Dark side of the fence: ornamental plants as a source of wild-growing flora in the Czech Republic

Odvrácená strana plotu: okrasné rostliny v České republice jako zdroj spontánní flóry

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Ornamental plants constitute an important source of alien, and potentially invasive species, but also include a substantial part of native flora and consist of taxa that occur both in the wild and in cultivation; yet garden floras are largely ignored in ecological studies. We studied ornamental plants in the Czech Republic in order to provide detailed information, based on field sampling, on the diversity of taxa grown in cultivation in private gardens. Sampling was done in accessible public areas, private gardens and private areas in villages, town- and city neighbourhoods, garden allotments, cemeteries, areas of dispersed farmhouse settlements not accessible to the public, and in new urban sprawl. The data can be used to estimate the propagule pressure of individual taxa, measured in terms of the frequency with which they are planted in the gardens. To make the data comparable across sites, we adopted a two-level approach that resulted in producing a detailed list (including all the taxa recorded) and an aggregated list (merging closely related and similar taxa, which was necessary in order to assess the frequency of planting across sites). Each species on the detailed list was assigned an origin, status, life history and cultivation requirements. Comparing the field records with national checklists of both native and alien vascular plants we quantified particular components of the ornamental flora. The floristic inventories for 174 sites yielded 1842 taxa on the detailed list, consisting of 1642 species (standard binomials), 9 cultivars assigned to genera, 147 hybrids and hybridogenous taxa, and 44 taxa identified at higher than species level. Of these taxa 1417 (76.9%) were alien and 420 (22.8%) native. The ornamental flora consisted of not-escaping aliens, escaping aliens and cultivated natives. Of the recorded taxa, 841 (45.6%) occur both in cultivation and the wild. The aggregated list comprised 1514 taxa and resulted from merging 533 taxa from the detailed list into 205 taxa. Most alien ornamentals are native to Asia and Americas. The proportion of escaped and not-escaping aliens significantly differed from wild aliens in the spontaneous flora with underrepresentation of escaped, which originated from Australia, Africa and the Mediterranean area. Taxa from Africa and anecophytes were overrepresented and those from Australia, the Mediterranean and other parts of Europe underrepresented among not escaping aliens. The assessment of planting frequency revealed that 270 taxa were found at more than 25% of the sites, while

584 (40%) occurred at only one or two sites. Winter annuals and shrubs are most represented among the commonly planted aliens; the only native species with comparably high planting frequencies among the aliens, are *Vinca minor*, *Hedera helix* and *Aquilegia vulgaris*. Related to the invasion potential of ornamental garden flora we analysed the recorded taxa with respect to the transient/persistent character of their occurrence. The core (persistent) part of the flora comprised 599 taxa (32% of the total number of taxa) and the transient 240 (13%) taxa. The "grey zone" between the two included 1003 taxa (55%). The results reported here provide quantitative insights into the role of horticulture as a major pathway of plant invasions.

K e y w o r d s: cultivated plants, Czech Republic, invasion, naturalization, ornamental flora, transient flora, urban areas

Introduction

Ornamentals are an abundant group of plants, including both native and alien species, which are extremely variable in terms of their life form and cultivation needs. They form an important component of the human environment, because they are grown in a broad spectrum of habitats such as gardens, public spaces (e.g. town squares or cemeteries), indoors (as houseplants), open land (e.g. in belts along roads), floriculture plantations and specialist garden collections. Traditionally, ornamental plants are studied separately from spontaneous flora, usually as a subject of garden architecture (Groening & Wolschke-Bulmahn 1989), floricultural industry (Wijnands 2005, Xia et al. 2006) and ethnobotany (Vogl et al. 2004). In the last decade, however, there was a major shift in interest and ornamental plants are now frequently included in ecological studies. The two main research areas in which ornamental plants are an important subject of study are invasion ecology, with horticulture being a major pathway for the introduction of alien plants (Reichard & White 2001, Křivánek et al. 2006, Dehnen-Schmutz et al. 2007, Hanspach et al. 2008, Kempel et al. 2011, Razanajatovo et al. 2015), and urban ecology in which ornamentals are an integral component of the environment (e.g. Kowarik 1990, Sukopp 2002, Gaston et al. 2005, 2007, Yang et al. 2015).

From the plant invasion perspective, horticulture is a major source of propagule pressure, which is a key factor in invasion biology (Křivánek et al. 2006, Botham et al. 2009, Lockwood et al. 2009, Simberloff 2009, Pyšek & Richardson 2010, Hulme 2011, Pyšek et al. 2015) and the stock from which new alien plants can escape into the wild is continually increasing. Huge numbers of imported species, imperfect legislation and insufficient resources, both financial and human, however, are major constraints to controlling this species pool and predicting future invasions (Roy et al. 2013). Garden escapes contribute significantly to local and regional pools of alien species (Mack 2000, Reichard & White 2001, Dehnen-Schmutz et al. 2007), and among these species there is generally a greater proportion of those that reach more advanced stages of the invasion process and become naturalized or even invasive (Kowarik 2005, Pyšek et al. 2011). The reasons for the invasion success of ornamentals are mainly a high and long-term propagule pressure, reduced risk of failure due to protection from unsuitable environmental conditions and sufficient time for them to adapt to local conditions (Mack 2000), and following escape there is an abundance of suitable habitats in urbanized areas that serve as entry points for the establishment of alien species (e.g. Chytrý et al. 2008, Pyšek et al. 2010, Jehlík 2013, Pyšek & Chytrý 2014). However, the majority of biodiversity studies ignore cultivated ornamental plants, and focus only on habitats with spontaneous flora (Chytrý et al. 2015, Kaplan et al. 2015). Until ornamentals escape, they are considered to be unimportant in urban areas and hence not included in regional floras, with the exceptions of specialized handbooks such as the 5th volume of the Rothmaler series (Jäger et al. 2008). However, while the wild-growing flora of towns and cities has been thoroughly studied for a long time (e.g. Višňák 1995, Pyšek 1998, Sukopp 2002, Chocholoušková & Pyšek 2003, Aronson et al. 2015, Čeplová et al. 2015), the species diversity and composition of the cultivated ornamental flora, especially in private gardens, has never been assessed on a regional scale in the ecological literature, despite the role of these gardens as primary sources of propagules of alien species.

Collecting field data on the pool of cultivated plants raises some methodological issues related mainly to taxonomy. In comparison to the wild-growing flora the ornamental flora contains a large number of cultivars, hybrids, polyploid groups and species complexes (Crane & Lawrence 1934, Anderson 2006) that appear to be autonomous entities, although their taxonomic rank varies. The taxonomic identity of many garden plants, especially the so-called "homeless plants" (Zohary 1962), or anecophytes, often remains unclear because of unknown parental taxa and the evolutionary processes that occurred during their cultivation and breeding. Therefore, the prediction of possible escape and invasion success of these taxa is difficult as invasiveness can be affected by small genetic differences in source populations (Lehrer et al. 2006, Ross et al. 2008, Pyšek et al. 2013). Another difficulty is linked to the fact that many garden ornamentals are a transient component of diversity. Within local or regional floras, it is possible to differentiate between persistent, core species, with rather stable distributions, and transient species, the presence and distribution of which depends more on chance events associated with fluctuations in climate, or rare and accidental transport opportunities (MacArthur 1960, Magurran & Henderson 2003, Coyle et al. 2013) rather than on their life-history traits and ecology; this division can be applied both to native and alien species. Transience is a typical feature of occurrences beyond the natural edges of species distribution ranges. The more pronounced the transient component of a flora, the more difficult it is to estimate the number of taxa. For the ornamental flora, the transient pool includes many species that may escape from cultivation and become invasive in the future.

The aim of this study was to provide the first detailed information on the diversity of taxa grown in cultivation in private gardens in the Czech Republic and, based on sampling that took the regional, climatic and cultural heterogeneity in this country into account, to estimate the size of the species pool of this flora. For a subset of the garden flora, we provide an estimate of the propagule pressure, measured in terms of the frequency with which these plants are cultivated in private gardens. Finally, the data are compared with the national checklists of both native and alien vascular plants (Danihelka et al. 2012), to quantify the components of the ornamental flora, including its core and transient parts, and discuss its potential for escape from cultivation and naturalization.

Methods

Study area

The Czech Republic is in central Europe and includes an area of 78,867 km^2, the majority of which is located in the temperate broad-leaved deciduous forest zone (Chytrý 2012, Divíšek et al. 2014). The climate is determined largely by the altitudinal range, which is from 115 to 1602 m, and the mean annual temperature and annual sum of precipitation range from 5.0 to 9.5 °C and 320 to 1450 mm, respectively (Tolasz et al. 2007). This country includes 6248 urban areas (municipalities: cities, towns and villages), which are separate legal entities and vary in size, human population density and other socioeconomic factors. The size of the municipalities range from Prague, the capital, with 1.2 million inhabitants, to small villages harbouring less than 50 permanent residents. There are 4867 municipalities with fewer than 1000, and 467 with fewer than 100 inhabitants. The whole country is relatively homogenous in terms of social, cultural and economic diversity due to the small differences between social strata, regions and cities vs villages (Ritschelová 2015).

The current concept of what constitutes a garden, gardening methods and the choice of ornamental species in the Czech Republic is a result of a continuum of historical processes stemming from three main cultural sources: (i) Traditional rustic gardens are mostly fenced and include hoed patches where ornamental plants are cultivated alongside vegetable and fruit crops. (ii) Luxurious walled gardens that form parts of originally aristocratic or religious estates; they were inspired by similar sites abroad and are characterized by a park-like structure with lawns, trees and shrubs. (iii) Since the beginning of the 1990s, a modern style of garden design was introduced mainly by landscape architects and commercial gardening companies, and their floristic composition has been gradually changing.

Sites studied

We recorded the ornamental flora at 174 urban localities (further referred to as 'sites'; see Fig. 1 for distribution and Electronic Appendix 1 for details of the sites sampled). The sites were selected so as to cover representative areas of the environmental and cultural conditions that are assumed to affect the diversity of local ornamental floras. This ensured that a wide range of urban and climatic types and a great diversity of ornamental flora recorded at the landscape scale were included in this study. The sites sampled included villages, town- and city neighbourhoods, garden allotments, cemeteries, areas of dispersed farmhouse settlements and the new urban sprawl, which is a significant feature of the last few decades. Data collected in villages of up to ~2000 inhabitants were merged and a village considered as a single site, whereas in towns and cities, one or more sites of similar urban character, were included in this study.

At each site the ornamental flora was recorded in private gardens and public areas. At least five gardens per site were studied in detail and other gardens were surveyed from behind the fence. The data were thus collected in (i) plantations in accessible public areas, such as streets or urban parks, (ii) private gardens accessible with the owner's permission, (iii) non-accessible private areas that could only be inspected visually from the outside, mostly front gardens or building frontages with window boxes and green entrances. Plants grown in garden centres and ornamental plantations outside urban areas were not included.

Selection of taxa for recording and collection of field data

At each site sampled, all plants (alien and native) other than spring geophytes and conifers cultivated for ornamental purpose in private gardens and public areas, as defined

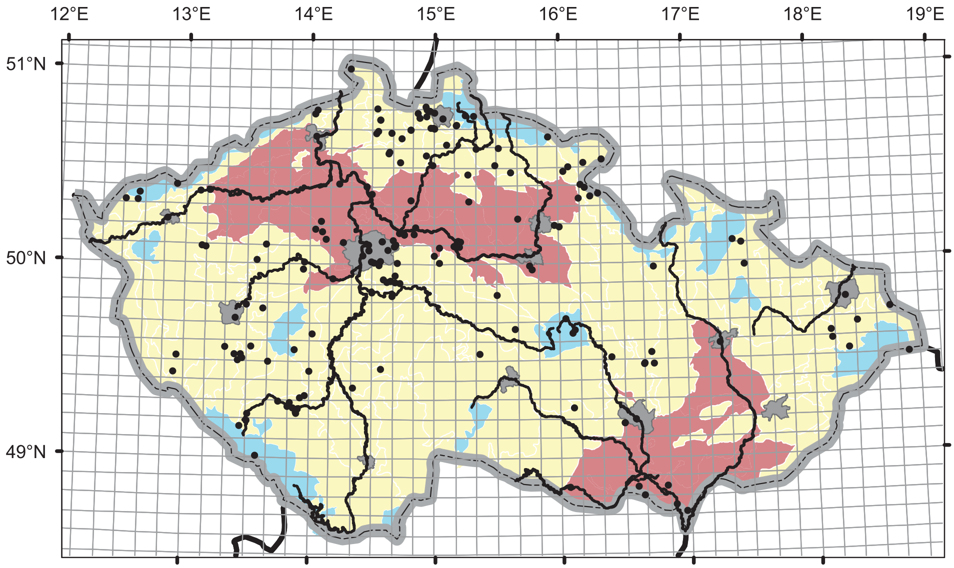


Fig. 1. – Map showing the sites sampled in the Czech Republic (see table in Electronic Appendix 1 for their descriptions). Phytogeographical regions (see Kaplan 2012 for their description) are indicated by using different colours: red – thermophyticum, yellow – mezophyticum, blue – oreophyticum. Position of large cities in the Czech Republic is shown by grey areas.

above, were recorded. Only species planted for ornamental purpose were considered. Spring geophytes were not included for practical reasons, namely because repeated visits to sites in order to record both spring and summer aspects were not logistically feasible. Conifers were excluded because only a few species are naturalized or invasive in the Czech Republic (Pyšek et al. 2012b), and many sterile plants are grown that are very difficult to identify. Grassland species cultivated as common components of garden lawns were also excluded. However, weedy plants growing in garden beds and among vegetables or fruit trees grown as ornamentals were included. The latter were included if their ornamental status and gardening care was confirmed by the owner or self-evident (such as, e.g., a flowering solitary specimen of *Erigeron annuus* growing in a hoed and otherwise weeded patch). Potted plants that were overwintered inside but summered in gardens were also included in the inventory.

The data were collected between June and August of 2011–2013 by 11 botanists (Electronic Appendix 1). Specimens of critical taxa were collected for herbarium or photographed for later identification.

Recorded plants and their names

We adopted a two-level approach that resulted in producing two species lists. All identified taxa of vascular plants recorded at the sites sampled were included on (i) a 'detailed list', which became the basis for producing (ii) an 'aggregated list' in which closely related taxa and those similar in appearance were merged to reduce the uncertainty associated with their identifications. The main purpose of the aggregated list was to assess the frequency of planting across sites. Moreover, by aggregating the species we reduced the potential bias attributable to a recorder's identity in identifying taxa or estimating species diversity.

We followed the approach adopted by major garden floras for the area studied (Jäger et al. 2008, Cullen et al. 2011), which use broad and flexible taxonomic concepts. As none of the available taxonomic sources contained all of the plants we recorded during our survey, we combined four different sources to create the above lists. For cultivated ornamentals we used the taxonomy and names used in the Rothmaler field guide to ornamental and utility plants for Germany (Jäger et al. 2008), which proved to be suitable also for the garden floras of the Czech Republic. The names for remaining taxa were successively adopted from the following sources: the Checklist of the vascular plants of the Czech Republic (Danihelka et al. 2012), the European Garden Flora (Cullen et al. 2011) and The Plant List (2013).

Intraspecific taxa and cultivars were not distinguished, except for taxa listed in the above sources by the genus name followed by the name of the cultivar (e.g. *Thymus* 'Elfin' in Jäger et al. 2008). We also did not distinguish between garden cultivars or planted wild forms of the same species (e.g. in *Bellis perennis* and *Phalaris arundinacea*). Unsupported names are used only in few cases, such as those widely accepted in botanical or gardening literature (e.g. *Ptilotus exaltatus*, *Viburnum ×pragense*), or informal physiognomy designations defined ad hoc (in *Hebe* spp. and *Bambusoideae* only).

The following forms of names were used in the aggregated list: (i) binomials, sometimes supplemented by the abbreviations cf. or aff.; (ii) aggregate designations for a group consisting of a limited number of species whose identity is known but they are not distinguished in the aggregated list (e.g. the entry *Achillea chrysocoma* & *A. tomentosa* includes only these two species); (iii) aggregate designations including an unknown number of species of which only some were identified (e.g. within *Colchicum* sp. et hybr., only *C. autumnale* was recorded but many other species or nothospecies are supposed to occur); (iv) broadly defined ad hoc designations for taxa about which more detailed information is lacking (e.g. *Alstroemeria* spp., *Epimedium* hybr., *Clematis patens* hybr.).

Quantitative measures of occurrence

The total number of sites at which a taxon in the aggregated list was recorded was used as a quantitative measure of the taxon's 'planting frequency'. Further, for each taxon at each site its local population size (termed 'abundance') was estimated using an ordinal scale: 1 – present in one garden at a site (low abundance), 2 – present in more than one garden but less than 30% of the gardens (medium abundance), 3 – commonly occurring in more than 30% of the gardens at a site (high abundance).

Species status, life history and regions of origin

Each species on the detailed list was assigned the following attributes: origin status, geographic region of origin (native range), life history and cultivation requirements (character of planting). The origin status was classified based on data in Pyšek et al. (2012b) and Danihelka et al. (2012). We distinguished five groups (Fig. 2): (i) 'wild natives' (native taxa growing in the wild and not recorded as cultivated in this study); (ii) 'cultivated

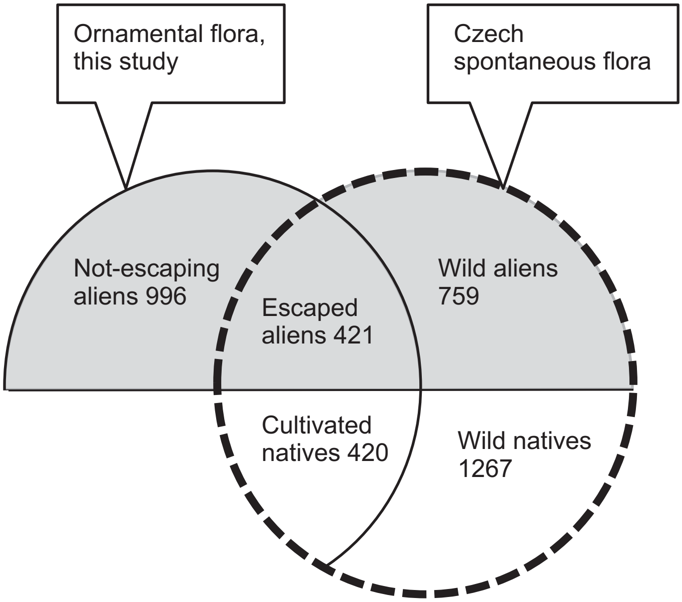


Fig. 2. – The comparison of the garden survey data collected for this study with the spontaneous flora of the Czech Republic (Danihelka et al. 2012 adjusted, see Methods for details; excluding conifers and spring geophytes). Eight taxa of unclear origin were excluded. Alien species are depicted in grey. The following groups are distinguished: wild natives (native taxa only growing in the wild and never cultivated); cultivated natives (growing both in the wild and in cultivation); wild aliens (alien taxa only growing in the wild); escaped aliens (growing both in the wild and in cultivation); not-escaping aliens (only grown in cultivation).

natives' (native taxa growing in the wild but also recorded as cultivated in this study); (iii) 'wild aliens' (alien taxa growing in the wild and not recorded as cultivated in this study); (iv) 'escaped aliens' (recorded as cultivated in this study and also known to grow in the wild following escape from cultivation); (v) 'not-escaped aliens' (only grown in cultivation and never found in the wild in the Czech Republic). Finally, the invasion status of each alien species (sensu Richardson et al. 2000, Blackburn et al. 2011) occurring in the wild in the Czech Republic was classified as casual, naturalized or invasive in this country (following Pyšek et al. 2012a, b). Geographic origin was classified at a broad level of continents (Africa, Asia, Americas, Europe and Australia including New Zealand). The Mediterranean area was distinguished as a separate region because of its importance as the source of numerous crops and ornamental species, and an important source of the alien flora of the Czech Republic (Pyšek et al. 2012a, b). Species of hybrid origin or those that originated in cultivation (anecophytes) were classified as of separate origin.

Each taxon was classified into one or more of the following life-history categories: (i) annual, (ii) overwintering herbaceous plant (i.e. biennial or perennial), (iii) shrub or (iv) tree (based on Jäger et al. 2008, Cullen et al. 2011). Woody dwarf shrubs such as *Calluna vulgaris* were classified as shrubs, soft-branched semi shrubs such as *Lavandula* spp., as overwintering herbaceous plants and shrubs. For species that are variable in terms of their life histories, the classification reflects life forms in which the taxon occurs in the Czech Republic.

Cultivation demands and persistence in the flora

Cultivation requirements were used as an additional criterion for assessing the transience/persistence of the recorded species' occurrence. We distinguished the following types: (i) standard outdoor flowerbed plants, both those that overwinter in gardens and annuals that survive harsh conditions in the seed stage; (ii) frost-sensitive plants requiring indoor overwintering, i.e. potted perennials such as *Agave americana* and outdoor geophytes such as *Canna indica*; (iii) plants requiring specific habitats such as walls, rock gardens or garden ponds; and (iv) plants usually considered non-ornamental, such as crops or weeds, but occasionally planted for decoration.

Each species was classified as forming a persistent (core) or transient part of the flora. This categorization was based on their status (taken from Pyšek et al. 2012b), cultivation requirements and abundances. Native species, all naturalized alien species, and locally abundant or scattered casual aliens were classified as core species. Frost-sensitive cultivated plants and casual aliens that vanished or are known from a single occurrence were classified as transient. The grey zone between these two clearly defined groups includes cultivated overwintering taxa and rare casual aliens.

Comparison with the flora of the Czech Republic

To compare the results of our inventory of garden floras with the national flora, we used the recent checklist of vascular plants of the Czech Republic that also includes some commonly cultivated plants (Danihelka et al. 2012). To make this comparison feasible, we excluded from the national checklist (i) cultivated plants not escaping from cultivation and (ii) microspecies of genera for which garden floras use broader taxonomical concepts (e.g. some agamospecies or sterile hybrids in the genus *Carex*). This simplified list is referred to as a 'spontaneous flora'.

Statistical analyses

To test for differences in the proportion of species in groups of various life forms and invasion status, we used count data analysed in row × column contingency tables, with GLM with log-link function and Poisson distribution of errors (Crawley 2007). If significant differences between the groups were found, G-tests were used to test which groups of species are more or less represented than expected by chance (Řehák & Řeháková 1986). Estimates of the total number of species occurring in gardens, based on the shape parameters of the species–area relationship curves (Chao and Jacknife methods), were calculated using the package vegan in R (Oksanen et al. 2013).

Results

Diversity of ornamental flora and its comparison with spontaneous flora

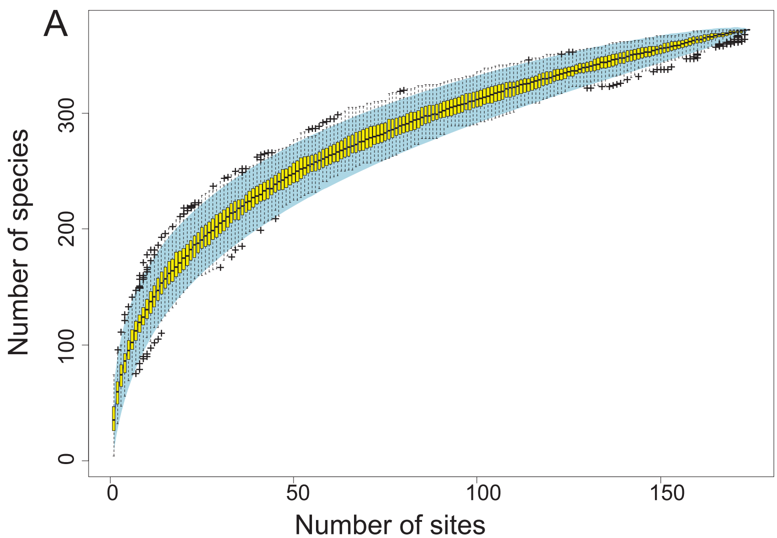
It is noteworthy, that this inventory is not a full list of species planted as ornamentals in gardens in the Czech Republic and, therefore, its comparison with the complete list of alien flora needs to be interpreted with this fact in mind. Floristic inventories for 174 sites yielded 1842 taxa on the detailed list, consisting of 1642 species (standard binomials), 9 cultivars assigned to genera, 147 hybrids and hybridogenous taxa and 44 taxa identified at higher than species level (Electronic Appendix 2). This flora includes not-escaping aliens, escaping aliens and cultivated natives (Fig. 2). Of the total number, 1417 (76.9%) taxa were alien and 420 (22.8%) native. The remaining eight taxa (0.3%: *Minuartia* sp., *Ophrys* sp., *Pulmonaria officinalis* agg., *Rubus fruticosus* agg., *Soldanella* sp., *Sorbus aria* agg., *Tragopogon* sp. and *Trollius* sp.) were not assigned a status because their identification was ambiguous; these genera include both native and alien species in the Czech Republic and were excluded from the analyses. Of the total national flora (as of Danihelka et al. 2012) consisting of 2859 taxa, 2026 (70.9%) were recorded only in the wild. Of the 1834 recorded ornamental species 841 (45.6%) occur both in cultivation and in the wild.

Using the broad classification of sites presented in Electronic Appendix 3, there were 74 sites located in towns (these on average harboured 210 ornamental taxa in the gardens sampled), 89 in villages (200 taxa) and 11 in scattered built-up areas (199 taxa). The aggregated list, comprising 1514 taxa, resulted from merging 533 taxa from the detailed list into 205 taxa of broader circumscriptions. Species–area relationships for the sites sampled, based on the aggregated list, are similar for cultivated native and alien ornamental taxa (Fig. 3). Both curves show a steady cumulative increase of ~2 new species per site, with signs of deceleration but are not asymptotic for the 174 sites sampled, indicating that the actual number of taxa in the Czech ornamental flora is higher than we recorded. The native spontaneous flora in the Czech Republic grouped according to the criteria cited above comprises 1678 taxa (Fig. 2). This estimate based on the species–area relationships using two different methods (Chao and Jacknife) indicates ~1900–2100 taxa, among which ~500 are native cultivated and ~1400–1600 cultivated aliens, both escaping and not-escaping (Table 1). By using the algorithm for calculating the species–area relationship curve, it is predicted that an additional ~200 sites would be needed to record the total diversity of the ornamental flora in the Czech Republic.

Ornamental flora as a source of plant invasions

Comparison of the proportion of cultivated alien taxa (escaped and not-escaping) among the total ornamental flora with the proportion of aliens (escaped and wild) in the spontaneous flora of the Czech Republic reveals that the former were significantly more represented (51% vs 37%; χ^2 46.7, df =1, $P < 0.0001$). Of the total of 1423 alien taxa recorded at the sites sampled, 422 are known to have escaped from cultivation in the Czech Republic (based on Pyšek et al. 2012b), which is 29% of the total diversity of spontaneously occurring alien flora in this country. Among the 421 taxa that have escaped cultivation, 261 are classified as casual, 128 as naturalized and 32 invasive. All species classified as invasive based on Pyšek et al. (2012b) are marked in Electronic Appendix 2 by an asterisk.

Related to the invasion potential of the ornamental garden flora is its transience/persistence continuum. The core part of the ornamental flora comprised of 599 taxa (32% of the total number recorded in the detailed list), of which 419 were native, 160 naturalized aliens, and 20 casual aliens with locally abundant or scattered distributions. The transient part of the ornamental flora consisted of 240 (13%) taxa, among which 198 were frost-sensitive and 42 casuals with a single record in the wild, or extinct. The "grey zone" between the two included 1003 taxa (55%), containing all the other cultivated not winter-hardy aliens recorded at both high and low frequencies and also 199 rare casual wild aliens.



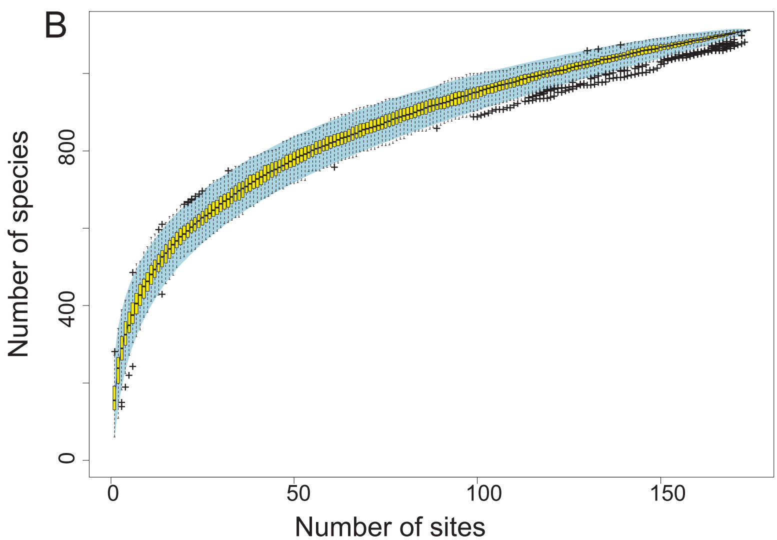


Fig 3. – Species–area relationship for native (A) and alien (B) species recorded at the 174 sites sampled, based on the aggregated list. The 'area' is the number of occupied sites. Area of the site was used as a weighting covariate. Asymptotes of individual curves estimated by different methods are shown in Table 1.

Table 1. – Estimates of the total number of species (excluding conifers and spring geophytes) based on the shape parameters of species–area relationship curves. Observed data are the number of species recorded in our survey, Chao and Jacknife are estimates of total species number.

	Observed number of taxa	Estimated number of taxa	
		Chao	Jacknife
All aliens (escaped+cultivated)	1107	1536+66	1421+42
Native taxa	377	502+10	484+18

Taxonomic and biogeographical patterns

The detailed list of the ornamental flora comprised 151 plant families, 59 of which were represented by one species, and only 11 contributed at least 2% of the total species number. Not-escaping cultivated aliens and cultivated natives belonged to a wide range of families, 127 and 83, respectively, whereas escaped aliens belong to only 47 families. The families of the ornamentals most frequently recorded, merged across groups of taxa, were the *Asteraceae*, *Rosaceae*, *Lamiaceae*, *Poaceae* and *Plantaginaceae*. Some cultivated plants belonged to families that are rare or absent in the Czech spontaneous flora, such as *Cactaceae*, *Myrtaceae*, *Aizoaceae*, *Magnoliaceae* and *Gesneriaceae* (Table 2, Electronic Appendix 2). The ornamental genera richest in species were *Sedum* (35 species), *Salix* (24), *Lonicera* (20), *Geranium* (19), *Rosa* (19), *Saxifraga* (19), *Carex* (18), *Prunus* (18), *Campanula* (17), *Allium* (14), *Silene* (14) and *Veronica* (14); most of them are also species-rich in the Czech spontaneous flora (Danihelka et al. 2012). This is different from the pattern recorded for wild natives where the genera richest in species include e.g. *Carex*, *Trifolium*, *Rumex*, *Bromus* and some with apomictic taxa such as *Rubus* and *Hieracium* (Danihelka et al. 2012).

Most alien ornamental taxa are native to Asia (357; 25.6%) and the Americas (354; 25.4%), with those from other parts of Europe or the Mediterranean area making up 13.1% (184) and 19.2% (268), respectively. Only 36 taxa recorded in our survey are native to Australia. Taxa of unclear provenance or of garden origin (anecophytes) comprised 8.6% (151) of the total (see Table 2 and Electronic Appendix 2 for distribution of alien taxa in families cross-tabulated with regions).

In terms of regions of origin both escaped ($\chi^2 = 26.6$, df = 6, $P < 0.001$) and not-escaping aliens ($\chi^2 = 303.2$, df = 6, $P < 0.001$) differed significantly from wild non-natives in the spontaneous flora. Australia, Africa and the Mediterranean area were strongly underrepresented among the regions of origin of escaped aliens. Plants from Africa and anecophytes were overrepresented and those from Australia, the Mediterranean and other parts of Europe underrepresented among not escaping aliens.

Life histories

On the detailed list, there were 205 annuals, 1121 overwintering herbaceous plants, 512 shrubs and 119 trees. The groups of taxa distinguished based on their origin significantly differed in the representation of their life histories (not escaping aliens vs wild aliens: $\chi^2 = 797.5$, df = 3, $P < 0.001$; escaped aliens vs wild aliens: $\chi^2 = 263.2$, df = 3, $P < 0.001$). Annuals were underrepresented and shrubs overrepresented among both groups of cultivated aliens (escaped and not-escaping) as compared to the number of aliens in the spontaneous flora (Table 3).

Frequency and abundance

Frequency and abundance were estimated only for the taxa on the aggregated list. Of the 1452 taxa on this list, 270 taxa were recorded at more than 25% of the sites. The frequencies of the 10 most common taxa (*Lavandula angustifolia* & *L.* ×*intermedia*, *Hosta* spp., *Paeonia lactiflora* & *P. officinalis* & hybr., *Buxus sempervirens*, *Phlox paniculata*, *Iris germanica* hybr., *Bergenia cordifolia* & *B. crassifolia*, *Vinca minor*, *Syringa vulgaris*,

Table 2. – The numbers of cultivated (not escaping and escaped; our data) and wild aliens (from spontaneous flora) classified according to families (abbreviated by using the first letters of the family name) and regions of origin. Only 20 most frequent families are shown (see Electronic Appendix 2 for complete data). Note that a species can be included in more than one region of origin. In grey are marked regions of origin with higher than 20% representation within the family.

Family / Origin	Cultivated, not escaping aliens									Cultivated, escaped aliens									Wild aliens							
	Af	As	Am	Aus	Med	Eur	ane	Total		Af	As	Am	Aus	Med	Eur	ane	Total		Af	As	Am	Aus	Med	Eur	ane	Total
Aste	12	9	37	7	18	10	5	98	Aste	1	4	26	1	19	11	5	**67**	Poac	9	18	20	3	68	9	6	133
Rosa	0	33	10	1	5	6	18	73	Rosa	0	16	10	0	7	8	2	**43**	Aste	3	8	21	1	39	22	27	121
Lami	2	8	9	2	16	4	6	47	Lami	0	2	1	0	13	6	3	**25**	Amar	1	19	19	6	19	17	5	86
Plan	0	3	12	9	6	5	2	37	Poac	1	5	3	1	4	2	1	**17**	Bras	2	11	3	0	43	25	1	85
Aspa	9	6	8	0	5	0	4	32	Bras	0	0	0	0	10	6	0	**16**	Faba	0	2	0	0	37	7	0	46
Cras	5	10	4	0	4	7	0	30	Ranu	0	2	0	0	8	4	1	**15**	Lami	0	2	1	0	17	10	4	34
Saxi	0	8	7	0	0	6	5	26	Faba	0	1	6	0	3	4	1	**15**	Apia	0	2	0	0	17	7	1	27
Poac	0	11	6	0	5	3	1	26	Cary	0	1	0	0	8	4	1	**14**	Cary	0	3	0	0	13	5	3	24
Capr	0	12	2	0	4	0	8	26	Cras	0	4	0	0	4	4	0	**12**	Bora	0	4	1	0	10	5	2	22
Faba	1	7	6	0	3	2	4	23	Sola	0	2	7	0	1	1	0	**11**	Onag	0	1	5	0	0	1	13	20
Eric	0	6	9	0	2	6	0	23	Papa	0	2	1	0	6	2	0	**11**	Poly	1	4	2	1	2	4	6	20
Ranu	0	7	4	0	1	4	5	21	Amar	0	2	4	0	1	3	0	**10**	Plant	0	0	2	0	16	1	0	19
Cary	0	4	1	0	5	8	1	19	Apia	0	1	0	0	6	3	0	**10**	Papa	0	1	1	0	11	4	0	17
Prim	0	10	1	0	3	2	2	18	Saxi	0	2	1	0	1	3	2	**9**	Gera	0	1	0	0	12	3	0	16
Olea	0	10	1	0	2	0	4	17	Sapi	0	2	2	0	1	1	1	**7**	Rosa	0	2	1	0	2	5	6	16
Gera	2	2	0	0	5	2	6	17	Plan	0	0	0	0	3	4	0	**7**	Malv	0	2	3	1	6	1	2	15
Camp	0	3	3	2	3	5	1	17	Capr	0	1	3	0	2	1	0	**7**	Sola	1	2	7	0	5	0	0	15
Sali	0	4	0	0	1	4	4	13	Bora	0	0	1	0	2	4	0	**7**	Euph	0	1	2	0	7	1	0	11
Sola	0	0	7	0	0	0	5	12	Poly	0	5	0	0	0	0	1	**6**	Ranu	0	2	0	0	6	3	0	11
Berb	0	5	3	0	1	0	3	12	Malv	0	0	0	0	3	1	1	**5**	Rubi	0	0	0	0	6	5	0	11
Total number of species																										
	84	278	241	34	136	94	125			4	79	113	2	132	90	29			18	87	101	12	371	148	88	
Total number of families																										
								127									83									47

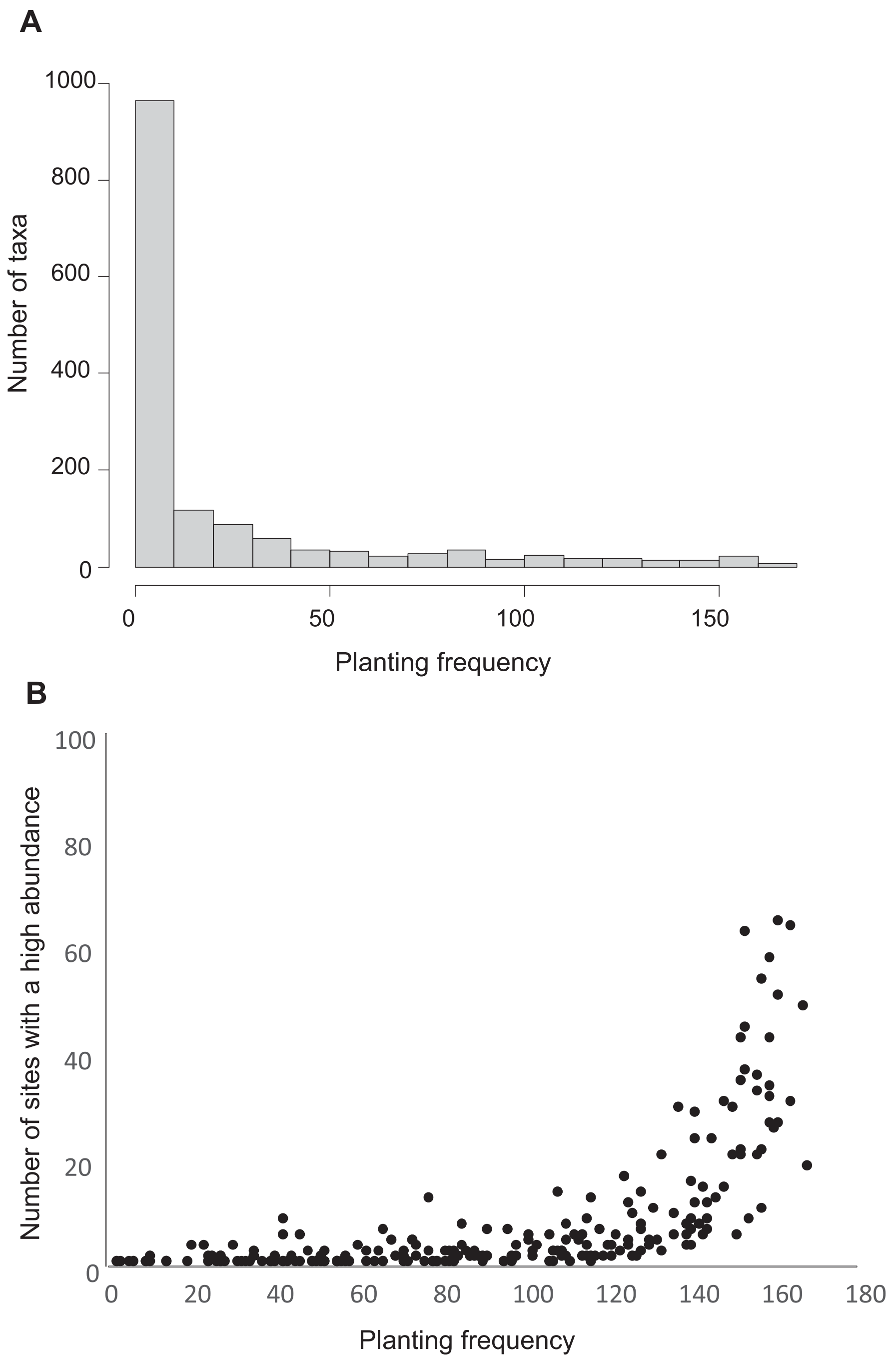


Fig 4. – (A) The distribution of planting frequencies of the taxa recorded. (B) Relationship between the number of sites at which the taxon reaches the high abundance (defined as commonly occurring in more than 30% of gardens within the site) and its planting frequency (the number of sites in which it was recorded, n = 174). Based on the aggregated list. For detailed information see Electronic Appendix 2.

Cerastium tomentosum & *C. tomentosum* hybr.) ranged from 168 to 159 of the total of 174 sites (Electronic Appendix 2). The majority of these common taxa were alien winter annuals and alien shrubs. Considering their status, the only native species with similarly high planting frequencies were *Vinca minor* (160 sites, but note that the native status of this species is still in dispute; Slavík 2000), *Hedera helix* (153) and *Aquilegia vulgaris* as the most common species within the aggregated taxon *Aquilegia* spp. et hybr. (159). Of the rare taxa, 584 (40%) occurred at only one or two sites (Fig. 4A).

Table 3. – Distribution of life histories in the groups of taxa. Asterisks indicate significant differences from proportions expected by chance derived from the number of aliens in the spontaneous flora (G-test; ** 0.01–0.001, *** < 0.001, the sign indicates over- or underestimation). Note that a species can be included in more than one life history group.

Status/life history	Annual	Overwintering herb	Shrub	Tree
Native	11	324	68	31
Not-escaping alien	–75***	+587***	+351***	+57**
Escaped alien	–119***	+217*	+94***	+32***
Wild alien (Czech spont. flora)	380	191	6	0

There were 232 taxa (15%) that were abundant at least at one site, 841 (56%) that were of medium abundance at most, and 441 (29%) that were uncommon at all sites. For the taxa with the high abundance, the relationship between the number of sites at which they were abundant and their planting frequency was not linear (Fig 4B, Electronic Appendix 2). Considering a range of frequencies the majority of taxa were locally highly abundant at a small number of sites. The number of sites at which a taxon was highly abundant abruptly increased for taxa with planting frequency exceeding ~60–70%. Taxa in this part of the plots occurred at many sites (high frequency) and were often very abundant and comprised some of the most popular Czech ornamentals, such as *Hosta* spp. and *Phlox paniculata*. Species reaching high abundances associated with low planting frequencies were often those confined to specific ecological conditions (e.g. *Athyrium filix-femina* and *Digitalis purpurea* in gardens at high altitudes, or *Tagetes patula* and *Dahlia ×hortensis* grown mainly in rustic gardens). In contrast, some species are frequently planted but seldom abundant (e.g. *Lavandula officinalis*, *Yucca filamentosa*), and others rarely planted and never abundant (e.g. many annuals and rock garden species such as *Gazania* spp. and *Pulsatilla* spp.).

Discussion

Can we estimate the diversity of the ornamental flora?

An important feature of the ornamental flora is the high proportion of species occurring at low frequencies. These rare species, together with some specific properties of garden ornamental flora and a high proportion of transient species make the comparison with standard floras difficult. The transient component (12% of the total number of taxa recorded in our survey) or species classified in the grey zone between transient and core species (59%) form the majority of the garden flora, but individually, these species are of marginal ecological importance. The examples of species considered transient include sensitive subtropical ornamentals such as *Angelonia salicifolia* and *Lobelia tupa*, rarities such as *Artemisia tridentata*, *Maihuenia poeppigii* and *Pinguicula balcanica*, and some ornamentals formerly cultivated that have recently disappeared, such as *Silphium perfoliatum* (Electronic Appendix 2); their occurrence is mostly restricted to a single or a few sites. The phenomenon of transience is in fact the main reason why the exact number of taxa in the ornamental flora remains unknown; many rare species are never recorded in surveys like ours due to their random spatial and temporal distribution. Therefore, any estimate of the total pool of taxa in an ornamental flora based on an extrapolation from core species' numbers needs to have been collected from a large geographic area, which includes various urban habitats. Even then, it is difficult to draw a clear line between the core and transient component of the flora.

The prevalence of rare species in our sample is similar to those previously reported (Smith et al. 2006, Acar et al. 2007, Loram et al. 2008a, b, Marco et al. 2010), with the majority of garden taxa occurring at low frequencies. The large proportion of rare species can be explained mainly by socioeconomic factors, which combine conformity (for example, a species-rich front garden is often a part of a particular life style and used to show off the owner's social status) and individualistic choice (free combination of species from a large available pool of taxa; Daehler 2008, Marco et al. 2010). The concept of transient status of many such species, describing the unstable component of the local flora, relates to dark diversity (Pärtel et al. 2011), which are the species that could be potentially present in a plant community but not recorded at a given site. However, the dark diversity concept is applicable to vegetation with predictable species composition, which is hardly the case reported here. Ornamentals that could be potentially present in the Czech Republic include the vast majority of the World's temperate flora and even many subtropical species, which makes the notion of dark diversity in garden floras less useful than in vegetation studies.

To minimize the taxonomic bias in order to facilitate the comparison of the ornamental flora with the spontaneous one, we closely followed the taxonomic approach used in regional floras. To obtain representative and robust data at the landscape level, the complete inventories of individual sites were made, and the sites were selected so as to cover the variation in the size of settlements, altitudinal and climatic range, geological diversity and biogeography, and by accounting for these factors, also the socioeconomic diversification that they underlie. Our results are highly scale-dependent, which is a common feature of biodiversity studies (Crawley & Harral 2001). Such an effect is manifested in the distribution of species such as *Agave americana*, *Bougainvillea glabra* and *Phoenix* spp., that are typical of large houses with well-lit halls or winter gardens where these plants can be kept over winter. At the scale of individual gardens, these species are rare (they occur at low abundances) but their frequencies at the site scale are rather high, as in each village or city there is at least one such house or villa (Thompson et al. 2003). Overall, the sampling of whole settlements, compared to inventories of individual gardens, overestimates the proportion of rare species in the total flora, but we compensated for this by introducing measures of abundance.

Czech ornamental flora in numbers

Some insights into the size of the actual Czech ornamental flora in private gardens are provided by the estimate based on the species–area relationship, and can be further elaborated by using information from botanical gardens. For a rough comparison of the number of taxa we recorded with the species pool of the Czech botanical gardens, we used data from the online catalogue of botanical gardens (http://www.florius.cz; accessed September 2015), which lists ~47,000 names of different taxonomic ranks. To make this data comparable with the results of our survey, the list was aggregated into ~18,000 taxa at species level comparable in status to the taxonomic concepts we used. Of this number, ~16,000 species (89%) were not recorded in gardens during our survey (on the detailed list) or are reported as native or alien species in the Czech flora. We recorded some species that are not included in the botanical garden catalogue (e.g. *Saxifraga tridactylites* and *Clematis pitcheri*), but the difference between the lists is mainly due to greenhouse species of tropical origin that are listed in the catalogue but not grown in small gardens. However, if the collection rarities and plants demanding extraordinary care are included, ornamentals highly outnumber the spontaneous flora.

Data from ornamental plantations comparable to our sample are rare; there are data on a limited number of private gardens in towns or small residential areas. In the city of Sheffield in the UK, 61 urban domestic gardens were surveyed, and of the 1166 species found there, 70% were alien (Smith et al. 2006). Similar data are available for Lauris, an urbanized Mediterranean rural area in France (Marco et al. 2010), and the city of Trabzon in Turkey (Acar et al. 2007), where alien species make up 88% and ~75% of the total floras, respectively. Data on ornamental floras in nine villages in Bulgaria, Montenegro, Greece and Croatia indicate 75–80% of the taxa are alien taxa (J. Sádlo, unpublished data). The results of the present study (1834 taxa; 77% of alien) suggest that the percentage of non-native taxa in the garden flora of the Czech Republic is very similar to these published findings, even though this study covered a much a wider range of urban areas.

Considering taxonomic diversity, biogeography and life forms, escaped aliens occupy an intermediate position between not-escaping and wild aliens, but are closer to the former. This pattern is largely determined by the natural distribution of the introduced taxa. For example in the *Poaceae*, main source of wild aliens is the Mediterranean area (due to many annual weeds such as *Bromus*), the cultivated taxa come from Asia (such as *Bambusoidae*, which are mostly unable to escape from cultivation), and escaped aliens originate from a wide range of regions such as Asia, the Mediterranean area and Americas. Similarly, in the *Lamiaceae*, both wild taxa and escaped aliens are often of European or Mediterranean origin, whereas cultivated taxa are usually not from Europe (probably as most of local species suitable for horticulture have already proved their ability to escape) but from the Americas, Asia and the Mediterranean area (subtropical genera such as *Plectranthus*).

Stochasticity, propagule pressure and escape from cultivation

A large percentage of the ornamental taxa in our sample grow both in cultivation and in the wild in the Czech Republic. This overlapping groups comprise native species and wild aliens (Fig. 2), accounting for 45% of the ornamental flora as recorded by our study, and 24% of the total spontaneous flora (Danihelka et al. 2012, Pyšek et al. 2012b).

Among the 100 most abundant ornamentals recorded in this survey 59% are wild aliens and 16% cultivated natives.

It needs to be kept in mind that the naturalization of aliens introduced as ornamentals begins during cultivation (Mack 2000, Pyšek et al. 2011). Many cultivated species indicate their potential to escape or naturalize by self-sowing in the garden beds (e.g. *Echinacea purpurea*) or by spreading clonally after a strong disturbance (e.g. *Campsis radicans*). Several wild aliens are often transferred back from the wild into cultivation (e.g. *Heracleum mantegazzianum*, *Solidago* spp.). Other species are directly released from gardens into the wild, which is at present the case for some wetland plants such as *Typha laxmanii* or *Sarracenia* spp. Other observed phenomena include repeated "back and forth movement" of plants between gardens and nature (e.g. *Aster amellus* and *Crocus* spp.), associated genetic changes resulting from selection by breeding for special traits (e.g. white-flowered *Polemonium caeruleum*), hybridization (e.g. *Primula veris* hybrids and *Aquilegia vulgaris* hybrids) or introduction of non-native races of native species (*Campanula persicifolia* subsp. *sessiliflora* and *Geranium sanguineum* var. *striatum*). Interestingly, many rare native species are much more frequently recorded in cultivation than in the wild, and new localities are known to be a result of planted source populations and may be important for in situ conservation (see Coomes & Ban 2004). For example, *Prunus tenella* naturally occurs at as few as three sites in southern Moravia (Chrtek 1992, www.florabase.cz), but was recorded at 51% of the sites we sampled and throughout most of the Czech Republic. Moreover, it is often encountered growing outside gardens in adjacent ruderal habitats.

Our inventory yielded 32 species classified as invasive in the Czech Republic (Pyšek et al. 2012b). Among these, those with high planting frequencies were mostly tall herbaceous plants or woody plants occupying a wide range of habitats (e.g. *Symphoricarpos albus*, *Solidago canadensis*, *Parthenocissus* sp.). Many of these invasive aliens belong to taxonomically rather difficult groups and genera, including hybrids or cultivars (e.g. *Aster novi-belgii* agg., *Prunus cerasifera*, *Lupinus polyphyllus* agg.). In contrast, invasive aliens that are rarely planted as ornamentals include many short weedy herbaceous plants that are typical of ruderal habitats (e.g. *Conyza canadensis*, *Echinochloa crus-galli* and non-ornamental forms of *Oxalis corniculata*). In some species, awareness of their problematic status has resulted in them being partly eliminated from cultivation and from the wild (*Heracleum mantegazzianum*). Nevertheless, many invasive aliens are still popular among gardeners, beekeepers and landscape architects. Even though their significant negative impacts are well known, some of them are widely planted throughout this country (e.g. *Symphoricarpos albus*, *Solidago canadensis*, *Prunus cerasifera* and *Lupinus polyphyllus*; Hejda et al. 2009).

As our data implies, the ornamental flora, being continuously enriched by new species, cultivars, varieties and hybrids, is a huge reservoir of potentially new naturalized or even invasive species. Even if new introductions ceased immediately, there are many species already introduced that could escape and naturalize (Kowarik 1995, Hulme et al. 2009), creating an invasion debt (Essl et al. 2011). Assessed based on their invasion potential, alien ornamentals planted in private gardens range from (i) highly invasive taxa already present in the country's flora such as *Impatiens glandulifera* and *Lupinus polyphyllus*, (ii) species that are most likely "safe" provided environmental conditions do not change (see Dehnen-Schmutz 2011), to taxa (iii) that can be considered "safe" based on the fact that they have been cultivated for a long time without escaping (e.g. *Hosta* spp. and *Hydrangea macrophylla*). However, many species are rarely or cultivated for only a short period, and their naturalization might turn out to be an open window of opportunity rather than an increase in propagule pressure. This is the case of taxa that are rarely planted but capable of thriving as highly invasive species in suitable environments, such as *Alyssum murale*.

An important issue related to the association of horticulture with the spontaneous flora is the direct impact of planted taxa have on natural processes by hybridizing with wild native species (Krahulcová et al. 1996, Daehler & Carino 2001, Stace & Crawley 2015, Vítová et al. 2015) or competing for pollinators (Chittka & Schürkens 2001, Jakobsson et al. 2009, Morales & Traveset 2009). Thus, a robust and scientifically based assessment of the propagule pressure of ornamental plants and their species pools is an important first step towards understanding the role of ornamental plants, and horticulture in general, in plant invasions and their impact on biodiversity (Humair et al. 2014). In this paper, by attempting to approximate the diversity of ornamentals based on real sampling, we set the scene for a deeper understanding and quantification of complex landscape processes connected with the cultivation and escape of ornamental plants.

See www.preslia.cz for Electronic Appendices 1–3

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Souhrn

Přestože je zahradní flóra v ekologických studiích většinou přehlížena, je důležitým zdrojem nepůvodních a často i invazních druhů rostlin. Okrasné rostliny zahrnují nejen druhy nepůvodní, ale ve velké míře i druhy původní. Tato studie, založená na terénním výzkumu v České republice, přináší nové informace o diverzitě okrasné flóry ve vztahu k flóře spontánní. Výzkum probíhal ve veřejném prostoru a v soukromých zahradách ve městech, vesnicích, osadách, zahrádkářských koloniích a hřbitovech. Získané údaje o četnosti pěstování jednotlivých druhů tak mohou sloužit jako odhad přísunu diaspor. Sestavili jsme dva seznamy rostlin, a to detailní, zahrnující všechny v terénu zaznamenané taxony, a agregovaný, vzniklý sloučením blízce příbuzných druhů, jejichž určování je obtížné, přičemž druhý seznam byl využit pro odhad frekvence pěstování. Ke každému taxonu v detailním seznamu jsme přiřadili informaci o tom, zda se jedná o druh původní, anebo zavlečený (v tom případě i o oblasti původního rozšíření), životní formě a pěstebních nárocích. Pro srovnání se spontánní flórou jsme použili seznamy původních a nepůvodních druhů rostlin České republiky, které jsme upravili tak, aby odpovídaly taxonomickému pojetí používanému při naší inventarizaci zahrad. Celkem jsme navštívili 174 obcí nebo městských částí, ve kterých jsme zaznamenali 1842 taxonů. Z nich 1642 bylo možné určit do druhu, 9 kultivarů do rodu, 147 bylo kříženců a 44 taxonů se podařilo určit jen na úrovni agregátu nebo jiného vyššího ranku. Z uvedeného počtu je 1417 (76,9 %) taxonů v České republice nepůvodních a 420 (22,8 %) původních. Okrasnou flóru jsme rozdělili na nezplaňující nepůvodní druhy, zplaňující nepůvodní druhy a pěstované původní druhy. Ze zaznamenaných druhů je 841 (45,6 %) jak pěstovaných, tak zplaňujících. Na agregovaném seznamu bylo 1514 taxonů, z nichž 205 vzniklo sloučením 533 taxonů z detailního seznamu. Většina nepůvodních okrasných rostlin pochází z Asie a Severní a Jižní Ameriky. Podíl zplaňujících nepůvodních druhů je větší než zastoupení této skupiny ve spontánní flóře České republiky. Rostliny původem z Austrálie, Afriky a Středozemí zplaňují méně často než rostliny pocházející odjinud. Analýza frekvence pěstování ukázala, že 270 taxonů bylo zaznamenáno ve více než 25 % obcí nebo městských částí, zatímco 584 (40 %) taxonů se vyskytovalo jen v jedné nebo dvou obcích. Jednoletky (letničky) a keře jsou nejčastější životní formy mezi pěstovanými nepůvodními druhy. Pouze několik původních druhů, jmenovitě *Vinca minor*, *Hedera helix* a *Aquilegia vulgaris*, se pěstuje se stejně velkou frekvencí, jaká byla zjištěna pro nejčastěji pěstované nepůvodní druhy. S ohledem na invazní potenciál byly druhy rozděleny podle charakteru rozšíření na druhy přechodně se vyskytující (transientní) a přetrvávající. Přetrvávající část okrasné flóry tvoří 599 taxonů (32 %) a transientní 240 (13 %) taxonů. Do „šedé zóny" mezi těmito dvěma ostře vymezenými skupinami spadá 1003 (55 %) taxonů.

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