



Original article

Plant invasions in Ukraine

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ABSTRACT

We present a comprehensive review of the plant invasions of 42 alien species and their impact on vegetation cover in Ukraine. Among these species, those currently posing the greatest threat to the environment have been identified. The structural features of this group were analyzed. In the life form spectrum the phanerophytes and therophytes are dominant, in the ecological spectrum the mesophytes are dominant, and kenophytes predominate at the time of immigration. Among the examined species, plants of North American origin predominate, agriophytes prevail by their degree of naturalization, and ergasiophytes are predominant by their way of entry. The participation of invasive species in natural and anthropogenic plant communities and biotopes was analyzed. These species are a stable component of grasses, scrub and forest habitats. Most of these invasive plants (33 species) are observed in anthropogenic habitats (I). Slightly fewer species of the studied group prefer habitat types E (25), F and G (22 each), although the largest invasions are observed exactly in these biotopes. Invasive species are characterized by eurytopicity. Four species have the greatest ecological plasticity, each of these is found in six types of habitats: *Ailanthus altissima* (B, F, G, I, J, H), *Amaranthus retroflexus* (C, E, F, G, I, J), *Opuntia humifusa* (B, E, F, G, H, I) and *Xanthium albinum* (B, C, E, F, G, I). *Erigeron canadensis* is found in five habitat types (C, E, F, G, I). The studied group is characterized by an insignificant regional specificity of the species composition, high invasive potential and stability of population reproduction.

KEY WORDS: kenophytes, ergasiophytes, invasiveness, invasibility of plant communities, types of biotopes, Ukraine

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1. Introduction

Invasive species and the negative effects of their impacts are one of the major threats to the existence of biodiversity. Study of the features of phytinvasions, the identification of invasive patterns, ways and mechanisms of distribution of the most successful species demonstrates trends in the evolution of flora and vegetation types. The rates of invasion, migration strategies and success of alien species depend on the natural conditions and biota heterogeneity of the regions, as well as on the peculiarities of their economic and socio-historical

relations. The natural conditions and features of historical and socio-economic development of Ukraine have contributed to the introduction and distribution of alien plants since ancient times. For two periods, before and after the middle of the 20th century, formation and development of alien flora of Ukraine appears different. The expansive species, such as *Amaranthus retroflexus*, *Ambrosia artemisiifolia*, *Cyclachaena xanthiifolia* (Nutt.) Fresen, which have completely changed the ruderal plant communities of several regions comprise the stable component of alien flora. The species composition of the alien fraction was very unstable,

but most alien plants have remained so far. Since the second half of the 20th century, the rate of expansion has slightly slowed, but the participation and role of invasive species in the vegetation cover demonstrate steady growth, in anthropogenic habitats especially. The outbreaks of phyt invasion have been characterized by fluctuations of population abundance of plants of alien species due to historical anthropogenic and / or environmental changes. The qualitative and quantitative structural changes of the flora and vegetation occur at different levels due to the complication and amplification of their vegetation cover adventisation (increasing alien species richness and rates of introduction, distribution, naturalization, coenotic role of plants). Growth of the invasive potential of species, together with the growing transformation of the vegetation cover along with climate change, leads to a redistribution of the species composition, a rise in the invasibility of plant communities and the emergence of new ecological niches and plant communities of various ranks, and also has caused widespread conversion of natural ecosystems and the structure of the natural flora (PROTOPOVA, 1991; PROTOPOVA ET AL., 2002).

1.1. A brief study of the research on plant invasions in Ukraine

The study of different aspects of the invasive species group over 220 years of history is related to the general research of the flora of Ukraine and its regions. Plant invasion as a biogeographical

problem was assessed for the first time in Ukraine by V. Taliev and M. Kotov. In the second half of the 20th century, a comprehensive study was initiated by PROTOPOVA (1973). In this research the alien flora of Forest Steppe and Steppe of Ukraine and some invasive patterns were described. Special research interest on invasive species dates from the end of 20th and the early 21st centuries and is related to publications by MARIYUSHKINA (1986), MARIYUSHKINA ET AL. (1987), PROTOPOVA ET AL. (2002, 2009, 2010, 2012, 2013, 2015), PROTS (2013), PROTS & VYKHOR (2014), BURDA ET AL. (2015), DVIRNA (2015, 2019), KUCHER (2015), STASIUK (2015), DIDUKH ET AL. (2016), ZAVIALOVA (2017), TOKARYUK ET AL. (2018), SHEVERA ET AL. (2018). Publications on these themes are listed in the regularly updated bibliographical guide (ALIEN SPECIES..., 2021). The state of plant invasions in Ukraine has been analyzed, the species composition of invasive plants of certain regions, including transformers, has been established (PROTOPOVA ET AL., 2009, 2010, 2012, 2014, 2015), the time of cultivation/spontaneous introduction and distribution were reconstructed, participation in plant communities was analyzed. The regional features of invasive species related to natural conditions, to the degree of anthropogenic transformation of vegetation cover and to socio-economic specifics of the regions have been revealed.

The aim of the study is to characterise the invasiveness of alien species in different vegetation types and biotopes, and invasibility of plant communities of Ukraine.

Table 1. Expansion of alien plant species in Ukraine in the 19th–21st centuries

Species	Year and localities of cultivation and first records (escaped, spontaneously)	Region of invasiveness	The beginning and duration of expansion			
			Second half of the 19 th	20 th		
				1900–1940	1941–1975	1976–2000
<i>Acer negundo</i> L.	Cultivated: 1809 – Osnoviansky park (Kharkiv Obl.), 1814 – Nikita Bot. Gard. (Crimea), 1816 – Kremenets Bot. Gard. (Ternopil Obl.), 1825 – Trykraty park (Mykolaiv Obl.), 1865 – Velyko-Anadol' park (Donetsk Obl.), etc. Escaped: Middle of the 19 th	All regions (banks of reservoirs)		+	+	+
<i>Ailanthus altissima</i> (Mill.) Swingle	Cult.: 1809 – Osnoviansky park (Kharkiv Obl.), 1813 – Nikita Bot. Gard., 1820 – Simferopol, Sevastopol, Theodosia (Feodosia) in Crimea Escaped: 1830 – Crimea, without concrete data	Crimea, Steppe, Western Forest Steppe			+	+
<i>Amaranthus retroflexus</i> L.	1819 – as a weed from all of the territory	Crimea, Steppe, Forest Steppe, Polissia	+	+	+	+
<i>Ambrosia artemisiifolia</i> L.	Cult.: 1914 – vill. Kudashivka (Dnipropetrovsk Obl.) Spontaneously: 1925 – Kyiv, territory of grain elevator	Steppe, Forest Steppe, Crimea		+	+	+
<i>Amelanchier spicata</i> (Lam.) K. Koch	Cult.: 1893 – Kyiv Escaped: ?	Polissia				+

<i>Amorpha fruticosa</i> L.	Cult.: 1809 – Osnovianskyi park (Kharkiv Obl.), 1811 – Kremenets Bot. Gard., 1815 – Nikita Bot. Gard., 1830 – parks of Odesa, Trykraty park; active cultivated from 1960s Escaped: ?	All regions (banks of reservoirs)				+	+
<i>Anisantha tectorum</i> (L.) Nevski	Archaeophyte	Steppe	+	+	+	+	+
<i>Apera spica-venti</i> (L.) P. Beauv.	Archaeophyte	Steppe	+	+	+	+	+
<i>Asclepias syriaca</i> L.	Cult.: 1859 – Kharkiv, 1863 – Bot. Gard. of Imperial University of St. Volodymyr in Kyiv Escaped: 1849 – territory of Chernihiv gub., Starodubsky Distr. (now Russian Federation), 1878 – vill. Kozyn (Kyiv Obl.)	Polissia, Forest Steppe				+	+
<i>Bidens frondosa</i> L.	Cult.: 1816 – Kremenets Bot. Gard. Spontaneously: 1970 – Kaniv (Cherkasy Obl.)	All regions (banks of reservoirs)				+	+
<i>Bupleurum fruticosum</i> L.	Cult.: 1814 – Nikita Bot. Gard.; later in other towns of the Southern Coast of Crimea, and Odesa; before 1821 – Kremenets Bot. Gard. Spontaneously: 1885 – Alupka	Crimea	+	+	+	+	+
<i>Cenchrus longispinus</i> (Hack) Fernald	Cult.: ?, probably in 1930s Spontaneously: 1950 – vill. Luch (Kherson Obl.)	Steppe			+	+	+
<i>Centaurea diffusa</i> Lam.	First records: 1853 – vill. Verbka, Balta, 1854 – Savran and vill. Okny (Odesa Obl.)	Steppe, Forest Steppe	+	+	+	+	+
<i>Echinocystis lobata</i> (Michx.) Torr. et A. Gray	Cult.: at the end of the 19 th and the first part of 20 th . Escaped: 1933 – vill. Didivtsi (Transcarpathia Obl.)	Transcarpathia, Western Forest Steppe, Polissia				+	+
<i>Elaeagnus angustifolia</i> L.	Cult.: 1814 – Nikita Bot. Gard. 1830 – Odesa parks Escaped: 1925 – Foros and Sudak (Crimea)	Crimea, Black Sea Coast, Steppe		+	+	+	+
<i>Elodea canadensis</i> Michx.	Cult.: ? Escaped: 1884 – Kherson; 1889 – vill. Maliutynka (Kyiv Obl.) and Kyiv; 1912 – Odesa	All regions (reservoirs)		+	+	+	+
<i>Erigeron annuus</i> (L.) Dumort.	Cult.: without concrete data Escaped: ? – Korsun (now Korsun-Shevchenkivskyi, Cherkasy Obl.)	Forest Steppe, Polissia			+	+	+
<i>Erigeron canadensis</i> L.	Cult.: 1816 – Kremenets Bot. Gard. Escaped: 1827 – Elisavetgrad (now Kropyvnytskyi), 1844 – Lubny (Poltava Obl.), 1857 – Crimea (Sudak valley), 1859 – Bukovina (without data)	All regions (sandy soils)	+	+	+	+	+
<i>Fraxinus ornus</i> L.	Cult.: 1821 – Nikita Bot. Gard. Escaped: the end of 19 th from Kuchuk-Lambat to Foros (Crimea). From the P. Pallas opinion (1999) plants of this species was cultivated in Crimea before 1793	Crimea	+	+	+	+	+
<i>Fraxinus pennsylvanica</i> Marshall	Cult.: the end of 18 th Escaped: ?	All regions (banks of reservoirs, forest edge)				+	+
<i>Grindelia squarrosa</i> (Pursh) Dunal	Cult.: 1942 – Bot. Gard. of Acad. of Sci. of Ukrainian RSR (Kyiv) Spontaneously: 1949 – between Iavkino and Novo-Poltavka vill. (Mykolaiv Obl.); 1969 – Nikita Bot. Gard.	Steppe, South of Forest Steppe, Crimea			+	+	+
<i>Helianthus tuberosus</i> L.	Cult.: probably before 19 th Escaped: ?	All regions (banks of reservoirs)				+	+
<i>Heracleum mantegazzianum</i> Sommier et Levier	Cult.: 1927 – Osmoloda forestry Escaped: 1954 – vill. Osmoloda (Ivano-Frankivsk Obl.)	Western Forest Steppe, Polissia, Transcarpathia				+	+
<i>Heracleum sosnowskyi</i> Manden	Cult.: 1949 – Bot. Gard. of Acad. of Sci. of Ukrainian RSR (Kyiv); 1960–70s in collective and soviet farms on the Western Ukraine Escaped: ?	Polissia, Western Forest Steppe, Transcarpathia				+	+
<i>Impatiens glandulifera</i> Royle	Cult.: 1930s – Transcarpathia Obl. and other Western Ukraine Escaped: 1938 – vill. Osiy	Transcarpathia, Northern and Western Forest					+

	(Transcarpathia Obl.); 1939 – vill. Mykhaylivka (Khmelnysky Obl.)	Steppe, Polissia					
<i>Impatiens parviflora</i> DC.	Cult.: 1893 – Dubliany (Lviv Obl.) Escaped: 1908 – Lviv and Ukrainian Carpathian without concrete data	Forest Steppe, Polissia		+	+	+	+
<i>Jacobaea maritima</i> (L.) Pelsér & Meijden	Cult.: probably the first half of 19 th Escaped: 1842 – Alupka–Yalta (Crimea)	Crimea	+	+	+	+	+
<i>Lupinus polyphyllus</i> Lindl.	Cult.: 1927 – Vinnytsia Escaped: 1959–1960 – Transcarpathia Obl.?	Forest Steppe, Polissia				+	+
<i>Lycium barbarum</i> L.	Cult.: 1812 – Nikita Bot. Gard. Escaped: 1822 – Podolia, after 1855 – Kyiv and sporadically throughout Ukraine	Crimea, Forest Steppe		+	+	+	+
<i>Opuntia humifusa</i> (Raf.) Raf.	Cult.: Probably in the first years of foundation of Nikita Bot. Gard. (1812–1827), 1882 – Italian cemetery in Gasfort mountain (Sevastopol, Crimea) Escaped: first half of 20 th	Crimea		+	+	+	+
<i>Padus serotina</i> (Ehrh.) Ag.	Cult.: ≈ 1860 – Krasnokutskyi (Karazinskyi) Garden; 1905 – Sofiyivka (Uman, Cherkasy Obl.); 1916 – Mariupol Forest Research Station (Zaporizhzhia Obl.); 1931 – Veseli Bokoven'ky Dendrology Park (Kirovohrad Obl.); 1932 – Valky Sort Station (Kharkiv Obl.) Escaped: ?	Polissia				+	+
<i>Partenocissus inserta</i> (A. Kern.) Fritsch.	Cult.: 1915 – Bot. Gard. of Chernivtsi University Escaped: ?	All regions (forest, forest edge)				+	+
<i>Reynoutria japonica</i> Houtt.	Cult.: the End of 19 th – Middle of 20 th ; 1902 – vill. Iabluniv (Ivano-Frankivsk Obl.); 1905 – Nogaïsk (now Prymors'k) (Zaporizhzhia Obl.) Escaped: 1928 – Rachiv Reg. (Transcarparhia Obl.), 1932 – Bolekhiv (Ivano-Frankivsk Obl.)	Transcarpathia, Western Forest Steppe, Polissia					+
<i>Rhamnus alaternus</i> L.	Cult.: 1812 – Nikita Bot. Gard. Escaped: 1860?, vill. Nikita, near Bot. Gard.	Crimea	+	+	+	+	+
<i>Robinia pseudoacacia</i> L.	Cult.: End of 18 th – without concrete data; 1804, Osnovianskyi park (Kharkiv Obl.), 1813 – Nikita Bot. Gard.; the Middle of 20 th – Odesa Escaped: 1855 – Sevastopol (Crimea)	Polissia, Forest Steppe, Steppe, Crimea		+	+	+	+
<i>Rudbeckia laciniata</i> L.	Cult.: the End of 19 th – the beginning of the 20 th – Western Ukraine Escaped: 1903 – vill. Serednie (Transcarparhia), 1909 – vill. Jordaneshty (Chernivtsi Obl.)	Transcarpathia, Ciscarpathia, Western Forest Steppe, Polissia (banks of reservoirs)				+	+
<i>Salix fragilis</i> L.	Archaeophyte	All regions (banks of reservoirs)			+	+	+
<i>Solidago canadensis</i> L.	Cult.: 1876 – Maramorosh region (Transcarpathia Obl.) and Western Ukraine, 1886 – Crimea Escaped: 1886 – Central Ukraine without concrete data	Polissia, Forest Steppe, Ciscarpathia, Transcarpathia					+
<i>Symphotrichum × salignum</i> (Willd.) Nesom	Cult.: ? Escaped: 1872 – Galicia, Bukovina	Polissia, Forest Steppe, Transcarpathia					+
<i>Tripleurospermum inodorum</i> (L.) Sch. Bip.	Archaeophyte	Polissia, Right-Bank Forest Steppe		+	+	+	+
<i>Ulmus pumila</i> L.	Cult.: 1894 – Bot. Gard. of Imperial University of St. Volodymyr in Kyiv; the first half of the 20 th (≈ 1917) – Bila Tserkva Escaped: ?	Steppe				+	+
<i>Xanthium albinum</i> (Widd.) H. Scholz	Spontaneously: 1928 – Nyzhniosirogoskyi Distr., without concrete localities (Kherson Obl.) and vicinity of Mykolaiv	All regions (banks of reservoirs)			+	+	+

2. Study area

Ukraine is located within the Forest, Forest-Steppe and Steppe zones, has two mountain systems (Ukrainian Carpathians, Crimean Mountains), and the Southern Coast of Crimea is located in ecoregion of Crimea Submediterranean forest complex. All these zones contain smaller classification units. Each one of these is characterized by a distinct vegetation cover type with a distinct species composition, including invasive plants, and by the state of its preservation (PROTOPOPOVA & SHEVERA, 2019).

2.1. A short history of development of the territory of Ukraine

In Steppe, Forest Steppe and partially Forest zones the beginning of development dates back to 5th-3rd millennia B.C. During this period, numerous sites of Trypillia culture existed from the Right Bank of the Dnipro to the southwestern borders of the country. In the east and south of the Steppe and Forest Steppe the Timber-Grave culture dominates later (18th–12th century B.C.). From the 7th century B.C. the settlement of modern Ukraine began from the southeast by the Scythians, Sarmatians and Alans, and then from the northwest by the Goths and again from the east by the Huns, which led to a great migration of people. At the same time, on the coast of the Black and Azov Seas, the Ancient Greek colonization took place, and in the Middle Ages – the Byzantine, Venetian and Genoese colonization of the Northern Black Sea Coast and the Crimea. At the same time, a large trade route connecting the Baltic and Black Seas passed through the country. From Scythian times, trade links with neighbouring and more remote regions have been traced. Migration of nomads through the Ukrainian steppes in Antiquity and the early Middle Ages, and frequent wars and military conflicts has contributed to the enrichment of the flora with non-native species, including from the Ancient Mediterranean. Thus, Ukraine has a long history of its development, which differs depending on the region.

Of great importance was the introduction of new plant species into cultivation, the centre of which were first monastic gardens, and later physic and botanical gardens and parks. In the middle of the 19th century the beginning of intensive anthropogenic transformation of the environment took place: urbanization, industrial development intensified, the development of railways (1863) and other transportation routes began. These transformations have contributed to the constant and substantial introduction of alien plant species, both directly from North America

and other continents, and mostly from secondary centres of introduction. Some of the introduced species of non-native plants quickly naturalized and showed a high degree of invasiveness.

3. Materials and methods

The data from the authors' field research (from 1965 till now), as well as the results of the review of scientific publications about alien plants (ALIEN SPECIES..., 2021), herbarium collections (CHER, CWU, DNZ, DSU, KHEM, KHER, KW, KWHA, KWHU, LW, LWS, LWKS, MSUD, SIMF, UU, YALT and other) have been critically analyzed.

The comparative morphological-ecological-geographical method is used in this study. The taxonomic nomenclature of plants corresponds to POWO (PLANTS OF THE WORLD ONLINE) with modifications. The types of biotopes have been used according to EUNIS habitat classification. The nomenclature of syntaxa has been used in accordance with "Vegetation of Europe" (MUCINA ET AL., 2016) and "Prodrome of the Vegetation of Ukraine" (DUBYNA ET AL., 2019).

4. Results

One of the key issues in the studies of invasive plants and their impacts on biodiversity is species composition, which is largely determined by the degree of naturalization of certain non-native species within the vegetation, in some regions or zones and in all of Ukraine. Species composition of invasive plants, as well as a number of other their characteristics, differ in the various regions of Ukraine. However, the composition and characteristics vary depending on environmental conditions and their transformation and implementation of plant strategies. Based on the research of the naturalization of alien species, their current distribution, coenotic role in the vegetation cover and habitats in different regions of Ukraine and analysis of the development of plant invasions within different periods (PROTOPOPOVA, 1991; PROTOPOPOVA ET AL., 2002, 2009, 2010, 2012, 2014, 2015, 2019; BURDA ET AL., 2015; ZAVIALOVA, 2017; SHEVERA ET AL., 2018) a group of 42 species of invasive plants was identified (Table 1). The main criteria for the selection of these species was the generalization of these characteristics of phytointvasions for the entire territory of Ukraine. Some species that were previously in an expanding state, but now have reduced their invasive activity compared to others and occupied a potential area (*Amaranthus albus* L., *A. blitoides* S. Watson, *Cyclachaena xanthiifolia*),

were not included in this group. Neither does this group include species that have local environmental outbreaks (for example, *Geranium sibiricum* L.), nor those species whose increase in activity is fluctuating or of a narrowly local nature (*Pistia stratiotes* L., *Azolla* sp. div.).

According to the analysis of plant invasions in Ukraine, their state for the period between 1850 and 2021 shows significant quantitative dynamics. In the second half of the 19th century, 9 species of invasive plants (for example *Amaranthus retroflexus*, *Erigeron canadensis*, *Centaurea diffusa*) were known, between 1900–1940 there were 18, 1941–1975 – 24, 1976–2000 – 38, 2001–2021 – 42. The severe recent growth is likely due to a significant increase in the number of introduced species, which is due to the revival of economic trade relations and migration processes. Plant invasions continue at the present time and new species appear (e. g., *Symphyotrichum x salignum*, *Impatiens glandulifera*, *Reynoutria japonica*, *Solidago canadensis*).

The results of the reconstruction of the dynamics of the distribution of invasive species on the territory of Ukraine have shown the diversity in the trends of the invasive processes. The large-scale migrations of *Ambrosia artemisiifolia* and *Xanthium albinum* were offensive for a long time. The six invasive species from the studied group were distributed radially. From the local center of the entry and naturalization the spreading of thirteen species has begun. Their progressive and stable distribution took place in a certain direction. The distribution of 30 species from the studied group has achieved expansion. For the most part, this type of widespread colonisation characterizes the invasive plants of North American origin (23 species). The East Asian and Caucasian origin is represented by 2 species each; Mediterranean, Mediterranean-Iranian and Asian origins are represented by 1 species each.

According to the analysis of the basic characteristics on this group of the invasive species we found that the life forms are significantly dominated by phanerophytes (including nanophanerophytes) – 16, and slightly less therophytes – 12 (Fig. 1). In relation to moisture most of these invasive species are xeromesophytes (19), with slightly less mesophytes (13), which corresponds to the ecological structure of both alien factions of regional floras and the flora of Ukraine in general. By the time of immigration kenophytes (38) prevail, by origin (Fig. 2) – North American species (23), according to degree of naturalization – agriophytes, and from the way of entry – ergasiophytes (31).

Alien plants species that have been actively spreading since the last quarter of the 20th

century, immediately showed a higher invasiveness. We no longer observe the distinct migration trends that have characterized the distribution of invasive species in the past. Over the last 50 years the majority of invasive species has become widespread in all anthropogenic habitats in Ukraine. The peculiarity of these invasive processes in the modern period is the compaction of species habitats due to the development of semi-natural habitats and the strengthening of the coenotic role of some species in plant communities. This is facilitated by the increasing invasiveness of plant communities, which is growing due to the fragmentation of natural vegetation, the impact of anthropogenic transformation and climate change.

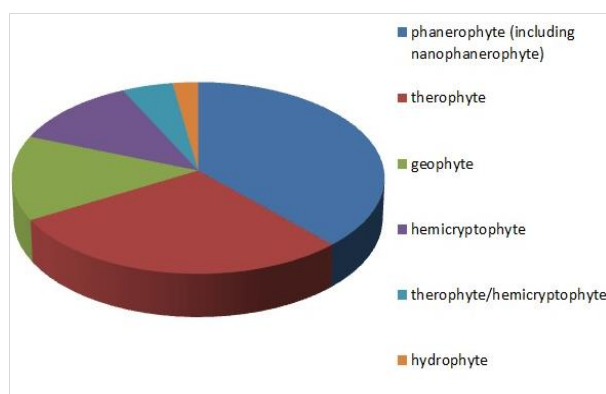


Fig. 1. Distribution of invasive species by their life form

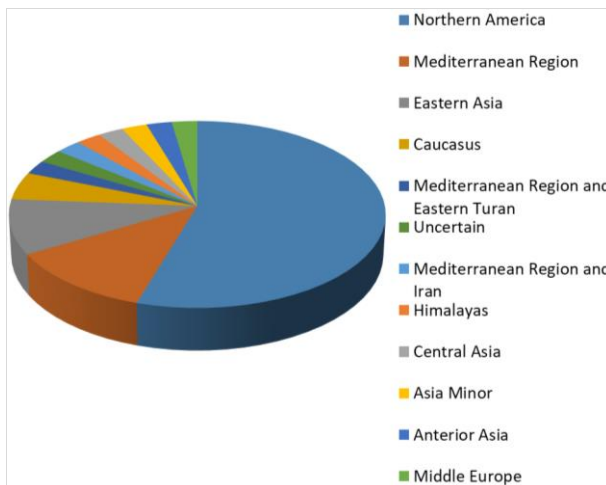


Fig. 2. Distribution of invasive species by their origin

Our analysis of the different vegetation types and habitats in Ukraine has showed an increase of the participation and coenotic role of invasive species in general. We also noted an increase of spectra of plant communities with the participation and high coenotic role of invasive species at the regional level. The results of the research are summarized by types of vegetation and presented below. Among all the types represented in the vegetation of Ukraine, we consider the classes of natural (forest, scrub, aquatic and wetland,

grasslands, coastal, chasmophytic, and other vegetation types) and anthropogenic (ruderal) vegetation. Threats from invasions of species communities for biodiversity are generalized for Ukraine at the zonal, regional and partially biotopes levels (Table 1).

4.1. Forest vegetation

Acer negundo and *Salix fragilis* are transformer species of floodplain forests. In the Ukrainian Carpathians, they displace aboriginal species of the genus *Salix* L., *Amelanchier spicata* and *Padus serotina*, are spread rapidly in the North of Ukraine, and interfere with the formation of undergrowth of aboriginal species in coniferous and mixed forests. *Amorpha fruticosa* and *Robinia pseudoacacia* are a stable component of the forests of Cl. *Pyrolo-Pinetea sylvestris* Korneck 1974, *Alnetea glutinosae* Br.-Bl. et Tx. ex Westhoff et al. 1946. *Bupleurum fruticosum* is a transformer species in the shrub layer of forests of the Cl. *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959 on the Southern Coast of Crimea. Transformer species of the tree layer in these communities are *Fraxinus ornus* and *Rhamnus alaternus*. Together with other foreign evergreen woody-shrub plants (*Quercus ilex* L., *Laurus nobilis* L., *Phillyrea* spp., *Viburnum tinus* L., etc.) *Rhamnus alaternus* forms communities that are specific in composition and structure. Such communities are similar to phytocoenoses of the Cl. *Quercetea ilicis* Br.-Bl. ex A. Bolòs et O. de Bolòs in A. Bolòs y Vayreda 1950. *Partenocissus inserta* prevents the development of the grass layer, sometimes occupying large areas by a 100% projected cover abundance, in almost all types of forest communities. *Echinocystis lobata* is also a threat in the West and North of Ukraine in the humid forests of the Cl. *Alnetea glutinosae*, *Salicetea purpurea* Moor 1958. In the North and West of Ukraine, from the beginning of summer, in many types of forests, the grass layer is formed by *Impatiens parviflora*, completely replacing natural species. Wetlands with plant communities of the Cl. *Alno glutinosae-Populetea albae* P. Fukarek et Fabijanić 1968 are occupied by *Impatiens glandulifera*. In the Greek juniper forests of some areas of the Mountain Crimea, the grass cover is significantly transformed by *Opuntia humifusa*.

4.2. Scrub vegetation

Acer negundo is a stable component of disturbed phytocoenoses of the Cl. *Crataego-Prunetea* Tüxen 1962. Other species that significantly affect the structure of communities of this class are *Lycium barbarum* and *Elaeagnus angustifolia*. On the edges

of downy oak forests, juniper and pistachio woodlands, also on coastal slopes of the Southern coast of Crimea, monodominant scrubs are formed by *Bupleurum fruticosum*, sometimes transforming and displacing the rare plant communities listed in the [GREEN DATA BOOK OF UKRAINE](#) (2009) with the participation of *Cistus tauricus* C. Presl. *Amorpha fruticosa* forms the coenoses of All. *Rubro caesii-Amorphion fruticosae* Shevchyk et V. Solomakha 1996 on alluvial deposits. The invasion of this species disturbs the structure of scrub communities.

4.3. Aquatic and wetland vegetation

Bidens frondosa invasion transforms the phytocoenoses of wetland vegetation. It is a constant species and a dominant one in communities of the Cl. *Bidentetea* Tx et al. ex von Rochow 1951, which are observed in the basins of large and small rivers almost everywhere. Therefore, it will continue to be a threat (Table 1). In turn, this invasion reduces the resistance of wetland phytocoenoses and creates favourable conditions for the entry of other alien species (*Rudbeckia laciniata*, *Impatiens glandulifera*). *Rudbeckia laciniata* changes the composition and structure of communities of the Cl. *Phragmito-Magnocaricetea* Klika in Klika et Novák 1941 in the West of Ukraine, and *Symphyotrichum x salignum* does the same in the North of Ukraine. Increased projective cover abundance and significance in the communities of the *Phragmito-Magnocaricetea* class is characteristic of *Impatiens parviflora* and *Impatiens glandulifera*. In general, river floodplains are the centres of growth and the migration corridors that are actively used for distribution by invasive plants. Among the invasive species of the studied group, the dispersal by river migration corridors of *Bidens frondosa*, *Amorpha fruticosa*, *Partenocissus inserta*, *Reynoutria japonica*, *Echinocystis lobata*, *Heracleum sosnowskyi* and *H. mantegazzianum* has been observed. Their invasions have transformed the vegetation cover not only along the banks of the longest rivers (Dnipro, Dniester, Southern Bug and other), but also of their tributaries too. *Elodea canadensis* is a transformer species of aquatic vegetation of the classes *Potamogetonetea* Klika in Klika et Novák 1941 and *Lemnetea* O. de Bolòs et Masclans 1955, which can be found throughout Ukraine.

4.4. Grasslands

The allelopathic properties and large above-ground phytomass of *Asclepias syriaca* prevent the development of the vegetation of the Cl. *Molinio-Arrhenatheretea* Tx. 1937. *Solidago canadensis*

and *Erigeron annuus* invasions completely change the structure of communities of this class, which causes a reduction in the area of meadows. *Lupinus polyphyllus* is rapidly spreading into the *Molinio-Arrhenatheretea* communities, increasing the projective cover and currently threatening the natural meadows of all regions of Ukraine except the steppe zone and the Crimea (Table 1). The invasion of *Echinocystis lobata* is dangerous for the hygrophilous communities of meadow vegetation of Polissya, which in some places completely changes the structure and species composition of coenoses. *Robinia pseudoacacia* threatens the communities of the class *Trifolio-Geranietea sanguinei* T.Müller 1962, especially in the Steppe and in the southern Forest Steppe. *Heracleum sosnowskyi* and *H. mantegazzianum* not only pose a threat to all types of meadow communities, but are also extremely dangerous to humans due to the likelihood of burns.

Anisantha tectorum has spread onto the disturbed areas of the Steppe, especially after fires and depletion by grazing, and so has *Ambrosia artemisiifolia* along the roads. *Centaurea diffusa* has a significant projective cover in steppe coenoses. *Festuco-Brometea* Br.-Bl. et Tx. Ex Soó 1947 includes *Grindelia squarrosa*, which changes the composition and structure. The expansion of *Ulmus pumila* leads to areas overgrown with communities of the *Festuco-Brometea* class even on the territory of protected areas (Department of the Luhansk Nature Reserve "Striltsivsky Steppe", Natural Reserve "Yelanetsky Steppe"). In the southern and eastern regions, there is the overgrowth of steppe communities due to the invasion of *Elaeagnus angustifolia*.

The wormwood steppes in the Crimea are threatened by the invasion of *Opuntia humifusa*. *Erigeron canadensis* poses a threat to psammophytic steppes, changing the structure of such plant communities and showing allelopathic properties.

4.5. Coastal vegetation

Xanthium albinum actively invades sandy beaches, and is a constant species in the plant communities of the Cl. *Cakiletea maritimae* Tx. et Preising in Tx. ex Br.-Bl. et Tx. 1952. Vegetation of the Cl. *Crithmo-Staticetea* Br.-Bl. in Br.-Bl. et al. 1952 on the southern coast of Crimea is threatened by the invasion of *Jacobaea maritima*. On the beaches, coastal rocks and soft cliffs of the Black Sea coast *Ailanthus altissima* forms monodominant communities.

4.6. Chasmophytic vegetation

The diagnostic species of the All. *Elytrigio nodosae-Rhoion coriariae* Korzhenevsky et Ryff ex Didukh et Mucina 2014 of the order *Onosmato polyphyllae-Ptilostemonetalia echinocephali* Korzhenevsky 1990 Cl. *Drypidetea spinosae* Quézel 1964 is *Ailanthus altissima*. The above-mentioned alliance includes plant communities of denuded shale slopes of the Southern coast of Crimea. Vegetation of *Sedo-Scleranthetea* Br.-Bl. 1955 class in the Crimean Mountains is transformed by *Opuntia humifusa*, which prefers the outcrops of conglomerates and shales.

4.7. Ruderal vegetation

Acer negundo forms the plant communities in artificial forests of the All. *Chelidonio-Acerion negundo* L. Ishbirdin et A. Ishbirdin 1989. *Robinia pseudoacacia* and *Fraxinus pennsylvanica* throughout Ukraine are among the main species of artificial forests belonging to the Cl. *Robinietea* Jurko ex Hadač. et Sofron 1980. *Symphotrichum xsalignum* forms specific phytocoenoses on fires and felled areas, in addition, this species forms monodominant communities in other anthropogenically disturbed habitats. *Ailanthus altissima* is a stable component of artificial forests in South of Ukraine. *Amaranthus retroflexus*, *Ambrosia artemisiifolia*, *Anisantha tectorum*, *Conyza canadensis*, *Xanthium albinum* are the constant species of classes *Sisymbrietea* Gutte et Hilbig 1975, *Papaveretea rhoeadis* S. Brullo et al. 2001, *Artemisietea vulgaris* Lohmeyer et al. in Tx. ex von Rochow 1951, within which can form monodominant communities due to their high seed productivity. *Reynoutria japonica*, *Helianthus tuberosus* and *Grindelia squarrosa* transform ruderal communities due to large above-ground phytomass. The plant communities of the azonal vegetation types (meadows, floodplain forests), and some other phytocoenoses (psammophytic, chasmophytic) with available ecological niches are characterized by the highest invasibility. Invasions of plant communities of zonal vegetation types (steppes, forests) are observed much less often.

These examples illustrate the success of invasions of some alien species in phytocoenoses of different classes and types of vegetation. The participation of *Echinocystis lobata* in the communities of classes *Epilobieteae angustifolii* Tx. et Preising ex von Rochow 1951, *Alno glutinosae-Populetea albae* and the hygrophilous alliance of the Cl. *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968 has been established. Narrower ecological amplitudes, but stable positions in phytocoenoses have other invasive species, in particular *Amelanchier spicata*

(in *Crataego-Prunetea*) or *Fraxinus pennsylvanica* – as a component of communities of classes *Robinietea*, *Salicetea purpureae*.

A number of species with high invasiveness, such as *Anisantha tectorum*, *Grindelia squarrosa*, *Elaeagnus angustifolia* and some other, not only show coenotic activity, but also form new communities. An effective way of naturalization in the coenosis is hybridization between native and alien species. In this way, *Salix fragilis* displaces the aboriginal species of *S. alba* L. from riparian willows and willow-poplar forests everywhere. These hybridizations may compromise the genetic integrity of native taxa to the point of causing extinctions. One of the long-term consequences of such hybridization is increasing opportunities for replacement of the native species on invasive non-aboriginal or their hybrids in natural phytocoenoses. The ecological outbreak of *Xanthium albinum* was accompanied by its interspecific hybridization with other species of the genus – archaeophyte *X. strumarium* and kenophyte *X. ripicola*. As a result, almost all over the territory, both species were assimilated by *Xanthium albinum*, in the populations of which there are now also many hybrids, which is most often the characteristic of the South of the Steppe of Ukraine. *Centaurea diffusa* hybridizes with species of "cornflower flora" of the lower Dnieper and other native taxa, such as *C. margarita-alba* Klokov, *C. sterilis* Steven, *C. steveniana* Klokov, *C. majorovii* Dumbadze, *C. lavrenkoana* Klokov. The hybridization between *Heracleum mantegazzianum* and *H. sphondylium* L., and possibly *H. sosnowskyi* has been recorded. *Reynoutria japonica* forms inverse hybrids with *R. ×bohemica* Chrtek & Chrtková of different ploidy. Some species are naturalized in semi-natural and natural plant communities due to mutations and race formation.

There are equally diverse patterns of relationships between invasive plants and habitat types: B – Coastal habitats, C – Inland surface waters, E – Grasslands and land dominated by forbs, mosses or lichens, F – Heathland, scrub and tundra, G – Woodland, forest and other wooded land, H – Inland unvegetated or sparsely vegetated habitats, I – Regularly or recently cultivated agricultural, horticultural and domestic habitats, J – Constructed, industrial and other artificial habitats (according to EUNIS habitat classification). Most invasive plants (33 species) are observed in anthropogenic habitats (I), among which the most common are artificial plantations, where wild ergasiophytes grow spontaneously. Slightly fewer species of the studied group prefer habitat types E (25), F and G (22 each), but it is in them that the largest

invasions are observed. In aquatic and coastal habitats, the variety of invasive plants is lower: in coastal habitats (B) 11 species are most often observed, and in freshwater reservoirs (C) 7 species, but they are capable of significant transformation of their environment. Some alien invasive species inhabit artificial (J) and natural (H) habitats with poorly developed vegetation – four and two species, respectively. However, if in natural habitats with chasmophytic vegetation the value of invasive species is small, then in the vegetation of artificial habitats they often play a major role.

4.8. Biotope

Invasive species are characterized by eurytopicity, most of which successfully inhabit a variety of habitats, both natural and anthropogenic (Figs. 3 and 4). The greatest ecological plasticity characterizes four species from the studied group of the invasive plants, each of which is found in six types of habitats: *Ailanthus altissima* (B, F, G, I, J, H), *Amaranthus retroflexus* (C, E, F, G, I, J), *Opuntia humifusa* (B, E, F, G, H, I) (Fig. 5), *Xanthium albinum* (B, C, E, F, G, I). *Erigeron canadensis* is found in five habitat types (C, E, F, G, I). Nine species are each noted in four types of habitats: *Anisantha tectorum* (B, E, F, G), *Bupleurum fruticosum* (B, F, G, I) (Fig. 6), *Centaurea diffusa* (B, E, F, I), *Lycium barbarum* (B, E, F, I), *Partenocissus inserta* (E, F, G, I), *Reynoutria japonica* (E, F, G, I) (Fig. 7), *Rhamnus alaternus* (B, F, G, I), *Robinia pseudoacacia* (B, F, G, I), *Solidago canadensis* (C, E, G, I). The same number of species has been recorded for three different types of habitats: *Acer negundo* (G, I, J), *Ambrosia artemisiifolia* (C, E, I), *Amorpha fruticosa* (B, G, I), *Asclepias syriaca* (E, F, I) (Fig. 8), *Elaeagnus angustifolia* (B, F, I), *Fraxinus ornus* (F, G, I), *Grindelia squarrosa* (E, F, I), *Impatiens glandulifera* (E, G, I), *Padus serotina* (F, G, I). The most invasive species (15) were observed in two types of habitats: *Amelanchier spicata* (F, G), *Apera spica-venti* (E, I), *Cenchrus longispinus* (E, I), *Echinocystis lobata* (E, G), *Elodea canadensis* (C, I), *Fraxinus pennsylvanica* (I, J), *Helianthus tuberosus* (E, I), *Heracleum mantegazzianum* (E, I), *Heracleum sosnowskyi* (E, I), *Rudbeckia laciniata* (E, I), *Salix fragilis* (F, G), *Senecio cineraria* (I, B), *Symphyotrichum × salignum* (E, I), *Tripleurospermum inodorum* (E, I), *Ulmus pumila* (F, I). Four species are characteristic of only one type of habitat: *Bidens frondosa* (C), *Erigeron annuus* (E), *Impatiens parviflora* (G), and *Lupinus polyphyllus* (E). Thus, the most easily invaded natural habitats are types E, F and G, the most eurytopic species are: *Ailanthus altissima*, *Amaranthus retroflexus*, *Opuntia humifusa* and *Xanthium albinum*.

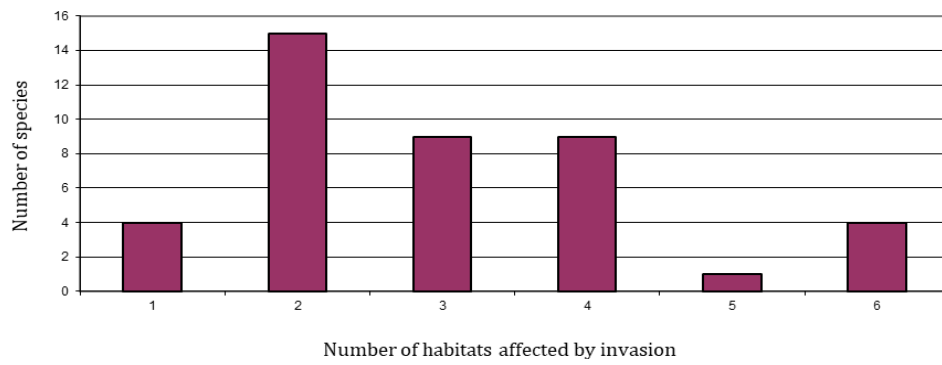


Fig. 3. Distribution of species into groups, depending on the number of invaded habitat types

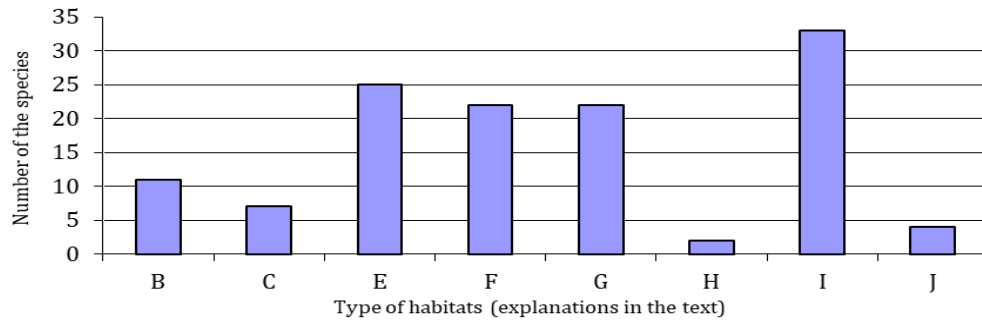


Fig. 4. Distribution of invasive species by their habitat types



Fig. 5. *Opuntia humifusa* (Raf.) Raf. in Crimea



Fig. 6. *Bupleurum fruticosum* L. in Crimea



Fig. 7. *Reynoutria japonica* Houtt. in Transcarpathia

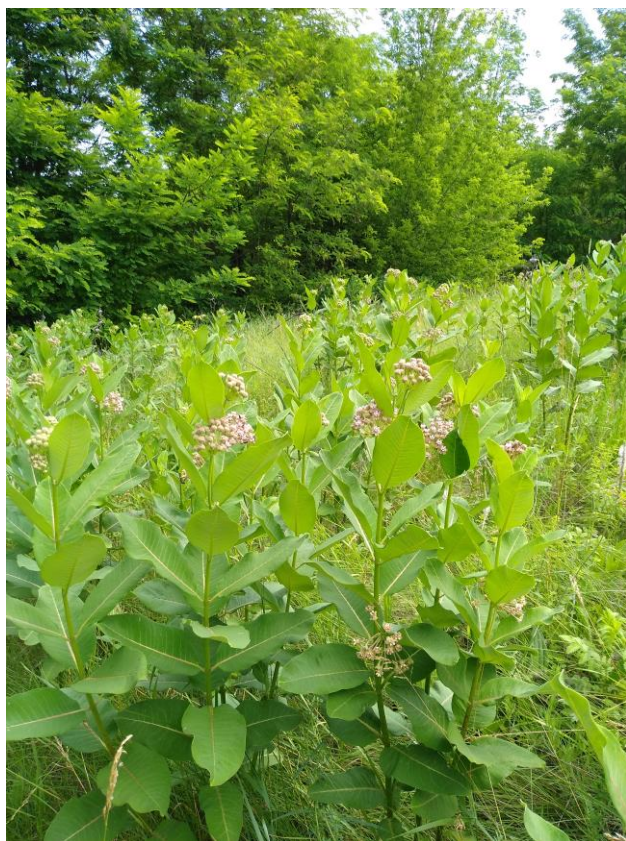


Fig. 8. *Asclepias syriaca* L. in Forest Steppe

5. Discussion

The studied group of plants includes some invasive species that have managed to overcome only the E-barrier, but their impact on the species composition of plant communities is significant. This indicates their high invasiveness. The examined species form significant monodominant communities, inhibiting the regeneration of other species, mainly weeds. Also the studied invasive species form the new associations or acting as constant or diagnostic species in these syntaxa.

For example, *Ambrosia artemisiifolia* is diagnostic and / or the dominant species of ass. *Ambrosietum artemisiifoliae* Vițălariu 1973, ass. *Ambrosio artemisiifoliae-Chenopodietum albi* Marjushkina et Solomakha 1985 (Cl. *Stellarietea mediae* Tx. et al. in Tx. 1950), ass. *Eragrostio minoris-Polygonetum arenastri* Oberd. 1954 corr. Mucina in Mucina et al. 1993 (Cl. *Polygono-Poetea annuae* Rivas-Mart. 1975). *Ambrosia artemisiifolia* is a constant species for such syntaxa: ass. *Amaranthetum blitoidis-retroflexi* Solomakha 1988, ass. *Conyzo canadensis-Lactucetum serriolae* Lohmeyer in Oberd. (Cl. *Stellarietea mediae*), ass. *Achilleo millefolii-Grindelietum squarrosae* Kostylev in Solomakha et al. 1992, ass. *Ambrosio artemisiifoliae-Xanthietum strumariae* Kostylev in Solomakha et al. 1992 (Cl. *Artemisietea vulgaris*).

Thus, *Ambrosia artemisiifolia* is distributed throughout the whole of Ukraine. But in the Steppe, Forest Steppe and the southern part of Polissia distribution of this species is common, in other regions it occurs sporadically. It is one of the most coenotically active species and diagnostic for some associations of ruderal vegetation. *Ambrosia artemisiifolia* is most often observed in the plant communities of classes *Stellarietea mediae* and *Artemisietea vulgaris*. The participation of *Ambrosia artemisiifolia* in plant communities of ass. *Echinochloo-Setarietum pumilae* Felföldy 1942 corr. Mucina in Mucina et. al. 1993 and ass. *Ambrosio artemisiifoliae-Chenopodietum albi* corresponds to high fidelity at the Centre and West of Ukraine. The participation of *Ambrosia artemisiifolia* in plant communities of ass. *Cirsio setosi-Lathyretum tuberosi* Smetana 2002, ass. *Achilleo millefolii-Grindelietum squarrosae*, ass. *Ambrosio artemisiifoliae-Xanthietum strumariae* (Cl. *Artemisietea vulgaris*) corresponds to high fidelity in the western part of Northern Black Sea region. In phytocoenoses of ruderal vegetation *Ambrosia artemisiifolia* has a projective cover range from 25% (*Galio-Urticetea* Passarge ex Kopecký 1969) to 50% (*Stellarietea mediae*).

One of the threats of invasive species is their direct impact on rare plant species and rare plant communities. For example, the significant impact of *Bupleurum fruticosum*, *Opuntia humifusa*, *Jacobaea maritima* to native biodiversity was recorded in Crimea.

Bupleurum fruticosum interferes with the restoration of rare species (listed in the Red Data Book of Ukraine and the regional Red List of the Autonomous Republic of Crimea) – *Juniperus excelsa* M. Bieb. and *Cistus tauricus* C. Presl – are dominants of the tree and shrub layers of the ass. *Cisto-Arbutetum andrachnis* Didukh, Vakarenko et Shelyag-Sosonko ex Didukh 1996 (*Jasmino fruticantis-Juniperion excelsae* Didukh, Vakarenko et Shelyag-Sosonko ex Bonari et al. 2021; *Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014; *Pinetea halepensis* Bonari et Chytrý in Bonari et al. 2021), respectively. Phytocoenoses of this association are listed in the **GREEN DATA BOOK OF UKRAINE** (2009).

Opuntia humifusa interferes with the restoration of rare species (listed in the Red Data Book of Ukraine and the regional Red List of the Autonomous Republic of Crimea) – *Juniperus excelsa* M. Bieb. and *Pinus brutia* var. *pityusa* (Steven) Silba – the dominants of the tree layer, and displaces *Stipa pontica* P.A. Smirn., *Helianthemum ledifolium* (L.) Mill. subsp. *lasiocarpum* Jacques & Hérincq and other rare species of herb layer of

associations *Achnathero bromoidis-Pinetum brutiae* Didukh 1996 nom. corr. 2021 and *Linosyri-Juniperetum excelsae* Didukh, Vakarenko et Shelyag-Sosonko ex Didukh 1996 (*Jasmino fruticantis-Juniperion excelsae* Didukh, Vakarenko et Shelyag-Sosonko ex Bonari et al. 2021; *Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014; *Pinetea halepensis* Bonari et Chytrý in Bonari et al. 2021). Phytocoenoses of these associations are listed in the [GREEN DATA BOOK OF UKRAINE](#) (2009).

Jacobaea maritima displaces the rare species listed in the Red Book of Ukraine and the regional Red List of the Autonomous Republic of Crimea – *Crithmum maritimum* L., *Glaucium flavum* Crantz, *Apocynum venetum* L. subsp. *sarmatiense* Woodson, which are diagnostic species and dominants of the association *Crithmo-Elytrigietum bessarabicae* Korzhenevsky et Klyukin in Korzhenevsky 2001 (*Elytrigio bessarabicae-Lactucion tataricae* Korzhenevsky ex Didukh et Mucina in Mucina et al. 2016; *Crithmo-Staticetalia* Molinier 1934; *Crithmo-Staticetea* Br.-Bl. in Br.-Bl. et al. 1952). Rare habitats are listed in Resolution 4 of the Bern Convention (the Emerald Habitats).

The species composition of the group of invasive plants in each of the botanical and geographical regions of Ukraine (except Crimea) differ slightly, which indicates the high invasiveness of all species, their ecological plasticity and diverse adaptive strategies. Species with transcontinental and transzonal types of area, are mainly distributed in the western, most often forest areas. In particular species of North American and East Asian origin adapt most successfully to the natural conditions of Ukraine. The species with an adjacent-zonal area is smallest proportion in the studied group, mostly this species are represented of Mediterranean origin. The latitudinal gradient tends to decrease the number of invasive species in a southern direction ([PROTOPOPOVA & SHEVERA](#), 2019). In general, the success of alien species invasiveness depends on the natural conditions of the territory and the invasibility of plant communities. In Ukraine, such conditions are mostly characterized by anthropogenic habitats with ruderal vegetation. However, a significant number of natural habitats are threatened by invasions, and even more plant communities contain invasive plants with a high coenotic role. The different strategies of invasive species in the secondary range should be noted. Thus, species such as *Ambrosia artemisiifolia*, *Amaranthus retroflexus*, *Xanthium albinum* have a very high eurytopicity, but they "drop out" from the semi-natural coenoses with increasing participation

of native species. In case of repeated transformation, the free niches are occupied first due to the seed bank being formed earlier in the soil. Invasive species with a different strategy (*Bidens frondosa*, *Elodea canadensis*, *Impatiens parviflora*) more often repopulate the biotopes of a certain type, where they have a high projective cover and remain in coenoses for a long-term period.

6. Conclusions

The obtained results show that invasive species are often quite stable components of grass, scrub and forest habitats in Ukraine. The most competitive ones occupy the dominant positions in such habitats and transform the environment due to the realization of their invasiveness. As a rule, anthropogenic habitats are places of their primary introduction and adaptation of alien species, and for the plants which have appeared incapable of competing with aboriginal species in their natural conditions. The anthropogenic biotopes remain the main habitats of invasive species in the secondary area of species range for a long-term time.

In general, the main features of the studied group are insignificant regional specificity of the species composition, high invasiveness and stability of the population reproduction. All invasive species are a part of the synanthropic fraction of the flora of Ukraine, a significant number of types of natural vegetation and natural types of habitats. The distributions of most of the studied species within Ukraine show expansion.

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