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Forewarned Is Forearmed: Documentation on the Invasion Risk of *Asclepias speciosa* in Greece and Europe

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Abstract: Biological invasions threaten biodiversity and agroecosystems, and early warning systems can minimise the spread of invasive alien species with limited resources. This study documents the presence of the alien plant *Asclepias speciosa* Torr., native to North America, that was first discovered in 2022 on Mount Vrontou, Central Macedonia, Northern Greece. This is the second European record of this alien species, after Lithuania, confirming its adaptability to contrasting European biogeographical regions. To enable future monitoring, this study provided new data on morphological traits of the species (above-ground parts), climatic tolerance (precipitation and temperature regimes), habitats with co-occurring species, pollinators, current reproductive potential, and seed germination at controlled temperatures (10 °C, 15 °C, and 20 °C). The high probability of misidentification with the highly invasive *A. syriaca* in European inventories supports the theory that *A. speciosa* may have been present in Europe long before it was officially reported. The lack of an EU-mandated reassessment of *A. syriaca* monitoring raises concerns regarding the potential invasion risk of *A. speciosa* in European natural and semi-natural areas or agricultural lands. Inspection mechanisms, early warning systems, and preventive measures are therefore essential to protect local biodiversity and agriculture from potential *A. speciosa* invasion, a risk that may be exacerbated by climate change.

Keywords: bioclimatic profiling; invasive alien species; non-native plants; milkweeds; seed germination

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1. Introduction

The genus *Asclepias* L. was originally described by Carl Linnaeus in 1753, who named it in honour of Asklepios (*Ασκληπιός* in Greek or Latin Aesculapius), the god of medicine and healing in ancient Greece, probably due to the plant's long history of medicinal use [1]. Linnaeus described the common milkweed as *A. syriaca* L., based on the mistaken belief that this species, native to North America, originated from Syria [2]. The genus *Asclepias* L. s. str. (Apocynaceae, Asclepiadoideae) includes approximately 120 species native to North and South America and South Africa [3]. Most species are distributed in North America and the Caribbean, with ten species occurring in South America [4–8].

In Europe, the alien members of the genus *Asclepias* s. str. have been reported as alien naturalised species, namely, *Asclepias curassavica* L., *A. incarnata* L., *A. syriaca* L. [9,10], and *A. speciosa* Torr. [4], while, in several countries of Southern Europe, species of the closely related genus *Gomphocarpus* R. Br. have also been reported, e.g., *Gomphocarpus fruticosus* (L.) W.T.Aiton (*Asclepias fruticosa* L.) and *Gomphocarpus physocarpus* E.Mey. (*Asclepias physocarpa* (E.Mey.) Schltr.) [9,11–13]. Undoubtedly, *A. syriaca* is the most widespread and invasive species of this genus in South and Central European countries [14–18], while *A. curassavica* and *A. incarnata* have only been recorded as casual or locally naturalised aliens in different regions of Europe [9,19,20]. In Greece, *A. curassavica* with bright orange-red flowers, *Gomphocarpus fruticosus*, and *G. physocarpus* have been reported as established alien species [9] (http://www.alienplants.gr, accessed on 25 October 2024), while *Asclepias speciosa* Torr. has only recently been reported as a new alien plant in Northern Greece [21].

Asclepias speciosa shares several morphological traits with *A. syriaca*, the common milkweed, and it has been highlighted that the former may often be misidentified as the latter [4]. Since the introduction of *A. syriaca* in Europe in 1629 [22] for ornamental and various other purposes such as its potential for fibre and latex production, *A. syriaca* has become established in many regions of Europe, and it has spread increasingly over the last decades. It should be emphasised that the presence of *A. speciosa* in Europe was only indirectly revealed for the first time in southern parts of Lithuania [4] during an extensive assessment of *A. syriaca* in the country in relation to the implementation of the EU Regulation on Alien Invasive Species at the national scale in Lithuania. The reassessment of deposited herbarium specimens in Lithuania has revealed several cases of misidentified *A. syriaca* instead of *A. speciosa*. These herbarium studies have shown that *A. speciosa* was originally collected in Lithuania in 1962 [4]. Based on information from herbarium labels, the latter study has shown that *A. speciosa* occurred in the wild of Lithuania for almost 60 years prior to the official report, and, therefore, it can be considered a naturalised alien plant in Lithuania [4]. This species might have been introduced to Lithuania at the end of the 19th century or the beginning of the 20th century as an ornamental plant, perhaps was later cultivated by local people in their gardens or as a melliferous plant, and later escaped from cultivation [4]. The reproductive behaviour of *A. speciosa* is characterised by a high production of wind-dispersed seeds coupled with asexual reproduction by creeping lateral rhizomes, which allows the species to spread rapidly and establish colonies in new territories [23]. In its alien range in Europe, *A. syriaca* invades habitats that have already been degraded, at least to some extent, by anthropogenic disturbance [24]. It is a highly competitive alien species with a tall and shady habit, vegetative spread, drought tolerance, and allelopathic potential [22,25], which can actively modify its local environment as a transformer species [26–28]. Although such facts are not known to the same extent for the similar and closely related *A. speciosa*, both species share remarkable similarities in terms of plant habit, reproductive strategies, and ecology. The diversity of natural and anthropogenic habitats occupied by *A. speciosa* in its native (USA) and alien (Lithuania) ranges include several grassland habitat types and wetlands as well as road verges, disturbed lands, and arable lands, respectively, thus rendering it as a colonising grassland species and/or a weed of arable lands [4], thus posing a potential threat for agriculture. The latter rings a bell for the detailed study of *A. speciosa* at the earliest possible stages regarding its future naturalisation and invasion in Europe or species-specific management measures. In this context, Geographic Information Systems (GISs) have been widely applied in studies on invasive species. GIS is an effective supporting tool for the automated recognition of invasive species distributions through remote sensing [29], in predicting the potential spatial distribution of alien species [30], and for developing risk assessments on the potential impacts of invasive species on native species within their ecosystems [31]. Additionally, the ecological preferences of alien species can be retrieved through a GIS application in a similar fashion with cases of rare species threatened with extinction [32].

The present study focused on documenting the ecological traits of the pilot wild-growing population of *A. speciosa* (showy milkweed) recently reported for the first time from Northern Greece [21]; this population has been closely monitored over the last two years with observations preceding the latter study. The native range of *A. speciosa* includes parts of the western half of North America, from California to British Columbia and Central Canada and south to Texas. In its native range, *A. speciosa* is adapted to a wide range of soil types and moisture conditions, from riparian sites to dry sites [33]. However, little is known about the climatic preferences that shape or limit its natural distribution. Although *A. speciosa* was reported as an established alien plant in Europe only a few years ago [4] and as a new alien plant in Greece only a few months ago [21], knowledge about its climatic preferences and introduced population dynamics in Greece or Europe is still limited and its naturalisation and invasion status remain largely unknown. As Greece is only the second country, after Lithuania, to report the presence of *A. speciosa* [4], the present study aimed at documenting the presence of *A. speciosa* in the Greek territory as early and as completely as possible in terms of the first habitats occupied, the local climatic regimes tolerated, and the current reproductive potential enabled; such features may facilitate the first assessment of *A. speciosa* in terms of its current establishment, naturalisation, and invasion status [34]. The documentation provided in this study also represents a baseline assessment for future monitoring schemes and heralds early warning efforts aimed at preventing the potential invasion of this alien species in Greece and Europe.

2. Materials and Methods

2.1. Field Research and Informed Field Identification of the Focal Species

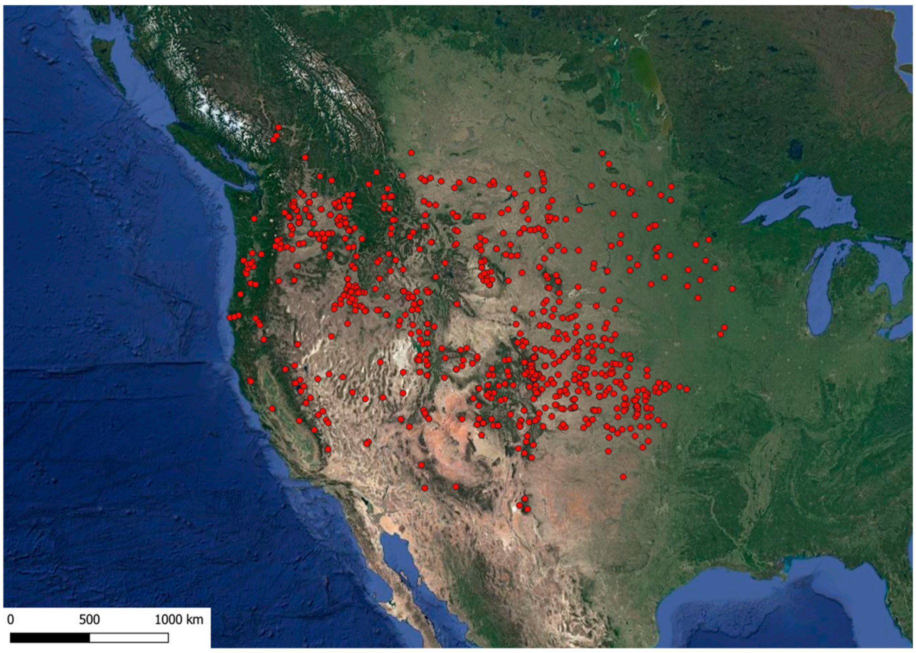
Field research on the occurrence of *A. speciosa* started in July 2022, following the accidental discovery of a colony of this species near Kapnofyto, Serres (Northern Greece) by Catherine Dijon. Since then, regular botanical surveys were carried out in the vicinity, covering an area of about 500 m^2 around the discovered colony, with the aim of recording any other *A. speciosa* plants. A total of nine (9) visits were made to the site from 2022 to 2024 (16 July 2022, 21 July 2022, 10 October 2022, 16 February 2023, 10 June 2023, 29 June 2023, 8 July 2023, and 26 July 2024) to assess the state of the wild-growing populations during the flowering or in the fruiting of *A. speciosa*. During the fieldwork, the morphological characteristics, flowering time, and habitat elements of *A. speciosa* were recorded along with the relative abundance of co-occurring plant species in the DAFOR scale, i.e., D: dominant >75%, A: abundant 51–75%, F: frequent 26–50%, O: occasional 11–25%, and R: rare 1–10% [35]. During the seventh visit on 8 July 2023, the stem height, number of leaf pairs, leaf blade length width, petiole length, number of inflorescences per plant, inflorescence diameter, number of flowers in inflorescence, and flower diameter were also recorded for seven representative wild-growing individuals of *A. speciosa*.

Given the morphological similarities between *A. syriaca* and *A. speciosa*, it has been highlighted that the former can often be misidentified as the latter [4], leading to biased or confusing results. A quite reliable and visible character for distinguishing these two species in the wild is leaf veining. Lateral veins in the leaf blades of the middle cauline leaves of *A. speciosa* are mainly alternate and branch off the main vein at a narrow angle, whereas those of *A. syriaca* are usually opposite and branch off at a wider angle [4]. The distinctive large corona of *A. speciosa* as well as the densely white-tomentose pedicels may also serve as characters that clearly distinguish *A. speciosa* from *A. syriaca*.

2.2. Mapping of Native and Alien Ranges for Species-Specific Bioclimatic Profiling

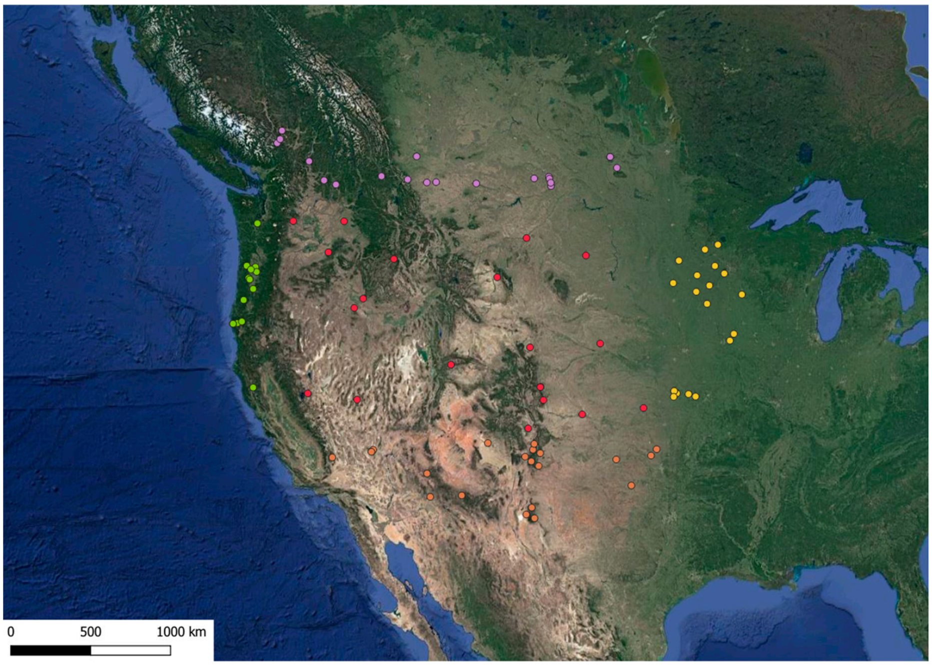
The native range of *A. speciosa* was determined using available data from the Global Biodiversity Information Facility (GBIF) database [36]. Some data points of the GBIF sourced from iNaturalist.org and Pl@ntNet were excluded to ensure data reliability. Furthermore, records of three sites from the Eastern United States were also excluded because they did not represent the natural range of the species according to the Plants of the World Online (POWO) database [3] and most likely represent *A. speciosa* as a garden ornamental or garden escape. Initially, 1173 distribution points were retrieved from the GBIF, and, after data filtering, 1154 points were retained in the final dataset for map construction. The distribution maps were generated using QGIS Desktop 3.36.0 (Figure 1). To develop the ecological profile of *A. speciosa* within its native range (Figure 1A), a subset of 100 points was selected from the total 1154 distribution points. This selection included the 20 most extreme distribution points in each cardinal direction (east, west, north, and south), with the addition of another 20 more inner points (central distribution area between the extreme east, west, north, and south distribution points). These inner or more central points were selected based on factors such as the overall central distribution pattern and the variation in elevation range (Figure 1B). The bioclimatic profile was constructed using this subset of points. Historical climate data were obtained from the WorldClim database, which provides minimum, maximum and average temperatures, as well as precipitation, and 19 bioclimatic variables [36,37]. The climate data, with a spatial resolution of 1 km^2 and a pixel size of 30 arcsec, were integrated with the selected distribution points using ArcMap 10.8.1.

The same methodology was used to construct the bioclimatic profile for the non-native (alien) range of the species. In this case, the previous historical climate data were linked to the two currently known distribution sites of *A. speciosa* in Europe (Southern Lithuania and Northern Greece as reported in this study) [4,21].



(**A**)

Figure 1. *Cont.*



(**B**)

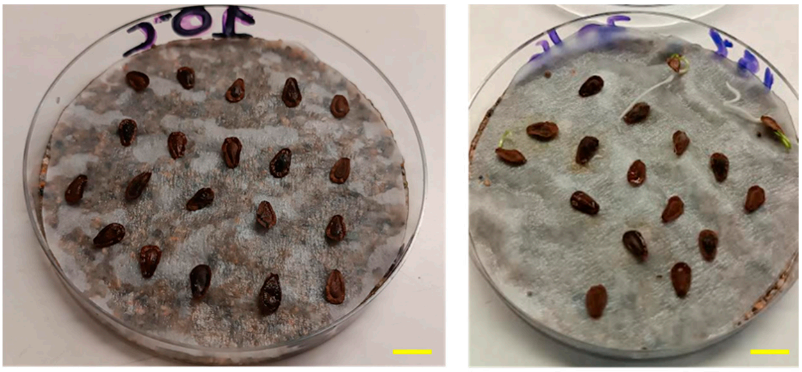
Figure 1. (**A**) Distribution points (n = 1154) of *Asclepias speciosa* according to the Global Biodiversity Information Facility (GBIF) database [36,37] after filtering out records sourced from non-expert platforms, and (**B**) selected distribution points (n = 100) covering the extremes of its native range, used here to generate the bioclimatic profile in its native range.

2.3. Seed Collection

Fruits of *A. speciosa* (follicles) containing mature seeds were collected on 16 February 2023 from three of the remaining wild individuals growing in the target area near Kapnofyto, Northern Greece. After collection, the seeds were cleaned manually and then spread on filter paper under laboratory conditions and air dried for one week. The dry seeds were stored in a glass container at 3–5 °C before being used in the germination experiment.

2.4. Seed Germination Tests

The germination experiments started at the end of June 2023 at the Laboratory of Floriculture, School of Agriculture, Aristotle University of Thessaloniki (Thermi, Greece). Three temperature-controlled growth chambers (CRW-500SD, Chryssagis, Athens, Greece) were used to determine the effect of temperature on seed germination. Specifically, seeds were incubated for germination at three constant temperatures of 10 °C, 15 °C, and 20 °C with a 12 h light/12 h dark photoperiod. Due to the limited number of seeds available, 20 seeds were used at each temperature. For each temperature treatment, the seeds were placed in 9 cm sterile plastic Petri dishes on filter paper (Figure 2A). A layer of moist sterile sand was placed under the filter paper to maintain moisture. The Petri dishes were then randomly placed on the shelves of the growth chambers, with a 12 h light/12 h dark photoperiod, and the substrate (filter paper and sand) was kept moist as required throughout the whole experimental period. The germinated seeds (Figure 2B) were counted and removed weekly over a period of ten weeks. A seed was considered germinated when a radicle of at least 2 mm in length emerged through the seed coat (Figure 2B) [38].



(A) (B)

Figure 2. (**A**) Seeds of *Asclepias speciosa* placed in a Petri dish, and (**B**) germinated seeds with visible radicles (scale bar in yellow: 5 mm).

The germinated seeds were sown in plastic pots (6.5 cm × 6.5 cm × 8 cm in dimension and 260 mL in volume) filled with a 3:1 (v/v) mixture of enriched fine peat (type TS1, Klassmann) and perlite, used to prepare the substrate filling the pots, and then covered with a thin layer of sterile sand to keep the substrate moist. The pots were placed on an unheated bench in the greenhouse. The pots were watered every two to three days to ensure sufficient moisture for proper growth of the seedlings. The germinated seeds developed into normal seedlings (with root, hypocotyl, cotyledons, epicotyl, and primary leaves) within two months (Figure 3A,B).

(A) (B)

Figure 3. Two- (**A**) and twelve-month-old (**B**) plants of *Asclepias speciosa* cultivated in artificial conditions in Greece (scale bar in yellow: 10 mm).

In the germination experiment, the proportion of germinated seeds at each incubation temperature was calculated by dividing the number of germinated seeds by the total number of seeds incubated at that temperature (20 seeds tested per treatment). To compare these germination ratios between different incubation temperatures, we used the z-test for proportions. The z-test for proportions is appropriate when comparing the proportions of two independent groups, i.e., the proportions of seeds germinated at different temperatures. While the z-test is typically ideal for larger sample sizes due to the Central Limit Theorem, smaller sample sizes may still allow its use under certain conditions. According to statistical guidelines, the z-test can be used when the sample size (n) and the expected number of successes (np) and failures ($n(1 - p)$) are all greater than five (5) [39,40]. In our study, each group had 20 seeds, and, given the observed germination rates, these conditions were likely to be met. The z-test assumes that the sample proportions approximate a normal distribution for large sample sizes. Despite the rather small sample size of 20 seeds here, previous studies have shown that the normal approximation can remain reasonable in similar biological contexts [41]. Furthermore, the z-test is robust to deviations from normality, especially when comparing proportions within smaller sample sizes, as is often the case in agricultural and ecological studies where germination rates tend to stabilise and follow predictable patterns [42]. Our primary focus was on comparing proportions across multiple temperature treatments rather than estimating means with associated variability, so the z-test for proportions was chosen as straightforward and appropriate.

3. Results

3.1. Original Documentation on the Occurrence of Asclepias speciosa in Greece

A wild-growing population of *A. speciosa* (Figure 4) was originally discovered in Northern Greece on 16 July 2022 by the second author of this study. The first recorded individuals of this alien species were growing 1.9–2.1 km south-east of the centre of the village of Kapnofyto, in the municipality of Sintiki, the regional unit of Serres, Central Macedonia, Greece. The site is located on the lower part of Mount Vrontous, at an altitude of 540 m above sea level.

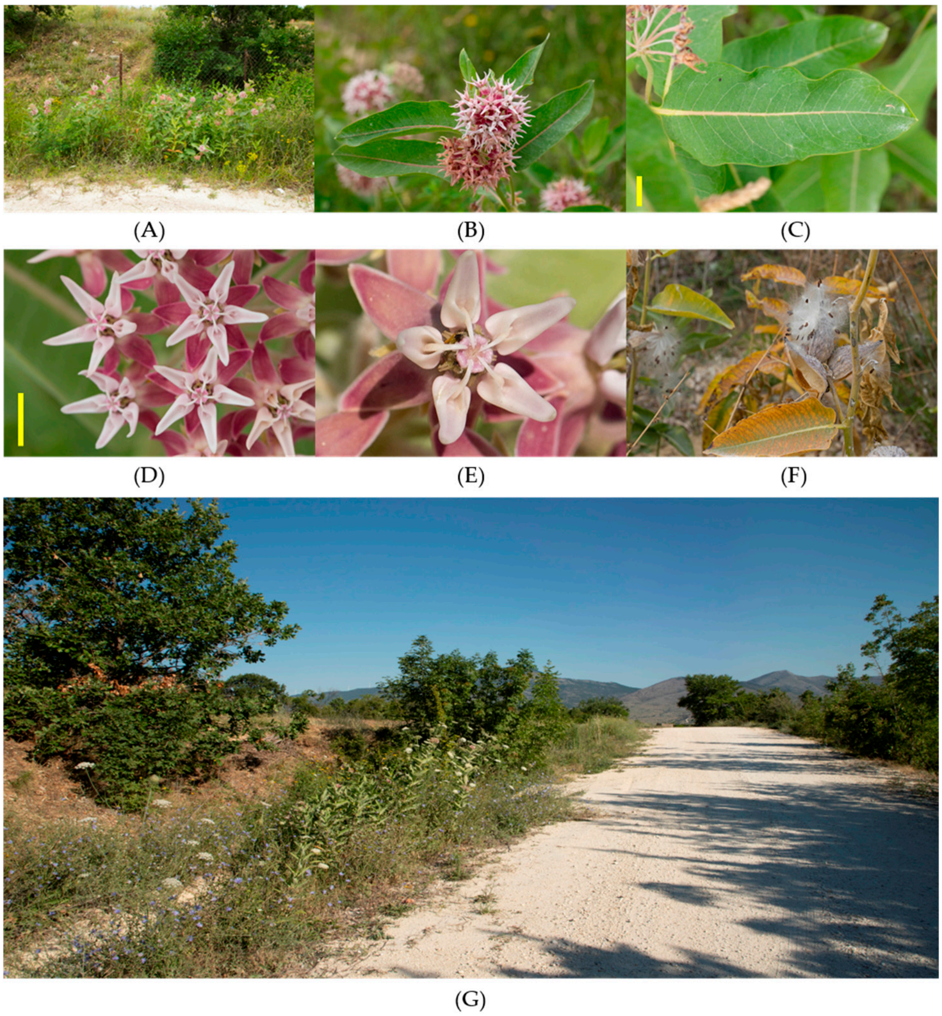


Figure 4. *Asclepias speciosa* near the village of Kapnofyto, Northern Greece: (**A**) colony of naturalised wild individuals in flower; (**B**,**C**) inflorescences and characteristic leaf venation (yellow line: 1 cm); (**D**,**E**) close-ups of flower clusters and an individual flower (yellow line: 1 cm); (**F**) follicles with mature seeds bearing white silky hairs for wind dispersal; and (**G**) general aspect of the original collection site. Photographs by Catherine Dijon.

3.2. Morphological Traits in the Invaded Area

The detected colony of wild plants found in Kapnofyto, Northern Greece (Figure 4), was taxonomically identified by several characteristics as *Asclepias speciosa*, an herbaceous perennial plant with extensive rhizomes. The usually tomentose stems of the plants were stout, simple, and reached a height of 67–123 cm in summer. The grey-green leaves (a total of 43 young and mature leaves from the 8th to 11th pairs from the base were measured on seven plants) were opposite, shortly petiolate (0.5–1.1 cm long), 7.6–15 cm long to 3.7–8.6 cm wide, oval to rather narrowly elliptic or ovate-lanceolate, densely white-tomentose to pilose on the underside, and rather glabrous on the upper side (Table 1). The stems and foliage exuded a milky latex sap when cut. The large fragrant umbellate inflorescences (2–6 per plant, 7.3–9.9 cm in diameter) were developed in loose clusters of 9–28 flowers with densely white-tomentose pedicels (Table 1).

Table 1. Morphological parameters studied on seven *Asclepias speciosa* individuals in the field.

Parameter (Unit)	Range of Values
Stem height (cm)	67.0–123.0
Number of leaf pairs	8.0–11.0
Length of leaf blade (cm)	7.6–15.0
Width of leaf blade (cm)	3.7–8.6
Length of petiole (cm)	0.5–1.1
Number of inflorescences per plant	2.0–6.0
Diameter of inflorescence (cm)	7.3–9.9
Number of flowers in inflorescence	9.0–28.0
Diameter of flowers (cm)	2.1–2.5

The conspicuously large and showy flowers (2.1–2.5 cm in diameter) had lanceolate calyx lobes 4–8 mm long; the purplish-pink corolla had reflexed pale pink lobes 10–15 mm long, and the appendage (hood) was long-attenuate, subulate, inflexed above the style, and glabrous. The anthers were connate, 2.5–3 mm long, with deltoid apical appendages. The fruits (follicles) were fleshy, ovoid-lanceolate, with an attenuated apex 6–9(–12.5) cm long, and were developed on upwardly curved pedicels. The dark reddish-brown, ovoid seeds (ca. 6 mm $\times$ 3.5 mm) with a marginal wing and an apical tuft of white silky hairs were numerous per follicle (split on one side in autumn for seed dispersal). Each seed had a tuft of white silky hairs, allowing them to be effectively dispersed by wind (Figure 4F). These features fulfil the key characters and fall within the range of the description of *A. speciosa* [33]. To provide an indication of the morphological characteristics of the alien colony of *A. speciosa* in Greece, nine morphological parameters were examined in situ in seven plant individuals illustrating their variability (Table 1).

3.3. Population Size and Habitat

The alien plants of *A. speciosa* were growing wild in a shallow roadside ditch, on a calcareous substrate. The road was not asphalted, had little traffic, and was mainly used by local farmers. The observed plant colony was located 500 m north of the Kapnofyto artificial lake, which serves as a water source for irrigation of nearby crops and is also used by fire-fighting helicopters to prevent the spread of wildfires in the surrounding area. There was also a water reservoir located 150 m north of the locality. Within a 10 m radius around the *A. speciosa* individuals, we recorded several native Greek wild plants as co-occurring species that characterise the natural state of the habitat or the niche occupied by the alien colony of *A. speciosa*. The *A. speciosa* plants were found growing close to the shade of two *Quercus pubescens* Willd. trees to the west and a group of *Fraxinus ornus* L. trees to the south. The east side of the road currently overlooks a ravine with a dense tree cover of (relative abundance in parenthesis) *Quercus pubescens* (D), *Q. coccifera* L. (A), and *Acer heldreichii* Orph. ex Boiss. (O). On the hilly west side of the road, the vegetation consisted mainly of lower perennials and some shrubs. From the northwest to the southwest side of the *A. speciosa* location, we noticed the following plant species: *Quercus pubescens* (F), *Quercus coccifera* (F), *Fraxinus ornus* (O), *Cistus creticus* L. (A), *Daucus carota* L. (A), *Lonicera etrusca* Santi (O), *Cichorium intybus* L. (F), *Centaurea macedonica* Boiss. (F), *Xeranthemum annuum* L. (F), *Delphinium consolida* L. (*Consolida regalis* Gray) (F), *Lomelosia argentea* (L.) Greuter & Burdet (F), *Onosma heterophylla* Griseb. (F), *Achillea crithmifolia* Waldst. & Kit. (F), *Jasione heldreichi* Boiss. & Orph. (F), *Hypericum olympicum* (O), *Campanula scutellata* (O), and *Silene frivaldszkyana* (R). Among them, only *C. intybus* may be considered as a native ruderal or synanthropic plant [34] associated with anthropogenic activities [43].

The population of *A. speciosa* was found on a single location on 16 July 2022. A total of 20 flowering individuals with a few follicles were counted on an area of approximately 2.5 m × 1 m (area of occupancy). Mature seeds were collected from only three individuals on 16 February 2023, as the wind had probably dispersed seeds from other fruiting individuals, as evidenced by empty follicles. On 10 June 2023, we revisited the locality to check the colony after the heavy rains and storms of the spring. The colony was found to be in good condition and persisted despite the gully erosion that had damaged the road and carried a lot of alluvial deposits into the ditches. On 29 June 2023, we noticed that some plants (>10) were leaning due to the alluvium that had partially covered some stems. However, the road had been partially repaired. On this day, we counted 36 plant individuals in an area of about 3 m × 1 m (area of occupancy). A few days later, a construction machine dug the trench completely, destroying most of the aerial parts of the plants. The soil removed from the ditch was thrown into a deeper ditch on the opposite side of the road. On 8 July 2023, we found only a single flowering plant in good condition. Some of the other plants found alive were without tops or lying down, and some small plants had no flowers. The remaining living plants were all growing close to the road and not in the ditch.

The next visit to the site was on 26 July 2024. The colony was found to be in good condition and consisted of 50 plants ranging in height from 50 cm to 123 cm, with 15 plants in flower and at least five of these bearing follicles. All plants were in the upper part of the ditch and on the roadside, with none present at the bottom of the ditch, having been uprooted during ditch maintenance work in 2023. From the few remaining roots left after the disturbance in 2023, the colony recovered over an area of approximately 0.7 m × 3 m. No plants were observed on the east side of the road, although some soil and some uprooted *A. speciosa* plants from the ditch had been displaced there by the construction machinery in 2023. Despite the near destruction of the plants in late June 2023, the colony at the same site appeared to be able to recover, probably through vegetative renewal.

No evidence of herbivory was recorded in the Greek colony of *A. speciosa*, probably due to the milky latex sap content, which makes the aerial parts as unpalatable for grazing animals [33].

3.4. Local Pollinators for Asclepias speciosa in Its Alien Range

In this newly recorded population of *A. speciosa* in Greece, the attractiveness of *A. speciosa* flowers to many local insects was recorded (Figure 5).

The visiting insect species recorded were *Apis mellifera* (Linnaeus, 1758; Hymenoptera: Apidaea), *Macroglossum stellatarum* (Linnaeus, 1758; Hymenoptera: Sphingidae), *Limenitis reducta* (Staudinger, 1901; Lepidoptera: Nymphalidae), *Lycaena tityrus* (Poda, 1761;

Lepidoptera: Lycaenidae), *Cetonia aurata* (Linnaeus, 1758; Coleoptera: Scarabaeidae), *Sarcophaga carnaria* (Linnaeus, 1758; Diptera: Sarcophaginae), *Aphis nerii* (Fonscolombe, 1841; Hemiptera: Aphididae), *Camponotus* sp. (Hymenoptera: Formicidae), *Rhynocoris iracundus* (Poda, 1761; Hemiptera: Reduviidae), and *Lygaeus* sp. (Hemiptera: Lygaeidae). It is likely that the pollinia (cohesive pollen mass) of *A. speciosa* may attach to the legs of pollinators (at least to some of the recorded insect species) and are transported to other flowers.

Figure 5. *Cont.*

(G) (H)

(I) (J)

Figure 5. Local native insect species visiting the flowers of *Asclepias speciosa* in the invaded area of Northern Greece, such as the Lepidoptera *Limenitis reducta* (**A$_1$**,**A$_2$**, illustrating the outer and inner sides of the wings) and *Lycaena tityrus* (**B**), the Hymenoptera *Apis mellifera* (**C**), *Macroglossum stellatarum* (**D**), and *Camponotus* sp. (**I**); the Coleoptera *Cetonia aurata* (**D**,**G**,**H**), the Hemiptera *Rhynocoris iracundus* (**E**), *Lygaeus* sp. (nymph) (**F**), and *Aphis nerii* (**J**). Photographs by Catherine Dijon.

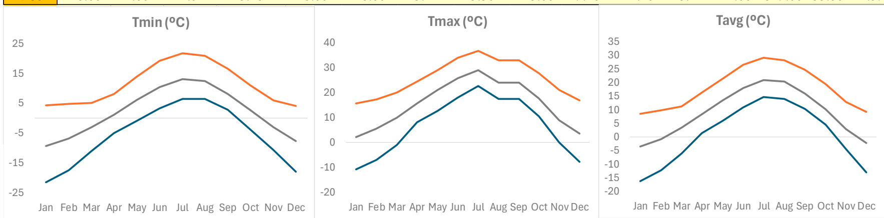
3.5. Bioclimatic Preferences of Asclepias speciosa in Native Range

Based on the natural distribution of *A. speciosa* in North America (Figure 1), the bioclimatic profile revealed a wide range of ecological tolerance for *A. speciosa* (Figure 6). The native populations of *A. speciosa* appear to thrive in areas and natural habitats that experience low winter temperatures, with minimum mean monthly temperature in January (−3.63 °C ± 6.04 °C), while the mean temperature rises above freezing by March (3.38 °C ± 4.05 °C) and continues to rise into the summer months, peaking in July (20.91 °C ± 3.21 °C). After this peak, temperatures gradually decrease again towards the winter months. The data suggest that *A. speciosa* is highly resilient to cold regimes and is naturally adapted to regions with harsh winter conditions (mean of T_{min} = −9.33 °C ± 6.45 °C in January). However, native populations of *A. speciosa* seem to avoid areas with high summer temperatures (mean of T_{max} = 28.78 °C ± 3.17 °C in July). This fact underlines the species' preference for temperate climates with moderate summer heat, which probably determines the extreme natural distribution limits in its native range. Regarding precipitation data, *A. speciosa* naturally occurs in habitats within its native range that are characterised by moderate precipitation levels, both during the coldest months (154.74 mm ± 210.37 mm) and the warmest (164.01 mm ± 88.50 mm) months of the year. As evidenced by the rainfall patterns during the driest periods in its native range (56.14 mm ± 21.28 mm), rainfall does not drop to zero (Figure 5); the latter indicates that the species can persist in environments where there is a consistent moderate amount of moisture throughout the year. The overall bioclimatic pattern suggests that, although *A. speciosa* is tolerant of varying rainfall patterns in its native range, it is still dependent on at least minimal precipitation, even in the driest seasons (Figure 6).

Temperature and precipitation regimes for 100 native sites of *Asclepias speciosa* in USA

Months	Minimum Temperature, Tmin (°C)				Maximum Temperature, Tmax (°C)				Average Temperature, Tavg (°C)				Precipitation (mm)			
	Tmin	Tmax	Tmean	std	Tmin	Tmax	Tmean	std	Tmin	Tmax	Tmean	std	Pmin	Pmax	Pmean	std
Jan	-21.50	4.20	-9.33	6.45	-11.00	15.40	2.07	6.04	-16.30	8.40	-3.63	6.04	5.00	298.00	52.46	73.11
Feb	-17.60	4.70	-6.87	5.43	-7.20	17.10	5.27	5.44	-12.30	9.70	-0.79	5.24	6.00	250.00	44.31	57.74
Mar	-11.10	5.10	-3.02	4.00	-1.20	19.90	9.79	4.45	-6.10	11.20	3.38	4.05	10.00	258.00	52.99	52.19
Apr	-5.10	8.00	1.13	3.16	7.90	24.30	15.41	3.42	1.40	16.20	8.27	3.10	7.00	329.00	55.80	77.59
May	-1.00	13.90	6.00	3.29	12.60	28.90	20.77	3.18	6.00	21.30	13.38	3.08	10.00	131.00	58.38	30.83
Jun	3.20	19.10	10.43	3.72	17.80	33.80	25.57	3.44	10.80	26.40	17.99	3.38	6.00	137.00	58.97	35.40
Jul	6.40	21.70	13.03	3.68	22.40	36.50	28.78	3.17	14.70	29.10	20.91	3.21	4.00	117.00	51.78	31.66
Aug	6.40	20.80	12.37	3.45	17.20	32.70	23.76	3.02	13.90	28.20	20.34	2.98	8.00	117.00	52.46	29.66
Sep	2.80	16.50	8.07	3.27	17.20	32.70	23.76	3.02	10.20	24.60	15.92	2.93	11.00	114.00	47.63	24.29
Oct	-4.00	10.90	2.59	3.09	10.40	27.70	17.44	3.29	4.40	19.30	10.01	2.96	12.00	132.00	45.44	28.35
Nov	-10.70	5.90	-3.01	3.97	-0.20	20.90	8.78	4.26	-4.40	12.90	2.89	3.80	8.00	305.00	56.93	68.71
Dec	-18.00	4.00	-7.81	5.46	-8.00	16.60	3.42	5.30	-13.00	9.20	-2.20	5.12	7.00	329.00	55.80	77.59

	Min	Max	Mean	std
Annual Mean Temperature (Bio_1)	2.78	17.43	8.87	3.15
Mean Diurnal Range (Bio_2)	9.79	20.35	13.82	2.23
Isothermality (Bio_3)	22.77	51.94	36.99	7.49
Temperature Seasonality (Bio_4)	361.66	1292.49	893.52	235.01
Max Temperature of Warmest Month (Bio_5)	22.70	36.50	28.99	3.04
Min Temperature of Coldest Month (Bio_6)	-21.50	4.00	-9.36	6.43
Temperature Annual Range (Bio_7)	19.50	49.40	38.35	6.80
Mean Temperature of Wettest Quarter (Bio_8)	-3.68	26.70	13.67	7.86
Mean Temperature of Driest Quarter (Bio_9)	-11.53	21.07	3.09	10.57
Mean Temperature of Warmest Quarter (Bio_10)	13.67	27.87	19.80	3.12
Mean Temperature of Coldest Quarter (Bio_11)	-13.83	9.12	-2.21	5.45
Annual Precipitation (Bio_12)	191.00	1947.00	627.69	382.53
Precipitation of Wettest Month (Bio_13)	28.00	329.00	101.21	67.57
Precipitation of Driest Month (Bio_14)	4.00	28.00	14.65	6.20
Precipitation Seasonality (Bio_15)	12.95	87.51	52.94	15.45
Precipitation of Wettest Quarter (Bio_16)	75.00	932.00	273.70	192.60
Precipitation of Driest Quarter (Bio_17)	19.00	100.00	56.14	21.28
Precipitation of Warmest Quarter (Bio_18)	31.00	343.00	164.01	88.50
Precipitation of Coldest Quarter (Bio_19)	19.00	877.00	154.74	210.37



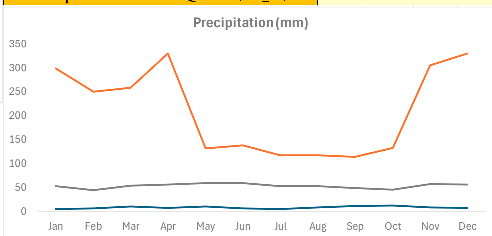
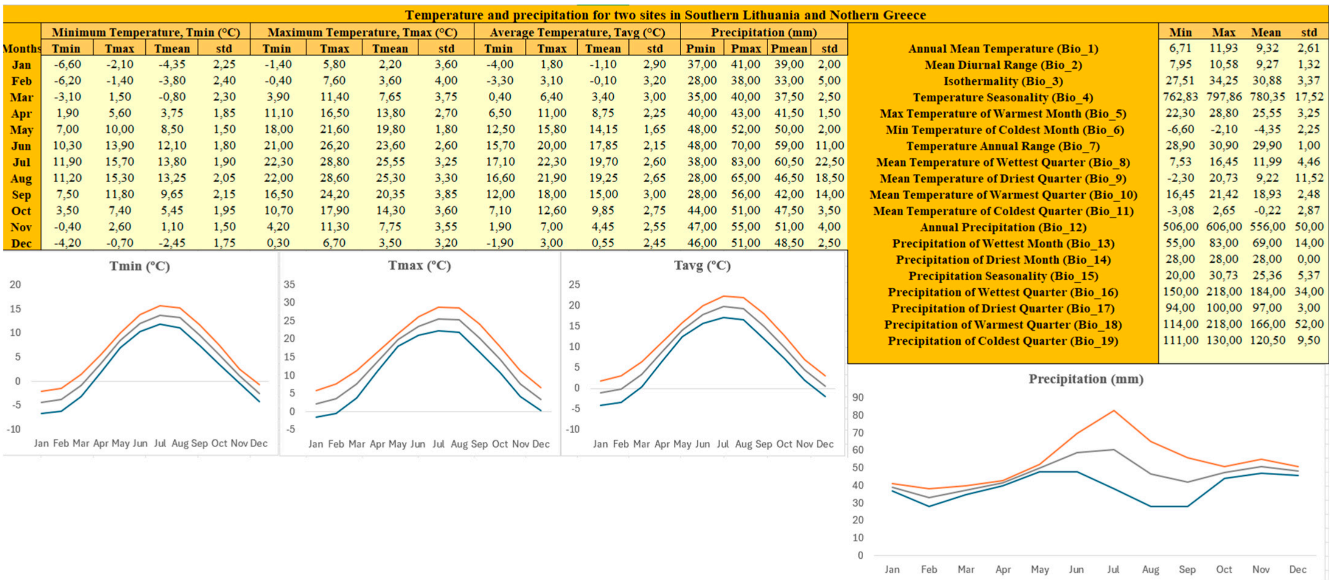


Figure 6. Bioclimatic profile across the native range of wild-growing populations of *Asclepias speciosa* [3] using 100 selected distribution points (see Section 2), which are linked in the GIS to geodatabases (WorldClim version 2.1) to provide values for minimum, maximum, and mean monthly temperatures (°C), monthly precipitation (mm), and calculated values for 19 bioclimatic variables (minimum, maximum, mean, and standard deviation are shown based on 1970–2000 data). The colours of the plotted lines indicate the minimum (blue), maximum (orange), and mean (grey) monthly values for temperature (°C) and precipitation (mm).

3.6. Bioclimatic Preferences of Asclepias speciosa in Its Alien Range

The bioclimatic profile of *A. speciosa* in its non-native (alien) range in Europe currently is exemplified by one locality in Southern Lithuania and another in Northern Greece (Figure 7). Despite its limited occurrence, the bioclimatic profiling showed that the alien populations of this species can thrive in regions with relatively low winter temperatures. In January, mean monthly temperatures were shown to reach −1.10 °C ± 2.90 °C, while, in March, temperatures were shown to rise above freezing, reaching a mean of 3.40 °C ± 3.00 °C. Temperatures in these areas were shown to increase gradually, reaching a maximum of 19.70 °C ± 2.60 °C in July. In August, temperatures remained relatively high, averaging 19.25 °C ± 2.65 °C, before gradually decreasing towards the winter months. At these European sites, the alien populations of this species probably experienced persistently low temperatures (mean temperature of the coldest quarter is −0.22 °C ± 2.87 °C, with the minimum of T_{min} reaching −6.6 °C in January). Conversely, even during the warmest periods, temperatures did not become excessively high, as indicated by the mean temperature of the warmest quarter (18.93 °C ± 2.48 °C), or the observation of the maximum of T_{max} ever recorded in July (28.80 °C). This profile suggested the option that the alien populations of *A. speciosa* can tolerate cooler climates and do not prefer regions with extreme heat, even in its non-native (alien) range (Figure 6). The precipitation data also suggested that *A. speciosa* alien populations could thrive in regions with relatively consistent precipitation throughout the year. During the coldest season, the average precipitation was 120 mm ± 9.5 mm (Bio 19), while, during the warmest season, it increased to 166 mm ± 52 mm (Bio 18). Even during the driest season, the alien populations of this species still seemed to receive a significant amount of precipitation, with an average of 97 mm ± 3 mm (Bio 17). This suggested that *A. speciosa* can adapt to environments with stable moisture availability in its alien range, even during drier periods (Figure 7).



Temperature and precipitation for two sites in Southern Lithuania and Nothern Greece

Months	Minimum Temperature, Tmin (°C) Tmin	Tmax	Tmean	std	Maximum Temperature, Tmax (°C) Tmin	Tmax	Tmean	std	Average Temperature, Tavg (°C) Tmin	Tmax	Tmean	std	Precipitation (mm) Pmin	Pmax	Pmean	std
Jan	-6,60	-2,10	-4,35	2,25	-1,40	5,80	2,20	3,60	-4,00	1,80	-1,10	2,90	37,00	41,00	39,00	2,00
Feb	-6,20	-1,40	-3,80	2,40	-0,40	7,60	3,60	4,00	-3,30	3,10	-0,10	3,20	28,00	38,00	33,00	5,00
Mar	-3,10	1,50	-0,80	2,30	3,90	11,40	7,65	3,75	0,40	6,40	3,40	3,00	35,00	40,00	37,50	2,50
Apr	1,90	5,60	3,75	1,85	11,10	16,50	13,80	2,70	6,50	11,00	8,75	2,25	40,00	43,00	41,50	1,50
May	7,00	10,00	8,50	1,50	18,00	21,60	19,80	1,80	12,50	15,80	14,15	1,65	48,00	52,00	50,00	2,00
Jun	10,30	13,90	12,10	1,80	21,00	26,20	23,60	2,60	15,70	20,00	17,85	2,15	48,00	70,00	59,00	11,00
Jul	11,90	15,70	13,80	1,90	22,30	28,80	25,55	3,25	17,10	22,30	19,70	2,60	38,00	83,00	60,50	22,50
Aug	11,20	15,30	13,25	2,05	22,00	28,60	25,30	3,30	16,60	21,90	19,25	2,65	28,00	65,00	46,50	18,50
Sep	7,50	11,80	9,65	2,15	16,50	24,20	20,35	3,85	12,00	18,00	15,00	3,00	28,00	56,00	42,00	14,00
Oct	3,50	7,40	5,45	1,95	10,70	17,90	14,30	3,60	7,10	12,60	9,85	2,75	44,00	51,00	47,50	3,50
Nov	-0,40	2,60	1,10	1,50	4,20	11,30	7,75	3,55	1,90	7,00	4,45	2,55	47,00	55,00	51,00	4,00
Dec	-4,20	-0,70	-2,45	1,75	0,30	6,70	3,50	3,20	-1,90	3,00	0,55	2,45	46,00	51,00	48,50	2,50

	Min	Max	Mean	std
Annual Mean Temperature (Bio_1)	6,71	11,93	9,32	2,61
Mean Diurnal Range (Bio_2)	7,95	10,58	9,27	1,32
Isothermality (Bio_3)	27,51	34,25	30,88	3,37
Temperature Seasonality (Bio_4)	762,83	797,86	780,35	17,52
Max Temperature of Warmest Month (Bio_5)	22,30	28,80	25,55	3,25
Min Temperature of Coldest Month (Bio_6)	-6,60	-2,10	-4,35	2,25
Temperature Annual Range (Bio_7)	28,90	30,90	29,90	1,00
Mean Temperature of Wettest Quarter (Bio_8)	7,53	16,45	11,99	4,46
Mean Temperature of Driest Quarter (Bio_9)	-2,30	20,73	9,22	11,52
Mean Temperature of Warmest Quarter (Bio_10)	16,45	21,42	18,93	2,48
Mean Temperature of Coldest Quarter (Bio_11)	-3,08	2,65	-0,22	2,87
Annual Precipitation (Bio_12)	506,00	606,00	556,00	50,00
Precipitation of Wettest Month (Bio_13)	55,00	83,00	69,00	14,00
Precipitation of Driest Month (Bio_14)	28,00	28,00	28,00	0,00
Precipitation Seasonality (Bio_15)	20,00	30,73	25,36	5,37
Precipitation of Wettest Quarter (Bio_16)	150,00	218,00	184,00	34,00
Precipitation of Driest Quarter (Bio_17)	94,00	100,00	97,00	3,00
Precipitation of Warmest Quarter (Bio_18)	114,00	218,00	166,00	52,00
Precipitation of Coldest Quarter (Bio_19)	111,00	130,00	120,50	9,50

Figure 7. Bioclimatic profile of the pilot wild populations of *Asclepias speciosa* in its current alien range (Southern Lithuania and Northern Greece) linked in the GIS with geodatabases (WorldClim version 2.1) with values of minimum, maximum, and mean monthly temperatures (°C), monthly precipitation (mm), and calculated values for 19 bioclimatic variables (minimum, maximum, mean, and standard deviation are shown based on data from 1970 to 2000). The colours of the plotted lines indicate the minimum (blue), maximum (orange), and mean (grey) monthly values for temperature (°C) and precipitation (mm).

3.7. Seed Germination of *Asclepias speciosa* in the Alien Range

The number of germinated seeds of *A. speciosa* was significantly affected by temperature (Table 2). At an incubation temperature of 15 °C, significantly more seeds germinated (9 out of 20) compared to 20 °C (2 out of 20). However, no significant differences in the number of germinated seeds were observed between the incubation temperatures of 10 °C and 15 °C (6 and 9 out of 20 seeds, respectively) or between 10 °C and 20 °C (6 and 2 out of 20 seeds, respectively).

Table 2. Comparisons of the numbers of germinated seeds between the incubation temperatures. Ratios (proportions) of germinated seeds at each incubation temperature are calculated. The z-test is used for comparisons between ratios.

<table>
<tr><th colspan="2" rowspan="2">Ratios</th><th colspan="3">Comparison of the Ratios</th></tr>
<tr><th>z-Value</th><th>p-Value</th><th>Conclusion</th></tr>
<tr><td>10 °C</td><td>15 °C</td><td rowspan="2">−0.980</td><td rowspan="2">0.339</td><td rowspan="2">Non-significant difference</td></tr>
<tr><td>0.30 [1]</td><td>0.45</td></tr>
<tr><td>10 °C</td><td>20 °C</td><td rowspan="2">1.581</td><td rowspan="2">0.130</td><td rowspan="2">Non-significant difference</td></tr>
<tr><td>0.30</td><td>0.10</td></tr>
<tr><td>15 °C</td><td>20 °C</td><td rowspan="2">2.479</td><td rowspan="2">0.023</td><td rowspan="2">Significant difference</td></tr>
<tr><td>0.45</td><td>0.10</td></tr>
</table>

[1] At each incubation temperature, the ratio of germinated seeds was calculated by dividing the number of germinated seeds by the total number of seeds incubated at that temperature.

The seeds incubated at 15 °C began to germinate after the first week (Figure 8), and germination was completed six weeks after the start of the germination test. In contrast, seeds incubated at 10 °C and 20 °C started germination two weeks later than those at 15 °C.

The germination of seeds incubated at 10 °C was completed after eight weeks, whereas those incubated at 20 °C completed germination after six weeks.

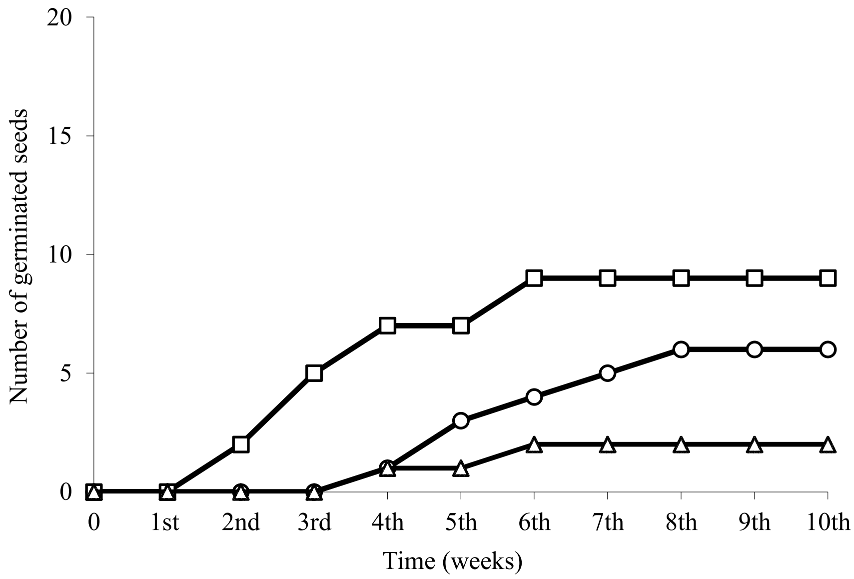


Figure 8. Diagram illustrating the cumulative number of germinated seeds of *Asclepias speciosa* incubated at 10 °C, 15 °C, and 20 °C (○ 10 °C, □ 15 °C, and Δ 20 °C).

4. Discussion

4.1. Period of First Introduction and Mode of Introduction

Most probably, the area around the village of Kapnofyto and the exact locality where *A. speciosa* was originally found in Northern Greece in 2022 has not been botanically investigated for many years. For example, it is known that, in May 2006, Eckhard Willing carried out a systematic botanical collection routine along roads and adjacent habitats in Northern Greece, including the area south-west of the village of Kapnofyto in Serres, stopping every 5 km to collect specimens, but no record of *A. speciosa* was reported at that time [21]. In addition, several visits made by Kit Tan in the late 1990s and early 2020s on the way to Achladohori in north-eastern Greece were retrospectively reviewed, but there were no records of *A. speciosa* [21]. The wild population of *A. speciosa* discovered in Northern Greece on 16 July 2022 confirms the assumptions of Kit and Sister Pachomia regarding the recent arrival of this species in Greece [21]. It can therefore be concluded that the species arrived in Greece in the early 2020s. Subsequent thorough inspections of the area carried out by the second author of this study as well as from other collectors [21] have not yielded additional wild-growing populations of *A. speciosa* in the area. The same locality from which *A. speciosa* was recently reported as a new record for the Greek flora [21] certainly lacks descriptive precision and geospatial accuracy; the original collection locality of *A. speciosa* in Greece as reported here is 1.9 km to 2.1 km south-east of the centre of the village of Kapnofyto (depending on whether the distance is calculated from the centre of the village or its fringe).

One can only speculate how *A. speciosa* was introduced to the Greek locality where it was discovered. Given that *A. speciosa* is already traded worldwide as a highly valued garden ornamental (e.g., https://www.beanplace.co.uk/products/asclepias-speciosa, etc., accessed on 24 October 2024), it is likely that *A. speciosa* was introduced into Greece as an ornamental plant (e.g., in the nearby village of Kapnofyto) and perhaps was later dumped by the roadside where the alien colony was established. Such a mode of introduction is also known for *A. syriaca* in Bulgaria and Lithuania [44], where viable seeds or rhizomes are most often discarded with garden waste to dump sites and riversides, allowing the establishment and further colonisation of suitable nearby habitats. The closely related and similar *A. syriaca* was first cultivated in Europe for ornamental and melliferous purposes, as a potential fibre plant, for biofuel and latex production [45]. In the 18th and 19th centuries, numerous studies on its potential uses had been carried out, for example, in Germany and Russia, with its cultivation abandoned or revived from time to time [46]. It is highly probable that the same purpose of introduction may apply to the Greek *A. speciosa* as well, or even to other neighbouring areas such as Southern Bulgaria; however, the latter species may have been overlooked or misidentified with *A. syriaca* in at least a number of cases as it happened in Lithuania [4].

4.2. Detection and Monitoring Issues

Asclepias syriaca is the most widespread and invasive species of the genus *Asclepias* in some Southern and Central European countries [14–18]. *Asclepias syriaca* has been observed in the Adriatic-Ionian region, and its occurrences have increased in the last two decades [47]. Due to its invasiveness and significant negative impact on native European (including Balkan) habitats and agroecosystems, *A. syriaca* has been included in the list of alien species of European Union concern (EU 2016/1142, EU 2017/1263) by the provisions of the Regulation of the European Parliament and of the Council of 22 October 2014 on Invasive Alien Species (EU Regulation 1143/2014). According to a field study conducted in Slovakia, *A. syriaca* does not affect species diversity but significantly reduces the cover of native plant species. The same study argues that *A. syriaca* does not pose a threat to soil nematode communities but has a negative impact on native plants [48]. Although *A. syriaca* occurs in several countries of the Balkan Peninsula, and its Bulgarian records are very close to the nearby border with Northern Greece [23,44] where *A. speciosa* was first found as documented herein, the former species (*A. syriaca*) has not been officially reported from Greece. Nevertheless, the resemblance of *A. syriaca* to the quite variable but similar in habit *A. speciosa* has been associated with misidentification problems [4], highlighting that the latter species (*A. speciosa*) has long been overlooked or misidentified due to resemblance to *A. syriaca*, especially when plants are examined or recorded at the vegetative stage. According to the latter study [4], the possible occurrence of *A. speciosa* in other regions of Europe cannot be excluded, and the discovery of *A. speciosa* in Northern Greece is consistent with this hypothesis.

The initial introduction event of *A. speciosa* into Greece is not yet known. The possible ornamental cultivation of the species in nearby urban areas (e.g., in the village of Kapnofyto) in the recent past could partly address this inquiry, as the seeds are rather easily dispersed by animals, with clothes, transport, and wind, suggesting that the initial individuals may have escaped from a garden. However, given the documented misidentifications in Lithuania [4], another possibility that cannot be easily excluded and should be further investigated is that *A. speciosa* was established in Bulgaria a long time ago without being recognised by local scientists; this implies that at least some of the records of *A. syriaca*, which is regularly monitored in Bulgaria [23,44], may actually refer to *A. speciosa,* in a similar fashion to what was proven in the case of Lithuania [4]. In such an unfortunate case (*A. speciosa* still unrecognised, undocumented, or under the guise of *A. syriaca*), seeds of *A. speciosa* could have been accidentally introduced into Kapnofyto in Northern Greece (where this new alien plant was found) by strong wind currents or through anthropochory and zoochory (attached to human clothing or animal fur) directly from the adjacent border area in Bulgaria, where milkweed specimens had been misidentified as *A. syriaca* [23,44] instead of *A. speciosa*. However, to verify or reject this scenario, further inspection and verification of collected specimens is required, as was performed, for example, in Lithuania [4].

4.3. Implications Concerning the EU Regulation

According to the requirements of the EU Regulation 1143/2014, the invasion of *A. syriaca* in native plant communities in Europe should be regularly monitored due to the fragmentary information available; however, confusion with the closely related and similar *A. speciosa* should also be carefully assessed to avoid biased assessments [4]. As evidenced in the alien range of the species (Lithuania and Greece), *A. syriaca* can be most easily distinguished from *A. speciosa* based on the shape and size of the flowers at the flowering, on the morphology of hoods during fruiting stages or even observing leaves and pedicels at the vegetative stage. At the flowering stage, the two species differ in the number of flowers in the inflorescence. Although the diameter of the inflorescence is almost the same in both species, those of *A. speciosa* in the alien range of the species (Europe) are more lax and contain almost half as many flowers (mean 36.2 ± 7.2) as those of *A. syriaca* (61.2 ± 19.5) [4]. During fruiting, the hoods of *A. speciosa* as evidenced in the alien range of the species (Europe) are 10–13 mm long, with an elongated tongue-like apex, and the horns are longer and apparently curved inwards, while the hoods of *A. syriaca* are 3.5–5.0 mm long, with a rounded apex, and the horns are short and only slightly curved inwards [4]. At the vegetative stage, another reliable key character that can be used in monitoring programmes is the indumentum of the pedicels: the pedicels of *A. speciosa* are densely covered with short white hairs as evidenced in the alien range of the species (Europe), whereas those of *A. syriaca* are glabrous or have only a few such hairs [4]. Furthermore, several leaf characteristics are equally reliable for distinguishing *A. speciosa* and *A. syriaca*., i.e., the leaf blade of the middle cauline leaves of *A. speciosa* is broadly ovate or elliptic and widest at its slightly cordate base (as evidenced in the alien range of the species in Europe), whereas the leaf blade of *A. syriaca* is ovate or elliptic with a rounded or slightly cuneate base, widest near the middle [4]. Additionally, the leaves of *A. speciosa* are significantly longer and wider than those of *A. syriaca* [4]. These key flowering or vegetative characteristics should be carefully considered in monitoring protocols of *A. syriaca* across Europe, especially during fieldwork as such key characters can ensure informed and precise taxonomic identification [4, taxonomic key for diagnosis] as well as unbiased invasion/distribution results.

4.4. Bioclimatic Profiling in Native and Alien Ranges

The GIS has long been used to analyse the potential and current spatial distribution of target species, to assess populations and ranges, or to measure and monitor biodiversity patterns in attempts to identify management priorities [49–52]. The GIS has also been used as a tool for the specific comparisons of ecological patterns between local and regional scales in habitat suitability studies or for analysing the impact of alien species on native plants [53] using static information from botanical collections to evaluate species distribution ranges, or to unveil ecological preferences with respect to local climatic regimes [32,54] or for invasive alien species such as *Solanum elaegnifolium* Cav. in Greece [55]. The bioclimatic profile first-time constructed herein for *A. speciosa* according to its native range has revealed that the species thrives in temperate environments, showing tolerance to relatively low winter temperatures, but it is less well suited to moderate-to-high summer heat regimes. Consistent precipitation throughout the year appears to be a critical factor in the persistence of the species populations in its native habitats. The large standard deviations observed in this bioclimatic profile were rather expected, reflecting the species' broad geographic and altitudinal distribution [33], which covers a wide range of longitudes (from 92° W to 124° W), latitudes (32° N to 50° N), and elevations from sea level to 5443 m above sea level.

The bioclimatic profile of the non-native (alien) distribution range of *A. speciosa* in Europe closely matches the climatic conditions of its native range in North America, suggesting that the European sites invaded to date are within the species' preferred ecological range. The climatic conditions in the non-native European sites appear to be within the ecological tolerance of the species and may represent possible extremes (Southern Lithuania, Northern Greece) within which the species may continue to spread as an invasive alien species. The latter may prove to have significant implications for a large part of the European territories, especially due to the climate crisis.

4.5. Reproductive Potential and Pollinators

In North America, the fragrant flowers of the native populations of *A. speciosa* attract butterflies, bees, and other insects [33]. A total of 128 beneficial insects have been recorded for *A. speciosa* in central Washington State, WA, USA [56]. In its native range, *A. speciosa* is known to be one of the primary larval hosts for the monarch butterfly (*Danaus plexippus* Linnaeus, 1758; Lepidoptera: Nymphalidae), providing an example of a specialist plant–insect relationship, with the monarch butterfly caterpillar feeding exclusively on members of the genus *Asclepias*. As a result, restoration programmes involving *A. speciosa* are specifically undertaken in its native range to support and enhance *Danaus plexippus* populations [56]. In its alien range in Northern Greece, nearly a dozen of local insect species was reported to visit *A. speciosa* flowers, likely providing effective pollination services and facilitating fruit and seed development. Noteworthy among them there was a native seed bug species (*Lygaeus* sp.; Hymenoptera: Lygaeidae). Taking into account that the common milkweed bug, *Lygaeus kalmii* (Stål, 1874; Hymenoptera: Lygaeidae) feeds almost predominantly with flower nectar and milkweed seeds of *A. speciosa* within its native range [57], it becomes apparent that a corresponding sister seed bug species of Greece's entomofauna has already responded positively to the introduction of the alien showy milkweed.

In the case of alien ornamental plants, the lack of seed production due to pollen sterility or a lack of compatible pollen is known to act as an initial barrier to their invasion success, providing insight into why some ornamental species fail to become invasive [58]. Furthermore, it has been reported that, in some cases, insufficient pollinator services can hinder invasion success [58]. In the herein study, in situ detected pollination services and seed formation, and the ex situ germination of *A. speciosa* were demonstrated as possible for the first time and were found be effective, thus providing evidence regarding the fully accomplished naturalisation of *A. speciosa* in Northern Greece. Previous studies [45] have mentioned that roads and associated anthropogenic disturbance regimes can induce the spread of the closely related and similar *A. syriaca*, highlighting that management and prevention measures should be applied along roadsides. As this is also true for other perennial alien invasive plants of American origin [55], and, due to similar habitat preferences and reproductive strategies of *A. syriaca* and *A. speciosa*, such management and prevention measures should probably also be applied to *A. speciosa*.

The present study is the first to confirm the potential for sexual reproduction of the alien *A. speciosa* in Northern Greece. In the Kapnofyto nearby area, we noticed that the colony of *A. speciosa* expanded between 2022 and 2023 by vegetative renewal, probably spreading by long rhizomes. However, we did not find any new populations that were established around the primary site due to seed dispersal and subsequent germination. It has been argued that a major obstacle to the spread of this species in its alien range is the apparent absence of sexual reproduction in the studied populations in Lithuania [4], as the absence of sexual reproduction significantly reduces the possibility of spreading and occupying new habitats. However, this is not the case for the Greek occurrence of *A. speciosa*, as well-developed fruits and ripe seeds were regularly observed in situ, and ex situ seed tests performed herein proved that the seeds were able to germinate well at 15 °C without cold stratification to overcome dormancy mechanisms. This field study in Northern Greece revealed that *A. speciosa* can establish colonies that spread through long underground rhizomes and can set ripe fruits with viable seeds, while the ex situ germination experiments performed herein showed that its viable seeds are able to germinate appropriately without innate restrictions. This dual mode of reproduction—both sexual and asexual—as herein documented for the first time in its alien range, renders *A. speciosa* as a potentially strong invader in Greece. Therefore, early warning systems should be enabled to monitor its future invasion before it is too late to act.

4.6. Seed Germination of Asclepias speciosa in Its Invaded Range

The present study documented that *A. speciosa* can set fruits regularly in Northern Greece and that its seeds are ripe in their follicles by early autumn, waiting for wind dispersal throughout fall and during winter unlike with reports from Lithuania [4].

According to Baskin and Baskin [59], *Asclepias* seeds can exhibit physiological dormancy that can be broken by cold stratification. However, seed dormancy has been found to be highly variable both within and between different *Asclepias* species and populations, and the duration of cold stratification required to break dormancy may also vary [60]. A previous study has reported that, in most *A. speciosa* populations [60], the germination rates may exceed 80% at alternating temperatures of 15/25 °C with significant variation in seed dormancy between populations (half with no dormancy, half requiring a cold stratification period of 2–4 weeks to fully break dormancy). Notably, in populations where dormancy has been present, the germination rate of seeds without cold stratification could still reach approximately 55% [60]. Another study reported that *A. speciosa* seeds are often dormant, requiring cold stratification for germination with considerable variation among populations [33]. Consequently, the proposed germination protocols for *A. speciosa* to date indicate clearly that cold stratification is not always necessary for seed germination [61,62].

In the present study, the germination of *A. speciosa* seeds ripened in its alien range was investigated for the first time, and the collected seeds were not subjected to cold stratification. Nevertheless, 9 out of 20 seeds (45%) germinated at an incubation temperature of 15 °C. It is likely that cold stratification would have further improved the germination rates of *A. speciosa* seeds. Incubation temperature had a significant effect on seed germination. Increasing the controlled temperature from 15 °C to 20 °C resulted in a significant decrease in the number of germinated seeds. A similar trend was observed in a previous study [60], where ca. 30% decrease in germination can be observed when increasing the alternating incubation temperature from 15/25 °C to 20/30 °C. Therefore, it is possible that cold stratification may mitigate the effect of temperature on germination of *A. speciosa*, allowing seeds to germinate over a wider range of temperatures. Undoubtedly, further research into seed germination of *A. speciosa* in its alien range is needed, with additional experiments to fully determine the germination requirements of the species, as well as the exact type of seed dormancy in its alien range. In the non-native distribution range in Europe, the mature seeds are naturally dispersed in autumn or during winter, and the germination of a proportion of them without dormancy probably occurs in October–November when climatic conditions such as temperature (around 10 °C) and adequate soil moisture due to precipitation are favourable for the survival of the seedlings, depending, however, on how low the winter temperatures are. Physiologically dormant seeds are likely to be first exposed to low winter temperatures, with germination occurring possibly later in early spring. Once a new colony is established, it can spread vegetatively through long rhizomes. This dual mode of reproduction should be considered in future monitoring programmes focusing on *A. speciosa*.

4.7. Potential Invasion and Need for Early Warning Systems

Although *A. speciosa* has only recently been reported from Europe [4], and even more recently from Greece [21], the invasion impact within its alien range has not yet been assessed in detail since it may be masked by *A. syriaca* [4]. In this context, several European studies on *A. syriaca* providing relevant insights into the potential ecological impact of this species are particularly important and may refer to *A. speciosa*, as *A. syriaca* and *A. speciosa* share similar morphology, reproduction potential, and ecology [4]. For example, several studies have shown the effect of *A. syriaca* on native flora [17] and fauna [48] or agricultural cultivars [63–67], including the allelopathic effects of root extracts on three agricultural cultivars with negative effects on both seed germination and the seedling growth of crops [64,67], thus impacting agricultural production. In addition to being a transformer species, the spread of *A. syriaca* seems unrestricted by dry soils and anthropogenic soil disturbance, which may further induce its invasion in both agricultural lands and natural landscapes [65]; it may also play a causative role in deep soil drought events in the invaded areas, mainly due to its deep and extensive underground system [66,68]. Given that *A. syriaca* is considered to be an important and problematic alien invasive species in Europe [23,47], especially in Central and Northern Europe [14,16,17,44,63–66] with *A. speciosa* being probably similarly problematic and possibly guised under *A. syriaca*, it is suggested herein that both species should be carefully surveyed and monitored, while previous distribution records and deposited herbarium specimens should be revisited and re-examined [4].

Monitoring and management plans for *A. syriaca* have been studied on several levels, using either conventional [65,68] or modern means and methods such as hyperspectral remote sensing technology and respective data [69,70]. Over the years, conventional management with herbicides [71] or biological control agents [72,73] have also been tested to control its invasion. The results were in most cases short-term [69,70] and not very promising, as *A. syriaca* continued invading new territories, sometimes even leading to new secondary invasions [69]. *Asclepias syriaca* remains a major threat to agriculture, native biodiversity, and ecosystem functioning, especially in the light of climate change. Considering that some studies have reported that plant-derived smoke can enhance the seed germination of *A. syriaca* [74], the invasion of this species in Mediterranean habitats may also succeed due to the increased likelihood of local wildfires in Southern European countries during the hot summer months in times of climate crisis [75]. With this in mind, and despite the lack of relevant information for *A. speciosa*, the management plans for *A. speciosa* should be preferably focused on early warning and detection mechanisms at the earliest possible stage, coupled with eradication measures at local scales.

5. Conclusions

The newly discovered wild population of *A. speciosa* in Greece is the second in Europe after Lithuania and the first one in the Balkans and Southern Europe. The latter record confirms the ability of this North American species to adapt to different biogeographic regions of Europe. To this end, and with the aim of facilitating future monitoring programmes, the present study documented for the first time the original alien population of *A. speciosa* in terms of morphological traits, ecological (climate and habitat) preferences, population dynamics, pollinators, seed germination ability, and invasion potential at the south-eastern extreme of its European (non-native) range. Although *A. speciosa* has only recently been reported from Europe, it is suggested that *A. speciosa* may have been present in European territories long before these official reports in national or regional inventories, due to the documented potential for misidentification with the highly invasive *A. syriaca*. This issue should therefore be carefully considered, as *A. speciosa* may represent a new invasion case of a cryptic nature with consequences for agricultural lands and (semi-) natural landscapes. Currently, there are no studies addressing the invasiveness of *A. speciosa* in Europe, and no re-inspection procedure is planned or applied to the *A. syriaca* monitoring schemes currently imposed by the EU Regulation across Europe. Given the strong morphological similarity, ecological affinities and similar reproductive strategies of *A. speciosa* and *A. syriaca,* it is herein proposed that *A. speciosa* could pose a significant new invasion risk to European territories. Therefore, inspection mechanisms, early warning systems, and preventive measures are crucial to protect local biodiversity and agriculture from potential invasion by *A. speciosa*, a risk that may be exacerbated by climate change.

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