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Research Article

Unintentional seed dispersal via container-grown garden plants: Seed density and composition vary among exporter countries

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Abstract

The global ornamental plant trade is well-known as an important source of non-native plants, but the unintentional dispersal of seeds as contaminants of this trade is rarely considered and largely understudied. We sampled the substrate of imported container-grown plants in six garden centres in Hungary to answer the following questions: (i) What species' seeds are present in the substrate of imported garden plants and in what quantity? (ii) Do the substrates of plants imported from different countries contain seeds in different density and composition? (iii) Do characteristics of the host garden plants affect the number and diversity of seeds found in their substrate? In the studied 60 litres of substrate samples, we detected altogether 2,181 seeds of 80 taxa. On average, 1 litre of substrate contained 36 seeds of five species. Most species were non-native in Hungary and 48% of the samples contained at least one seed of a recently introduced, emerging neophyte. We found that the substrate of plants imported from different countries contained seeds in different number, diversity, and composition**.** Thus, the structure of the horticultural trade network can have an effect on the non-native flora of importing countries. Furthermore, the substrate of needle-leaved ornamental species contained more seeds than the substrate of broadleaved ornamentals. Our findings provide further evidence that the ornamental plant trade can disperse a large number of seeds of numerous species and introduce new non-native species into the importing countries. We conclude that this introduction pathway deserves greater attention in invasion biology.

Key words: Alien plants, container plants, contaminant pathway, horticultural trade, invasive species, plant nursery, plant trade

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Introduction

Being able to understand and foresee biological invasions is increasingly important in the era of global change (Bradley et al. 2010; Pyšek et al. 2020). The activities of humans are the most important factors driving biological invasions (Pyšek et al. 2010; Bertelsmeier et al. 2017). Trade and transport shape invasions especially strongly (Perrings et al. 2005; Meyerson and Mooney 2007), with most harmful invasive species reaching new regions through trading activities (Levine and

D'Antonio 2003). The monetary value of imports into a country is also clearly linked to the number of non-native species in that country (Vilà and Pujadas 2001; Westphal et al. 2008). Therefore, the characteristics of trade and transport networks can even be used to assess invasion risk and the propagule pressure associated with specific commodities (Chapman et al. 2017). The volume of international trade is expected to increase in the coming decades (Chateau et al. 2015), likely resulting in a further increase in the number of non-native species worldwide.

The likelihood of a species becoming invasive in a region depends on the introduction pathway by which it reached the particular region (Hulme et al. 2008a; Pyšek et al. 2011). Information on what species are introduced via a specific pathway can therefore facilitate risk assessment and import regulations (Hulme et al. 2008b; Saul et al. 2017) and reduce non-native species introductions (Hulme et al. 2008a; Novoa et al. 2020). The transport and introduction phases of invasions are clearly highly relevant for invasive species management and policy, yet these phases are less researched than the spreading phase and the effects of invasive species (Chapman et al. 2017). It was also emphasised by many authors that more effort and resources should be concentrated on the introduction stage of invasions (Leung et al. 2002; Westphal et al. 2008; Simberloff et al. 2013). Based on the above considerations, it is vital to have a comprehensive view of the different pathways by which species are introduced into new regions (Essl et al. 2015; Chapman et al. 2017).

A high proportion of the non-native plant species worldwide have been deliberately introduced as ornamental plants (Haeuser et al. 2018; Dawes et al. 2025), but unintentional introductions are also known to be a prominent source of non-native invasive species (Lambdon et al. 2008; Lehan et al. 2013). In the Czech Republic, for example, 772 plant taxa were listed as introduced unintentionally (Pyšek et al. 2022), while 446 (51%) of the listed 878 alien plant species in Hungary were accidentally introduced into the country (Csiky et al. 2023). Unintentionally introduced non-native species frequently reach new regions as contaminants in traded commodities (Hulme et al. 2008a). According to Pyšek et al. (2009), 403 plant species have been introduced to Europe as contaminants of commodities (e.g., via seeds and mineral materials), which constitute 17% of all recorded non-native species. Intentional releases and escapes from cultivation are well-recognized introduction pathways; therefore, their relative importance is already declining (Hulme et al. 2008a; Seebens et al. 2023). On the other hand, the number of new introductions through other pathways (such as the contaminant, stowaway, and corridor pathways) is still increasing (Hulme et al. 2008a; Seebens et al. 2017).

Most studies demonstrating that invasions are closely linked to international trade considered trade as a whole, such as the total value of imports (e.g., Vilà and Pujadas 2001; Westphal et al. 2008). More recently, the live plant trade has been found to be more closely related to the distribution of invasive species than trade in general (Chapman et al. 2017). The international live plant trade experienced a significant growth in recent decades (Hinsley et al. 2025), and is a considerable part of global commerce, with an export value of USD 11.8 billion in 2024 (International Trade Center 2025). Horticultural trade, considering both live plants and horticultural substrates (growing media), has been shown to disperse a range of plant pathogens (e.g., Liebhold et al. 2012; Bienapfl and Balci 2014), invertebrates such as insects and snails (Sæthre et al. 2010; Moore et al. 2016), and even vertebrate species (Silva-Rocha et al. 2015; Rato et al. 2023). In certain areas, many different non-native species have been first documented in plant nurseries and garden centres, such as snails (Bergey et al. 2014; Páll-Gergely et al. 2020) and planarians (Lazányi et al. 2024), which also suggests that they presumably reached the new sites via the horticultural trade. Several non-native plant species have also been first detected in nurseries and garden centres (e.g., Hoste et al. 2009; Molnár et al. 2024; Sonkoly et al. 2025), but direct assessments of the dispersal of plant propagules as contaminants of horticultural stock are rare. The viable seed content of imported container-grown plants was studied in Alaska (Conn et al. 2008) and in Norway (Bruteig et al. 2017), and the unordered additional plant species and seeds accompanying aquatic plants ordered from plant vendors throughout the USA were assessed by Maki and Galatowitsch (2004). However, to our knowledge, there are no other studies of this issue so far.

Propagule pressure is consistently positively correlated with establishment success (Cassey et al. 2018) and it is considered one of the most important factors determining the success of biological invasions (Colautti et al. 2006; Lockwood et al. 2005). Thus, deepening our understanding of it is vital for anticipating future invasions (D'Antonio et al. 2001; Cassey et al. 2004). Unfortunately, direct information on propagule pressure is difficult to obtain (D'Antonio et al. 2001; Eschtruth and Battles 2011), especially for plants and other organisms introduced via small propagules which are challenging to detect and identify. As the live plant trade is now recognised as a pathway for accidental non-native plant introductions (mostly in the form of contaminant seeds), it is timely to increase our knowledge of the species dispersed via this pathway and the propagule pressure it generates. However, invasive species policy in ornamental horticulture generally overlooks the accidental dispersal of contaminant plant species (see e.g., Barbier et al. 2013; Hulme 2015; Hulme et al. 2018). Even a recent review summarising the environmental and societal risks of the international ornamental plant trade has ignored contaminant plant species and only focused on the animal species hitchhiking on traded live plants (Hinsley et al. 2025). To prevent the introduction and spread of plant pests and diseases, EU legislation allows importing live plants together with growing media from non-member countries only if the growing medium meets strict phytosanitary requirements outlined in Annex VII of Commission Implementing Regulation (EU) 2019/2072 (European Commission 2019). However, these regulations are designed primarily to address plant health concerns and not to prevent the accidental introduction of non-native seeds. Moreover, the trade of live plants and their associated growing media between EU member countries is subject to much less strict regulations. The EU Plant Passport, outlined by Regulation (EU) 2016/2031 (European Parliament and Council of the European Union 2016), guarantees that the plant has been inspected regularly and it is free from quarantine pests and diseases, but it does not account for contaminating seeds in the growing medium.

Based on the above considerations, it is timely to gain more knowledge on what plant species are dispersed as contaminants of container-grown plants and in what quantities. Identifying the factors that influence seed density and composition of container substrates is also essential for improving our ability to anticipate introductions and to design more effective preventive measures and policy instruments. The exporter country of the plant may be such an influencing factor (see Bruteig et al. 2017). The substrates of container-grown plants arriving from different countries may contain different amounts of seeds and in different composition due to several reasons, including differences in their regional flora or in the weed management practices employed by the nurseries (Conn et al. 2008; Stewart et al. 2017). Some characteristics of the garden plants may also influence the number and diversity of seeds in the substrates (see e.g., Conn et al. 2008). For example, it usually takes more time to grow woody plants than herbaceous ones, which provides more time for seeds to accumulate in their substrates. Species with slow growth rates also take more time to reach a marketable size than fast-growing species, therefore they may also be more likely to accumulate seeds in their containers.

In this study, we sampled the substrate of recently imported container-grown garden plants in multiple garden centres in Hungary to answer the following questions: (i) What species' seeds are introduced as contaminants of the substrate of garden plants and in what quantity? (ii) Do the substrates of garden plants imported from different countries contain seeds in different density and composition? (iii) Do characteristics of the garden plants affect the number and diversity of seeds found in their substrate?

Methods

Sampling and germination

To assess the viable seed content of the substrate of imported container-grown plants for garden use (hereafter 'garden plants'), we took substrate (i.e., growing media) samples from the containers of recently imported perennial garden plants in six garden centres in North-Eastern Hungary in the spring of 2023 (Table 1, Fig. 1). We aimed to sample the substrate of recently imported plants to avoid collecting seeds and other generative propagules (hereafter referred to as 'seeds' for simplicity) that may have been accumulated in the containers due to exposure to the local seed rain. To this end, garden centre employees assisted us in selecting plant batches that had arrived earlier that spring, thereby ensuring that the sampled substrates had not been exposed to local seed rain. We collected a total of 60 one-litre samples (see Suppl. material 1). Each sample was pooled from multiple containers of the same garden plant species and batch, which were chosen based on the availability of batches that arrived recently. For large garden plants, whose containers were also large and available in limited numbers, the one-litre sample was collected from as few as two containers. In contrast, for small garden plants, samples were pooled from 10 to 20 containers, which also helped to avoid damaging the roots. We aimed to sample approximately the upper 5 cm layer of the substrates, and in cases when the surface of the substrate was covered with a mulch layer (wood shavings or pine bark), we excluded the mulch layer from the sample.

Table 1. The location of sampled garden centres in NE Hungary, and the number of substrate samples taken from them. One pooled sample is 1 litre of substrate.

Code	Settlement	Coordinate	Sampling date (2023)	Number of pooled samples
GC01	Miskolc	48.137°N, 20.780°E	29 March	9
GC02	Debrecen	47.508°N, 21.603°E	30 March	8
GC03	Debrecen	47.525°N, 21.660°E	30 March	9
GC04	Nyékládháza	47.988°N, 20.845°E	3 April	9
GC05	Sajószöged	47.948°N, 20.987°E	13 April	8
GC06	Debrecen	47.544°N, 21.586°E	13 April	17

Figure 1. **A.** Sampling the substrate of a batch of *Cedrus deodara* 'Feelin Blue'; **B.** Sampling the substrate of a batch of *Cupressocyparis leylandii* 'Gold Rider'; **C.** *Eclipta prostrata* and a few other seedlings emerging from a substrate sample; **D.** Plants previously transplanted and waiting for identification; **E.** *Eleusine indica* emerging from a sample; **F.** *Symphyotrichum squamatum* germinated from a sample and flowering in the greenhouse; **G.** Individual transplanted for later identification (subsequently identified as *Dittrichia viscosa*). The individuals shown in the photographs are authors of the study and have provided consent for their inclusion. Photographs by J. Sonkoly.

Employees also provided information about the country of origin of the plants: 42 of the sampled garden plant batches were imported from Italy, 16 from the Netherlands and two from Spain (see Suppl. material 1).

The collected samples were then transported to the laboratory of the Department of Ecology, University of Debrecen (Hungary). We used the method of Ter Heerdt et al. (1996) to reduce sample volume, which involves washing the samples through two sieves (mesh size 0.2 mm and 2.8 mm). This method eliminates fine particles by washing them out, while large particles are retained by the coarse mesh, considerably reducing sample volume. The concentrated samples were then spread on the surface of steam-sterilised potting soil in balcony planters (sized approximately 60 cm × 20 cm × 15 cm). Each balcony planter contained a one-litre sample and we also set up five planters only containing sterilised potting soil (no sample) to detect seed contamination during the germination period. Therefore, altogether 65 balcony planters were used in the experiment, which were kept in an unheated greenhouse in the botanical garden of the University of Debrecen. The germination period lasted from 17 April 2023 to 16 November 2023, during which the samples were watered daily. Emerging seedlings were regularly counted, identified and removed. We transplanted the plants that were not yet identifiable into separate pots. The transplanted plants (155 individuals) were further grown until they could be identified, but not later than November 2024, i.e., the end of the second vegetation season.

Calculations and analyses

We categorised the detected species into native and non-native categories based on the checklist of alien vascular plants of Hungary (Csiky et al. 2023). Non-native species were further categorised based on residence time, thereby distinguishing between archaeophytes and neophytes. Neophyte species were further categorised into established neophytes and emerging neophytes, because recently introduced species, which are not yet established in the region represent the highest biosecurity risk. The checklist of Csiky et al. (2023) also categorises species based on invasion status (casual, naturalised, invasive or transformer), and we treated casual neophytes and recently introduced species, which are not yet included in the checklist, as emerging neophytes. Naturalised, invasive, and transformer neophytes were treated as established neophytes.

First, we analysed the effect of the exporter country on the number of seeds and the number of species detected in the samples. As only two samples were from garden plants imported from Spain, those two samples were excluded from analyses based on the country of origin, and only samples originating from Italy and the Netherlands were compared. Although samples were collected across six garden centres, garden centre could not be included as a random effect in the analysis due to complete confounding with origin country (some garden centres imported from only one country). However, as we specifically targeted recently imported plants in order to minimise the effect of the local conditions in different garden centres, we can reasonably assume that the detected numbers of seeds and species primarily reflect the conditions in the origin country and the source nurseries. Therefore, we chose to analyse the effect of origin country rather than that of the garden centre. Because the seed numbers were overdispersed, we constructed a negative binomial generalised linear model (GLM) using the *glmmTMB* package in R (Brooks et al. 2017). However, there was severe heteroscedasticity (significant Levene's test) that persisted even after excluding an extreme outlier and explicitly modelling the variance using the *dispformula* parameter. Therefore, we used the non-parametric Wilcoxon rank-sum test to compare seed numbers between origin countries, which is robust to the observed heteroscedasticity. On the other hand, the number of species met model assumptions and was analysed using a negative binomial generalized linear model (*glmmTMB*).

To assess differences in seed community compositions between samples originating in different countries, we performed permutational multivariate analyses of variance (PERMANOVAs) with Bray-Curtis dissimilarity, using the *adonis2* function from the *vegan* package in R (Oksanen et al. 2026). We assessed homogeneity of multivariate dispersions using the *betadisper* function in the *vegan* package, followed by a permutation test (999 permutations). No significant differences in dispersion were found, validating the PERMANOVA results. Principal coordinates analysis (PCoA) was used to visualise the compositional differences between samples originating in different countries because it is more stable with sparse datasets and tied dissimilarities than non-metric multidimensional scaling (NMDS).

To assess the effect of the garden plants' taxonomy on the number and diversity of seeds found in their substrates, we categorised the garden plants into families based on the Plants of the World Online database (POWO 2025; see Suppl. material 1). Samples of the substrates of plants belonging to families represented by fewer than five species in our dataset were excluded from this model. It was not possible to include the origin country of the sample in the model because the family of the garden plant was confounded with origin country (some families were only represented among Italian samples). It was also not possible to analyse the effect of plant family separately in Italian samples to avoid the confounding effect of origin country, because most of the families were represented by too few samples in this reduced dataset. Therefore, we shifted the analysis from the taxonomic level to the functional level. The garden plants were clearly separable into two large groups based on leaf habit: (i) needle or scale-leaved species (Conifers), and (ii) broadleaved species (Angiosperms, mostly dicots). Thus, we pooled plant families based on their leaf habit and compared substrate samples of needle-leaved versus broadleaved garden plants. We did not distinguish between woody and herbaceous garden plants because almost all sampled garden plants were woody species. (Suppl. material 1). We then analysed the effect of leaf habit only on the 42 samples originating from Italy, therefore avoiding the confounding effect of origin country in this analysis. Because both seed numbers and species numbers were overdispersed, we constructed negative binomial generalized linear models (GLMs) for both variables, using the package *glmmTMB*. Model assumptions (tested using the *DHARMa* package, Hartig 2024) were met for both variables in this restricted subset.

Finally, because almost all samples from needle-leaved garden plants originated from Italy, we wanted to verify that the observed effect of origin country was not a spurious result of needle-leaved plants being overrepresented among Italian samples. To this end, we restricted the dataset to samples from broadleaved plants and analysed the effect of origin country on both seed numbers and species numbers on this restricted dataset, using negative binomial generalized linear models (GLMs).

All analyses were carried out in R version 4.3.2 (R Core Team 2023). Nomenclature follows Euro+Med PlantBase (http://www.europlusmed.org). The native versus non-native status of species and their invasion status in Hungary was given according to the Pannonian Database of Plant Traits (PADAPT, Sonkoly et al. 2023). Invasiveness in Europe is based on Kalusová et al. (2024); we considered a species as invasive in Europe if it is invasive in at least one region of Europe.

Results

In total, the 60 one-litre samples contained 2,181 germinating seeds. Fourteen seedlings died before they could have been identified (< 1% in total, one monocot and 13 dicots), the remaining 2,167 seedlings belonged to 80 taxa, 74 of them identified at the species level (more information in Suppl. material 2). Most of the individuals were identified on the species level, except for one *Cerastium*, three *Digitaria*, five *Juncus*, two *Trifolium*, and 8 *Typha* seedlings which died before further identification was possible or did not develop diagnostic features by the end of the second vegetation season (November 2024). *Juncus ranarius* and *J. bufonius* seedlings were pooled as *Juncus bufonius/ranarius* because they died before they could have been distinguished without doubt. The number of seedlings from one-litre samples ranged between 0 and 783, with a mean of 36.35 seedlings/L. Only two of the sixty samples were free of contaminating seeds. The number of taxa germinated from one-litre samples ranged between 0 and 22, with a mean of 5.38 taxa/L (excluding the unidentified individuals, see Suppl. material 1).

The most abundant species were *Sagina procumbens* (957 seedlings), *Cardamine occulta* (221 seedlings), *Euphorbia maculata* (201 seedlings), *Portulaca oleracea* (77 seedlings), and *Oxalis corniculata* (76 seedlings) (see Suppl. material 3). In contrast, the majority of taxa were represented by 1–5 individuals. The majority of taxa were present in 1–5 samples (61 species), while the most common species were *E. maculata* (in 31 samples), *P. oleracea* (in 19 samples), and *S. procumbens* (in 17 samples, see Suppl. material 3). Seven species (*Digitaria sanguinalis*, *Erigeron canadensis*, *Euphorbia maculata*, *Oxalis corniculata*, *Poa annua*, *Portulaca oleracea*, and *Sonchus oleraceus*) were detected in samples originating from all three countries, even though only two samples originated from Spain. Half of the taxa were detected in samples collected in only one of the garden centres, but five species were detected in samples from all garden centres (*C. occulta*, *E. maculata*, *P. oleracea*, *S. procumbens*, and *S. oleraceus*, see Suppl. material 3).

The majority of the detected species were non-native in Hungary (48 species, Suppl. material 3). Seven of the species we detected have only recently been reported from the country (i.e., not included in the alien checklist of Csiky et al. 2023, but reported by other since then), while *Dittrichia viscosa* has not been reported from Hungary yet. On average, 78.8% of the seeds detected in each sample belonged to species non-native in Hungary, and 91.7% of the samples contained at least one seed of a non-native species. When we differentiated between long-established archaeophyte and neophyte species, an average of 45.1% of all seeds detected in each sample belonged to neophyte species, and 85% of the samples contained at least one seed of a neophyte species. We also distinguished between established neophytes and emerging neophytes. We found that an average of 12.1% of all seeds detected in each sample belonged to emerging neophyte species, and 48.3% of the samples contained at least one seed of an emerging neophyte. On average, 28.6% of the seeds detected in each sample belonged to species considered to be invasive in Hungary, and 73.3% of the samples contained at least one seed of a species invasive in Hungary. 53.9% of the seeds detected belonged to species invasive in at least one region of Europe and 86.7% of the samples contained at least one seed of a species invasive in Europe.

Both the number of seeds and the number of species were significantly higher in samples originating from Italy compared to samples originating from the Netherlands ($W = 160$, $p = 0.002$ for seed number, $\chi^2(1)=12.194$, $p < 0.001$ for species number, Fig. 2). PERMANOVA revealed that the country of origin ($F = 2.541$, $R^2=0.046$, $p = 0.001$, Fig. 3) had a significant effect on the seed composition of the samples.

The leaf habit of the garden plant (analysed only on samples originating from Italy to avoid the confounding effect of origin country) had a significant effect on the number of seeds ($\chi^2(1)=4.655$, $p = 0.031$), with samples from needle-leaved garden plants containing more seeds than samples from broadleaved species (Fig. 4). However, leaf habit did not have a significant effect on the number of species detected in the substrate ($\chi^2(1)=1.627$, $p = 0.202$, Fig. 4). To verify that the observed effect of origin country was not a spurious result of needle-leaved garden plants being overrepresented among Italian samples, we analysed the effect of origin country separately on the subset of broadleaved plants. Within this restricted dataset, both the number of seeds ($\chi^2(1)=12.361$, $p < 0.001$) and the number of species ($\chi^2(1)= 6.9112$, $p = 0.009$) remained significantly higher in the Italian samples.

Discussion

Human activities such as trade and transport have long been recognised as the main driving forces of non-native species introductions and biological invasions (Hulme 2009; Bullock et al. 2018). Ornamental plants are known to be the main sources of naturalised and invasive plant species worldwide (Pergl et al. 2016; van Kleunen et al. 2018). In contrast, the accidental dispersal of contaminant seeds associated with the international live plant trade has not been given considerable attention so far. Here we provide evidence that the substrate of container-grown garden plants imported from distant countries can contain large numbers of seeds – mostly of non-native plant species. Moreover, the seed density and composition of the substrates can differ among exporter countries.

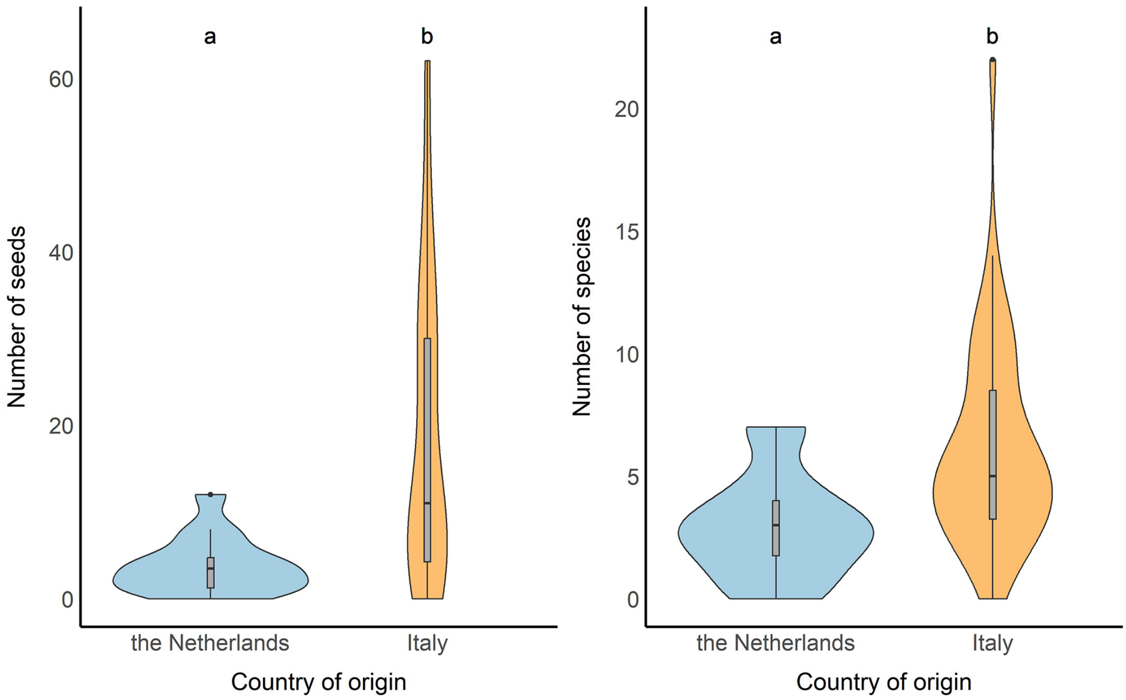

Figure 2. The number of seeds and the number of species in one-litre samples taken from the substrate of garden plants imported from the Netherlands (n = 16) and from Italy (n = 42). Note that outlier values are not shown on the seed number plot to improve the readability of the plot. Significant differences (based on Wilcoxon rank sum test in the case of seed numbers and negative binomial GLM in the case of species numbers) are indicated with different letters above the bars.

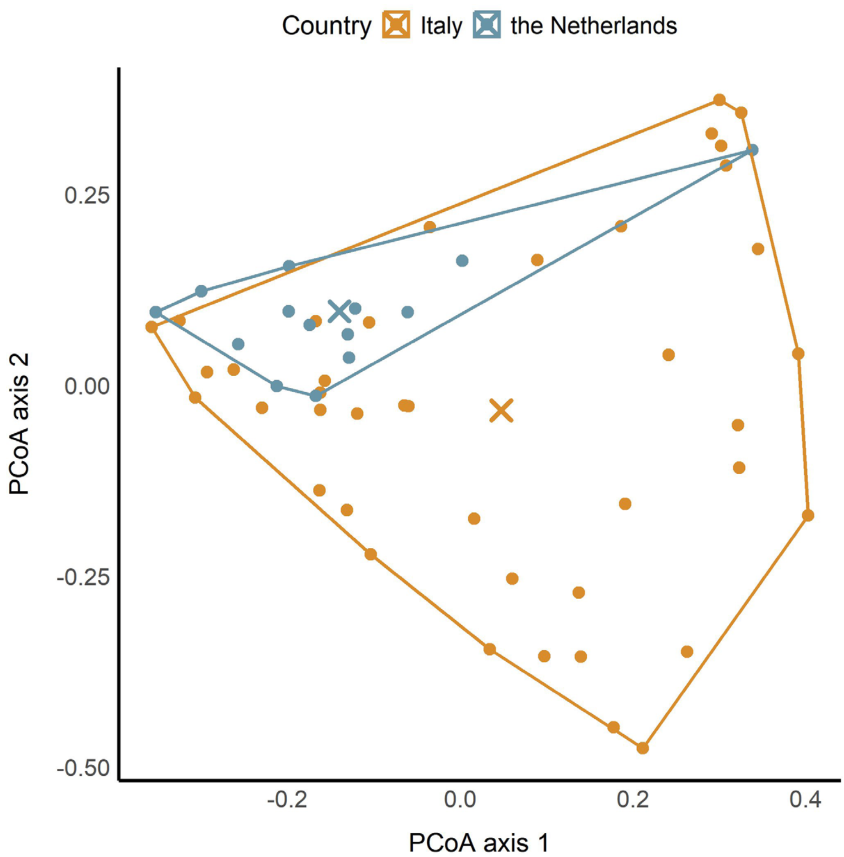

Figure 3. Principal Coordinates Analysis (PCoA) of the seed composition of samples by country of origin. The first two PCoA axes explained 12.1% and 9.5% of the variation in community composition, respectively. The × symbols indicate the centroids of the two groups.

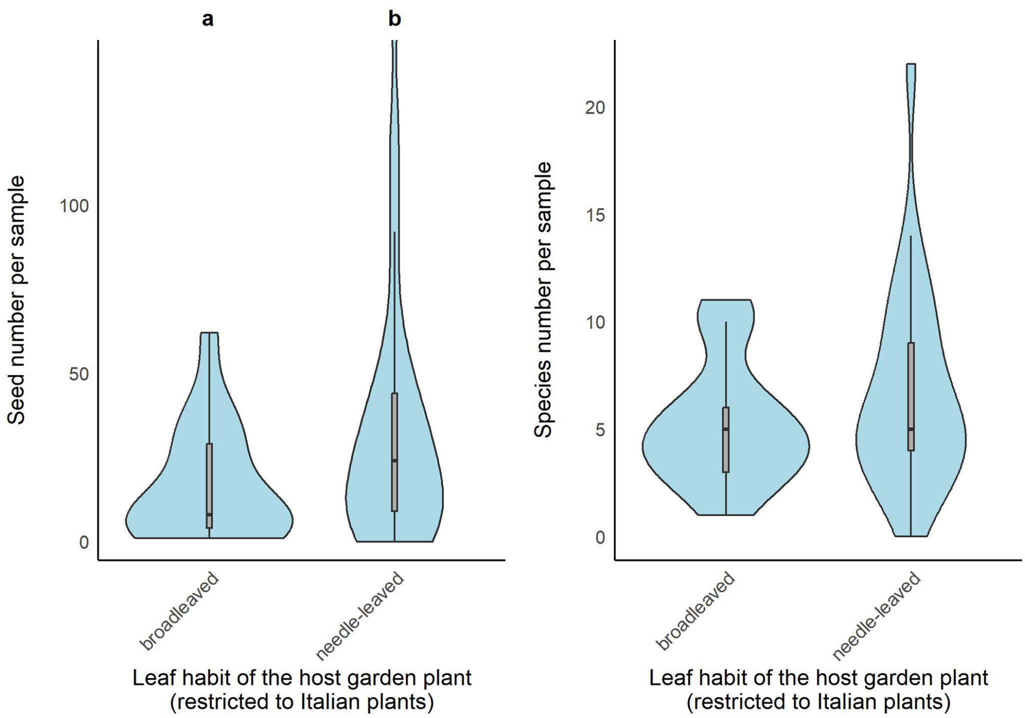

Figure 4. The number of seeds and the number of species in one-litre samples taken from the substrate of broadleaved (n = 17) and needle-leaved garden plants (n = 25) originating from Italy. Note that outlier values are not shown on the seed number plot to improve the readability of the plot. Significant differences based on negative binomial GLMs are indicated with different letters above the bars.

Nurseries producing container-grown ornamental plants are exposed to intensive disturbance and high propagule pressure due to the constant inflow of potting substrates and other horticultural materials. Resource availability in nurseries is also high due to fertilizer use. All these factors can contribute to the high invasibility of these facilities (Davis et al. 2000; Davis and Pelsor 2001; Colautti et al. 2006); therefore, it is not surprising that they have been repeatedly found to be inhabited by numerous non-native species (see e.g., Conn et al. 2008; Hoste et al. 2009; Sonkoly et al. 2025). We found that a very high proportion of the detected species belonged to non-native species, but most of these are already widespread throughout Europe (e.g., *Erigeron canadensis*, *Galinsoga quadriradiata*, *Oxalis corniculata*). However, more than 10% of the seeds belonged to emerging neophytes. As species that are not yet established (as well as not yet introduced species) are the ones that can potentially induce new invasions, they are especially important from a biosecurity perspective. Almost half of the samples contained at least one seed of an emerging neophyte, indicating that this is a common phenomenon. The high proportion of emerging neophytes suggests that the trade of container plants not only has a role in distributing the seeds of native and already established non-native species, but also in introducing new species and a considerable number of seeds belonging to species that are still at the early stages of the invasion process. For example, *Gnaphalium pensylvanicum* is a species native to North and South America, whose spread has only been documented in Western and Southwestern Europe so far (Verloove et al. 2023). The only documented occurrence of *G. pensylvanicum* in Hungary is from the container of an ornamental plant in a garden centre (Sonkoly et al. 2025). *Dittrichia viscosa* is native to the Mediterranean Basin and has been introduced to some other parts of Europe, but it is not yet considered as an invasive species in most European countries (Kalusová et al. 2024) and it has not yet been reported from Hungary. *Symphyotrichum squamatum*, a species native to South America, is already considered invasive in several European countries (see e.g., Arianoutsou et al. 2010; Uludağ et al. 2017), but it mainly spreads in Southern Europe and has only recently been reported from Hungary (Takács et al. 2025). Some seeds of ornamental plant species were detected as well, but in surprisingly low numbers: three seedlings of *Nerium oleander* germinated from the substrate of conspecific individuals and one seedling of *Lonicera nitida* was detected in the substrate of *Taxus* × *media* 'Hillii' individuals.

There were seven species (*Digitaria sanguinalis*, *Erigeron canadensis*, *Euphorbia maculata*, *Oxalis corniculata*, *Poa annua*, *Portulaca oleracea*, *Sonchus oleraceus*) which we detected in samples originating from all three countries, even though there were only two samples from Spain. These species frequently grow in the containers of ornamental plants according to our experiences during sample collection, and according to previous results as well (Sonkoly et al. 2025). Forty-five of the species we documented (60.8%) were also detected in samples from the containers of plants imported to Norway (Bruteig et al. 2017). The plant species that were represented by the highest numbers of seeds in our study also considerably overlap with the species Bruteig et al. (2017) reported as the most abundant species germinating from the samples. Case et al. (2005) listed 26 species as common nursery weeds in the USA, 14 of which were also found in our study. The detected non-native species also show a great overlap with the non-native species detected in a survey assessing the non-native flora of nurseries and garden centres in Hungary (Sonkoly et al. 2025). Based on these findings, we can presume that there is a limited set of plant species that are particularly successful in colonizing plant nurseries in Europe and the USA, and therefore able to build up a considerable seed bank inside the containers.

The average number of seeds per litre of substrate in our study (36.4 seeds/L) was considerably higher compared to the seed densities found by Conn et al. (2008) in Alaska. They found the highest number of seeds in the soil of balled-and-burlapped trees and shrubs (20.2 seeds/L), followed by small and large container-grown woody plants (7.8 seeds/L and 3.2 seeds/L, respectively). The number of taxa detected per litre was also much higher in our study. Conn et al. (2008) found the highest number of species in the soil of large container-grown woody plants (1.8 species/L), while we found an average of 5.4 species/L. A report by Bruteig et al. (2017) assessed the seed content of the substrate of container plants imported to Norway. They reported a total of 17,123 seedlings from 650 litres of samples (26.3 seeds/L), which is comparable to the seed density in our study, although they did not provide the number of seeds per litre directly. It is important to consider that the sampling method used and sampling depth may also influence seed densities and, to some extent, may be the explanation for different studies finding contrasting seed densities. In this study, we assessed the seed content in approximately the upper 5 centimetres of the substrate, meaning that these values are not necessarily applicable to the deeper layers of substrate in the containers.

The substrates of plants imported from Italy contained seeds in significantly higher density and diversity than the substrates of plants imported from the Netherlands. Substrates of plants imported from different countries also had significantly different seed compositions, although the variance explained was rather low. Species documented exclusively in the substrates of plants imported from the Netherlands were almost all native and widely distributed throughout Europe (e.g., *Hypochaeris radicata*, *Juncus inflexus*, *Urtica urens*). Conversely, many species found only in the substrates of Italian plants are primarily distributed in Southern Europe.

Some of these are native to the region (*Dittrichia viscosa*, *Polypogon virdis*), while others are non-native species that have mainly colonised Southern Europe so far (e.g., *Eclipta prostrata*, *Euphorbia prostrata*, and *Symphyotrichum squamatum*). Although further studies are needed to corroborate our findings, they suggest that the substrate of garden plants imported from different countries can be considerably different in terms of seed numbers and species composition, which was also observed by Bruteig et al. (2017). Different countries have different floras and environmental conditions, and the weed management practices applied by nurseries may vary between countries (Conn et al. 2008; Stewart et al. 2017), likely contributing to the observed differences in seed contamination between countries. These differences may also be related to the different range of species imported from the two countries; plants imported from Italy mostly belonged to the Cupressaceae and Pinaceae families, while plants imported from the Netherlands belonged to a more diverse range of families, but were typically not Conifers (see Suppl. material 1). On the other hand, our analysis showing that the effect of origin country was significant on both seed numbers and species numbers even after restricting the dataset to broadleaved species suggests that the observed difference is primarily caused by factors other than the different range of plants imported from the two countries. Furthermore, substrate mixes are likely already contaminated with seeds before potting (see e.g., Case et al. 2005; Sonkoly et al. 2022), and different nurseries and countries may use different types of substrates.

The origin country of the sampled plants was not independent of the garden centre from where the sample was taken, as some garden centres imported from only one country, making it impossible to consider the potential confounding effect of the local conditions in the different garden centres by including the garden centre in the models. However, as the sampled garden plants were freshly imported, there was little opportunity for local seed contamination or for ecological filtering by the garden centres' local environment. Based on this, it is reasonable to assume that the observed differences in seed and species numbers between samples originating from Italy and the Netherlands primarily reflect the conditions in the origin country and/or the source nurseries, rather than local garden centre conditions.

The sampled garden plants' leaf habit appeared to be associated with differences in the seed content of its substrate; substrates of needle-leaved plants contained more seeds than substrates of broadleaved plants. It is well-established that species with needle or scale-like leaves have low specific leaf area (SLA; e.g., Reich et al. 1995, 1997), which is characteristic to species with a resource-conservative strategy and low growth rates (Shipley 2006; Poorter et al. 2009), while broadleaved species generally have higher SLA and grow faster. Therefore, the leaf habit of the garden plants may be associated with the length of time they spend in the nursery before being sold at a retail, during which time seeds can accumulate in their substrate (Conn et al. 2008), possibly explaining the observed differences. It may also be possible that broadleaved plants intercept a larger portion of the seed rain while needle-leaved and scale-leaved plants may present less of an obstruction for seeds, allowing more seeds to reach the substrate. As the substrate of needle-leaved garden plants contained more seeds and needle-leaved plants are overrepresented among Italian samples, we also tested whether the effect of country is still present exclusively among broadleaved plants. Italian samples contained more seeds and species even when restricted to broadleaved garden plants, verifying that the observed country effect is not just a spurious finding resulting from the overrepresentation of needle-leaved plants among Italian samples.

The global horticultural trade has experienced considerable growth over the last two decades, with the export value of live plants approximately doubling during this time (Hinsley et al. 2025). In Norway, for example, the imports of container-grown garden plants have quadrupled between 1997 and 2016 (Bruteig et al. 2017). Italy and the Netherlands are the largest exporters of live plants globally (Hinsley et al. 2025). In 2021, the Netherlands exported almost 300 million kilograms of garden plants, mostly to other European countries (de Waart et al. 2025). Given that the substrates of these plants likely make up a considerable proportion of this mass, a vast number of seeds are undoubtedly dispersed accidentally with them each year. Due to the huge number of incoming seeds and the diverse array of species, it is highly likely that some species introduced with imported garden plants will become naturalised in the new area (see also Hoste et al. 2009). As disturbed, resource-rich 'habitats' embedded in intensively used, urbanized landscapes, garden centres have high invasibility (Davis et al. 2000; D'Antonio et al. 2001), and, when exposed to high propagule pressure of certain plant species, they are very likely to become starting points of invasions (Lockwood et al. 2005; Vedder et al. 2021). Moreover, climate warming is likely to reduce existing climatic limitations for many species, facilitating their naturalisation and potential invasion (Walther et al. 2009; Dullinger et al. 2017). Therefore, the large number and diversity of seeds entering Central Europe as contaminants of container-grown plants from Italy (and possibly other Mediterranean countries) will be even more likely to trigger invasions as temperature rises (Seebens et al. 2015).

Information on the risks posed by the unintentional introduction of species as contaminants of particular commodities is essential to design effective policy measures aimed at controlling invasions (Essl et al. 2015). Increasing evidence shows that biological invasions are largely driven by global trade networks (e.g. Levine and D'Antonio 2003; Westphal et al. 2008; Chapman et al. 2017), and detailed information on these networks is expected to improve risk assessments and support the development of effective policies (Banks et al. 2015; Paini et al. 2016). Improving our knowledge of which commodities are responsible for transporting specific contaminant species could therefore enhance the accuracy of invasion predictions. In particular, the live plant trade has been shown to be more strongly associated with invasions than trade in general (Chapman et al. 2017). Data on species accidentally transported via horticultural trade could facilitate more precise risk assessments (Essl et al. 2015), as the trade volume of horticultural commodities may serve as a proxy for propagule pressure for these species (Chapman et al. 2017). On the other hand, detailed and up-to-date information on the volume and spatial structure of the live plant and horticultural trade would also be needed to quantify propagule pressure (Colautti et al. 2006) and assess the risk posed by non-native species dispersed via these commodities (Hulme 2009). These considerations highlight the need to pay greater attention to the accidental introduction of species as contaminants in the global horticultural trade.

In conclusion, our findings confirm that a great number of seeds can be entering new regions as contaminants of the horticultural trade, many of which are recently introduced, emerging neophyte species. Although the germination and establishment success of these seeds will ultimately determine these species' invasion potential, their high propagule pressure significantly increases the likelihood of initiating new invasions. We found that container-grown plants imported from different countries introduced seeds in different numbers and composition, suggesting that the structure of the horticultural trade network may have an influence on the non-native flora of importing countries, with potential consequences for biological invasions. Characteristics of the imported container plants may also have an effect on the number of seeds dispersed in their substrate, but the effect of exporter country seems to be more important. Finally, our findings suggest that although the global horticultural trade has mostly been considered as a pathway for deliberate non-native plant introduction so far and the accidental dispersal of seeds as contaminants in the horticultural trade has been studied much less frequently, increased attention to the contaminating seeds in horticultural trade is urgently needed. We also emphasise that more effort and research needs to be devoted to the less researched transport and introduction phases of biological invasions in general.

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Supplementary material 1

Samples

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Data type: xlsx

Explanation note: Information about the substrate samples (sampling date and location, ornamental plant, number of seeds germinated, number of taxa detected, etc.).

Link: https://doi.org/10.3897/neobiota.107.184691.suppl1

Supplementary material 2

Germination results

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Data type: xlsx

Explanation note: Detailed results of the germination study (species × sample matrix).

Link: https://doi.org/10.3897/neobiota.107.184691.suppl2

Supplementary material 3

Species data

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Data type: xlsx

Explanation note: Detailed information about the detected species (number of seeds germinated, invasions status, etc.).

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Additional information

Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.