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Emerging invasion threat of the liana *Celastrus orbiculatus* (Celastraceae) in Europe

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Abstract

The woody vine *Celastrus orbiculatus* (Celastraceae), Oriental bittersweet, is an alien species that recently has been found to be spreading in Europe. Many aspects of its biology and ecology are still obscure. This study evaluates the distribution and habitats, as well as size and age of stands of *C. orbiculatus* in Lithuania. We investigated whether meteorological factors affect radial stem increments and determined seedling recruitment in order to judge the plant's potential for further spread in Europe. We studied the flower gender of *C. orbiculatus* in four populations in Lithuania and found that all sampled individuals were monoecious, although with dominant either functionally female or male flowers. Dendrochronological methods enabled us to reveal the approximate time of the first establishment of populations of *C. orbiculatus* in Lithuania. The youngest recorded individual with fruits was determined to be 10 years old. Analysis of radial increments revealed no reliable correlations with meteorological conditions. Therefore, we conclude that climatic conditions in the region are favourable for the growth, reproduction, and invasion of this species. *C. orbiculatus* produces viable seeds, successfully reproduces and spreads within and around the established stands. The presence of seedlings and two- to four-year-old saplings in the population confirms constant generative recruitment. Available information on the distribution of *C. orbiculatus* in Europe revealed its existence in 13 countries. In total, 58 occurrences of this species have been recorded in Europe so far. We consider that the lag period lasted until 2005 and that the exponential population growth phase has now set in. In Lithuania, the invaded area is quite small (0.51 ha); however, the total estimated invaded area in Europe could be about 250 ha. At the current stage of invasion and distribution in Europe, measures for control, management, and eradication of *C. orbiculatus* have a chance of being effective and economically feasible.

Keywords

dendrochronology, dioecious plants, distribution, flower gender, habitats, reproduction, seedlings

Introduction

Lianas are strong competitors with trees for above- and belowground resources (Toledo-Aceves and Swaine 2008; Ladwig and Meiners 2010; French et al. 2017). Although vines and climbers are prevalent in gaps of tree stands and on forest edges where they compete intensely with trees, most of them are shade tolerant and can wait for favourable light conditions for a longer period of time (Baars and Kelly 1996; Schnitzer et al. 2000; Allen et al. 2007; French et al. 2017). When favourable conditions set in, lianas respond with high growth rates, reducing growth and recruitment of trees and shrubs (Greenberg et al. 2001; Leicht and Silander 2006; Ladwig and Meiners 2010). Thus, the impact of native, and particularly of invasive, lianas on biodiversity, habitats, and economically important trees make them a matter of serious ecological concern (McNab and Meeker 1987; Grauel and Putz 2004; Pavlovic and Leicht-Young 2011; Addo-Fordjour and Rahmad 2015). Special attention was paid to the spread and invasion of lianas in many European countries quite recently. However, only three species of lianas, i.e. *Parthenocissus quinquefolia*, *Lonicera japonica* and *Vitis vinifera* have been included in the list of the 150 most widespread alien species in Europe (Lambdon et al. 2008), whereas at a country or regional level, the number of invasive and potentially invasive lianas is often higher. Fast spread and invasion of several species of the genus *Vitis* has been observed in Italy (Ardenghi et al. 2014; Ardenghi and Cauzzi 2015). *Pueraria montana* var. *lobata* (*P. lobata*) is considered to be invasive in Switzerland (Gigon et al. 2014). *Parthenocissus inserta* has been included in the Black List of the Czech Republic (Pergl et al. 2016).

Implementing the European Union Regulation 1143/2014 on invasive alien species, a horizon scanning for potentially invasive alien species has revealed 98 species that pose particular danger in the EU (Roy et al. 2015). *Celastrus orbiculatus* was listed among the alien species with a potentially negative impact on biodiversity and was prioritised for pest risk analysis (Roy et al. 2015; Tanner et al. 2017).

Celastrus orbiculatus was introduced to Europe as an ornamental plant at around 1860. Soon after its introduction, in 1863, it was first offered for sale to the public as an ornamental plant in Siebold's nursery (The Netherlands) catalogue (Del Tredici 2014). According to Adolphi et al. (2012), this species was first reported to have escaped in Germany in the early 1950s near Lohr am Main, but was then erroneously identified as *C. scandens*. To date, *C. orbiculatus* has been recorded as a casual or naturalised species in 13 European countries (Stace 1997; Verloove 2006; Purcel 2010; Pyšek et al. 2012; Tokarska-Guzik et al. 2012; Leonhartsberger 2013; Adolphi 2015; Beringen et al. 2017; Gudžinskas et al. 2017; Alberternst and Nawrath 2018, etc.).

Celastrus orbiculatus was introduced to the United States from Asia in the late 19th century, and has become naturalised in the Eastern States where it occupies large areas of disturbed temperate forests, alluvial woods, and roadsides (Merriam 2003; Pande et al. 2007; Leicht-Young et al. 2007, 2013; Kuhman et al. 2013; Horton and Francis 2014). This species causes changes in ecosystem productivity and structure (Ladwig and Meiners 2010; Hoosein and Robinson 2015), but most seriously it threatens the native congener, *C. scandens*, by hybridisation (Leicht and Silander 2006; Leicht-Young et al. 2007; Zaya et al. 2015). In New Zealand, *Celastrus orbiculatus* started to spread in 1981. Almost two decades later it became quite frequent and is considered as a threat to native ecosystems (Williams and Timmins 2003).

Quite recently a risk assessment of *C. orbiculatus* for the EU, with special focus on the Netherlands, has been performed (Beringen et al. 2017). However, this risk assessment was based mainly on studies from North America and on a few surveys on this species from several European countries. Important results of several other investigations that have not been evaluated in the previous risk assessment (Beringen et al. 2017) have revealed new important information about the invasiveness and performance of *C. orbiculatus* in the Baltic Region and in Central Europe (e.g. Purcel 2010, 2011; Gudžinskas et al. 2017; Alberternst and Nawrath 2018).

Despite the increased number of studies on *C. orbiculatus*, many of its biological and ecological properties, which have an important effect on the spread and emerging invasion, were insufficiently known in Europe. Therefore, we started to investigate established populations of *C. orbiculatus* in Lithuania, which are at the north-eastern limit of current naturalisation of this species in the southern part of the boreal biogeographic region of Europe. The aims of this study were (a) to analyse the current distribution of *C. orbiculatus* in Lithuania and Europe, (b) to evaluate the size of *C. orbiculatus* populations and occupied habitats in Lithuania, (c) to assess allocation of flowers by the gender; (d) to evaluate the age of individuals and approximate time of population establishment, (e) to study radial increment rates and possible relationships with meteorological conditions, (f) to investigate generative reproduction and sapling density in an invaded habitat. The results of this study provide information for a better understanding of *C. orbiculatus* reproduction, spread and invasion to natural, seminatural and human-made habitats.

Materials and methods

Study species

Celastrus orbiculatus Thunb. (Celastraceae R. Br.) is a deciduous woody vine that climbs by means of twining about a support. Cane-forming stems are located just above the ground and liana-forming stems are in the canopy layer where it climbs through the tree trunk and branches. (Leicht-Young et al. 2007; Zhixiang and Funston 2008). Flowers frequently are functionally unisexual because of abortion or reduction of male or female parts, thus the plants are usually dioecious, sometimes monoecious, though plants develop both unisexual and perfect flowers (Brizicky 1964; Gleason and Cronquist 1991; Burnham and Santana 2015). This species is native to East Asia and its range includes Central and North Japan, Korean Peninsula, Far East of Russia and China north of the Yangtze River and tolerates a very wide range of climates (Ohwi 1965; Williams and Timmins 2003; Zhixiang and Funston 2008).

Mapping of distribution

A distribution map of *C. orbiculatus* 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). A distribution map of *C. orbiculatus* in Europe was compiled using data of available published reports (hereafter referred to in the text). We also used data from our studies and some unpublished (acknowledged personal reports, herbaria) information on occurrences of this species. The map was created employing the same base-map, grid cells and "AFE Editor" software as used for the "Atlas Florae Europaeae" map compilation (Kurtto et al. 2004).

Study sites

We performed field studies on four populations of *C. orbiculatus* in Lithuania during the growth season of 2016 and flower gender was studied in June of 2018. We also surveyed a newly discovered population in Vandžiai (Raseiniai distr.) in September of 2018. Therefore, population size and habitats of *C. orbiculatus* were evaluated in five sites in Lithuania (Table 1). Additionally, in July 2019, we surveyed two previously unregistered sites of *C. orbiculatus* in Girionys (Kaunas distr., Lithuania) and in Ķemeri village (Jūrmala city, Latvia). Herbarium specimens of this species from all sites were collected by the authors and deposited at the Herbarium of the Institute of Botany of the Nature Research Centre (BILAS).

Sampling procedures

Population size and habitat characteristics

The areas of small populations were measured using measurement tape, whereas the size of large populations with complicated configuration was measured by applying geographical coordinates established at certain points of the stand perimeter. The area occupied by *C. orbiculatus* was calculated using online software provided from the Spatial Information Portal of Lithuania (www.geoportal.lt). The quantity of fruits was estimated visually. When solitary fruits were found on the lateral branches of a *C. orbiculatus* individual, its fruit yield was classified as poor, whereas for individuals having one or more fruits on most of their axillary cymes on a lateral branch, its fruit yield was classified as abundant.

The height of trees in the habitats and height of *C. orbiculatus* in the trees were measured with a height measurement device (Haglöf EC II, Sweden). Coverage of plants (in per cent) of different vegetation layers was estimated visually. We identified habitat types following the Interpretation Manual of European Union Habitats (Rašomavičius 2012; European Commission 2013) according to the ecological features, vegetation structure and species composition.

Table 1. Geographical characteristics of the studied *Celastrus orbiculatus* sites in Lithuania.

Site	Latitude (N) / Longitude (E)	Altitude (m a.s.l.)
Paneriai (Vilnius city)	54.6344, 25.1526	150
Visoriai (Vilnius city)	54.7403, 25.2606	174
Babrungėnai (Plungė distr.)	55.9986, 21.8699	158
Palanga city	55.9591, 21.0915	10
Vandžiai (Raseiniai distr.)	55.3017, 23.4276	58

Analysis of flower gender

Flower gender of *Celastrus orbiculatus* was studied in four populations (Babrungėnai, Palanga, Paneriai and Visoriai) at the beginning of June of 2018. We sampled from two to five mature and clearly identifiable separate individuals from each population, 12 individuals in total. Ten lateral branches (usually 15–20 cm long) at 1–3 m high from the ground with several inflorescences were taken from each plant, labelled and placed into separate plastic bags and brought to the laboratory for further analysis. At the laboratory, the number of inflorescences and number of flowers in each inflorescence was counted starting from the base of branch and inflorescence. Each flower was studied under the binocular microscope and dissected, when necessary, to estimate its gender. Flowers with developed anthers and undeveloped pistil and ovary were treated as functionally male, flowers with developed pistil and ovary but undeveloped anthers were treated as functionally female flowers (Figure 1).

Study of seedlings and saplings

The density of *C. orbiculatus* seedlings and saplings was estimated in three parallel 20-meter-long transects in Paneriai Forest in early September 2016. The transects were at a distance of approx. 30 m between the previous transect. Transects were selected in an area free of ground cover of *C. orbiculatus* shoots. The first transect was arranged in the central part of the *C. orbiculatus* stand with the densest and highest mature individuals, the second transect was selected at the edge of the stand with mature individuals, and the third transect was in an area free of mature *C. orbiculatus* individuals. The transects were divided into 20 sampling plots of 1 m^2 using a frame with all sides of 1 m. The number of seedlings and saplings grown from seeds was counted. Individuals grown from seeds in the year of the study were ascribed to the group of seedlings, whereas elder individuals (two or more years old) were identified as saplings. We distinguished seedlings from saplings by the level of stem lignification. Saplings and individuals grown from underground shoots were distinguished by the shape of their leaves and the character of the shoot. In each transect, we also measured the height of 10 randomly selected seedlings and 10 saplings.

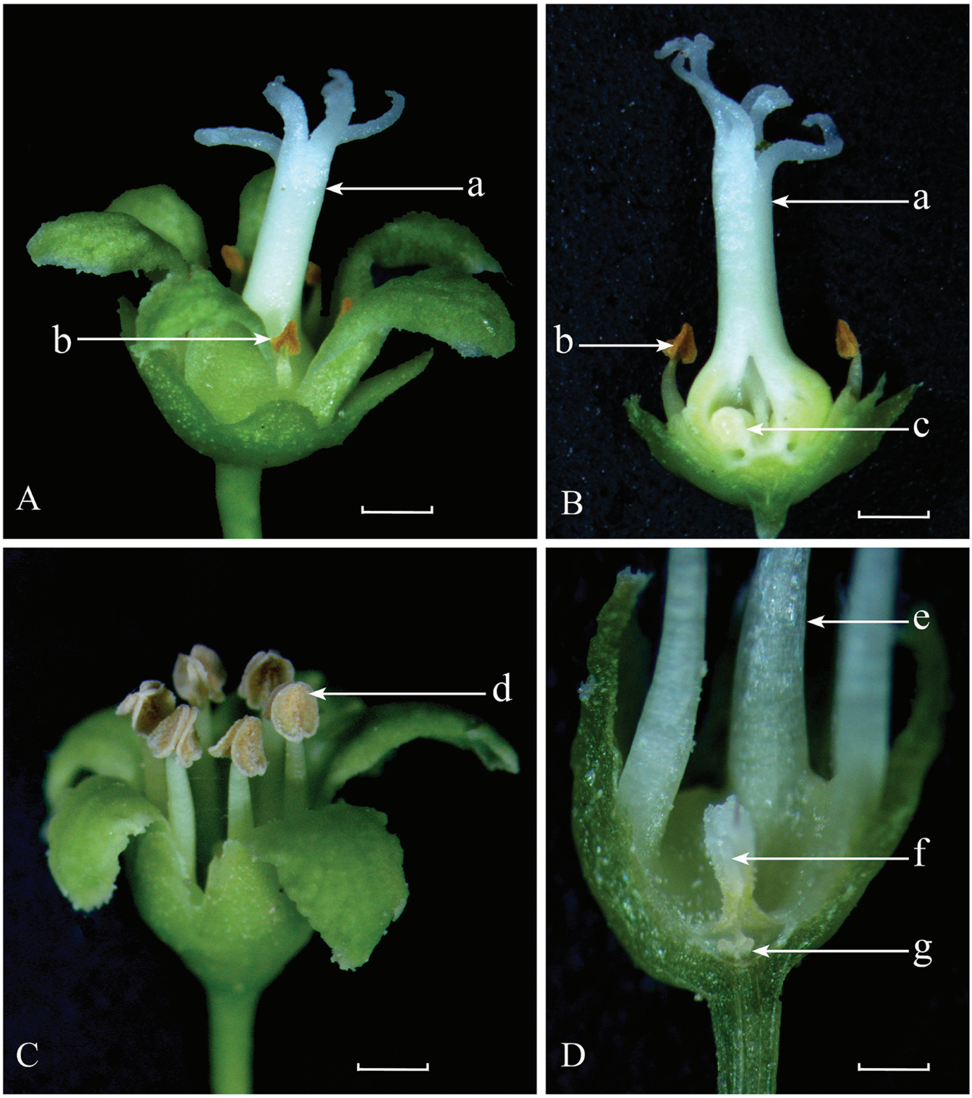

Figure 1. Flowers of *Celastrus orbiculatus*. **A** Functionally female flower with developed pistil (**a**) and staminodes (**b**) **B** longitudinal section of functionally female flower (petals removed) with developed pistil (**a**), staminodes (**b**) and ovules in the ovary (**c**) **C** functionally male flower with developed stamens (**d**) **D** longitudinal section of functionally male flower with filaments of developed stamens (**e**), pistillode (undeveloped pistil, **f**) and ovary with aborted ovules (**g**). Scale bars: 1 mm (**A–C**); 2 mm (**D**).

Evaluation of plant age and radial growth

Stems of *C. orbiculatus* for dendrochronological analysis were sampled in three populations (Babrungėnai, Visoriai and Paneriai) at the end of the growth period in September 2016. The population of Palanga was not sampled the same way because of an insufficient number of primary stems. Two series of samples were collected in the population of Paneriai Forest: the first series was collected in the - presumably - oldest part of the population, another series in the peripheral part of the stand, at 40–50 m from the first sampling site. Ten of the largest individuals from each sampling area were selected and 15–20-cm-long stem sections were cut with a saw at ground level. Samples were numbered, diameters measured with a caliper and placed into paper bags for drying at ambient temperature for three months.

Before counting annual rings, sections of ca. 5 cm were cut from each dried sample of the stem and one of its surfaces sanded and polished. Polished surfaces of the samples were stained with original stain prepared from the powder of *Curcuma* rhizomes boiled in vegetable oil (5 g of powder and 20 ml of vegetable oil). Prepared cross-sections of *Celastrus orbiculatus* stems were examined under a binocular microscope (LEICA EZ4), the annual rings of the xylem were counted and the width of annual rings was measured with an accuracy of 0.1 mm.

Information on the monthly minimum temperatures and the amount of precipitation in the period from 1989 to 2016 was provided by the Hydrometeorological Service under the Ministry of Environment of Lithuania. The data was used to evaluate the impact of meteorological factors on the radial stem growth of *C. orbiculatus*.

Statistical analyses

The normality of data distribution was evaluated using the Shapiro-Wilk test. Comparison of normally distributed data sets (pooled seedling and sapling density, width of annual rings) was performed applying ANOVA several-sample F-test and Tukey's post-hoc pairwise comparisons. Two normally distributed data sets of seedling and sapling height were compared applying Student's t-test. Because seedling and sapling density in the studied plots were distributed non-normally, comparison of their densities was analysed applying non-parametric Kruskal-Wallis H-test and Mann-Whitney post-hoc pairwise comparisons. Correlations between normally distributed data sets of annual ring width and meteorological parameters were calculated applying Pearson's rank correlation test. The significance level of statistical tests was set at $p < 0.05$. Dependence of stem age and its diameter were evaluated using linear bivariate model. Descriptive statistical analysis results include mean values and standard deviations (mean ± SD), in analyses of seedling and sapling density also including minimum, maximum and median. All calculations were performed using PAST 3.20 (Hammer et al. 2001).

Results

Distribution

Currently, *C. orbiculatus* occurs in six localities in southeastern (Paneriai and Visoriai, Vilnius city), central (Vandžiai, Raseiniai distr. and Girionys, Kaunas distr.) and western (Babrungėnai, Plungė distr. and environs of Palanga city) parts of Lithuania

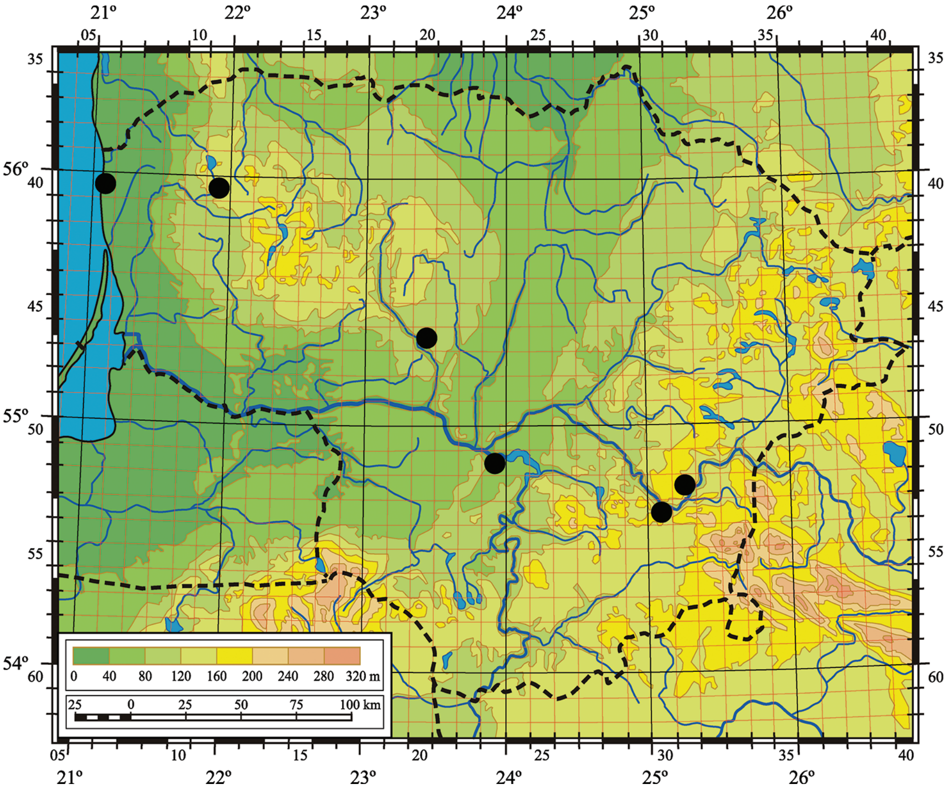

Figure 2. Current distribution of *Celastrus orbiculatus* in Lithuania mapped on to the local grid.

(Figure 2). This species was first recorded in the environs of Palanga city in 2014. In the same year, *C. orbiculatus* was also found in Visoriai. Two localities of this species were recorded in 2016 (Babrungėnai and Paneriai). Localities in Vandžiai and Girionys were discovered in 2018 and 2019, respectively.

Information on the distribution of *C. orbiculatus* in Europe was quite dispersed over numerous publications and other sources of information. According to these sources *C. orbiculatus* has been recorded in 13 European countries: Austria (Leonhartsberger 2013; Sauberer and Till 2015), Belgium (Verloove 2006, 2013), the Czech Republic (Červinka and Sádlo 2000; Pyšek et al. 2012; Pergl et al. 2016), Germany (Brandes 2011; Adolphi et al. 2012; Adolphi 2015; Alberternst 2018; Alberternst and Nawrath 2018), Latvia, Lithuania (Gudžinskas et al. 2017), the Netherlands (Beringen et al. 2017), Norway (Gederaas et al. 2012; Beringen et al. 2017), Poland (Purcel 2010, 2011), the European part of Russia (Morozova 2014, without exact locality), Sweden (Beringen et al. 2017), Ukraine and United Kingdom (Stace 1997; Beringen et al. 2017; BSBI 2018). In total, 58 sites of occurrence of this species have been reported so far and they fall into 42 grid cells of the "Atlas Florae Europaeae" (Figure 3).

Analysis of the spread dynamics of registered *C. orbiculatus* populations in Europe revealed very slow increase of sites of occurrence (on average three new sites per 10 years)

Figure 3. Distribution of *Celastrus orbiculatus* in Europe mapped on to the grid of the *Atlas Florae Europaeae*.

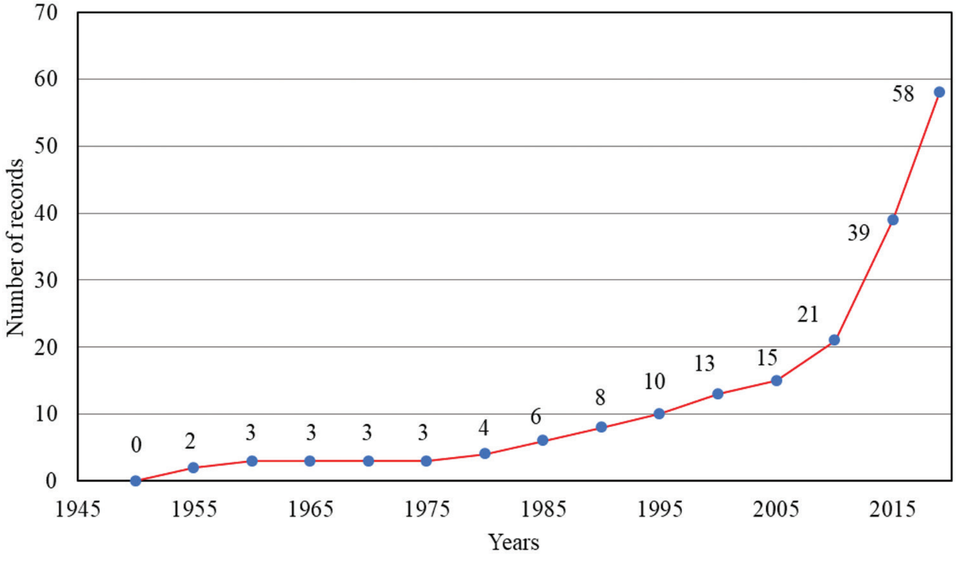

Figure 4. Cumulative curve of *Celastrus orbiculatus* record number in Europe.

from its first report in Europe in 1953 (Adolphi et al. 2012) until 2005; this period corresponds to the lag phase. From 2005 onwards, the number of registered new occurrences started to increase rapidly, on average almost three sites per year (Figure 4). The increase of occurrences since 2005 may be recognised as the start of the exponential growth phase.

Habitats

Four of the studied populations (Paneriai, Visoriai, Babrungėnai and Vandžiai) were in forest habitats and one population (Palanga) on the edge of a forest. In Paneriai Forest, the plants occupied an approximately 70-year-old *Pinus sylvestris* stand with admixture of *Acer platanoides* and *Quercus robur* in the second tree layer (Table 2). The population in Visoriai was recorded in an approximately 60-year-old *Betula pendula* stand with admixture of *Picea abies* and *Populus tremula* in both tree layers. In Babrungėnai, the population of *Celastrus orbiculatus* occupied a forest glade under a low-voltage power transmission line and a surrounding approximately 50-year-old tree-stand of almost equal proportions of *Pinus sylvestris*, *Picea abies* and *Betula pendula*. The stand of *C. orbiculatus* in Vandžiai (Raseiniai distr.) occupies an about 20-year-old woodland composed of *Betula pendula*, *Alnus incana* and *Tilia cordata*. The stand was in a transitional zone between broad-leaved forest and alluvial forest habitats (Table 2). Near Palanga, the stand of *Celastrus orbiculatus* was on a shrubby edge of the dry pine forest on dunes and occupies a transitional area between the forest and sandy grassland.

The studied forest habitats invaded by *C. orbiculatus* had characteristic vertical structure of the tree and shrub layers and their cover (excluding *C. orbiculatus*) ranged from 40% to 60% and from 30% to 60%, respectively (Table 2). Normal development of the tree and particularly of the shrub layer suggests that this species invaded already stabilised habitats without significant disturbances.

In Lithuania, *C. orbiculatus* occurs in quite different types of habitats. The population in the environs of Palanga occupies a transitional area between a habitat of wooded dunes (2180 Wooded dunes of the Atlantic, Continental and Boreal region) and sand grasslands (6120* Xeric sand calcareous grasslands). In Paneriai, this species occupies mature pine forest (9010* Western Taiga) and the transitional zone to spruce forest (9050 Fennoscandian herb-rich forests with *Picea abies*). In Visoriai, *C. orbiculatus* grows in stadial forest dominated by *Betula pendula* with an admixture of *Picea abies*, which according to the ecological conditions and species composition is close to the herb-rich spruce forest habitat (9050 Fennoscandian herb-rich forests with *Picea abies*). The stand of *C. orbiculatus* in Vandžiai invaded a young *Betula pendula* stand situated in the transitional zone between alluvial forest (91E0 Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior*) and broad-leaved forest (9020* Fennoscandian hemiboreal natural old broad-leaved deciduous forests).

Population size and characteristics

In Paneriai Forest, a dense stand of this species with mature individuals occupies an area of 2600 m^2. The total area of the stand, including recorded seedlings and saplings, comprises 3640 m^2. At the Vandžiai site (Raseiniai distr., Central Lithuania) the species occupies 880 m^2 while the other studied stands of *C. orbiculatus* were significantly smaller (Table 2). Thus, the total area occupied by this species in all registered populations in Lithuania approximates to 0.51 ha.

Table 2. Characteristics of the studied *Celastrus orbiculatus* sites.

Character	Site				
	Paneriai	Visoriai	Babrungėnai	Palanga	Vandžiai
Area occupied by the stand of *Celastrus orbiculatus* (m^2)	3640	480	90	20	880
Age of the dominant trees (years)	70	60	50	–	20
Maximum height of the tree layer (m)	24	17	15	–	15
Coverage of the tree layer (%)	60	50	50	–	40
Coverage of the shrub layer (%)	60	30	60	20	50
Coverage of the herb layer (%)	40	30	30	60	20
Coverage of the bryophyte layer (%)	60	10	5	20	5
Maximum height of *Celastrus orbiculatus* (m)	18	14	10	3	14
Coverage of *Celastrus orbiculatus* in the tree layer (%)	15	20	10	–	20
Coverage of *Celastrus orbiculatus* in the shrub layer (%)	50	40	30	10	60
Coverage of *Celastrus orbiculatus* in the herb layer (%)	60	30	60	50	60
Total coverage of *Celastrus orbiculatus* in all layers (%)	70	60	70	50	70

In all studied sites, *C. orbiculatus* shoots were distributed over all vegetation layers and in all cases it was the dominant species in the entire community. Its total coverage ranged from 50% to 70% (Table 2). In four studied sites, shoots of *Celastrus orbiculatus* reached the tree canopy layer and the height of the tallest individuals ranged from 10 to 18 m, though its coverage in this layer was quite low (Table 2). Much higher coverage of *C. orbiculatus* in forest habitats was in the shrub layer, ranging from 30% to 60% (mean 45%). The highest mean coverage (52%) of this species was recorded in the herb layer, where it ranged from 30% to 60%.

Flower gender

Analysis of flower (n = 1913) gender of 12 individuals revealed that all plants were monoecious, whereas dioecious or polygamo-dioecious individuals were not found. In all studied individuals either functionally female or male flowers prevailed, from 74.2% to 84.3% and from 76.5% to 84.9%, respectively (Table 3). Individuals with mostly functionally female or male flowers were recorded in the Paneriai and Palanga populations, whereas the Visoriai and Babrungėnai populations consisted of only individuals with prevailing functionally male flowers.

We noted that functionally female flowers of individuals with prevailing male flowers were usually arranged in the proximal part of lateral branches, at the first to the third node, and in the proximal part of the inflorescence. In individuals with prevailing female flowers, functionally male flowers were usually arranged in inflorescences at the distal part of a branch or at the apex of the inflorescence.

The existence of monoecious individuals in all studied sites explains the pattern of *C. orbiculatus* fructification. At the Babrungėnai and Visoriai sites, the set of *C. orbiculatus* fruits in 2016 was poor because dioecious individuals bearing only dominant male flowers were recorded. In Palanga and in Paneriai, some individuals produced

Table 3. Distribution of flowers by gender in the studied individuals of *Celastrus orbiculatus* from four populations in 2018.

Site	Number of individuals	Number of studied flowers	Prevailing gender of flowers	Gender of flowers			
				female		male	
				number	%	number	%
Paneriai	1	138	male	25	18.1	113	81.9
	2	147	female	116	78.9	31	21.1
	3	124	female	92	74.2	32	25.8
	4	161	female	135	83.9	26	16.1
	5	235	female	198	84.3	37	15.7
Visoriai	1	156	male	27	17.3	129	82.7
	2	131	male	23	17.6	108	82.4
	3	166	male	39	23.5	127	76.5
Babrungėnai	1	152	male	30	19.7	122	80.3
	2	126	male	19	15.1	107	84.9
Palanga	1	170	male	32	18.8	138	81.2
	2	207	female	171	82.6	26	17.4

abundant fruits in 2016. In both these sites individuals with dominant functionally female and dominant functionally male flowers were registered.

Seedlings and saplings

In all sampling plots of the central part of the *C. orbiculatus* stand, we recorded 162 seedlings and saplings, and their mean density was 8.10 ± 1.94 individuals/m^2 (Table 4). ANOVA test revealed significant differences among the studied transects ($F (2, 57) = 81.29$, $p < 0.001$). In the periphery of the stand, where generative individuals were absent, and in transects located outside the stand, the density of seedlings and saplings was statistically significantly lower than in the central part of the stand (Tukey's pairwise comparison, $Q = 13.81$; $p < 0.001$ and $Q = 16.95$, $p < 0.001$, respectively). The difference between density of seedlings and saplings at the periphery of the stand and outside of the main stand was statistically insignificant ($Q = 3.14$, $p = 0.076$). Nevertheless, in both these transects seedling and sapling density was considerable so that one can expect further extension of the population (Table 4).

Analysis of the proportions of seedlings and saplings revealed that in the central part of the stand saplings prevailed (55.55%), whereas on the periphery and outside the main stand seedlings prevailed (54.10% and 52.63%, respectively). Density of seedlings and saplings in the centre of the stand was statistically significantly higher than in the other two transects (Table 5). However, we did not find significant differences of seedlings and saplings between transects on the periphery and outside the stand (Mann-Whitney U-test, $U = 138.00$, $n = 40$, $p = 0.081$).

Two- and three-year-old saplings were almost equally presented in all transects. Four-year-old saplings were recorded in the central part of the stand only. The height of the

Table 4. Total number of *Celastrus orbiculatus* seedlings and saplings in the studied transects (Paneriai Forest, Vilnius), their density (mean ± SD), minimum and maximum number in sampling plot and median. The same letter indicates statistically significant differences according to Tukey's pairwise comparison ($p < 0.001$).

Transect location	Sampling plots (n)	Total number	Density (individuals/m²)	Minimum	Maximum	Median
Centre	20	162	8.10 ± 1.94^{ab}	5	12	8
Periphery	20	61	3.05 ± 1.50^{a}	0	6	3
Outside	20	38	1.90 ± 1.41^{b}	0	5	2

Table 5. Number, percentage and density (mean ± SD, individuals/m²) of *Celastrus orbiculatus* seedlings and saplings in three transects in Paneriai Forest (Vilnius). The same letter indicates statistically significant differences according to Mann-Whitney pairwise comparison ($p < 0.001$).

Transect location	Seedlings			Saplings		
	Number	%	Density	Number	%	Density
Centre	72	44.45	3.60 ± 1.67^{ab}	90	55.55	4.50 ± 1.15^{ab}
Periphery	33	54.10	1.65 ± 1.26^{a}	28	45.90	1.4 ± 0.88^{a}
Outside	20	52.63	1.00 ± 0.97^{b}	18	47.37	0.90 ± 0.91^{b}

measured seedlings ranged from 4 cm to 10 cm. Mean height of seedlings was 6.70 ± 1.58 cm. The height of saplings ranged from 9 cm to 19 cm and their mean height was 13.03 ± 2.70 cm. Saplings were significantly taller than seedlings (Student's t-test, $t = 11.07$, $n = 60$, $p < 0.001$). Two four-year-old saplings were 18 cm and 19 cm in height.

Age of stands and individuals

According to the number of annual rings, the oldest analysed population of *C. orbiculatus* was that at Visoriai, in which the oldest recorded living stem was 21 years old; the oldest dead stem was 30 years old, and mean age of sampled stems was 11.9 ± 4.7 years (Table 6). Thus, the first individual in this population settled here in 1987. The second oldest population was that at Paneriai and the oldest sampled stem in the central part of the stand was 18 years old. Therefore, the population of Paneriai Forest established itself around 1999. The age of sampled stems in the central part of the site ranged from 11 to 18 years. The age of the largest sampled stems in the periphery of the stand ranged from 6 to 11 years (Table 6). The population of *C. orbiculatus* at Babrungėnai was younger than at the other sites and the oldest stem was 11 years old. Thus, this population originated there as late as 2006. As the population at Palanga was quite small, we sampled one of the largest stems that was 10 years old. Thus, this population also originated in 2006.

Table 6. Age and stem diameter of studied *Celastrus orbiculatus* stems (n = 10 in each stand) and estimated year of the stand initiation.

Features	Visoriai	Paneriai		Babrungėnai
		Centre	Periphery	
Age of the oldest living stem (years)	21	18	11	11
Age of the youngest stem (years)	7	11	6	3
Age of the oldest dead stem (years)	30	–	–	–
Estimated year of the stand initiation	1987	1999	2006	2006
Diameter of the oldest living stem (mm)	47.5	42.1	18.0	15.7
Mean age of stems (years)	11.9 ± 4.7	13.2 ± 2.3	9.6 ± 1.9	6.9 ± 3.0
Mean diameter of stems (mm)	20.4 ± 12.8	25.8 ± 8.7	14.6 ± 2.7	11.99 ± 2.4

Stem diameter and radial increment

The diameter of sampled stems of *C. orbiculatus* was strongly correlated with their age (R^2 = 0.73, p < 0.001, n = 40). However, analysis of same age stem diameters revealed a significant variation. The diameter of 11-year-old stems (n = 10), comprising the largest age group among the sampled stems, ranged from 11.2 mm to 25.4 mm (mean 17.7 ± 3.9 mm). Variation of diameter of same aged stems in the same habitat suggests a significant effect of the stem position and competition with other stems, height of foliage, light availability, etc.

The mean width of annual rings (n = 376) of the xylem of *C. orbiculatus* of all studied stems (n = 40) was 0.77 ± 0.26 mm. The minimum width of annual rings in the studied plants was 0.3 mm, the maximum width was 1.7 mm, and the median width of annual rings was 0.7 mm. We compared the width of annual rings formed from 2006–2016 and found no statistically significant differences among years (F (10, 99) = 0.56, p = 0.84). Also, differences could not be detected by pairwise comparison between years. However, we found statistically significant differences among annual ring width of the same age (11-year-old) stems (F (9, 100) = 16.93, p < 0.001). Pairwise comparison also revealed significant differences between annual ring width in stems both from the same site and from different sites.

Results from the analysis of the relationships of annual ring width and radial increment of the stem diameter with meteorological factors were quite unexpected. No statistically reliable correlations were found between annual ring widths and mean annual temperature (r = 0.16, p = 0.64), mean winter temperature (r = –0.01, p = 0.84), mean summer temperature (r = 0.21, p = 0.53), minimum winter temperature (r = –0.10; p = 0.43), and annual precipitation (r = 0.12; p = 0.72).

Discussion

Distribution

The currently recorded localities of *C. orbiculatus* in Lithuania are in different regions of the country and separated by distances ranging from 10 km to 130 km. Therefore, we suppose that escaped populations of *C. orbiculatus* have originated from different sources. Considering the common cultivation of this species in gardens and for landscaping in Lithuania (Navasaitis 2008), Latvia (Laiviņš et al. 2009) and other European countries (Stace 1997; Beringen et al. 2017), its further spread is expected. The species is dispersed by several vectors, including birds (Purcel 2011; Alberternst 2018; Alberternst and Nawrath 2018); thus, we can presume that this species is more widely distributed, but that many existing populations still have not been identified.

Beringen et al. (2017) questioned whether new sites of *C. orbiculatus* in Europe originate from the dispersal of seeds by berry-eating birds, or from the dumping of garden waste. Studies by Purcel (2011), Alberternst (2018), and Alberternst and Nawrath (2018) confirmed that birds are important vectors for spreading this species both in proximity of the invaded area as well as at quite long distances. We suppose that at least one of the Lithuanian sites in Babrungėnai, situated under low-voltage power lines, is a result of bird dispersal from areas of cultivation. However, we were not able to identify a source of seeds in the area around Babrungėnai (within 1 km range). There is also a high probability that birds have dispersed seeds of *C. orbiculatus* from Vilnius Botanical Garden or another place of cultivation to Paneriai Forest (Vilnius). The nearest known place of cultivation is about 8 km away. In Visoriai, *C. orbiculatus* seeds or vegetative parts could have been introduced via wastes from gardens that are located about 0.5 km away from the site. In the environs of Palanga, *C. orbiculatus* was probably introduced from a place of cultivation which is approx. 0.8 km to the north. Seeds or fruits could have been brought in by strong winds, birds or human activity. The population at Vandžiai is probably a relic of former cultivation.

The map of its current distribution (Figure 3) shows higher concentrations of occurrences in western and eastern Germany (17 sites of the total 58 sites registered till the end of 2019), southern Sweden, western Poland and Lithuania. Our analysis of the occurrence and distribution of this species in Central Europe leads us to consider that this plant should be classified as having a restricted range. If the rate of spread and records of new occurrences continue at the same rate as during the last 15 years, *Celastrus orbiculatus* may become widespread in Europe within the next decade.

Habitats

In its native range in East Asia, *C. orbiculatus* grows mainly in mixed forests, along forest margins and on grassy slopes (Zhixiang and Funston 2008). In the invasive range in North America, it occupies a very wide range of habitats: wet and dry forests, old-growth forests, areas of forests damaged by wind-throws, abandoned fields, reforested areas, slopes, dunes and various anthropogenic or heavily disturbed habitats (Leicht-Young et al. 2007; Pavlovic and Leicht-Young 2011, etc.). Similar habitats are occupied in New Zealand (Williams and Timmins 2003). Studies of *C. orbiculatus* spread in North America have revealed that coniferous forests are less favourable habitats and large areas of these forests may act as a barrier against spread of this species (Merow et al. 2011).

However, results of our study suggest that forest habitats dominated by coniferous trees are suitable for *C. orbiculatus* and forests belonging to the western taiga, wooded dune and herb-rich spruce forest habitats are also prone to the invasion of this liana.

In Europe, *C. orbiculatus* most frequently has been found in areas close to urban environments and occupying human-made or disturbed habitats; however, in Austria, Germany and Poland this species has been found occurring in natural or seminatural habitats located at significant distances from urban areas (Purcel 2010; Adolphi et al. 2012; Leonhartsberger 2013; Adolphi 2015; Sauberer and Till 2015; Alberternst and Nawrath 2018, etc.). Beringen et al. (2017) concluded that *Celastrus orbiculatus* is able to establish itself and invade alluvial (91E0 Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior*) and riparian (91F0 Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *Ulmus minor*, *Fraxinus excelsior* or *Fraxinus angustifolia*, along major rivers) forest habitats on moist soils. In Lithuania, *C. orbiculatus* was found to invade a wider range of natural habitats than has been reported from other European countries. The ability of this species to invade dry dune woodlands, grasslands, pine, spruce alluvial and riparian forests of high conservation value is of particular concern. Due to the ability of this species to establish itself in alluvial and riparian habitats, it may very well intensively spread along watercourses in the future.

Celastrus orbiculatus affects all layers of the vegetation in the invaded habitats. Its coverage in the tree canopy layer was quite low in Lithuania, although it substantially reduces light availability in the lower vegetation layers. We detected the highest coverage of *Celastrus orbiculatus* in the shrub and herb layers. Even higher total coverage, ranging from 80% to 100%, of this species has been recorded in Hessen, Germany (Alberternst and Nawrath 2018). This species hinders light penetration and interferes with all plant growth, especially of shrubs and young trees. *Celastrus orbiculatus* also affects mature and young trees and shrubs by girdling their stems and hindering organic matter flow in the phloem. Furthermore, *C. orbiculatus* increases the load of biomass on the upper part of a tree, thus increasing the likelihood of wind damage (Horton and Francis 2014).

Population size and characteristics

Registered populations of *C. orbiculatus* currently occupy an area of 0.51 ha in Lithuania. However, information on the area occupied by this species in other European countries is incomplete. Probably the largest area occupied by *C. orbiculatus* is in Poland, Lubuskie province. There, about 170 ha in the environs of World War II fortifications are occupied by *C. orbiculatus* with very dense stands on about 9 ha (Purcel 2010). In Neuwied (Germany), a stand of *C. orbiculatus* occupies about 2 ha along a railway (Adolphi et al. 2012). Alberternst and Nawrath (2018) estimated that in Hessen (Germany) stands of various density of *C. orbiculatus* occupied ca. 44.6 ha in 2017. In Austria, in the environs of Graz, a stand of *C. orbiculatus* stretches over a length of 50 m along the River Mur and there the liana climbs in trees and covers riparian areas (Leonhartsberger 2013). The total area occupied by *C. orbiculatus* in all European countries is currently estimated at approx. 250 ha. However, as new occurrences of *C. orbiculatus* are being recorded in Europe almost every year, the actual distribution and occupied area could very well be larger than currently known.

Flower gender

Individuals of *C. orbiculatus* are known to be either functionally dioecious (Brizicky 1964), functionally monoecious (Hou 1955) or polygamo-dioecious (Gleason and Cronquist 1991). Our study, though based on only 12 sampled mature individuals, revealed that only monoecious individuals were present in the four studied populations in Lithuania. The fact that in all studied populations we found monoecious individuals explains the presence of a certain amount of ripe fruits (Gudžinskas et al. 2017). Interestingly, in 2019 we recorded an individual of *C. orbiculatus* in Ķemeri (Latvia) with solitary fruits and we suppose that this plant is also monoecious with prevailing functionally male flowers.

The available information on the generative reproduction of *C. orbiculatus* in Europe is controversial. Verloove (2013) noted that *C. orbiculatus* hardly flowers in Belgium and, therefore, its further spreading by sexual reproduction would seem rather unlikely. But, in contrast, at least in some of the sites in Germany, *C. orbiculatus* flowers and produces quite large amounts of seeds (Adolphi et al. 2012; Adolphi 2015). Purcel (2010, 2011) recorded generative spread of this species within and around large stands as well as in a range of 3–5 km from the sites of initial introduction. Abundant reproduction by seeds has been recorded in Hessen, Germany (Alberternst and Nawrath 2018). The different reproductive behaviour of *C. orbiculatus* reported from various regions of Europe may possibly be caused by the different structure of populations according to the gender of flowers (Hou 1955; Brizicky 1964; Gleason and Cronquist 1991; Burnham and Santana 2015). Regional differences of the gender allocation in *C. orbiculatus* populations can be a result of separate introduction events from different sources.

The existence of monoecious individuals of *C. orbiculatus* in Lithuania supports the assumption that monoecious or polygamo-dioecious plants in other populations in Europe also exist. Thus, when monoecious or polygamo-dioecious individuals occur in an area, there are no obstacles for their sexual reproduction (Herron et al. 2007; Ladwig and Meiners 2010; Burnham and Santana 2015), further spread and invasion even in cases of solitarily growing individuals.

Seedlings and saplings

Celastrus orbiculatus does not form a persistent seedbank; almost all seeds germinate in spring and the light intensity does not affect their germination (Dreyer et al. 1987; Van Clef and Stiles 2001; Ellsworth et al. 2004a; Beringen et al. 2017). Relatively high proportions of seedlings survive under poor illumination conditions and seeds can wait for a certain time for forest habitat disturbances and creation of favourable light conditions for their proliferation (Greenberg et al. 2001; Ellsworth et al. 2004b).

Our research revealed significant densities of *C. orbiculatus* seedlings and saplings within limits of its dense stand with mature individuals, on the periphery and in proximity of the stand without mature individuals. The quite slow growth rate during the first three to four years, as revealed by our study, confirms that saplings form so-called seedling banks (Ellsworth et al. 2004b). We were not able to establish whether elder saplings were absent because of their death, poor seed production in certain years and absence of generative reproduction, or because on the fifth year they produce long shoots and become undistinguishable from shoots grown from roots and underground stems. Nevertheless, the results of this study revealed that *C. orbiculatus* is capable of reproducing by seeds and thus may easily expand its population even in undisturbed forest habitats.

There is insufficient information regarding the time point when individuals of *C. orbiculatus* grown from seeds reach maturity. Silveri et al. (2001) reported that in North America in newly established populations of seed origin, individuals of 12 years of age reached the generative stage. Seedlings and saplings grow slowly in the first few years, at least in forest habitats. Our study revealed that four-year-old saplings in a dense stand were up to 19 cm high. Under favourable light conditions saplings grow faster than under the canopy (Silveri et al. 2001). In the population of Palanga, a single sampled individual in a well-illuminated habitat on the forest edge was eight years old and produced fruits. Therefore, we conclude that individuals grown from seeds in well-illuminated habitats can reach the reproductive stage at approx. 10 years. Individuals grown from root-suckers grow very fast and four-year-old shoots can already reach the reproductive stage (Silveri et al. 2001; Ellsworth et al. 2004a).

Propagule pressure is among the most significant factors affecting the spread and invasiveness of plant species (Warren et al. 2013). Extensive cultivation as well as increase of naturalised populations of *C. orbiculatus* in Europe plausibly increase its propagule pressure on the native habitats and threatens further invasion.

Age of stands and individuals

The dendrochronological methods employed in this study enabled us to determine the approximate time of establishment of populations of *C. orbiculatus* and the age of their generative maturity.

Studies on the age structure of *C. orbiculatus* in the area of the Hudson River Estuary (New York State, USA) revealed that the oldest individuals were about 20 years old and their diameter was up to 70 mm, while the mean stem diameter of 5–7-year-old individuals was 17.5 mm (Hoosein and Robinson 2015). In New Zealand, the main stems of *C. orbiculatus* were commonly 50–60 mm in diameter, and the largest recorded stem was 140 mm in diameter. Most of the studied stems in New Zealand were 10–12 years old, whereas one stem collected on North Island at Clova Bay had 32 visible annual rings (Williams and Timmins 2003).

We found that the oldest living stem in the studied populations in Lithuania was 21 years old, and a dead stem (most probably quite recently strangled by other stems of *C. orbiculatus*) was 30 years old. The diameter of the oldest living stem was 47.5 mm. Significant differences in stem diameters in the area of the Hudson River Estuary, USA (Hoosein and Robinson 2015), on the North Island of New Zealand (Williams and Timmins 2003), and plants studied in Lithuania may be due to different habitat conditions. The individuals that we studied grew in undisturbed forest habitats, whereas in the USA and New Zealand most of the sampled plants grew in variously disturbed or forest fringe habitats (Williams and Timmins 2003; Hoosein and Robinson 2015). Thus, slower growth rate and, therefore, stem diameter, in Lithuania was probably caused not only by significant differences in climatic conditions as compared to those in the area of the Hudson River Estuary and in New Zealand, but also by stronger competition of the native species and light availability. Unfortunately, there are no published data on the age, stem diameter, and radial increment of *C. orbiculatus* from other regions of Europe and habitats within the plant's native range.

Stem diameter and radial increment

We analysed the effect of the meteorological factors in Lithuania on the radial growth of *C. orbiculatus* stems and found no specific relationships. The absence of reliable correlations between the width of annual rings and the mean annual temperature, mean winter temperatures, mean summer temperatures, minimum winter temperatures and annual precipitation suggests that climatic conditions in Lithuania are optimal for this species. Surprisingly, even prolonged very cold winter temperatures below –25 °C (in 2003, 2006, 2010, 2012) and occasionally below –30 °C (in 1997) did not damage *C. orbiculatus* shoots significantly to inhibit radial increments in the following growth period. The sites of the three largest and oldest populations studied in Lithuania fall in the first hardiness zone (H1) (Cullen et al. 2011). Thus, areas with moderately cool climates with few periods of severe cold during the winter are suitable for this species and these are areas threatened by its invasion. Beringen et al. (2017) concluded that large areas of Europe might be susceptible to the invasion of *C. orbiculatus* based on an analysis of the climatic conditions in the native range of this species in East Asia and the invasive range in North America. Conditions within the entire Atlantic, continental, and southern boreal biogeographic regions of Europe are likely to be suitable for the establishment of this liana.

Conclusions

Celastrus orbiculatus is spreading in Europe, although its range is still restricted. Climatic conditions are suitable for this species in the Atlantic and continental biogeographic regions, as well as in the southern part of the boreal biogeographic region of Europe. It invades a wide range of forest habitats and poses a threat to dry grasslands, dunes, forest fringe communities of high conservation value, as well as diverse anthropogenic habitats.

Celastrus orbiculatus, at least in Lithuania, but probably also in other European countries, is represented not only by dioecious, but also by monoecious individuals. Thus, even in cases of the occurrence of solitary individuals or small groups of monoecious plants, it produces viable seeds and successfully reproduces sexually. Considering its current distribution and the quite frequent cultivation of *C. orbiculatus* in gardens, most likely it will steadily spread into new areas. Nevertheless, it is still possible to stop the spread of this liana and to reduce the risk of its further invasion.

The effectiveness of control and eradication measures of invasive plant populations is highest when the occupied area is rather small (Blackwood et al. 2010; Epanchin-Niell and Hastings 2010). Control and eradication of *C. orbiculatus* are time- and cost-consuming tasks (Ellsworth et al. 2004a; Pavlovic and Leicht-Young 2011; Beringen et al. 2017). However, considering that total area currently occupied by *C. orbiculatus* in Europe as being ca. 250 ha, its effective control and eradication is still feasible and cost-effective.

Increasing public awareness about the threat of *C. orbiculatus* invasion is among the most important tasks aiming to reduce the possibility of its spread from gardens. Further surveillance of exiting stands of *C. orbiculatus* and search for invaded but still overlooked areas should be performed involving citizens, amateur botanists, and specialists.

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