DOI: 10.12905/0380.phyton62-63-2023-0075 Published online 9 Mar 2023

First inventory of the invasive alien plant species along Nestos River (East Macedonia, NE Greece)

Spyros Tsiftsis[1] & Theodora Merou[1]

with 3 figures and 2 tables

Key words: NE Greece, Nestos River, floodplain areas, Natura 2000, invasion, IAS.

Summary

Tsiftsis S. & Merou T. 2023. First inventory of the invasive alien plant species along Nestos River (East Macedonia, NE Greece). – Phyton (Horn, Austria) 62–63: 75–86, with 3 figures and 2 tables.

Invasive alien species constitute a great threat to biodiversity and habitats at a global scale. River floodplains contain very sensitive habitats (e.g., alluvial areas, riparian forests, wetlands) that are highly threatened by invasive alien species commonly transported and introduced into countries through transboundary river systems. In the present study, the invasive alien plant species in the habitats of the Nestos river delta were identified and mapped, using a 200 × 200 m grid. Six plant species displaying invasive behavior (*Acer negundo*, *Ailanthus altissima*, *Amorpha fruticosa*, *Phytolacca americana*, *Robinia pseudoacacia*, *Solanum elaeagnifolium*) have been found along the Nestos River system. *Phytolacca americana* was the most widely distributed species (recorded in 82 grid cells), followed by *Robinia pseudoacacia* (67 grid cells) and *Amorpha fruticosa* (63 grid cells). Judging by the number and distribution of the grid cells invaded by *Amorpha fruticosa*, it is already rather widespread in the area, but it still shows the most aggressive invasive behavior as compared to the other five. Consequently, if the rate of expansion remains uncontrolled, large meadows that are close to the river will be fully covered by *Amorpha fruticosa* in the next couple of years. The continuous monitoring of the distribution and possible expansion of invasive alien species in the study area would be critical for applying successful control management programs.

1. Introduction

The transfer of species from one area to another is a worldwide phenomenon and has been known since ancient times. For example, the common pheasant (*Phasianus colchicus*), named after the river Phasis in Transcaucasia, was brought to Greece by the ancient Greeks around 1300 B.C. (Cassey & al. 2015). Domestic or wild animal and plant species have been introduced for food (e.g., game), for their ornamental value, or as pets (Tella 2011). Nowadays, globalization, the newly developed means of transportation and the increase in the people's income have enabled the transportation of goods from all parts, even the most remote, of the world. In this way, species are intentionally or unintentionally transferred, and their distribution range is expanded. Species that have been introduced into areas outside their natural range by human activities are called alien species or introduced species (Richardson & al. 2011).

Many of those non-native species have adapted easily to new environments and expanded rapidly, displaying a highly competitive behavior. Therefore, they are considered as invasive alien species (IAS). Their rates of colonization have recently accelerated due to various factors (e.g., habitat modification, human transportation), but also due to global climate change, as climatic zones shift and their potential ranges expand (Clout & Williams 2009). It is estimated that more than 11,000 alien species have been introduced into the European Union recently, while 15 % of them present invasive behavior, thus being harmful to biodiversity (European Union 2011). For this reason, the European Commission issued the Invasive Alien Species Regulation on January 1st, 2015, as Regulation (EU) 1143/2014. This regulation is in agreement with Action 16 of Target 5 of the EU 2020 Biodiversity Strategy, as well as with Aichi Target 9 of the Strategic Plan for Biodiversity 2011–2020 under the Convention of Biological Diversity. Three distinct types of measures are referred to in the EU Regulation: (a) prevention, (b) early detection and rapid eradication, and (c) management of the IAS in the territory of the European Union.

[1]) International Hellenic University, Department of Forest and Natural Environment Sciences, 1st km Dramas – Mikrochoriou, P.O. Box 172, 66132 Drama, Greece; corresponding author: S. Tsiftsis (e-mail: stsiftsis@for.ihu.gr)

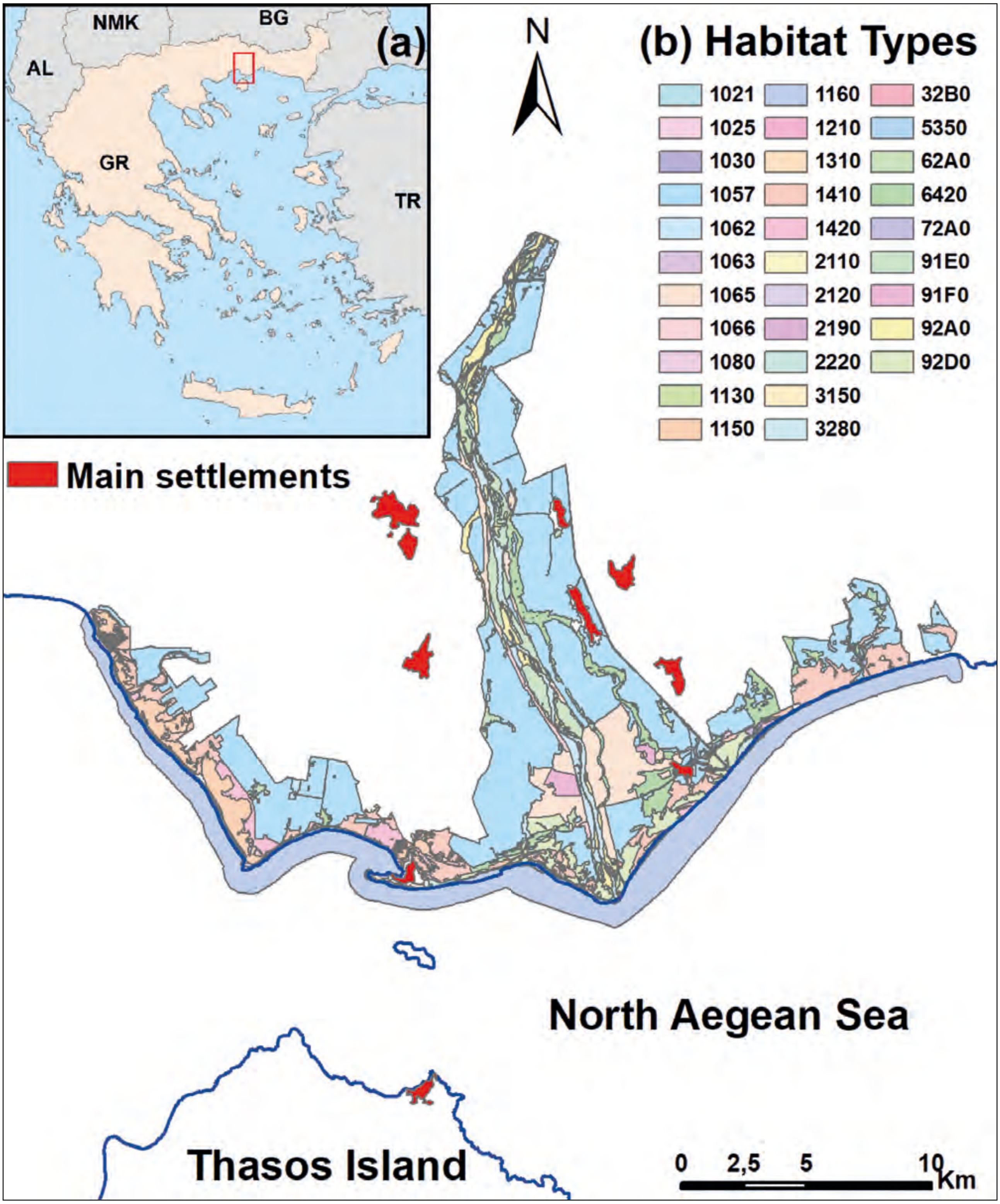

Fig. 1. (a) Map of Greece showing the Nestos Delta area. – (b) Overview of the Nestos Delta and adjacent coastal areas. The various color shades assigned to 31 of the 32 habitat types (compare Table 1) are not distinguishable at this small scale. The most extensive portions of the river delta proper (also shown at a larger scale in Fig. 3) are covered by: Arable cultivated land (1057), Plantations with forest trees (1065), coastal lagoons (1150), Mediterranean tall humid herb grasslands of the Molinio-Holoschoenion (6420), Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Alno-Padion, Alnion incanae, Salicion albae) (91E0), *Salix alba* and *Populus alba* galleries (92A0), Riparian mixed forests of *Quercus robur, Ulmus laevis* and *Ulmus minor, Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (Ulmenion minoris) (91F0).

Table 1. Habitat types in the Nestos Delta area.

Code no.	Habitat type
1021	Concentrations of agricultural infrastructures
1025	Roads
1030	Areas of gravel or/and sand extraction
1057	Arable cultivated land
1062	Abandoned crops
1063	Rivers
1065	Plantations with forest trees
1066	Fruit trees and plantations
1080	Natural water collections
1130	Estuaries
1150	Coastal lagoons
1160	Large shallow inlets and bays
1210	Annual vegetation of drift lines
1310	*Salicornia* and other annuals colonizing mud and sand
1410	Mediterranean salt meadows (Juncetalia maritimi)
1420	Mediterranean and thermo-Atlantic halophilous scrubs (Sarcocornetea fruticosi)
2110	Embryonic shifting dunes
2120	Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes)
2190	Humid dune slacks
2220	Dunes with *Euphorbia terracina*
3150	Natural eutrophic lakes with Magnopotamion- or Hydrocharition-type vegetation
3170	Mediterranean temporary ponds (not shown in Fig. 1b)
3280	Constantly flowing Mediterranean rivers with Paspalo-Agrostidion species and hanging curtains of *Salix* and *Populus alba*
32B0	Euro-Siberian annual communities of muddy river banks
5350	Pseudomaquis
62A0	Eastern sub-mediterranean dry grasslands (Scorzoneratalia villosae)
6420	Mediterranean tall humid herb grasslands of the Molinio-Holoschoenion
72A0	Reed thickets
91E0	Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Alno-Padion, Alnion incanae, Salicion albae)
91F0	Riparian mixed forests of *Quercus robur, Ulmus laevis* and *Ulmus minor, Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (Ulmenion minoris)
92A0	*Salix alba* and *Populus alba* galleries
92D0	Southern riparian galleries and thickets (Nerio-Tamaricetea and Securinegion tinctoriae)

Although some alien species have positive impacts on the new environments into which they have been introduced (Chiba 2010), most of them have caused dramatic changes at different levels of organization in ecosystems. For example, they are considered responsible for accelerating the extinction of native species, altering the genetic composition of native species populations, reducing the abundance and the number of species in an area, reducing ecosystem productivity, affecting nutrient cycling and regional hydrology, and changing habitat structure (Vilà & al. 2011, Ricciardi & al. 2013). The identification of these impacts has led the scientific community to map out immediate management measures and to propose legal actions against IAS, although this has not been completely successful as introductions still happen, though often unintentionally (Regulation (EU) 1143/2014). However, it should be noted that preventing the introduction of alien species is usually considered more beneficial than managing these taxa after they have been introduced into a new area (Simberloff & al. 2013).

In Europe, floodplains are occupied by very sensitive habitats (e.g., alluvial areas, riparian forests, wetlands) threatened by numerous factors (Pyšek & Prach 1994, Schnitzler & al. 2007, Pegg & al. 2022). Among them, a wide range of species-rich freshwater ecosystems of very high environmental value have been identified (European Environment Agency 2016). River systems also serve as transport corridors for invasive plants by transporting downstream vegetative matter and seeds (Gallé & al. 1995). The expansion of IAS in wetland habitats through this mechanism poses direct threats to native species in these habitats (Pegg & al. 2022).

In northern Greece, transboundary rivers, such as the Axios, Strymon, Nestos, and Evros, are ideal transport corridors for alien plant species (e.g., *Amorpha fruticosa*) that can expand their range with the help of running water (Pedashenko & al. 2012). However, this is not the only way by which alien plant species can be transported and established in floodplain areas. Over the last few decades, many alien plant species have been imported into Greece, both intentionally (e.g., ornamental and medicinal plants) and unintentionally, using several pathways of introduction (Arianoutsou & al. 2010). Despite the large number of alien species that have been recorded in Greece, not all of these are invasive. Only 50 of the 343 alien species recorded in Greece show an invasive behavior, having been naturalized and established in a variety of habitats (Arianoutsou & al. 2010).

The Nestos (Mesta) is one of the most important rivers in Bulgaria and northern Greece. It originates from Mount Rila in southern Bulgaria, between the mountain ranges of Aimos and Rodopi. In total, the river is 234 km in length and its basin covers an area of 5,749 km^2, 130 km and 2,280 km^2 of which lie in Greece (Samaras & Koutitas 2008). Before it reaches the sea, the main river spreads over the coastal plain of Chrysoupolis and expands as a deltaic system with freshwater lakes and ponds forming the Nestos Delta (Fig. 1).

According to Mallinis & al. (2011), the plain area along the river was changed substantially after the second world war. In 1945, the entire floodplain area of Nestos River was still highly dominated by forests and wetlands. Significant landscape transformation was observed in the 1960s when agricultural areas greatly increased and forested areas declined, due to the establishment of intensive agriculture. A major reduction of wetland areas was also noticed due to their conversion mainly into rangelands.

However, despite the substantial decline in the natural landscapes of the wider area, the region still holds the most extensive riparian forest in Greece (Vasilopoulos 2005). Moreover, the floodplain of Nestos River is of high ecological significance because of its large number of important habitats. It has been classified as a wetland of international importance and was included in the Ramsar Convention in 1971. The area is also protected by the Bern Convention, by European Commission Directives, and by Greek law. Finally, it belongs to the Natura 2000 Network, a designation which includes regions of special environmental interest (Dafis & al. 1997).

According to the 'Monitoring Report for Terrestrial Habitats' (Ministry of Environment and Energy), 32 habitat types are present in the Nestos area (Fig. 1b, Table 1). Most of these are natural formations corresponding to habitat types of good conservation status. Moreover, some of these habitats also form types of priority. For instance, the riparian forest of Kotza Orman has been diminished substantially in recent years and requires specific management measures, in order to maintain its distinct physiognomy. The natural forests of Kotza Orman are classified in two Habitat Types, namely 'Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior*' (habitat 91E0*), and 'Riparian mixed forests of *Quercus robur, Ulmus laevis* and *Ulmus minor, Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (Ulmenion minoris)' (habitat 91F0). The total area of these natural forests is about 500 hectares, and it is believed that alien species can change their floristic composition, light conditions, and soil characteristics (Vasilopoulos 2005).

During field surveys, performed over the last few years, a number of alien species with invasive behavior have been observed in the floodplain area of Nestos River in NE Greece. These species have been observed both in grasslands and in the riparian forest. Thus, the aims of the present study were:

(a) to identify the alien plant species that show invasive behavior, and (b) to map their distribution and provide information about their invasiveness.

2. Materials and methods

In order to identify the alien plant species with invasive behavior, we first compiled the list of alien species occurring in the study area. For this purpose, an exhaustive literature review was carried out and this list was enriched with personal observation data obtained during field surveys conducted in previous years. After compiling the list of alien species in the study area (13 species in total, see Table 2), we conducted numerous field excursions to determine the invasiveness of these species and to map their distribution. The field excursions were carried out in two consecutive years (2021 and 2022), from the beginning of species flowering, during summer, until late September.

To map the distribution of the invasive alien plant species in the study area, we used a grid with a cell size of 200 × 200 m. During fieldwork, we recorded the geographical coordinates at each site where the studied IAS was found, the altitude, the habitat according to the EUNIS codes (EUNIS 2022), and specific information regarding the impact of the IAS on different components of the environment (e.g., local biodiversity, human activities).

The nomenclature of the plant species follows Dimopoulos & al. (2013), whereas codes of the Habitat Types presented in Fig. 1b and Table 1 are according to the 'Interpretation manual of European Union habitats' (European Commission 2013).

3. Results and discussion

Based on the available literature sources and personal observation data, 13 potential IAS have been reported in the wider study area (Table 2). However, only six of them (marked with an asterisk in Table 2) were considered to present an invasive behavior and were surveyed during the field excursions: *Acer negundo, Ailanthus altissima, Amorpha fruticosa, Phytolacca americana, Robinia pseudoacacia* and *Solanum elaeagnifolium*. The degree of the negative impacts that these species may cause was mainly determined by their spreading ability as well as by their high competiveness (Roy & al. 2015).

Several field excursions were performed during the two sampling periods (2021–2022), aiming at recording the distribution of the six above-mentioned IAS. They were recorded in a significant number of grid cells, indicating that the area is strongly affected by their expansion. The number of 200 × 200 m grid cells in which the six invasive alien plant species have been recorded is presented in the right column of Table 2.

Acer negundo (Box elder, Ash-leaf maple)

Acer negundo was introduced in Europe as a horticultural plant centuries ago and was also used as urban greenery (in parks and tree plantations

Table 2. Potentially invasive and invasive (*) alien species recorded in the area of Nestos River. The right column shows the number of grid cells where the six invasive alien species have been recorded.

Taxon	**Family**	**Chorology**	**Number of grid cells (200 × 200 m)**
**Acer negundo* L.	Sapindaceae	N American	31
**Ailanthus altissima* (Mill.) Swingle	Simaroubaceae	Paleotropical	3
Amaranthus deflexus L.	Amaranthaceae	S American	
**Amorpha fruticosa* L.	Fabaceae	N American	63
Datura stramonium L.	Solanaceae	Cosmopolitan	
Eleusine indica (L.) Gaertn.	Poaceae	Cosmopolitan	
Medicago sativa L. subsp. *sativa*	Fabaceae	Paleotemperate	
Paspalum distichum L.	Poaceae	Neotropical	
**Phytolacca americana* L.	Phytolaccaceae	N American	82
**Robinia pseudoacacia* L.	Fabaceae	N American	67
**Solanum elaeagnifolium* Cav.	Solanaceae	S American	5
Sporobolus indicus (L.) R. Br.	Poaceae	Tropical Asian	
Xanthium spinosum L.	Asteraceae	S American	

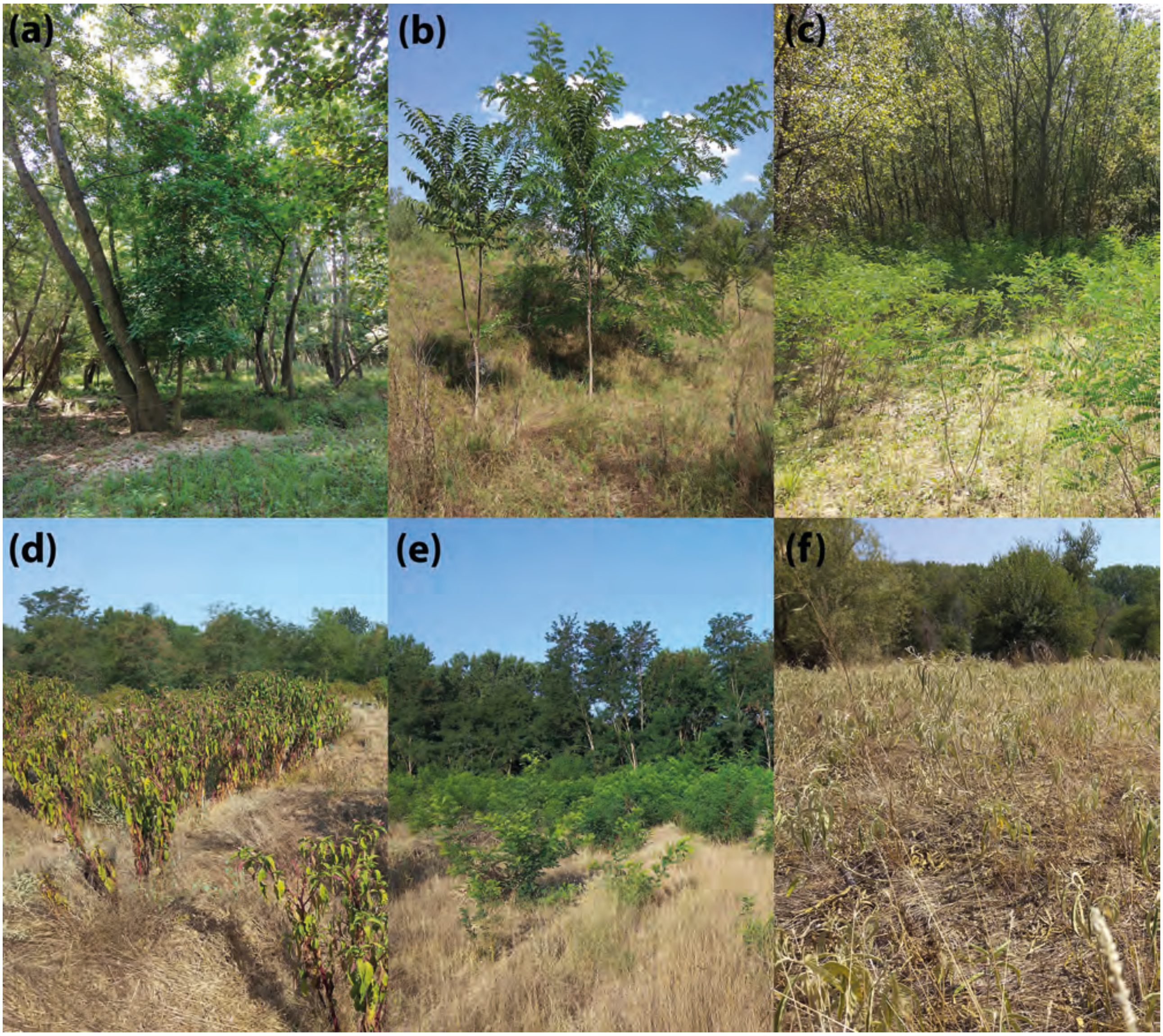

Fig. 2. (a) *Acer negundo* growing in alluvial forest with *Alnus glutinosa* (91E0). – (b) *Ailanthus altissima* growing in dry grassland. – (c) Thickets of *Amorpha fruticosa* found under native *Populus nigra* forest (92A0). – (d) Groups of individuals of *Phytolacca americana* in dry grassland (62A0). – (e) Expansion of *Robinia pseudoacacia* and establishment in dry grassland. – (f) Dry grassland with a large population of *Solanum elaeagnifolium*.

along city roads) in Greece. It is a fast-growing tree species, although short-lived, which can tolerate a broad range of environmental conditions. It has been widely planted in cities and parks because it is resilient in conditions of increased atmospheric pollution, and it can tolerate heat and drought stress. On the other hand, it can also grow in temporarily or permanently water-logged areas (Howell & Benson 2000). Its winged fruits enable long distance dispersal and it can be found in areas far from the places where it was planted. As a result, it has become one of the most invasive plant species occurring in riparian forests all around Europe (Sikorska & al. 2019), such as Białowieża in Poland (Adamowski & al. 2002). Once established in a riparian area, it is considered that it will affect other dominant tree species and will alter vegetation composition.

Acer negundo was found in the Nestos area in habitat type 91E0, i.e. alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Alno-Padion, Alnion incanae, Salicion albae), in the lower tree layer and more rarely in the understory and the canopy. Although the pressure of *Acer negundo* on native tree species is not yet very high, it is expected that its share in the tree layer will increase strongly in the course of succession and affect the habitat type. For a comprehensive description of its negative impacts on riparian forests, see Sikorska & al. (2019).

In total, *Acer negundo* (Fig. 2a) was recorded in 31 grid cells along Nestos River (Fig. 3a, Table 2), almost always between the two embankments that have been constructed for flood control.

In general, *Acer negundo* occurs in the form of isolated or scattered individuals, a fact that could be attributed to the capability of its seeds for long distance dispersal. Although it was never found in dense thickets, we observed a large number of young plants in the understory of alluvial forests with *Alnus glutinosa* (91E0). This might indicate that the alluvial forests of the area will be strongly affected by the replacement of *Alnus glutinosa* with *Acer negundo* in the future. Moreover, scattered individuals have been recorded in grassland communities but their effects on these habitats were very limited. This was because the regeneration of *Acer negundo* in grassland communities is not always easy, and thus, its expansion seems to be rather difficult.

According to the EUNIS typology, *Acer negundo* has been found in the following habitats of the study area: G1.2: Mixed riparian floodplain and gallery woodland; G1.3: Mediterranean riparian woodland; E2: Mesic grasslands.

Ailanthus altissima (Tree of heaven)

Ailanthus altissima was first introduced to Europe (France) in the 1740s and subsequently planted as an ornamental in several European countries. It has spread and been naturalized across large areas of Europe and is now considered as an invasive species that can rapidly spread onto disturbed sites or fragmented landscapes (Enescu & al. 2016). Moreover, it can invade riparian forests, shrublands, and mesic and xeric woodlands (Kowarik & Säumel 2007). Therefore, it seriously threatens biodiversity and ecosystem functions also in Greece (Fotiadis & al. 2011).

In total, *Ailanthus altissima* (Fig. 2b) has been recorded in 3 grid cells along Nestos River (Fig. 3b, Table 2). In all three grid cells, only a small number of individuals have been recorded so far. Thus, for the time being, *A. altissima* can be considered as a rather uncommon alien species in the study area. However, it is only a matter of time that *A. altissima* will expand and establish in other parts of the area where it will affect various natural and semi-natural habitats. It usually forms dense thickets, where all other plant species are going extinct – a quite destructive effect on local species composition and diversity, also due to the allelopathic effects of phytotoxic compounds from roots and leaves (e.g., Heisey 1990, De Feo & al. 2003).

According to the EUNIS typology, *Ailanthus altissima* has been found in the following habitats of the study area: E1: Dry grasslands.

Amorpha fruticosa (False indigo)

Amorpha fruticosa was reported for the first time in Greece in 2000, where it was found along Strymon River and its delta (NE Greece) (Karagiannakidou-Iatropoulou & al. 2000). Since then, *A. fruticosa* expanded its distribution range and now it is found in 7 out of the 13 phytogeographical areas of Greece. According to the CABI Compendium (2016), *A. fruticosa* is a fast-growing, deciduous shrub occurring in wetlands and disturbed habitats. It is native to North America but has spread across Asia and several European countries. Although it is believed that it was introduced in some countries as an ornamental plant, in Greece it was introduced from the other Balkan countries via the main transboundary rivers. *Amorpha fruticosa* is classified among the most aggressive IAS in Europe due to its high reproductive capacity, as it usually forms dense thickets and outcompetes native flora, changing successional patterns and reducing biodiversity. As it prefers riverbanks (poplar or willow galleries, almond willow-osier scrubs), unvegetated or sparsely vegetated shores, water-fringing reed-beds, riverine and lakeshore scrubs (Anastasiu & al. 2008), its numerous buoyant fruits are usually dispersed on the water surface (by wind or downstream) and can germinate far away from the parental plants; moreover, it also spreads vegetatively by sprouting, and stems can root at the nodes (e.g., Szigetvári 2002). Despite all negative impacts that *A. fruticosa* may cause, the foliage of this shrub constitutes a valuable forage for grazing animals, and it has also been proposed as a good beekeepers' plant providing considerable quantities of nectar and pollen, similar to *Robinia pseudoacacia*.

Although *Amorpha fruticosa* was first observed along Nestos River a few years ago, it has rapidly expanded, forming dense thickets and directly affecting plant species richness and distribution patterns. It was found in 63 grid cells (Figs. 2c and 3c, Table 2), mostly in large numbers and primarily in grassland communities where it gradually became the dominant species. However, it has also invaded alluvial forests with *Alnus glutinosa* and native forests with *Populus nigra*. In both cases, the numbers of individuals were smaller than in the open grassland habitats, especially in the alluvial forests with *Alnus glutinosa*. Obviously, the *Amorpha fruticosa* populations in open habitats are more dynamic and more disastrous to native vegetation. However, the fact that it was also found in *Populus nigra* forest patches might indicate that these patches could be seriously threatened in the future (Pedashenko & al. 2012). *Populus nigra* cannot regenerate under the pressure of IAS and this primary forest tree species would successively be replaced by *Amorpha fruticosa* after several years.

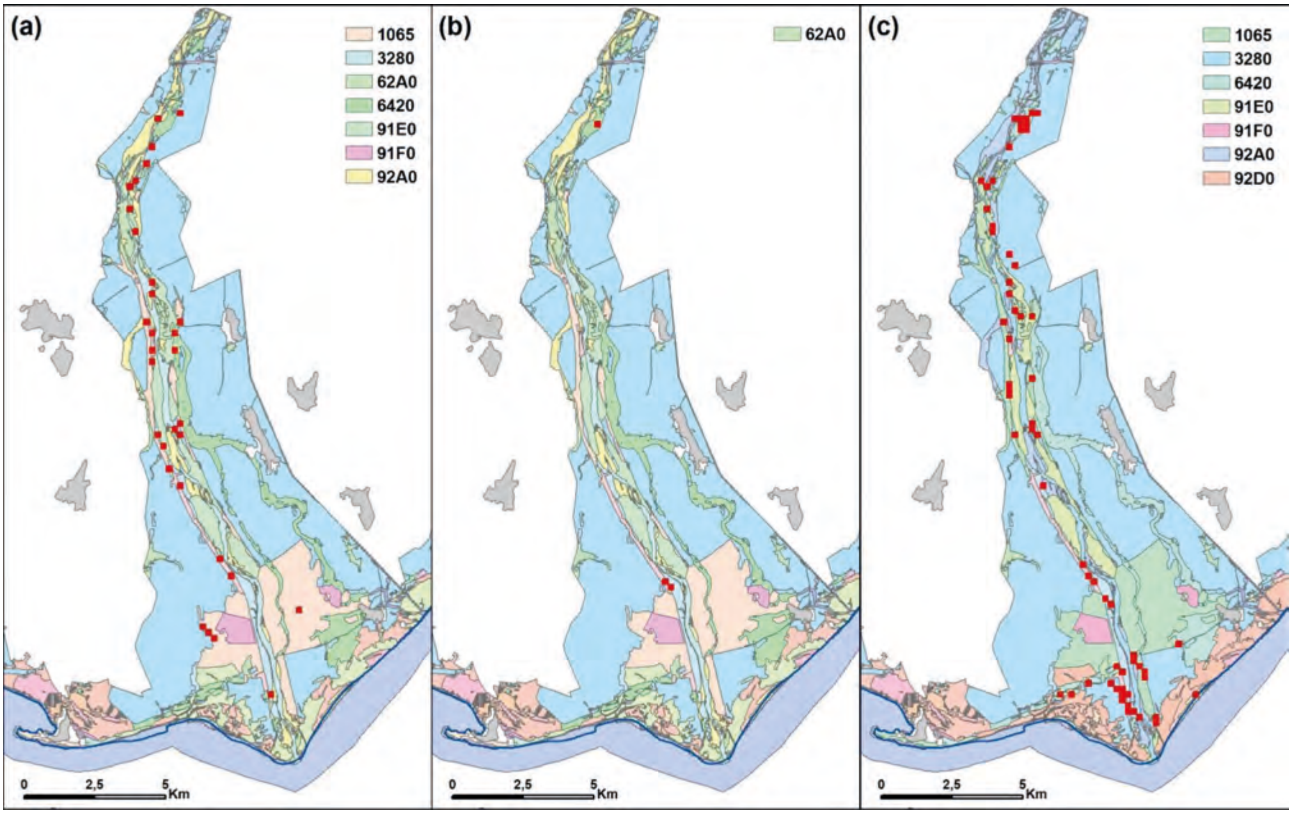

Fig. 3 (a–c). Distribution (red squares) of the studied invasive alien species along Nestos River. (a) *Acer negundo*. – (b) *Ailanthus altissima*. – (c) *Amorpha fruticosa*. – The color and number codes refer to the main habitat types invaded by each species (see Table 1). Larger settlements are shown in gray.

According to the EUNIS typology, *Amorpha fruticosa* has been found in the following habitats of the study area: C1.6: Temporary lakes, ponds and pools; C2.5: Temporary running waters; E3: Seasonally wet and wet grasslands; F9: Riverine and fen scrubs; G1.2: Mixed riparian floodplain and gallery woodland; G1.3: Mediterranean riparian woodland.

Phytolacca americana (Pokeweed)

Phytolacca americana was first introduced in the Mediterranean in the 17th century (Balogh & Juhász 2008) but it now also occurs in several other European countries (EPPO 2022). Its fruits are eaten by birds and thus their seeds are dispersed over long distances.

In terms of the number of grid cells in which it has been recorded so far, *Phytolacca americana* (Fig. 2d) was the most widespread IAS occurring along Nestos River (Fig. 3d, Table 2). It was recorded in 82 grid cells but it was not as dangerous as other alien species, e.g., *Amorpha fruticosa*. In general, it was mostly found in dry grasslands in isolated individuals or small groups. Although it was also found in the understory of forested areas, the number of individuals was small and, based on our evaluation, not able to cause serious problems to the dominant tree species.

According to the EUNIS typology, *Phytolacca americana* has been found in the following habitats of the study area: E1: Dry grasslands; E2: Mesic grasslands; G1: Broadleaved deciduous woodland; G1.2: Mixed riparian floodplain and gallery woodland; G1.3: Mediterranean riparian woodland.

Robinia pseudoacacia (Black locust)

Robinia pseudoacacia is widely distributed in Greece, as it was formerly planted to stabilize soil and to prevent erosion, especially in degraded cropland on slopes, with shallow soils and poor yields caused by surface runoff and subsequent soil erosion. After abandonment of cultivation, a large portion of these areas was restored with *R. pseudoacacia*, following rules of the European Agricultural Fund for Rural Development (EAFRD) (Papaioannou & al. 2016). In the Nestos area, *R. pseudoacacia* had been grown in plantations to replace natural vegetation formations during the last century. The criteria for its selection were mainly its ability to grow fast and to produce timber of high quality. It was cultivated in several localities, and old planta-

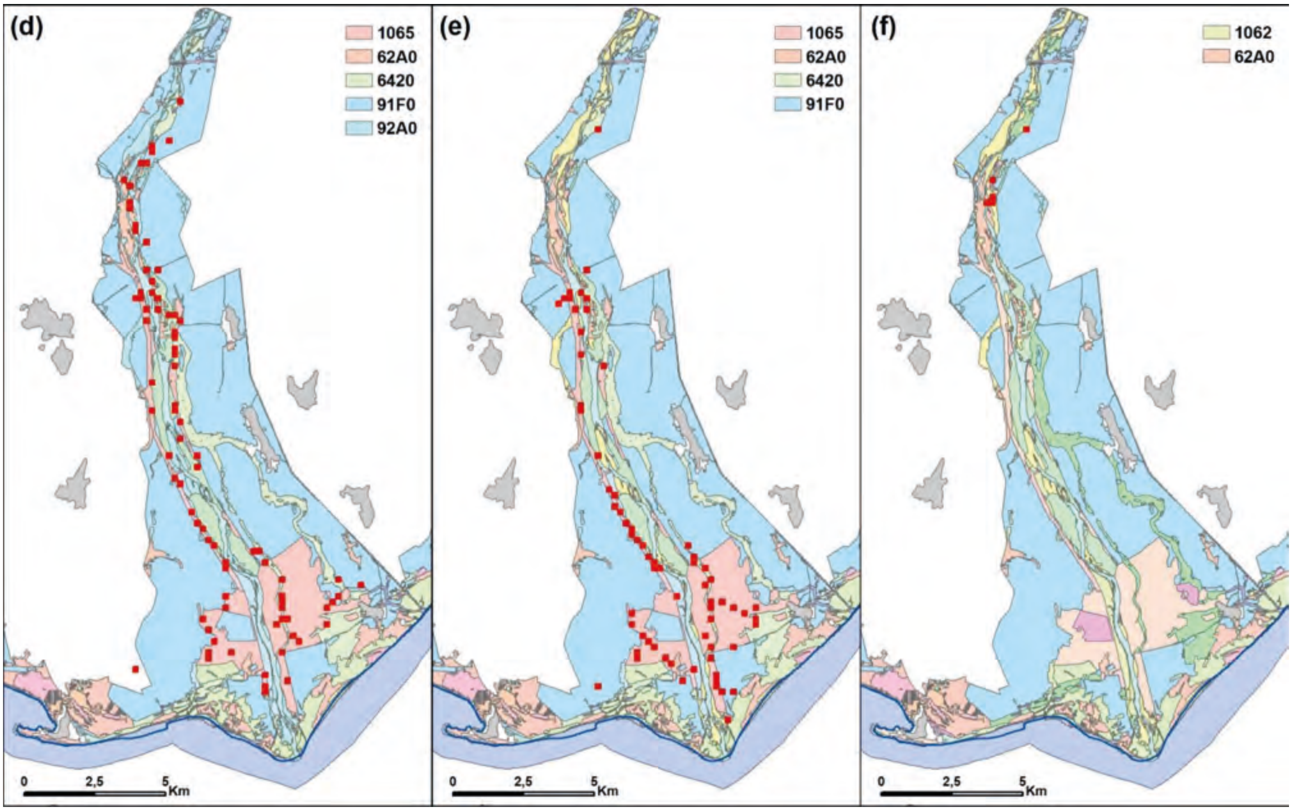

Fig. 3 (d–f). Distribution (red squares) of the studied invasive alien species along Nestos River. (d) *Phytolacca americana*. – (e) *Robinia pseudoacacia*. – (f) *Solanum elaeagnifolium*. – The color and number codes refer to the main habitat types invaded by each species (see Table 1). Larger settlements are shown in gray.

tions still exist in the area. *Robinia pseudoacacia* can easily spread from any place where it has been introduced, and invade natural and semi-natural habitats (mostly dry and mesic grasslands), and affect biodiversity. As a result, vital space for other species is being reduced and this causes problems to wild and domestic animals (Vasilopoulos 2005). Despite the species' numerous uses for humans, its negative environmental impacts forced European authorities to list it among the most competitive IAS in Europe (Sádlo & al. 2017).

In total, *Robinia pseudoacacia* (Fig. 2e) has been recorded in 67 grid cells along Nestos River (Fig. 3e, Table 2). It is the second most widespread IAS in the study area, in terms of the number of occupied grid cells.

According to the EUNIS typology, *Robinia pseudoacacia* has been found in the following habitats of the study area: E1: Dry grasslands; E2: Mesic grasslands; G1: Broadleaved deciduous woodland.

Solanum elaeagnifolium (Silverleaf nightshade)

Most probably, *Solanum elaeagnifolium* was introduced in Europe unintentionally from Texas in the 1930s (Economidou & Yannitsaros 1975, Uludag & al. 2016). The invasion started from the Mediterranean Basin and expanded into other areas of the continent, and *S. elaeagnifolium* is now classified among the most aggressive IAS in Europe. According to Krigas & al. (2021) its range in Greece has increased by 1750 % during the last few decades, which indicates its great invasiveness and rapid spread.

Solanum elaeagnifolium has been recorded in only 5 grid cells along Nestos River (Figs. 2f and 3f, Table 2), although it is a common species in Greece where it can be found in cultivated, abandoned, managed or disturbed lands, pastures, urbanized areas, and roadsides (Krigas & al. 2021). This scarcity in the study area can be attributed to the fact that many grassland communities along Nestos River are classified as mesic or temporary wet grasslands, which are not very suitable for the plant. However, the populations in the invaded grid cells are already characterized by the typical large numbers of individuals affecting the physiognomy of the plant communities. Moreover, as a poisonous plant to both humans and cattle, *S. elaeagnifolium* is not affected by grazing. On the contrary, as grazing reduces the competitive capacities of the valuable forage plants, it finds the necessary space for its expansion and thus it can become the dominant species within a few years after being established in an area.

According to the EUNIS typology, *Solanum elaeagnifolium* has been found in the following habitats of the study area: E1: Dry grasslands.

4. Conclusions

The impacts of IAS occurring in the Nestos area are still relatively low, although locally extensive. The highest negative impact was inflicted by *Amorpha fruticosa*, the invasion of which was very aggressive. In July 2018, only a few very small shrubs of *A. fruticosa* were observed in specific grassland areas along Nestos River. Today there are quite dense bushes 2–3 meters high, with many small plants extending toward the river. It is believed that, if the rate of expansion persists, broad strips along the river will in large part be covered by *A. fruticosa* within the next couple of years. Similar problems have been identified in other European countries (e.g., in Romania, Kucsicsa & al. 2018), the reason why the species is classified among the most aggressive IAS in Europe.

Apart from *Amorpha fruticosa* as the fastest and apparently most competitive invader, it is expected that both *Acer negundo* and *Robinia pseudoacacia* will negatively affect natural habitats in the long term. Unfortunately, it is not possible to exactly predict their invasiveness as both species are trees and vegetation succession is a very slow process. However, specific action should be taken to reduce their further spread because invasive tree species have been identified as a major threat to riparian forests elsewhere. They are able to outcompete native species (e.g., *Salix* spp., *Populus* spp.) and to alter succession dynamics (Sikorska & al. 2019).

In the present study, the first systematic mapping of the distribution of invasive alien plant species occurring along Nestos River was attempted. The results can form the basis for studying the impacts of these plant species on the natural ecosystems of the area. It is highly recommended to continuously monitor the distribution and expansion of the IAS in the study area and, following their trends, to apply management measures for controlling them.

Acknowledgements and funding

We cordially thank Dr. Christian Scheuer and one anonymous reviewer who greatly improved an earlier version of the manuscript. The study was supported by the IASON Project ('Invasive Alien Species Observatory and Network Development for the Assessment of Climate Change Impacts in Black Sea Deltaic Protected Areas', BSB - 1121), implemented within the Joint Operational Programme Black Sea Basin 2014–2020.

References

Adamowski W., Dvorak L. & Ramanjuk I. 2002. Atlas of alien woody species of the Białowieża Primaeval Forest. – Phytocoenosis (New Series) 14: 1–304.

Anastasiu P., Negrean G., Başnou C., Sîrbu C. & Oprea A. 2008. A preliminary study on the neophytes of wetlands in Romania. – In: Rabitsch W., Essl F. & Klingenstein F. (eds). Biological Invasions – from Ecology to Conservation. – NeoBiota 7: 181–192.

Arianoutsou M., Bazos I., Delipetrou P. & Kokkoris, Y. 2010. The alien flora of Greece: taxonomy, life traits and habitat preferences. – Biological Invasions 12: 3525–3549.

Balogh L. & Juhász M. 2008. American and Chinese pokeweed (*Phytolacca americana* L., *Ph. esculenta* van Houtte). – In: Botta-Dukát Z. & Balogh L. (eds.). The most important invasive plants in Hungary, p. 35–46. – Institute of Ecology and Botany, Hungarian Academy of Sciences; Vácrátót, Hungary.

CABI Compendium 2016. *Amorpha fruticosa* (false indigobush). – CABI Digital Library. https://www.cabidigitallibrary.org/doi/10.1079/cabicompendium.5001.

Cassey P., Vall-Llosera M., Dyer E. & Blackburn T. M. 2015. The biogeography of avian invasions: history, accident and market trade. – In: Canning-Clode J. (ed.). Biological Invasions in Changing Ecosystems: Vectors, Ecological Impacts, Management and Predictions, p. 37–54. – De Gruyter Open Ltd.; Warsaw.

Chiba S. 2010. Invasive non-native species' provision of refugia for endangered native species. – Conservation Biology 24(4): 1141–1147.

Clout M. N. & Williams P. A. 2009. Invasive Species Management: A Handbook of Principles and Techniques. – Oxford University Press; Oxford.

Dafis S., Papastergiadou E., Georghiou K., Babalonas D., Georgiadis T., Papageorgiou M., Lazaridou T. & Tsiaousi V. 1997. The Greek Habitat Project Natura 2000: an overview. – Greek Biotope/Wetland Centre; Thessaloniki.

De Feo V., De Martino L., Quaranta E. & Pizza C. 2003. Isolation of phytotoxic compounds from tree-of-heaven (*Ailanthus altissima* Swingle). – Journal of Agricultural and Food Chemistry 51: 1177–1180.

Dimopoulos P., Raus T., Bergmeier E., Constantinidis T., Iatrou G., Kokkini S., Strid A. & Tzanoudakis D. 2013. Vascular plants of Greece: An annotated checklist. – Englera 31: 1–372. – Botanischer Garten und Botanisches Museum Berlin-Dahlem; Hellenic Botanical Society, Athens.

Economidou E. & Yannitsaros A. 1975. Recherches sur la flore adventice de Grèce: V. Distribution et écologie de *Solanum elaeagnifolium* Cav. – Revue de Biologie et d'Écologie Méditerranéenne 2: 29–44.

Enescu C. M., Houston Durrant T. & Caudullo G. 2016. *Ailanthus altissima* in Europe: distribution, habitat, usage and threats. – In: San-Miguel-Ayanz J., de Rigo D., Caudullo G., Houston Durrant T. & Mauri A. (eds.). European Atlas of Forest Tree Species, p. 61. – Publications Office of the European Union; Luxembourg.

EPPO 2022. EPPO Global Database - *Phytolacca americana*. https://gd.eppo.int/taxon/PHTAM [accessed 23 Nov 2022].

EUNIS 2022. European Nature Information System. http://eunis.eea.europa.eu/ [accessed 20 Nov 2022].

European Commission 2013. Interpretation manual of European Union habitats. - EUR 28 DG Environment - Nature and Biodiversity.

European Environment Agency 2016. Flood risks and environmental vulnerability — Exploring the synergies between floodplain restoration, water policies and thematic policies. EEA Rep. No. 1/2016. – European Environment Agency; Copenhagen, Denmark. Publications Office of the European Union; Luxembourg.

European Union 2011. The EU Biodiversity Strategy to 2020. – European Commission. Publications Office of the European Union; Luxembourg.

Fotiadis G., Kyriazopoulos A. P. & Fraggakis I. 2011. The behaviour of *Ailanthus altissima* weed and its effects on natural ecosystems. – Journal of Environmental Biology 32(6): 801–806.

Gallé L., Margóczy K., Kovács E., Györffy G., Körmöczy L. & Németh L. 1995. River valleys: are they ecological corridors? – Tiscia 29: 53–58.

Heisey R. M. 1990. Evidence of allelopathy by tree-of-heaven (*Ailanthus altissima*). – Journal of Chemical Ecolology 16(6): 2039–2055.

Howell J. & Benson D. 2000. Predicting potential impacts of environmental flows on weedy riparian vegetation of the Hawkesbury-Nepean River, south-eastern Australia. – Austral Ecology 25(5): 463–475.

Karagiannakidou-Iatropoulou V., Konstantinou M. & and Lavrentiadou S. 2000. Flora, vegetation and ecological management of Strymon river delta (NE Greece). – 2nd Balkan Botanical Congress, Istanbul Turkey, p. 257–262.

Kowarik I. & Säumel I. 2007. Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. – Perspectives in Plant Ecology, Evolution and Systematics 8(4): 207–237.

Krigas N., Tsiafouli M. A., Katsoulis G., Votsi N.-E. & van Kleunen M. 2021. Investigating the invasion pattern of the alien plant *Solanum elaeagnifolium* Cav. (Silverleaf Nightshade): Environmental and human-induced drivers. – Plants 10(4): 805.

Kucsicsa G., Grigorescu I., Dumitraşcu M., Doroftei M., Năstase M. & Herlo G. 2018. Assessing the potential distribution of invasive alien species *Amorpha fruticosa* (Mill.) in the Mureş Floodplain Natural Park (Romania) using GIS and logistic regression. – Nature Conservation 30: 41–67.

Mallinis G., Emmanoloudis D., Giannakopoulos V., Maris F. & Koutsias N. 2011. Mapping and interpreting historical land cover/land use changes in a Natura 2000 site using earth observational data: The case of Nestos delta, Greece. – Applied Geography 31: 312–320.

Papaioannou A., Chatzistathis T., Papaioannou E. & Papadopoulos G. 2016. *Robinia pseudoacacia* as a valuable invasive species for the restoration of degraded croplands. – Catena 137: 310–317.

Pedashenko H. P., Apostolova I. I. & Vassilev K. V. 2012. *Amorpha fruticosa* invasibility of different habitats in lower Danube. – Phytologia Balcanica 18(3): 285–291.

Pegg J., South J., Hill J. E., Durland-Donahou A. & Weyl O. L. F. 2022. Impacts of Alien Invasive Species on Large Wetlands. – In: Dalu T. & Wasserman R. J. (eds.). Fundamentals of Tropical Freshwater Wetlands, p. 487–516. – Elsevier; Amsterdam, The Netherlands.

Pyšek P. & Prach K. 1994. How important are rivers for supporting plant invasions? – In: de Waal L. C., Child L. E., Wade P. M. & Brock J. H. (eds.). Ecology and management of invasive riverside plants, p. 19–26. – John Wiley & Sons Ltd.; Chichester, New York, etc.

Richardson D. M., Pyšek P. & Carlton J. 2011. A compendium of essential concepts and terminology in invasion ecology. – In: Richardson D. M. (ed.). Fifty Years of Invasion Ecology: The Legacy of Charles Elton, p. 409–420. – John Wiley & Sons Ltd.; Oxford.

Ricciardi A., Hoopes M. F., Marchetti M. P. & Lockwood J. L. 2013. Progress toward understanding the ecological impacts of non-native species. – Ecological Monographs 83(3): 263–282.

Roy H. E., Adriaens T., Aldridge D. C., Bacher S., Bishop J. D. D., Blackburn T. M., Branquart E., Brodie J., Carboneras C., Cook E. J., Copp G. H., Dean H. J., Eilenberg J., Essl F., Gallardo B., Garcia M., García-Berthou E., Genovesi P., Hulme P. E., Kenis M., Kerckhof F., Kettunen M., Minchin D., Nentwig W., Nieto A., Pergl J., Pescott O., Peyton J., Preda C., Rabitsch W., Roques A., Rorke S., Scalera R., Schindler S., Schönrogge K., Sewell J., Solarz W., Stewart A., Tricarico E., Vanderhoeven S., van der Velde G., Vilà M., Wood C.-A. & Zenetos A. 2015. Invasive Alien Species - Prioritising prevention efforts through horizon scanning. ENV.B.2/ETU/2014/0016. Final report. – European Commission; Brussels.

Sádlo J., Vítková M., Pergl J. & Pyšek P. 2017. Towards site-specific management of invasive alien trees based on the assessment of their impacts: the case of *Robinia pseudoacacia*. – NeoBiota 35: 1–34.

Samaras A. G. & Koutitas C. G. 2008. Modelling the impact on coastal morphology of the water management in transboundary river basins. The case of River Nestos. – Management of Environmental Quality 19(4): 455–466.

Schnitzler A., Hale B. W. & Alsum M. E. 2007. Examining native and exotic species diversity in European riparian forests. – Biological Conservation 138: 146–156.

Sikorska D., Sikorski P., Archiciński P., Chormański J. & Hopkins R. J. 2019. You can't see the woods for the trees: Invasive *Acer negundo* L. in urban riparian forests harms biodiversity and limits recreation activity. – Sustainability 11(20): 5838.

Simberloff D., Martin J.-L., Genovesi P., Maris V., Wardle D. A., Aronson J., Courchamp F., Galil B., García-Berthou E., Pascal M., Pyšek P., Sousa R., Tabacchi E. & Vilà M. 2013. Impacts of biological invasions: what's what and the way forward. – Trends in Ecology and Evolution 28(1): 58–66.

Szigetvári C. 2002. Initial steps in the regeneration of a floodplain meadow after a decade of dominance of an invasive transformer shrub, *Amorpha fruticosa* L. – Tiscia 33: 67-77.

Tella J. L. 2011. The unknown extent of ancient bird introductions. – Ardeola 58(2): 399–404.

Uludag A., Gbehounou G., Kashefi J., Bouhache M., Bon M.-C., Bell C. & Lagopodi A. L. 2016. Review of the

current situation for *Solanum elaeagnifolium* in the Mediterranean Basin. – EPPO Bulletin 46(1): 139–147.
Vasilopoulos G. 2005. Analysis of the floristic structure and study of succession on the natural and anthropogenous plant societies of Nestos' riparian forest. – MSc Thesis, School of Biology, Aristotle University of Thessaloniki [in Greek with English summary].
Vilà M., Espinar J. L., Hejda M., Hulme P. E., Jarošík V., Maron J. L., Pergl J., Schaffner U., Sun Y. & Pyšek P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. – Ecology Letters 14(7): 702–708.

(Received 30 Dec 2022, accepted 6 Feb 2023)