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Historical reconstruction of the invasions of four non-native tree species at local scale: a detective work on *Ailanthus altissima*, *Celtis occidentalis*, *Prunus serotina* and *Acer negundo*

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Abstract

Reconstructing the history (spatio-temporal patterns) of biological invasions at a small spatial scale is challenging, notably because the required data are often not available in sufficient quantity and quality. In this study, we present a mixed approach using six different data sources to explore the spreading history of four non-native invasive tree species, *Ailanthus altissima*, *Celtis occidentalis*, *Prunus serotina* and *Acer negundo* in a high conservation value foreststeppe habitat with an area of 1000 ha (Peszér Forest, Central Hungary). We carried out a literature search, compiled all the archived and currently valid data of the National Forestry Database (NFD) in a GIS database, conducted a full-coverage field survey, mapped all the large/old tree specimens and carried out annual ring counts, performed a hotspot analysis on the abundance data provided by the field survey and gathered local knowledge. Each of these approaches proved indispensable and their complementary use made it possible to reconstruct the invasion history of all four tree species. According to the available source literature, *P. serotina* was first planted in the area in 1937 and the first known occurrence of *A. altissima* could also be traced back to the 1930s. The examination of large specimens of *C. occidentalis* and querying the NFD for data related to *A. negundo* provided evidence that these species have been present in the area since at least the 1940s. However, based on the NFD and local knowledge, it is certain that the rapid expansion of the four tree species occurred simultaneously and only around the turn of the millennium, with a lag of at least 60-70 years. The exploration of local knowledge revealed three possible explanations, which interestingly also coincided in time. With the change in the political regime, the intensity of forest use started to decrease in the 1990s, the population of game was drastically reduced at the end of the decade and droughts became more frequent from 2000 onwards. The field survey clearly showed that these tree species were 2-3 times more prevalent and abundant than the relevant NFD data indicated. Finally, the primary hotspots of *A. altissima* and *A. negundo* overlapped with the locations of their first known occurrences, while in the case of *C. occidentalis* and *P. serotina*, they did not. However, local knowledge revealed that the former two had been ignored since at least the 1950s, while the latter two were occasionally planted until the 1990s. It is likely that the primary hotspots of *C. occidentalis* and *P. serotina* indicate the locations of these undocumented plantations.

Keywords

forest management, forest-steppe, full-coverage mapping, hotspot analysis, local knowledge, National Forestry Database, population eruption

Introduction

For thousands of years, humans have been moving tree species from one place to another for many purposes, such as cultivation, trade or during war (Sîrbu 2007). In general, the introduction of non-native species first soared in the Age of Discovery and was boosted once again by increased mobility during the Industrial Revolution (Hulme 2009, Nyssen et al. 2018). However, it is fair to say, no earlier period compares to our New Era of Globalisation when the rate of human-mediated introductions has grown by several orders of magnitude in just a few decades (Rejmánek 2014). This trend indisputably correlates with the exponential growth of international trade (Bradley et al. 2012, Lenzner et al. 2020, Hulme 2021) and is likely to continue in the future (Seebens et al. 2021). Various studies have shown that, as the frequency of introduction events (i.e. propagule pressure (Lockwood et al. 2005)) increases, so does the chance of a successful invasion (Veltman et al. 1996, Drake et al. 2005, Simberloff 2009, Koontz et al. 2018). On the other hand, as the emblematic case of the rabbits in Australia illustrates (Alves et al. 2022), there are certain situations where a few introductions are sufficient to trigger a massive invasion (Zayed et al. 2007, Arca et al. 2015). Naturally, the success of an invasion is also determined by a combination of numerous other factors, such as invasiveness (the propensity of an introduced species to invade the recipient community), invasibility (the sensitivity of the recipient community to the establishment and spread of an introduced species), disturbance regime, genetic background and the spatio-temporal variation of these (Lozon and MacIsaac 1997, Richardson and Pyšek 2006, Dlugosch and Parker 2008 , Rejmánek et al. 2013). In any case, answering the complex questions of invasion biology also requires us to explore the history of a specific invasion to provide a basic framework. However, this task poses a variety of challenges, due to the lack of available data in most cases (Rabitsch 2010, Chong et al. 2017). In this paper, we present a mixed approach by historically exploring the invasion of four non-native tree species on a local scale. We focus on *Ailanthus altissima* (Mill.) Swingle, *Celtis occidentalis* L., *Prunus serotina* Ehrh. and *Acer negundo* L., which, in Hungary (and in many other countries), not only threaten a whole range of habitats and species, but also cause serious problems to, for example, certain economic and maintenance sectors.

An increasing number of studies have attempted to reconstruct the invasion history of various taxa at global (Ryan et al. 2019), continental (Scholler and Böllmann 2004, Haubrock et al. 2022), national (Briscoe Runquist et al. 2019), regional (Morris et al. 2013, Botella et al. 2022) or mixed (Pyšek et al. 2007) scales. However, at a local scale, it is usually very difficult to find historical data in sufficient quantity and quality to complete this task. In the case of plant species, herbarium collections (Crawford and Hoagland 2009, Antunes and Schamp 2017), horticultural (Dehnen-Schmutz et al. 2007) and forestry inventories (Lugo 2004, Brus et al. 2019) can be the first sources to provide important input data besides published and grey literature (e.g. studies available only in libraries, unpublished studies). Aerial photographs and satellite imagery might also be helpful if the species in question can be well distinguished on a textural, phenological or spectral basis (Bradley 2014). The techniques of hyperspectral imaging spectroscopy and light detection and ranging (LiDAR) are relatively new, but could become indispensable tools for documenting or even preventing invasions in the future (Huang and Asner 2009, Bolch et al. 2020). In addition to the studies focusing on analysing the dynamic processes of invasive species, based on historical data, many studies have uncovered past events from recent (well-recorded) spatio-temporal data or have used a mixed approach. Today, with new genomic methods, thousands of genes can be easily and reliably analysed at the population level to determine introduction pathways, the first establishment locations and the subsequent spreading dynamics (Cristescu 2015, Vallejo-Marín et al. 2021, Byrne et al. 2022). In the case of tree and shrub species, invasion histories can also be revealed by evaluating measured or estimated phenological traits, such as size (and derived age) distribution, the extent of colonies and the density of seedling recruitment (Deckers et al. 2005, Wangen and Webster 2006, Holmes et al. 2014). These methods generally require field data collected at high sampling intensities and are probably best suited for investigations at landscape or local scales. Over the past two decades, questionnaires, interviews and other social surveys have become increasingly important tools in conservation and ecological research (White et al. 2005, Bennett et al. 2017). Several papers have been published on the social perception of invasive species (Oxley et al. 2016 , Kapitza et al. 2019, Kowarik et al. 2021, Meinhardt et al. 2022), including some in which local knowledge was a key factor in revealing past conditions (Middleton 2012).

The first global database of invasive tree and shrub species was launched in the early 1990s after 12 years of data collection (Binggeli 1996). It included 653 species, 347 of which were tree species. A new database was not published until much later (Richardson and Rejmánek 2011), first with 622 species and after an update (Rejmánek and Richardson 2013), 751 species, including 434 tree species. Today, several international databases provide information on invasive species (e.g. CABI, EPPO, GBIF, ISSG). In Europe, at the beginning of the 20th century, (Goeze 1916) listed 2,645 non-native woody species in parks and gardens (in: Kowarik (1995)); however, it would be difficult to give an exact number today. Some tree species are considered highly invasive in most European countries and are frequently managed, such as *A. negundo*, *A. altissima*, *P. serotina*, *Robinia pseudoacacia* L. and *Quercus rubra* L. (Monaco and Genovesi 2014, Braun et al. 2016). Some species and cultivars of taxa that are still widely planted, such as *Acacia* spp., *Eucalyptus* spp., *Populus* spp., *Salix* spp. *Pinus* spp. and other conifers, can also cause significant conservation, economic or health problems (Lorenzo et al. 2010, Brundu and Richardson 2016, Silva-Pando 2021, Campagnaro et al. 2022). The Management List of non-native invasive tree and shrub species of Hungary currently comprises 16 species (Bartha 2020). The list only includes species that are either: a) still present in small areas, but no known control method is available, so they are likely to spread rapidly or b) already widespread and can only be realistically controlled at small scales, typically in areas of high conservation importance. Since the early 2000s, significant effort has been put into controlling *A. altissima*, *A. negundo*, *C. occidentalis*, *Elaeagnus angustifolia* L., *Fraxinus pennsylvanica* Marshall, *P. serotina*, *R. pseudoacacia* and *Amorpha fruticosa* L. in the country (Csiszár and Korda 2015). It should be noted, however, that *R. pseudoacacia* needs to be discussed separately from the others, as it remains one of the most important tree species of economic value in the country (Rédei et al. 2017).

Most of the woody species were deliberately introduced in new areas, causing ecological or concomitant economic problems (Richardson and Rejmánek 2011). On the other hand, many of them remain in use and provide income for people (Kull et al. 2011, Brundu et al. 2020). For centuries, botanic gardens and arboreta have been regarded as centres of plant introduction and have played a primary role in the transfer of propagating material for agricultural, industrial, forestry and horticultural purposes (Heywood 2011, Nyssen et al. 2018, Galbraith and Cavallin 2021). It is telling that almost all of the invasive plant species causing problems at the global level can still be found in many living collections (Hulme 2015). The first seeds of Europe's most problematic invasive tree species were also sent to botanic gardens and different collections. *A. altissima* was first brought to Paris in the 1740s (Hu 1979), then introduced to a botanic garden in Chelsea (London) and a private collection in Busbridge, England in 1751 (Swingle 1916), while the first *P. serotina* and *R. pseudoacacia* trees were raised by botanists in Paris in the early 17th century (Goeze 1916 , Wein 1930, Peabody 1982). A literature review of the main invasive tree species at the national scale (Korda 2018) has shown that those species had been introduced to Hungary by the early 1800s at the latest, with the very first records originating from botanical gardens and city parks. It is interesting to note that, for example, the promotion and dissemination of *A. altissima* in the country can ultimately be traced back to the caring work of one person over four decades. Despite their pivotal role in the history of many invasive plant species, botanical gardens place great emphasis on invasive plant research, knowledge dissemination and prevention through risk assessment programmes today

(Galbraith and Cavallin 2021). In our time, ornamental horticulture and forestry (including agroforestry) play the most important role in maintaining and establishing pathways for invasive woody species and many herbaceous plants (Reichard and White 2001, Hulme et al. 2018, van Kleunen et al. 2018).

Modern forestry (i.e. organised forestry (Lundmark et al. 2017)) was born in Europe at the beginning of the 19th century, by which time, vast areas had been deforested and the remaining forests were generally over-exploited (Kaplan et al. 2009). Therefore, forest engineers, who were already being trained in the academies, had to carry out large-scale afforestation and forest restoration works as soon as possible to meet the growing human population's increasing demand for wood. This process tested the suitability of various non-native tree species for large-scale commercial use and selected species were planted on a large scale. Eventually, with the inevitable spread of monocultures in the 20th century, these tree species became an integral part of European plantation forestry (Nyssen et al. 2018).

Today, 21% of the total area of Hungary (i.e. about 2 million hectares) is covered by forests, of which 460,000 ha are made up of *R. pseudoacacia*, 100,000 ha by hybrid poplar clones (*Populus* × *euramericana* (Dode) Guinier) and 180,000 ha by coniferous (mainly *Pinus sylvestris* L. and *Pinus nigra* J. F. Arnold) plantations. The six most problematic invasive tree species – *A. altissima*, *A. negundo*, *C. occidentalis*, *E. angustifolia*, *F. pennsylvanica* and *P. serotina* – are estimated to be present on a total of 22,000 ha at the stand level (National Land Centre 2022). In addition, these species are present in most parts of the country and are only absent in the higher-elevation parts of the mountain forests (Bartha et al. 2022). It can be concluded that, after the introduction of these tree species, they were used for many purposes in the country. In plantation forestry, particularly in sandy areas, these species were most often used in combination with others to provide a second canopy layer (shading) and have also been found to be suitable for soil conservation, humus enrichment, boundary marking or stabilising bare surfaces (e.g. sand dunes). From the second half of the 20th century, the interest of foresters in these species declined significantly, because it was recognised that they cannot be controlled by the commonly-used forestry technologies and that they are economically worthless in terms of wood and processability (Korda 2018).

This paper aims to offer a multivariate approach for reconstructing tree invasion histories at local scales. Our work focuses on the invasion of *A. altissima*, *C. occidentalis*, *P. serotina* and *A. negundo* in a 1000–ha forest-steppe habitat complex. We attempted to: (i) identify the first introduction localities, (ii) determine the spread patterns up to the present and (iii) reveal and discuss the key factors that may have played a key role in the invasions of these four tree species. To achieve this, we: 1) conducted a literature review, 2) processed the relevant archives and currently valid data of the National Forestry Database, 3) carried out a fine-scale field survey, 4) located the largest specimens in the area, 5) performed a hotspot analysis on the recent data and 6) collected local knowledge. Finally, we would like to point out the limitations of each source.

Materials and methods

Study area

The Peszér Forest is located on the northern edge of the Danube–Tisza interfluve in the Kiskunság Region, Central Hungary (47.0996°N 19.3000°E, 95–107 m a.s.l.). This 1628–ha site is part of the European Natura 2000 network (HUKN 20002) and includes forests, scrublands and grasslands of high conservation value. We focused on areas classified as forest by land use, covering a total of 1083 ha and comprising a large central block and some smaller blocks of the Szalag Forest (also protected on the state level) (Fig. 1). In the following, we will refer to this particular area as a whole as Peszér Forest. The Peszér Forest is located in the continental forest-steppe zone, but there is also a minor sub-Mediterranean climatic influence (Kun et al. 2021). The annual precipitation is between 500 and 600 mm and the mean temperature is 11°C (Tölgyesi et al. 2019). However, soil properties also play a pivotal role in the composition of the vegetation in the Hungarian lowlands (Fekete et al. 2014). Locally, the dominant soil type is calcareous sand with low to medium fertility (Vadász et al. 2016), but, in the past, foresters have also tried to afforest saline and clay soils.

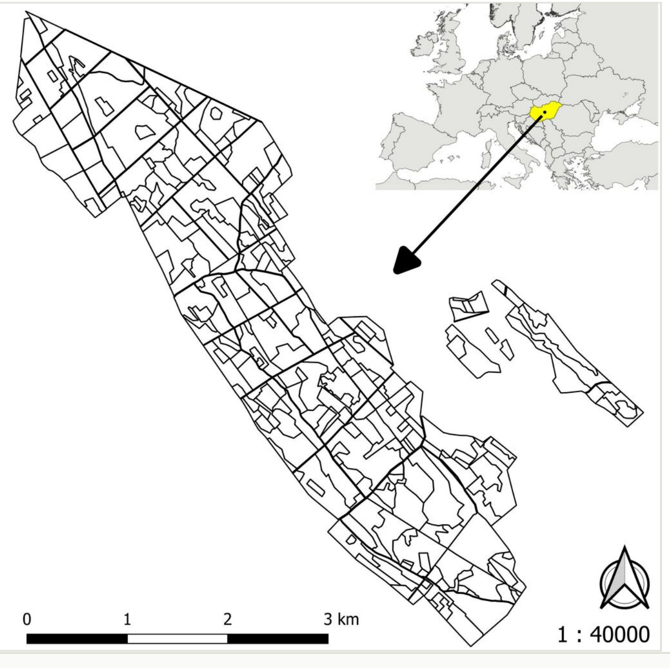

Figure 1.

The location of the Peszér Forest in Hungary and its subdivision to forest subcompartments in 2019.

For centuries, access to Peszér Forest was restricted as it was primarily used by its landlords for hunting. At the same time, local residents were allowed to produce firewood in the forest, which was typically done with short rotation coppice management. Although the intensification of forest use had already begun by the early 20th century, it only became predominant from the beginning of the communist era in the 1950s (Molnár et al. 2022). At this time, (semi)natural habitats were replaced with plantations of *R. pseudoacacia*, *Pinus* spp. and *Populus* × *euramericana* cultivars. Despite this, many forest patches of high nature value have been preserved and significant conservation efforts are now underway to improve conservation conditions. Forest management is also becoming more moderate and is moving towards the exclusive use of native tree species. Currently, Peszér Forest hosts more than 10% of the entire Carpathian Basin's Eurosiberian steppic woods with *Quercus* spp. (91I0) habitats, a priority natural habitat type of Community interest under the EU Habitats Directive. In terms of tree volume, *Populus* × *canescens* (Aiton) Sm. (a natural hibrid of *Populus alba* L. and *Populus tremula* L.), *Quercus robur* L. and *R. pseudoacacia* dominate. The stands are often characterised by incomplete canopy closure, usually resulting in a dense and well-developed shrub layer consisting of *Crataegus monogyna* Jacq. and *Ligustrum vulgare* L. The herb layer is characterised by a mixture of forest, grassland and forest-steppe species. The studied area consists of a total of 300 forest subcompartments (Fig. 1). In Hungary, the subcompartment is the preferred forest management unit, in spatial, administrative and practical terms as well.

Data collection and analyses

The history of the spread of the most frequent invasive tree species in Hungary, including the four species subject to our study, was examined in a book based on 1,775 literature sources (Korda 2018). In addition to this work, we reviewed all the issues of the two most important Hungarian forestry journals (Erdészeti Lapok (published since 1862) and Erdészettudományi Közlemények (published since 1899)), which have been fully digitised. Finally, when collecting local knowledge, we also looked for any grey literature that respondents might have available.

In Hungary, the National Forestry Database (NFD) is required to be updated every 10 years according to the Forest Management Plan; however, this deadline can be extended by a few years upon request. In the NFD, each sub-compartment has its standard data sheet, which contains the most important information about the environmental, compositional and structural characteristics, in addition to information about the most recent management activities. All relevant information on the four tree species could be obtained basically from three sections: 1) a list of major tree species based on an admixing ratio (a percentage value calculated on the basis of the relative wood volume of all the tree species present and a tree species can be considered major if it reaches 5%), 2) a list of accompanying tree species (with an admixing ratio below 5%) and 3) the comment box where any other information (e.g. conservation implications, shrub and herb layers) can be noted. With respect to the tree species listed in the major tree species section, several other details, such as the age and origin (seed or sprout), are also indicated. The occurrence of the studied tree species in the first section suggests a more massive, stand-level presence, whilst records in the other two sections generally indicate a lower prevalence (e.g. spatially sporadic/patchy occurrence or just saplings). Therefore, data from these two sections were processed together as follows. Raw NFD data were obtained from the National Land Centre (2023) for Peszér Forest for the years 1958, 1971, 1982, 1992, 2002 and 2016, the latter representing the currently valid data. We processed the standard data sheets for each period and each sub-compartment (1,686 standard data sheets in total) to extract all the data about the four tree species included in this study, then created a set of GIS layers, arranging the data in chronological order (Suppl. material 1). Finally, the prevalences of the species records (including all records) and, separately, the prevalences of the main tree species records were calculated for each of the four tree species for each period.

When designing field surveys, one of the first tasks is to determine the sampling intensity at which data should be collected. In our case, instead of specifying a particular sampling intensity, we chose to carry out a spatially explicit, full-cover survey of the entire area. A 25 × 25 m grid was created in the GIS, covering the site. Grid cells are referred to as survey units (SU – 625 m^2). We aimed to thoroughly investigate each SU to record the occurrence and abundance of the studied invasive tree species. SUs crossed by subcompartment borders (i.e. the cells containing more than one overlapping forest subcompartment) were split into separate polygons with different shapes and sizes. Of these, SUs covering at least 100 m^2 were taken into account. This allowed us to survey the subcompartments with a spatial coverage of 93–98%. In cases where it was not possible to carry out a quantitative survey (e.g. virtually impenetrable scrub layer), only occurrence (presence/absence) data were collected by careful visual observation. We designed the survey protocol to be as simple as possible to make data collection quick and easy. Data were collected in a GIS environment using field tablets and the ArcPad software. For each of the four invasive tree species, abundance data were recorded for three size classes. The first size class included specimens with a diameter measured at breast height exceeding 5 cm (dbh ≥ 5 cm). These adult specimens were directly counted. The vast majority of seed-bearing adult specimens belonged to this group. An estimated average diameter was also recorded in the case of each invasive tree species in each SU. The second size class included all the young saplings that have not yet reached the 5 cm dbh threshold, but have already reached a minimum height of 20-30 cm. The number of specimens (shoots/ramets) was directly counted between 1 and 10, rounded to the nearest ten between 10 and 100 or rounded up to thresholds of 150, 250, 500 or 1000 shoots as the upper maximum. Saplings in the latter group were considered viable and had a good chance of reaching free-to-grow status. The third size class referred mainly to the seedlings, the number of which was recorded as an ordinal variable with categories representing 1–10, 10–100, 100–1000 and > 1000 specimens. This group was only recorded during the growing season, as seedlings proved difficult to detect in winter without foliage. For each sub-compartment, we also compared the current NFD data with the results of our own field survey. To achieve this, a threshold was set, above which a mass presence can be ascertained. The criteria were: 1) the density of the dbh ≥ 5 cm class reached 100 specimens/ha and/or 2) the density of the dbh < 5 cm class reached 1000 specimens/ha and 3) a given tree species was present in at least one-fourth of the 625 m^2 survey units of the subcompartment. Meeting any of these criteria, the tree species are so abundant that their specimens must be easily visible in the field and should, therefore, be recorded in the NFD. The field survey was carried out in 510 field days between October 2017 and April 2019 within the framework of the OAKEYLIFE project (2017–2022).

In addition to the three classes, specimens with dbh ≥ 30 cm were point-mapped and recorded individually in each SUs. Following an official permit procedure in 2021, the largest specimens were felled to obtain their annual ring counts. We also recorded information that might indicate earlier planting, for example, specimens of similar age arranged in rows.

It can be generally assumed that, on the local scale, the current largest hotspots may reflect the locations of the first introductions. To identify the main spatial clusters of the invasive tree species, local Gi* statistics (Getis and Ord 1992, Getis and Ord 1996) were performed in QGIS version 3.22 using the Hotspot Analysis Tool (Oxoli et al. 2017). A total of eight runs were carried out, based on the abundance values of the dbh ≥ 5 cm and dbh < 5 cm size classes by the four tree species. As a result of the analyses, a unique Z-score was calculated for each SU with an associated p-value (the values may, of course, vary by species and size class in the same SUs). This therefore enables the ranking of all SUs and visualising the results. For the spatial representation, the natural breaks (Jenks) setting was used in the case of SUs with a positive Z-score (hotspot) at $p < 0.05$. Hotspots containing SUs in the top 1% of the Z-score scale were defined as primary hotspots. Finally, the locations of the first known introductions and the primary hotspots were compared for each tree species and dbh class.

During the OAKEYLIFE project, local knowledge about the area was continuously collected. However, only 12 key informants were found who could provide useful information on the history of invasive tree species. Informants were between 40 and 85 years old and worked or had worked in the Peszér Forest for at least a decade in forestry or conservation positions. Due to the small sample size, it would not have made sense to conduct a statistically assessable questionnaire or similar survey; instead, informal conversations and unstructured interviews were carried out with each person on multiple occasions. Each time, the following recurring questions were asked: 1) when and how were the four tree species introduced to the area, 2) were these species planted somewhere/anywhere, 3) when did their populations explode and 4) what might be the cause of their population explosion?

Results

Information available in literature

The review of literature on the local presence of the four invasive tree species identified four sources that provided relevant information for the research. The first records of *A. altissima* were found in a 1964 journal article, which discussed the species in a comprehensive manner (Faragó 1964). In his work, the author gave the age and the exact location (a subcompartment ID) of the specimens studied. The oldest specimen was 25 years old and the site was located on the north-western edge of the Peszér Forest. Thus, it can be concluded that *A. altissima* was already present in Peszér Forest in the 1930s.

For *P. serotina*, the date and place of the first introduction could be identified with certainty from the other three sources identified. In 1937, an experimental forest was established in Peszér Forest, referred to as the Arboretum. It was later taken over by the National Forest Institute in the 1950s, which further developed it, planting and studying various non-indigenous woody species (Kolossváry 1961). However, the date of the first introduction of *P. serotina* is clearly described in a short communication (Babos 1954); the first experimental stand of the tree species was established in 1937 by a leading forest engineer. This information is confirmed by another short communication much later (Bidló and Faragó 1991), in which the authors also include the ID of the relevant forest subcompartment. Thus, for *P. serotina*, the place and time of the first introduction are known with certainty.

No data were found in literature about the first introduction (planting) of *C. occidentalis* and *A. negundo*.

Information stored in the National Forestry Database

In general, the NFD data showed that the tree species became more and more frequent in Peszér Forest in each subsequent period after their first appearance, with the greatest increase occurring at the turn of the millennium (Table 1).

Table 1.

Ailanthus altissima, *Celtis occidentalis*, *Prunus serotina* and *Acer negundo* in Peszér Forest over the last 60 years, based on the data of the National Forestry Database (1958-2016) and the recent field survey (2017-2019). N: Number of forest subcompartments. P (%): prevalence of a tree species in the study area (in relation to N). Pm (%): prevalence of a tree species as a major tree species in the study area (in relation to N). In theory, the currently valid (2016) forestry data and the field survey results should be very similar. However, the apparent difference highlights the under-representation of invasive tree species in the NFD.

Year / Species	*A. negundo*		*A. altissima*		*C. occidentalis*		*P. serotina*	
	P (%)	Pm (%)	P (%)	Pm (%)	P (%)	Pm (%)	P (%)	Pm (%)
1958 (n = 496)	0.8	0.4	0	0	0	0	0	0
1971 (n = 198)	0.5	0	0.5	0	0	0	0	0
1982 (n = 198)	2.0	0	3.5	0	2.0	0	0	0
1992 (n = 209)	4.8	0	8.6	0	2.9	0	0	0
2002 (n = 285)	8.4	0.4	25.6	0.4	33.7	0	15.8	0.4
2016 (n = 300)	13.0	1.3	48.7	8.3	47.3	0.7	18.0	0.3
2017-2019 (n = 300)	36.3	4.3	82.0	27.7	95.3	25.0	64.3	5.3

The earliest records of *A. negundo* were also found in the NFD. The presence of this species was indicated on four of the standard data sheets compiled in 1958. In the case of two forest subcompartments, this species was even listed amongst the major tree species. In the case of one of these subcompartments, the admixing ratios of *P.* × *canescens* and *A. negundo* were 90% and 10%, respectively. The age of this forest stand was recorded to be 18 years and it originated from seeds, clearly indicating an artificially reforested stand. The situation was more complicated for the other subcompartment. The data sheet indicated 60-year-old oaks and 50-year-old wild pears, with *R. pseudoacacia* as the dominant species and *P.* × *canescens* and *A. negundo* as accompanying species. No age data were provided, but the origin was marked as root sprouting. This information in the database indicated that *A. negundo* had previously been present and felled, but the subcompartment was reforested via root (and stump) sprouting. The average felling age of *R. pseudoacacia* in the country is 31 years (Rédei et al. 2017), but many stands are cut earlier to be used in the manufacturing of specific products, for example, fence posts. The 1958 NFD data, therefore, suggest that *A. negundo* must have been present in this area by the 1940s at the latest. It is interesting to note that it was not recorded again amongst the major tree species until 2002. Compared to the detailed field survey (see the next sub-heading), it appeared to be three times under-represented in the currently valid 2016 NFD data (Fig. 2).

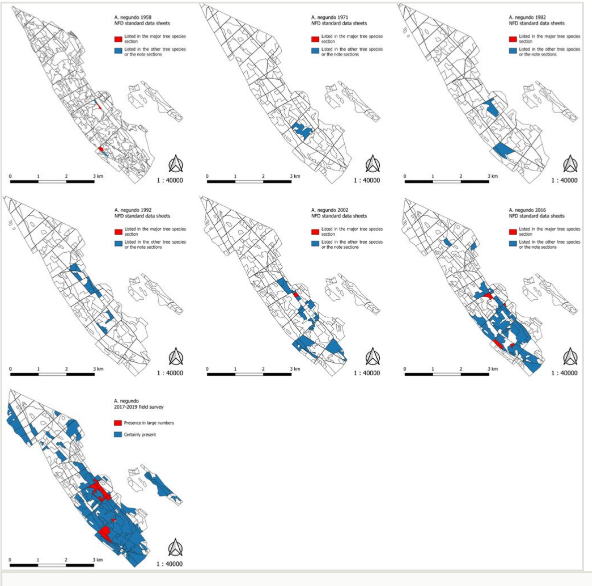

Figure 2.

Reconstruction of the spread of *A. negundo* in Peszér Forest, based on the data of the National Forestry Database available since 1958 and its recent status according to the currently valid (2016) forestry data (National Land Centre 2023) (Suppl. material 1) and – in comparison – the recent field survey (2017-2019).

A. altissima was first indicated by the NFD to be locally present in 1971. At that time, it was only reported from one subcompartment (the above-mentioned experimental forest). The experimental forest is located next to the forest subcompartment from which the first known occurrence (the 1930s) originates. It is, therefore, possible that it was also present here before and that it occupied an area intersected by the boundary of the two forest subcompartments, forming a larger patch. In terms of prevalence, a significant increase was indicated in 2002, when it was listed as a major tree species for the first time. Compared to the detailed field survey, the under-representation in the currently valid NFD data was about twice as high in terms of prevalence and three times as high in the case of the major tree species (Fig. 3).

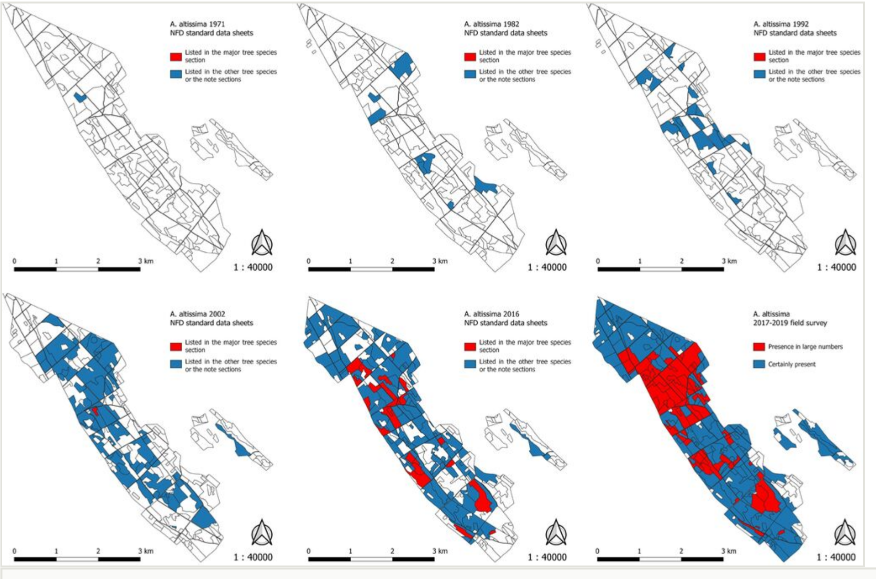

Figure 3.

Reconstruction of the spread of *A. altissima* in Peszér Forest, based on the data of the National Forestry Database available since 1958 and its recent status according to the currently valid (2016) forestry data (National Land Centre 2023) (Suppl. material 1) and – in comparison – the recent field survey (2017-2019).

The first occurrence of *C. occidentalis* in the NFD dates back to 1982. However, it was recorded in four forest subcompartments at the same time. The NFD data suggest that the invasion of this species may have started suddenly at the turn of the millennium, as it was reported in 2002 in a large part of the study area. *C. occidentalis* appeared amongst the major tree species for the first time in the currently valid 2016 NFD data, but it was still significantly under-represented compared to the field survey results (Fig. 4).

The greatest surprise was clearly the case of *P. serotina*, which was not listed in the standard data sheets until 2002 (Fig. 5), despite its documented planting in 1937. However, the tree species was then recorded in 45 subcompartments at the same time and, in one case, it was recorded amongst the major tree species. Compared to the results of the detailed field survey, it was three times under-represented in the currently valid NFD data, both in terms of prevalence and as a major tree species.

In the note section of the NFD data, a massive presence of *A. altissima* (numerous) was indicated for the first time in 1982, at its first known location of occurrence (the above-mentioned experimental forest) and in two adjacent subcompartments. However, according to a key informant, at that time and even much later, only the multitude of root suckers was indicated. In 2002 and especially in 2016, however, the NFD data include the frequent use of the word numerous and similar terms, not only for *A. altissima*, but also for *P. serotina* and *C. occidentalis*.

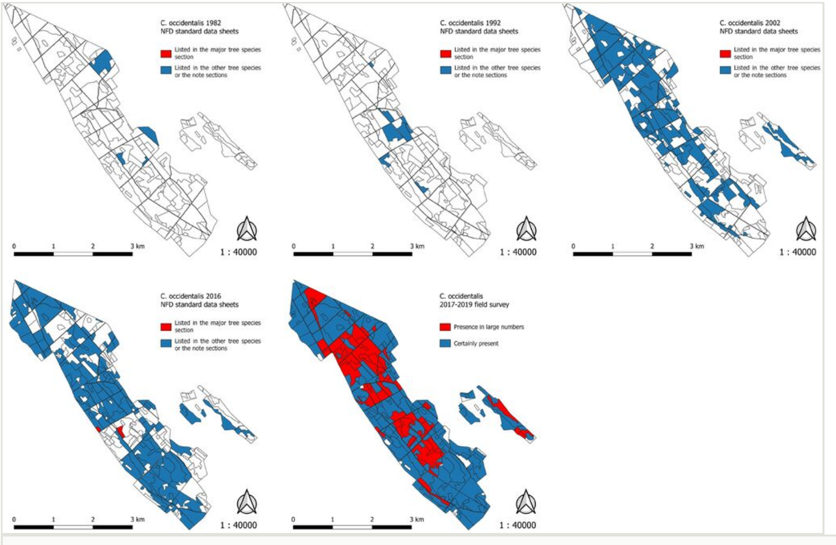

Figure 4.

Reconstruction of the spread of *C. occidentalis* in Peszér Forest, based on the data of the National Forestry Database available since 1958 and its recent status according to the currently valid (2016) forestry data (National Land Centre 2023) (Suppl. material 1) and – in comparison – the recent field survey (2017-2019).

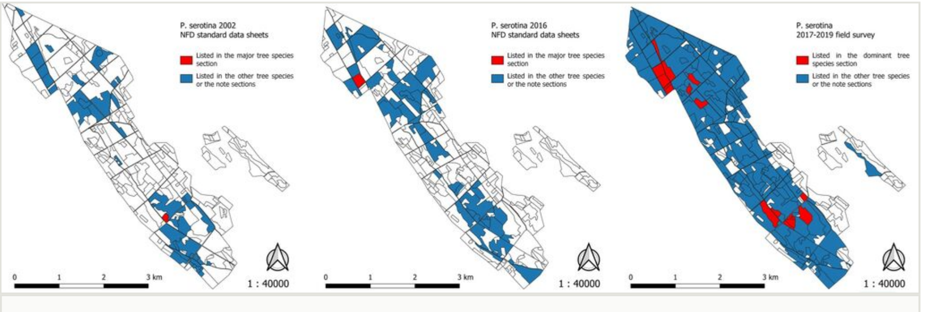

Figure 5.

Reconstruction of the spread of *P. serotina* in Peszér Forest, based on the data of the National Forestry Database available since 1958 and its recent status according to the currently valid (2016) forestry data National Land Centre 2023 (Suppl. material 1) and – in comparison – the recent field survey (2017-2019).

Results of the field survey

During the field data collection, 262 out of 300 subcompartments of the study area (1083 ha) were surveyed with a total of 16,056 SUs, covering 910 ha (see an example in Fig. 6). In the case of the four studied invasive tree species in total, 98,136 specimens were recorded (directly counted) in the dbh ≥ 5 cm size class, while the estimate for the dbh < 5 cm size class resulted in a figure of 2,175,000 specimens in the subcompartments assessed on a quantitative basis. In the case of seedlings, the data collected were ultimately used only as occurrence data, being not suitable for estimating abundance values. It was impossible to survey 32 subcompartments with a total area of 103 ha due to the impenetrable shrub cover; therefore, only occurrence (presence/absence) data were collected at these locations. The completely closed vegetation cover in these stands prevents the mass regeneration of invasive (and any native) tree species, so these stands most likely host an insignificant part of the overall local populations of the four studied invasive tree species. Another 30 ha could not be surveyed due to ongoing forestry activities and, finally, the remaining 40 ha covers the road network and other non-assessable elements of the study area. Overall, of the 300 subcompartments examined, *A. altissima*, *C. occidentalis*, *P. serotina* and *A. negundo* were found in 246 (82%), 286 (95%), 193 (64%) and 109 (36%) subcompartments, respectively. In the same order, the mass presence was calculated to be 27.7%, 25%, 5.3% and 4.3% of the forest subcompartments, according to the criteria described in the methodology.

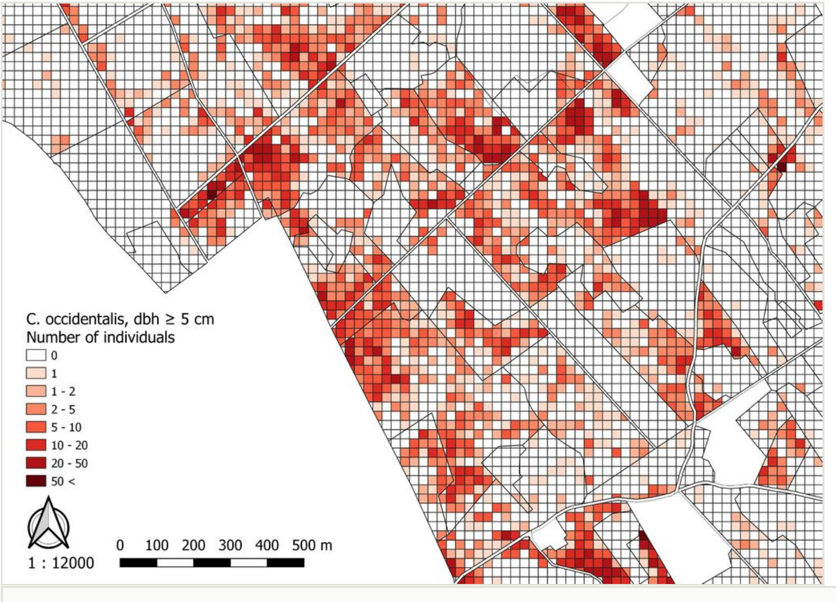

Figure 6.

Example illustration of the field survey conducted in 2017-2019, based on the 25 x 25 m survey units. The map shows the distribution and abundance of the dbh ≥ 5 cm class of *C. occidentalis* according to a chosen abundance category display in the north-western part of Peszér Forest. Subcompartments with a continuous white background could not be surveyed.

Results of annual ring counts

During the field survey, 58 specimens of *A. altissima* with a dbh ≥ 30 cm were recorded (Fig. 7). Of these, five specimens reached 40 cm dbh and one specimen had a dbh of over 50 cm. This latter specimen was felled and subjected to an annual ring count, revealing its age to be 48 years old.

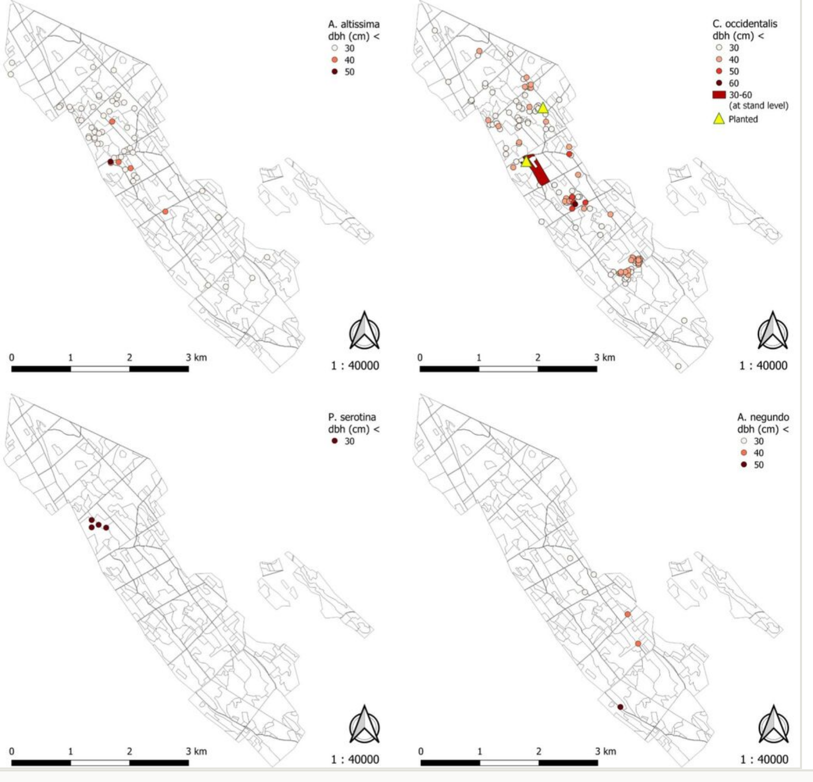

Figure 7.

Occurrences of larger specimens of *A. altissima*, *C. occidentalis*, *P. serotina* and *A. negundo* (dbh ≥ 30 cm) in Peszér Forest. In the case of *C. occidentalis*, the forest subcompartment containing many large specimens and the identified plantings are shown separately.

Compared to the above-mentioned species, more specimens with larger diameters (dbh ≥ 30 cm) were recorded in the case of *C. occidentalis*. Furthermore, a key forest subcompartment for the history of the tree species was identified (Fig. 7). It was located directly under the northern forester's house of Peszér Forest and contained hundreds of specimens with a dbh exceeding 30 cm. On the other hand, the largest trees (with dbh values between 50 and 65 cm) were arranged in rows, suggesting that they had been planted at the same time. Altogether three specimens were cut down, which were found to be of the same age, 75 (+ a few) years (an exact age could not be determined due to the interference of the innermost rings). With this information, the earliest known occurrence of *C. occidentalis* was identified and it can be concluded that this species has been present in

Peszér Forest since at least the 1940s. Apart from the key subcompartment, one additional case was documented in the north-eastern part of the forest where it was certain that the specimens had been planted on purpose (Fig. 7). The dbh of these specimens ranged between 15–20 cm and were located on the side of a sand dune arranged in a few rows, admixed with *R. pseudoacacia*. Some of these specimens were felled and a ring count revealed their age to be 30 years. This information clearly proved that *C. occidentalis* was planted in Peszér Forest even after the 1980s. A further 125 larger specimens were recorded scattered throughout the area, 83 with a dbh ≥ 30 cm, 36 with a dbh ≥ 40 cm, five with a dbh ≥ 50 cm and one exceeding a dbh of 60 cm. These individuals were not subjected to ring counts.

In the case of *P. serotina*, only four specimens reaching 30 cm dbh were found, relatively close to each other, which were not subjected to ring counts.

Altogether six larger specimens of *A. negundo* were found, three with a dbh ≥ 30 cm, two with a dbh ≥ 40 cm and one with a dbh just over 50 cm. As with *A. altissima*, the age of this latter specimen did not exceed 50 years.

Results of the hotspot analyses

Hotspot analyses on the field survey data resulted in the identification of one or two primary hotspots in the case of the four studied invasive tree species and the two dbh classes. In addition to these, other clusters of varying shapes and sizes were also found (Fig. 8). The extreme values and distributions of the Z-scores were different for the four invasive tree species and the two dbh classes, but the lowest positive Z-score was 1.96 in all cases at a significance level of $p < 0.05$. For *A. altissima*, a significantly positive Z-score was obtained for 3509 SUs in the dbh ≥ 5 cm class and for 2924 SUs in the dbh < 5 cm class. For *C. occidentalis*, the results were 2967 SUs and 3684 SUs, for *P. serotina*, 1948 SUs and 1929 SUs and for *A. negundo*, 1325 SUs and 1547 SUs. The upper extremes of the Z-scores (indicating the degree of aggregation) for *A. altissima*, *C. occidentalis*, *P. serotina* and *A. negundo* were 30, 23.7, 48.3 and 67.2 in the dbh ≥ 5 cm class and 27.2, 27.8, 56.6 and 37.5 in the dbh < 5 cm class, respectively. This suggests that *P. serotina* and *A. negundo* occur in a more aggregated spatial pattern in the study area than *A. altissima* and *C. occidentalis*.

In the case of *A. altissima*, one primary hotspot could be identified for both dbh classes, located on the north-western edge of Peszér Forest. There is a perfect overlap between the primary hotspot and the first known occurrence of this tree species, which means that, 80 years after its first introduction, it is most abundant where it was probably first established. Adjacent to this, there is a large and partially contiguous set of clusters of SUs with lower Z-scores. In addition, a larger, isolated patch in the mid-western part of the study site can be highlighted.

For the dbh ≥ 5 cm class of *C. occidentalis*, two primary hotspots were identified, one in the northernmost part of the study area and the other in the central part. For the dbh < 5 cm class, a twin primary hotspot was identified in the same forest subcompartment in the northern part of the Forest. However, there are also several isolated hotspots scattered throughout the area, with lower Z-scores even appearing in the most remote and more-or-less isolated eastern part of the study area (Szalag Forest). Although the first known occurrence of the tree species is located in a hotspot with lower Z-scores, the primary hotspots for both dbh classes are located elsewhere.

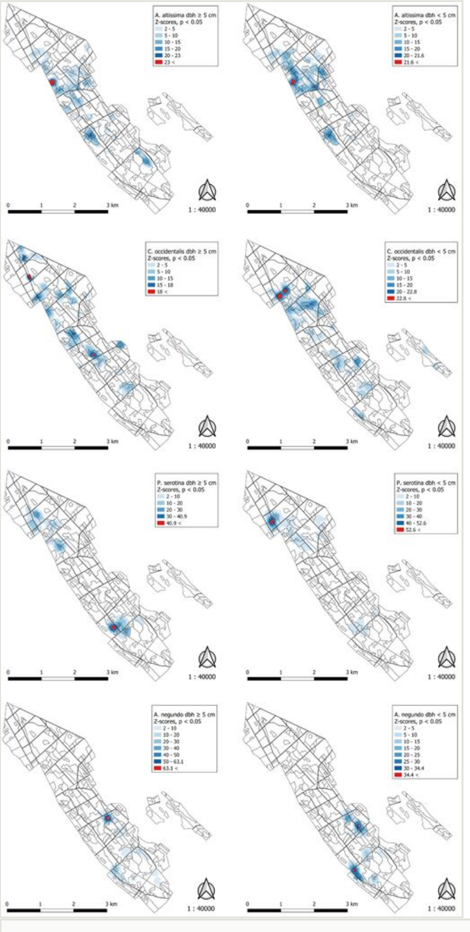

Figure 8.

Results of the hotspot analyses for *A. altissima*, *C. occidentalis*, *P. serotina* and *A. negundo* by the dbh ≥ 5 cm and the dbh < 5 cm classes. Z-scores with $p < 0.05$ are displayed according to natural breaks (Jenks). Survey units with Z-scores in the upper 1% are highlighted with red (primary hotspots).

The situation proved to be much simpler for *P. serotina* and *A. negundo*. For the dbh ≥ 5 cm class of *P. serotina*, a distinct primary hotspot can be observed in the central-southern part of the study area and a larger patch with lower Z-scores in the north-western part. For the dbh < 5 cm class, the situation is partially reversed, with the primary hotspot being located in the north-western part. Outside of these, only hotspots with generally low Z-scores could be identified. The experimental forest, where *P. serotina* was introduced for the first time, does not coincide with the primary hotspots, but a lower Z-scored hotspot still appears there.

In the case of *A. negundo*, one primary hotspot was identified for the dbh ≥ 5 cm and two for the dbh < 5 cm class in the southern and central parts of the study area. However, the spatial patterns showed a relatively close overlap. Similarly to *A. altissima*, the first known occurrences and primary hotspots of *A. negundo* are (almost) identical.

Results of collecting local knowledge

The exploration of local knowledge also revealed important information on the spread of the four invasive tree species. All 12 key informants confirmed that the studied invasive tree species started to expand spectacularly only after the turn of the millennium. Furthermore, exponential increases in seed quantities (mass germination events) became a common phenomenon even later, basically from the 2010s onwards, similarly to the dynamics observed in other forests in the region. On a causal basis, it can be assumed that significant changes must have taken place in some respects in the 2000s and perhaps even in the 1990s. One informant specifically pointed out that, from 2000 onwards, drought-prone springs and summers became more frequent, accompanied by increasingly mild winters. In his opinion, this must have been a factor in the start of the mass spread of *A. altissima*, as its young shoots did not freeze at all in the winter and it seemed to tolerate hot summers very well. Another important piece of information for this period is that, until the late 1990s, the fallow deer (*Dama dama*) population was kept at a very high level (around 100 individuals) by the game management company. However, after a new game manager took over, the population was reduced to almost zero within 1–2 years. The last crucial finding for this period is summarised in the statements of two foresters and one professional conservationist active at the time. Since the 1990s, there have been numerous consultations (or heated debates) between the locally competent Forestry Directorate and the National Park Directorate, which ultimately resulted in a decrease in the intensity of land use. On the one hand, this meant a reduction in the frequency and spatial extent of annual forestry works and, on the other hand, it facilitated the development of a dense shrub layer in the forest stands and on many clearings. One informant noted that this change may have been a factor in the rapid invasion of tree species. In regard to the times before the 1990s, only two senior foresters could provide reliable data. By the 1960s, foresters in the region no longer attached importance to *A. altissima* and *A. negundo*, as their wood properties proved to be poor and they were considered “junk trees”. In addition, it was recognised that the intensive sprouting of *A. altissima* can negatively affect the growth of the major tree species intended to be cultivated. For these reasons, planting this species in Peszér Forest had certainly been avoided since that time. However, the situation was different for *C. occidentalis* and *P. serotina*. It turned out that the two tree species were planted until the beginning of the 1990s, especially in areas with the lowest productivity (e.g. on higher parts of sand dunes). Although these species were never planted as major trees, it was quite frequent to plant these as admixed species in the *R. pseudoacacia* and *P.* × *canescens* plantations.

The key pieces of information from the data collected are summarised in Fig. 9 and Table 2.

Table 2.

Summary of the key information collected during the research by data source. The underlining indicates the source of the first known, identified occurrence.

Tree species / sources	***Acer negundo***	***Ailanthus altissima***	***Celtis occidentalis***	***Prunus serotina***
Literature	no data	certainly present since the 1930s (Faragó 1964)	no data	first planted in 1937 in the forest's experimental stand (Babos 1954, Kolossváry 1961, Bidló & Faragó 1991)
First appearance in the National Forestry Database	1958 (18 years old individuals), certainly present since the 1940s	1971	1982	2002 (!)
Sampling older specimen	maximum 50 years old specimens	maximum 50 years old specimens	certainly present since the 1940s: 75 (+5) years old specimens	no older specimens are present
Utilisation in forestry	certainly avoided at least since the 1950s	certainly avoided at least since the 1950s	planted on an ad hoc basis even in the 1980s and 1990s, for example, to bind sand dunes	planted on an ad hoc basis even in the 1980s and 1990s, for example, to bind sand dunes
Field survey (dbh ≥ 5 cm class)	12,000 individuals; 8.2 cm average dbh; 7.2% frequency in SU-s	43,900 individuals; 8 cm average dbh; 24.7 % frequency in SU-s	26,900 individuals; 8.6 cm average dbh; 33.2% frequency in SU-s	15,300 individuals; 7.7 cm average dbh; 13.6% frequency in SU-s
Field survey (dbh < 5 cm class)	approx. 61,000 individuals; 28% frequency in SU-s	approx. 1,100,000 individuals; 44 % frequency in SU-s	approx. 890,000 individuals; 78% frequency in SU-s	approx. 110,000 individuals; 28% frequency in SU-s
Hotspot analysis	The first known occurrences and the primary hotspots are almost identical	The first known occurrence and the primary hotspot are identical	The first known occurrence and the primary hotspots are at different locations	The first plantation and the primary hotspots are at different locations

Discussion

The four invasive tree species studied have been present in Peszér Forest since at least the 1930s or 1940s. A definitive source for the date of the first introduction was found only for *P. serotina* (1937), but the data indicate that the other three species could not have been present much earlier either. The first specimens of *P. serotina* and *C. occidentalis* were certainly planted. However, the characteristics of the first known occurrences of *A. altissima* (around the experimental forest) and *A. negundo* (already amongst the major tree species and seed sources at its first mention) suggest that they were also introduced deliberately. According to the NFD data and the local knowledge, each of the tree species barely expanded for 60–70 years and, after the turn of the millennium, their populations suddenly exploded.

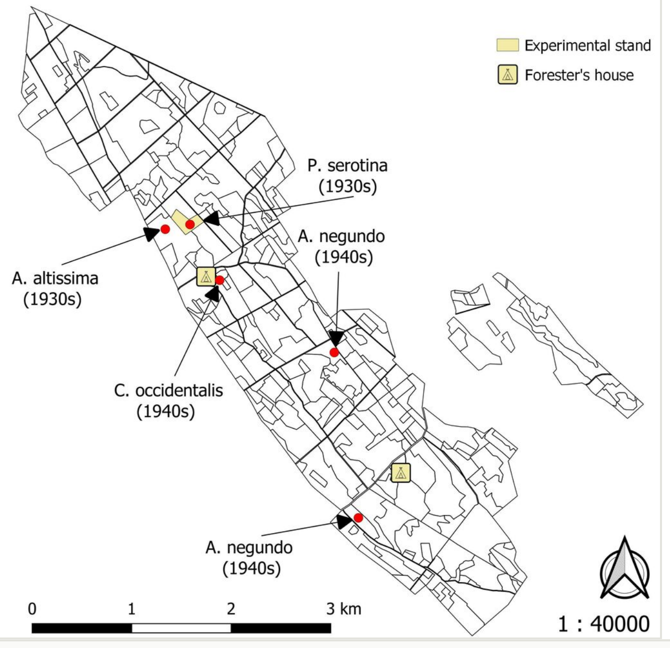

Figure 9.

The first known occurrences of the four invasive tree species, based on all data sources. *A. altissima*: literature; *C. occidentalis*: live specimens; *P. serotina*: literature; *A. negundo*: National Forestry Database (National Land Centre 2023) (Suppl. material 1). The forester's houses and the experimental forest are also indicated.

For invasive species, the lag time (or lag phase) is the period from first introduction to successful spread, i.e. invasion in the classical sense (Hengeveld 1989). Since the lag time depends on a myriad of factors and can vary even for the same species, it is usually impossible or very difficult to predict (Coutts et al. 2018). In Germany, a study on 184 woody species found these values to be 131 years for shrubs and 170 years for trees on average (Kowarik 1995). The work also included *A. altissima* with a lag phase of 122 years, *A. negundo* with 183 years and *P. serotina* with one of the shortest lag times, 29 years. Research conducted in Australia found an average lag time of 85 years for woody species (Caley et al. 2007), whilst it can be even shorter in the Tropics, averaging 14 years (Daehler 2009). All four tree species are able to reach seed-bearing age relatively early. *A. altissima* can reach flowering age at 3–5 years (Kowarik and Säumel 2007) and 10–20 years old specimens tend to have the best seed production (Miller 1990). In Belgium, Deckers et al. (2005) showed that *P. serotina* can produce seeds as early as 4 years old and the majority of specimens examined had been reproducing since 7 years of age. *A. negundo* was reported to reach seed-bearing age after 7–11 years (Overton 1990), but it is likely that, in invaded areas, the first seeds may be produced even earlier. No precise data were found for *C. occidentalis*, but in Peszér Forest, younger trees with a dbh of 2–3 cm and a total height of 3–4 m can already produce viable seeds (pers. obs.). As the species can grow an average of 40 cm/year in the first 6 years (Krajicek 1965), seed production is also likely to start within 10 years. In addition, all four species are able to regrow from stumps after felling to a significant extent and these robust shoots can flower within 1–2 years (pers. obs.). In any case, by the 1950s or 1960s at the latest, the foresters of the time should have seen the advance of the tree species if their invasion had started immediately. However, *A. altissima*, *C. occidentalis* and *P. serotina* appeared in the NFD much later than the first known occurrences and a significant increase in the abundance of all four species occurred simultaneously at the turn of the millennium.

For a given species, the lag time can depend on: 1) the characteristics of population growth and range expansion (inherent lag), 2) changes in the environmental conditions and 3) changes in genetic factors (prolonged lags) (Hobbs and Humphries 1995, Crooks and Soulé 1999). Of the three main groups of explanation, only the third can be excluded with high probability. On the one hand, no more than 10–15 generations of these tree species could have existed in Peszér Forest before the 2000s and, on the other hand, it is unlikely that all of these species would have undergone genetic changes at the same time that could have triggered their invasion. However, it is expected that, once the first viable seeds appear, the population and range of an introduced invasive tree species will eventually start to increase. For inherent lags, this increase is constant and can be described by classical population growth models, such as an exponential function or a quadratic function of time (Hengeveld 1989, Crooks 2005). The available NFD data do not allow such calculations; however, a simple increase in the population alone would not explain why all four species invaded at almost the same time anyway. However, since the NFD data show that the four species have been appearing steadily in new stands over the decades, it is likely that these species had become frequent enough in Peszér Forest by the turn of the millennium to allow a sudden outbreak. Nevertheless, the phenomenon that lasted for 60–70 years was most likely a prolonged lag, eventually brought to an end by environmental changes. Local knowledge has revealed three very important environmental changes at the turn of the millennium, each of which might have strong explanatory power. Firstly, the management of the forest changed, secondly, drought years became more frequent and thirdly, the game population was decimated.

Forest management activities and, in particular, the resulting disturbances, undeniably play a key role in biological invasions. Felling changes canopy closure conditions, leading to increased light availability, while the movement of machinery and the transportation of timber can cause drastic soil disturbance in addition to propagule dispersal. This can act as a major driver in the invasion process, as has already been shown for *A. altissima* (Carter and Fredericksen 2007, Rebbeck et al. 2017), including Peszér Forest (Erdélyi et al. 2021) and other coppice forests (Radtke et al. 2013). Canopy structure has also been demonstrated to be a decisive factor in *P. serotina* invasion (Closset-Kopp et al. 2007, Vanhellemont et al. 2010, Jagodziński et al. 2019), supporting its long-described gap-dependence in its native range (Auclair and Cottam 1971). In many respects, *C. occidentalis* has similar characteristics to *P. serotina*, for example, it also has excellent shade tolerance and spreads via endozoochory. In Peszér Forest, its saplings start to grow immediately after the slightest opening of the canopy or even the shrub layer (pers. obs.). In Europe, the invasion of *A. negundo* is worst in riparian forests and similar habitats with temporary waters and is generally discussed in terms of flooding-related disturbances and biotic regulation (Saccone et al. 2010, Porté et al. 2011, Sikorska et al. 2019). In Peszér Forest, it was only able to spread in the lowest-lying parts with the best water supply, but even in the larger clear-cuts, the explosions in its seed quantities are moderate compared to *A. altissima* (pers. obs.). Today, all tree species respond quickly to forestry interventions, but until the 2000s, these were rather subdued. The regime change of 1989–1990, which marked the end of the communist (socialist) period in Hungary, probably played an important role in this significant change. In general, there have been major transformations in all sectors, including forestry (e.g. the privatisation of many state-owned forests) and nature conservation (e.g. the first separate Nature Conservation Law in 1996). In the socialist era, both newly-planted and coppiced stands were treated at high frequency to remove unwanted vegetation. Most of the forest stands of Peszér Forest were plantations or coppice forests, consisting only of the main tree species planted. Manual labour was usually available (partly due to guaranteed employment (Bandzak 1994)) and usually performed by local residents. This was fundamentally altered following the regime change and labour shortages have been a growing problem in the sector ever since. Due tothis and many other reasons, financial management of the various field operations has become increasingly challenging. At the same time, the advocacy power of nature conservation has increased and the mutually beneficial and inevitable decision has finally been taken to reduce the intensity of interventions. As a result, the shrub cover is now dense and continuous almost everywhere in the Forest; however, during this time, not only shrubs, but invasive tree species could have grown up as well, probably in much larger numbers without the frequent interventions.

Climate change can directly or indirectly play a role in the invasion of many species by altering the nature of vectors and pathways, the abiotic properties of the recipient environment and the biotic interactions of the recipient community (Hulme 2017, Robinson et al. 2020). Furthermore, the increasing weather anomalies and associated catastrophic events can trigger very rapid population explosions (Geerts et al. 2013, Walsh et al. 2016). With rising mean annual temperatures, the frequency and severity of drought events in Hungary have become significantly higher since the 1990s and this has particularly severe consequences for the Danube–Tisza Interfluve (Fiala et al. 2014). The tragic droughts of 2000 and 2003, for example, were specifically mentioned by one key informant: “Those were such unbearable days that we couldn't stay out in the field. And it was only after the drought years that I first saw *A. altissima* seedlings appearing in very large numbers everywhere”. *A. altissima* and in particular its seedlings have long been known to be sensitive to frost, but at the same time tolerant of droughts (Kowarik and Säumel 2007). The former property is also clearly indicated by the X-ray experiments carried out in Hungary in the 1960s with the aim of making the seedlings resistant to frost (Karai 1963). A study conducted in the Mediterranean Region has identified an average annual temperature threshold (11.1°C), above which the species can no longer spread (Motti et al. 2021). The mean annual temperature in Hungary is between 8 and 11°C, but it is interesting to note that this value is around 11°C in the study area as well. In any case, the lack of long winters and rising temperatures favour the invasion of *A. altissima*. A North American study, using a climate envelope approach, has shown that both *P. serotina* and *C. occidentalis* are amongst the 25 native tree species whose range will show the greatest latitudinal shifts due to climate change (McKenney et al. 2007). Another study on *P. serotina* also outlined significant shifts in North America and predicted an increase in its invasion in Europe (Segura et al. 2018). However, in Hungary, the invasion of *A. negundo* is not expected to increase much in essentially dry forests such as Peszér Forest, but it will certainly persist for a long time in habitats with a better water supply.

The impact of large herbivores on plant invasions can be diverse, as they can accelerate (Vanhellemont et al. 2010), mitigate (Rossell et al. 2007) or have mixed effects (Knapp et al. 2008) on the spreading processes. *A. altissima* is consumed by large mammals in North America, but typically less than other tree species (Kowarik and Säumel 2007). In Hungary, a study in non-native forests showed that red deer (*Cervus elaphus*) hardly consume it even when it is present in large numbers. *C. occidentalis*, on the other hand, was particularly favoured (Mátrai et al. 2004). In Peszér Forest, besides the fallow deer, the roe deer (*Capreolus capreolus*) and the European hare (*Lepus europaeus*) are also present, but none of them is browsing *A. atissima*, although signs of tasting and bark stripping sometimes occur. This is also true for both *P. serotina* and *A. negundo*, but definitely not for *C. occidentalis*, which is essentially the only invasive tree species that is favoured by the animals and regularly browsed when young (pers. obs.). However, the drastic reduction of the fallow deer population in the late 1990s must have had some impact on the vegetation as well. In addition to browsing, game species influence their environment in many other ways, such as trampling, which is another important direct effect. If large numbers of individuals are present, it has been shown that, in parallel with palatable plant species, unpalatable plant species can also undergo a significant decline due to severe soil disturbance (Heckel et al. 2010). In addition, one informant described the fallow deer as “the goat of the lowlands”, which implies that it can eat a wide variety of plants when the palatable ones are not present. In conclusion, the reduction of the game population probably favoured *C. occidentalis*, but at the same time, it may have also provided more favourable conditions for the regeneration of the other three tree species.

All six approaches applied in the research proved to be important and provided new information on an individual basis as well. The circumstances of the first introduction of *P. serotina* and *A. altissima* were answered by the most basic source, the literature. The four relevant sources were cited in Korda (2018), but either in insufficient detail or in phrasing that did not allow a local link to be identified. Therefore, it was worth revisiting the main forestry journals. Two sources were also obtained in print from foresters during the collection of local knowledge. These were not necessary in our case, as those had been digitised a few years earlier, but it is still an indication that important written material may be in the possession of the people who live in the landscape. The earliest data on *A. negundo* were provided by the NFD and the increasing prevalence of all four species could be tracked on distribution maps created using the database. However, *A. altissima* and *C. occidentalis* did not appear in the NFD until about 40 years later and *P. serotina* 65 years later than their first known introductions. In addition, the four tree species have been found to be generally under-represented in the current NFD. These databases form an essential basis for many forest-related research and policy-making efforts, but in all cases, limitations must be recognised and conclusions must be drawn with caution (Thompson et al. 2007, Traub and Wüest 2020, Yanai et al. 2023). At larger scales, NFDs and similar databases (e.g. forest inventories) can definitely provide a strong basis for assessing recent and potential occurrences (Campagnaro et al. 2022), investigating causal relationships (Zhai et al. 2018, Lázaro-Lobo et al. 2021) or carrying out risk assessments (Bindewald et al. 2021) concerning invasive tree species. However, as our results show, smaller-scale studies on this topic are likely to require higher-resolution data and supplementary sources.

The detailed field survey clearly showed that the problem is much greater in the area than any other database could suggest. However, collecting field data on a larger scale with a similar effort would probably be unfeasible due to the costs and manpower required. On the other hand, it provides crucial data for the long-term optimisation of conservation and forest management activities in target areas of high conservation value and, hence, for reducing costs. For example, in the OAKEYLIFE project, data on invasive tree species collected at a resolution of 25 × 25 m were used as the basis for several decisions (e.g. reconstruction or rehabilitation at the habitat patch level) and resource prioritisation. The documentation of large tree specimens during the field survey allowed the identification of the earliest known occurrence of *C. occidentalis*. The data also showed the preferences of forest managers, i.e. which tree species are most often left behind during felling. *C. occidentalis* appeared to be the first once again when using this approach. Comparing the positions of the large tree specimens and the results of the hotspot analyses, an overlap can generally be seen, but the central hotspots (survey units with the highest Z-scores) and largest tree specimens are in the same location only in the case of *A. negundo*. However, the spatial distribution of large tree specimens is essentially determined by case-by-case decisions made during logging, so further conclusions regarding spreading histories should be drawn with caution on this basis alone.

The identification of hotspots is a common methodological approach in studies aiming to explore the past and present status of invasive species and to make predictions about their future spread (Ibáñez et al. 2009, O'Neill et al. 2021, Schneider et al. 2021, Yang et al. 2023). In this work, the analysis allowed the identification of current differences in spatial distributions and abundances, but also enabled indirect conclusions to be drawn about differences between the tree species and some past events. For *A. altissima* and *A. negundo*, the locations of the central hotspots and the first known introductions were nearly identical, but not so for *C. occidentalis* and *P. serotina*. The reason for this difference could be two-fold. Firstly, in terms of life history traits, *A. altissima* shares many similarities with *A. negundo*, whereas *C. occidentalis* is more similar to *P. serotina*. For example, the former two spread via anemochory (dispersion usually over shorter distances) and are very light-demanding, whereas the latter two spread via endozoochory (allows jump-dispersal) and have excellent shade tolerance. Secondly, the exploration of local knowledge revealed that *A. altissima* and *A. negundo* did not have any use in the area, while *C. occidentalis* and *P.*

serotina had been purposefully planted for a long time. In Hungary, *C. occidentalis* had been widely used to bind sand dunes (Korda 2018) and its central hotspots in Peszér Forest were located in exactly such areas. In the case of *P. serotina*, the northern central hotspot was located in a newly-established part of the Forest, which was planted only in the 1960s (new afforestation efforts in the north-western part (1958–2002) can be traced in Fig. 2). Due to the short time span, it is unlikely that the species here have become abundant only through spontaneous processes. It follows that hotspot analysis may allow the identification of potential planting sites for invasive tree species in cases where no documentation was made.

Finally, local knowledge has also proved to be of paramount importance, especially in understanding the population explosions at the millennium and the utilisation of the tree species. However, because of the time that has passed, informants have often been unable to pinpoint the exact places and times in question. Thus, for research at the local scale, this approach can be recommended primarily as a complement to the quantitative methods.

Conclusions

Unravelling the history of the spread of invasive tree species is an undeniably difficult task. While large-scale historical reconstructions can be carried out using one or two types of data sources and usually do not require targeted prior field data collection, a similar approach at the local scale is unlikely to be successful due to the low data density. In this study, six approaches were used simultaneously and each of these sources independently provided key information. This illustrates the need for as many different sources as possible in such relatively small study areas, as they can complement each other. The mixed approach can be applied to other tree species and areas as well, for example, a similar work is replicable in virtually any forested area in Hungary. In most cases, the invasion history of a species cannot be fully explored and this is also true for the four tree species in Peszér Forest. At the same time, a well-supported story can act as a strong argument for identifying these species as a problem not only for conservation, but also for various economic sectors and the general public. In Hungary, *C. occidentalis* is still a popular park tree and is also available in some garden stores and there are also (undocumented) examples of *P. serotina* being planted in some forest landscape units. However, this occasional use of the tree species in our time is negligible compared to the previous two centuries (Korda 2018). We have now reached the point where efforts to manage invasive tree species are already underway. Although the complete eradication of tree species from an area with the size of Hungary is going to remain unthinkable for a long time, good results have been achieved on a small scale (Csiszár and Korda 2015). The most labour-intensive part of managing invasive tree species is the removal of seedlings and young saplings, but this does not require any specialised skills, so anyone can do it. As volunteering plays an increasing role in conservation, more and more people are getting involved in data collection (Johnson et al. 2020) and the active management (Dechoum et al. 2019) of invasive species as well. To further stimulate interest, it is necessary to present this complex problem not only from a variety of ecological or economic angles, but also from a historical perspective.

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Conflicts of interest

The authors have declared that no competing interests exist.

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Supplementary material

Suppl. material 1: Derived data of *Ailanthus altissima*, *Celtis occidentalis*, *Prunus serotina* and *Acer negundo* from the National Forestry Database and its archives.

doi

Authors: Arnold Erdélyi

Data type: excel file

Brief description: Data derived from the National Forestry Database for the investigated invasive tree species from the forest management periods 1958, 1971, 1982, 1992, 2002 and finally 2016, valid at the time the study was conducted.

Download file (461.83 kb)