comprised 180 alien woody species frequently planted and acclimatized in the Czech Republic: all 28 species that are at present widely planted for timber in forests (Křivánek *et al.*, 2006), and 152 species commonly planted in parks and gardens. The latter group was selected from the total of 1691 park and garden woody species on the basis of their residence time, frequency of planting, and horticultural importance. Only species planted in the Czech Republic for at least 60 years and well adapted to the conditions of target region were considered (a similar time criterion as applied by Reichard & Hamilton, 1997). Species only planted in specialized collections, not offered in garden catalogues, or planted in parks in the Czech Republic were excluded. The selection was based on summarizing literature sources (Koblížek, 2000), on 121 garden catalogues, covering the period since year 1852 up to present, and on the occurrence of woody species in 823 chateau parks in the countryside (Hieke, 1984, 1985) and in 13 large parks of Prague (B. Gregorová *et al.*, unpublished). An effort was made to include species with comparable intensity of planting in the country, implying comparable propagule pressure. Under such assumption, the potential invasiveness of species does not depend on the frequency of planting but on their geographical and ecological traits.

Concerning the invasion status, 17 species on the list were invasive, 9 naturalized but non-invasive, 31 casual aliens, and 123 were never reported to escape from cultivation (see Appendix S1 in Supplementary Material; status taken from Pyšek *et al.*, 2002). Classification of the invasion status follows Richardson *et al.* (2000) and Pyšek *et al.* (2004). Casual species do not form self-replacing populations outside cultivation and rely on repeated introductions for their persistence. Naturalized species reproduce consistently and sustain populations over many life cycles without direct intervention by humans. Invasive species are a subset of naturalized, that have the potential to spread over a considerable area. Environmental weeds (pests) are alien species that invade natural vegetation, usually adversely affecting native biodiversity and/or ecosystem functioning (Pyšek *et al.*, 2004).

Taxonomic nomenclature follows Koblížek (2000).

Accuracy and reliability of tested schemes

For each scheme, accuracy and reliability for Central Europe were calculated following Smith *et al.* (1999). Accuracy indicates the probability of correct classification, i.e. the proportion of known invasive species that would be correctly assessed as invasive [$A_i = (I_r/I_t) \times 100$; where I_r is the number of invaders that were rejected by the system, and I_t was the total number of invaders assessed], and that of known non-invasive species that would be correctly identified as non-invasive [$A_n = (N_a/N_t) \times 100$; where N_a was the number of non-invader species accepted and N_t the total number of non-invaders assessed]. Overall accuracy [$A_o = (N_a + I_r)/(N_t + I_t)$], including both components, was used to compare the suitability of the schemes tested.

To set up the bottom level for the acceptance of each scheme for Central Europe, we followed overall accuracy A_o in the prime region of its development as calculated by Smith *et al.* (1999). These values were 76% for Reichard–Hamilton and 85% for the WRA scheme based on the figures from Australia and New Zealand; the latter was taken as the acceptable level of overall accuracy for our data.

Reliability takes into account that any sample of species rejected by a screening system will include a proportion of non-invasive species wrongly classified as invaders. It has two components: the probability that an accepted species will become invader, $P_{ai} = I_a/(N_a + I_a)$, and the probability that a rejected species would have been an invader, $P_{ri} = I_r/(N_r + I_r)$. When assessing the reliability of prediction schemes, the base-rate effect must be taken into account. This effect refers to the fact that it is much harder to predict rare events. The overall base-rate probability for a species to become invasive is a product of three probabilities, i.e. the rate at which it escapes from cultivation and becomes casual, the rate of naturalization, and the rate of the naturalized species becoming a pest (Smith *et al.*, 1999). The base-rate for alien woody plants in the Czech Republic was calculated following Smith *et al.* (1999) with the only difference of using the category invasive instead of pest for the latter probability. Nonetheless, as 11 of the 17 invasive species in the data set are environmental weeds with serious impact (Křivánek *et al.*, 2004), the figure obtained can be compared with those given in Smith *et al.* (1999).

RESULTS

The WRA+Daehler model provided the best results. The basic WRA model rejected all invasive species but also 3.5% (5 species) of non-invasive taxa. Sixty-four percent (91 species) of non-invaders were accepted and 32.5% (46) were suggested for further analysis. Using the WRA+Daehler model led to the final acceptance of 83.8% (119) of non-invaders; further evaluation was still needed for 13.0% (18) of species (Fig. 1, see Appendix S1 in Supplementary Material). On average, the data allowed to answer 37 questions of 49 posed by the scheme.

The Reichard and Hamilton's decision tree model was least successful. It rejected only 35.0% (6) of invasive species and 47.0% (8) were suggested for further evaluation. This model was the only one that accepted some invaders (3 species, 18.0%). One of the accepted species (*Quercus rubra*) is considered a pest in the Czech Republic (Křivánek *et al.*, 2004). The Reichard–Hamilton model accepted 65.0% (92) of non-invasive species and recommended 22.0% (31) for further evaluation. The number of non-invasive species rejected (19, i.e. 13.0%) was also highest of the three models tested (Table 1, Fig. 1).

Overall accuracy was highest for the WRA+Daehler model (85.5%); the additional analysis of species recommended for

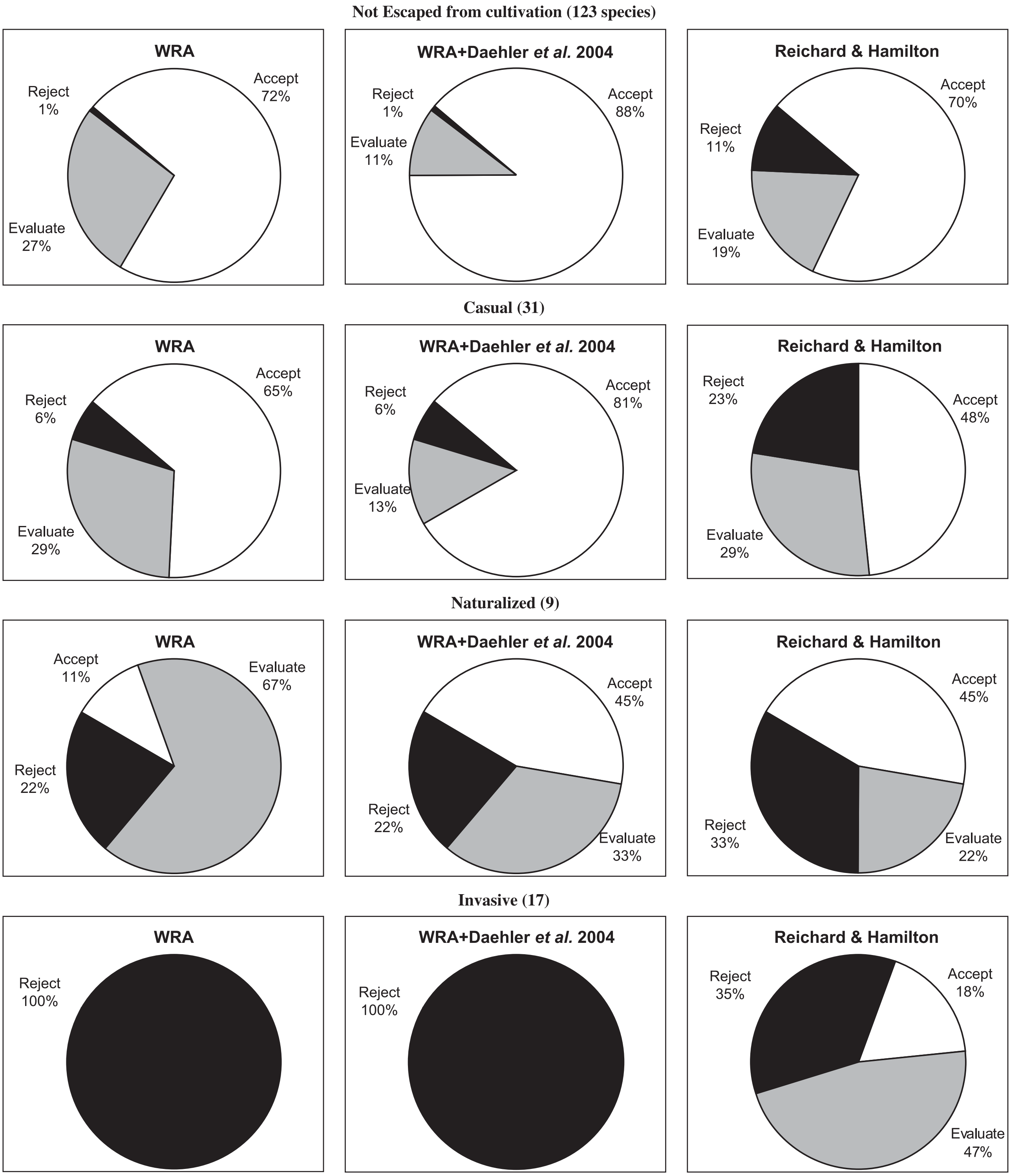

Figure 1 Results of three risk assessment schemes (see text for details) applied to 180 alien woody species commonly planted in the Czech Republic. Percentage of species rejected, accepted, or suggested for further evaluation is indicated for particular groups differing in invasion status. Definition of categories follows Richardson *et al.* (2000) and Pyšek *et al.* (2004).

further evaluation increased the accuracy of the basic WRA scheme by 17.6%. The accuracy of the basic WRA scheme (67.9%) was still higher than that of the Reichard–Hamilton model (61.6%) (Table 1).

Both WRA-based schemes rejected all invasive species, so the probability that an accepted species would become an invader was null. On the other hand, the probability that a rejected species would have been an invader was 77.3%. A low number of

Table 1 Accuracy and reliability of tested models evaluated according to Smith *et al*. (1999)

	Species number						Accuracy (%)			Reliability (%)	
Model	I_r	I_a	I_t	N_a	N_r	N_t	A_i	A_n	A_o	P_{ai}	P_{ri}
WRA	17	0	17	91	5	142	100.0	64.1	67.9	0.0	77.3
WRA+Daehler	17	0	17	119	5	142	100.0	83.8	85.5	0.0	77.3
Reichard & Hamilton	6	3	17	92	19	142	35.3	64.8	61.6	3.2	24.0

I, number of invasive species; *N,* number of non-invasive species; r, rejected; a, accepted; t, total; A_i, accuracy of correctly identifying invaders; A_n, accuracy of correctly identifying non-invaders; A_o, overall accuracy; P_{ai}, the probability that a species accepted will become an invader; P_{ri}, the probability that a rejected species would have been an invader. See text for details on particular screening models.

rejected invasive species in the Reichard–Hamilton's model yielded a 3.2% probability that an accepted species would invade but that only 24.0% of rejected species would invade (Table 1).

Of casual aliens, 6% (WRA and WRA+Daehler) and 23% (Reichard–Hamilton) were rejected. The number of casual species recommended for further evaluation was reduced from 29% (WRA) to 13% (WRA+Daehler), and 65% and 81% of casuals were accepted by WRA and WRA+Daehler, respectively. Reichard–Hamilton's model accepted 48% of casuals and 29% were recommended for further analysis. Both WRA schemes rejected 22% of naturalized species. Percentage of naturalized species recommended for acceptance by the WRA scheme (11%) increased to 45% in the WRA+Daehler model, as the number of species recommended for further evaluation decreased from 67% to 23%. Reichard–Hamilton's scheme rejected 33% of naturalized species, 45% were accepted, and 22% required further evaluation (Fig. 1).

DISCUSSION

For the reasons outlined above, our study focused on risk assessment schemes applicable to woody plants in Central Europe. Nevertheless, there are other screening systems and some of them yielded promising results: the model developed for South African fynbos vegetation (Tucker & Richardson, 1995), EPPO Pest Risk Assessment (http://www.eppo.org/QUARANTINE/quarantine.htm), or risk assessment of new environmental weeds in Central Europe (Weber & Gut, 2004). The fynbos model was designed for application to very specific conditions — fire-prone, nutrient-poor shrublands — that do not occur in Central Europe. The EPPO screening procedure was primarily developed for plant and insect pests of agricultural habitats and cannot be used to predict invasions to natural vegetation. The risk assessment scheme developed for environmental weeds in Switzerland was not used here because it is very similar to the WRA scheme and its overall accuracy, calculated for 47 plants invasive in temperate Europe and 193 aliens that have failed to naturalize in Switzerland, was as low as 65% (Weber & Gut, 2004). The present study therefore focused on testing the two models developed for Australian vegetation (Pheloung, 1995; Pheloung *et al*., 1999) and alien woody species in North America and Hawaii (Reichard & Hamilton, 1997; Reichard, 2001).

Reichard and Hamilton's decision tree is relatively easy to use. Only seven questions need to be answered, using the binary mode. In North America, 90% of 235 tested woody species were correctly assessed with this scheme, 97.1% of invasive species were rejected, and 70.8% of non-invasive were accepted; the overall accuracy was 76% (Reichard & Hamilton, 1997; Smith *et al*., 1999; but see Rejmánek *et al*., 2005a; pp. 110–111 for some problems with the categorization of species as 'non-invasive' in this scheme). The scheme is now being used in botanical gardens and horticultural practice in the USA (S. Reichard, pers. comm.). However, when applied to Central Europe, this scheme rejected only 35% of invasive species and accepted 65% of non-invasive. The overall accuracy was 14% lower than in the region for which it was developed. Primary reason for this failure could be that the model ignores climatic factors in native distribution area of tested species. Many species rejected as potentially invasive in our test of this model are not suited to the Central European climate because of severe winter seasons and frost. This, in combination with a strong emphasis on whether or not a species is invasive elsewhere, leads to misclassification of some non-invasive species as pests (see Appendix S1 in Supplementary Material). For example, *Buddleja davidii* is a serious invader in Australia, Mediterranean basin, and European regions with oceanic climate (Weber, 2003). In the Czech Republic, however, it was only reported as casual for the first time recently (Pyšek *et al*., 2002) because it is limited by frost. Other incorrectly classified harmful species are *Paulownia tomentosa* (invasive in North America; planted in the Czech Republic since 1844), *Gleditschia triacanthos* (South Africa and Australia, 1785), *Morus alba* (South Africa, 1835), and *Wisteria sinensis* (North America, 1913). All these species have been planted in the Czech Republic for a sufficiently long period to have become adapted to the local climate.

In our data set, the criterion of being invasive elsewhere appeared less important than suggested in the Reichard–Hamilton scheme; this criterion is also included in the WRA screening procedure. In our tested group, 38 species are reported as invasive elsewhere (Reichard, 1997; Bingelli *et al*., 1998; Haysom & Murphy, 2003; Weber, 2003). All seven species reported as invasive both elsewhere and in the Czech Republic were rejected by both WRA schemes, and six of them by the Reichard–Hamilton scheme, too. On the other hand, the Reichard–Hamilton scheme rejected also 13 of 17 species not escaped from cultivation in the

Czech Republic. WRA rejected 11 not escaped species and the WRA+Daehler provided best results, rejecting only one such species. The invasive-elsewhere criterion is generally considered very important for the assessment of potentially invasive species and sometimes it is even taken as the only permanent predictor of invasion (Williamson, 1999).

Taxonomic classification is another source of bias when transferring screening system of Reichard and Hamilton from one area to another. Stressing the invasiveness of other species within the genus/family and using it as an important decision attribute make the results rather sensitive to the differences in generic concept used in different areas. Although many invasive species belong to genera containing a single invasive species, membership to a large genus becomes a sort of 'the mark of Cain' for all its representatives. The probability that a large genus includes an invasive species is higher than for small genera and the simple system of answering yes or no does not take into account how large a proportion of species within the genus are invasive. Because of the invasion of *Acer negundo* (*Negundo aceroides*) in the Czech Republic, decision on other casually occurring or even non-escaping maples was postponed to further analysis (see Appendix S1 in Supplementary Material). A pest species *Quercus rubra* is an example of the one most seriously misclassified; it was accepted while two other non-escaping oaks were recommended for further screening. The results within genera *Prunus* and *Robinia* were also biased by the 'genus invasiveness' concept. Finally, absence of vegetative growth is an attribute of non-invasiveness in the North American system. Although vegetative growth is considered as an important attribute of successful invader (Kolar & Lodge, 2001; Weber & Gut, 2004), some successful invaders in Central Europe do not reproduce vegetatively. From the tested list, this holds for *Mahonia aquifolium, Lycium halimifolium, Pinus strobus*, and *Quercus rubra*, but only the first species was rejected (see Appendix S1 in Supplementary Material). To conclude, it appears that the low number of questions on which the Reichard and Hamilton's system is based makes the scheme easy to use in situations for which it was developed, but limits its applicability elsewhere.

WRA was developed for Australia and New Zealand (Pheloung, 1995; Pheloung *et al*., 1999) and successfully tested in Hawaii and other Pacific islands (Daehler & Carino, 2000; Daehler *et al*., 2004). Pheloung *et al*. (1999) tested 370 plant species alien to Australia, representing both weeds and useful taxa from agriculture, the environment, and other sectors. All serious pests and 84% non-harmful but invasive species were rejected and only 7% of non-invasive species were rejected or recommended for further analysis. When applied to Hawaii, WRA rejected 99% of invasive species (Daehler & Carino, 2000). In other Pacific islands, 95% of invasive species were rejected and 85% of non-invasive species were accepted. By using additional decision tree, Daehler *et al*. (2004) were able to cut down the portion of species recommended for further analysis from 24% to 8%. The results yielded by the WRA model with additional decision tree in the Czech Republic were even better than in Australia and Pacific region. All invasive species were rejected and 83.8% of non-invasive were accepted. This implies that the WRA screening procedure, as modified by Daehler *et al*. (2004), might be potentially suitable for a wider range of geographical regions.

Of the 127 woody species reported as escaping from cultivation in the Czech Republic, 54 are naturalized (42.5%) and there are 11 (20.3%) pests among the latter. These values are much higher than predicted by the Tens Rule (Williamson, 1996) and compare to those found in vertebrates (Jeschke & Strayer, 2005). It implies that woody plants are very successful as invaders, compared to other plant groups. All three schemes reflected a clear trend of increasing proportion of rejected species as naturalization process progressed from casual to naturalized to invasive stage. In general, results obtained for casual and naturalized but non-invasive species are not too encouraging regardless of the scheme used. Not surprisingly, it is more difficult to predict the behaviour of species that escaped from cultivation but are not yet invasive. Many woody species have long lag-phases to invasions and the number of invasive aliens will increase in the future even if introductions ceased instantly (Kowarik, 1995). In our study, we attempted to reduce this bias by testing only those species that are planted for sufficiently long period in the Czech Republic, but it is clear that species yet to become invasive increase the variation in possible outcome of invasion, hence affecting the accuracy of the risk assessment schemes.

The overall accuracy of the best fit model (WRA+Daehler) achieved in conditions of Central Europe was 86% (compared to 68% for WRA and 62% for Reichard–Hamilton). Nevertheless, the predictive power of risk assessment schemes is higher for identifying invasive and harmful species than for finding safe non-invasive species. The level of misclassifications tends to be higher for species that will probably never become invasive than for harmful invaders; the number of potentially rejected non-invasive aliens is relatively high because of low base-rate effect of occurrence of invasive species (Smith *et al*., 1999). Data are available for the Czech Republic that allow to quantify successful transition from one step of invasion process to the next and demonstrate that predicting invasions is indeed about predicting rare events. The potential pool of woody aliens introduced to the Czech Republic includes 4360 taxa (M. Křivánek, unpublished data). Of these, only 2.9% are known to have escaped from cultivation, 1.7% persist as casuals, and 0.8% are naturalized. Only 0.4% (one in 257 species) are invasive and 0.25% (one in 396) are harmful pests. These numbers can be related to the accuracy of the three tested schemes. Of the total source pool of 4360 taxa, 4343 are currently not invasive. If the percentage of false predictions obtained by the tested schemes (Fig. 1) is approximated to these 4343 species, 608 (WRA+Daehler), 1390 (WRA), and 1650 (Reichard–Hamilton) species that are probably safe in terms of potential invasion would be rejected.

Smith *et al*. (1999) also document that a scheme can be ignored if the economic loss caused by introduction of a harmful species is not eight times higher than a loss caused by its rejection. This approach, however, does not take the identity of species in question and habitat invaded into account. The damage to natural ecosystems is in most cases irreversible, hence difficult to compare to an economic loss resulting from unrealized opportunity. The rejection of a potentially harmless species can be in many cases compensated by an introduction of another harmless species, alien or native. It is possible that continuing commercial use of some harmful species reflects the inertia of forestry authorities rather than economic reasons. For example, *Pinus strobus* has been planted in the Czech Republic for more than two centuries; it invades unique natural sandstone habitats. The invasion of this species has been one of the most dramatic by woody species in this country (Hadincová *et al*., 1997). It does not produce a good quality timber and could be replaced in many cases by aliens that are not invasive in the Czech Republic, such as *Pseudotsuga menziesii* or *Abies grandis* (Forest Management Institute 1994); yet new plantations of *P. strobus* are being established (Czech Statistical Office, 2002). This example indicates that a decision whether to introduce a prediction scheme or to discard it cannot be based solely on the value of accuracy and reliability it provides. Schemes achieving high levels of accuracy in different geographical and ecological situations, such as the WRA model elaborated by Daehler *et al*. (2004), represent a valuable tool with a capacity to diminish the risk of invasion by newly introduced species.

Our study was performed on woody species commonly planted in the Czech Republic but all the species tested are planted in a wider area of Central Europe; most of them were introduced to other parts of Europe prior to their introduction to the Czech Republic (Svoboda, 1976, 1981). This makes the results of the present study applicable to the temperate climate of Central Europe in general.

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SUPPLEMENTARY MATERIAL

The following material is available online at http://www.blackwell-synergy.com/loi/ddi

Appendix S1 List of species used in the present study and results of their evaluation using the three tested prediction schemes.

Appendix S1. List of species used in the present study and results of their evaluation using the hree tested prediction schemes: WRA (Pheloung *et al.* 1999); WRA with additional decision tree analysis (Daehler *et al.* 2004); Reichard and Hamilton (1997) scheme. Species with WRA score < 1 are accepted, those with > 6 rejected, and those with 1–6 recommended for further analysis. ? – not enough data to perform the evaluation. WRA - Total results means recommendation for species after both WRA schemes: WRA and WRA+Daehler. Nomenclature follows Koblížek (2000). See text for details on particular screening models.

Species	**Status in the CR**	**Reichard & Hamilton**	**WRA Outcome**	**WRA Score**	**WRA + Daehler**	**WRA-Total Result**
Abies balsamea	not escaped	accept	accept	-5	-	accept
Abies cephalonica	not escaped	accept	accept	-6	-	accept
Abies concolor *	not escaped	accept	accept	-2	-	accept
Abies grandis *	not escaped	accept	accept	-5	-	accept
Abies homolepis	not escaped	accept	accept	-6	-	accept
Abies nordmanniana *	not escaped	accept	accept	-4	-	accept
Abies pinsapo	not escaped	accept	accept	-5	-	accept
Abies procera *	not escaped	accept	accept	-7	-	accept
Abies veitchii	not escaped	accept	accept	-4	-	accept
Acer ginnala	casual	reject	evaluate	2	accept	accept
Negundo aceroides *	invasive	reject	reject	11	-	reject
Acer rubrum	not escaped	further analysis	accept	-2	-	accept
Acer saccharinum	casual	further analysis	accept	-2,5	-	accept
Acer tataricum	not escaped	further analysis	accept	-1	-	accept
Aesculus ×carnea	casual	accept	accept	-5	-	accept
Aesculus flava	not escaped	accept	accept	-6	-	accept
Aesculus hippocastanum *	casual	further analysis	accept	-3	-	accept
Aesculus parviflora	not escaped	further analysis	accept	-4	-	accept
Ailanthus altissima *	invasive	reject	reject	13	-	reject
Amelanchier canadensis	not escaped	accept	accept	-1	-	accept
Amorpha fruticosa	invasive	reject	reject	7	-	reject
Aristolochia durior	not escaped	further analysis	evaluate	3	accept	accept
Berberis gagnepainii	not escaped	accept	evaluate	1	accept	accept
Berberis julianae	not escaped	accept	evaluate	1	accept	accept
Berberis thunbergii	not escaped	reject	reject	7	-	reject
Betula lenta	not escaped	accept	accept	-5	-	accept

Betula papyrifera	not escaped	accept	accept	-4	-	accept
Buddleja alternifolia	not escaped	accept	accept	-5	-	accept
Buddleja davidii	casual	reject	accept	-0,5	-	accept
Buxus sempervirens	not escaped	accept	accept	-1	-	accept
Campsis radicans	not escaped	accept	accept	-3	-	accept
Caragana arborescens	not escaped	accept	evaluate	3	accept	accept
Caragana frutex	not escaped	accept	evaluate	2	accept	accept
Castanea sativa *	casual	accept	accept	-6	-	accept
Catalpa bignonioides	casual	reject	accept	-0,5	-	accept
Celastrus scandens	not escaped	accept	accept	-1	-	accept
Celtis occidentalis	casual	accept	accept	-5	-	accept
Cerasus serrulata	not escaped	further analysis	accept	-2,5	-	accept
Colutea arborescens	naturalized	further analysis	evaluate	5,5	accept	accept
Cornus florida	not escaped	accept	accept	-3	-	accept
Corylus colurna	casual	accept	accept	-4	-	accept
Cotinus coggygria	casual	further analysis	accept	-4	-	accept
Cotoneaster bullatus	casual	accept	accept	-1	-	accept
Cotoneaster horizontalis	casual	further analysis	evaluate	1	?	evaluate
Crataegus crus-galli	casual	accept	accept	-1	-	accept
Cryptomeria japonica	not escaped	accept	accept	-8	-	accept
Deutzia scabra	casual	reject	evaluate	1	accept	accept
Eleagnus angustifolia	casual	further analysis	reject	7	-	reject
Eleagnus commutata	not escaped	accept	evaluate	1	accept	accept
Euonymus fortunei	not escaped	further analysis	evaluate	3	accept	accept
Euonymus latifolius	not escaped	accept	evaluate	2	accept	accept
Exochorda racemosa	not escaped	reject	evaluate	3	accept	accept
Forsythia suspensa	casual	accept	accept	-2	-	accept
Fraxinus americana *	not escaped	further analysis	accept	-5	-	accept
Fraxinus ornus	naturalized	accept	evaluate	3	?	evaluate
Fraxinus pennsylvanica	invasive	accept	reject	10	-	reject
Ginkgo biloba	not escaped	accept	accept	-4	-	accept
Gleditschia triacanthos	not escaped	reject	evaluate	4,5	accept	accept
Gymnocladus dioicus	not escaped	accept	accept	-1	-	accept
Hamamelis virginiana	not escaped	accept	accept	-1	-	accept
Hippophaë rhamnoides	casual	further analysis	reject	7	-	reject
Holodiscus discolor	not escaped	accept	accept	-2	-	accept
Hydrangea arborescens	not escaped	accept	accept	-1	-	accept

Hydrangea paniculata	not escaped	reject	evaluate	3	accept	accept
Hydrangea petiolaris	not escaped	accept	evaluate	3	accept	accept
Chaenomeles japonica	casual	accept	accept	-2	-	accept
Chaenomeles speciosa	not escaped	accept	accept	-2	-	accept
Chamaecyparis lawsoniana	casual	accept	accept	-4	-	accept
Chamaecyparis nootkatensis	not escaped	accept	accept	-2	-	accept
Chamaecyparis obtusa	not escaped	accept	accept	-5	-	accept
Chamaecyparis pisifera	not escaped	accept	accept	-2	-	accept
Chionanthus virginicus	not escaped	accept	accept	-1	-	accept
Ilex aquifolium	not escaped	further analysis	evaluate	2,5	?	evaluate
Juglans cinerea	not escaped	accept	accept	-5	-	accept
Juglans nigra *	casual	accept	accept	-5	-	accept
Juglans regia *	naturalized	accept	accept	-1	-	accept
Juniperus chinensis	not escaped	accept	accept	-6	-	accept
Juniperus squamata	not escaped	accept	accept	-8	-	accept
Juniperus virginiana	not escaped	accept	accept	-2	-	accept
Kalmia latifolia	not escaped	accept	evaluate	1	?	evaluate
Kerria japonica	not escaped	reject	evaluate	4,5	?	evaluate
Koelreuteria paniculata	not escaped	accept	accept	-3	-	accept
Laburnum anagyroides	naturalized	accept	evaluate	5	accept	accept
Larix kaempferi	not escaped	accept	accept	-1	-	accept
Laurocerasus officinalis	casual	reject	evaluate	5	accept	accept
Liriodendron tulipifera	not escaped	accept	accept	-5	-	accept
Lonicera caerulea	not escaped	accept	accept	-1	-	accept
Lonicera henryi	not escaped	accept	evaluate	1	accept	accept
Lonicera maackii	not escaped	reject	evaluate	2,5	accept	accept
Lonicera nitida	not escaped	accept	accept	-1	-	accept
Lonicera periclymenum	not escaped	reject	evaluate	5	?	evaluate
Lonicera tatarica	casual	reject	evaluate	5	?	evaluate
Lycium halimifolium	invasive	further analysis	reject	8,5	-	reject
Magnolia ×soulangeana	not escaped	accept	accept	-6	-	accept
Magnolia acuminata	not escaped	accept	accept	-3	-	accept
Magnolia hypoleuca	not escaped	accept	accept	-1	-	accept
Magnolia kobus	not escaped	accept	accept	-1	-	accept
Mahonia aquifolium	invasive	reject	reject	8	-	reject
Malus baccata	not escaped	accept	accept	-9	-	accept
Malus floribunda	not escaped	accept	accept	-7	-	accept

Morus alba	not escaped	reject	evaluate	2,5	evaluate	evaluate
Morus nigra	not escaped	further analysis	evaluate	1,5	evaluate	evaluate
Padus serotina *	invasive	reject	reject	7	-	reject
Parthenocissus inserta	invasive	further analysis	reject	12	-	reject
Parthenocissus quinquefolia	naturalized	further analysis	reject	7	-	reject
Parthenocissus tricuspidata	not escaped	reject	evaluate	5	?	evaluate
Paulownia tomentosa	casual	reject	evaluate	5,5	accept	accept
Phellodendron amurense	not escaped	accept	accept	-5	-	accept
Philadelphus coronarius	casual	accept	accept	-2	-	accept
Physocarpus opulifolius	invasive	accept	reject	8	-	reject
Picea bicolor	not escaped	accept	accept	-6	-	accept
Picea engelmanni *	not escaped	accept	accept	-4	-	accept
Picea glauca *	not escaped	accept	accept	-3	-	accept
Picea jezoensis	not escaped	accept	accept	-5	-	accept
Picea mariana *	not escaped	accept	accept	-4	-	accept
Picea omorika *	not escaped	accept	accept	-3	-	accept
Picea orientalis	not escaped	accept	accept	-5	-	accept
Picea pungens *	not escaped	accept	accept	-2	-	accept
Picea sitchensis	not escaped	accept	accept	-5	-	accept
Pinus aristata	not escaped	further analysis	accept	-1	-	accept
Pinus banksiana *	not escaped	reject	accept	-1	-	accept
Pinus cembra *	not escaped	accept	accept	-3	-	accept
Pinus contorta *	not escaped	reject	accept	-2	-	accept
Pinus flexilis	not escaped	further analysis	evaluate	1	evaluate	evaluate
Pinus jeffreyi	not escaped	further analysis	accept	-3,5	-	accept
Pinus leucodermis	not escaped	accept	accept	-3	-	accept
Pinus nigra *	naturalized	reject	evaluate	1	evaluate	evaluate
Pinus parviflora	not escaped	further analysis	accept	-2	-	accept
Pinus peuce	not escaped	accept	accept	-1	-	accept
Pinus ponderosa	not escaped	further analysis	accept	-3	-	accept
Pinus strobus *	invasive	further analysis	reject	10	-	reject
Pinus wallichiana	not escaped	further analysis	accept	-2,5	-	accept
Platanus ×hispanica *	casual	accept	accept	-2	-	accept
Platanus occidentalis	not escaped	accept	accept	-3	-	accept
Platycladus orientalis	casual	accept	accept	-2	-	accept
Populus ×canadensis *	invasive	further analysis	reject	7	-	reject
Populus balsamifera	casual	further analysis	accept	-2	-	accept

Populus lasiocarpa	not escaped	further analysis	accept	-6,5	-	accept
Populus simonii	not escaped	further analysis	accept	-2,5	-	accept
Pseudotsuga menziesii *	naturalized	reject	evaluate	1	evaluate	evaluate
Pterocarya fraxinifolia	not escaped	accept	accept	-2	-	accept
Pyracantha coccinea	not escaped	accept	accept	-2	-	accept
Quercus coccinea	not escaped	further analysis	accept	-1	-	accept
Quercus palustris *	not escaped	further analysis	accept	-3	-	accept
Quercus rubra *	invasive	accept	reject	7	-	reject
Rhus typhina	invasive	further analysis	reject	13	-	reject
Ribes aureum	casual	further analysis	evaluate	1	?	evaluate
Ribes sanguineum	not escaped	accept	evaluate	1	?	evaluate
Robinia pseudoacacia *	invasive	reject	reject	19	-	reject
Robinia viscosa	not escaped	further analysis	evaluate	2,5	accept	accept
Rosa multiflora	not escaped	reject	evaluate	3	?	evaluate
Sarothamnus scoparius	invasive	further analysis	reject	9	-	reject
Sequoiadendron giganteum	not escaped	accept	accept	-6	-	accept
Sophora japonica	not escaped	accept	accept	-1	-	accept
Sorbaria sorbifolia	naturalized	reject	reject	7	-	reject
Swida alba	not escaped	accept	evaluate	1	?	evaluate
Swida sericea	naturalized	accept	evaluate	3	accept	accept
Symphoricarpos albus	invasive	further analysis	reject	10	-	reject
Symphoricarpos orbiculatus	casual	further analysis	evaluate	4	?	evaluate
Syringa ×chinensis	not escaped	further analysis	accept	-5	-	accept
Syringa josikaea	not escaped	accept	evaluate	3	accept	accept
Syringa vulgaris	invasive	further analysis	reject	9	-	reject
Tamarix gallica	not escaped	further analysis	accept	-2,5	-	accept
Taxodium distichum	not escaped	accept	accept	-1	-	accept
Thuja occidentalis	not escaped	accept	evaluate	1	evaluate	evaluate
Thuja plicata	not escaped	accept	accept	-2	-	accept
Thuja standishii	not escaped	accept	accept	-2	-	accept
Tilia americana	not escaped	accept	accept	-5	-	accept
Tilia euchlora	not escaped	accept	accept	-2	-	accept
Tilia tomentosa	casual	accept	accept	-3	-	accept
Tsuga canadensis	not escaped	accept	accept	-3	-	accept
Tsuga mertensiana	not escaped	accept	accept	-4	-	accept
Viburnum farreri	not escaped	accept	evaluate	1	accept	accept
Viburnum lentago	not escaped	accept	accept	-1	-	accept

Viburnum prunifolium	not escaped	accept	evaluate	1	accept	accept
Viburnum rhytidophyllum	not escaped	accept	evaluate	1	?	evaluate
Vitis coignetiae	not escaped	further analysis	evaluate	1	accept	accept
Vitis riparia	casual	accept	evaluate	2	accept	accept
Weigela florida	not escaped	accept	accept	-3	-	accept
Wisteria sinensis	not escaped	reject	evaluate	3,5	accept	accept

* species planted in both parks and forests