Journal of Pest Science (2026) 99:104
https://doi.org/10.1007/s10340-026-02063-9

REVIEW

25 years in Europe: a review of the results and knowledge gaps concerning the rapidly spreading invasive oak lace bug (*Corythucha arcuata*)

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Received: 18 December 2025 / Revised: 21 April 2026 / Accepted: 23 May 2026

Abstract
The oak lace bug (OLB, *Corythucha arcuata*), originally native to North America, is a rapidly spreading invasive insect in Europe. Since its first detection in Italy in 2000, it has been reported in 25 countries, with its expansion largely driven by human-mediated dispersal. OLB is a multivoltine species, and its spread is further facilitated by the fact that nearly all Eurasian deciduous oak species are potential hosts, and it can also feed on several other woody plants. As a result, OLB has the potential to occupy up to 30 million hectares of oak forests in Europe and even more in Asia. Some studies indicate that OLB has significant negative effects on oaks and associated ecosystems. It reduces photosynthetic activity in oaks, impairs seedling growth, and there are implications that it also decreases fecundity. These impacts weaken tree health and could threaten the diverse communities of herbivores dependent on oaks. OLB may also influence other ecosystem components, such as leaf litter, surface waters, and even human health. Although its population dynamics are influenced by climatic conditions, current evidence suggests that European winters do not strongly constrain its spread. Various chemical control methods and some biological control agents have been tested, but no effective and environmentally sustainable management strategy is currently available. The egg parasitoid *Erythmelus klopomor* is the only known specialist enemy of OLB in North America and represents a promising long-term control option. However, further research on its behavior and host range is necessary before considering its intentional introduction to Europe.

Keywords *Corythucha arcuata* · Invasive species · Leaf discoloration · Control measures · Oaks · Oak ecosystems · Escape from natural enemies · *Erythmelus klopomor*

Introduction

The introduction of non-native species outside of their native range is a major driver of environmental degradation, rapidly expanding across ecosystems, societies, and economies globally (Pyšek et al. 2017; Diagne et al. 2021). Invasive species (as defined by Simberloff and Von Holle 1999) are species that are introduced outside their native range and spread, with potential negative consequences. The ecological and economic impacts of these species are widely recognized (Williamson 1996; Wittenberg and Cock 2001; Pimentel 2002; Mollot et al. 2017; Blackburn et al. 2019; Haubrock et al. 2021). Among taxonomic groups, arthropods (excluding crustaceans) account for 28% of first records in new regions (Seebens et al 2021) with insects comprising approximately 87% of all alien arthropods in Europe (Roques 2010). However, invasive invertebrates are likely underestimated due to difficulties in their detection and identification (Keller et al. 2011).

Despite the probable underestimation, the number of non-native species established in Europe is generally increasing exponentially in terrestrial ecosystems (Hulme et al. 2008). This is not merely a local trend; it reflects the global increase (Seebens et al. 2017). Over the last 200 years this rate shows an increase, with 37% of all first records reported most recently (1970–2014) and no saturation in the accumulation of alien species (Seebens et al. 2017). This trend is expected to continue, because of the significant time lag between the introduction and spread

Subject Editor Tim Haye.

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Published online: 14 July 2026

of a species, which suggests that many future invasions are already underway (Kowarik 1995).

In Hungary 108 alien insect species with real or potential importance only for forestry have been recorded between 1881 and 2010. The rate of newly arrived species also showed a steep increase; more new species were recorded between 1981 and 2010 than between 1881 and 1980. Of these species the order Hemiptera (particularly aphids) represented 2/3 (Csóka et al. 2012). The lack of saturation in alien species accumulation has important implications for understanding biodiversity patterns (Seebens et al. 2017). Although regional species richness may increase, this would come at the cost of negative impacts on native ecosystems (Simberloff et al. 2013). Invasive invertebrates, in particular insects, can strongly affect biodiversity through competition, predation, habitat alteration or indirect effects such as disease transmission or sharing natural enemies (NRC 2002; Levine 2008; Lebouvier et al 2020; Liu et al. 2020). They may also hybridize with a native species (Jensen et al. 2005). The global appearance of non-native insects has also risen worldwide in the recent decades (Roques 2010; Csóka et al. 2017; Liebhold et al. 2017), and this trend is likely to continue.

In addition to ecological impacts, invasions impose substantial economic costs (Renault et al. 2022). Many invasive terrestrial invertebrate species alter the structure and functions of invaded ecosystems (Bertelsmeier et al. 2016; Holway et al. 2002), causing diverse economic consequences, that have likely increased steadily alongside rising establishment rates of alien terrestrial invertebrate species (Roques et al 2009; Seebens et al. 2017). Future range shifts driven by globalization and climate change will likely add to these effects (Bellard et al. 2013). Global economic costs for invasive terrestrial invertebrates were estimated to be US$ 712.44 billion, averaging US$ 11.40 billion annually since 1960, with rapid growth over time (Renault et al. 2022), highlighting a significant economic burden.

Ecosystem functioning depends on plants and consumers (Eisenhauer 2012; Hooper et al. 2000; Wardle 2013; Wardle and Peltzer 2017). Invasions can disrupt these interactions, altering the processes of ecosystems (Wardle and Peltzer 2017). Forests which are both ecologically and economically important are also threatened by the surge of invasions. One precedent is the severe defoliation, which can result in higher tree mortality and reduced growth (Brockerhoff and Liebhold 2017a, b) potentially shifting competition in favor of non-host trees, altering forest composition and long-term successional patterns (Morin and Liebhold 2015). These can indirectly affect host associated species, influencing wider food webs. Invasion of forests is increasing by many different taxa (Brockerhoff and Liebhold 2017a, b) mainly by fungi and arthropods.

One recent significant arthropod invader in Europe is the oak lace bug (*Corythucha arcuata* (Say) 1832—Hemiptera: Tingidae; abbreviated as 'OLB' further on). Current results show that it could significantly impact the oak ecosystems in its invaded range and cause economic loss and ecological harm. While information on its biology and effects is available (Gibson 1918; Connell and Beacher 1947), there are still many unanswered questions. We aim to shortly summarize the previously reviewed knowledge about OLB and add new empirical evidence about its biology, its natural enemies and the public and the stakeholders' awareness about it. It is also our goal to point out areas in need of research and highlight the currently researched and potential control options concerning the species.

Reviewing the origin and biology of the OLB

To understand the reasons why the OLB has become a successful invader and how it might impact the novel habitat, it is imperative to assess the current knowledge about the species in the place of its origin. The OLB is a member of the genus *Corythucha*. Its adults are 3.1 mm by 1.6 mm (Gibson 1918). They have broad, transparent, lacelike elytra and are flattened. They are cream-colored with a brown band near the apex and a faint brown band across the base of the elytra. A brown spot at the center of the costal margin and brown tumid elevations of elytra are usually prominent.

The native range of the species is the eastern part of the USA up to Southern Canada (Roques et al. 2009). It is multivoltine, meaning that depending on the local climate, it can have 2 or 3 generations per year (Connell and Beacher 1947). The females lay their eggs in larger groups on the underside of oak leaves. Both nymphs and adults feed by sucking on the underside, causing the upper side of the leaves to have grayish-yellow spots. The main hosts in the Nearctic region for the OLB are *Quercus alba* Linnaeus 1753, *Q. macrocarpa* Michaux 1801, *Q. montana* Willdenow 1805, *Q. muehlenbergii* Engelmann 1877, *Q. prinoides* Willdenow 1805 and other *Quercus* species (Fagaceae) (Johnson and Lyon 1976; Puttler et al 2014). Its primary host plants are all in the 'white oaks' group (Puttler et al 2014). However, feeding OLBs were also documented on *Castanea dentata* (Marshall) Borkhausen 1800 (Fagaceae), sometimes on *Malus domestica* (Suckow) Borkhausen 1803 (Rosaceae), maples (Aceraceae) or wild roses (Rosaceae). In its native range, the OLB can be found where the preferred host plants are present (Connell and Beacher 1947). In the Western USA it was recently found in Oregon, on white oak *Quercus garryana* Douglas ex Hook., 1839 (Rosetta 2017).

The references concerning OLB indicate that heavy infestation (which usually happens by late summer) may cause premature leaf fall (Solomon 1980) and the resulting discoloration decreases the ornamental value of trees (Connell and Beacher 1947). While one reference reports that chemical control is sometimes advised on shade or ornamental trees, natural enemies are generally effective (Van Driesche et al. 2013). In late autumn (October/November) only the adults of the OLB migrate to the over wintering microhabitats. Usually these are small gaps, such as raised bark pieces, crevices and forks in the branch. They can rarely be found under leaf litter, but most of the OLBs use stems, branches, and stumps on the ground (Paulin et al. 2021). We assume that such overwintering habits likely contributed to its introduction to Europe, as the adults in bark crevices of logs could have been transported with timber import from North America.

The OLB in Europe, Asia, and the circumstances supporting its spread

The first finding of the OLB in Europe, similarly to many other alien species (Occhipinti-Ambrogi 2002; Nunes et al. 2014, 2015; Tricarico et al. 2018), was documented in Northern Italy in 2000 (Bernardinelli 2000). By the end of 2024, its spread was recorded in the following years and countries (Fig. 1): 2002 Switzerland (Forster et al. 2005) and Turkey (Mutun 2003); 2005 Iran (Samin and Linnavuor 2011); 2012 Bulgaria (Dobreva et al. 2013); 2013 Hungary (Csóka et al. 2013), Croatia (Hrašovec 2013) and Serbia (Pap 2015; Poljaković-Pajnik 2015) 2015 Russia (Neimorovets et al. 2017); 2016 Albania (Csóka et al. 2019), Romania (Don et al 2016), Slovenia (Jurc et al. 2017), Ukraine (Shchurov et al. 2016) and Moldova (Derjanschi and Mocreac 2018); 2017 Bosnia and Herzegovina (Glavendekić et al. 2017a, 2017b) and France (Streito et al. 2018); 2018 Greece (Csóka et al. 2019) and Slovakia (Zúbrik et al. 2019); 2019 Austria (Sallmannshofer et al. 2019), North Macedonia (Sotirovski et al. 2019), Czechia (Mertelík and Liška 2020); 2021 Portugal (Gil and Grosso-Silva 2021), Germany (Wonsack and Thomas 2021) and Poland (Gierlasiński and Orzechowski 2023); 2022 Spain (Riba-Flinch 2022); and 2025 Belarus (Sinchuk et al. 2026). The OLB has heavy infestation in several of the 24 invaded countries, and feeding causes total discoloration of the leaves, usually by August–September or occasionally as early as late June (Paulin et al. 2020).

Fig. 1 Feeding spots of the oak lace bug on *Quercus petraea* [Matt.] Lieblein 1784. (Photograph taken by: György Csóka, University of Sopron, Forest Research Institute)

OLB has advanced fast over Europe, overcoming natural barriers and 'jumping' great distances. However, it did not achieve this expansion through its ability to spread actively. Its close relative, the sycamore lace bug (*Corythucha ciliata* (Say) 1932) has a recorded mean flight distance of 728.25 m for females and 329.11 m for males (Lu et al. 2019). The long-distance spread of the OLB is presumably mediated by human traffic, as first signs of invasion can be seen on roadsides and near railroads. A study focusing on the spread and distribution of the OLB in Italy also supports this. According to this research, insects were observed in over half of the sampling sites; and of the attacked sites, several had a heavy infestation level (Bracalini et al. 2023). Urban sites also showed more infestation compared to peri-urban ones (Bracalini et al. 2023) (Fig. 2).

Another major factor helping the OLB's invasion is the availability of host plants. A survey of 48 oak (*Quercus*) and several other tree species showed that the OLB could survive on a wide variety of plants (Csóka et al. 2019). Twenty-seven of the surveyed deciduous oak species (both in section Quercus and section Cerris) and many other woody plants can facilitate the spread of the OLB (Csóka et al. 2019; Bernardinelli 2006). In Europe, this means a minimum of 35 million hectares of oak forests; thus, the OLB does not suffer a scarcity of hosts to aid its further spread (Paulin et al. 2020).

There may be ways to reduce the speed of the OLB's future spread. One previously reported and reviewed strategy could be to increase tree diversity (Jactel et al. 2021), which can affect herbivory by attracting herbivores onto neighboring, non-preferred species ('associational susceptibility') (Barbosa et al. 2009) or by making preferred hosts less

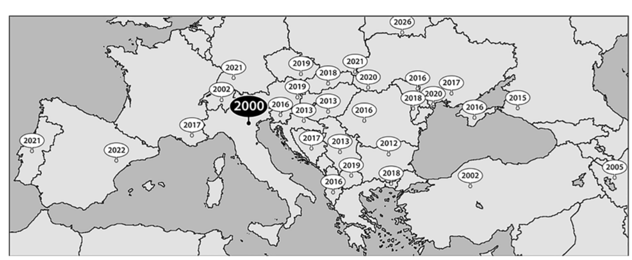

Fig. 2 The European distribution of the oak lace bug in 2025, with the year of first record for each country. (Figure belongs to: University of Sopron, Forest Research Institute)

apparent, reducing infestation ('associational resistance') (Jactel and Brockerhoff 2007). One research collaboration in five European countries was conducted to study the infestation intensity of the OLB in such conditions. Study plots with high (pure stands) and plots with low percentage of oak (mixed stands) were selected in five countries. Analysis showed that the level of tree infestation caused by the OLB differed only between countries but was not significantly affected by stand type (Hoch et al. 2023). Since very little is known about the OLB's behavior, there are currently limited number of explanations for this pattern. One such explanation would be that OLB can spill over from oaks to several other broadleaved tree or shrub species (Csóka et al. 2020), thus the exact species admixed in the oak forests can play a role. Based on the results of Hoch et al. (2023), this type of management in oak forests will not radically limit the OLB's spread.

Climatic conditions affecting the OLB

The previously described establishment and the spread of an alien invasive species can sometimes be hindered by abiotic conditions. In this case, the most likely limiter could be cold climate. Consequently, the OLB's overwintering in the field was studied to determine its endurance in cold conditions (Paulin et al. 2021). The results demonstrated that the OLB adults could survive rather cold winters with a mortality rate of ca. 50% or even less. One such case is the winter of 2016–2017 in Hungary, which was colder than average, with an estimated mean temperature around – 1 °C to 0 °C nationwide, compared to the normal of about 0.3 °C. Even then over 60% of the surveyed OLB adults survived (Csepelényi et al. 2017). Later, laboratory research also showed that while the OLB was a freeze-avoidant insect, there were adults that had super cooling points (the temperature at which the body fluids of the organism begin to freeze) as low as – 29 °C (Paulin et al. 2023a, b). The three separate samples (collected in November, January, and March) were stored for three weeks and withstood both – 3 °C and – 5 °C with mortality rates below 10%. The beginning of the following spring brought the mortality rates slightly up. This suggests some change over the winter period which helps the OLB cope with the cold conditions (Paulin et al. 2023a, b). Our results still indicate that the OLB can survive winter conditions in its invaded European range, and low winter temperatures will not hamper the species' spread (Paulin et al. 2021, 2023a, b).

Climatic conditions affect the development of OLB outside of winter as well, as is the case for many other arthropods (Aghdam et al 2009; Lactin et al. 1995; Zamani et al 2006). As mentioned in the second chapter, the number of OLB generations during a yearly period is determined by the local climate (Connell and Beacher 1947). In a study conducted by Bălăcenoiu et al. (2021a) in Romania, the OLB showed a seasonal dynamic that had two population peaks—one in July and the other in August. This pattern of the OLB's seasonal dynamics is also in line with the model of another long-established invasive species that shares a similar biology—the sycamore lace bug, *Corythucha ciliata* (Bălăcenoiu et al. 2021a). *C. ciliata* is a pest feeding and developing on trees of the Platanaceae family (Florian et al. 2022).

It was also repeatedly reported that air temperature and humidity significantly influenced the dynamics of the OLB population (Bălăcenoiu et al. 2021a). This means that within the invaded areas, the OLB will have at least two generations in a one-year period, and the already documented outbreaks will continue. Ciceu et al. (2024) using a comprehensive compiled dataset and a species distribution modeling framework developed predictive models to estimate both the realized niche and potential distributions of OLB in Europe. Their study revealed that, under current climate change scenarios, there is still potential for the invasive species to colonize new areas. Hungarian oak and Turkey oak natural distributions were said to be entirely suitable for the species; but only half of the range of the other main oak species (sessile and English oak) was suitable for colonization by OLB. Their models predicted that in the RCP 8.5 scenario the area suitable for colonization is expected to increase by up to 30%.

According to the models, two of the significant limiting factors were the number of degree days above 5 °C and number of degree days below 0 °C, highlighting the role of cold temperatures as a limiting factor. The cited research on the cold tolerance of the oak lace bug shows its potential to withstand extreme low temperatures before freezing and 3-week exposure to -5 °C without significant mortality (Paulin et al. 2023a, b). Consistent with this finding, Ciceu et al.'s model reflects a similar trend, indicating low values for the probability of occurrence in areas where the mean temperature of the coldest month drops below 5 °C.

Additionally, precipitation in the second and sixth months of the year plays a significant role in predicting the species' behavior. On the one hand, the suitability of the species is linked to drier winters, while on the other hand, it is associated with wetter springs/summers. This pattern can be explained by the species' life cycle. In April/May, the insects are active after overwintering and start searching for high-quality food sources, which shows preference for regions with abundant precipitation during this period. It also implies a preference for areas where their host species thrive. However, heavy rains during the period when the overwintered adult emerge, may lead to severe mortality (Ciceu et al. 2024).

Known and presumed impacts of the OLB on oak health, growth, and fecundity

As we must expect the continued presence of the OLB, it is important to know as much as possible about its impact. Since its effects in its native range have not been studied extensively as it has not played a major role in the ecosystem, the knowledge before its invasion in Europe is somewhat limited. In this chapter, we enlist the different studies examining the effects of the OLB on its hosts and try to highlight common grounds in the variety of results. The most apparent impact of the OLB is the yellow-grayish discoloration caused by the nymphs and adults feeding on the underside of the leaves (Fig. 1). In its native range, this effect was described as something that was detrimental to the ornamental value of shade trees (Connell and Beacher 1947). In European oak-dominated stands, at sites of heavy OLB feeding this discoloration was observed on the entire foliage by August or in some cases even earlier (Paulin et al. 2020).

The feeding of so many OLB generations can cause the discoloration to be observed on 100% of the foliage, and even remote sensing methods (MODIS, Sentinel, Google Earth, etc.) can be used to show severe infestation levels in several countries (Fig. 3) (Berta et al. 2018; Kern et al. 2021). Solomon (1980) reported that discoloration caused by OLB feeding may reduce photosynthetic activity. In Europe, a 58.8% decrease in photosynthesis and a 21.7% reduction in transpiration activity were measured during heavy OLB infestation (Nikolić et al. 2019). These infested leaves also have an earlier abscission, causing them to fall 1.5–2 months earlier (Solomon 1980). While these results indicate that OLB will negatively affect the trees, measuring the intensity and impact of herbivory is often difficult (Schowalter 2000). But in the USA and Canada for example, forest tree loss due to insects has been calculated to amount to as much as 14% and 22%, respectively (Harausz and Pimentel 2002). A study on oak trees showed that when trees were treated with insecticide (to keep defoliation below 5%) growth (determined from tree rings) was unaffected, but the number of acorns produced was up to four times higher in treated trees (Crawley 1985). It is highly unlikely that the effects of OLB on a lasting period would not severely impact the oaks' nutrient and water flow and consequently their health and reproduction. OLB may also be a vector of oak pathogens; as was the case with the elm phloem necrosis transferred by the elm leafhopper (*Scaphoideus luteolus* Van Duzee, 1894) (Baker 1948a, b, 1949).

Fig. 3 Drone image near Felsőtárkány (northern part of Hungary) showing discoloration on oaks caused by the oak lace bug in September 2024. (Photograph taken by: Marton J. Paulin, University of Sopron, Forest Research Institute)

The metabolism of oaks is already impacted by several outside factors, such as weather conditions or herbivores; this also affects their health and growth. Insects that defoliate oaks in spring are known to have a significant influence on radial growth (Colbert and Fekedulegn 2001; Muzika and Liebhold 1999). Knowledge about the effect of defoliation or damage that occurs later in the growing season (after July) is still lacking. It is quite clear that most of the oaks' radial growth occurs in the first part of the vegetation season; thus, it can be concluded that the damage caused by the OLB will not have serious impact on the radial growth in only one year. However, this effect is continuous, and over several years, the repeated infestation could have a significant influence; however there are no long-term studies that show clear evidence of this.

While it has not yet been proven, the possible influence the OLB has on oak health might also negatively affect the already insecure acorn yield. According to field inspections in Croatia and Hungary, early acorn abscission was at a higher rate, and acorn size was marked as below average in oak stands where OLB outbreaks occurred throughout multiple years (Franjević et al. 2018; Paulin et al. 2020). Coincidentally in 2018, when some of the observations about the acorn size were made, an unprecedented heat wave and drought was documented all over Europe. As drought impacts the fitness of trees negatively and possibly contributes to early acorn abscission and smaller size, its effects cannot be excluded. However, in later years, with less drought, we still observed similar symptoms in forests with high OLB infestation. The attempts to quantify these effects in Croatia or our own research in Hungary has not yet discovered a direct link (Franjević et al. 2018; Paulin et al. 2020). However, the growth of the acorns usually speeds up in July, during which time the negative physiological effects of the OLB intensify. It can therefore be assumed that the physiological effects of the OLB on oak foliage have or will have detectable effects on acorn crop. In that context, the Turkey oak's (*Quercus cerris* Linnaeus 1753) acorns develop for two years (Bartha et al. 1999), meaning that the OLB's effects will influence the acorn development throughout two years.

According to a study by Drekić et al. (2023), OLB may also impact the regeneration of oak forests. Their results indicated a significant decrease in the intensity of OLB attack on seedlings grown unshaded by the old trees (Drekić et al. 2023). Treatment by insecticide also caused a significant difference in the height of seedlings growing in shade in 2021, indicating that the cumulative effect of more intense OLB attacks has the potential to reduce oak seedling growth (Drekić et al. 2023). The health and regeneration of oaks is a crucial issue for Europe as oaks will become increasingly important for silviculture aiming to mitigate the effects of climate change (Stimm et al. 2021). The pedunculate oak (*Q. robur* Linnaeus 1753) is one of the most important tree species in European temperate deciduous forests, dominating lowland forests in a huge belt from Britain to the Ural Mountains (Bohn et al. 2007; Walter and Breckle 1989). Since all known Eurasian deciduous oaks are known hosts of OLB (Csóka et al. 2019) its impact, coupled with the already present dangers to these oaks' health (such as drought, defoliators, and pathogens) is highly likely to influence the natural regeneration of oaks in a negative way (Annighöfer et al. 2015; Reif and Gärtner 2007; Shaw 1968a, 1968b).

OLB's known and presumed interactions in oak ecosystems

Oaks are not only prominent and distinctive tree species in many natural territories in Europe, but also support a remarkably large variety of herbivorous arthropod species (Crawley 1983). In contrast to other tree species, oaks in all likelihood have the highest number in this regard. A total of 423 insect and mite species from the UK (Kennedy and Southwood 1984), 298 insects from Germany (Altenkirch 1986), and 672 insect species from Hungary (Csóka and Ambrus 2016) were reported as oak-associated herbivores (feeding on living plant tissue). It is this reason which would make OLB's impacts on oak health a possible danger to their ecosystems.

Invasive alien species can also cause major changes in the functioning of the ecosystem (Wardle and Peltzer 2017). While the highest number of species can usually be found on oaks in the first half of the year, the number of nymphs potentially feeding/developing on the leaves is still large in August/September (Kulfan et al. 2013). There are approximately 180 species (in Hungary alone) that are still feeding on oaks in late summer, during the highest OLB damage (Paulin et al. 2020). Because of the continuous being of the effect, it has a potential to seriously reduce the herbivore populations. The decrease in some of these insects could also significantly impact their predators.

Since we can presume that OLB may directly impact species that feed during late summer, other larvae feeding early in the vegetative period potentially hinder the OLB's proliferation. A study designed by Valdés-Correcher et al. (2023) aimed to document the effect of other herbivores' chewing damage on the OLB's feeding habits on four oak species: pedunculate (*Q. robur*), sessile (*Q. petraea* [Matt.] Lieblein 1784), Turkey oak (*Q. cerris*), and holm oak (*Q. ilex* Linnaeus 1753). Only eight OLBs survived on holm oak leaves; therefore, they excluded holm oak samples from sub sequent analyses. During laboratory experiments, they found that early herbivore chewing facilitated subsequent damage by the OLB to pedunculate, sessile, and Turkey oaks (Valdés-Correcher et al. 2023). They observed significant differences in the different hosts' sensitivity to the OLB between the three oak species (Valdés-Correcher et al. 2023). However, they found no evidence that early herbivory influenced the rank of sensitivity of different host species to the OLB (Valdés-Correcher et al. 2023).

Aside from the damage the OLB can cause to oak-associated species, there is a possibility of further impacts on oak forests. This theory is based on an event recorded on the sycamore lace bug (*C. ciliata*) causing mass fish mortality in several trout farms in the NW part of Greece (Savvidis et al. 2009). The feces and the adults of the bug were washed into the streams from the Platanus trees during the heavy rains. It was proven in ex situ experiments that the mass mortality of young trout in one of the trout farms was caused by the feces and adult bugs in the water (Savvidis et al. 2009). While nothing of this sort was caused by the OLB yet, due to the close relation between the two species, the potential similar effects of the OLB's mass abundance should be studied.

Since OLB's impact on oak health, oak leaves, and oak ecosystems has not been thoroughly studied yet, there could be other ways the OLB may affect other oak-associated species. There is the question of mycorrhizal fungi and litter decomposers. The health of mycorrhizal fungi is closely tied to the health of their host trees. OLB's impact in this case could also include economically important groups like truffles (the genus *Tuber*). Truffles can only be cultivated if they have a mutual symbiotic association with a list of species of specific trees like *Quercus* sp. (Győrfi 2010). Therefore, the impact of OLB could negatively influence some species of this genus. This is important, because these are economically important mushrooms, as they produce fruits with a characteristic aroma and flavor profile (Gryndler et al. 2014; Paolocci et al. 2004; Shah et al. 2020).

Forest ecosystems contain both aboveground and belowground components; both are integral for the continued working of the forests (Hooper et al. 2000; Wardle 2013). OLB overfeeding, aside from the previously mentioned effect on photosynthesis (Nikolić et al. 2019), could also induce changes in the chemical composition of leaves. Therefore, we are also convinced that studying how litter decomposers are at risk is also crucial.

Human-OLB interactions

With the widespread distribution of OLB and the large areas occupied by their host trees across both natural and urban environments, interactions between humans and OLB assumably will become more frequent. The previously mentioned close relative of the OLB, the sycamore lace bug, sporadically stings humans and has reportedly caused painful irritation on the skin (Dutto and Bertero 2013; Izri et al. 2015). No similar reports related to the OLB are known yet, but our own experience shows that it can cause similar symptoms (Paulin et al. 2020). In the future, people may experience such contact with OLB in oak-dominated forests along frequented hiking trails, as well as in public gardens, parks, roadsides plantings and private gardens.

Since the public's encounter with the OLB is predicted to become more frequent, it is also likely that in the future, the general population might be involved in making decisions and taking steps related to the OLB. To evaluate public awareness and familiarity with the OLB and the health of oak forests, a survey was distributed in 2020 using social networks and professional connections (Bălăcenoiu et al. 2021b). The survey was also circulated between foresters and stakeholders, in hopes of getting more replies from those with vested interest. Over 2000 people responded, from nine nations in Europe. Public awareness regarding the visible damage caused by the OLB was moderate (60%), but a vast majority (93%) of respondents considered it an issue (Bălăcenoiu et al. 2021b).

The knowledge and awareness around the OLB of respondents from countries where it is widespread was higher than that of people from countries where it is not. Based on the responses, forest managers and stakeholders believed that the OLB could affect photosynthesis and acorn crop, but the insect could not cause the death of trees (Bălăcenoiu et al. 2021b). Both stakeholders and respondents with ties to environmental NGOs speculate that the price of wood will decrease because of the OLB but believe that the insect and its effects would have no influence on property value. However, forest owners fear that people would avoid entering the forests with widespread OLB presence (Bălăcenoiu et al. 2021b). When asked about preventive or control measures against the OLB, the majority replied that mechanical trapping or biological control measures were preferable to chemical ones. Based on current research, the encounters between the public and the OLB seemingly have not yet reached a critical point. However, due to OLB's already widespread presence, as well as considering its future outbreaks, it is imperative to keep the general population in mind when considering control options.

Attempts of chemical control methods

The chemical control of the OLB was the least favored by the public, probably for its perceived negative effects (Bălăcenoiu et al. 2021c). However, since it is already extensively used and its application can in some isolated cases be beneficial, research is still necessary. There have been several trials regarding the OLB's chemical control. When using chemical control, systemic insecticides will probably have the highest efficacy, as both young and adult bugs feed on the underside of leaves and are likely well protected from pesticide exposure.

Serbian researchers tested four chemical insecticides: Bifenthrin with applied concentration 0.05%, Buprofezin—0.05%, Thiametoxam — 0.02% and Abamectin — 0.065%; they applied the chemicals using a backpack sprayer (Drekić et al. 2019). Experiments showed that 2 days after treatment, the effectiveness of Bifenthrin in suppressing the nymphs of oak lace bug was 100%, and the effectiveness of Thiametoxam was 99.34%. The other two insecticides were slightly less effective: Abamectin at 81.77% and Buprofezin at 64.98%. After ten days of application of insecticides, the effectiveness of Thiametoxam and Bifenthrin was 100%, while the effectiveness of Buprofezin increased to 81.50%, and Abamectin — up to 97.28%.

Later, still in Serbia, three more insecticides were tested, this time using a Stihl SR 420 mist blower: Deltamethrin with an applied concentration of 0.05%, Flonicamid— 0.014% and Acetamiprid — 0.025% (Drekić et al. 2021). The test results showed that two days after the treatment, the effectiveness of the drugs used based on the active ingredients Deltamethrin and Acetamiprid was 100%. Flonicamid had a significantly lower efficiency – 76.4%. 10 days after treatment with insecticides Deltamethrin and Acetamiprid, their effectiveness in suppressing the number of oak lace bugs was 99%.

The effect of insecticides against the OLB on a larger scale was tested in 2020 in Romania (Bălăcenoiu 2021c). In 2020, two types of synthetic insecticides were tested, using aerial spraying methods, for oak lace bug population control: contact pyrethroid Alfametrin (Alfametrin 10 CE over 'Forest A') and systemic insecticide (APIS 200 SE over 'Forest B'). Short term results showed a reduced population density of nymphs (by 91–96%) in all experimental areas. However, areas where contact insecticide was used were observed to be reinfested 22 days after treatment. Areas where systemic insecticide was used were observed to be reinfested more than a month later. The attack intensity showed stronger discoloration in areas treated with contact insecticide compared to areas treated with systemic insecticide.

Fora et al. (2024) recently tested the insecticide Spinosad (Laser™ 240 SC) against OLB nymphs in Romania.

Spinosad affects the nervous system of insects, rendering them inert. The active ingredient of Spinosad (Laser™ 240 SC) is derived from a naturally occurring soil bacterium, *Saccharopolyspora spinosa* Mertz and Yao, 1990; for this reason, the authors refer to it as a 'biological method' (not to be confused with 'biological control'). The study revealed that Spinosad diluted in water at 2 mL/4 L and 2 mL/2 L concentrations produced a high mortality. This mortality rate 3 days later was comparable to the impact of synthetic insecticides and reached 94% and 98%, respectively. Therefore, these laboratory experiments proved that Spinosad could be effectively used as a biological method against the OLB.

While these results of these tests suggest that the OLB can be controlled using spraying methods, the fact that there is at least 35 million hectares of potential hosts for the species means that no chemical control method is economically feasible; even more so when most tests reveal that only multiple sprayings produce the desired effect. However, in some cases (urban habitats, park trees, nurseries) it might be applicable with proper caution to human exposure. The high diversity of other insects in oak forests mentioned in a previous chapter means that such spraying treatments in or close to natural habitats are highly precarious. The chemical control of OLB in oak ecosystems, due to the high biodiversity supported by oaks, is altogether unacceptable at such a large scale, meaning that the likeliest regulation method is biological control.

Natural enemies and pathogens of the OLB in its invaded range

Since its first discovery in Europe, researchers have tried to find the native enemies of OLB with regulatory potential. On many occasions, different species were recorded feeding on some developmental stage of the OLB (such as coccinellids, lacewings, predatory bugs, velvet mites and spiders) but there has been no record since Paulin et al. (2020) that any of them had significant regulating influence on OLB populations. The OLB's rate of spread and the mass proliferations experienced in Europe can mostly be a result of its escape from the predators and parasitoids in its native range; the so-called enemy (or ecological) release hypothesis (Brockerhoff et al. 2006; Brockerhoff and Liebhold 2017a, b; Firlej et al. 2012). In North America, the OLB is mostly contained by its natural enemies (Solomon 1980).

Some common predators such as the *Formica rufa* group Linnaeus, 1761 (Hymenoptera: Formicidae), have been reported to avoid OLB, even if infected leaves fall to the ground near their anthill (Paulin et al. 2020; Fürjes-Mikó et al. 2025). Somewhat contrary to this we have yet unpublished research results from 2023, where we used Chauvin-traps (Chauvin 1966). The preliminary data showed that in a sessile oak forest, nearly 300 OLB adults were found in the traps of *F. rufa* ant hills. However it is yet unclear in what way (carried or fell in by accident) and in what condition (alive or dead) the OLB adults got into the traps.

There is partial information on local predators and parasitoids interacting with the OLB-s already widespread in Europe. There are reports about the larvae of *Chrysoperla carnea* (Stephens, 1836), *Pseudomallada* sp. (Neuroptera: Chrysopidae) and *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae) in Hungary preying on different stages of OLB (Paulin et al. 2020). In Italy, some spiders (Araneae: Salticidae) have been listed as native predators of the OLB (Bernardinelli and Zandigiacomo 2001). Yet neither country had any information on native enemies having any noticeable effect (Paulin et al. 2020).

In recent years, parasitoids of the OLB were studied in Bulgaria (Georgiev et al. 2024). Nymphs of OLBs were collected from European oak (*Q. robur*) and Turkey oak (*Q. cerris*) from five separate areas. After rearing, the following eulophid species (Hymenoptera: Eulophidae) were documented in the samples: *Tamarixia pubescens* (Nees, 1834), *Elasmus* sp., *Minotetrastichus* sp., *Pnigalio* sp. and *Sympiesis* sp. (Georgiev et al 2024). The presumed effect of these parasitoids was minor (0.1–0.3%) (Georgiev et al 2024). Since these eulophid species are recorded as parasitoids of species not closely related to lace bugs, it is likely that the samples were contaminated.

Entomopathogenic fungi found in Europe also have minor impact on OLB populations. The impact of four widespread entomopathogenic fungi on OLB was documented in Croatia and Slovakia (Kovač et al. 2020, 2021). These were: *Beauveria pseudobassiana* S.A. Rehner and Humber 2011, *Lecanicillium pissodis* Kope and I. Leal 2006, *Akanthomyces attenuatus* (Zare and W. Gams) Spatafora, Kepler and B. Shrestha 2017 and *Samsoniella alboaurantia* (G.Sm.) Mongkols., Noisrip., Thanakitp., Spatafora and Luangsa-ard 2018. The most effective fungus species seemed to be a *B. pseudobassiana* isolate. The OLB mortality rate was 80% and the fungal infection rate of adults was about 70% 14 days after treatment. However, this rate was only achieved in Petri dishes under laboratory conditions. Because of this, we think that the treatment mentioned in the paper (the application of a fungal inoculum on moss patches at the basis of oak trees) is not feasible as a long-term solution for such a large area of already infested oak forests. Our field surveys from several years, which were performed during sample collections in separate locations, showed a less than 0.001% mortality in field conditions (Paulin et al. 2023a, b). It is also worth noting that *B. pseudobassiana* is documented as a cosmopolitan entomopathogenic fungi (Rehner et al. 2011), which means that using such biological control agents could also impose risks upon the rest of the herbivore communities on oaks.

All observations so far show that predators and parasitoids already present in Europe do not show any regulating potential against the OLB. This case is similar to the close relative sycamore lace bug (*Corythucha ciliata*) which has been present in Europe for more than 60 years (Servadei 1966). The sycamore lace bug's case studies have pointed out that although the predation of *C. ciliata* is effective in laboratory conditions, it does not significantly inhibit its reproduction (and the effects it causes) in natural circumstances (Őszi et al. 2006). While there is a slight possibility that certain native enemies could be used to limit the OLB to some degree, the current evidence shows that considerable effort is required to achieve a significant impact. Based on this evidence none of the native predators, parasitoids, or even pathogens can effectively regulate the OLB in its current invaded range, and the most likely option is using classical biological control.

Possibility of classical biological control

Classical biological control relies on finding the natural enemies of a pest in its range of origin. These possible enemies are usually chosen because they are specialists (most probably parasitoids) and are observed to cause high mortality in the target species (Hawkins et al. 1993). Since there were Tingidae species that caused a significant economic impact in the past, we already have knowledge of egg parasitoids used against them in biological control methods. Such natural enemies of the Chrysanthemum lace bug, (*Corythucha marmorata* [Uhler, 1878]) (Puttler et al. 2006; Triapitsyn et al. 2024); the avocado lace bug, (*Pseudacysta perseae* [Heidemann, 1908]) (Peña et al. 2009), and the OLB were documented in the past (Puttler et al. 2014). The parasitoid, documented to control the avocado lace bug and the OLB, called *Erythmleus klopomor* (Triapitsyn et al. 2007) (Hymenoptera: Mymaridae) is the only native enemy which so far has been considered against the OLB (Paulin et al. 2026). We have conducted a few surveys of *E. klopomor*, and further studies are planned to help us better understand its ecology, particularly concerning the unintended side effects. Our unpublished preliminary results on *E. klopomor* seem promising, and our surveys have found no other parasitoid of the OLB eggs.

Low densities of OLB in the 7 states of the USA we visited compared to the invaded range in Europe can probably be attributed to the significant effect of the *Erythmelus*. Alternative explanation could be that European oaks are naïve, but it can be rejected since the American white oaks in the European arboreta and botanical gardens just as severely infected as the Euro-pean oaks (58). We have also recorded the presence of *E. klopomor* in five states previously undocumented, as well as producing preliminary parasitism rates of this Mymarid (Paulin et al. 2026). As *E. klopomor* was documented to parasitize several tingid species, mainly *Corythucha* spp. (Triapitsyn et al. 2024, 2007; Peña et al. 2009; Puttler et al. 2006), it is a very promising candidate for biological control. Even more encouraging is the fact that the OLB seems to be its preferred host (Puttler et al. 2006). However, to prevent undesirable side effects and to expand knowledge about the behavior and habitat of this parasitoid species, further research efforts are needed both in the field and under laboratory conditions.

Concluding remarks and possible future research

Based on all the available knowledge reviewed, the OLB has been proven to be a highly dangerous invader, necessitating more thorough research in certain areas. One such instance is that we still lack definite information about the OLB's pathways into Europe and Asia. These pathways may also facilitate the spread of other invaders in the future.

To the best of our knowledge, the importance of oaks in Europe is unquestionable. Their decline would cause a major economic disturbance, not just because of the decline in wood, but also because oak forests provide other beneficial services as well (e.g. truffles and other valuable mushrooms). In comparison to with other forests such as pine, oak forests are characterized by higher species diversity, stratification, litter production, and soil fertility (Shrestha 2003), meaning the damage of OLB could also potentially threatens these.

The oak forests of Europe are already showing decline due to several factors. Major agents of oak decline are the severe (in particular, repeated) defoliation of other insect larvae, the infection of powdery mildew, weather extremes (severe summer drought, winter frost and spring frost), other abiotic factors (groundwater level decrease, soil composition change) or a combination of these (Thomas 2008). At hydromorphic sites for example, intermittent soil moisture can intensify the impact of drought (Thomas 2008). In the temperate regions major outbreaks of decline only happen if two or more of these factors act in combination (Thomas 2008). When the decline starts, biotic factors such as the root pathogen *Gymnopus fusipes* (Bull.) Gray 1821 and the borers *Agrilus biguttatus* (Fabricius, 1776) or *Platypus cylindrus* (J.C.Fabricius, 1792) can contribute to the damage in later stages (Thomas 2008). There are other possible causal factors, whose importance still must be corroborated, but the fact that oaks are already under severe pressure cannot be denied.

The full extent of threats posed by OLB and the means of it has yet to be fully discovered. Wide scale studies on the OLB's effect on oak regeneration and growth are needed to take effective steps against the further decline of oak forests. Research on how OLB may influence oak health and the internal composition of leaves is essential, not just for preserving oaks, but to prevent the collapse of their ecosystems, which heavily rely on oak herbivores. Oaks rely on the parts of their ecosystems which have been underrepresented in research; such as mycorrhizal fungi and leaf decomposers. These components also need further examination.

While native enemies do not seem to have any significant effect on the OLB, because of the lack of scientific results, there still could be alternative ways to hinder its spread. Judging by what (Bălăcenoiu et al. 2021b) reported of the public's opinion on OLB, it is probable that local management options against it would be widely used. Unfortunately, there is no knowledge of such practices yet, but there are examples where the public's opinion in how pests are handled can influence how much financial support publicly favored control measures could get (Solino and Raposo 2022; Hayat et al 2024).

The total eradication of the OLB is impossible and native European predators and pathogens have had no success in reducing their population. Since no close relative native species of OLB exist in Europe, the chances of parasitoids already found in Europe meaningfully affecting the populations of OLB are slim. Entomopathogenic fungi have been studied, and have produced high mortality rates, but these results were acquired under laboratory circumstances. Reproducing these results under field conditions seems highly unlikely, also most of these fungi were not specialists. Their application in the diverse oak ecosystems could threaten other, non-target species as well. We consider the thorough investigation of promising classical biological agents, such as *Erythmelus klopomor*, as well as examining their possible non-target effects to be much needed. Long-term application of any other control method over the large area of the European oak forests is not feasible and would be immensely harmful to their diverse ecosystems.

There are chemical control options available against OLB. While some of these options have been studied and are available, they should only be applied after careful consideration for several reasons. One of the primary reasons, similarly to entomopathogenic fungi, is that the currently known and used chemicals are not selective, meaning that they damage the entire ecosystem where used. The other main argument is that due to the fact that OLB has multiple generations yearly, one treatment would not be enough to have a significant effect on the continuous population of OLB.

While the North American oak lace bug alone threatens European ecosystems in a complex way, it is but one of the newest additions to the already long list of agents responsible for the decline of oaks. The oak decline phenomenon has been known for a long time (Macháčová et al. 2022), but now OLB, with its multitude of effects, is part of the already accumulated pressures. Yet the impacts of OLB are not immediate and information about its effects is scattered. Comprehensive research targeting oak-dominated forests already infested by the OLB is required, in addition to studies on potential management and control methods.

Author contributions GC and MP wrote the manuscript. Both authors read and approved the manuscript.

Funding Open access funding provided by University of Sopron. Our research was funded from project'K 142858', implemented with the support of the Ministry of Innovation and Technology of Hungary from the National Research, Development and Innovation Fund, financed under the'K22-OTKA' funding scheme.

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflicts of interest The authors declare no competing interests.

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