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Spread and potential host range of the invasive oak lace bug [*Corythucha arcuata* (Say, 1832) – Heteroptera: Tingidae] in Eurasia

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Abstract

1. The North American oak lace bug feeds on leaves of “white oaks” in its native range. In Europe, it was first discovered in northern Italy in 2000. In the past years, it subsequently spread rapidly and population outbreaks were observed in several European countries. Here, we summarise the steps of its expansion.
2. To predict its potential host range, we checked 48 oak species in 20 sentinel gardens in seven countries between 2013 and 2018.
3. In total, 27 oak species were recorded as suitable hosts, 13 of them are globally new ones, 23 out of the 29 in section *Quercus* (~ white oaks, an intrageneric taxonomic unit within genus *Quercus*), including Asian oaks, native to Japan, Korea and China, and four out of five in section *Cerris* (another intrageneric unit of the same genus) were accepted as hosts. None of the species in section *Lobatae* (red oaks) or in the *Ilex* group was.
4. Host records were also collected in forest stands of ten countries. We found 11 oak species infested. Outbreak populations were most commonly found on *Q. robur*, *Q. frainetto*, *Q. petraea*, and *Q. cerris* – widespread and outstandingly important oaks species in Europe.
5. Based on our findings, we conclude that suitable hosts for oak lace bug are present in most of Europe and Asia. It means that lack of hosts will likely not restrict the further range expansion.

Keywords: *Corythucha arcuata*, host plants, non-native species, sentinel gardens, *Quercus* spp.

Running title: Area expansion and host range of the oak lace bug

Introduction

Insects are among the most numerous invaders worldwide (Kenis & Branco, 2010; Brockerhoff & Liebhold, 2017), and make up ca. 87% of the non-native arthropods introduced in Europe (Roques, 2010). Non-native insect species have appeared at an alarmingly increasing rate in Europe in recent decades (Roques, 2010; Kenis & Branco, 2010; Csóka *et al.*, 2012; Tuba *et al.*, 2012; Smith *et al.*, 2018). While some non-native insects spread slowly and do not cause detectable economic/ecological damage, others become invasive, rapidly expand their range and subsequently have rather severe effects within newly invaded area. Examples of recent rapid spreads within Europe are provided among many others by *Obolodiplosis robiniae* (Skuhrava *et al.*, 2007), *Harmonia axyridis* (Roy *et al.*, 2016), *Leptoglossus occidentalis* (Lesieur *et al.*, 2018) and *Halyomorpha halys* (Vétek *et al.*, 2018). Non-native species, on top of their potential of causing significant economic losses, may have impacts on natural processes in ecosystem functions (Simberloff, 2001, 2011; Kenis *et al.*, 2009; Wardle & Peltzer, 2017; Liebhold *et al.*, 2017).

One of the major determinants regarding a non-native insect's potential to become invasive is the availability of its hosts. If suitable hosts are absent or very rare in the newly invaded territory, the non-native insect species has limited chance to establish and become invasive.

The oak lace bug (*Corythucha arcuata* Say, 1832 – Heteroptera: Tingidae; abbreviated as “OLB” further on) is native and widespread in the eastern part of the United States and across southern Canada (Barber, 2010). The known host records from its native range are listed in Table 1. Surprisingly, only seven oak species out of more than 40 native to North America are named at the species level (Table 1). Most literature sources refer to the hosts of OLB as oaks, or slightly more accurately white oaks (section *Quercus* in genus *Quercus*). Morrill (1903) also recorded “English oak” (*Quercus robur*) as a preferred host in Massachusetts, but he used the scientific name of this species incorrectly (he gave *Q. rubra* instead of *Q. robur*). Non-oak hosts include *Castanea dentata*, *Acer* spp., *Malus* spp., *Pyrus* spp., and *Rosa* spp. without accurate species names (Connell & Beacher, 1947; Drake & Ruhoff, 1965; Drew & Arnold, 1977).

OLB was first discovered in Europe, in northern Italy in 2000 (Bernardinelli, 2000; Bernardinelli & Zandigiacomo, 2000; Figure 1.). Recognizing its potential importance, OLB was put on the EPPO Alert List in March 2001 and it remained until 2007, when it became clear that administrative efforts could not stop its further spread. Between April and July 2002, two specimens of OLB were caught in a

flight interception trap in southern Switzerland (Forster *et al.*, 2005). In the same year, OLB was found for the first time in Turkey, about 200 km east of Istanbul (Mutun, 2003). One specimen was found in Iran (Western Azerbaidjan) in 2005 (Samin & Linnavouri, 2011). By the summer of 2008, the distribution expanded significantly, reaching 28,000 km² only in Turkey (Mutun *et al.*, 2009). This population build-up in western Asia most likely acted as a prolific source for the spread north through the Balkans. However, a human-mediated accidental introduction from northern Italy to other countries could not be excluded.

In July 2012, OLB was found in Bulgaria (Dobrevna *et al.*, 2013). One year later, it appeared in Hungary (Csóka *et al.*, 2013), and was recorded at two distant (140 km in a straight line) locations almost at the same time. In 2013, it was also discovered in Croatia (Hrašovec *et al.*, 2013) and Serbia (Poljaković-Pajnik *et al.*, 2015; Pap *et al.*, 2015; Glavendekić, 2017). In Russia, OLB was first found in Krasnodar in 2015 (Neimorovets *et al.*, 2017). OLB was detected for the first time in 2016, again in several countries: Albania (E. Cota's pers. comm.), at two locations in Romania, rather far (at least 400 km) from each other (Don *et al.*, 2016; Chireceanu *et al.*, 2017). In autumn 2016, Jurc & Jurc (2017) also recorded it in Slovenia, close to the Croatian border. In Bosnia and Herzegovina, the first observation dates from 2017 (Glavendekić & Vukovic-Bojanović, 2017; Dautbašić *et al.*, 2018). In the same year it was detected in southwestern France (Streito *et al.*, 2018). In 2017, it was also found in southern Ukraine (V. Meshkova's pers. comm.). In May 2018, OLB has been recorded in north-eastern Greece (D. Avtzis' pers. comm.) and in June 2018, in southern Slovakia (Zúbrik *et al.*, 2018). A screening in south-eastern Austria in September 2019 confirmed its occurrence at 21 sites (Sallmanshofer *et al.*, 2019). Following the first records, fast range expansions were reported from almost all the countries (Csepelényi *et al.*, 2017a; Simov *et al.*, 2018). It should also be mentioned that the temporal sequence of the first records in different countries does not necessarily reflect a real pattern of the spread relating to time. It is more likely related to the timing of the intensive search after the species appeared in the given country. The countries where and the years when OLB was detected first are shown in Figure 1. The northernmost known record (N48.510889; E22.051056) in September 2019 is from eastern Slovakia (Zubrik's unpublished data). Population genetic studies may clarify the starting point and routes of the invasion (Estoup & Guillemaud 2010; Cristescu 2015). Although OLB adults can actively fly and they can also be passively dispersed by wind, their long-term dispersal is generally related to international road and rail traffic. The first infested locations in a

given region were often found at resting places near motorways or along rail lines (authors' unpublished observation).

By autumn 2016, the total area of invaded oak forests was about one million hectares in Russia, of which about 0.4 million was severely infested (oak crowns in large groups or in whole forest blocks suffered early discoloration exceeding 50% level). The total extent of the outbreak areas in 2017 exceeded 1.3 million hectares, in the oak forests of the Krasnodar Territory and the Republic of Adygea. Currently, the bug has spread to all the oak forests of the Black Sea coast, of the Krasnodar Krai region, from Anapa to the state border. There is still no indication that OLB has reached its potential distribution limits in Europe and Asia.

In this paper, we are summarising the present information available on the range expansion in Europe and the host range of the accidentally introduced and rapidly spreading invasive North American oak lace bug. In order to predict its further potential regarding hosts use in the invaded range, and the risk of its further area expansion, we checked 48 oak species in 20 sentinel gardens in seven countries between 2013 and 2018. These gardens can provide valuable data on the host range of non-native pests or pathogens (Roques *et al.*, 2017; Vettraino *et al.*, 2017). The data on potential host use is very important to evaluate and predict the potential to spread and cause damage.

Methods

We have been collecting data intensively on host use since 2013 in 20 sentinel gardens (i.e. botanical gardens and arboretums) in seven countries (Croatia, Hungary, Italy, Romania, Serbia, Slovakia, Slovenia) and forest stands in eleven ones (Bosnia and Herzegovina, Bulgaria, Croatia, Hungary, Italy, Romania, Russia, Serbia, Slovakia, Slovenia and Turkey). A list of the sentinel gardens is given in Table 2 and shown in Figure 2.

A total of 15 sentinel gardens were located in an area already invaded by the oak lace bug, and five of them were outside of the presently known range. These five (two in Hungary, two in Slovakia and one in Slovenia) were also checked for the presence of OLB since we consider arboretums and botanical gardens as potential "hot spots" of non-native insects and early detection points. We

assumed that invasive OLB might appear in such places even far from the core invaded area. We also collected information from the oak stands of the countries where OLB's presence was known for at least two years. Although the discolouration of the infested leaves is typical, we always checked the affected trees for presence of adults, moulted skins of larvae and egg clusters. These together can provide unequivocal signs of a plant being utilised as a host. We did not consider a tree species as a host if only adults were found on it. As an easily and passively spreading species, OLB can often land and be on plants which are not suitable hosts.

The overwintered adults can be found on the underside of leaves from April. Egg bunches are present from early May, larvae appear later in May. As OLB may have three overlapping generations per season, all developmental stages are noticed on the foliage from June until October.

The arboretums and botanical gardens in Hungary were visited two to six times, most of the sentinel gardens outside this country were visited once (see Table 2). The surveys (both in sentinel gardens and autochthonous oak stands) were made once a year from mid-July to late September. By this time, the symptoms become easily noticeable and unambiguous. Sample branches were regularly cut using long-handled loppers to check the presence of the different developmental stages.

The number of locations and of trees from different oak species varied depending on the species. The oaks native in the region were regularly sampled (>10) and at many locations (>10), the most exotic ones were generally rare and restricted to few places. While specimens of *Quercus robur*, for example, were present as a number of individual trees in most of the botanical gardens/arboretums surveyed, only single individual trees of some other species (i.e. *Q. aliena*, *Q. gambelii*, *Q. imeretina*, etc.) were available at one site only. This fact would make the statistical analysis of host preference rather difficult.

Oak stands were also surveyed by the authors in ten countries (Bosnia and Herzegovina, Bulgaria, Croatia, Hungary, Italy, Romania, Russia, Serbia, Slovenia and Turkey). The levels of infestation were classified as described below. The number of oak stands that were surveyed cannot be given precisely, but the total area reaches several thousand hectares. In different native oak stands, regularly no survey of single trees was necessary, since in most cases larger groups of them or even whole stands were severely infested, providing easily detectable symptoms. We categorised the infestation level on a 0–3 scale. The scale is described as follows:

- 0: No symptoms.
- 1: Symptoms/different developmental stages of OLB are sporadic, restricted to single leaf or smaller groups of them and can only be found with targeted, intensive search.
- 2: Symptoms/different developmental stages of OLB are found along whole branches that can easily be spotted on the tree.
- 3: Symptoms/different developmental stages of OLB cover whole trees or groups of them, sometimes even extensive stands of many hectares. Heavily infested trees/stands can be safely spotted from larger distance, or for instance with drones.

Results

Oak Hosts

We checked 48 different oak species in 20 sentinel gardens in seven countries. Presence of OLB was recorded at 15 locations in five countries (Croatia, Hungary, Italy, Romania and Serbia). A total of 27 out of 48 oak species were proved to be suitable OLB hosts. They are listed in Table 3. Only the locations with recorded presence of OLB are included in it. Of these 27, 15 were globally new host records for OLB (underlined in Table 3). The share of each intrageneric taxonomic unit from genus *Quercus* can be seen in Figure 3. Out of 29 species surveyed in section *Quercus* (white oaks), 23 (79.3%) can be hosts of the OLB, four out of the five ones (80%) belonging to section *Cerris* are suitable for it, and three of them were heavily infested at almost all locations. No symptoms were recorded on any of the North American red oaks within the section *Lobatae* and no species in the *Ilex* group (Mediterranean evergreen oaks) showed some of infestation (Table 3).

In forest stands of the ten countries involved in this study, we found 11 species of oaks (autochthonous in the given country) infested by OLB at different levels (Table 4 and Figure 4). All species showed signs of heavy infestation in some countries. So far, outbreak populations have most often been detected in *Q. robur*, *Q. frainetto*, *Q. petraea*, and *Q. cerris* stands.

Non-Oak Hosts

Thirty-three species of non-oak woody hosts belonging to ten plant families have been recorded in eight countries. These host records are provided in Table 5. Many of them are new host records.

Discussion

OLB's widely accepted host species belong to the two major sections of the genus *Quercus* (*Quercus* and *Cerris*). The taxonomic relatedness of the oak species included in this study seems to be a more important factor than their native ranges. White oaks (section *Quercus*) were infested almost independently from their native ranges, except for the North American ones, naturally present on the western coast of the USA. One species (*Q. gambelii*) showed a low level of infestation, the other one (*Q. garryana*) was not attacked. However, it should be mentioned that these species were represented by only single (and small) tree at only one botanical garden (Vácrátót, Hungary). Heavily infested species can be found both among the North American (*Q. alba*, *Q. macrocarpa*, etc.), European (*Q. robur*, *Q. petraea*, etc.) and even species with Far East origin (*Q. dentata*, *Q. mongolica*). Only one species from the section *Cerris* (*Q. acutissima* – native to Eastern Asia) was unattacked, but, this species was only surveyed at one place (Vácrátót, Hungary).

From our observations it is quite clear that the red oaks (section *Lobatae*) are not suitable hosts for OLB. None of these species (with one exception, see below) showed any signs of infestation, although most of them grow in a rather exposed environment, surrounded by heavily infested suitable hosts. We found only a very small (less than 1 cm²) spot with symptoms on *Q. imbricaria* (Szarvas, Hungary, 2015), but dead larvae were surrounding it, therefore we do not consider this oak species a suitable host. These results coincide with the observations of Morrill (1903), who reported three species of red oaks (*Q. coccinea*, *Q. ilicifolia*, *Q. laurifolia*) remained unaffected “although they stood so near to badly infested trees that their branches touched in some cases”. Trieff (2002) found OLB adults in the canopy of *Quercus rubra* during a knockdown fogging experiment in the USA. However, presence of adults itself does not provide proof that *Quercus rubra* is a suitable host, as it was mentioned earlier. Our results are also similar to those of Bernardinelli (2006a, b) who found the North American *Q. rubra* as unsuitable, versus native European oaks that are.

None of the three oak species belonging to the *Ilex* group had any feeding symptoms in the arboretums and botanical gardens visited. However, in a sentinel experiment in Croatia (seedlings were placed under a heavily infested *Q. robur* stand), even these species (*Q. ilex* and *Q. coccifera*) showed sporadic small symptoms of sucking. Therefore, it can be concluded that OLB's preferred hosts are present in the majority of the Europe. It should also be mentioned again that many central and even eastern Asian oaks (including natives of Japan, Korea and China) are suitable OLB hosts. These are globally new host records for OLB, meaning that eastbound range expansion of OLB is unlikely to be restricted by host availability. In surveys at the stand level, not surprisingly, *Q. cerris*, *Q. petraea*, *Q. pubescens* and particularly *Q. robur* were recorded as being most heavily attacked in all countries. These species are widely distributed and are among the most abundant on trees in the surveyed region. Summed up, only these four species are covering together more than 10 million hectares of forested land in Europe.

Climate may influence significantly the establishment and further spread of the non-native invasive insects. The milder and shorter winters could do it on the higher overwintering survival and the timing of spring emergence resulting more generations per year (Berzitis *et al.*, 2016; Pap *et al.*, 2018; Smith *et al.*, 2018; Ward *et al.*, 2018). Bernardinelli (2006b) compared climatic conditions of the native North American range and Europe and concluded that most of the latter is likely to provide suitable conditions for the establishment of OLB. In a recent study (Csepelényi *et al.*, 2017b), it was found that the relatively cold winter of 2016/2017 did not cause high overwintering mortality (not exceeding 50%) at two locations in south-eastern Hungary.

The long-term impact of the OLB damage is not yet known, but there are good reasons to assume that the "chronic" infestations will negatively influence in a significant manner the growth, health status and fecundity of the oak stands which already suffer from both the direct and indirect effects of climate change (Csóka, 1997; Csóka *et al.*, 2009). The heavily attacked leaves lose most of the chlorophyll in their upper surface, while the one in their underside tissues remains relatively unharmed. This is particularly important in terms of photosynthesis since ca. 80% of this process takes place in the palisade clorenchyma of the leaf upper surface (Lambers *et al.*, 1998). According to a recent Serbian study, the rate of photosynthetic and transpiration activity as well as the stomatal conductance decreased by 58.84%, 21.66% and 35.71%, respectively, compared to non-infested plants (Nikolić *et al.*, 2019). An unpublished study in Hungary resulted in a similar loss regarding the

photosynthetic activity in late June, at above 50% of the degree of leaf discolouration (I. Mészáros' pers. comm.). Further targeted experiments should be established in order to clarify OLB's long-term impact on health, growth and fecundity of the infested oaks.

It is also still unknown how the mass presence of OLB will influence the extremely species-rich herbivorous insect communities thriving on European oaks. Only in Hungary, at least 650 herbivore insect species were recorded feeding on oaks and more than 40% of them are strictly specialists (Csóka, 1998; 2006; Csóka & Szabóky, 2005). Mitchell *et al.* (2019) reported 2,300 species associated with *Q. petraea/robur* in the UK, of which 326 were found to be obligate associates (only found on these two oak species). It has already been found in Hungary that larvae of oak specialist notodontids (*Harpya milahuseri* and *Drymonia querna*) starve and then die on leaves severely infested by OLB (authors' unpublished observations).

Our survey in sentinel gardens and forest stands must be considered as an early, but evidently "snapshot" warning. By this, we mean that both the number of affected oak species and the level of infestation are likely to grow in the near future, particularly in most recently invaded areas. The host range, based on our results, could be considered as a "minimum" one. The datasets collected during our survey allows us to predict a further large-scale spread and even a wider host range within both Europe and Asia.

Insect outbreaks sometimes provoke otherwise unexpected host shifting together with range expansion (Castagneyrol *et al.*, 2016). As a consequence, we recorded 28 plant species within eight families as occasional hosts of OLB in eight recently invaded countries (Table 5). The family of Rosaceae was represented by 15 species, Betulaceae by three, Fagaceae, Ulmaceae, Sapindaceae and Malvaceae by two, the other two families (Cannabaceae and Cornaceae) by one each. Genera *Corylus* and *Rubus* were infested in the highest number of countries, and regularly with highest infestation rates. New host records are underlined in Table 5. However, the infestation levels were much lower on a regular basis than those on oaks at the same locations. But still, host shifting may further facilitate the spread of OLB even where the landscape is strongly fragmented and the oak forests do not adjoin each other.

The recent explosive spread and outbreaks of OLB in several European countries show that the dispersal ability and the potential damage by the species can hardly be properly evaluated upon its arrival, as a non-native. Some species do not show immediate invasiveness, and start to spread

rapidly only after a latent period of different lengths (Crooks 2005; Jaric *et al.*, 2018). The favourable weather conditions (likely mild winters allowing high overwintering survival) in several consecutive years may play a “triggering” role in the acceleration of the expansion and fast increase in abundance as it is assumed in the case of OLB.

Due to large-scale and potentially severe effects of OLB in the Eurasian oak forests, preferably international studies are further necessary.

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Web link: <http://oaks.of.the.world.free.fr> (date of the last visit: January 10th 2019)

Name	Common name	Native Range*
Section <i>Quercus</i> – white oaks		
<i>Q. alba</i> L. 1753	white oak	e North America
<i>Q. bicolor</i> Willd 1801	swamp white oak	ne USA; s Canada
<i>Q. macrocarpa</i> Michx. 1801	bur oak	e North America
<i>Q. montana</i> Willd. 1805	chestnut oak	s and e USA
<i>Q. muehlenbergii</i> Engelm. 1887	chinkapin oak	e and cl USA; Canada; ne Mexico
<i>Q. prinoides</i> Willd. 1801	dwarf chinkapin oak	e USA
<i>Q. stellata</i> Wangenh. 1787	post oak	c and se USA

Table 1: North American host records of OLB based on literature sources: (Morrill [1903]; Osborn & Drake [1917]; Connell & Beacher [1947]; Drake & Ruhoff [1965]; Connor [1988]; Torres-Miller [1995]; Drew & Arnold [1997]; Trieff [2002]; Kay *et al.* [2007]; Barber [2010]). Common names of the oaks follow Miller & Lamb (1985). Native ranges are taken from <http://oaks.of.the.world.free.fr>. e = eastern, ne = north-eastern, c = central, s = southern, se = south-eastern

No.	Name	Coordinates	Year(s) visited
Croatia			
1	Lisičine	N45.656667; E17.501944	2017
2	Zagreb	N45.805000; E15.970556	2017
Hungary			
3	Alcsútdoboz	N47.423333; E18.591944	2017
4	Budapest	N47.480833; E19.038333	2017
5	Erdőtelek	N47.689722; E20.313611	2017
6	Gödöllő	N47.567500; E19.383889	2015-2018
7	Kecskemét	N46.915833; E19.655556	2015-2017
8	Püspökladány	N47.334444; E21.090833	2015-2018
9	Sárvár	N47.253119; E16.941489	2016-2018
10	Sopron	N47.680161; E16.573414	2016-2018
11	Szarvas	N46.875556; E20.529444	2013-2017
12	Tiszaigar	N47.527500; E20.806111	2017-2018
13	Tiszakürt	N46.888611; E20.118889	2014-2017
14	Vácrátót	N47.707778; E19.234444	2013-2017
Italy			
15	Padua	N45.399167; E11.880278	2017
Romania			
16	Macea	N46.382222; E21.307222	2015-2016
Serbia			
17	Belgrade	N44.815833; E20.473333	2017
Slovakia			
18	Malacky	N48.439028; E17.030639	2017
19	Topolcianky	N48.422306; E18.413917	2017
Slovenia			
20	Volčji Potok	N46.191178; E14.612783	2017

Table 2: List of the sentinel gardens (botanical gardens and arboretums) surveyed between 2013 and 2018 in seven countries. Highlighted rows indicate locations where OLB has not yet been found.

Oak (<i>Quercus</i>) species	Native range	Country														
		Croatia		Hungary										Italy	Romania	Serbia
		Lisičine	Zagreb	Alcsútdoboz	Budapest	Erdőtelek	Gödöllő	Kecskemét	Püspökladány	Szarvas	Tiszaigar	Tiszakürt	Vácrátót	Padua	Macea	Belgrade
Section <i>Quercus</i>																
<i>Q. alba</i> L. 1753*	e North America	-	-	-	-	3	-	-	-	3	2	-	3	-	-	-
<i>Q. aliena</i> Blume 1850	c China, Korea, Japan	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
<i>Q. bicolor</i> Wild 1801*	ne USA, S Canada	-	-	-	-	-	-	-	-	2	-	1	2	+	-	-
<i>Q. dentata</i> Thunb. 1784	Japan, Korea, China, Spain, Portugal, the	0	-	-	-	-	-	3	-	-	-	-	2	-	-	-
<i>Q. faaginea</i> Lam. 1783	Baleares, Algeria, Morocco	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
<i>Q. frainetto</i> Ten. 1813	s Italy, The Balkans, s of the Black Sea	1	1	-	2	-	-	3	-	-	-	3	2	-	-	2
<i>Q. gambelii</i> Nutt. 1848	sw USA, n Mexico	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
<i>Q. garryana</i> Dougl. ex Hook. 1839	w USA (Pacific coast)	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-
<i>Q. hartwissiana</i> Steven 1857	s and e Bulgaria, Asia Minor, Caucasus	-	-	-	-	-	-	-	-	-	3	-	0	-	-	-
<i>Q. iberica</i> Steven ex Bieb. 1808	Transcaucasus, Balkans, nw Turkey, Crimea, n Iran	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
<i>Q. imeretina</i> Steven ex	w Caucasus	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-

Oak (<i>Quercus</i>) species	Native range	Country														
		Croatia			Hungary							Italy	Romania	Serbia		
		Lisičine	Zagreb	Alcsútdoboz	Budapest	Erdőtelek	Gödöllő	Kecskemét	Püspökladány	Szarvas	Tiszaigar	Tiszakürt	Vácrátót	Padua	Macea	Belgrade
<u>Woronov 1936</u>																
<i>Q. lobata</i> Née 1801	California	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-
<i>Q. lyrata</i> Walt. 1788	se USA, from New Jersey to Texas	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
<i>Q. macranthera</i> Fisch. & C.A.Mey ex Hohen 1838	Caucasus, n Iran, s of Caspian Sea, Armenia	-	-	-	-	3	3	-	3	3	-	1	-	+	-	
<i>Q. macrocarpa</i> Michx. 1801*	e North America	-	-	3	-	3	-	3	3	-	2	3	3	-	+	3
<i>Q. mannifera</i> Lindl. 1840	from e Turkey to n Iran	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-
<i>Q. mongolica</i> Fisch. ex Ledeb. 1850	China, Japan, Korea, Mongolia, e Russia, Sachaline Islands	-	-	-	-	-	-	-	-	3	-	3	-	-	-	-
<i>Q. muehlenbergii</i> Engelm. 1887*	e and c USA, Canada, ne Mexico	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-
<i>Q. pedunculiflora</i> K.Koch 1849	Asia Minor, Caucasus, Balkans	-	-	2	-	-	-	-	-	3	-	-	-	-	-	-
<i>Q. petraea</i> (Matt.) Liebl. 1784	Europe, w Asia,	1	1	2	-	3	2	-	-	-	-	3	3	-	+	-
<i>Q. polymorpha</i> Schltdl. & Cham. 1830	Atlantic slope of Mexico, Guatemala,	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-

Oak (<i>Quercus</i>) species	Native range	Country														
		Croatia			Hungary									Italy	Romania	Serbia
		Lisičine	Zagreb	Alcsútdoboz	Budapest	Erdőtelek	Gödöllő	Kecskemét	Püspökladány	Szarvas	Tiszaigar	Tiszakürt	Vácrátót	Padua	Macea	Belgrade
	sw Texas															
<i>Q. pontica</i> K.Koch 1849	Caucasus, Armenia, around Black Sea, n Turkey	-	-	-	3	-	-	2	-	3	-	3	2	-	-	-
<i>Q. prinoides</i> Willd. 1801*	e USA	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
<i>Q. pubescens</i> Willd. 1805	s Europe, w Asia, Caucasus Atlantic Coast	-	-	-	0	-	-	-	-	-	3	-	-	-	-	-
<i>Q. pyrenaica</i> Willd. 1805	(France, Spain, Portugal, Morocco)	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Q. robur</i> L. 1753	Europe, sw Asia, n Africa	3	3	3	-	3	3	3	3	3	3	3	3	3	+	3
<i>Q. serrata</i> Murray 1784	China, Taiwan, Japan, Korea	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-
<i>Q. stellata</i> Wangenh. 1787 *	c and se USA	-	-	-	-	-	-	-	-	-	2	-	0	-	-	-
<i>Q. virgiliana</i> Ten. 1835	s Europe, e Corsica, Italy, to the Black Sea	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Section <i>Cerris</i>																
<i>Q. acutissima</i> Carruth. 1861	Japan, n China, Korea, Himalaya,	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-

Oak (<i>Quercus</i>) species	Native range	Country														
		Croatia		Hungary										Italy	Romania	Serbia
		Lisičine	Zagreb	Alcsútdoboz	Budapest	Erdőtelek	Gödöllő	Kecskemét	Püspökladány	Szarvas	Tiszaigar	Tiszakürt	Vácrátót	Padua	Macea	Belgrade
<i>Q. cerris</i> L. 1753	Cambodia, Vietnam, Thailand s and se Europe, Asia Minor Syria,	-	1	3	3	3	2	2	3	3	3	3	3	-	+	-
<i>Q. libani</i> <u>G.Olivier 1801</u>	Lebanon, Asia Minor sw Italy,	-	-	-	-	-	-	3	3	-	-	3	1	-	-	-
<i>Q. trojana</i> <u>Webb 1839</u>	Balkans, Asia Minor	-	-	-	-	-	-	-	3	-	-	-	-	-	-	3
<i>Q. variabilis</i> <u>Blume 1851</u>	Japan, China, Korea, Taiwan, Tibet	0	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Section <i>Lobatae</i>																
<i>Q. buckleyi</i> Nixon & Dorr 1985	Texas, Oklahoma	-	-	-	-	-	-	-	-	-	0	-	0	-	-	-
<i>Q. coccinea</i> Münchh. 1770	e USA	-	-	0	-	0	0	-	-	0	-	0	0	-	-	-
<i>Q. ilicifolia</i> Wangenh. 1787	e USA	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-
<i>Q. imbricaria</i> Michx. 1801	se and c USA	-	-	-	-	0	0	-	-	-	0	0	0	-	-	-
<i>Q. laurifolia</i> Michx. 1801	se Virginia to s Florida and Texas	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-
<i>Q. laurina</i> Humb. & Bonpl. 1809	Mexico, Guatemala	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-

Oak (<i>Quercus</i>) species	Native range	Country														
		Croatia			Hungary								Italy		Romania	Serbia
		Lisičine	Zagreb	Alcsútdoboz	Budapest	Erdőtelek	Gödöllő	Kecskemét	Püspökladány	Szarvas	Tiszaigar	Tiszakürt	Vácrátót	Padua	Macea	Belgrade
<i>Q. palustris</i> Münchh. 1770	ne USA	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0
<i>Q. phellos</i> L. 1753	se USA	0	0	-	-	-	-	-	-	-	-	0	-	-	-	-
<i>Q. rubra</i> L. 1753	se Canada, e USA	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-
<i>Q. shumardii</i> Buckley 1860	s Ontario; e and c USA	-	-	-	-	-	-	-	-	-	-	0	-	-	-	-
<i>Q. velutina</i> Lam. 1785	e USA	-	-	-	-	-	-	-	-	-	0	0	-	-	-	-
<i>Ilex</i> group																
<i>Q. coccifera</i> L. 1753	Mediterranean region	0	-	-	0	-	-	-	-	-	-	-	-	-	-	0
<i>Q. ilex</i> L. 1753	s Europe	-	-	-	0	-	-	-	-	0	-	-	-	0	-	-
<i>Q. phillyreoides</i> A.Gray 1859	s Japan; c China; Korea	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-

Table 3: OLB oak hosts recorded in 15 sentinel gardens (arboretums and botanical gardens) in five countries. Oak names and native ranges come from <http://oaks.of.the.world.free.fr>. The oaks recorded as host in a native range are marked with “*”. The globally new host records are underlined. “+” means a recorded host, but no information on the infestation level. The Romanian data are based on Don *et al.* (2016).

e = eastern, ne = north-eastern, c = central, n = northern, s = southern, se = south-eastern,

sw = south-western

Oak species	Country									
	Bosnia and Herzegovina	Bulgaria	Croatia	Hungary	Italy	Romania	Russia	Serbia	Slovenia	Turkey
<i>Quercus castaneifolia</i> C.A.Meyer 1831	-	-	-	-	-	-	3*	-	-	-
<i>Quercus cerris</i> L. 1753	-	3	2	3	2	3	3*	3	-	-
<i>Quercus frainetto</i> Ten. 1813	-	3	-	-	2	2	-	-	-	-
<i>Quercus hartwissiana</i> Steven 1857	-	3	-	-	-	-	3*	-	-	-
<i>Quercus infectoria</i> G.Olivier 1801	-	-	-	-	-	-	-	-	-	3
<i>Quercus macranthera</i> Fisch. & C.A.Mey. ex Hohen 1838	-	-	-	-	-	-	-	-	-	3
<i>Quercus pedunculiflora</i> K.Koch 1849	-	3	-	-	-	2	-	-	-	-
<i>Quercus petraea</i> (Matt.) Liebl. 1784	3	3	-	2	2	2	3	3	-	3
<i>Quercus polycarpa</i> Schur 1851	-	3	-	-	-	-	-	-	-	-
<i>Quercus pubescens</i> Willd. 1805	-	3	1	1	2	-	3*	-	-	3
<i>Quercus robur</i> L. 1753	3	3	3	3	3	3	3*	3	2	3

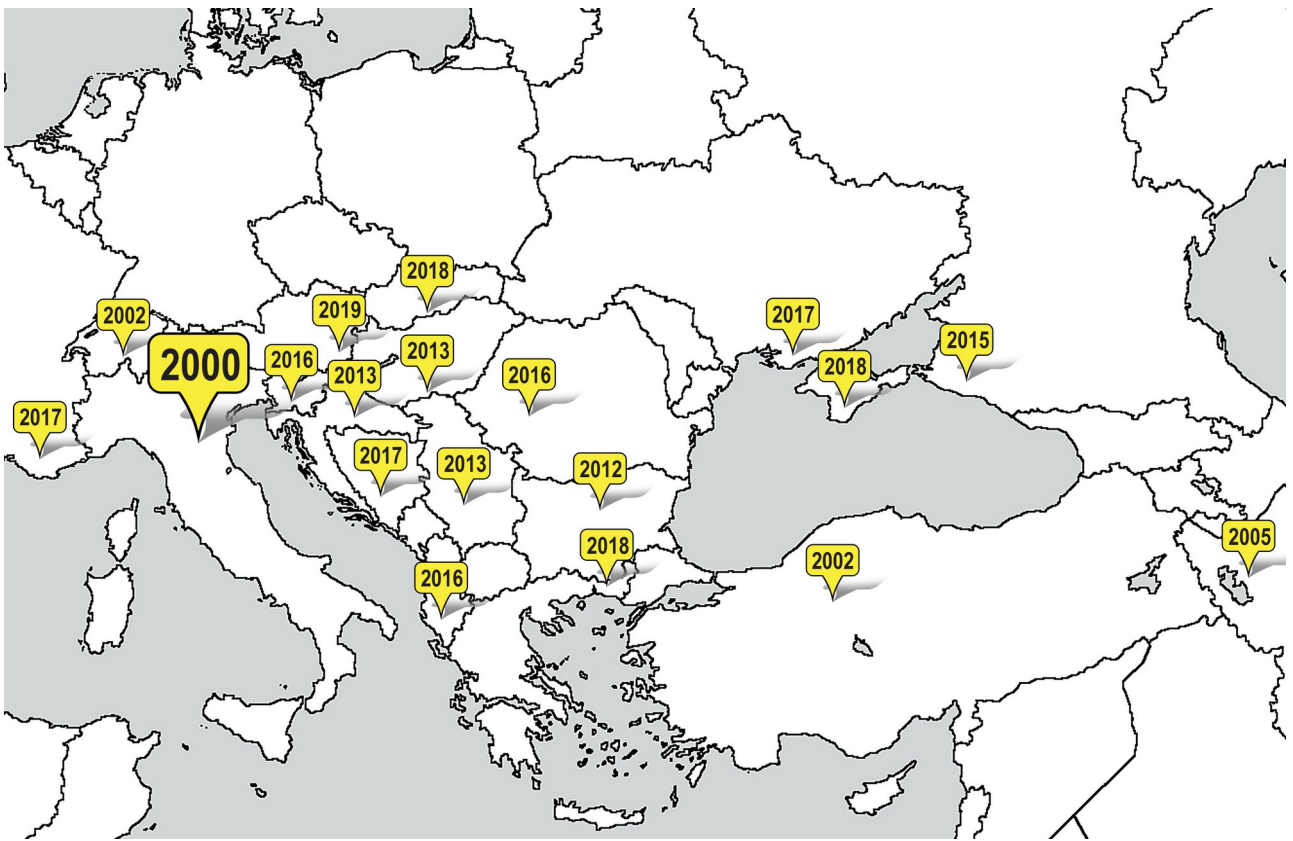
Table 4: Oak host records in forest stands in ten countries (data collected by the authors)

*Data from Neimorovets *et al.* (2017)

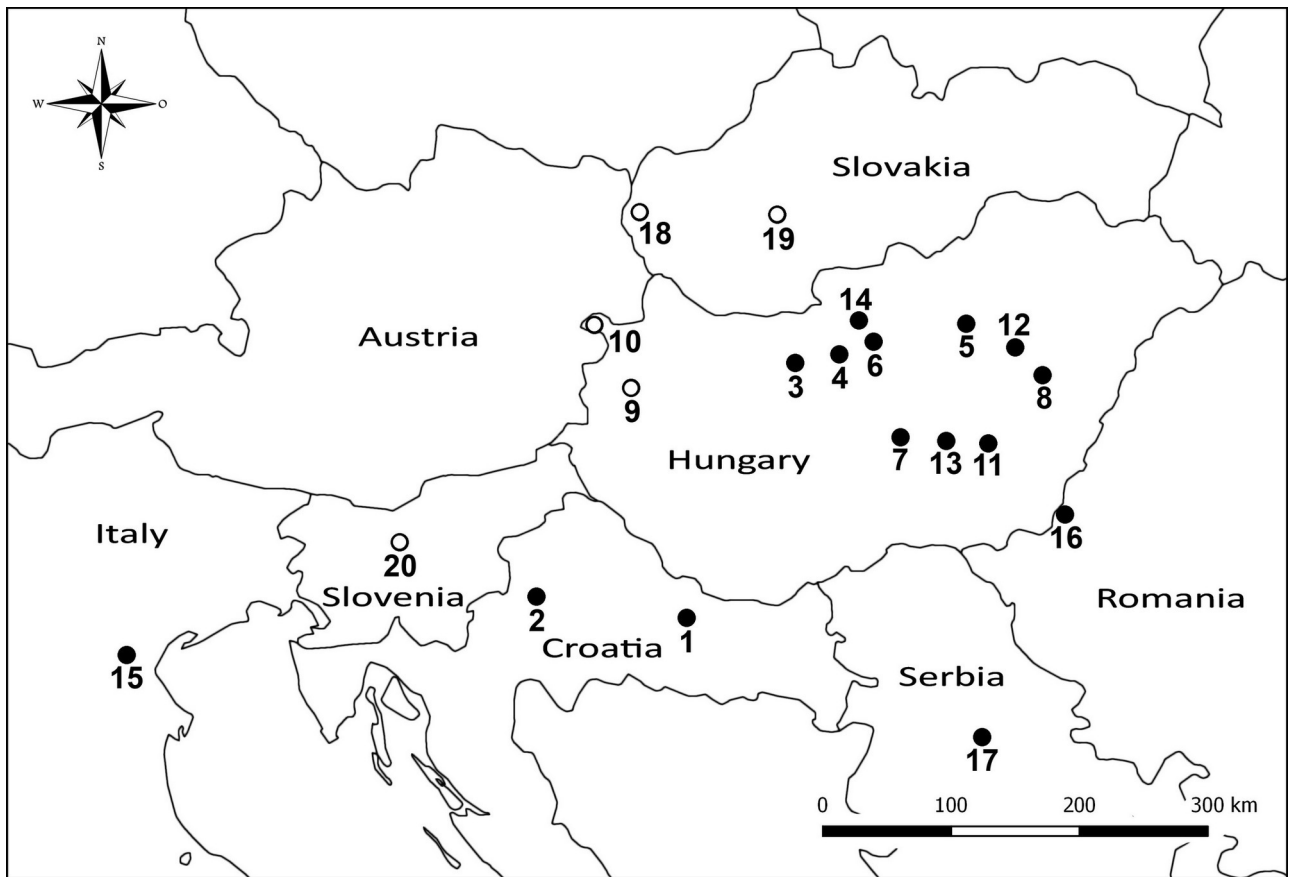
Species	Country							
	Bulgaria	Croatia	Hungary	Italy	Romania	Russia	Serbia	Turkey
Sapindaceae								
<i>Acer campestre</i> L. 1753	-	1	1	-	-	-	-	-
<i>Koelreuteria paniculata</i> Laxm. 1772	-	-	1	-	-	-	-	-
Cannabaceae								
<i>Celtis occidentalis</i> L. 1753	-	-	-	-	-	-	2	-
Fagaceae								
<i>Castanea sativa</i> Mill. 1768	2	-	-	-	-	-	-	-
<i>Fagus sylvatica</i> L. 1753	-	1	1	-	-	-	-	-
Betulaceae								
<i>Carpinus betulus</i> L. 1753	-	1	1	-	-	-	-	-
<i>Corylus avellana</i> L. 1753	-	1	2	3	-	-	2	-
<i>Corylus colurna</i> L. 1753	-	1	2	-	-	-	-	-
Cornaceae								
<i>Cornus sanguinea</i> L. 1753	-	1	-	-	-	-	-	-
Rosaceae								
<i>Chaenomeles japonica</i> (Thunb). Lindl. Ex Spach 1834	-	-	-	-	-	-	2	-
<i>Crataegus coccinea</i> L. 1753	-	-	-	2	-	-	-	-
<i>Crataegus monogyna</i> Jacq. 1775	-	-	-	-	-	-	2	-
<i>Crataegus</i> spp.	-	-	-	-	-	-	-	-
<i>Kerria japonica</i> (L.) DC. 1818	-	-	1	-	-	-	-	-
<i>Prunus lusitanica</i> L. 1753	-	-	-	1	-	-	-	-

Species	Country							
	Bulgaria	Croatia	Hungary	Italy	Romania	Russia	Serbia	Turkey
<u><i>Prunus serotina</i> Ehrh. 1784</u>	-	1	3	-	-	-	-	-
<u><i>Prunus serrulata</i> Lindl. 1830</u>	-	-	2	-	-	-	2	-
<u><i>Prunus spinosa</i> L. 1753</u>	-	-	2	-	-	-	-	-
<u><i>Prunus subhirtella</i> Miq. 1865</u>	-	-	-	1	-	-	-	-
<i>Pyrus communis</i> L. 1753	-	1	-	-	-	-	2	-
<i>Rosa canina</i> L. 1753	1	-	1	-	-	-	-	-
<i>Rosa</i> spp.	1	-	1	-	-	-	-	1
<i>Rubus caesius</i> L. 1753	1	2	3	-	-	-	3	-
<i>Rubus</i> spp.	1	-	-	-	-	-	-	-
<u><i>Sorbus aria</i> (L.) Crantz 1763</u>	-	-	1	-	-	-	-	-
<u><i>Sorbus scandica</i> Fr. 1817</u>	-	-	-	-	-	-	3	-
<u><i>Sorbus torminalis</i> (L.) Crantz 1763</u>	-	1	-	-	-	-	-	-
Ulmaceae								
<u><i>Ulmus glabra</i> Huds. 1762</u>	-	-	2	-	-	-	-	-
<u><i>Ulmus minor</i> Mill. 1768</u>	-	2	2	-	-	-	-	-
<i>Ulmus</i> spp.	-	-	-	-	1	3	-	-
Malvaceae								
<u><i>Tilia cordata</i> Mill. 1768</u>	-	-	2	-	-	-	-	-
<u><i>Tilia platyphyllos</i> Scop. 1771</u>	-	-	3	-	-	-	1	-
<i>Tilia</i> spp.	-	-	-	-	1	-	-	-

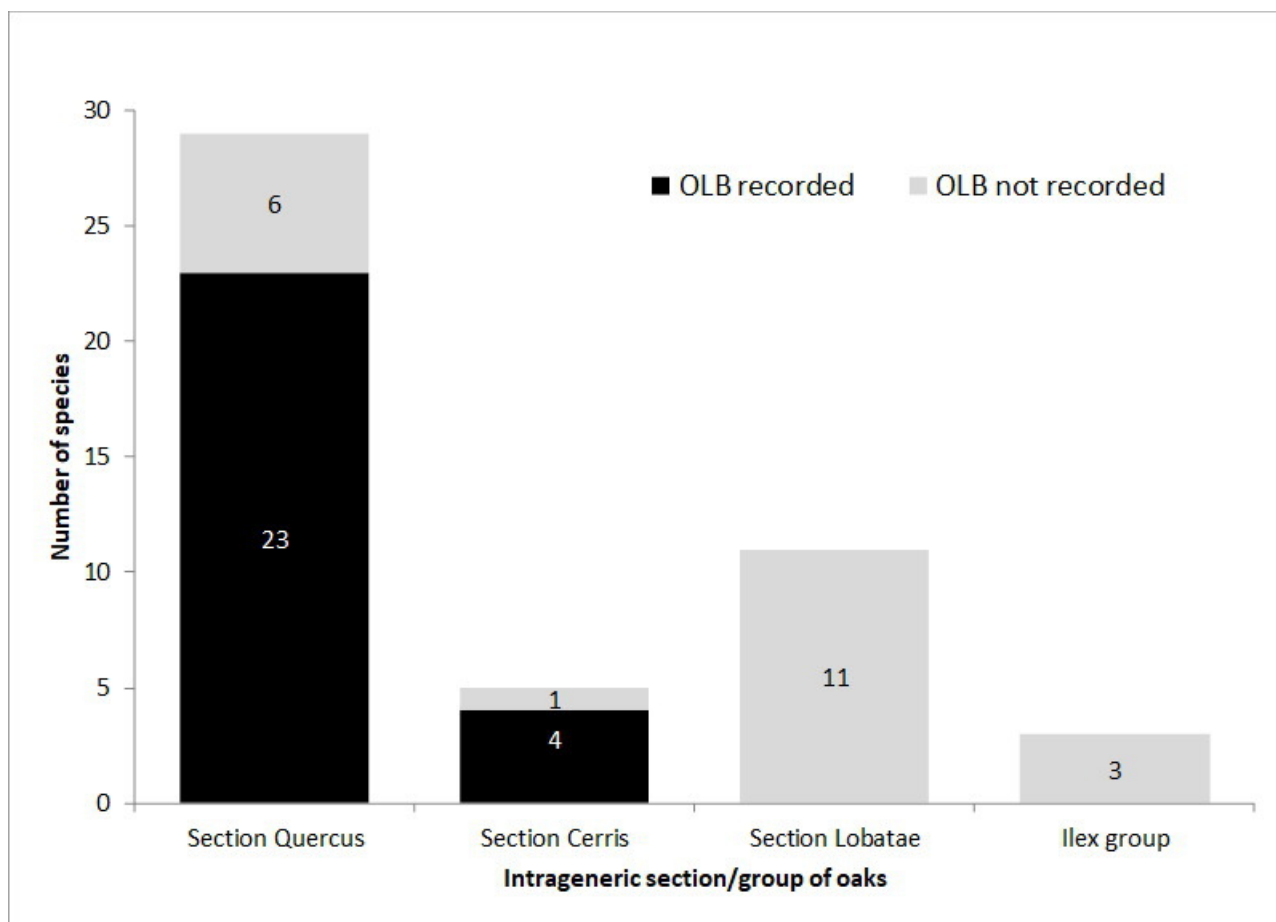
Table 5: Non-oak woody hosts recorded in eight countries with different levels (1–3) of infestation (data collected by the authors). New host records are underlined.



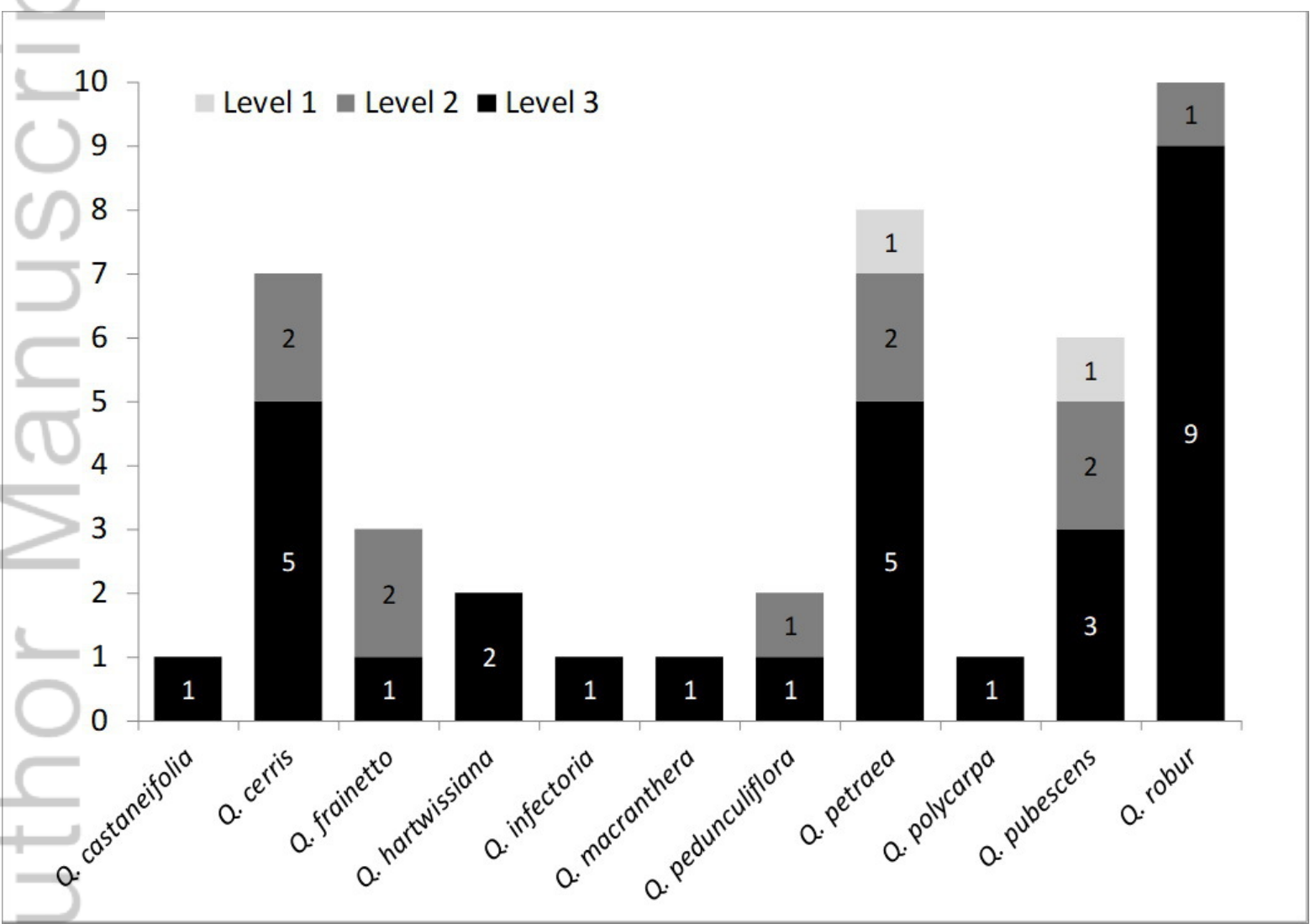
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AFE_12362_Fig 2.jpg



AFE_12362_Fig 3.jpg



AFE_12362_Fig 4.jpg