Research Article

Asclepias syriaca L. (Apocynaceae) and its invasiveness in the southern part of the Boreal region of Europe – evidence from Lithuania

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Abstract

Common milkweed, *Asclepias syriaca* L. (Apocynaceae), has become a problematic invasive species in southern regions of Europe and has been added to the list of invasive alien species of concern of the European Union. For a long time, this alien species had not been considered a potential invader in the northern regions of the continent. This study is an attempt to evaluate the potential invasiveness of *A. syriaca* in the southern part of the Boreal biogeographic region of Europe as by observations made in Lithuania. To this point, the plant has been recorded from 38 sites and the total area occupied by its stands is about 1.29 ha in the country. The size of *A. syriaca* stands at the different sites varies significantly, from a few individuals to stands covering an area of 0.74 ha. Most frequently, *A. syriaca* occupies anthropogenic herb stands, unmanaged xeric and mesic grasslands, and was recorded from arable field habitats. In eight of the 17 studied sites *A. syriaca* sets fruit and produces viable seeds. We suppose that stands setting fruit and producing viable seeds are represented by individuals of several genotypes, whereas some quite large stands are represented by vegetative descendants of one single individual and, therefore, fruit set is absent. Although most of the currently known stands are relics of former cultivation or escaped from areas of recent cultivation, at one site it is considered to be of seed origin. As by the quite large number of *A. syriaca* localities in Lithuania, its intense vegetative spread, and production of fruits and viable seeds, we predict further future spread and invasion in Lithuania. Thus, *A. syriaca* should also be treated as a potentially invasive species in other locations of the southern part of the Boreal biogeographical region of Europe.

Key words: distribution, fruit set, habitats, reproduction, seed germination

Introduction

The intentional introduction of alien plants has become a main source of the recently increasing number of invasive species throughout the world (Keller et al. 2011; Heywood and Sharrock 2013; Pergl et al. 2016). These plants spend a certain period under human care before starting to spread and becoming naturalized and, sometimes, even invasive (Richardson et al. 2000). However, the period from the introduction to the start of naturalization and invasion varies depending on the species and several factors, including propagule pressure, abiotic filters, plant traits, etc. (Theoharides and Dukes 2007). Therefore, it is important to understand

the patterns of the spread, the population dynamics, particular sexual and asexual reproductive features, habitat preferences, and other ecological requirements of the invasive or potentially invasive species (Pergl et al. 2020). This understanding is particularly important to define the strategy and measures for the eradication and control of an invasive species (Pluess et al. 2012).

The common milkweed, *Asclepias syriaca* L. (Apocynaceae), is a rhizomatous, 60–200-cm tall perennial herb, producing a white latex containing several toxic cardenolides. The plant is native to North America. In its native range it grows in well-drained sandy, clayey, or rocky calcareous soils along the banks of lakes, ponds, and waterways, in prairies and at forest margins (Bhowmik and Bandeen 1976; Bhowmik 1994; Hartzler and Buhler 2000). *Asclepias syriaca* was introduced to Europe in the 17th century (Bagi 2008) and for a long time it was cultivated mainly for ornamental purposes, as a melliferous plant, and was later propagated as a potential fiber plant, for biofuel, and latex production (Follak et al. 2018). Escaped plants first were noticed in the mid-19th century and since the mid-20th century it has started to spread intensively into natural, seminatural, and human-made habitats and has become an invasive species mainly in Western and Central Europe (Bagi 2008; Paukova et al. 2014; Tokarska-Guzik and Pisarczyk 2015; Dvirna 2018). The most widespread and invasive populations of this species occur in areas of southern parts of Central Europe (Bagi 2008; Konstantinović et al. 2008; Petrova et al. 2013; Dvirna 2018; Follak et al. 2018). Because of its invasiveness and significant negative impact on native habitats and its threat to agricultural lands, as by the provisions of the Regulation (EU) No. 1143/2014 of the European Parliament and of the Council of 22 October 2014 on Invasive Alien Species, *A. syriaca* was included in the list of the invasive alien species of (European) Union concern (EU 2017/1263).

According to the risk assessment of *Asclepias syriaca* for Europe (Tokarska-Guzik and Pisarczyk 2015), the invasion of this species is posing a threat to the stability of several natural ecosystems in the Continental, Mediterranean, and Pannonian biogeographic regions of Europe (Tokarska-Guzik et al. 2012). Within the Boreal biogeographic region of Europe, this species has been considered as naturalized in Lithuania only (Gudžinskas 1998; Gudžinskas et al. 2018). It has been recorded quite recently in Sweden (first noticed in 2005) where it is treated as potentially invasive (NOBANIS 2020; SLU Artdatabanken 2021) and in Latvia (first recorded in 2012) it is currently rated as a casual alien (Nāburga and Evarts-Bunders 2019).

In Lithuania, *Asclepias syriaca* appears to have been introduced in the first half of the 19th century (Dagys 1938; Pabrėža 2009), its spread having started in the second half of the 20th century, and was later classified as a locally naturalized species (Gudžinskas 1994, 1998). Over several of the last decades *A. syriaca* has been reported to occur at various sites in southern

Lithuania but had not been considered to pose a threat of invasion, because sexual reproduction had not been observed (Gudžinskas 1998; Gudžinskas et al. 2018). Thus, it appears now that Lithuania is the northeastern limit of its current naturalized range in Europe and, therefore, it is urgent to evaluate the plant's distribution, size of populations, occupied habitats, vectors of dispersal, and reproductive characteristics. These characteristics are particularly important for modelling the possible further spread of the species in the southern part of the Boreal biogeographical region of Europe.

The aim of this study was to estimate the potential of *Asclepias syriaca* invasion in Lithuania, i.e., in the southern part of the Boreal biogeographic region of Europe (Cervellini et al. 2020). In this study we aimed to find answers to a series of questions: What is the current distribution of *Asclepias syriaca* in Lithuania? How large are the areas occupied by its stands in the country? Which types of habitats does this species prefer and which could be affected in the future? In which sites does *A. syriaca* produce fruits and how many fruits are produced by individual shoots? Are the produced seeds viable and how might they facilitate the further spread of this species?

Materials and methods

Distribution

Our studies on the distribution, size of stands, and habitats occupied by *A. syriaca* were performed from June to October of 2018–2020. Data from previously published studies on the distribution of *A. syriaca* was also analyzed. During the study we visited previously known localities and searched for new sites using information obtained from various sources (professional botanists, staff of protected areas, citizens, etc.). Some localities were discovered by the authors while implementing other research projects.

A distribution map of *A. syriaca* in Lithuania was compiled applying a system of grid cells which were arranged according to geographical coordinates with sides of 6′ of latitude and 10′ of longitude (Gudžinskas 1993). All localities recorded in the same grid cell were marked by one symbol on the map. We used data of our studies and data of herbarium specimens deposited at the Herbarium of the Institute of Botany of the Nature Research Centre, Vilnius (BILAS). Samples of *A. syriaca* collected during this research were deposited at the same herbarium. A list of currently known localities for *A. syriaca* in Lithuania is presented in the Supplementary material (Table S1). The localities where this species is being cultivated were excluded from this study.

Stand size

The areas of small stands were measured using measurement tape. The area occupied by large stands of *A. syriaca* was calculated using online software provided from the Spatial Information Portal of Lithuania

(www.geoportal.lt) according to geographical coordinates established at certain points of the stand perimeter. The size of stands at all sites represents their state as of 2018–2020.

Habitats

Habitat types of *Asclepias syriaca* of the study sites were identified and named after EUNIS Habitat Classification (Davies et al. 2004) with later corrections and amendments (https://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification). The cover of *A. syriaca* was estimated visually in percent within the limits of its occupied area in all studied sites.

Fruit set

Surveys of the fruit set of *Asclepias syriaca* were performed from September to October 2018 and 2020 at 17 sites (Alešiškės, Aukštadvaris, Bagdononys, Bižai, Kalniškė, Kleboniškis, Krakiškės, Levonys, Meškučiai, Miegonys, Puvočiai, Radžiūnai, Šlapikai, Vandžiai, Verniejus, Zabarauskai, Žilvičiai). At each site we thoroughly surveyed stands of the species and recorded absence or presence of fruits. At seven sites (Alešiškės, Kalniškė, Meškučiai, Miegonys, Vandžiai, Verniejus, Zabarauskai) we randomly selected 30 stems with fruits with at least 1 m distance between them and counted the number of developed fruits. Stems, though with remnants of inflorescences but without fruits, were ignored.

Seed germination

At five sites (Alešiškės, Meškučiai, Miegonys, Verniejus, Zabarauskai) at the beginning of October 2018 we randomly selected 5 ripe or almost ripe (yellowish) fruits from different shoots, placed them into labelled paper bags and brought them to the laboratory for further analysis. At the laboratory fruits were dried for one month at ambient temperature. Dried fruits were opened, seeds extracted, separated from tuft of hairs and visually normally developed seeds were selected for the test of germination. Selected seeds were placed into paper bags and stored at room temperature until the testing of their germination. In May 2018, at the Meškučiai and Verniejus sites we also collected 1–3 intact fruits of the 2017 season that had survived through the winter.

Germination of seeds of *A. syriaca* from fruits ripened in 2017 was tested from May to June 2018, whereas germination of seeds from stands surveyed in 2018, was tested in March 2019. A total of 50 normally developed seeds (10 from each fruit) were sown on wet quartz sand in plastic boxes with cover and kept at room temperature (ca. 18–21 °C) under natural daylight illumination for four weeks. Each second day the seeds were sprayed with tap water. Seed germination was recorded at two-day intervals. Seeds with ca. 3-mm-long emerged roots were considered to be germinated.

Statistical analyses

The normality of data distribution was evaluated using the Shapiro-Wilk test. The results of descriptive statistics included mean values and standard deviations (mean ± SD). Because the number of fruits per stem was distributed non-normally, the non-parametric Kruskal-Wallis H-test and the Mann-Whitney post-hoc pairwise comparisons were applied. All calculations were performed using PAST 3.20 (Hammer et al. 2001).

Results

Distribution

The first documented record of cultivated *Asclepias syriaca* in Lithuania is from 10 July 1930, when C. Regel collected plants in a garden in Meškučiai village, Trakai county (currently in Kaišiadorys district; herbarium specimen in BILAS). Until quite recently it was thought that the first record of wild occurrence of *Asclepias syriaca* in Lithuania was made in 1962 in Žuvintas mire, Alytus district, South Lithuania (Galinis 1964). However, the study of the recovered herbarium specimen and analysis of currently existing plants from a nearby locality revealed that in fact they belong to another species, *Asclepias speciosa* Torr. (Gudžinskas et al. 2019).

Thus, escaped individuals of *A. syriaca* in Lithuania were first recorded on 15 July 1991, in Aukštadvaris village (Trakai distr.), on a dry hill slope at the cemetery. Seven sites of its wild stands were known until 2015: Verniejus village (1992, Trakai distr.), Meškučiai (1994, Kaišiadorys district), Naujamiestis (1995, Vilnius city), Vandžiai (1999, Raseiniai district), Prapuntai village (2001, Lazdijai district), and Miegonys (2014, Rokiškis district). In 2018, we started dedicated studies on the distribution and ecology of *A. syriaca* and found nine new wild sites of this species in Lithuania. In 2019, we recorded this species in seven and, in 2020, another 15 new localities. Until the end of 2020, this species was noticed in 38 localities (Table S1) mainly in the southern, eastern, and northeastern parts of the country; few localities were registered in the western part of Lithuania so far (Figure 1). Thus, most of the localities of this species are distributed on the Baltic and Žemaičiai elevations and only few localities occur in the lowland regions.

Size and density of stands

The size of the currently known stands of *A. syriaca* in Lithuania varies substantially (Table S1). Nine stands (23.7%) of this species were small and occupied from 1 m^2 to 10 m^2. They were formed usually by a few (Kukutėliai, Mažoji Riešė) or several dozen shoots (Buišiai, Lazdijai) and represent quite recently established populations. Stands of *A. syriaca* in eight localities (21.0%) occupied from 11 m^2 to 20 m^2 and the density of shoots tended to be higher. Mean cover of this species in such stands ranged from 40% to 70%.

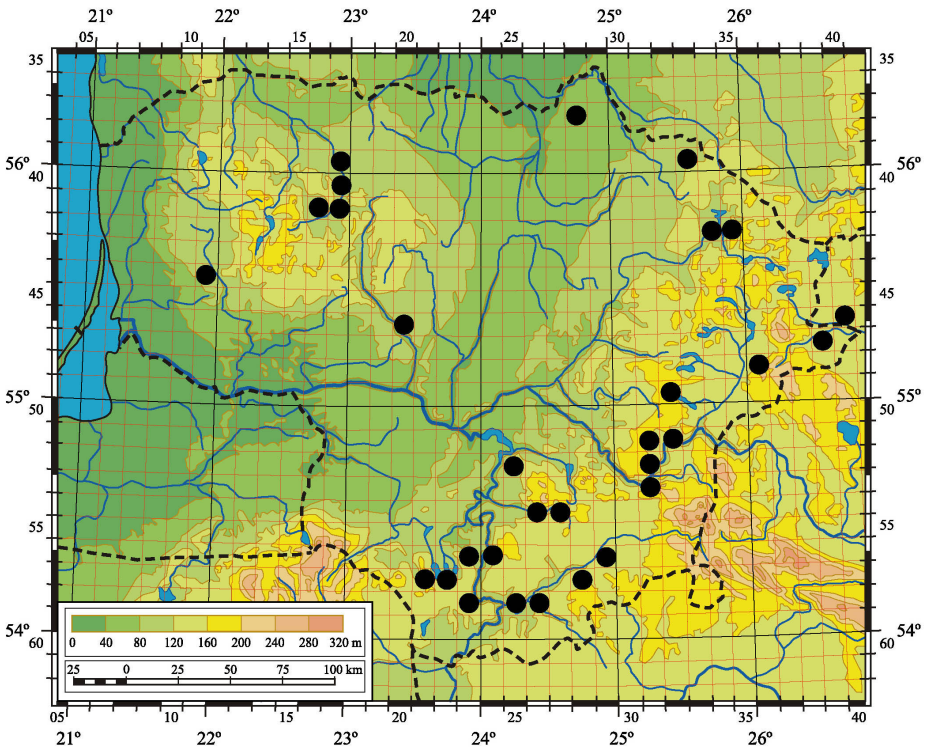

Figure 1. Current distribution of *Asclepias syriaca* in Lithuania (for details see Supplementary material Table S1).

Quite large stands, ranging from 21 m^2 to 100 m^2 (9 stands or 23.7%) and from 101 m^2 to 500 m^2 (9 stands or 23.7%) where almost as frequent as small and quite small stands. Exceptionally large stands, occupying more than 1000 m^2 comprised 7.9% (3 stands).

The largest currently known stand is in Meškučiai village and occupied 7390 m^2 in 2018. When the site was first discovered in 1994, the stand occupied 2130 m^2. Thus, in 24 years the size of the stand increased by 5260 m^2. A stand of *A. syriaca* in Verniejus village was discovered in 1992 and then occupied ca. 900 m^2, whereas in 2018 it occupied 1250 m^2, i.e., it increased by 350 m^2 in 26 years. A colony of this species in Aukštadvaris at the time of discovery in 1991 occupied ca. 40 m^2, whereas in 2018 it occupied 60 m^2. A rapid increase in size of a stand of *Asclepias syriaca* was noted in Miegonys village; in 2014, the stand was ca. 12 m^2, whereas four years later (in 2018) it occupied already 150 m^2.

Thus, the analysis revealed that in different localities the increment of the stand size ranged from ca. 1 m^2 per year (in Aukštadvaris site) to 219 m^2 per year (in Meškučiai site). In Verniejus, the stand increased on the average by 13 m^2 annually, whereas in Miegonys it increased by 35 m^2 per year. Currently, the total area of registered stands of *A. syriaca* in Lithuania occupy ca. 1.29 ha (Table S1).

Habitats

The analysis of habitats with *A. syriaca* in Lithuania revealed that this species invaded ten types of habitats (Table 1, Table S1). Small stands of

Table 1. Frequency of *Asclepias syriaca* invasion and areas occupied by its stands in habitats according to the EUNIS classification.

Habitat code	EUNIS habitat name	Number of sites	Percentage of sites in the habitat	Stand area (m^2)	Percentage of the total stand area
E1.D	Unmanaged xeric grassland	13	22.4	5593	43.4
E2.1	Permanent mesotrophic pastures and aftermath-grazed meadows	1	1.7	60	0.5
E2.6	Agriculturally improved, re-seeded and heavily fertilized grassland	2	3.5	26	0.2
E2.7	Unmanaged mesic grassland	9	15.5	572	4.4
E5.1	Anthropogenic herb stands	17	29.3	783	6.1
E5.2	Thermophile woodland fringes	3	5.1	3697	28.7
E5.4	Moist or wet tall-herb and fern fringes and meadows	5	8.6	1784	13.9
G5.1	Lines of trees	2	3.5	10	0.1
G5.6	Early-stage natural and seminatural woodlands and regrowth	4	6.9	251	1.9
I1.1	Intensive unmixed crops	2	3.5	98	0.8
	Total:	58	100	12874	100

A. syriaca usually were found to have invaded one habitat, whereas larger ones (occupying ca. 50 m^2 or more) frequently invaded habitats of two or three types. Therefore, the number of habitats exceeds the number of registered sites (Table 1). In most cases this species was recorded from grasslands (50 sites, 86.2%) and in several cases it occupied woodland (6 sites, 10.3%) and agricultural (2 sites, 3.5%) habitats.

Most frequently, *A. syriaca* in Lithuania was found to be invading anthropogenic herb stands (E5.1) and unmanaged xeric grassland (E1.D) habitats (Table 1). In unmanaged mesic grasslands (E2.7) this species was found to occur in nine sites. In moist or wet tall-herb and fern fringes and meadows (E5.4) *A. syriaca* was recorded for five sites and it occupies substantial areas at the Meškučiai and Verniejus sites. At two sites this species was found to have invaded agriculturally improved grasslands (E2.6). Although *A. syriaca* prefers open areas, we found that it can survive for a long time in early-stage natural and seminatural woodlands and regrowth habitats (G5.6) with a cover of trees and shrubs of up to 20%, occasionally of up to 60% (Kleboniškis). In two localities this species was recorded to occur in intensive unmixed crop (I1.1) habitats (Figure 2A), though the invaded area and the density of shoots in rye and barley crop fields was quite small. Thus, *A. syriaca* in Lithuania invades and tolerates habitats with a quite wide range of soil humidity (from dry to moist soils). It should be noted that only a small part of the invaded habitats was disturbed or modified by human activity, whereas a substantial part of grasslands was without evident recent disturbances.

Fruit set

Fruit set of *Asclepias syriaca* in 2018–2020 was absent in eight (Aukštadvaris, Bagdononys, Bižai, Krakiškės, Puvočiai, Radžiūnai, Šlapikai, and Žilvičiai) of 17 studied sites. Low fruit set was recorded in Kleboniškis and Levonys, where only two and five individuals, respectively, had one normally developed

Figure 2. Flowering *Asclepias syriaca* in intense unmixed crop (rye) habitat, 27 July 2020, Žilvičiai village, Lazdijai district (A) and individuals with fruits in unmanaged xeric grassland habitat, 14 September 2018, Meškučiai village, Kaišiadorys district (B). Photos by Z. Gudžinskas.

fruit each. In the other seven studied sites numerous individuals with fully developed fruits were recorded (Figure 2B). In Meškučiai, Verniejus, and Zabarauskai *Asclepias syriaca* fruit set was studied in moist tall-herb (E5.4) habitats, in Alešiškės and Vandžiai in unmanaged xeric grasslands (E1.D), in Miegonys sampled plants occurred in unmanaged mesic grassland (E2.7), and the colony in Kalniškė occupied an anthropogenic herb stand (E5.1) habitat.

Analysis of the number of developed fruits per shoot applying the Kruskal-Wallis test revealed significant differences between all studied sites ($H = 41.33$, $p < 0.001$) as well as between habitat types ($H = 35.11$, $p < 0.001$). The mean number of developed fruits in the pooled moist tall-herb habitats ($n = 90$) was 2.1 ± 1.2, in the pooled unmanaged xeric and mesic grasslands ($n = 90$) it was 3.8 ± 2.1, and in the anthropogenic herb stand ($n = 30$) it was 3.3 ± 1.99. According to the Mann-Whitney pairwise comparison, the number of fruits per shoot in the moist tall-herb habitats was statistically significantly different from the unmanaged xeric and mesic grasslands as well as from the anthropogenic herb stand habitat (Figure 3). At the level of individual shoot, the number of developed fruits ranged from one to six in the moist tall-herb habitats, from one to nine in the unmanaged xeric and mesic grasslands, and from one to eight fruits in the anthropogenic herb stand. The lowest mean number of developed fruits was recorded in Zabarauskai (1.8 ± 1.3), whereas the highest mean number was in the Alešiškės (4.2 ± 2.1) site. Thus, differences of fruit set were not observed between all unmanaged xeric, unmanaged mesic grasslands, and anthropogenic herb stands, and it was higher than in the moist tall-herb habitats (Figure 3).

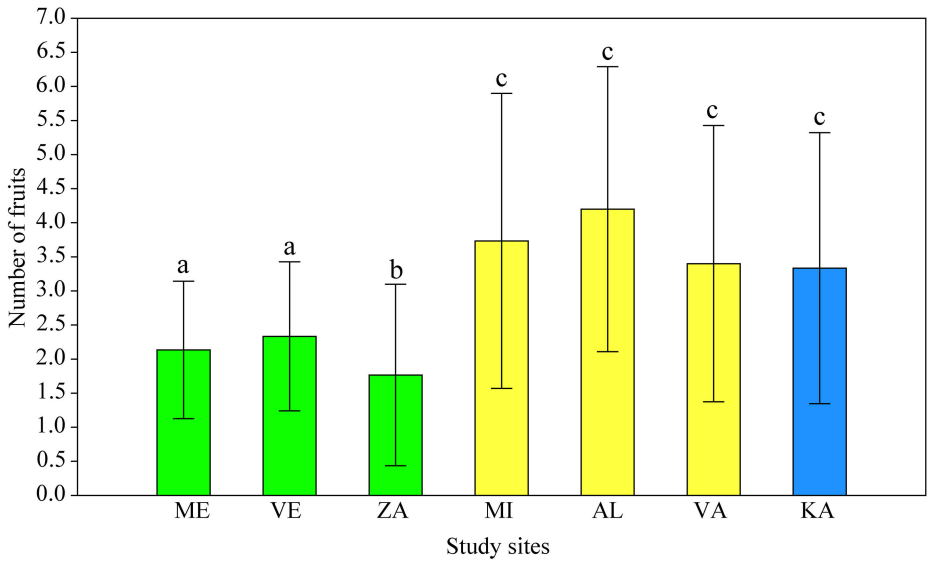

Figure 3. Mean fruit number per shoot of *Asclepias syriaca* in the studied sites in 2018. Whiskers denote standard deviation. Different letters above bars denote statistically significant differences between the mean number of fruits applying the Mann-Whitney post-hoc test. Abbreviations: Me – Meškučiai, Ve – Verniejus, Za – Zabarauskai (moist tall-herb and fern fringe and meadow habitats), Mi – Miegonys, Al – Alešiškės, Va – Vandžiai (unmanaged xeric and mesic grassland habitats), Ka – Kalniškė (anthropogenic herb stand habitat).

Seed germination

We tested germination of seeds that had overwintered in unopened fruits and were collected in May 2018 at the Meškučiai and Verniejus sites. Seeds from both localities started to germinate after 6–8 days and germination continued for another 12–15 days. The rate of overwintered seed germination was quite high: 76% of seeds germinated (n = 40) from the Meškučiai and 72% of seeds (n = 50) from the Verniejus site. Examination of the ungerminated seeds revealed that they were rotten (24% of seeds from Meškučiai and 28% from Verniejus).

The results of the test of seed germination that were collected in autumn of 2018 in the Alešiškės, Meškučiai, Miegonys, Verniejus, and Zabarauskai sites and stored at room temperature, showed significant differences as compared with seeds overwintered in the field. Seeds from the Meškučiai (54%) site showed the highest germination rate. The germination rate of seeds was 43% from Verniejus, 42% from Alešiškės, 34% from Miegonys, and 30% from the Zabarauskai sites (from each site n = 50). Although after the germination test some ungerminated seeds were rotten, almost the same number of seeds were intact, though did not germinate.

Discussion

Distribution

The current distribution of *A. syriaca* in Lithuania, in our opinion, is only partly known. During the two seasons of this study, mainly in the southern and eastern parts of Lithuania, we found 31 previously unrecorded localities. Thus, further investigations may reveal many more new localities

of this species, particularly in the vicinity of long-ago abandoned homesteads.

We believe that most of the currently known sites of *A. syriaca* originated by their spread from places of former cultivation (e.g., in Meškučiai and Verniejus), as, for instance, by rhizomes dumped with garden wastes (e.g., in Miegonys and Zabarauskai) or accidentally introduced with replacement soil (e.g., in Mažoji Riešė). The occurrence in the village of Kleboniškis appears to be of seed origin: this site is located 1800 m southeast of the exceptionally large stand in the village of Meškučiai, where *A. syriaca* steadily produces large numbers of fruits. The plants in Kleboniškis grow on a dry hill slope which is now overgrowing with young pines. The first author visited this spot in the 1990s and *A. syriaca* was absent then. Our presumption of the seed origin in this locality is also indirectly supported by the fact that *A. syriaca* grows in four groups irregularly scattered on the slope occupying from one to several square meters each. Furthermore, fruit set, although quite poor because of the habitat shading by young pine trees, appears to exclude a population origin from a single clone. It is quite possible that westerly winds transported seeds from the Meškučiai site in the late 1990s or early 2000s, prior to the dry grassland on the slope starting to become overgrown with pine trees.

In other European countries of the Boreal region, *A. syriaca* is much less frequent than in Lithuania. It has been recorded to have escaped at five sites and at several dozens of sites with unspecified status in Sweden (NOBANIS 2020; SLU Artdatabanken 2021) and two sites in Latvia (Nāburga and Evarts-Bunders 2019). In Sweden, it is considered to be potentially invasive (Tokarska-Guzik and Pisarczyk 2015), whereas in Latvia it is ascribed to the group of casual aliens, though its naturalization and further spread are to be anticipated (Nāburga and Evarts-Bunders 2019).

In Lithuania, *Asclepias syriaca* for a long time has been cultivated in gardens as an ornamental or at apiaries as a melliferous plant and is still found in many places in rural areas. Therefore, because of the existing propagule pressure (Rouget and Richardson 2003; Simberloff 2009; Lockwood et al. 2009) one can anticipate further spread and discovery of unknown localities. The highest probability to discover new localities of *A. syriaca* is in the northern, eastern, and southern parts of Lithuania where it, according to the results of our surveys, has been cultivated in gardens most frequently.

Size of stands

Most of the stands of *A. syriaca* in Lithuania are quite small and 14 of them occupy less than 100 m^2. However, considering the fast vegetative spread of this species by long rhizomes (Bagi 2008; Dvirna 2018), the occupied areas may increase significantly within a few years. A particularly intense increase of the invaded area was noticed in Meškučiai, where the previously

detected colony already had occupied a large area. Nevertheless, the previously identified small colony in Miegonys had also increased significantly over four years, on an average by 35 m^2 per year. In other sites, the area invaded by *A. syriaca* was smaller because of natural or artificial obstacles. For example, in Aukštadvaris the rate of colony increase was low because it occupied almost all suitable areas between the wooded slope of the ravine and the stone fence of the cemetery. In Verniejus the colony occupied almost the entire open area between the lake shore and the broadleaf woodland.

Information on the size of *A. syriaca* stands and occupied total area in Sweden is lacking (NOBANIS 2020; SLU Artdatabanken 2021). The stand of *A. syriaca* in Lucavsala, Latvia, occupies ca. 30 m^2, whereas the size of the stand at Dole railway station is unknown (Nāburga and Evarts-Bunders 2019). Thus, currently the plants occupy a quite small area in the Boreal region of Europe.

Trials of *A. syriaca* local eradication have not been performed in Lithuania so far. With the complicated control and eradication of this species in other European countries (Bakacsy and Bagi 2020), it must be considered difficult, time consuming, and an expensive task. It is known that the effectiveness of eradication measures of invasive plant stands is highest when the occupied area is rather small (Blackwood et al. 2010; Epanchin-Niell and Hastings 2010). Thus, considering the quite small (ca. 1.29 ha) invaded area in Lithuania, as well as in other countries of the Boreal region of Europe, eradication and control of its stands should be started as soon as possible. Delay in eradication and control may result in the increase of the invaded area by several fold, and, hence, hike the necessary investments for eradication in the future.

Habitats

The results of this study show that *A. syriaca* in Lithuania invades anthropogenic, seminatural, and natural habitats – however, most frequently it invades various types of grasslands, and only a small fraction of stands occupy woodland regrowth and agricultural habitats in winter- or summer-crop fields (Table 1). In other countries of the Boreal region of Europe the plant has been recorded in anthropogenic habitats, i.e., abandoned gardens, along roads and railways, or in garbage dumps (Nāburga and Evarts-Bunders 2019; NOBANIS 2020; SLU Artdatabanken 2021). In Central and Southern Europe, where *A. syriaca* is the most invasive (Bagi 2008; Novák et al. 2009; Follak et al. 2018), it most often occurs in dry grasslands, along roads and railways, in wastelands, abandoned orchards and arable lands, and in vineyards (Valachovič 1987; Stanković-Kalezić et al. 2008; Bakacsy and Bagi 2020). Thus, in the southern part of the Boreal region, *A. syriaca* also invades grassland habitats and climate changes may facilitate its spread over a large area of grasslands in the future.

In the southern regions of Europe, *A. syriaca* is considered a noxious weed of arable lands (Novák et al. 2009; Bakacsy and Bagi 2020); however, in Lithuania it is rare in this type of habitat and was detected only at two sites. The related species, *A. speciosa*, also has been recorded to occur in arable land habitats in Lithuania (Gudžinskas et al. 2019). Thus, further spread of *A. syriaca* to habitats of this type can be expected. It should be noted that during the plowing of cultivated fields, the rhizomes of *A. syriaca* can spread even further over a large area making its eradication even harder.

Occurrence of *A. syriaca* in the early stage within natural and seminatural woodlands and regrowth habitats in Lithuania, probably is a result of long-term abandonment of the area and its overgrowth by native trees and shrubs. However, the density of shoots in stands occurring under the canopy of trees (e.g., in Kleboniškis site) usually is quite small, plants poorly flower, and only a few fruits develop. Thus, to control or eradicate *A. syriaca*, afforestation of certain areas by native broadleaf or coniferous trees could be used. However, decline and extinction of *A. syriaca* stands in woodland habitats is a slow process and may take several decades.

Fruit set

In eight of the 17 studied localities no fruit set of *A. syriaca* was observed, although plants occupied quite large areas. Therefore, it is possible that all these sites consist of vegetative descendants of one plant and represent single clones. Absence of fruit set appears to be the case in stands of *A. syriaca* in Lithuania, which supposedly is composed of individuals originated from a single clone (Gudžinskas et al. 2019). It is known that most species of the genus *Asclepias* are primarily or completely self-incompatible (Wyatt and Broyles 1994), and viable seeds are produced in the case of flower pollination from pollen of a genetically distinct individuals. Self-compatible individuals are rare even in natural populations of some *Asclepias* species (Bookman 1984; Finer and Morgan 2003). *Asclepias syriaca* occasionally sets fruits after pollination from within the same clone, but self-compatibility is less than 5% (Kephart 1981; Kahn and Morse 1991).

The abundant fruit set in the studied sites at Alešiškės, Kalniškė, Meškučiai, Miegonys, Vandžiai, Verniejus, and Zabarauskai suggests that in these localities two or more genetically distinct clones of *A. syriaca* grow together. Considering the abundant visit of flowers by honeybees, bumblebees, and other insects (Wyatt and Broyles 1994; Howard and Barrows 2014), this appears to ensure successful cross-pollination, abundant fruit set, and production of viable seeds. In the case of the generative reproduction of a primarily small number of genetically distinct clones in a site, the number of genetically distinct individuals originated from the cross-pollination increases, thus, increasing further success of the generative reproduction in primarily self-incompatible plants. On the other hand, considering just a low level of self-compatibility of *A. syriaca* (Kephart 1981; Kahn and Morse

1991), occasional fruit set is possible even in areas occupied by a single clone. Thus, descendants grown from seeds may increase genetic diversity of individuals in the site and facilitate generative reproduction (Wilcock and Jennings 1999; Eckert 2000; Zhang and Zhang 2007).

The results of our study revealed that fruit set of *A. syriaca* in unmanaged xeric and mesic grassland as well as in anthropogenic herb stand habitats was similar and significantly higher than in moist tall-herb and fern fringe habitats. The light availability in moist tall-herb and fern fringe habitats, which occur along forest edges, is usually lower than in open xeric and mesic grassland and anthropogenic herb stand habitats. Studies performed in North America have revealed that light availability is strongly related with fruit production in *A. syriaca* and several other *Asclepias* species (Bhowmik and Bandeen 1976; Kephart 1981, 1987). It should be noted that fruit set of *A. syriaca* occurring in unmanaged xeric and mesic grassland habitats in Lithuania (mean 4.2 fruits per shoot) is comparable with the fruit set in the northern part of native area (4–6 fruits per shoot) in Canada (Bhowmik and Bandeen 1976).

Nāburga and Evarts-Bunders (2019) reported that in nurseries of Latvia *A. syriaca* sets fruits, produces viable seeds, and cases of self-sowing have been observed, however, they did not provide information about the fruit set in the escaped populations in the country. Although *A. syriaca* develop fruits in Sweden, information about seed viability and generative reproduction of this species from the country are also lacking (SLU Artdatabanken 2021).

Considering the observed abundant fruit set in at least seven sites of *A. syriaca* in Lithuania, we predict further spread of this species by seeds and its invasion, although initially slow, into new areas. Nāburga and Evarts-Bunders (2019) concluded that *A. syriaca* has a high potential of invasion in Latvia, although currently it has been classified as a casual alien there.

Seed germination

Seeds of *Asclepias syriaca* require a one-year period of after-ripening before they can germinate moderately well (Bhowmik and Bandeen 1976). Our tests revealed that seeds collected in springtime germinate better than seeds collected in autumn and sown after six months of storage at room temperature. Thus, seeds remaining in unopened fruits throughout the winter pass low temperature stratification and their germinability increases. Bhowmik and Bandeen (1976) reported that the highest germination rate (about 76%) of *A. syriaca* seeds has been found after 11 months of storage at room temperature. However, after six months of storage, seeds of *Asclepias syriaca* collected in Lithuania germinated quite well and the results are comparable with the 54% seed germination rate under laboratory conditions testing seeds from the native range in Canada (Bhowmik and Bandeen 1976) and 25–50% germination rate of seeds from the invasive range in Ukraine (Dvirna 2018).

It should be noted that one of the aims of our study was to test whether seeds produced in Lithuania are viable, therefore, exact seed germination rate and seed viability should be verified in the future with several replications. Nevertheless, our tests of seed germination confirmed that *A. syriaca* in Lithuania actually produces viable seeds and, thus, it is capable of generative reproduction and further spread. In the largest site of this species in Latvia (Lucavsala), no seedlings were found in 2016 (Nāburga and Evarts-Bunders 2019).

The summer and autumn of 2017 was unusually cool and moist in Lithuania. The amount of precipitation in this year exceeded the multi-annual mean by 55% and mean air temperature in summer and autumn was by 0.5–1.4 °C lower (Marcinonienė et al. 2018). However, *A. syriaca* produced fruits with viable seeds. We suppose that because of intense rains some fruits of *A. syriaca* did not open in autumn and remained intact until the late spring of 2018. Ripe fruits of *Asclepias* species split open and release seeds when becoming dry (Bhowmik 1994). During a rainy autumn at least some fruits remain unopened. Thus, prolonged seed release, at least in some years, appears to increase the invasive potential of the species (Rejmánek and Richardson 1996).

Conclusions

The current distribution of *Asclepias syriaca* in Lithuania in the wild and its presence in cultivation suggests that its distribution may increase in the future. Despite thorough studies, some sites of this species might have remained unnoticed, as *A. syriaca* frequently occurs in long-ago abandoned and secluded areas of former homesteads. Most of the currently registered localities of this species should be treated as relics of former cultivation, however, in several localities it has been introduced accidentally with garden wastes or soil. One locality of this species is assumed to be of seed origin.

Most frequently *A. syriaca* invades and forms large stands in dry or mesic grassland habitats, though moist forest fringe habitats are also prone to the invasion of this species. The start of spread of *A. syriaca* in arable lands raises major concerns, because it can facilitate its further fast spread over large areas and invasion into neighboring habitats. The total area currently occupied by *A. syriaca* in Lithuania is relatively small (ca. 1.29 ha), thus implementation of urgent measures of control and eradication of existing wild populations as well as eradication of cultivated stands could prevent its further spread to new localities.

With its vigorous vegetative spread, abundant fruit set, and production of viable seeds, *A. syriaca* should be considered a species with high potential of invasion in the southern part of the Boreal biogeographic region of Europe.

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Supplementary material

The following supplementary material is available for this article:

Table S1. List of *Asclepias syriaca* localities, year of record, occupied area, and invaded habitat type (including area occupied in the respective habitat type and cover by *Asclepias syriaca*) in Lithuania.

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