

Nurseries and garden centres act as hubs of alien plant invasions: a case study from Hungary

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Abstract: The growing global horticultural trade has a key role in the introduction of alien plant species into new areas, partly because it also entails the unintentional dispersal of many contaminant species over large distances. However, apart from sporadic reports of such contaminant species, this phenomenon is largely understudied. In order to study this, a systematic field survey of garden centres in Hungary was carried out to assess their role in unintentionally introducing invasive alien species. Twelve garden centres were surveyed in spring, summer and autumn and all individuals of alien species recorded. In addition to the pots and containers of plants for sale, all indoor and outdoor areas, such as flowerbeds, bare and covered surfaces, cracks in the pavement, lawns and other vegetated areas were surveyed. A total of 93,788 individuals of 67 alien species were recorded, seven of which were recorded for the first time in this country. Despite their small area, the studied garden centres hosted a large percentage of the local alien flora, indicating that they strongly accumulate alien species. There were large populations of many alien species, suggesting that garden centres can act as invasion hubs. Trait differences between the alien species in the garden centres and the regional alien flora indicate that the species most successful at colonizing garden centres are both good dispersers and possess an effective resource-acquisitive strategy. Thus, populations of alien plants in garden centres may be the source of local invasions. Moreover, individuals and seeds in the containers of ornamental plants are likely to be transported to distant areas by customers. Despite the limited spatial extent of this survey, the findings indicate that the horticultural trade may act not only as a source of plant introductions, but can also potentially influence the subsequent stages of the invasion process. Thus, there is a need for further studies on the role of species contaminating horticultural stock in alien plant invasions.

Keywords: alien species, horticulture, human-mediated dispersal, nursery industry, plant invasion

Introduction

Invasive alien species are one of the major drivers of environmental change worldwide (Díaz et al. 2019). As summarized in the review of Pyšek et al. (2020), invasive species can have a multitude of adverse effects, such as reducing biodiversity, disrupting food webs, altering habitat structure, and ultimately altering ecosystem functions and services (Ehrenfeld 2010, Vilà et al. 2011). In addition, invasive species can also be detrimental to human health and economy (Early et al. 2016, Haubrock et al. 2021). Global changes, including climate change and anthropogenic habitat conversion, as well as the rising rates of international trade and transport, are major drivers in the spread of invasive species (Bradley et al. 2010, Pyšek et al. 2020, Hulme et al. 2023), and climate change is expected to further increase the number and effect of plant invasions globally (Early et al. 2016, Dullinger et al. 2017). Hence, it is important to obtain a better understanding of the spread of invasive species.

Long-distance dispersal events play a crucial role in many large-scale ecological processes (Nathan 2006, Paulose & Hallatschek 2020), such as gene flow between distant populations (Clobert et al. 2012) and range shifts associated with changing landscapes and climates (Clark et al. 1999). Biological invasions are also more likely to be driven by long-distance dispersal events than local dispersal (Kot et al. 1996, Nathan 2006). As long-distance dispersal is very difficult to study, our understanding of it is still severely limited (Levin et al. 2003, Jordano 2017), which also prevents a full understanding of the processes underlying the spread of invasive species. Human activity has historically been a considerable factor in the dispersal of species, both accidentally and on purpose (Hulme 2009, Bullock et al. 2018). Moreover, due to the quickly rising rates of global trade and human mobility in the last century, humans have presumably become the major dispersal vector (Hodkinson & Thompson 1997). Humans can now also be considered as the main long-distance dispersal vector (Higgins et al. 2003, Taylor et al. 2012), suggesting that the increasing levels of globalization and human activity has led to more chances for long-distance spread.

Likely associated with the increased chances of long-distance dispersal, all evidence indicates that the rate of invasive species introductions at many locations is also increasing (Lockwood et al. 2005, Hulme 2009) and the spread of invasive species is widely considered to be mainly driven by international trade and transport, both in terrestrial and in aquatic ecosystems (Jenkins 1996, Perrings et al. 2005, Essl et al. 2015). Studies have demonstrated a clear link between the monetary value of imports and the number of invasive species in a country (Vilà & Pujadas 2001, Westphal et al. 2008, Dalmazzone & Giaccaria 2014), and the rate of invasive species accumulation in different species groups in the United States is well described by a model based on the cumulative value of imports (Levine & D'Antonio 2003).

Horticulture has always been one of the most significant human activities responsible for introducing invasive species into new areas (Kenis et al. 2007, van Kleunen et al. 2018), but the growing global horticultural trade (van Kleunen et al. 2018) is increasing the rate at which they are being introduced into new areas (Bradley et al. 2012, Liebhold et al. 2012). Ornamental species are widely known as the main source of introduced alien plants, many of which are capable of becoming naturalized and subsequently invasive in their introduced range (Pergl et al. 2016, Hulme et al. 2018). However, the global horticultural

trade is also responsible for the unintentional dispersal of many contaminant species (Hodkinson & Thompson 1997, Montagnani et al. 2022, Sonkoly et al. 2022).

Nurseries and garden centres (hereafter garden centres for simplicity) have been repeatedly shown to provide habitat for a wide range of plant species (e.g. Hoste et al. 2009, Gallego & Lumbreras 2013, Takács et al. 2020, Rigó et al. 2023), plant pathogens (Bienapfl & Balci 2014, Jung et al. 2016), molluscs (Bergey et al. 2014, Páll-Gergely et al. 2020) and planarians (Lazányi et al. 2024). Alien species found in the diverse anthropogenic microhabitats inside the garden centres can arrive there via various pathways. They can come from nearby populations, but also from much more distant locations via long-distance dispersal, for example, they may be dispersed on the clothing and footwear of the staff or the customers (Ansong & Pickering 2016, Lukács et al. 2024) or attached to vehicles (von der Lippe & Kowarik 2007, Taylor et al. 2012). Moreover, in addition to pathogens (e.g. De Groote et al. 2006, Bienapfl & Balci 2014), horticultural substrates are frequently contaminated with seeds and other plant propagules (Conn et al. 2008, Dyer et al. 2017, Sonkoly et al. 2022). Therefore, importing plants in containers is likely to disperse species over large distances and potentially introduce new alien species into garden centres, which can act as sites for multiplication and acclimatization for many of them.

To develop evidence-based and effective strategies for the prevention of further plant invasions, more research is needed on the role of the horticultural trade in the unintentional spread of alien plant species (van Kleunen et al. 2018). Although there are reports of noteworthy occurrences of alien plant species in garden centres (e.g. Gallego & Lumbreras 2013, Takács et al. 2020, Molnár V. et al. 2024, Dudáš et al. 2025), their occurrence has hardly been studied systematically (but see Hoste et al. 2009). Codes of conduct for the horticultural industry regarding invasive species also exist (e.g. Baskin 2002, Brundu et al. 2011), but these typically focus on the deliberately introduced ornamental plants rather than on the accidental introductions of contaminant species. To bridge this knowledge gap, we conducted systematic field surveys in order to assess which alien plant species occur in garden centres and what is their abundance. We hypothesized that (i) the number of alien species in garden centres is positively correlated with their size, (ii) relative to their size, garden centres host a disproportionately large proportion of the local alien flora, and (iii) alien species inhabiting garden centres differ from the regional alien flora in their ecological and dispersal traits.

Materials and methods

In 2019, three surveys (spring, summer and autumn, separated by 2–3 month intervals) of 12 ornamental plant retailers were carried out in and near the city of Debrecen, Hungary (Fig. 1). These included both nurseries and garden centres of different sizes from small, family-owned businesses to large franchises (ranging from ~1,200 m² to ~12,000 m² in area, see Table 1). Owners and/or managers were informed and gave their consent for the surveys. Repeated surveys in each season during the vegetation period ensured the finding of species with different phenologies. The whole area of each garden centre including both outdoor and indoor areas (buildings and greenhouses) was surveyed, which included examining the pots and containers of ornamentals for sale, as well as flowerbeds, bare soil or covered soil surfaces (with agrotexile or gravel), cracks in the pavement and

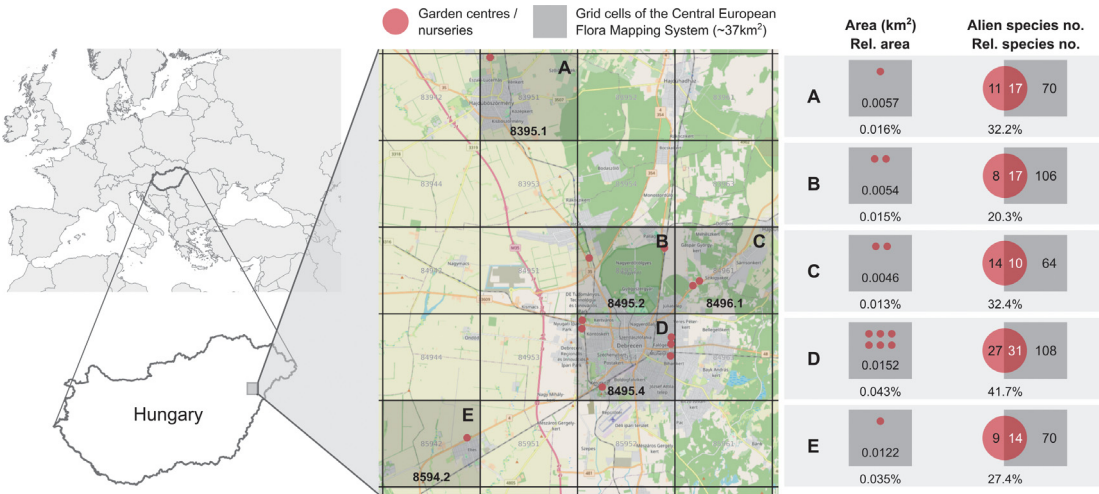


Fig. 1. Species numbers in the garden centres studied, located in and around the city of Debrecen, Hungary. The panel on the right (left column) shows the number of garden centres in each quarter-grid cell of the Central European Flora Mapping System (Niklfeld 1971), their total area and relative area compared to the total area of the grid cell. The right column shows the number of alien plant species recorded in the garden centres (separately for newly recorded species and those that have been known from the given grid cell), the number of alien plant species found in the respective grid cell according to the Vascular plants of Hungary online database (Bartha et al. 2021+) and not in the garden centres, and the percentage of grid-cell's alien species recorded in garden centres.

fugues, lawns and other vegetated areas. All spontaneously occurring individuals of all alien species were recorded, therefore excluding planted individuals and the plants offered for sale. Ornamental plant species (e.g. *Buddleja davidii*, *Pilea microphylla*, *Soleirolia soleirolii*) were also recorded if they occurred spontaneously (as a contaminant) in pots of other species or outside the pots. For species that spread clonally or form mats and in the case of extremely abundant species, the number of individuals was estimated. The native versus alien status of species in Hungary was assessed using the checklist of Csiky et al. (2023); neophytes and archaeophytes were both treated as aliens (see Supplementary Table S1). We treated *Oxybasis glauca* (whose native or alien status in Hungary is debated) as an alien species and therefore included it in the analyses. To compare the percentage of species in each invasion status category (casual, naturalized, invasive, and transformer) between the species documented in the garden centres and the regional alien flora, we considered the invasion status of the species according to Csiky et al. (2023). To compare the percentages in the two species lists, we used Pearson's chi-square test with a simulated P-value (via Monte Carlo simulation) because some cell counts were very low.

The area of the garden centres was measured using Google Earth. The correlation between the area of each garden centre and the number of species and individuals they host was tested using Spearman's rank correlations. The studied garden centres were scattered in five quarter grid cells (hereafter grid cells for simplicity) of the Central European Flora Mapping System (Niklfeld 1971, see Fig. 1). The list of alien species recorded in garden centres located in each grid cell was compared with the list of documented alien

species in the same grid cell, based on Bartha et al. (2021+). To test whether garden centres host a disproportionately large percentage of the local alien flora relative to their size, two metrics were calculated: (i) the percentage of each grid cell's area occupied by the garden centre(s), and (ii) the percentage of the documented alien species in each grid cell (including newly recorded species in the surveys) that were recorded in the garden centre(s) in that grid cell. The two metrics were compared using Wilcoxon rank sum test.

When comparing traits and ecological indicator values (EIVs) of the species found in the garden centres with the traits and EIVs of the total regional alien flora, we considered the alien checklist of Csiky et al. (2023) and obtained data from the Pannonian Database of Plant Traits (PADAPT; Sonkoly et al. 2023). We considered those traits which may influence the species' ability to colonize garden centres and for which data was available for the majority of the species. Based on these criteria, thousand-seed mass (TSM, g), plant height (cm), leaf area (LA, mm²), specific leaf area (SLA, mm²/mg), leaf dry matter content (LDMC, mg/g) and leaf dry weight (LDW, mg) were selected. As EIVs, we used the Borhidi-type indicator values (Borhidi 1995) for soil moisture (W_B), light intensity (L_B) and nutrient supply (N_B), which are based on the indicator values of Ellenberg et al. (1992) and also adapted to the Pannonian Ecoregion. For the species recorded in the garden centres, traits and ecological indicator values were also mainly obtained from the regional database PADAPT (Sonkoly et al. 2023), with missing trait values filled in wherever possible, either by new measurements carried out for the purpose of this analysis or data in the LEDA Traitbase (Kleyer et al. 2008). Traits and EIVs of the two species groups (i.e. recorded aliens vs. the regional alien flora) were compared using Wilcoxon rank sum tests. All statistical analyses were conducted in an R environment (version 4.3.2, R Core Team 2023). Nomenclature follows the Euro+Med PlantBase (2006+).

Results

A total of 93,788 individuals of 67 introduced species were recorded (Table 2, Fig. S1), seven of which are new records for Hungary: *Acalypha brachystachya*, *Fumaria capreolata*, *Gnaphalium pensylvanicum*, *Hylotelephium sieboldii*, *Oldenlandia corymbosa*, *Soleirolia soleirolii* and *Urtica pilulifera*. The majority of the species are neophytes (85%), and only 12% are archaeophytes (the status of 3% of the species was uncertain, see Supplementary Table S1). Most of the species are naturalized in Hungary (32 species), 15 are casual aliens (including the newly recorded species), 14 are invasive, and six of them are considered transformer species in Hungary (Table 1). The proportion of species in each invasion status category differed significantly between the species documented in the garden centres and the species of the regional alien flora (chi-square test, $\chi^2 = 26.798$, $P < 0.0001$), with a higher proportion of invasive and transformer species in the garden centres.

The five most abundant species were *Sagina procumbens*, *Oxalis corniculata*, *Cardamine occulta*, *Oxybasis glauca* and *Euphorbia maculata*, each with more than 10 thousand individuals. On the other hand, 13 species (19%) were each represented by a single individual (Table 2). On average, each species occurred in four of the 12 garden centres. Twenty-eight species (42%) were found in a single one, while six species (*Erigeron annuus*, *Erigeron canadensis*, *Euphorbia maculata*, *Oxalis corniculata*, *Oxalis dillenii* and *Sagina procumbens*) occurred in all the garden centres (Table 2).

Table 1. The location and approximate area of the garden centres studied, together with the number of species and number of individuals documented in them.

Code	Settlement and street name	Coordinates (N, E)	Outdoor area (m ²)	Greenhouse area (m ²)	No. of species	No. of individuals
1	Debrecen, Díszfaiskola street	47.583, 21.592	2,100	–	18	7,928
2	Debrecen, Hét vezér street	47.525, 21.660	1,600	–	29	7,974
3	Debrecen, Vértesi street	47.508, 21.603	2,700	160	29	10,223
4	Debrecen, Kócsag street	47.542, 21.584	1,600	–	31	8,084
5	Hajdúböszörmény, Külső Dorogi street	47.697, 21.507	5,700	1,800	28	5,756
6	Debrecen-Apafa, Route 4	47.587, 21.656	3,300	–	19	5,301
7	Debrecen, Balmazújvárosi street	47.544, 21.586	7,000	1,200	33	8,085
8	Ebes, Route 4	47.478, 21.487	12,000	6,400	12	24,877
9	Debrecen, Budai Nagy Antal street	47.533, 21.660	1,200	700	11	4,168
10	Debrecen, Budai Nagy Antal street	47.532, 21.660	1,500	400	16	1,440
11	Debrecen, Külső Sámsoni street	47.566, 21.682	1,400	1,400	16	2,448
12	Debrecen, Külső Sámsoni street	47.566, 21.683	3,200	–	17	7,504

Table 2. List of the spontaneously occurring invasive alien species in the garden centres studied with the number of recorded individuals and the number of garden centres where they were found. Invasion status in Europe and in Hungary are given according to Kalusová et al. (2024) and Csiky et al. (2023), respectively: nat – naturalized; inv – invasive; trans – transformer; n.l. – not listed in the given source. * species of Union concern (European Commission 2025), ^ species new to alien flora of Hungary. Note that some species are not listed in Csiky et al. (2023) but have been recorded in the country since then.

Species	Total number of individuals	Individuals inside containers	Individuals not in containers	Number of garden centres	Invasion status in Europe	Invasion status in Hungary
<i>Acalypha brachystachya</i> [^]	17	15	2	2	n.l.	n.l.
<i>Acer negundo</i>	1	1	0	1	inv	nat
<i>Acer saccharinum</i>	200	200	0	1	nat	nat
<i>Ailanthus altissima</i> *	4	1	3	4	inv	trans
<i>Amaranthus blitum</i>	94	51	43	10	inv	nat
<i>Amaranthus deflexus</i>	37	9	28	7	inv	nat
<i>Amaranthus powellii</i>	186	2	184	3	inv	nat
<i>Amaranthus retroflexus</i>	412	26	386	7	inv	nat
<i>Ambrosia artemisiifolia</i>	827	91	736	8	inv	nat
<i>Artemisia annua</i>	1	0	1	1	inv	inv
<i>Asclepias syriaca</i> *	1	0	1	1	inv	trans
<i>Buddleja davidii</i>	10	0	10	1	inv	nat
<i>Cardamine occulta</i>	11,395	7,642	3,753	11	nat	n.l.
<i>Chenopodium hybridum</i>	3	0	3	2	nat	nat
<i>Chenopodium murale</i>	8	5	3	1	nat	nat
<i>Chenopodium album</i>	95	21	74	7	nat	nat
<i>Chenopodium betaceum</i>	33	13	20	6	casual	nat
<i>Chenopodium ficifolium</i>	165	164	1	4	nat	nat
<i>Claytonia perfoliata</i>	1	1	0	1	nat	casual
<i>Commelina communis</i>	4	0	4	1	inv	nat
<i>Dysphania pumilio</i>	1	1	0	1	inv	nat
<i>Eclipta prostrata</i>	8	3	5	4	inv	n.l.
<i>Elaeagnus angustifolia</i>	1	1	0	1	inv	trans
<i>Epilobium ciliatum</i>	228	147	81	7	inv	nat
<i>Erigeron annuus</i>	4,529	1,498	3,031	12	inv	inv
<i>Erigeron canadensis</i>	1,629	528	1,101	12	inv	inv
<i>Erigeron sumatrensis</i>	52	0	52	2	inv	n.l.

Species	Total number of individuals	Individuals inside containers	Individuals not in containers	Number of garden centres	Invasion status in Europe	Invasion status in Hungary
<i>Euphorbia maculata</i>	10,113	4,352	5,761	12	inv	inv
<i>Euphorbia peplus</i>	758	109	649	8	inv	nat
<i>Euphorbia prostrata</i>	167	11	156	4	inv	nat
<i>Euphorbia serpens</i>	3,550	918	2,632	5	inv	nat
<i>Fumaria capreolata</i> [^]	1	1	0	1	nat	n.l.
<i>Galinsoga parviflora</i>	726	28	698	8	inv	inv
<i>Galinsoga quadriradiata</i>	73	47	26	5	inv	nat
<i>Geranium dissectum</i>	2	0	2	1	nat	nat
<i>Gleditsia triacanthos</i>	105	0	105	1	inv	nat
<i>Gnaphalium pensylvanicum</i> [^]	1	1	0	1	inv	n.l.
<i>Humulus japonicus</i> *	1	0	1	1	inv	inv
<i>Hylotelephium sieboldii</i> [^]	1	1	0	1	nat	n.l.
<i>Lepidium didymum</i>	2	2	0	1	inv	casual
<i>Microrrhinum minus</i>	21	0	21	1	inv	nat
<i>Oenothera biennis</i>	3	0	3	2	inv	inv
<i>Oldenlandia</i> cf. <i>corymbosa</i> [^]	26	26	0	2	n.l.	n.l.
<i>Oxalis corniculata</i>	15,662	8,614	7,048	12	inv	inv
<i>Oxalis dillenii</i>	6,011	1,789	4,222	12	inv	inv
<i>Oxalis stricta</i>	3,640	2,239	1,401	4	inv	inv
<i>Oxybasis glauca</i>	11,197	4,314	6,883	9	nat	nat
<i>Panicum dichotomiflorum</i>	15	0	15	1	inv	inv
<i>Panicum riparium</i>	44	36	8	2	casual	casual
<i>Parietaria judaica</i>	267	8	259	3	nat	nat
<i>Parthenocissus quinquefolia</i>	3	0	3	1	inv	nat
<i>Phytolacca americana</i>	1	0	1	1	inv	inv
<i>Pilea microphylla</i>	106	79	27	5	casual	n.l.
<i>Polycarpon tetraphyllum</i>	1	1	0	1	nat	nat
<i>Polypogon viridis</i>	11	6	5	1	nat	casual
<i>Populus x canadensis</i>	2	2	0	1	inv	nat
<i>Potentilla indica</i>	2	2	0	1	inv	inv
<i>Robinia pseudoacacia</i>	12	11	1	2	inv	trans
<i>Sagina procumbens</i>	17,672	4,714	12,958	12	nat	nat
<i>Senecio leucanthemifolius</i> subsp. <i>vernalis</i>	6	0	6	1	inv	nat
<i>Soleirolia soleirolii</i> [^]	5	5	0	1	inv	n.l.
<i>Solidago canadensis</i>	36	9	27	3	inv	trans
<i>Solidago gigantea</i>	207	139	68	4	inv	trans
<i>Ulmus pumila</i>	196	78	118	5	inv	inv
<i>Urtica pilulifera</i> [^]	1	1	0	1	nat	n.l.
<i>Veronica peregrina</i>	2,787	626	2,161	9	inv	nat
<i>Veronica persica</i>	412	4	408	6	inv	nat

Fifty-two of the 67 species occurred in the containers of ornamental plants. There were 15 species occurring only outside containers and 15 that occurred only in containers (Table 2). The majority of the individuals were found in outdoor areas (69.9%), while a much lower percentage was in greenhouses (30%, Supplementary Table S1), which reflects the areas of the outdoor and greenhouse areas as a percentage of the total area surveyed (Table 1). Regarding the different locations where alien species were found, pots and containers hosted the highest number of individuals (41.1%), followed by pavement (22.1%) and agrotextile (16.4%), while the remaining 20.4% were distributed among all other types of locations (Supplementary Table S1).

Each garden centre hosted an average of 7,816 individuals of 22 alien species. However, they varied considerably, with species numbers ranging from 11 to 33 and the total number of individuals ranging between 1,440 and 24,877 (Table 1). The number of species in a garden centre was not correlated with the area of the garden centre ($P = 0.314$), however, the number of individuals was significantly positively correlated with the area ($R = 0.606$, $P = 0.037$). The number of species and the number of individuals in a garden centre were also not correlated ($P = 0.105$).

The garden centres occurred in five grid cells of the Central European Flora Mapping System (Fig. 1). Although garden centres covered a very small fraction of the grid cells (ranging from 0.013% to 0.043%), they hosted high numbers of alien species. On average, 17.2% (ranging from 13.5% to 22.3%) of the already known alien flora of the grid cells were found in the comparatively tiny area of the garden centres. In addition, eight to 27 species in the garden centres in each grid cell were not previously documented in those grid cells. The garden centres host a disproportionately large proportion of the local alien flora relative to their size (Fig. 1).

When the alien species recorded in garden centres were compared with the regional alien flora in terms of traits and ecological indicator values (EIVs, see Supplementary Table S1), we found that they had significantly lighter seeds, higher specific leaf area (SLA), lower leaf dry matter content (LDMC), and higher EIVs for soil moisture and nutrient supply than the regional alien flora (Table 3).

Table 3. Traits and ecological indicator values (EIVs) of the alien species recorded in garden centres compared with those of the regional alien flora (Wilcoxon rank sum tests). Abbreviations: TSM – thousand-seed mass; LA – leaf area; SLA – specific leaf area; LDMC – leaf dry matter content; LDW – leaf dry mass; W_B , L_B , and N_B – ecological indicator values for soil moisture, light intensity and nutrient supply, respectively (Borhidi 1995).

	Regional alien flora (mean±SE)	Garden centres (mean±SE)	P-value
TSM (g)	30.1±6.1	10.5±4.3	< 0.0001
Plant height (cm)	306.1±24.2	434.7±114.1	0.636
LA (mm ²)	3,132±385	2,479±675	0.537
SLA (mm ² /mg)	23.5±0.8	31.0±2.3	< 0.0001
LDMC (mg/g)	247.5±5.2	212.9±11.7	0.015
LDM (mg)	196.4±28.5	119.8±33.1	0.058
W_B	4.5±0.1	5.1±0.2	0.005
L_B	7.4±0.1	7.2±0.2	0.205
N_B	5.4±0.1	6.5±0.3	0.001

Discussion

The role of horticultural trade in biological invasions has been mainly considered in the context of ornamental plants escaping cultivation and becoming invasive, and it has been much less considered as a pathway of accidental human-vectored dispersal (Bullock et al. 2018) of contaminant species. This study revealed that, despite their small area, the garden centres contained surprisingly large numbers of alien plant species. Many of these species had large populations, which could facilitate dispersal not just locally in the surrounding landscape, but also more widely, because customers may transport them over

long distances in the containers of the ornamental plants. The fact that the majority of the species were found inside the containers of ornamental plants supports our assumption that most accidental alien plant species arrive at the garden centres via shipments of ornamental plants. This is also supported by the presence of species that have not been previously recorded in Hungary.

The seven species recorded in Hungary for the first time fall into three categories: (i) species of Mediterranean origin, which presumably arrived in garden centres due to the increase in sourcing plants from Mediterranean countries, particularly Italy and Spain (Hoste & Verloove 2009): *Fumaria capreolata* and *Urtica pilulifera*; (ii) emerging species of (sub)tropical origin, which are not yet widespread, but have already been introduced to some temperate regions: *Acalypha brachystachya*, *Gnaphalium pensylvanicum*, and *Oldenlandia corymbosa*; (iii) ornamental species, which are probably present in garden centres due to their widespread cultivation: *Hylotelephium sieboldii* and *Soleirolia soleirolii*. Seventeen of the 67 species documented were also found in containers of ornamental plants in Belgium (Hoste et al. 2009), including two of the species new to the Hungarian flora (*F. capreolata* and *G. pensylvanicum*).

The most abundant alien species in garden centres were mostly already quite widespread both in Hungary and in Europe (Kalusová et al. 2024). However, the third most abundant species, *Cardamine occulta*, of which more than 11,000 individuals were recorded, was only included in the alien plant inventory of eight out of 55 European countries and territories up until 2022 (Kalusová et al. 2024) and was also only recently found in Hungary (Takács et al. 2020). This species has quickly spread in Europe in places where its occurrence can be attributed to the horticultural trade (see e.g. Leostin & Mayorov 2019, Šlenker et al. 2019, Pliszko 2020, Hruševár et al. 2021, Király et al. 2021, Kovács et al. 2023).

Both the number of species and the number of individuals were highly variable across the garden centres studied. We hypothesized that the number of alien species found in a garden centre is positively related to the size of the garden centre, as larger garden centres presumably have a larger incoming stock. A larger incoming stock can be associated with higher propagule pressure (i.e. a larger number of individuals released into the area), which is considered as one of the most important factors determining the success of invasive species (Lockwood et al. 2005, Colautti et al. 2006). In addition, a survey of land snails in plant nurseries revealed that the number of taxa occurring in a nursery was positively related to its area (Bergey et al. 2014). Despite this, there was no relationship between the size of a garden centre and the number of alien plant species it hosts. However, there was a significant positive relationship between the size of a garden centre and the number of alien plant individuals found in it. The highest numbers of alien species were recorded in garden centres that, rather than being the largest in area, were the busiest and offered the greatest diversity of plants for sale in our experience. This observation is in line with the key importance of propagule pressure, but, unfortunately, we have no data to test this assumption.

We also hypothesized that, relative to their size, garden centres host a disproportionately large percentage of the local alien flora. Although the garden centres cover only a very small fraction of the area of the flora mapping grid cells they are located in, they host a high percentage of the recorded alien flora within those grid cells, supporting this hypothesis. This result illustrates that garden centres strongly accumulate alien species

and that they can act as invasion hubs for several new invading species (Letnic et al. 2015). Human-vectored dispersal can result in spatially aggregated populations of alien species, which frequently occur in and around anthropogenic habitats (Bullock et al. 2018). These habitats can function as invasion hubs, from which established satellite populations of alien species can spread further into the landscape (Suarez et al. 2001, With 2002). Because eradicating such invasion hubs is a targeted and effective way of reducing the spread of invasive species (Moody & Mack 1988, Florance et al. 2011), their identification is a very important step in controlling this phase of invasion.

The hypothesis that alien species in garden centres differ from the regional alien flora in their traits was partially supported by the results. There was no difference between these two groups of species in terms of plant height and leaf size (expressed in terms of specific leaf area and leaf dry mass). On the other hand, the documented alien species had significantly lower LDMC and higher SLA compared to the regional alien flora, which indicates that they are placed on the leaf economic spectrum towards the fast-growing, resource-acquisitive strategies (Leishman et al. 2007). The fact that the recorded alien species had a lower seed mass is probably due to the presumed better dispersal ability (Guo et al. 2000, Tremlová & Münzbergová 2007) and longer seed persistence (Thompson et al. 1993, Zhao et al. 2011) of small-seeded species. Persistent seeds remain viable in containers throughout the potentially lengthy transportation process from wholesalers to garden centres (and eventually to the customer's gardens). These findings indicate that the species that are most successful at colonizing garden centres are both good dispersers and have a resource-acquisitive strategy (Wright et al. 2004, Pierce et al. 2014), because they need to be able to grow and reproduce quickly. Species with a slow growth rate, high stature or long life cycle also occasionally appear in garden centres, but they are less abundant and unlikely to establish self-sustaining populations within the garden centres. Thus, horticultural trade can play a role in their introduction, but the garden centres themselves play a less important role as invasion hubs for these species (Suarez et al. 2001, Letnic et al. 2015). Regarding ecological indicator values, the alien species in garden centres had significantly higher values for soil moisture and nutrient supply than the regional alien flora, which indicates the effect of fertilizer use and frequent irrigation in nurseries and garden centres.

Fifty-two of the recorded 67 species occurred in the containers of ornamental plants. As the customers regularly transport the containers over great distances, further long-distance dispersal of these species can be expected regularly (Hodkinson & Thompson 1997, Bergey et al. 2014). The 15 species not recorded in containers may have arrived in the garden centres from populations in the neighbouring area by other means of dispersal than as contaminants of horticultural stock. Individuals outside containers are not readily transported to distant areas, but as several species had populations of considerable size even outside the containers (*Cardamine occulta*, *Euphorbia* spp., *Oxalis* spp., *Veronica peregrina* etc.), they can exert sufficient propagule pressure to induce local invasions.

Regarding the genetic effects of accidental long-distance dispersal associated with the horticultural trade, it is likely that these long-distance dispersal events commonly lead to low genetic diversity in the introduced populations due to strong founder effects (Setsuko et al. 2020, Wu et al. 2023). On the other hand, long-distance dispersal by humans often transports many propagules or individuals of a species at a time (Bullock et al. 2018). If propagules arriving at a site are from different areas and the genetic makeup of the

species in its native range is spatially structured, the genetic diversity of such introduced populations may be higher than that in any of the native source populations (Lockwood et al. 2005, Smith et al. 2020), which can minimize Allee effects and founder effects (Wu et al. 2023). This supports the notion that the international horticultural trade not only has a key role in new species introductions, but also increases the chance of successful invasions due to the recurring introductions of alien plants into local outlets of the global horticultural trade (Dehnen-Schmutz et al. 2007), which increase the chances of novel genetic combinations and evolutionary shifts (Kolbe et al. 2004, Lockwood et al. 2005, Šlenker et al. 2018).

It is frequently suggested that managing and controlling invasive species is easiest and most cost-effective in the early stages of the invasion process (e.g. Rout et al. 2011, Simberloff et al. 2013, Chapman et al. 2016). Specifically, eradicating recently established satellite populations (Moody & Mack 1988, Florance et al. 2011) or reducing the probability of long-distance dispersal events that create such populations (Buckley et al. 2005, Shea et al. 2010) can be especially effective in controlling the spread of invasive species. Our results indicate that eradicating new populations of alien species in garden centres would be easier and more cost-effective than focusing the control measures on older and bigger populations. Therefore, early detection and eradication of satellite populations in garden centres should be a priority in invasive species management. In the meantime, there is a need to raise public awareness, thus both the managers and employees of plant nurseries and garden centres, as well as the customers should be educated and informed about the potential adverse consequences of new plant species introduced as contaminants in the containers of plants.

It has to be noted that our assessment of the role of garden centres as invasion hubs is somewhat limited due to the lack of reliable information on which species arrived at the garden centres by long-distance dispersal via the horticultural trade and which came from existing populations in the neighbouring areas. However, it does not refute the fact that even the species originally entering the garden centres from the neighbouring populations can be further dispersed by customers transporting the containers to distant areas. Furthermore, this survey was of a relatively small area; thus, the limited spatial extent of the study makes it difficult to draw general conclusions. Due to these limitations and the complexity of this phenomenon, many questions remain unanswered. For example, the propagule content of the containers of ornamental plants has been rarely studied (but see Cross & Skroch 1992, Conn et al. 2008). Assessing the different pathways by which propagules can reach these containers could also provide information about the step of the horticultural trade at which interventions could be the most effective.

Conclusions

This study is one of the few assessments of the accidental dispersal of plants as contaminants of plants offered for sale by the horticultural trade. The garden centres surveyed hosted large populations of alien species, therefore they may serve as invasion hubs. Propagule pressure of the populations in garden centres can be sufficient to result in local invasions. In addition, individuals occurring in containers and their seed bank are regularly transported to distant areas by customers, where they may establish new invasion

hubs. Thus, the horticultural trade may not only be a pathway of alien plant introductions, but also important in the subsequent stages of the invasion process. Due to the diverse range of species and the large number of propagules arriving with increasing inflow of horticultural stock, it is highly likely that at least some of them will be naturalized and ultimately become invasive in their new range. Although more attention has been paid to other introduction pathways such as deliberate introductions for ornamental purposes, this study indicates that plant species dispersed as contaminants of horticultural stock need to be better considered in invasion biology in order to reduce the threat they may present.

Supplementary materials

Fig. S1. Photographs of some of the recorded alien species and their habitats in the garden centres studied.

Table S1. Numbers of individuals of each species in different specific locations in garden centres and data on the traits of the species used in the analyses.

Supplementary materials are available at <https://www.preslia.cz>.

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Zahradní centra jako zdroj neúmyslného zavlékání nepůvodních rostlin a lokálních invazí – případová studie z Maďarska

Rostoucí globální zahradnický obchod hraje klíčovou roli při zavlékání nepůvodních druhů rostlin do nových oblastí, mimo jiné proto, že s sebou nese i neúmyslné šíření mnoha druhů na velké vzdálenosti. V Maďarsku jsme provedli systematický terénní průzkum dvanácti zahradních center, zaměřený na posouzení jejich role v neúmyslném zavlékání invazních druhů rostlin. Zaznamenali jsme všechny jedince nepůvodních druhů v květináčích a kontejnerech rostlin určených k prodeji i na všech vnitřních a venkovních plochách, jako jsou záhony, nezakryté i zakryté povrchy, dlažební spáry, trávnický a další plochy s vegetací. Celkem jsme zaznamenali 93 788 jedinců 67 nepůvodních druhů, sedm z nich bylo pro Maďarsko nových. Navzdory malé rozloze hostila studovaná zahradní centra značný podíl místní nepůvodní flóry, u mnoha druhů byly navíc zjištěny početné populace, což ukazuje, že nepůvodní rostliny v zahradních centrech mohou představovat zdroj lokálních invazí. Nepůvodní rostliny a jejich semena v kontejnerech s okrasnými rostlinami jsou navíc pravděpodobně zákaznický transportovány na velké vzdálenosti. Přes omezený rozsah tohoto výzkumu výsledky ukazují, že zahradnický obchod může fungovat nejen jako zdroj introdukcí rostlin, ale potenciálně může ovlivňovat i následné fáze invazního procesu.

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