



Plant communities with the dominant *Elaeagnus angustifolia* in Ukraine: classification and distribution

Liubov M. Borsukevych¹ · Svitlana M. Iemelianova^{2,3} · Vitalii P. Kolomiychuk⁴

Received: 30 July 2022 / Accepted: 23 February 2023

© The Author(s), under exclusive licence to Plant Science and Biodiversity Centre, Slovak Academy of Sciences (SAS), Institute of Zoology, Slovak Academy of Sciences (SAS), Institute of Molecular Biology, Slovak Academy of Sciences (SAS) 2023

Abstract

Elaeagnus angustifolia is one of the highly invasive shrubs in Ukraine, which escaped from the culture and started to form plant communities in different habitats. We aimed to: (i) analyze information about the history of cultivation, introduction, and current distribution of *E. angustifolia* in Ukraine; (ii) conduct a phytosociological classification of *E. angustifolia*-dominated stands in Ukraine; (iii) characterize the units described; (iv) compare synecological characteristics of different *E. angustifolia* communities; (v) reveal some reasons for the invasion success of *E. angustifolia* on the territory of Ukraine. We established that *E. angustifolia* is widespread nowadays in the steppe zone of Ukraine, but shows a tendency to expand its range northward. We identified four associations (*Lactuco tataricae-Elaeagnetum angustifoliae*, *Plantago arenariae-Elaeagnetum angustifoliae*, *Balloto nigrae-Elaeagnetum angustifoliae*, *Leymo sabulosi-Elaeagnetum angustifoliae*) and one community (*Elytrigia repens-Elaeagnus angustifolia*) with the dominance of oleaster in Ukraine. Using DCA-ordination, it was demonstrated that the main gradients of a plant community's differentiation are the climate's aridity-humidity and thermoregime of the territory. The invasion success of *E. angustifolia* is caused by anthropogenic pressure as well as the biological peculiarities of this species.

Keywords Classification · Invasion · Syntaxonomy · Ukraine · Vegetation

Introduction

Invasive plants are considered a significant threat to biodiversity and constitute a major component of anthropogenic global change (Vitousek 1994; Pyšek et al. 2012b). Invaders may have substantial environmental effects, changing the community's structure (Abbott 1992; Levine et al. 2003; Kettunen et al. 2009; Winter et al. 2009; Pyšek and Richardson 2010; Klein and Smith 2021), nutrient cycles (Zitler and Dawson 1989; Bermúdez de Castro et al. 1990; Simons and Seastedt 1999; Fridley and Frank 2017), trophic levels

(McCary et al. 2016; Wainright et al. 2021), hydrology (Calder and Dye 2001; Huddle et al. 2011; Le Maitre et al. 2015), and functioning of whole ecosystems (Mack et al. 2000; Manchester and Bullock 2000; Pimentel et al. 2001; Vilà et al. 2010, 2011; Stohlgren et al. 2011). Aliens with high invasive abilities can cause high economic losses and be a source of allergens that significantly worsen the quality of human life (Muñoz and Cavieres 2008).

Woody plants were not widely considered to be important invasive alien species until recently (Holm et al. 1977, 1997; Akobundu and Agyakwa 1987; Osada 1997; Raju 1998; Everitt et al. 2007; Richardson and Rejmánek 2011). But now in many parts of the world, this life-form features prominently on lists of invasive alien plants. In some areas, non-native woody species are among the most conspicuous and damaging invasive plants. They were moved by humans out of natural ranges for many purposes, and many species of trees and shrubs have become naturalized or invasive (Binggeli 1996; Richardson 1998; Richardson and Rejmánek 2004; Williams and Cameron 2006; Richardson 2011; Brundu and Richardson 2016; Wagner et al. 2017, Campagnaro et al. 2022).

✉ Svitlana M. Iemelianova
yemelianova.sv@gmail.com

¹ Botanical Garden of Ivan Franco National University of Lviv, Lviv, Ukraine

² Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

³ M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine

⁴ O.V. Fomin Botanical Garden of Taras, Shevchenko National University of Kyiv, Kyiv, Ukraine

Elaeagnus angustifolia (oleaster, russian olive, wild olive) is one of the highly invasive woody species that become invaders in different parts of the world (Knopf and Olson 1984; Olson and Knopf 1986; Brock 1998; Cagiotti et al. 1999; Haber 1999; Lesica and Miles 2001; Stannard et al. 2002; Botta-Dukát and Balogh 2008). Oleaster can replace ecologically (Pendleton et al. 2011) and culturally (Pretty Paint-Small 2013) important native trees and shrubs. Some biological and ecological traits of *E. angustifolia* give it a significant competitive advantage over native trees (Shafroth et al. 1995; Lesica and Miles 1999, 2001; Katz and Shafroth 2003; Pearce and Smith 2009; Reynolds and Cooper 2010). Wild olive, as a nitrogen-fixing species, alters nutrient dynamics in invaded areas (Follstad Shah et al. 2010; Reynolds and Cooper 2010; Mineau et al. 2011). The russian olive invasion has the potential to cause significant economic and resource losses (Wilson and Bernards 2009). The effects on recreation areas, grazing lands, irrigation channels, and other waterways present a chronic maintenance challenge to private and public land management (Olson and Knopf 1986; Lesica and Miles 2001). That is why it is crucial to study and monitor this invasive species for purposes of nature conservation and preventing biodiversity losses.

E. angustifolia belongs to the genus *Elaeagnus* of *Elaeagnaceae* (*Araliaceae*) family (Heywood 1993). This is a small deciduous tree or large thorny shrub that can grow quickly to a height of 10 m and a diameter of 30 cm, and it begins to bear fruit after 5–6 years (Kokhno 1986). It is generally rounded in shape with a loose arrangement of branches. Its stems, buds, and leaves have a dense covering of silvery to rusty scales. Leaves are simple, alternate, 1–3 inches long, lance-shaped, and silvery on both sides. Flowers appear in June–July. They are bell-shaped, single or clustered in the leaf axils, fragrant, yellowish on the inside, and silvery outside. The fruits are elliptical or oblong in shape, 10–30 × 6–20 mm long, light green to yellow in color, with silvery scales, hard and fleshy. Establishment and reproduction are primarily by seed, although some vegetative propagation also occurs (Chopyk et al. 1983; Prokudin 1987). Oleaster is a long-lived plant (80–100 years). Most commonly it grows along floodplains, riverbanks, stream courses, marshes, and irrigation ditches. This tree can tolerate a wide range of harsh environmental conditions such as drought, high soil salinity, or soil alkalinity. *E. angustifolia* can tolerate extended flooding and silting and thrives in a variety of soil types, from sand to dense clay. It can spread with a sharp change in the water regime. *E. angustifolia* requires a minimum of 20 cm of precipitation per year and has a high rate of evapotranspiration. Oleaster can colonize disturbed areas after fires in a short period of time (propagated by means of sprouts from roots and root crowns) (Protopopova et al. 2009).

Most authors suggest that *E. angustifolia* originated in the Irano-Turanian region (Sudnik-Wójcikowska et al. 2009). The general distribution of *E. angustifolia* covers the Caucasus, West Siberia (southern regions), Central Asia, Atlantic, and Central Europe, Mediterranean, Asia Minor, Iran, and NW China (Dzhungaria-Kashgaria). Its range in the east stretches from eastern Kazakhstan to Kashmir and NW India (POWO, 2022). The western limit of the *E. angustifolia* distribution is not set, as the species occurs sporadically in Central Europe, in such countries as Poland, Hungary, Czech Republic, and Slovakia (Tokarska-Guzik 2005; Botta-Dukát and Balogh 2008; Medvecká et al. 2012; Pyšek et al. 2012a). Within its native range, it mainly grows along riverbanks, on stony slopes, in open sandy areas, coastal dunes, and littoral zones; in the mountains up to 700–1300 m a.s.l. (Minchenko 1974; Tsvelev 2002, 2004). The plant was introduced as an ornamental in North America in the late 1800s and quickly became a very serious problem in many states (Lesica and Miles 1999). It has spread from its initial plantings in the 17 western states with no direct human assistance and nowadays is well-established outside of cultivation. In much of the central and northeastern United States, it is generally described as only occasionally or rarely escaping from cultivation; absent in 13 states in the southeast (Olson and Knopf 1986). It grows especially well in riparian habitats and has been documented as out-competing the native plains cottonwood (*Populus carolinensis*).

E. angustifolia has started to spread as an invasive species in Ukraine's steppe region over the past decade (Protopopova et al. 2006). Moreover, it is considered a “transformer” species that significantly influences the species composition of the plant communities in the steppe zone of Ukraine (Protopopova et al. 2009). It changes the vegetation of the Steppe and Black Sea regions, causes the overgrowth of river valleys and grasslands in saline coastal depressions, and forms thickets that change the lighting regime of the herb cover, which is reflected in the species composition and structure of plant communities. Even though this species has become naturalized in azonal plant communities (mostly in floodplains and along rivers), there is a clear trend towards its active spread in sand arenas, seacoasts, saline meadows, and sometimes in the psammophytic steppe (Protopopova et al. 2009).

The first report about vegetation with *E. angustifolia* dated to 1989 and indicated that the *Elaeagneta angustifoliae* formation occurred in elevated areas of riverbeds, and across the sand dunes of the rivers Danube, Dnipro, Don, and Kuban (Dubyna and Shelyag-Sosonko 1989). In the early 2000s, such authors as Dubyna et al. (2003) and Karnatovska (2006) described the *Elaeagnus angustifolia* community.

V. Golub and co-authors (Golub et al. 2002; Golub and Kuzmina 2004) were the first who described the new

phytosociological associations with *E. angustifolia*. In 2002, they identified and in 2004 validated three new associations in the Lower Volga Valley – *Elaeagnatum angustifoliae*, *Artemisio austriacae-Elaeagnatum angustifoliae*, and *Plantagini majoris-Elaeagnatum angustifoliae*. They had assigned them to the class *Nerio-Tamaricetea*.

At the same time, in Ukraine, T. Chynkina (2002) in the mouth of the Dnipro River described an association with the same name – *Elaeagnatum angustifoliae*. This association was not published as valid because the publication contained only a synoptic table. Furthermore, this association was erroneously attributed to the alliance *Salicion elaeagni*, which unites vegetation of wet gravel substrates on mountain river banks. In the “Prodrome of Vegetation of Ukraine” (Dubyna et al. 2019) this association was presented as *Elaeagnatum angustifoliae* Chynkina 2002 **nom. inval.** with the reference to the Articles 3o and 5 of the 3^d edition of International Code of Phytosociological Nomenclature (ICPN) (Weber et al. 2000).

Due to the fact that *E. angustifolia* is actively spreading in Ukraine nowadays and has a high ability to form plant communities, we set out to do the following: (1) Analysis of information about the history of cultivation, invasion, and current distribution of *E. angustifolia* in Ukraine; (2) Phytosociological classification of *E. angustifolia*-dominated stands in Ukraine; (3) Detailed characteristic of identified units; (4) Comparison of synecological characteristics of different communities; (5) Determination of some reasons for the invasion success of *E. angustifolia* on the territory of Ukraine.

Materials and methods

Study area

Ukraine is divided into three physiogeographic zones (forest, forest-steppe, and steppe) (Fig. 1), which are distinguished by the types of landscapes, their geological, geomorphological structure, and climatic features (the southward increase of continentality). The forest zone (Polissia) is a region of lowlands covered with glacial, fluvio-glacial, and alluvial deposits occupied mostly by mixed (coniferous-broad-leaved) and broad-leaved forests, as well as bogs, fens, and wetlands (National Atlas of Ukraine 2007). The Ukrainian Forest-Steppe is a slightly undulating plain dominated by a thick loess stratum that overlies various geological layers cut by gullies and ravines. Forests (broad-leaved hornbeam-and-oak, oak, hornbeam, poplar, and willow) occupy 13% of the area. The large flat areas with different chernozems are covered by different types of grasslands (Marynych 1993).

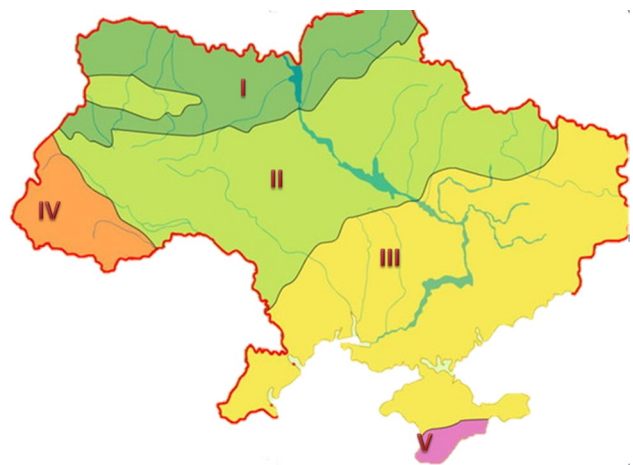


Fig. 1 Geographical regions of Ukraine (zone limitations are marked by a continuous line). I – forest zone (Polissia), II – forest-steppe zone, III – steppe zone, IV – Ukrainian Carpathians, V – Crimean Mountains

Our main study was conducted in the steppe zone of Ukraine, which is about 231 000 km² in area (40% of the territory of Ukraine). The Ukrainian Steppe encompasses most of the western segment of the Eurasian Steppe, known as the Black Sea (or Pontic) steppe province, with a semiarid climate and chernozem or chestnut soils (Marynych 1993). The annual precipitation across the steppe zone of Ukraine decreases southward from 450 mm along the forest-steppe margin to 300 mm at the Perekop Isthmus. The moisture deficit is caused by 900–1 000 mm of annual evaporation. The small rivers in the Steppe tend to be seasonal and dry up in summer. The large rivers, such as Dnipro and Southern Bug, carry their waters in transit. The small lakes, often in pody, are seasonal; the large lakes are of the coastal, liman type, many with saline water (Marynych and Shyshchenko 2005). The Ukrainian Steppe is frequently differentiated according to climatic and soil conditions into three subzones. The northern subzone is characterised by natural vegetation of meadow fescue and feather grass on ordinary, medium humus content (6–8%) in chernozems. The middle subzone, extending along the Black Sea coastal plain eastward towards the northern coast of the Azov Sea, is characterised by narrow-leaved fescue and feather grass on southern chernozems (5–6% humus content) and dark chestnut soils (3–4% humus content). The southern subzone, which straddles Perekop Bay and Syvash Lake, consists of the dry wormwood-grassland steppe on chestnut and solonetz soils (2–3% humus content) (National Atlas of Ukraine 2007).

Data set

Initially, we collected 245 phytosociological vegetation plots with the presence of *E. angustifolia* from both (i) unpublished

Table 1 Overview of the dataset used for classification of *Elaeagnus angustifolia* stands in Ukraine

Authors	Number of plots	Source
Borsukevych L.	79	Private database
Kolomiychuk V.	56	EU-UA-006 “Vegetation database of Ukraine and adjacent parts of Russia”
Solomakha I., Umanets O.	31	Solomakha et al. 2015
Karnatovska M.	30	Karnatovska 2006
Smetana M.	17	Smetana 2002
Moysiyenko I.	9	Solomakha et al. 2015
Dubyna D., Vakarenko L., Dziuba T.	7	Dubyna et al. 2020
Davydova A.	5	Davydova 2020
Dubyna D.	4	Dubyna and Dziuba 2014
Solomakha I.	4	Solomakha et al. 2015
Dziuba T., Tymoshenko P.	3	Dubyna and Dziuba 2014

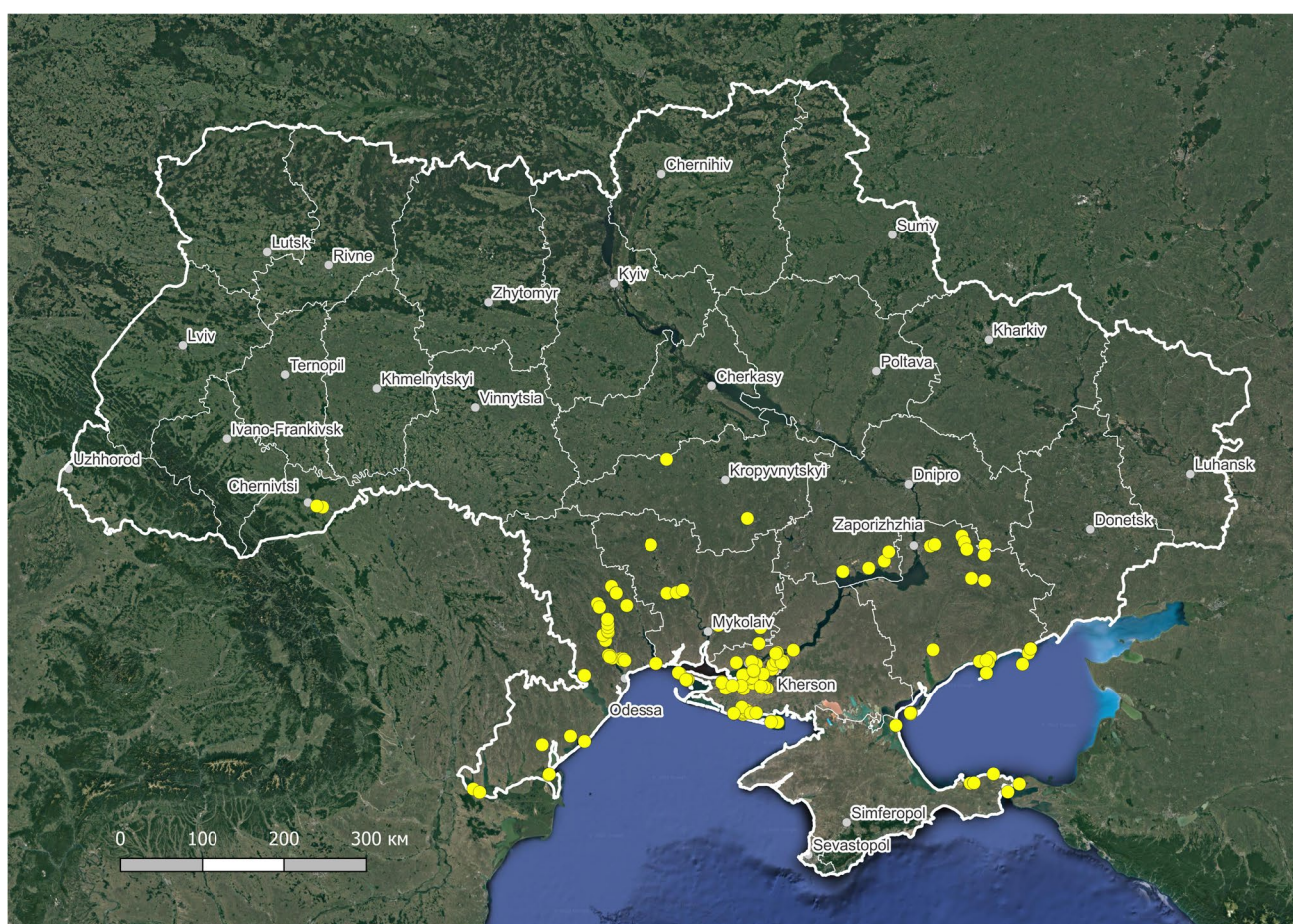


Fig. 2 Distribution map of vegetation plots which was compiled from sources listed in Table 1

field research (79 relevés made by L. Borsukevych) and (ii) local literature (166 relevés from 7 sources) or databases (Table 1; Fig. 2). All relevés were sampled using the Braun-Blanquet approach (Braun-Blanquet 1964) with the

seven-grade scale of abundance and dominance of species. All relevés were stored in the Turboveg for Windows 2.92 database (Hennekens and Schaminée 2001) and processed in JUICE 7.1 software (Tichý 2002). Relevés lacking geographical

coordinates were georeferenced using the Google Earth program (www.google.com/earth, n.d.). Since we wanted to classify only the canopy dominated by *E. angustifolia* we excluded the relevés with species below 25%. After such filtering, the resulting dataset included 207 relevés. All vegetation layers were combined into a single layer. As bryophytes and lichens were not recorded in the majority of plots, they were excluded from the dataset. We also removed all records of juvenile trees and shrubs, as well as records of vascular plant species that were not identified at the species level.

Data analysis

To build the classification, we used both agglomerative and divisive classification algorithms. In the first step of data analysis, we used a modified TWINSpan algorithm (Roleček et al. 2009) with three “pseudospecies” cut levels (0, 5, 25%) and the Sørensen coefficient (Sørensen 1948) as a measure of cluster heterogeneity. Our aim at this point was to identify probable affiliation of the *E. angustifolia*-dominated stands at the level of higher syntaxonomical units. For this purpose, we ran data processing using more than 2700 relevés of Ukrainian floodplain forests (Borsukevych L., unpublished data). Our expert knowledge and literature analysis led us to suppose that *E. angustifolia* is most likely associated with the alliance *Artemisio scopariae-Tamaricion ramosissimae*. For this reason, we also included in the data processing the nomenclatural type of the abovementioned alliance (association *Calamagrostio-Tamaricetum ramosissimae* Simon et Dihoru 1963). In the second step, to distinguish the vegetation units at the level of association, we made beta-flexible clustering (beta = -0.25, Bray-Curtis dissimilarity, log-transformed percentage abundances) in PC-ORD software (McCune and Mefford 2006). Crispness analysis (Botta-Dukát et al. 2005) showed the highest support for classification into five groups. The content of clusters was analyzed by diagnostic, constant, and dominant species in JUICE (Tichý 2002). The diagnostic value of the species was assessed using the *phi* coefficient based on the fidelity concept (Chytrý et al. 2002). The threshold values for the *phi* coefficient are taken at the level of 0.25. Highly diagnostic species have a *phi* coefficient that exceeds 0.5. Species with a non-significant diagnostic value were excluded based on Fisher’s exact test ($P < 0,001$). Vegetation units are presented using a synoptic table with the percentage frequency of species and modified fidelity index (*phi* coefficient) in superscript. To determine the high-constant species we used the index of constancy at more than 50% and constant species at more than 25%. For dominant species, we considered those with a mean cover of > 25% and frequency of > 10%.

Ecological differentiation was conducted using DCA-ordination (Hill and Gauch 1980) in the R program

(Venables et al. 2008) operated from JUICE (Tichý 2002). Indicator values were adopted from Ya. Didukh (2011).

Distribution maps were created using the open Source QGIS (v. 3.22).

We harmonised the nomenclature of vascular plants according to the Euro + MedBase (2006). Names of high-rank syntaxa follow Mucina et al. (2016).

Results

History of cultivation and modern distribution

We found that the russian olive has been planted as an ornamental plant since the 19th century (Protopopova et al. 2006). In private gardens near Odessa it was mentioned in 1830 (Palimpestov 1855), and in the Nikita Botanical Garden in Crimea since 1879 (Zgurovskaya 1984). *E. angustifolia* was purposefully imported for planting in forest belts in southern Ukraine, as it could withstand the harsh arid and high-temperature southern climate conditions. Since the mid-20th century, *E. angustifolia* has been occurring more and more frequently as it was the main tree species planted in windbreaks in the steppe zone (Sudnik-Wójcikowska et al. 2009). Protective forest belts with russian olive were actively created in the 1950 and 1960s. The plant was cultivated along railways, roads, and in artificial plantations in the Black Sea and Azov Sea areas (Matyakin 1952).

The first data of escaped *E. angustifolia* was reported in Crimea (near Foros and Sudak) in 1925 (Protopopova et al. 2006). After rapid and effective naturalization, the wild olive from the artificial forest belts has spread spontaneously to natural territories due to its abundant fruit reproduction, and was actively dispersed in the Northern Black Sea region until the end of the 20th century. Nowadays, *E. angustifolia* is one of the most commonly planted shrubs in shelterbelts in southern Ukraine (Protopopova et al. 2006). In the forest-steppe zone, the oleaster occurs rarely, usually as a solitary shrub or growing in small groups. For example, in the middle part of the Dnipro River (Kaniv Nature Reserve), Shevchyk et al. (1996) mentioned only single oleaster shrubs, which do not threaten any vegetation. The analysis provided by K. Norenko (2016) revealed the presence of northernmost isolated populations of *E. angustifolia* in the central part of the Kyiv region (Ukrayinka, Dudari, and Velykyi Bukryn villages of Myronivskiy district), in the south of Zhytomyr region (Khazhyn village of Berdychiv district) and in the central part of Rivne region (Zdolbuniv). These locations almost coincide with the northern border of the forest-steppe zone and the southern border of the forest zone (Polissia). In the southern part of Ukraine, it most often occurs in the basins of small rivers, where salinization processes occur. In the deltas of the Danube, Dniester, Southern

Bug, Ingulets, Dnipro, and on the Cis-Dunay islands *E. angustifolia* sporadically spreads among the willow-poplar floodplain woods of the coastal strip, in areas with increased soil mineralization. It also penetrates overgrazed pastures, stony slopes of ravines, and rocky screes, and occurs on dry soils roadsides, wastelands, and fallows.

Vegetation classification

The first TWINSPAN division separated *E. angustifolia*-dominated stands from other forest and shrub vegetation, highlighting a quite marked floristic distinction between them and a noticeable relation to the vegetation of tamarisks riverine scrubs (Fig. 3, group of clusters lined in blue color). We extracted this group of vegetation plots for further analysis. With the second division using PC-ORD we obtained 5 clusters due to floristic differences and environmental conditions (Fig. 4; Table 2). We assigned every cluster to different phytosociological associations or communities and below we provide their characteristics in distribution, habitat preferences, structure, and species composition. The distribution of each vegetation unit is shown in Fig. 5.

Cluster 1. Association *Lactuco tataricae-Elaeagnetum angustifoliae* Sokolova, Ermolaeva, Kolomiychuk 2021 (Table 2, column 1) (Fig. 5, 6).

(incl. *Lactuco tataricae-Elaeagnetum angustifoliae juncetosum maritimae* Sokolova, Ermolaeva, Kolomiychuk. 2021 (art. 4e))

Synonym: *Elytrigio elongatae-Elaeagnetum angustifoliae* I. Solomakha et al. 2015 (art. 5).

Name-giving taxa: *Elaeagnus angustifolia* L., *Lactuca tatarica* (L.) C. A. Mey.

Nomenclatural type (Sokolova et al. 2021)¹: Page 64, table 1, relevé 5 (*holotypus*), Braun-Blanquet scale – *Elaeagnus angustifolia* 3; *Agrostis maetotica* 1; *Calamagrostis epigejos* 1; *Elytrigia obtusiflora* 1; *Bromus squarrosus* +; *Cynanchum acutum* +; *Juncus maritimus* +; *Lactuca tatarica* +; *Phragmites australis* +; *Festuca regeliana* r.

Syntaxonomy note. In Ukraine, plant communities of this association were provided by different authors with different names and statuses. First, within Oleshkivski Sands M. Karnatovska (2006) described *E. angustifolia* stands with a noticeable proportion of halophyllous species as a community *Elaeagnus angustifolia* var. *Plantago salsa*. Later, I. Solomakha et al. (2015) in the Black Sea Region provided the association *Elytrigio elongatae-Elaeagnetum angustifoliae* as a new. But authors didn't mention the nomenclatural type of this association. For these reasons, it was published as invalid. In 2021 Sokolova et al. (2021) within Tuzla Island

proposed the association *Lactuco tataricae-Elaeagnetum angustifoliae* with two subassociations: *Lactuco tataricae-Elaeagnetum angustifoliae juncetosum maritimae*, which is characterized by a high frequency of halophyllous plants; and *Lactuco tataricae-Elaeagnetum angustifoliae artemisietosum arenariae*, which significantly differs by the presence of psammophytic species. The first subassociation was described incorrectly according to Article 4e of ICPN (Theurillat et al. 2021) because since 2021 the subassociation that includes the type of the name of the association must automatically get the epithet “typicum”. But the very association was published validly and we consider this name to indicate *E. angustifolia* stands on saline soils.

Diagnostic species: *Calamagrostis epigejos*, *Calystegia sepium*, *Carex extensa*, *Cirsium alatum*, *Cynanchum acutum*, *Elytrigia elongata*, *Juncus maritimus*, *Limonium meyeri*, *Phragmites australis*, *Plantago cornuti*, *Puccinellia distans*, *Scorzonera parviflora*, *Sonchus palustris*.

Constant species: *Daucus carota*, *Elaeagnus angustifolia*, *Galium aparine*, *Gypsophila perfoliata*.

Dominant species: *Elaeagnus angustifolia*, *Elytrigia elongata*.

Structure and composition. The shrub layer usually consists only of *E. angustifolia*. In some localities, oleaster is accompanied by *Populus nigra* (10–15%) and single plants of *Ulmus pumila* or *Tamarix tetrandra*. The cover of the shrub layer varies from 35 to 70%. Coverage of the herb layer is usually higher than 55%. *Elytrigia elongata* is a significant dominant of the herb layer. Among other common species are halophytes (*Artemisia santonicum*, *Carex extensa*, *Juncus gerardi*, *J. maritimus*, *Limonium meyeri*, *Plantago maritima* subsp. *ciliata*, *P. cornuti*, *Tripolium pannonicum*, *Typha laxmannii*), some psammophytes (*Calamagrostis epigejos*, *Leymus racemosus* subsp. *sabulosus*, *Plantago arenaria*, *Secale sylvestre*) and ruderal plants (*Centaurea diffusa*, *Erigeron canadensis*, *Sysimbrium polymorphum*). Plant communities are characterized by medium species richness (9–18 species in the relevé with a total taxa number of 129).

Synecology. These are halophyllous stands concentrated on the flat areas with turf-meadow or sandy soils with a diverse degree of salinity. The community inhabits previously covered areas by salt meadows or salt steppe grasslands.

Distribution. The association sporadically occurs in the Black Sea and Azov Sea regions, inhabiting central zones of sandy spits, lowlands with the close occurrence of mineralized ground waters, and coastal areas remote from the sea.

Variability. The stands occurring in the Azov Sea region are richer in halophytes than those in the Black Sea region. Some true halophytes, such as *Artemisia santonicum*, *Carex extensa*, and *Juncus maritimus*, appear in the Azov Sea region alongside *Elytrigia elongata* as

¹ Species names in nomenclatural types were given in the original form.

Table 2 Shortened synoptic table of the vegetation with the dominance of *Elaeagnus angustifolia* in Ukraine

No. of cluster	1	2	3	4	5
No. of relevés	69	22	48	15	53
<i>Elytrigia elongata</i>	65 ^{70.0}	5			6
<i>Cynanchum acutum</i>	52 ^{39.1}		4	33	13
<i>Limonium meyeri</i>	33 ^{38.0}			7	11
<i>Puccinellia distans</i>	19 ^{36.6}		2		
<i>Calystegia sepium</i>	26 ^{34.2}		4	7	2
<i>Phragmites australis</i>	51 ^{33.2}		21	33	9
<i>Carex extensa</i>	13 ^{32.7}				
<i>Juncus maritimus</i>	13 ^{32.7}				
<i>Plantago cornuti</i>	13 ^{29.5}				2
<i>Sonchus palustris</i>	13 ^{29.2}		2		
<i>Calamagrostis epigejos</i>	43 ^{27.7}	41 ^{24.6}	4	7	9
<i>Cirsium alatum</i>	9 ^{26.6}				
<i>Scorzonera parviflora</i>	10 ^{25.2}				2
<i>Bromus hordeaceus</i>	4	82 ^{83.1}			4
<i>Bassia laniflora</i>		73 ^{82.5}			
<i>Lomelosia argentea</i>	1	73 ^{81.4}			
<i>Plantago arenaria</i>		77 ^{75.7}		13	2
<i>Silene subconica</i>		59 ^{73.2}			
<i>Picris hieracioides</i>	10	68 ^{70.9}	2		
<i>Alyssum turkestanicum</i>		50 ^{66.7}			
<i>Crepis ramosissima</i>	1	50 ^{65.4}			
<i>Achillea micrantha</i>	1	55 ^{62.1}		7	2
<i>Chondrilla juncea</i>	3	68 ^{60.9}		20	8
<i>Poa bulbosa</i>		55 ^{60.5}		7	6
<i>Trifolium arvense</i>		36 ^{56.0}			
<i>Jacobaea borysthena</i>		36 ^{56.0}			
<i>Polygonum arenarium</i>	1	36 ^{54.5}			
<i>Erigeron canadensis</i>	9	55 ^{54.4}	2		11
<i>Anisantha sterilis</i>	7	77 ^{50.3}	38		32
<i>Euphorbia seguierana</i>	1	50 ^{49.9}		20	2
<i>Xeranthemum annuum</i>		27 ^{48.0}			
<i>Dianthus platyodon</i>		27 ^{48.0}			
<i>Cynodon dactylon</i>	14	55 ^{41.4}	2	20	13
<i>Daucus carota</i>	33	64 ^{36.2}	40		15
<i>Linum austriacum</i>		18 ^{36.1}			2
<i>Secale sylvestre</i>	10	45 ^{34.6}		33 ^{19.0}	4
<i>Helichrysum arenarium</i>		14 ^{33.5}			
<i>Gypsophila paniculata</i>		14 ^{33.5}			
<i>Herniaria polygama</i>		14 ^{33.5}			
<i>Eryngium campestre</i>		36 ^{32.3}	2	20	11
<i>Onosma arenaria</i>		9 ^{27.2}			
<i>Cuscuta monogyna</i>		9 ^{27.2}			
<i>Centaurea breviceps</i>		9 ^{27.2}			
<i>Cirsium vulgare</i>	1		71 ^{71.4}		13
<i>Taraxacum officinale</i>	1		58 ^{65.7}		8
<i>Fallopia convolvulus</i>			48 ^{63.4}		2
<i>Ballota nigra</i>			56 ^{61.2}		13
<i>Galium aparine</i>	26		79 ^{60.0}		26
<i>Sambucus nigra</i>	1		48 ^{59.0}		6
<i>Conium maculatum</i>			40 ^{56.7}		2
<i>Schedonorus arundinaceus</i>	4		44 ^{56.3}		2
<i>Galium mollugo</i>			33 ^{51.4}		2
<i>Lepidium draba</i>	1		50 ^{51.1}	7	13
<i>Achillea millefolium</i>	7	23	54 ^{49.9}		
<i>Rhamnus cathartica</i>			27 ^{47.9}		
<i>Arctium lappa</i>			29 ^{47.6}		2
<i>Lactuca serriola</i>	7		42 ^{47.3}	7	2
<i>Fumaria officinalis</i>			23 ^{43.8}		

Table 2 (continued)

<i>Potentilla reptans</i>	7		33 ^{43.0}		4
<i>Cynoglossum officinale</i>		5	33 ^{42.2}		8
<i>Torilis japonica</i>			27 ^{40.5}	7	
<i>Cornus sanguinea</i>			21 ^{39.1}		2
<i>Althaea officinalis</i>	6	5	35 ^{38.9}		9
<i>Convolvulus arvensis</i>			35 ^{37.7}	7	15
<i>Carex cuprina</i>	1		19 ^{37.4}		
<i>Chaiturus marrubiastrum</i>			17 ^{37.1}		
<i>Carex hirta</i>			17 ^{37.1}		
<i>Festuca rubra</i>			17 ^{37.1}		
<i>Geum urbanum</i>			23 ^{37.0}		6
<i>Glechoma hederacea</i>			19 ^{36.8}		2
<i>Pyrus communis</i>	1		17 ^{34.9}		
<i>Poa trivialis</i>	1		17 ^{34.9}		
<i>Hordeum murinum</i>			17 ^{34.3}		2
<i>Artemisia absinthium</i>	4		29 ^{34.1}		13
<i>Prunus cerasifera</i>			21 ^{33.6}	7	
<i>Agrimonia eupatoria</i>			21 ^{32.8}		8
<i>Arctium tomentosum</i>	1		17 ^{32.3}		2
<i>Prunus spinosa</i>			12 ^{32.0}		
<i>Ranunculus acris</i>			12 ^{32.0}		
<i>Cirsium arvense</i>	10		38 ^{31.9}		26
<i>Leonurus cardiaca</i>			15 ^{31.6}		2
<i>Atriplex sagittata</i>	3		21 ^{30.1}		8
<i>Hordeum jubatum</i>			10 ^{29.2}		
<i>Heracleum sphondylium</i>			10 ^{29.2}		
<i>Humulus lupulus</i>	3		19 ^{28.3}	7	
<i>Polygonum aviculare</i>	3		15 ^{27.7}		2
<i>Epilobium hirsutum</i>	6		15 ^{26.6}		
<i>Linaria vulgaris</i>	1		10 ^{26.4}		
<i>Lamium amplexicaule</i>			12 ^{26.1}		4
<i>Lathyrus pratensis</i>			8 ^{26.0}		
<i>Dactylis glomerata</i>			8 ^{26.0}		
<i>Geranium sylvaticum</i>			8 ^{26.0}		
<i>Lithospermum officinale</i>			8 ^{26.0}		
<i>Carex spicata</i>			8 ^{26.0}		
<i>Aristolochia clematitis</i>			8 ^{26.0}		
<i>Plantago major</i>			10 ^{25.7}		
<i>Leymus racemosus</i>	12			80 ^{77.5}	
<i>Centaurea odessana</i>	1			53 ^{66.2}	
<i>Linaria genistifolia</i>	1	9		60 ^{65.9}	
<i>Silene conica</i>				33 ^{53.5}	
<i>Cakile maritima subsp. euxina</i>				33 ^{53.5}	
<i>Crambe maritima</i>	10			47 ^{52.9}	4
<i>Xanthium orientale subsp. riparium</i>	9			53 ^{52.5}	15
<i>Eryngium maritimum</i>			2	33 ^{51.2}	
<i>Anisantha tectorum</i>	9		21	60 ^{49.6}	11
<i>Alyssum hirsutum</i>		5		33 ^{45.2}	4
<i>Artemisia arenaria</i>	4			27 ^{42.4}	
<i>Jurinea longifolia</i>				20 ^{40.8}	
<i>Ephedra distachya</i>				20 ^{40.8}	
<i>Teucrium polium</i>				20 ^{35.8}	4
<i>Gypsophila perfoliata</i>	28 ^{17.5}			40 ^{35.0}	8
<i>Lactuca tatarica</i>	25		21	47 ^{33.5}	8
<i>Verbascum pinnatifidum</i>				13 ^{33.1}	
<i>Amaranthus retroflexus</i>				13 ^{33.1}	
<i>Tamarix tetrandra</i>	1			13 ^{30.6}	
<i>Melilotus albus</i>	17 ^{14.2}			27 ^{30.3}	2

Table 2 (continued)

<i>Amorpha fruticosa</i>	10 ^{7.5}		2	20 ^{27.6}	
<i>Bromus squarrosus</i>	7			27 ^{27.3}	17 ^{11.2}
<i>Dichodon viscidum</i>				13 ^{27.3}	4
<i>Tragopogon dubius subsp. major</i>	1			13 ^{25.5}	4
<i>Galium humifusum</i>	14		6	13	42 ^{36.8}
<i>Jacobaea erucifolia subsp. arenaria</i>					11 ^{30.4}
<i>Hordeum murinum subsp. leporinum</i>	1				11 ^{27.8}
<i>Achillea setacea</i>					9 ^{27.7}
<i>Atriplex tatarica</i>	1		1		17 ^{25.8}
<i>Carex colchica</i>		36 ^{31.5}		33 ^{27.1}	2
<i>Elytrigia repens</i>	22	9	98 ^{53.4}	7	89 ^{44.1}
<i>Cichorium intybus</i>	20	5	35	13	42 ^{22.0}
<i>Poa angustifolia</i>	10	27	42 ^{22.2}		36 ^{15.3}
<i>Plantago lanceolata</i>	4	23	25 ^{14.4}	7	15
<i>Artemisia austriaca</i>	7	9	8	27 ^{22.2}	9
<i>Chenopodium album</i>	3	18	27 ^{21.7}		15
<i>Elaeagnus angustifolia</i>					
	100	100	100	100	100

Percentage frequency and modified fidelity index (phi coefficient × 100) superscripted are shown. Only species with frequency more than 25% and phi coefficient more than 0.25 in at least one column are included and shaded in grey (with phi > 50 in dark grey; with phi < 50 in light grey). Species within clusters are arranged in descending order of fidelity index

co-dominants. At the same time, stands of this association across the Black Sea coast are usually characterized by *Elytrigia elongata* dominance and a higher proportion of ruderal plants which can tolerate soil salinity. On the Azov Sea coast, stands of association grow in conditions of higher soil moisture that manifest in the frequent presence of some helophytes (*Bolboschoenus maritimus*, *Phragmites australis*, *Typha laxmannii*).

Cluster 2. Association ***Plantago arenariae-Elaeagnum angustifoliae* I. Solomakha, Vorobyov, Moysiyyenko ex Borsukevych, Iemelianova, Kolomyichuk ass. nov.** (Table 2, column 2) (Fig. 5, 7).

Synonyms: *Plantago arenariae-Elaeagnum angustifoliae* I. Solomakha et al. 2015 (art. 2b, 5); *Gypsophilo paniculatae-Elaeagnum angustifoliae* I. Solomakha et al. 2015 (art. 2b, 5).

Name-giving taxons: *Elaeagnus angustifolia* L., *Plantago arenaria* Waldst. & Kit.

Nomenclatural type. Holotypus: Karnatovska (2006: table B6.8, relevé 2) M. Karnatovska, Ukraine, Kherson Region, Kahovskyi district, Korsunka village, Kozacholagerska arena, plot size 25 m², cover of shrub layer 70%, cover of herb layer 60%. Braun-Blanquet scale – *Elaeagnus angustifolia* 4; *Achillea micrantha* 1; *Agropyron cristatum*

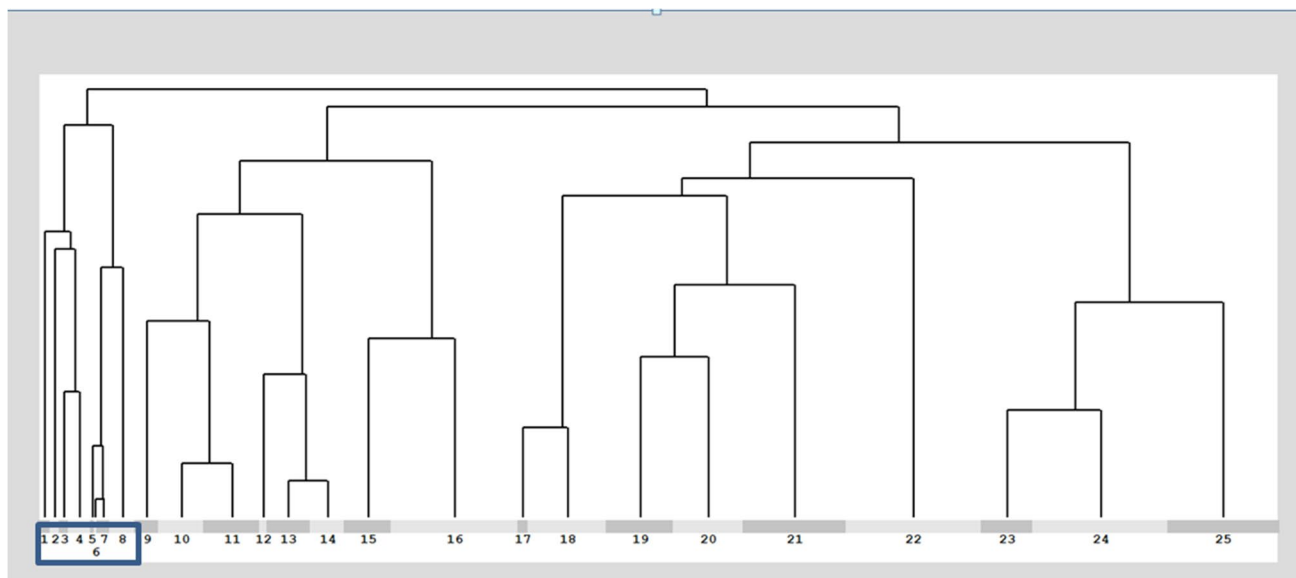


Fig. 3 Hierarchical dendrogram of vegetation classification using TWINSpan modified with three pseudospecies cut levels (0, 5, 25%) and Sørensen coefficient. A group of clusters lined in blue unites *Elaeagnus angustifolia*-dominated stands

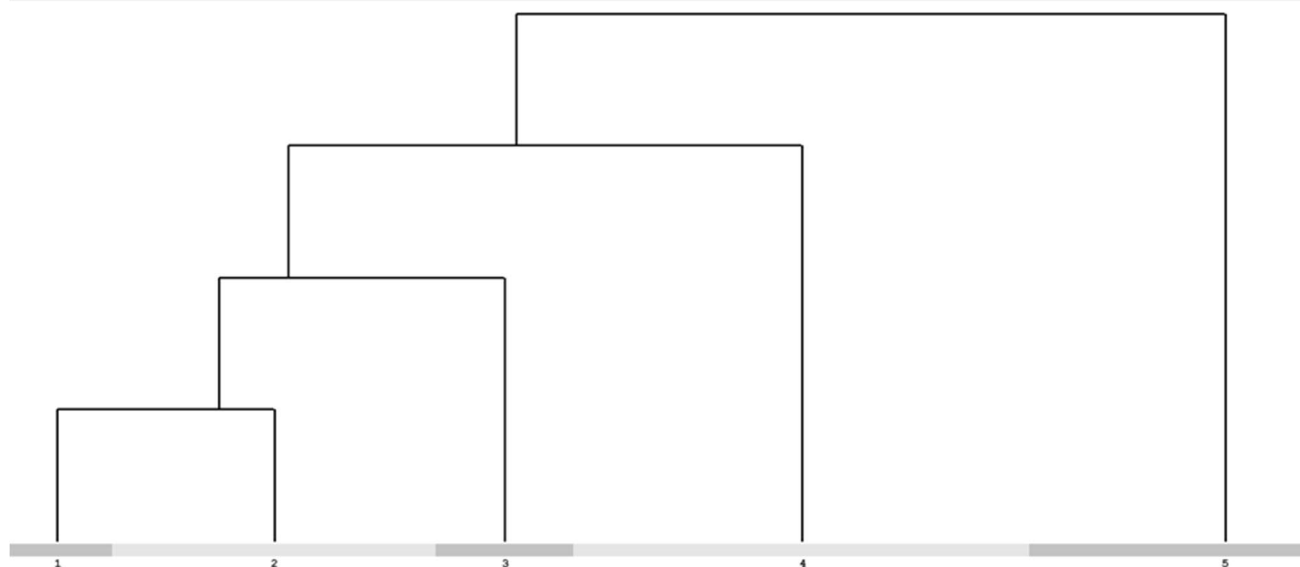


Fig. 4 Dendrogram of analyzed vegetation plots obtained by the beta-flexible clustering (beta = -0.25, Bray-Curtis dissimilarity, log-transformed percentage abundances). Clusters: 1 – *Lactuco tataricae-Elaeagnetum angustifoliae*, 2 – *Plantago arenariae-Elae-*

agnetum angustifoliae, 3 – *Balloto nigrae-Elaeagnetum angustifoliae*, 4 – *Leymo sabulosi-Elaeagnetum angustifoliae*, 5 – *Elytrigia repens-Elaeagnus angustifolia* community

Fig. 5 Distribution maps of vegetation units. Numbers mark: 1 – *Lactuco tataricae-Elaeagnetum angustifoliae*, 2 – *Plantago arenariae-Elaeagnetum angustifoliae*, 3 – *Balloto nigrae-Elaeagnetum angustifoliae*, 4 – *Leymo sabulosi-Elaeagnetum angustifoliae*, 5 – *Elytrigia repens-Elaeagnus angustifolia* community

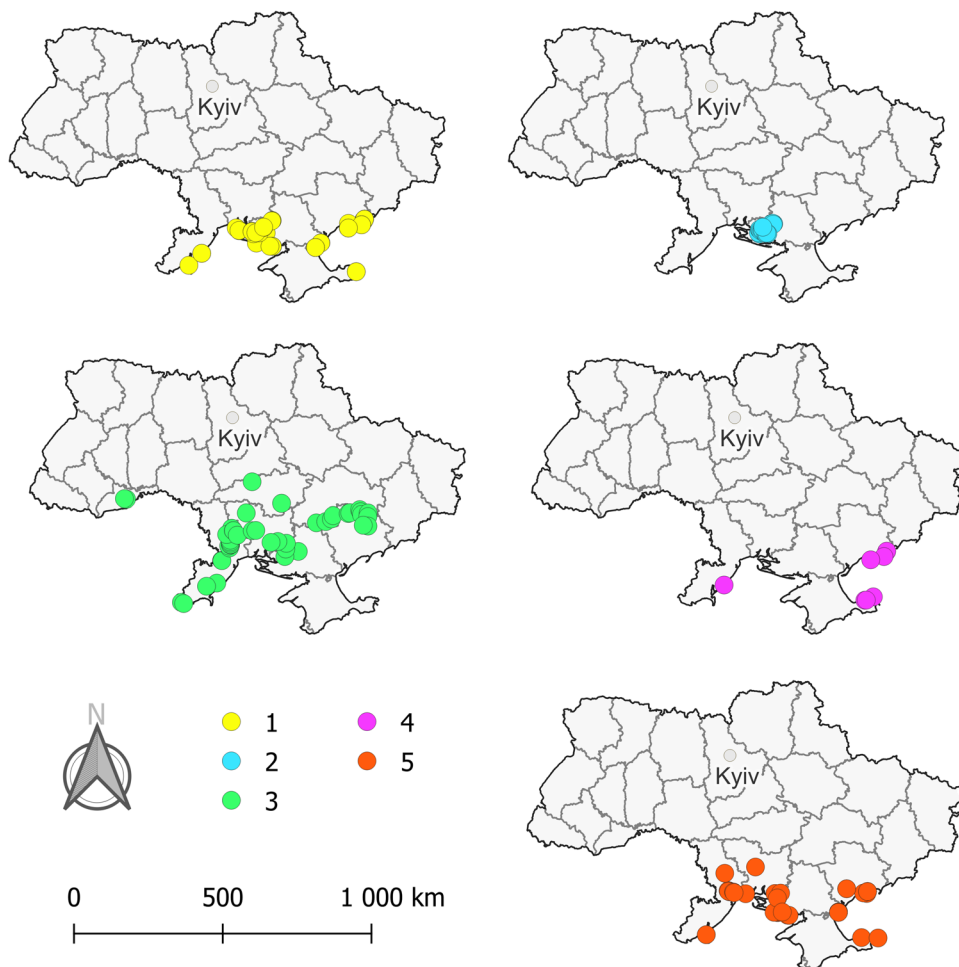




Fig. 6 Typical stands of association *Lactuco tataricae-Elaeagnetum angustifoliae* (near Vylkovo, Odessa Region. Foto by L. Borsuk-evych)



Fig. 7 Typical stands of association *Plantago arenariae-Elaeagnetum angustifoliae* (Oleshkivski Sands, Kherson Region. Foto by L. Borsuk-evych)

1; *Alyssum turkestanicum* 1; *Bassia laniflora* 1; *Bromus hordeaceus* 1; *Carex colchica* 1; *Chondrilla juncea* 1; *Crepis ramosissima* 1; *Cynodon dactylon* 1; *Dianthus platyodon* 1; *Euphorbia seguierana* 1; *Eryngium campestre* 1; *Erysimum montanum* 1; *Helichrysum arenarium* 1; *Herniaria polygama* 1; *Linaria genistifolia* 1; *Lomelosia argentea* 1; *Picris hieracioides* 1; *Plantago arenaria* 1; *Poa bulbosa* 1; *Polygonum arenarium* 1; *Silene subconica* 1; *Trifolium arvense* 1; *Xeranthemum annuum* 1; *Cuscuta monogyna* +; *Onosma arenaria* +; *Phelipanche purpurea* +; *Astragalus onobrychis* r.

Syntaxonomy note. For the first time this association was mentioned by Solomakha et al. (2015) on the territory of

northern Black Sea Region. The authors proposed this name on the basis of phytosociological data collected by M. Karnatovska, who described it as community *Elaeagnus angustifolia* var. *Pleconax subconica*. But they didn't provide any vegetation plots and didn't mention any nomenclatural type. Here, based on the relevés of M. Karnatovska (2006), we validate the name *Plantago arenariae-Elaeagnetum angustifoliae*. We also considered the association *Gypsophilo paniculatae-Elaeagnetum angustifoliae* I. Solomakha et al. 2015 as a synonym. Unfortunately, in this case, Solomakha et al. (2015) also didn't provide any phytosociological data or nomenclatural type. But analyzing the synoptic table and diagnostic species presented by authors in their book (Solomakha et al. 2015), we decided to include this community into *Plantago arenariae-Elaeagnetum angustifoliae* as a synonym.

Diagnostic species: *Achillea micrantha*, *Alyssum turkestanicum*, *Anisantha sterilis*, *Bassia laniflora*, *Bromus hordeaceus*, *Carex colchica*, *Centaurea breviceps*, *Chondrilla juncea*, *Crepis ramosissima*, *Cuscuta monogyna*, *Cynodon dactylon*, *Daucus carota*, *Dianthus platyodon*, *Erigeron canadensis*, *Eryngium campestre*, *Euphorbia seguierana*, *Gypsophila paniculata*, *Helichrysum arenarium*, *Herniaria polygama*, *Jacobaea borysthena*, *Linum austriacum*, *Lomelosia argentea*, *Onosma arenaria*, *Picris hieracioides*, *Plantago arenaria*, *Poa bulbosa*, *Polygonum arenarium*, *Secale sylvestre*, *Silene subconica*, *Trifolium arvense*, *Xeranthemum annuum*.

Constant species: *Calamagrostis epigejos*, *Elaeagnus angustifolia*, *Poa angustifolia*.

Dominant species: *Elaeagnus angustifolia*.

Structure and composition. This community represents the psammophytic stands of *E. angustifolia*. A shrub layer with a cover of 50–60% reaches in height of 6–7 m. The herb layer is often dense (covering 60 to 75%) and rich in species those are characteristic of classes *Koelerio-Corynephoretea canescentis* (*Calamagrostis epigejos*, *Chondrilla juncea*, *Cynodon dactylon*, *Polygonum arenarium*, *Silene subconica*) and *Helychriso-Crucianelletea maritimae* (*Carex colchica*, *Eryngium campestre*, *Lomelosia argentea*, *Onosma arenaria*, *Secale sylvestre*). Phytocoenoses are characterized by relatively low species diversity. Usually, 14–20 species are recorded in each plot, and only sometimes a number of species reach 28–32. Since the herb layer is situated under the sparse canopy of oleaster it often dries up and burns in summer. Cattle grazing causes the presence of weeds and alien species (*Ambrosia artemisiifolia*, *Carduus crispus*, *Centaurea diffusa*, *Erigeron canadensis*, *Tribulus terrestris*, *Xanthium strumarium*). In total, the flora of the association is composed of 65 taxa.

Synecology. Occurs on the lowland areas between dunes on sandy soils with low groundwater levels.



Fig. 8 Typical stands of association *Balloto nigrae-Elaeagnetum angustifoliae* (near Ostritsa, Chernivtsi Region. Foto by L. Borsukevych)

Distribution. The association for now is known only across Lower Dnipro Arenas (Oleshkivski Sands).

Cluster 3. Association *Balloto nigrae-Elaeagnetum angustifoliae* Borsukevych in Borsukevych, Iemeljanova, Kolomiychuk ass. nov. (Table 2, column 3; Table 3) (Fig. 5, 8).

Synonym: *Elaeagnetum angustifoliae* sensu Chynkina 2002 (art. 3o, 5).

Name-giving taxons: *Ballota nigra* L., *Elaeagnus angustifolia* L.

Nomenclatural type. Holotypus: L. Borsukevych (Table 3, relevé 38), 02.06.2019, Mykolaiv region, Veselynovo district, Novyi Gorodok village, Chychykliya River, 47.421667°N, 31.641667°E, plot size 100 m², cover of shrub layer 70%, cover of herb layer 90%. Braun-Blanquet scale – *Elaeagnus angustifolia* 4; *Elytrigia repens* 3; *Festuca rubra* 2; *Galium aparine* 2; *Lolium perenne* 2; *Poa pratensis* 2; *Polygonum aviculare* 2; *Schedonorus arundinaceus* 2; *Anisantha sterilis* 1; *Ballota nigra* 1; *Chenopodium album* 1; *Fallopia convolvulus* 1; *Hordeum murinum* 1; *Stellaria media* 1; *Achillea millefolium* +; *Ambrosia artemisiifolia* +; *Armoracia rusticana* +; *Cicuta virosa* +; *Cirsium vulgare* +; *Daucus carota* +; *Leonurus cardiaca* +; *Medicago falcata* +; *Plantago lanceolata* +; *Torilis japonica* +; *Veronica arvensis* +; *Viola arvensis* +; *Xanthium strumarium* +; *Dipsacus fullonum* r; *Lactuca tatarica* r; *Plantago major* subsp. *intermedia* r; *Prunus cerasifera* r; *Rhamnus cathartica* r; *Sambucus nigra* r.

Syntaxonomy note. We decided to include association described by T. Chynkina (2002) with the name *Elaeagnetum angustifoliae* as the synonym. Since vegetation plots are not presented in this or other papers of the author, we could not compare these units in detail and be completely

sure of the correctness of our syntaxonomical resolution. However, a comparison of the floristic composition according to the synoptic table presented in the Ph.D. thesis of T. Chynkina (2003) gave us reason to suppose that the community described in the Dnipro Estuary region was most similar to the association, which we describe under the name *Balloto nigrae-Elaeagnetum angustifoliae* in terms of species composition and ecological requirements.

Diagnostic species: *Achillea millefolium*, *Agrimonia eupatoria*, *Althaea officinalis*, *Arctium lappa*, *A. tomentosum*, *Aristolochia clematitis*, *Artemisia absinthium*, *Atriplex sagittata*, *Ballota nigra*, *Carex cuprina*, *C. hirta*, *C. spicata*, *Chaiturus marrubiastrum*, *Cirsium arvense*, *C. vulgare*, *Conium maculatum*, *Convolvulus arvensis*, *Cornus sanguinea*, *Cynoglossum officinale*, *Dactylis glomerata*, *Elytrigia repens*, *Epilobium hirsutum*, *Fallopia convolvulus*, *Festuca rubra*, *Fumaria officinalis*, *Galium aparine*, *G. mollugo*, *Geranium sylvaticum*, *Geum urbanum*, *Glechoma hederacea*, *Heracleum sphondylium*, *Hordeum jubatum*, *H. murinum*, *Humulus lupulus*, *Lactuca serriola*, *Lamium amplexicaule*, *Lathyrus pratensis*, *Leonurus cardiaca*, *Lepidium draba*, *Linaria vulgaris*, *Lithospermum officinale*, *Plantago major*, *Poa trivialis*, *Polygonum aviculare*, *Potentilla reptans*, *Prunus cerasifera*, *P. spinosa*, *Pyrus communis*, *Ranunculus acris*, *Rhamnus cathartica*, *Sambucus nigra*, *Schedonorus arundinaceus*, *Taraxacum officinale*, *Torilis japonica*.

Constant species: *Anisantha sterilis*, *Chenopodium album*, *Cichorium intybus*, *Daucus carota*, *Elaeagnus angustifolia*, *Poa angustifolia*.

Dominant species: *Anisantha sterilis*, *Elaeagnus angustifolia*, *Elytrigia repens*, *Galium aparine*.

Structure and composition. This vegetation unit represents the species-rich mesophyllous *E. angustifolia* stands that are characterized by a higher ratio of nitrophyllous plants. The shrub layer is dense (60–80%) and rich in species. Oleaster is often accompanied by *Acer negundo*, *A. tataricum*, *Amorpha fruticosa*, *Crataegus monogyna*, *Fraxinus pennsylvanica*, *Morus alba*, *M. nigra*, *Prunus avium*, *P. mahaleb*, *Pyrus communis*, *Salix × rubens*, *Tamarix gracilis*, *Ulmus laevis*, *U. minor*. The herb layer has a total cover of 60–90% and often is differentiated into two- or three sub-layers. The upper sub-layer consists of the dominant *Elytrigia repens* (with a cover of 40–60%) and other tall herbs, usually ruderal ones (*Anisantha sterilis*, *Arctium lappa*, *A. tomentosum*, *Artemisia absinthium*, *A. vulgaris*, *Cannabis sativa*, *Carduus acanthoides*, *Cichorium intybus*, *Daucus carota*, *Lactuca serriola*, *Solidago canadensis*, *Verbascum blattaria*). The middle sub-layer frequently consists of nutrient-demanding plants characteristic of the class *Artemisietea vulgaris* (*Ambrosia artemisiifolia*, *Aristolochia clematitis*, *Berteroa incana*, *Bryonia alba*, *Echium vulgare*, *Potentilla reptans*), together with representatives of *Epilobietea*

Table 3 Phytosociological relevés of the association *Ballota nigrae-Elaeagnretum angustifoliae*

No. of relevé	1	2	3	4	5	6	7	8	9	10	11	12
Field number	1785	1706	1716	1712	1702	1708	1704	1703	1654	1699	1697	1698
Plot size, m2	100	100	100	100	100	100	100	100	100	100	100	100
Altitude	116	13	9	19	29	18	5	3	4	5	5	5
Cover of shrub layer, %	60	50	40	40	50	60	60	55	50	70	70	50
Cover of herb layer, %	95	95	95	90	85	95	80	95	70	100	100	100
<i>Elaeagnus angustifolia</i>	4	3	3	3	3	4	4	4	4	4	4	4
<i>Elytrogia repens</i>	2	2	1	1	+	2	2	1	2	2	4	3
<i>Cirsium vulgare</i>	+	+	+	r	.	.	+	r	.	.	r	+
<i>Taraxacum officinale</i>	+	+	.	.	+	+	+	.	r	.	.	.
<i>Fallopia convolvulus</i>	.	+	1	.	.	+	+	.	.	.	+	.
<i>Ballota nigra</i>	+	3	+	+	.	1	.	+	+	2	1	+
<i>Galium aparine</i>	1	2	1	.	1	1	2	.
<i>Sambucus nigra</i>	1	.	.	.	r	+	1	.
<i>Conium maculatum</i>	1	+	+	+	.	+	.	.	.	2	1	2
<i>Schedonorus arundinaceus</i>	.	.	.	4	5	.	3	2	.	.	.	r
<i>Galium mollugo</i>	.	.	2	1	+	.	.	1	1	.	.	+
<i>Lepidium draba</i>	.	1	2	+	1	+	2	.	4	+	1	1
<i>Achillea millefolium</i>	+	.	+	+	.	+	.	+
<i>Rhamnus cathartica</i>	2	.	+	r	.	.
<i>Arctium lappa</i>	.	.	.	r	r
<i>Lactuca serriola</i>	+	.	.	+
<i>Fumaria officinalis</i>	+	.	+
<i>Potentilla reptans</i>	2
<i>Cynoglossum officinale</i>	+	.	+	+	.	r
<i>Torilis japonica</i>	.	.	.	1	.	.	.	+
<i>Cornus sanguinea</i>	+
<i>Althaea officinalis</i>	+	.	.	+	1	.	1	+
<i>Convolvulus arvensis</i>	.	+	+	.	.	+	.	1	+	.	+	.
<i>Carex cuprina</i>	+	.	.	.	+	.	1
<i>Chaiturus marrubiastrum</i>
<i>Carex hirta</i>
<i>Festuca rubra</i>	1	.	.	.
<i>Geum urbanum</i>	+	+
<i>Glechoma hederacea</i>
<i>Pyrus communis</i>	r
<i>Poa trivialis</i>

Table 3 (continued)

<i>Cirsium vulgare</i>	+	+	+	+	+	r	+	+	+	+	+	+	.
<i>Taraxacum officinale</i>	+	1	+	+	+	+
<i>Fallopia convolvulus</i>
<i>Ballota nigra</i>	+	.	.	2	2	1	2	2	2	2	2	2	2
<i>Galium aparine</i>	2	2	3	4	2	2	2	2	2	2	2	2	2
<i>Sambucus nigra</i>	.	+	.	.	.	1	1	1	1	1	1	1	.
<i>Conium maculatum</i>	.	.	.	+
<i>Schedonorus arundinaceus</i>	.	.	2	+	.	.	.	1	1	1	1	1	.
<i>Galium mollugo</i>	.	.	1	1
<i>Lepidium draba</i>	.	1	1	2	1	2	2	2	2	2	2	2	.
<i>Achillea millefolium</i>	.	.	+	+	+	+	+	+	+	+	+	+	+
<i>Rhannus cathartica</i>	.	.	.	r
<i>Arctium lappa</i>	.	.	+
<i>Lactuca serriola</i>	.	+	.	+	.	+	+
<i>Fumaria officinalis</i>
<i>Potentilla reptans</i>	1	1	.	.	.	1	1	.
<i>Cynoglossum officinale</i>	r
<i>Torilis japonica</i>	1
<i>Cornus sanguinea</i>
<i>Althaea officinalis</i>	+	+	2	+	+	+
<i>Convolvulus arvensis</i>	1	1	1	1	1	1	1	.
<i>Carex cuprina</i>	.	3
<i>Chaeturus marrubiastrum</i>	r	+
<i>Carex hirta</i>	2
<i>Festuca rubra</i>	2
<i>Geum urbanum</i>
<i>Glechoma hederacea</i>	3	1	.	2	2	.
<i>Pyrus communis</i>	.	.	1	r
<i>Poa trivialis</i>	1
<i>Hordeum murinum</i>
<i>Artemisia absinthium</i>	.	.	+	2	+
<i>Prunus cerasifera</i>
<i>Agrimonia eupatoria</i>	+
<i>Arctium tomentosum</i>	.	+
<i>Prunus spinosa</i>
<i>Ranunculus acris</i>	.	+
<i>Cirsium arvense</i>	.	.	+	1
<i>Leonurus cardiaca</i>
<i>Atriplex sagittata</i>
<i>Hordeum jubatum</i>
<i>Heraclium sphondylium</i>	.	.	+

Table 3 (continued)

Altitude	121	2	126	1	60	31	17	23	23	2	30	9
Cover of shrub layer, %	60	70	60	70	80	80	70	95	90	60	85	70
Cover of herb layer, %	100	90	100	95	100	100	100	90	95	100	95	100
<i>Elaeagnus angustifolia</i>	4	4	4	4	3	3	3	3	3	4	5	4
<i>Elytrigia repens</i>	4	3	4	3	2	4	4	1	1	.	2	2
<i>Cirsium vulgare</i>	.	+	+	.	+	+	.	r	r	.	r	+
<i>Taraxacum officinale</i>	+	.	+	+	+	.	.	+	+	r	+	+
<i>Fallopia convolvulus</i>	+	1	+	1	+	.	.	+	+	2	+	+
<i>Ballota nigra</i>	.	1	.	.	.	2	.	1	1	+	.	+
<i>Galium aparine</i>	2	2	.	1	2	4	4	5	5	5	4	5
<i>Sambucus nigra</i>	+	r	.	.	1	3	3	4	4	1	+	.
<i>Conium maculatum</i>	2	.	1	1	+	.	2
<i>Schedonorus arundinaceus</i>	.	2	2	1	.	.	1	1	1	.	2	4
<i>Galium mollugo</i>	1	.
<i>Lepidium draba</i>
<i>Achillea millefolium</i>	+	+	+	+	+	+
<i>Rhamnus cathartica</i>	.	r	+	.	.	.	r	.
<i>Arctium lappa</i>	r	r	+	.	.	+	r	.
<i>Lactuca serriola</i>	1	.	.	.	1	+	+	+	+	.	.	.
<i>Fumaria officinalis</i>	+	.	+	+	.	.	.	r	r	.	.	.
<i>Potentilla reptans</i>	.	.	.	2	.	.	.	1	1	1	2	.
<i>Cynoglossum officinale</i>	r	r	r	.	.	+
<i>Tortilis japonica</i>	.	+	1	+
<i>Cornus sanguinea</i>	2	+	.	+	+	.	.	+
<i>Althaea officinalis</i>	.	.	+	+	+
<i>Convolvulus arvensis</i>	+
<i>Carex cuprina</i>
<i>Chaiturus marrubiastrum</i>	+	+	.	.	.
<i>Carex hirta</i>	1	.	2	+	2	.
<i>Festuca rubra</i>	3	2	.	.	+
<i>Geum urbanum</i>	+	+	.	+	.
<i>Glechoma hederacea</i>	.	.	.	1	1
<i>Pyrus communis</i>	r	+
<i>Poa trivialis</i>	1	.	.	1	1	2	1	+
<i>Hordeum murinum</i>	.	1	.	+	.	.	.	2	2	.	.	.
<i>Artemisia absinthium</i>
<i>Prunus cerasifera</i>	.	r	.	.	.	+	.	r	r	.	.	.
<i>Agrimonia eupatoria</i>	.	.	1	.	.	r	.	r	r	.	.	.
<i>Arctium tomentosum</i>	.	.	+	+	+	.	.	r
<i>Prunus spinosa</i>	.	.	+
<i>Ranunculus acris</i>	.	.	1

Table 3 (continued)

Cerastium fontanum subsp. vulgare*Vicia villosa*

+

Locality 1 - Kirovograd region, Ustynivka rajon, Berezivka river near Lebedyne 48°07'33.4"N 032°35'59.0"E; 2 - Odessa region, Ivanovo rajon, Velykyy Kujalnyk river near Ivanovo 46°58'28.9"N 030°28'35.5"E; 3 - Mykolajiv region, Vesselynovy rajon, Chycklija river near Ivanovka 47°21'53.0"N 031°22'56.5"E; 4 - Odessa region, Mykolajiv rajon, Tylygul river near Strukovo 47°21'58.8"N 030°35'46.8"E; 5 - Odessa region, Ivanovo rajon, Malyy Kujalnyk river near Maslovo 46°53'08.7"N 030°26'13.3"E; 6 - Odessa region, Ivanovo rajon, Velykyy Kujalnyk river near Konopljane 47°03'04.0"N 030°28'16.9"E; 7 - Odessa region, Ivanovo rajon, Malyy Kujalnyk river near Baranovo 46°56'02.3"N 030°24'05.6"E; 8 - Odessa region, Ivanovo rajon, Malyy Kujalnyk river near Maslovo 46°52'42.5"N 030°26'21.0"E; 9 - Odessa region, Tatarbunary rajon, river near Zovtyj Jar 45°52'08.9"N 029°54'30.8"E; 10 - Odessa region, Blajivka rajon, ponds near Jasky 46°30'52.4"N 030°07'18.8"E; 11 - Odessa region, Blajivka rajon, ponds near Jasky 46°31'10.5"N 030°06'34.1"E; 12 - Odessa region, Blajivka rajon, ponds near Jasky 46°31'08.6"N 030°06'45.6"E; 13 - Odessa region, Ivanovo rajon, Velykyy Kujalnyk river near Ivanovo 46°57'53.4"N 030°28'56.5"E; 14 - Odessa region, Shyriajevo rajon, Velykyy Kujalnyk river near Petroverivka 47°15'29.7"N 030°19'04.4"E; 15 - Mykolajiv region, Snegirevka rajon, Ingulets river near Novotymofivka 46°50'48.2"N 032°46'26.7"E; 16 - Mykolajiv region, Snegirevka rajon, Ingulets river near Novotymofivka 47°00'40.1"N 032°47'55.7"E; 17 - Odessa region, Ivanovo rajon, Velykyy Kujalnyk river near Sherovo 47°00'50.9"N 030°28'28.0"E; 18 - Mykolajiv region, Arbuzyanka rajon, Pivdennyj Bug river near Pankratovo 47°51'31.3"N 031°07'58.4"E; 19 - Zaporizzia region, Gulijajpole rajon, Gajchur river near Pryluky 47°45'34.1"N 036°11'00.8"E; 20 - Odessa region, Remi rajon, channel near Novosilske 45°16'28.2"N 028°32'05.4"E; 21 - Zaporizzia region, Volniansk rajon, Mokra Moskovka river near Bekarivka 47°51'43.4"N 035°26'03.6"E; 22 - Mykolajiv region, Zovtneve rajon, Ingul river near Kalynivka 47°02'05.5"N 032°09'36.2"E; 23 - Zaporizzia region, Novomykolajivka rajon, Verhnia Tera river near Terstianka 47°53'05.7"N 035°53'00.1"E; 24 - Zaporizzia region, Novomykolajivka rajon, Gajchur river near Zarichne 47°51'13.8"N 036°11'44.0"E; 25 - Kherson region, Beryslav rajon, Dnipro river near Otradokamianka 46°46'41.2"N 033°17'42.0"E; 26 - Dnipropetrovsk region, Apostolovo rajon, channels near Dniepr near Grushivka 47°35'09.3"N 034°02'42.1"E; 27 - Dnipropetrovsk region, Tomakivka rajon, river near Topyla 47°47'14.3"N 034°44'21.8"E; 28 - Zaporizzia region, Zaporizzia rajon, Mokra Moskovka river near Natalivka 47°50'45.0"N 035°22'08.4"E; 29 - Mykolajiv region, Zovtneve rajon, river near Pervomajske 47°03'38.3"N 032°26'35.3"E; 30 - Dnipropetrovsk region, Nikopol rajon, channels near Dniepr near Prydniprovsk 47°37'14.8"N 034°26'08.3"E; 31 - Zaporizzia region, Pology rajon, Konka river near Pology 47°29'39.5"N 036°11'17.7"E; 32 - Zaporizzia region, Novomykolajivka rajon, Verhnia Tera river near Barvinivka 47°48'45.5"N 035°55'09.3"E; 33 - Zaporizzia region, Novomykolajivka rajon, Verhnia Tera river near Novoviktorivka 47°56'47.8"N 035°50'45.6"E; 34 - Odessa region, Tatarbunary rajon, Nerushaj river near Bashtanivka 45°46'40.0"N 48°14'24.2"N 026°09'25.9"E; 35 - Chernivtsi region, Gertsia rajon, bank of the Prut river near Ostritsa 48°15'06.2"N 026°04'13.9"E; 36 - Chernivtsi region, Novoselytsia rajon, bank of the Prut near Bojanivka river near Novyy Gorodok 47°22'19.8"N 031°31'45.0"E; 39 - Kirovograd region, Kropyvnytskyy rajon, Gruzka river near Kirovograd 48°35'46.6"N 032°16'00.9"E; 38 - Mykolajiv region, Veselynovy rajon, Chycklija river near Novyy Gorodok 47°22'19.8"N 031°31'45.0"E; 39 - Kirovograd region, Novomyrhorod rajon, Velyka Vys river near Myrolubivka 48°42'58.1"N 031°22'33.5"E; 40 - Kherson region, Tsurupynsk rajon, Konka river near Oleshky 46°37'53.6"N 032°44'05.6"E; 41 - Zaporizzia region, Gorihiv rajon, Konka river near Bilogirria 47°31'02.8"N 035°59'25.0"E; 42 - Odessa region, Ivanovo rajon, Velykyy Kujalnyk river near Konopljane 47°05'51.9"N 030°28'06.1"E; 43 - Dnipropetrovsk region, Tomakivka rajon, Zarianochka river near Zaria 47°41'37.3"N 034°40'14.7"E; 44 - Odessa region, Mykolajiv rajon, Tylygul river near Strukovo 47°21'56.7"N 030°36'08.3"E; 45 - Odessa region, Mykolajiv rajon, Tylygul river near Strukovo 47°21'56.7"N 030°36'08.3"E; 46 - Odessa region, Remi rajon, Orlovsk 45°18'30.8"N 028°26'20.2"E; 47 - Odessa region, Mykolajiv rajon, Tylygul river near Skosarivka 47°26'06.61"N 030°31'44.92"E; 48 - Odessa region, Berezivka rajon, Tylygul river near Chyzevo 47°14'16.8"N 030°45'39.3"E

angustifoliae (*Aegopodium podagraria*, *Alliaria petiolata*, *Anthriscus sylvestris*, *Chelidonium majus*, *Galium aparine*, *Geum urbanum*, *Impatiens parviflora*, *Leonurus cardiaca*, *Torilis japonica*) and *Molinio-Arrhenatheretea* (*Lolium perenne*, *Schedonorus arundinacea*, *S. pratensis*, *Vicia cracca*). The most frequent dominants of the bottom layer are climbing plants (*Convolvulus arvensis*, *Fallopia convolvulus*) and some low-growing herbs (*Polygonum aviculare*, *Argentina anserina*). In total, the floristic structure of the association is formed by 252 species (from 24 to 41 per plot).

Synecology. The stands prefer riparian zones along rivers (especially small rivers) with turf-meadow or loamy soils. Typically, stands are not flooded but concentrated in areas with high groundwater levels. Low salinity is also characteristic of stands' habitats.

Distribution. Commonly occurs in the river valleys in the steppe zone of Ukraine. We also observed two localities in the Chernivtsi region in the valley of the Prut River that indicate *E. angustifolia* spreading across other parts of Ukraine, where it not only has a stable population but also forms a plant community and appears as a coenoses-forming and diagnostic species.

Cluster 4. Association *Leymo sabulosi-Elaeagnetum angustifoliae* (Sokolova, Ermolaeva, Kolomiychuk 2021) Borsukevych, Iemelianova, Kolomiychuk ass. nov. et stat. nov. (Table 2, column 4) (Fig. 5, 9).

Basyonym: *Lactuco tataricae-Elaeagnetum angustifoliae artemisietosum arenariae* Sokolova, Ermolaeva, Kolomiychuk 2021.

Nomenclatural type (Sokolova et al. 2021): Page 64, table 1, relevé 8 (*holotypus*), Braun-Blanquet scale – *Artemisia arenaria* 3; *Elaeagnus angustifolia* 3; *Atriplex littoralis* +; *Crambe pontica* +; *Elytrigia obtusifolia* +; *Lactuca tatarica* +; *Limonium meyeri* +; *Leymus sabulosus* r.



Fig. 9 Typical stands of association *Leymo sabulosi-Elaeagnetum angustifoliae* (near Berdiansk, Zaporizhzhia Region. Foto by V. Kolomiychuk)

Syntaxonomy note. As we mentioned above, within the association *Lactuco tataricae-Elaeagnetum angustifoliae* T. Sokolova et al. (2021) described subassociation *Lactuco tataricae-Elaeagnetum angustifoliae artemisietosum arenariae*, which characterized a high proportion of species of coastal habitats (dunes and sandy beaches). Based on the results of our clustering and ordination analysis, we considered, that compared to the association's nomenclatural type as well as other data in our dataset, these stands are completely different. That is why we propose to change the status of this subassociation by raising it to the level of association and assigning the name *Leymo sabulosi-Elaeagnetum angustifoliae*.

Diagnostic species: *Alyssum hirsutum*, *Amaranthus retroflexus*, *Amorpha fruticosa*, *Anisantha tectorum*, *Artemisia arenaria*, *Bromus squarrosus*, *Cakile maritima* subsp. *euxina*, *Carex colchica*, *Centaurea odessana*, *Crambe maritima*, *Dichodon viscidum*, *Ephedra distachya*, *Eryngium maritimum*, *Gypsophila perfoliata*, *Jurinea longifolia*, *Lactuca tatarica*, *Leymus racemosus* subsp. *sabulosus*, *Linaria genistifolia*, *Melilotus albus*, *Silene conica*, *Tamarix tetrandra*, *Teucrium polium*, *Tragopogon dubius* subsp. *major*, *Verbascum pinnatifidum*, *Xanthium orientale* subsp. *riparium*.

Constant species: *Artemisia austriaca*, *Cynanchum acutum*, *Elaeagnus angustifolia*, *Phragmites australis*, *Secale sylvestre*.

Dominant species: *Elaeagnus angustifolia*.

Structure and composition. This type represents *E. angustifolia* species-poor stands that are located closest to the sea and affected by waves. Oleaster dominantes in the shrub layer (the cover does not exceed 50–60%) and grows to 1.5–2.5 m high. Xerophyllous woody species (e.g., *Ailanthus altissima*, *Hippophaë rhamnoides*, *Prunus cerasifera*, *Rosa canina*, *Tamarix gracilis*, *T. tetrandra*) accompany *E. angustifolia* in some areas. At most of the sites, the herb layer is rather sparse (almost never higher than 20–30%), slightly stratified into sub-layers, and poor in species. Elements of the classes *Ammophiletea* (*Argusia sibirica*, *Artemisia arenaria*, *Asparagus maritimus*, *Crambe maritima*, *Eryngium maritimum*, *Gypsophila perfoliata*, *Leymus racemosus* subsp. *sabulosus*, *Salsola soda*) and *Cakiletea maritimae* (*Cakile maritima* subsp. *euxina*, *Lactuca tatarica*, *Polygonum maritimum*, *Salsola tragus*) dominate here. Ruderal species (e.g., *Amaranthus retroflexus*, *Anisantha tectorum*, *Cichorium intybus*, *Diplotaxis muralis*, *Erigeron annuus*, *Marrubium peregrinum*, *Melilotus albus*, *Onopordum acanthium*, *Stellaria media*), as well as representatives of the classes of psamphytic vegetation (*Calamagrostis epigejos*, *Carex colchica*, *Centaurea odessana*, *Ephedra distachya*, *Euphorbia seguierana*, *Festuca beckeri*, *Poa bulbosa*, *Secale sylvestre*, *Seseli tortuosum*, *Silene conica*) are also frequent in the species composition of this association. The total number of species reaches 99, in some relevés – 11–15.

Synecology. The stands occur on spits of sandy or sandy-pebbly seacoasts. They prefer open, dry, well-lit habitats and often grow in contact with psammophytic coastal vegetation.

Distribution. This association was documented across the Azov Sea coast. Probable distribution of this association related to similar habitats across the Black Sea coast as well.

Cluster 5. *Elytrigia repens*-*Elaeagnus angustifolia* community (Table 2, column 5) (Fig. 5, 10).

Syntaxonomy note. *E. angustifolia* stands with the dominance of *Elytrigia repens* in the herb layer were described by Shibanova and Ovcharova (2021) in Altai Krai of Russia as an association *Elytrigio repentis-Elaeagnetum angustifoliae*. This vegetation tends to occupy meadow solonchak and meadow-chestnut solonetz soils. The species composition of this vegetation is characterized by a high proportion of graminoids and an abundant appearance of ruderal plants resulting from grazing pressure. In Ukraine similar plant community spreads on slightly saline soils and often affected by grazing. Despite vegetation association described by Russian authors differs by the presence of some Asian species, such as *Artemisia nitrosa*, *Glycyrrhiza uralensis*, *Hordeum brevisubulatum*, *Parasenecio hastatus*, *Sibbaldianthe bifurca*, etc., in general, species composition of both communities appears quite similar by the high frequency of steppe and ruderal species. Considering the significant geographical remoteness of Ukraine and Altai, as well as the low sharpness of this vegetation unit, we decided to assign such kind of the *E. angustifolia* stands status community so far. But it is evident that further studies of this vegetation in Ukraine and adjacent areas are necessary. With the appearance of new data, this issue could be resolved in the future.



Fig. 10 Typical stands of *Elytrigia repens*-*Elaeagnus angustifolia* community (near Tatarbunary, Odessa Region. Foto by L. Borsuk-evych)

Diagnostic species: *Achillea setacea*, *Atriplex tatarica*, *Elytrigia repens*, *Galium humifusum*, *Hordeum murinum* subsp. *leporinum*, *Jacobaea erucifolia* subsp. *arenaria*.

Constant species: *Anisantha sterilis*, *Cichorium intybus*, *Cirsium arvense*, *Elaeagnus angustifolia*, *Galium aparine*, *Poa angustifolia*.

Dominant species: *Elaeagnus angustifolia*, *Elytrigia repens*.

Structure and composition. Xerophyllous oleaster stands of overgrown character, with physiognomy determined by grasses (mostly *Elytrigia repens*). The canopy usually consists of *E. angustifolia* and thermophyllous shrubs such as *Crataegus monogyna*, *Gleditsia triacanthos*, *Morus alba*, *Prunus armeniaca*, *Rosa canina*, *R. corymbifera*, *R. majalis*, *Tamarix ramosissima*. The cover of the shrub layer is usually higher than 60%. The herb layer cover depends on the shrub layer density and can vary from 15 to 60%. *Elytrigia repens* is a significant dominant species of the herb layer. A species-rich group of xerophyllous steppe taxa (e.g. *Achillea setacea*, *Artemisia austriaca*, *Astragalus onobrychis*, *Bromopsis inermis*, *Eryngium campestre*, *Festuca valesiaca*, *Galium humifusum*, *Medicago falcata*, *Poa angustifolia*, *Salvia nutans*, *Thalictrum minus*) is characterized by high constancy in the community. It is also remarkable the occurrence of some ruderal plants – *Anisantha sterilis*, *Artemisia absinthium*, *Centaurea diffusa*, *Cichorium intybus*, *Cirsium arvense*, *Daucus carota*, *Lepidium draba*, *Tanacetum vulgare*. The number of species varies from 15 to 22 (the total count is 257).

Synecology. Stands prefer flat areas in river valleys with meadow and chestnut soils and chernozems.

Distribution. This community is widespread across the whole steppe zone of Ukraine.

Ecological ordination of vegetation units

The DCA ordination (Fig. 11) showed that identified units are distributed along the first ordination axis from the mesophytic association *Balloto nigrae-Elaeagnetum angustifoliae* (cluster 3) to xerophyllous stands of *Plantago arenariae-Elaeagnetum angustifoliae* (cluster 2). The main factors that determine the differentiation of vegetation dominated by *E. angustifolia* are climatic gradients – aridity-humidity of climate and thermoregime of the territory. That is why cluster 3 that corresponds to the mesophyllous stands (association *Balloto nigrae-Elaeagnetum angustifoliae*) is situated in the left part of the DCA diagram. This vegetation is more common in the northern part of the steppe zone where the amount of precipitation higher than in other parts of study area. Xerophytic and mesoxerophytic stands of the associations *Lactuco tataricae-Elaeagnetum angustifoliae* (cluster 1) and *Plantago arenariae-Elaeagnetum angustifoliae* (cluster 2) are located in the right part of the ordination

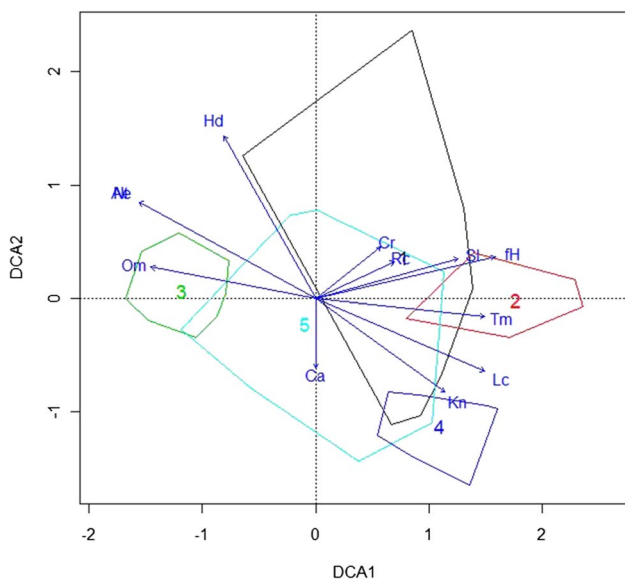


Fig. 11 DCA-ordination of the resulted clusters. Numbers in the centroids correspond to the cluster number in the text. Environmental vectors: Hd – moisture, fH – variability of damping, Rc – soil acidity, Sl – salt regime of a soil, Ca – carbonate content in a soil, Nt – nitrogen content in a soil, Ae – soil aeration, Tm – thermal regime, Om – humidity of climate (ombroregime), Kn – continentality of climate, Cr – cryoregime, Lc – light. Eigenvalues: 1st axis (DCA1) 0.5794, 2nd axis (DCA2) 0.3485

diagram. They are concentrated in areas with higher average annual temperatures and higher indicators of the radiation balance. It was also found that the salt regime of the soil causes the ecological separation of *Lactuco tataricae-Elaeagnetum angustifoliae* (cluster 1). *Elytrigio repentis-Elaeagnus angustifoliae* community (cluster 5) is concentrated in the central part of diagram and indicates its transition nature, not only by moisture, but also by other edaphic factors, including soil acidity and salinization. The DCA diagram revealed that the higher temperatures and more continental climate determine the ecological separation of coastal stands, which belong to the association *Leymo sabulosi-Elaeagnetum angustifoliae* (cluster 4). Almost all units are well separated from each other, with the exception of clusters 1 and 5, which we have interpreted as association *Lactuco tataricae-Elaeagnetum angustifoliae* and *Elytrigia repens-Elaeagnus angustifolia* community, and which occupy similar soil types across all study area.

Discussion

Elaeagnus angustifolia is one of the most widespread alien shrubs in Ukraine, especially in the steppe zone (Sudnik-Wójcikowska et al. 2009). We found that it took russian olive more than five decades to spread widely across the whole country, which reflects a pattern commonly observed for invasive horticultural plants (Ewel et al. 1999; Reichard and

White 2001). This time range was caused by a low rate of introduction at the beginning of the 20th century and significantly greater rates in the 1930 and 1940s due to the development of government afforestation programs. Another reason is the approximately ten-year period before newly established *E. angustifolia* individuals become reproductively mature and provide seeds for engraftment on the new areas (Lesica and Miles 2001). It was also noted by Katz and Shafroth (2003) that *E. angustifolia*, which was introduced to the western part of North America by 1900s, became prominent outside cultivated areas until 2–5 decades later (Olson and Knopf 1986). The same time lag was recorded in Altai Krai (Shibanova and Ovcharova 2021). Only in the last 20 years wild olive started to form its own natural stands and affect native vegetation. The shelterbelts (windbreaks, forest belts) and tree plantings in the immediate vicinity of settlements are the main sources of diaspores.

The current spread of *E. angustifolia* in Ukraine is related to anthropogenic landscape changes. In particular, a system of large artificial water reservoirs and the engineering of the Dnipro River system of dams were built to prevent uncontrolled flooding (Sudnik-Wójcikowska et al. 2009). Because the floodplain and alluvial regimes were completely transformed by such ecological changes, the environment, particularly plant and soil cover, was negatively affected. It caused the area of anthropogenically altered wetlands with high salinization levels to grow. Within drained areas, where water canals and riverbeds were before, young populations of *E. angustifolia* are actively expanded. Over the last 20 years changes in Ukrainian agriculture have led to decreased land cultivation and grazing intensity, especially in the steppe zone. As a result many abandoned agricultural fields became areas where *E. angustifolia* could spread unhindered, with the subsequent affection of various vegetation and habitat types (Protopopova et al. 2009). The active *E. angustifolia* invasion across the steppe zone is also related to the environment mesophytization in the region.

Excessively moist areas and ongoing floods are the main factors restricting the distribution of *E. angustifolia*. Yet, at the landscape level, *E. angustifolia* is mostly actively naturalizing on river floodplains and habitats near water bodies. In unsalted habitats with sufficient moisture, shrubs of *E. angustifolia* are in more favorable natural and climatic conditions and reach a height of 10 m. In saline or dry habitats, only low shrubs of *E. angustifolia* are noted. The species’ gravitation to the moist soil correlates with the results of research by American scientists (Katz and Shafroth 2003). In the USA, *E. angustifolia* has the status of a coastal species; its habitat is accompanied by river networks and frequently flooded meadows with rich soils.

In Ukraine, there is a definite trend towards the active expansion of *E. angustifolia* in different vegetation types, from sand steppes to halophytic and coastal grasslands (Protopopova et al. 2009). In general, *E. angustifolia* is a

consistent dominant in studied stands. In the shrub layer, which reaches in the height of 3–5 m and has a coverage of 50–80%, oleaster accompanied usually some native (*Cornus sanguinea*, *Fraxinus excelsior*, *Hippophaë rhamnoides*, *Prunus* spp., *Rosa* spp., *Salix cinerea*, *Ulmus glabra*, *U. pumila*) and alien (*Acer negundo*, *Ailanthus altissima*, *Amorpha fruticosa*, *Fraxinus pennsylvanica*, *Gleditsia triacanthos*, *Salix* × *fragilis*, *Ulmus pumila*) species. Because of the presence of tall grasses (such as *Calamagrostis epigejos*, *Leymus racemosus* subsp. *sabulosus*, *Phragmites australis*), the herb layer can reach a height of up to 1.5 m. It has a very diverse species composition that is provided by the co-occurrence of species that are characteristic of several vegetation classes, both natural and anthropogenic. The representatives of *Festuco-Brometea*, *Koelerio-Corynephoretea canescentis*, *Festuco-Puccinellietea*, *Epilobietea angustifoliae*, *Chenopodietaea*, *Artemisietea vulgaris* classes have a high frequency. Lianas – *Humulus lupulus*, *Parthenocissus quinquefolia* or *Vitis vinifera* – are also frequent. The moss layer has minor importance in most of the *E. angustifolia* stands.

In vegetation overviews, the classification of vegetation with *E. angustifolia* as well as its rank in the hierarchical classification system was quite debatable. Different authors classified the russian olive's community differently at the higher levels. Thus, some of the authors recognized this vegetation type to the class *Nerio-Tamaricetea* (Golub and Kuzmina 2004). This point of view was followed by some Ukrainian scientists (Dubyna et al. 2003; Solomakha et al. 2015). Other phytosociologists placed vegetation with *E. angustifolia* within floodplain forests (Chynkina 2002; Dubyna and Dziuba 2014). The authors of "Prodrome of Vegetation of Ukraine" (Dubyna et al. 2019) agreed on the necessity of including these plant communities in the class *Salicetea purpurea*. The authors argue that shrub communities with a diagnostic block including *Tamarix ramosissima*, *Hippophaë rhamnoides* and *Elaeagnus angustifolia*, in contrast to the oleander-tamarisk shrubs of the Mediterranean (*Nerio-Tamaricetea*) confined mainly to the delta areas of large rivers in the southern part of Ukraine. They are floristically and ecologically, as well as physiognomically, closer to the coenoses *Artemisio scopariae-Tamaricion ramosissimae* – an alliance distinguished by Romanian phytocoenologists (Simon and Dihoru 1963). However, the position of this alliance in the class *Salicetea purpureae*, which unites the vegetation of floodplain tree-scrub vegetation, require further research.

It is also necessary to pay special attention to relict extra-zonal temperate deciduous inland sandy woods, so-called "kolky", for understanding the syntaxonomical frame of *E. angustifolia* stands across this habitat type. Despite the quite similarity of species composition with the psammophytic stands of *Artemisio scopariae-Tamaricion ramosissimae* this vegetation is different by origin and environmental conditions. In Ukraine, for the first time this vegetation was mentioned by Umanets and Solomakha (1999), who

described a new alliance – *Asparago tenuifolii-Quercion roboris*, to unite all relict woodlands with *Betula borys-thenica*, *Populus tremula* and *Quercus robur* within inland sandy dunes of Ukraine. The authors placed this vegetation in the class *Salicetea purpurea*. The same syntaxonomical position for this vegetation was proposed by M. Karnatovska (2006), who provided its special study. In 2015 I. Solomakha and co-authors (2015) proposed a new vegetation class for these plant communities – *Dactylo glomerati-Populetea tremulae*. These syntaxonomical proposals weren't considered and were discussed in the current vegetation overview of Ukraine (Dubyna et al. 2019). That is why the status and syntaxonomical position of this vegetation is still unclear in Ukraine. In Europe, the most similar vegetation type belongs to the alliance *Fragario vescae-Populetales tremulae* within the class *Brachypodio pinnati-Betuletea pendulae*.

It is also necessary to conduct special research on an artificial plantations of oleaster. In this study, we did not include them in the analysis. We assume that they may belong to the class *Robinietaea* which represents artificial tree and shrub plantations. However, to confirm this hypothesis, it is necessary to conduct a separate analysis using data from the mentioned class.

Based on our results and taking into account the above syntaxonomic discussion, we propose the following syntaxonomic scheme of *E. angustifolia* stands in Ukraine:

SALICETEA PURPUREAE MOOR 1958

Tamaricetalia ramosissimae Borza et Boşcaiu ex Dolţu et al. 1980

Artemisio scopariae-Tamaricion ramosissimae Simon et Dihoru 1963

Lactuco tataricae-Elaeagnetum angustifoliae Sokolova, Ermolaeva, Kolomiychuk 2021

Balloto nigrae-Elaeagnetum angustifoliae Borsukevych in Borsukevych, Iemelianova, Kolomiychuk ass. nov.

Leymo sabulosi-Elaeagnetum angustifoliae Borsukevych, Iemelianova, Kolomiychuk ass. nov.

Elytrigia repens-Elaeagnus angustifolia community [Salicetea purpurea].

??? Class

??? Order

??? Alliance *Asparago tenuifolii-Quercion roboris* Umanets et Solomakha 1999.

Plantago arenariae-Elaeagnetum angustifoliae I. Solomakha, Vorobyov, Moysiienko ex Borsukevych, Iemelianova, Kolomiychuk ass. nov.

Conclusion

We provide the first classification of vegetation dominated by *Elaeagnus angustifolia* on the territory of Ukraine and identified four associations – *Lactuco tataricae-Elaeagnetum angustifoliae*, *Plantago arenariae-Elaeagnetum angustifoliae*, *Balloto nigrae-Elaeagnetum angustifoliae*, *Leymo sabulosi-Elaeagnetum angustifoliae* and *Elytrigia repens-Elaeagnus angustifolia* community. We showed that climate is the main factor that determines the distribution of wild olive stands within Ukraine. Our results give us the information we need to set up a monitoring system for *E. angustifolia*, which is one of the most aggressive invasive species in Ukraine.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

- Abbott RJ (1992) Plant invasions, interspecific hybridization and the evolution of new plant taxa. *Trends Ecol Evol* 7(12):401–405. [https://doi.org/10.1016/0169-5347\(92\)90020-C](https://doi.org/10.1016/0169-5347(92)90020-C)
- Akobundu IO, Agyakwa CW (1987) A handbook of west african weeds. International Institute of Tropical Agriculture, Ibadan
- Bermúdez de Castro F, Aranda Y, Schmitz MF (1990) Acetylenedereducing activity and nitrogen inputs in a bluff of *Elaeagnus angustifolia* L. *Orsis* 5:85–89
- Binggeli P (1996) A taxonomic, biogeographical and ecological overview of invasive woody plants. *J Veg Sci* 7:121–124. <https://doi.org/10.2307/3236424>
- Botta-Dukát Z, Chytrý M, Hájková P, Havlová M (2005) Vegetation of lowland wet meadows along a climatic continentality gradient in Central Europe. *Preslia* 77(1):89–111
- Botta-Dukát Z, Balogh L (2008) The most important invasive plants in Hungary. *Vacratot*
- Braun-Blanquet J (1964) *Pflanzensociologie. Grundzuge der Vegetationskunde*. 3 Aufl. Springer Verlag, Wien–New-York
- Brock JH (1998) Invasion, ecology and management of *Elaeagnus angustifolia* (russian olive) in the southwestern U.S.A. In: Starfinger U, Edwards K, Kowarik I, Williamson M (eds) *Plant Invasions: ecological mechanisms and human responses*. Backhuys Publishers, Leiden
- Brundu G, Richardson DM (2016) Planted forests and invasive alien trees in Europe: A Code for managing existing and future plantings to mitigate the risk of negative impacts from invasions. *NeoBiota* 30:5–47. <https://doi.org/10.3897/neobiota.30.7015>
- Cagiotti MR, Ranfa A, Marinangeli F, Maovaz M (1999) Invasive species in urban and suburban coenosis in central Italy. In: 5th International Conference of Ecology of Invasive Alien Plants, La Maddalena, Sardinia, Italy
- Campagnaro T, Brundu G, Burrascano S, Celesti-Grappow L, La Mantia T, Sitzia T, Badalamenti E (2022) Tree invasions in Italian forests. *For Ecol Manag* 521:120382. <https://doi.org/10.1016/j.foreco.2022.120382>
- Chopyk VI, Dudchenko LG, Krasnova AN (1983) *Dikorastyshchie poleznyie rasteniya Ukrainy*. Spravochnik. Kyiv, Naukova Dumka
- Calder ID, Dye P (2001) Hydrological impacts of invasive alien plants. *Land Use Water Resour Res* 7:1–12. <https://doi.org/10.22004/ag.econ.47855>
- Chynkina TB (2002) Syntaxonomy of the forest vegetation of the estuary of Dnipro. In: Yu.D. Kleopov and modern botanical science, Kyiv
- Chynkina TB Syntaxonomy and anthropogenic dynamic of the vegetation of the Dnipro Estuary Region., Dissertation MM (2003) Gryshko National Botanical Garden
- Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. *J Veg Sci* 13:79–90. <https://doi.org/10.1111/j.1654-1103.2002.tb02025.x>
- Davydova AO (2020) Phytodiversity of NNP “Dzharylhatsky”: structure, dynamics, protection. Dissertation, M.G. Kholodny Institute of Botany NAS of Ukraine
- Didukh YaP (2011) The ecological scales for the species of Ukrainian flora and their use in synphytoindication. Kyiv, Phytosociocentre
- Dubyna DV, Dziuba TP (2014) Syntaxonomical diversity of vegetation of the Dnipro River mouth region. VI. Classes *salicetea purpureae*, *Alnetea glutinosae* *Veg russia* 25:13–29
- Dubyna DV, Dziuba TP, Iemeljanova S, Bagrikova NO, Borysova OV, Borsukevych LM, Vynokurov DS, Gapon SV, Gapon YuV, Davydov DA, Dvoretzky TV, Didukh YaP, Zhmud OI, Kozyr MS, Konishchuk VV, Kuzemko AA, Pashkevych NA, Ryff LE, Solomakha VA, Felbaba-Klushyna LM, Fitsaylo TV, Chorna GA, Chorney II (2019). In: Iakushenko DM (ed) *Prodrome of Vegetation of Ukraine*. Shelyag-Sosonko YuR, Naukova dumka, Kyiv
- Dubyna DV, Ennan AA, Vakarenko LP, Dziuba TP, Shykhaleyeva GM, Kyrushkina HM (2020) *Encyclopedia of the Kuyalnyk estuary. Vegetation*. Odesa, “Astroprint”
- Dubyna DV, Shelyag-Sosonko YuR (1989) *Plavni Prychernomor'ya*. Kyiv, Naukova Dumka
- Dubyna DV, Shelyag-Sosonko YuR, Zhmud OI, Zhmud MY, Dvoretzkyi TV, Dziuba TP, Tymoshenko PA (2003) Danube biosphere reserve. Roslynni svit. Kyiv, Phytosociocentre
- Euro + Med 2006+ [continuously updated]: Euro + Med PlantBase – the information resource for Euro-Mediterranean plant diversity. Published at <http://www.europlusmed.org>. Accessed 28 June 2022
- Everitt JH, Lonard RI, Little CR (2007) *Weeds in South Texas and Northern Mexico*. Tech University Press, Texas
- Ewel JH, Dowd DJ, Bergelson J, Daehler CD, D'Antonio CM, Gomez LD, Gordon DR, Hobbs RJ, Holt A, Hopper KR, Hughes CE, LaHart M, Leakey RRB, Lee WG, Loope LL, Lorence DH, Louda SM, Lugo AE, McEvoy PB, Richardson DM, Vitousek PM (1999) Deliberate introductions of species: research needs. *Bioscience* 49:619–630
- Follstad Shah JJ, Harner MJ, Tibbets TM (2010) *Elaeagnus angustifolia* elevates soil inorganic nitrogen pools in riparian ecosystems. *Ecosystems* 13:46–61. <https://doi.org/10.1007/s10021-009-9299-4>
- Fridley JD, Frank DA (2017) Invasive plants accelerate nitrogen cycling: evidence from experimental woody monocultures. *J Ecol* 105(4):1105–1110. <https://doi.org/10.1111/1365-2745.12732>
- Golub VB, Kuzmina EG (2004) Community with the dominance of *Elaeagnus angustifolia* in the Lower Volga Valley. *Izvestiya NC RAN. Special issue* 2:317–322
- Golub VB, Kuzmina EG, Barmin AN (2002) Communities with *Elaeagnus angustifolia* predominating in the Lower Volga valley, Ukrainian. *Phytosoc Coll Ser* 1(18):86–91
- Google Earth. (n.d.). www.google.com/earth, Google Inc., Mountain View

- Haber E (1999) Invasive exotic plants of Canada, factsheet no 14: russian-olive. National Botanical Services, Ottawa
- Hennekens SM, Schaminée JHJ (2001) Turboveg, a comprehensive database management system for vegetation data. *J Veg Sci* 12:589–591. <https://doi.org/10.2307/3237010>
- Heywood VH (1993) Flowering plants of the World. Oxford University Press, New York
- Hill MO, Gauch H (1980) Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42:47–58. https://doi.org/10.1007/978-94-009-9197-2_7
- Holm L, Doll J, Holm E, Pancho J, Herberger J (1997) World weeds. Natural histories and distribution. Wiley, New York
- Holm LG, Plucknett DL, Pancho JV, Herberger TP (1977) The world's worst weeds. Distribution and biology. University Press, Honolulu
- Huddle JA, Awada T, Martin DL, Zhou X, Pegg SE, Josiah SJ (2011) Do invasive riparian woody plants affect hydrology and ecosystem processes? *Great Plains Res* 21:49–71
- Karnatovska M Flora and vegetation of Low Dnipro Arenas., Dissertation (2006) M.G. Gryshko National Botanical Garden
- Katz GL, Shafroth PB (2003) Biology, ecology, and management of *Elaeagnus angustifolia* L. (russian olive) in western North America. *Wetlands* 23:763–777. [https://doi.org/10.1672/0277-5212\(2003\)023\[0763:BEAMOE\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2003)023[0763:BEAMOE]2.0.CO;2)
- Kettunen M, Genovesi P, Gollasch S, Pagad S, Starfinger U, ten Brink P, Shine C (2009) Technical support to EU strategy on invasive species (IAS) – Assessment of the impacts of IAS in Europe and the EU (final module report for the European Commission). Institute for European Environmental Policy (IEEP), Brussels
- Klein P, Smith CM (2021) Invasive Johnsongrass, a threat to native grasslands and agriculture. *Biologia* 76:413–420. <https://doi.org/10.2478/s11756-020-00625-5>
- Knopf FL, Olson TT (1984) Naturalization of russian-olive: implications to Rocky Mountain wildlife. *Wildl Soc Bull* 12:289–298
- Kokhno NA (1986) Derevyia i kustarniki kultiviruemye v Ukraini SSR. Pokrytosemennye. Naukova dumka, Kiev
- Le Maitre DC, Gush MB, Dziki S (2015) Impacts of invading alien plant species on water flows at stand and catchment scales. *AoB PLANTS* 7:plv043. <https://doi.org/10.1093/aobpla/plv043>
- Lesica P, Miles S (1999) Russian olive invasion into cottonwood forests along a regulated river in north-central Montana. *Can J Bot* 77:1077–1083
- Lesica P, Miles S (2001) Natural history and invasion of russian olive along eastern Montana rivers. *West N Am Nat* 61:1–10
- Levine JM, Vilà M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc R Soc Lond* 270:775–781. <https://doi.org/10.1098/rspb.2003.2327>
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710. [https://doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)
- Manchester SJ, Bullock JM (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. *J Appl Ecol* 37:845–864. <https://doi.org/10.1046/j.1365-2664.2000.00538.x>
- Marynych OM (ed) (1993) Geographical encyclopedia of Ukraine. Kyiv, Ukrainian Encyclopedia
- Marynych OM, Shyshchenko PG (2005) Physical geography of Ukraine. Kyiv, Znannya
- Matyakin GI (1952) Lesnyie polezashchitnyie polosy i mikroklimat. Moskow, Geographfiz
- McCary MA, Mores R, Farfan MA, Wise DH (2016) Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: a meta-analysis. *Ecol Lett* 19(3):328–335. <https://doi.org/10.1111/ele.12562>
- McCune B, Mefford MJ (2006) PC-ORD. Multivariate analysis of ecological data. Version 5. MjM Software, Glenden Beach, Oregon, U.S.A
- Medvecká J, Kliment J, Májeková J, Halada L, Zaliberová M, Gojdičová E, Feráková V, Jarolímek I (2012) Inventory of the alien flora of Slovakia. *Preslia* 84:257–309
- Minchenko NF (1974) *Elaeagnus* L. In: Rubtsov LI (ed) Trees and shrubs. Spravochnik. Kyiv, Naukova Dumka
- Mineau MM, Baxter CV, Marcarelli AM (2011) A non-native riparian tree (*Elaeagnus angustifolia*) changes nutrient dynamics in streams. *Ecosystems* 14:353–365. <https://doi.org/10.1007/s10021-011-9415-0>
- Mucina L, Bültmann H, Dierßen K, Theurillat JP, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, Gavilán García R, Chytrý M, Hájek M, Di Pietro R, Iakushenko D, Pallas J, Daniéls FJA, Bergmeier E, Santos Guerra A, Ermakov N, Valachovič M, Schaminée JHJ, Lysenko T, Didukh YaP, Pignatti S, Rodwell JS, Capelo J, Weber HE, Solomeshch A, Dimopoulos P, Aguiar C, Hennekens SM, Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Appl Veg Sci* 19:3–264. <https://doi.org/10.1111/avsc.12257>
- Muñoz AA, Cavieres LA (2008) The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. *J Ecol* 96:459–467. <https://doi.org/10.1111/j.1365-2745.2008.01361.x>
- National Atlas of Ukraine (2007) Rudenko LG (Ed) Kyiv, DNPV “Kartographiya”
- Norenko KM (2016) Border of areal of *Elaeagnus angustifolia* L. in the Right Bank of Dnipro in Ukraine. *Naukova zapysky NaUKMA* 184:57–60
- Olson TE, Knopf FL (1986) Naturalization of russian olive in the western United States. *West J Appl For* 1:65–69
- Osada T (1997) Colored illustrations of naturalized plants of Japan. Hoikusha, Osaka, Japan
- Palimpstov I (1855) Slovar selskohoziaystvennykh rasteniy. Odessa
- Pearce CM, Smith DG (2009) Rivers as conduits for long-distance dispersal of introduced weeds: example of russian olive (*Elaeagnus angustifolia*) in the Northern Great Plains of North America. In: Van Devender TR, Espinosa-García FJ, Harper-Lore BL, Hubbard T (eds) Invasive plants on the move: Controlling them in North America. Arizona-Sonora Desert Museum, Tucson, AZ
- Pendleton RL, Pendleton BK, Finch D (2011) Displacement of native riparian shrubs by woody exotics: effects on arthropod and pollinator community composition. *Environ Nat Resour J* 16:25
- Pimentel D, McNair S, Janecka J, Wightman J, Simmonds C, O'Connell C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agric Ecosyst Environ* 84(1):1–20. [https://doi.org/10.1016/S0167-8809\(00\)00178-X](https://doi.org/10.1016/S0167-8809(00)00178-X)
- POWO (2022) Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on <http://www.plantsoftheworldonline.org>. Accessed 05 Dec 2022
- Pretty Paint-Small V (2013) Linking culture, ecology and policy: the invasion of Russian olive (*Elaeagnus angustifolia* L.) on the Crow Indian Reservation, south-central Montana, USA. Ph.D. dissertation. Fort Collins, Colorado State University
- Prokudin YuN (Ed) (1987) Opredelitel vyshych rasteniy Ukrainy. Kyiv, Naukova Dumka
- Protopopova VV, Shevera MV, Melnik RP (2006) The history of introduction and present distribution of *Elaeagnus angustifolia* L. in the Black Sea Region of Ukraine. *Chornomorskyi Bot J* 2:5–13. <https://doi.org/10.14255/2308-9628/06.22/1>
- Protopopova VV, Shevera MV, Mosyakin SL, Solomakha VA, Solomakha TD, Vasilyeva TV, Petryk SP (2009) Invasive plants in

- the flora of the Northern Black Sea Region (Ukraine). Phytosociocentre, Kyiv
- Pyšek P, Danihelka J, Sádlo J, Chrtěk J, Chytrý M, Jarošík V, Kaplan Z, Krahulec F, Moravcová L, Pergl J, Štajerová K, Tichý L (2012a) Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. *Preslia* 84:155–255
- Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012b) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Glob Change Biol* 18:1725–1737. <https://doi.org/10.1111/j.1365-2486.2011.02636.x>
- Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and health. *Annu Rev Environ Resour* 35:25–55. <https://doi.org/10.1146/annurev-envir-033009-095548>
- Raju RA (1998) Prevalent weed flora in Peninsular India. Allied Publishers, New Delhi
- Reichard SH, White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. *Bioscience* 51:103–112. [https://doi.org/10.1641/0006-3568\(2001\)051\[0103:HAPOI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0103:HAPOI]2.0.CO;2)
- Reynolds LV, Cooper DJ (2010) Environmental tolerance of an invasive riparian tree and its potential for continued spread in the south-western U.S. *J Veg Sci* 21:733–743. <https://doi.org/10.1111/j.1654-1103.2010.01179.x>
- Richardson DM (1998) Forestry trees as invasive aliens. *Conserv Biol* 12:18–26
- Richardson DM (2011). In: Simberloff D, Rejmánek M (eds) *Trees and shrubs. Encyclopedia of biological invasions*. University of California Press, Berkeley
- Richardson DM, Rejmánek M (2004) Invasive conifers: a global survey and predictive framework. *Divers Distrib* 10:321–331
- Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species – a global review. *Divers Distrib* 17:788–809. <https://doi.org/10.1111/j.1472-4642.2011.00782.x>
- Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. *J Veg Sci* 20:596–602. <https://doi.org/10.1111/j.1654-1103.2009.01062.x>
- Shafroth PB, Auble GT, Scott ML (1995) Germination and establishment of the native plains cottonwood (*Populus deltoides* Marshall subsp. *monilifera*) and the exotic russian-olive (*Elaeagnus angustifolia* L.). *Conserv Biol* 9:1169–1175
- Shevchyk VL, Solomakha VA, Voytuk YuO (1996) Syntaxonomy of vegetation and list of flora of the Kaniv National Reserve. *Ukrain Phytosociolog Collect* 1(4):1–119
- Shibanova AA, Ovcharova NV (2021) Plant communities with naturalized *Elaeagnus angustifolia* L. as a new vegetation element in Altai Krai (Southwestern Siberia, Russia). *Acta Biol Sibirica* 7:49–61. <https://doi.org/10.3897/abs.7.e58204>
- Simon T, Dihoru G (1963) Die Tamarix-auen am Flusse Buzău in Rumänien. *Annales Universitatis Scientiarum de Rolando Eötvös Nominatae, Sectio Biologica* 6:159–173
- Simons SB, Seastedt TR (1999) Decomposition and nitrogen release from foliage of cottonwood (*Populus deltoides*) and russian-olive (*Elaeagnus angustifolia*) in a riparian ecosystem. *Southwest Nat* 44:256–260
- Smetana MG (2002) Syntaxonomy of steppe and ruderal vegetation of Kryvorizhia. *Kryvyi Rig*
- Sokolova TA, Ermolaeva OYu, Kolomiychuk VP (2021) Tree and shrub vegetation of Tuzla Island (Kerch Strait. *Sci South Russia* 17(4):61–71. <https://doi.org/10.7868/S25000640210407>
- Solomakha IV, Vorobyov YeO, Moisiyenko II (2015) Vegetation of forest and shrubs of the Northern Black Sea region. Kyiv, Phytosociocentr
- Sørensen TJ (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation of danish commons. *Kongelige Danske Videnskabernes Selskab Biologiske Skrifter* 5(4):1–34
- Stannard M, Ogle D, Holzworth L, Scianna J, Sunleaf E (2002) History, biology, ecology, suppression and revegetation of russian-olive sites (*Elaeagnus angustifolia* L.). USDA – National Resources Conservation Service, Boise, ID, USA
- Stohlgren T, Pyšek P, Kartesz J, Nishino M, Pauchard A, Winter M, Pino J, Richardson DM, Wilson RJU, Murray BR, Phillips ML, Ming-Yang L, Celesti-Grapow L, Font X (2011) Widespread plant species: natives versus aliens in our changing world. *Biol Invasions* 13:1931–1944. <https://doi.org/10.1007/s10530-011-0024-9>
- Sudnik-Wójcikowska B, Moisiyenko I, Slim P, Moraczewski I (2009) Impact of the invasive species *Elaeagnus angustifolia* L. on vegetation in pontic desert steppe zone (Southern Ukraine). *Pol J Ecol* 57(2):269–281
- Tichý L (2002) JUICE, software for vegetation classification. *J Veg Sci* 13:451–453. <https://doi.org/10.1111/j.1654-1103.2002.tb02069.x>
- Theurillat JP, Willner W, Fernández-González F, Bültmann H, Čarni A, Gigante D, Mucina L, Weber HE (2021) International Code of Phytosociological Nomenclature. 4th edition. *Appl Veg Sci* 24:e12491. <https://doi.org/10.1111/avsc.12491>
- Tokarska-Guzik B (2005) The establishment and spread of alien plant species (kenophytes) in the flora of Poland. *Prace Nauk. Uniw*
- Tsvelev NN (2002) About genera *Elaeagnus* (Elaeagnaceae) in russia and bordered countries. *Bot J* 87(11):74–86
- Tsvelev NN (2004) *Elaeagnus* L. In: Tsvelev NN (Ed) *Flora of the Eastern Europe*. Moscow-Sankt-Peterburg
- Umanets OY, Solomakha IV (1999) Syntaxonomy of vegetation of the Black Sea Biosphere Reserve. III. Ivano-Rybalchanska site. *Ukrainian Phytosociological Collection, Series A* 14:84–102
- Venables WN, Smith DM, R Development Core Team (2008) An Introduction to R: Notes on R, A Programming Environment for Data Analysis and Graphics. <https://onlinebooks.library.upenn.edu/webbin/book/lookupid?key=olbp44950>
- Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Front Ecol Environ* 8:135–144. <https://doi.org/10.1890/080083>
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, 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. *Ecol Lett* 14(7):702–728. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology* 75:1861–1876
- Wagner V, Chytrý M, Jiménez-Alfaro B, Pergl J, Hennekens S, Biurrun I, Knollová I, Berg C, Vassilev K, Rodwell JS, Škvorc Ž, Jandt U, Ewald J, Jansen F, Tsiripidis I, Botta-Dukát Z, Casella L, Attorre F, Rašomavičius V, Čušterevska R, Schaminée JHJ, Brunet J, Lenoir J, Svenning J-C, Kačič Z, Petrášová-Šibíková M, Šilc U, García-Mijangos I, Campos JA, Fernández-González F, Wohlgemuth T, Onyschenko V, Pyšek P (2017) Alien plant invasions in european woodlands. *Divers Distrib* 23:969–981. <https://doi.org/10.1111/ddi.12592>
- Wainright CA, Muhlfelda CC, Elsera JJ, Bourretd SL, Devlina SP (2021) Species invasion progressively disrupts the trophic structure of native food webs. *PNAS* 118(45):e210217911. <https://doi.org/10.1073/pnas.210217911>

- Weber HE, Moravec J, Theurillat J-P (2000) International Code of Phytosociological nomenclature. *J Veg Sci* 11:739–768. <https://doi.org/10.1111/avsc.12491>
- Williams PA, Cameron EK (2006) Creating gardens: the diversity and progression of european plant introductions. In: Allen RB, Lee WG (eds) *Biological invasions in New Zealand*. Springer-Verlag, Berlin
- Wilson R, Bernards M (2009) *Weeds of Nebraska: russian olive biology, identification, distribution, control*. University of Nebraska-Lincoln Extension Publication
- Winter M, Schweiger O, Klotz S, Nentwig W, Andriopoulos P, Arinoutsou M, Basnou C, Delipetrou P, Didziulis V, Hejda M, Hulme PE, Lambdon PW, Pergl J, Pysek P, Roy DB, Kühn I (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proc Natl Acad Sci USA* 106(51):217–221. <https://doi.org/10.1073/pnas.0907088106>
- Zgurovskaya LN (1984) *Raskazy o dereviakh Kryma*. Simpheropol, Tavria
- Zitzer SF, Dawson JO (1989) Seasonal changes in nodular nitrogenase activity of *Alnus glutinosa* and *Elaeagnus angustifolia*. *Tree Physiol* 5:185–194

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.