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Infestation intensity by the invasive oak lace bug, *Corythucha arcuata* (Say) in mixed and pure oak stands

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Abstract

There has been accumulating evidence for effects of tree species composition on herbivory with many examples of lower damage by specialist feeders in tree species rich forests. In a joint study in five Central and Southeastern European countries, we studied the effect of tree species richness on infestation intensity of the oak lace bug, *Corythucha arcuata* (Say) (Heteroptera, Tingidae), an invasive pest on oak trees that has spread rapidly across the Balkan Peninsula and Central Europe. Intensity of infestation by *C. arcuata* on oaks was assessed on three or four study plots with high (pure stands) and three or four plots with low percentage of oak (mixed stands) in each country. Ordinal regression analysis showed that intensity of infestation of trees by *C. arcuata* differed between countries; no significant effect of stand type (mixed or pure) on infestation levels was detected. When analysing the percentage of trees in the highest infestation class, stand type had a significant effect with more intensive infestation in pure stands. We conclude that mixed stands will not prevent severe infestation but may help mitigating the impact of established *C. arcuata* populations.

KEYWORDS

associational resistance, *Corythucha arcuata*, diversity, host tree concentration, invasive forest pest

1 | INTRODUCTION

Alien invasive forest insects negatively affect forest ecosystems worldwide, having ecological as well as socio-economic impact (Brockerhoff & Liebhold, 2017). Classical biological control is one approach to compensate for the often observed insufficient natural control in the invaded range (Kenis et al., 2017). In addition, tree species composition may also help mitigating the impact of the invasive pest. There is evidence that damage by specialized herbivores is lower in mixed stands than in pure stands (recent meta-analysis by Jactel et al., 2021). More evidence is needed for such effects on invasive pests. In this study, we used the oak lace bug, *Corythucha* *arcuata* (Say, 1832) (Heteroptera, Tingidae), a tingid bug native to North America, as an example. About 10 years after the first record in Europe and Asia Minor in 2000 in Italy (Bernardinelli & Zandigiacomo, 2000) and 2002 in Turkey (Mutun, 2003), it began its rapid spread in the Black Sea region, as well as across the Balkan Peninsula to Central Europe, reaching Austria and the Czech Republic in 2019 (summarized in Csóka et al., 2020; Paulin et al., 2020) and South-West Germany in 2021 (Wonsack & Thomas, 2021). In 2019, the total area infested by *C. arcuata* in Croatia, Hungary, Serbia, Romania and European Russia was estimated to be 1.75 million ha (Paulin et al., 2020). Severe infestation of oaks causes discoloration and drying of leaves, a symptom that can be easily observed and that is also commonly recognized by the public (Bălăcenoiu, Japelj, et al., 2021). The damage has remained at high level in the infested areas in consecutive years since the introduction; therefore, negative long-term effects on oak health can be expected. A remote sensing study showed that the NDVI of infested oak forests decreased in the first 2–3 years after first damage by *C. arcuata* and remained at reduced level in the following years, indicating continuously high damage (Kern et al., 2021). Sucking of nymphs and adults damages the leaf tissue and leads to reduction of photosynthetic activity by almost 60% (Nikolić et al., 2019). After hibernation, adults move to fresh oak leaves where eggs are deposited after some time of maturation feeding. Two to three generations can develop in a season leading to accumulating damage and visible symptoms to the leaves (Bălăcenoiu, Simon, et al., 2021; Paulin et al., 2020). Because most radial growth of oaks occurs in the first half of the growing season, feeding by *C. arcuata* does not appear to have a dramatic effect on annual wood increment; however, a cumulative effect from repeated damage seems likely (Paulin et al., 2020). This repeated damage over a long period of time can also have additional negative effects on oak health since it acts together with already long-lasting negative impacts of other biotic factors such as defoliators like the gypsy moth, *Lymantria dispar*, oak powdery mildew, *Erysiphe* spp., and climate extremes, including prolonged drought periods and heat waves (Drekić et al., 2020; Pap et al., 2018; Stojanović et al., 2021). A negative impact of extended *C. arcuata* feeding damage on acorn crop is expected, although a study in Croatia could not yet quantify such effects (Franjević et al., 2018; Paulin et al., 2020). Continuous outbreaks of *C. arcuata* will probably have negative effects on other herbivores feeding on oak foliage, particularly species that develop later in the growing season (Paulin et al., 2020).

Unfortunately, no feasible options for control of this invasive pest are currently available in forests and woodlands, and hence, a continual spread of the pest across Europe appears inevitable (Williams et al., 2021). Chemical control achieves significant short-term reduction of the pest but does not prevent re-infestation of treated areas in the same season (Bălăcenoiu, Nețoiu, et al., 2021; Drekić et al., 2021). Therefore, while also considering non-target effects as well as legal restrictions, pesticide treatments are not a sensible option in forest settings. It is crucial to look for alternative measures to reduce the damage. There is a lack of research on the impact of native natural enemies on population dynamics of *C. arcuata*, reports of native fungal pathogens attacking the insect being one exception (Kovač et al., 2020). Also for the closely related *Corythucha ciliata*, an invasive pest on *Platanus* spp., records of natural enemies in Italy exist (Tavella & Arzone, 1987). Published information on the impact on the population over time since establishment is lacking. Nevertheless, exploring options for biological control either by importing natural enemies from the native range (classical biological control) or augmenting native enemies in the invaded range – e.g., entomopathogenic fungi as studied by Kovač et al. (2021) – will be important. In addition, it is of great interest to determine whether site conditions in forest, and in particular the density of host tree species, influence infestation by *C. arcuata* in order to develop silvicultural management approaches.

There has been accumulating evidence that damage by specialized herbivores is lower in mixed stands than in monocultures (Barbosa et al., 2009; Kambach et al., 2016; Letourneau et al., 2011). A recent meta-analysis showed that such a significant effect was consistent across feeding guilds of forest pests (Jactel et al., 2021). There are only a few studies addressing the effect of plant species composition on invasive forest pests. For *C. arcuata*, we are aware of one study from the Ukraine with limited sample size (Meshkova et al., 2020). The findings corroborate previous meta-analyses that already concluded that feeding damage by specialized herbivores is lower in mixed than in pure forest stands (Jactel et al., 2005; Jactel & Brockerhoff, 2007). Explanations for these effects of plant mixture on herbivory are based on the enemies and resource concentration hypotheses (Root, 1973). The enemies hypothesis, i.e. a higher effectiveness of natural enemies in more complex environments (Russel, 1989), is not expected to be relevant in the case of *C. arcuata* since records of natural enemies attacking this species in Europe are sporadic and do not indicate significant impact on the population (Paulin et al., 2020). On the other hand, resource concentration could be important. The probability of finding a host tree can be lower for a specialist herbivore in mixed stands due to lower host abundance and reduced apparency of hosts, both physically and chemically, due to mixed emission of cues from hosts and non-host trees (Jactel et al., 2021). *C. arcuata* must be considered a specialist developing on species of the genus *Quercus* from the sections Quercus and Cerris, while sections Lobatae and Ilex are not suitable (Csóka et al., 2020). Hosts from other genera, such as *Tilia*, *Ulmus*, *Corylus* or several Rosaceae can be infested; but this occurs more as a spillover from nearby oak trees (Csóka et al., 2020).

In the present study, we compared *C. arcuata* infestation levels in pure or oak-dominated forest stands with 75%–100% oak (*Q. robur* and *Q. petraea*) and forest stands where oaks are only intermixed. This was done in five countries in Central and Southeastern Europe along a gradient of the invasion front. Study sites were located in different oak forest types and ranged from 83 to 411 m elevation. Nevertheless, we are aware that the sites do not cover the entire range of *C. arcuata* in Europe. We compared sites in areas where *C. arcuata* has only recently spread and infestation intensity was low (in Austria and Hungary) and sites in areas where *C. arcuata* has been established for more than 5 years and is present in high densities (in Slovenia, Croatia, and Serbia). We hypothesised that infestation levels will be lower in mixed forests than in pure or oak-dominated forests. Moreover, we expected this effect to be more pronounced at an earlier stage of invasion, assuming that the invader will be more successful to establish when hosts are easier to access in pure stands than in mixed stands.

2 | MATERIALS AND METHODS

2.1 | Sampling sites

Sampling sites were established in six to eight forest stands of at least 1 ha in size in each of the participating countries (Austria, Croatia, Hungary, Serbia, and Slovenia). Half of the selected stands per country were either pure oak stands or stands dominated by oak (*Q. robur* or *Q. petraea* covering at least 75% of the stand area; referred to as "pure stands"). The other half of the stands were mixed forests with oak (*Q. robur* or *Q. petraea* covering less than 60% of the stand area; referred to as "mixed stands"). The percentage of oak in the forest was assessed in the field by visual estimate. All sites were mature forests with mean DBH of analysed oak trees on the site ranging from 30 to 56 cm in Austria, 25 to 73 cm in Croatia, 15 to 63 cm in Hungary, 52 to 72 cm in Serbia, and 46 to 72 cm in Slovenia. Typically, one site with high and one site with low oak percentage were located in close vicinity and had comparable site characteristics (Figure 1 and Table S1). Study sites in Austria and Slovenia were located in the area of oak hornbeam forests in the colline zone without direct influence by rivers. The Hungarian study sites were in the area of colline oak-hornbeam-Scots pine forests with only small watercourses. On the other hand, sites in Croatia and Serbia were riparian forests. The former were located in mixed deciduous forests in the colline zone, characterized by nutrient-rich soil and poorly drained soil types, influenced by the Drava and Danube Rivers. Study sites in Serbia were located within the main complexes of pedunculate oak forests along the Danube and Sava Rivers (see Table S1 for characteristics of sites). The sites in Austria and Hungary were at an earlier stage of invasion by *C. arcuata* based on previous records and had lower infestation levels by *C. arcuata* compared to sites in Croatia, Serbia, and Slovenia.

2.2 | Sampled trees

Per sampling site, 15 mature oak trees (either *Q. robur* or *Q. petraea*) were randomly chosen for assessment of *C. arcuata* infestation. Trees were evenly distributed across the sampling site; no trees located directly on the forest edge were included. Tree species, diameter, and social class after Kraft (following Eichhorn et al., 2020) of each inspected oak were recorded.

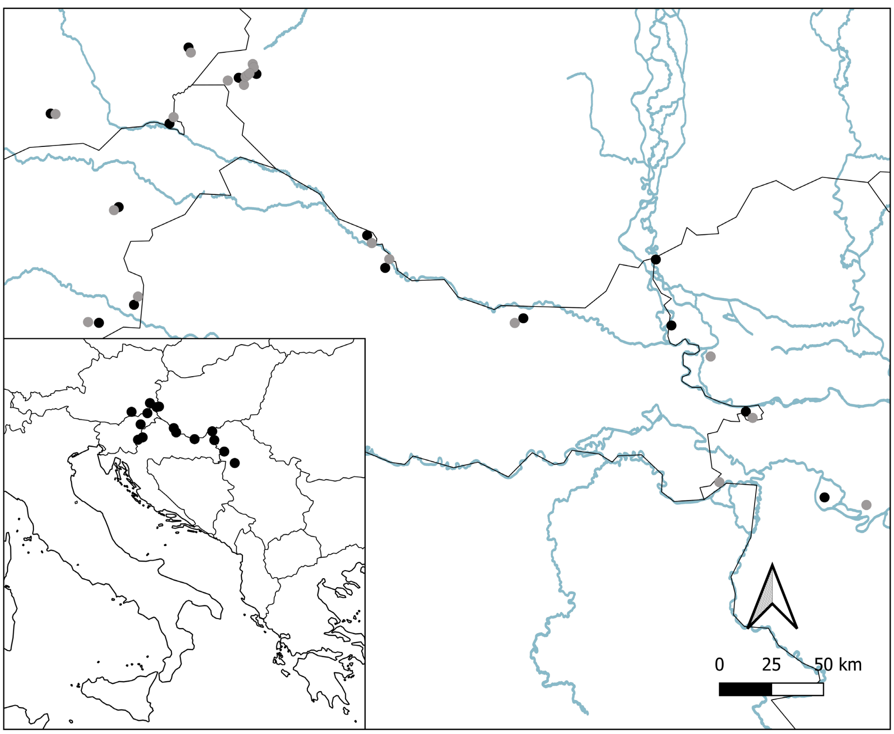

FIGURE 1 Sampling sites used in this study. Pure oak stands (oak ≥75%) are shown in black, mixed oak stands (oak ≤60%) are shown in grey. The small insert gives an overview (symbols do not differentiate between the stand types). Black lines indicate borders of countries and coastlines, blue lines indicate rivers. The map has been prepared using EuroGeographics for the administrative boundaries (https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units/countries#countries20; accessed 18.7.2023) and European Union's Copernicus Land Monitoring Service information (https://doi.org/10.2909/393359a7-7ebd-4a52-80ac-1a18d5f3db9c; accessed 27.10.2023). [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Assessment of *C. arcuata* infestation

Corythucha arcuata infestation per tree was assessed following a simple semi-quantitative method following Csóka et al. (2020) that was also feasible in closed stands. Presence/absence of symptoms therefore concerned the part of the crown visible from the ground. Each tree was inspected for signs and symptoms of *C. arcuata* (discoloration, faeces, groups of eggs and nymphs) from the ground using binoculars. In cases of doubt, a telescopic pole saw was used to cut twig samples for confirmation. Four classes of infestation (based on Csóka et al., 2020) were recorded: (0) no symptoms; (1) symptoms and different developmental stages of *C. arcuata* are sporadic, restricted to single leaves or smaller groups of leaves and can only be found with targeted intensive search; (2) symptoms and different developmental stages of *C. arcuata* are found along whole branches and can easily be spotted on the tree, parts of the crown are without symptoms; (3) symptoms and different developmental stages of *C. arcuata* cover the whole tree, the whole visible crown is affected. All sites were assessed between August 15 and September 15, 2021; at this time, feeding damage by *C. arcuata* has been accumulating since spring and is readily visible.

2.4 | Data analysis

The data followed an ordinal distribution and therefore we used an ordinal regression to model infestation intensity by *C. arcuata* (i.e. the dependent variable). The independent variables were the stand type ("mixed" or "pure") and the country. Stand location was used as a random factor to account for potential spatial autocorrelation. Variables were checked for multicollinearity. First, a full model including all variables was made, followed by a model selection process based on the Akaike Information criterion (AIC). Models which were less than 4 AIC units from the best model were averaged and the full averaged model was taken. The ordinal regression was done with the "clmm" function in the "ordinal" package (Christensen, 2015) using the statistical program R (R Core Team, 2023). Visualization was done with the package ggplot2 (Wickham, 2016). The model averaging was done with the package "MuMIn" (Barton, 2022).

For the influence of the variables on the percentage of trees in infestation class 3 (highest infestation class), we used a general linear model with binomial error structure, including the proportion of class 3. Total number of trees per plot was included as weight.

3 | RESULTS

Corythucha arcuata occurred on all study sites and infested most of the studied oak trees. Overall, only 5% of assessed trees were without signs of infestation. Intensity of infestation varied between the countries (Figure 2). In Austria and Hungary, 35.6% and 41.7% of oaks, respectively, were in the higher infestation classes 2 and 3.

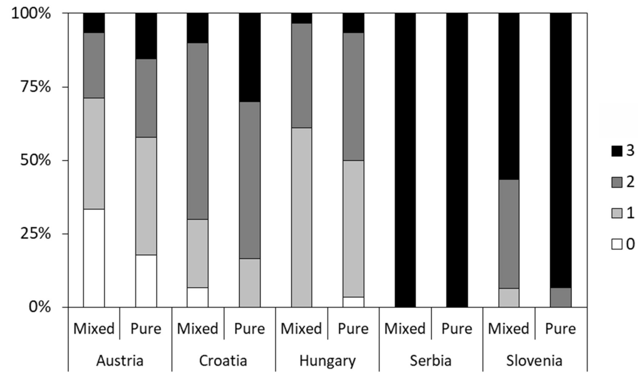

FIGURE 2 Frequency of *Corythucha arcuata* infestation classes on mixed (oak ≤60%) and pure (oak ≥75%) plots in Austria and Hungary (areas with early stage of invasion) and in Croatia, Serbia and Slovenia (areas with established populations).

This percentage was 76.7% in Croatia, 96.7% in Slovenia and 100% in Serbia.

Two models within 4 AIC units were shown to include country, followed by stand type (Table 1). For the impact on different countries, it was shown that Slovenia and Croatia had a higher impact than Austria. The stand type did not show a significant association (Table 2, Figure 3). The model analysing the percentage of trees in class 3 (the highest infestation class) showed a significant effect of stand type, meaning that pure oak stands tended to have a higher percentage of highly infested trees (Table 3).

4 | DISCUSSION

Impact by *C. arcuata* on oak foliage differed greatly between the regions covered by our study. Since study plots were on one hand located at the edge of the invasive range of *C. arcuata* in Austria and Western Hungary and on the other in areas where the species has been firmly established, i.e. in Slovenia, Croatia and Serbia, this was not unexpected. Both personal observation of the authors as well as remote sensing data (Kern et al., 2021) indicate that no reduction of leaf damage has occurred since invasion in the area of our study. Consequently, country significantly affected intensity of infestation in our model analysis. We did not find a significant effect of stand type (mixed or pure oak forest) on the level of infestation. However, the proportion of trees in the highest infestation class (class 3) on the study plots was higher in pure stands. It remains open to which extent these findings conform to frequently reported examples of associational resistance in forests against herbivores, as recently reviewed in Jactel et al. (2021). As outlined in the introduction, *C. arcuata* is a specialist herbivore for which such effects should be more important than for a polyphagous species.

Admixture of non-host trees can lead to reduced damage by invasive herbivorous insects, as it has been shown for the gall wasp *Dryocosmus kuriphilus* in Italy (Guyot et al., 2015) or the bark scale *Matsucoccus feytaudi* in Corsica (Rigot et al., 2014). The gall wasp may

No.	(Int)	Country	Stand type	df	logLik	AICc	Delta	Weight
4	+	+	+	9	−359.463	737.3	0.00	0.766
2	+	+		8	−361.681	739.6	2.37	0.234
3	+		+	5	−388.792	787.7	50.44	0.000
1	+			4	−389.993	788.1	50.80	0.000

TABLE 1 Model selection showing the ranks of the models from the lowest to the highest AICc, the delta from the lowest AICc and the weight of the model. Models which were less than 4 AIC units from the best model were used (model number in bold).

<table>
<tr><th>Variable</th><th>Estimate</th><th>Std. error</th><th>z Value</th><th>p (>|z|)</th></tr>
<tr><td>0|1</td><td>−2.1509</td><td>0.6043</td><td>3.559</td><td>0.000372</td></tr>
<tr><td>1|2</td><td>1.8939</td><td>0.5890</td><td>3.215</td><td>0.001304</td></tr>
<tr><td>2|3</td><td>5.2460</td><td>0.6507</td><td>8.062</td><td><2e-16</td></tr>
<tr><td>CountryCroatia</td><td>2.7079</td><td>0.6875</td><td>3.938</td><td>8.2e-05</td></tr>
<tr><td>CountryHungary</td><td>1.2520</td><td>0.7174</td><td>1.745</td><td>0.080943</td></tr>
<tr><td>CountrySerbia</td><td>27.3873</td><td>54.1484</td><td>0.506</td><td>0.613009</td></tr>
<tr><td>CountrySlovenia</td><td>6.3296</td><td>0.8663</td><td>7.307</td><td><2e-16</td></tr>
<tr><td>Factor(stand.type)Pure</td><td>1.1750</td><td>1.1750</td><td>1.000</td><td>0.317310</td></tr>
</table>

TABLE 2 Full average model after model selection of intensity of *Corythucha arcuata* infestation and independent variables country and stand type ("mixed" or "pure").

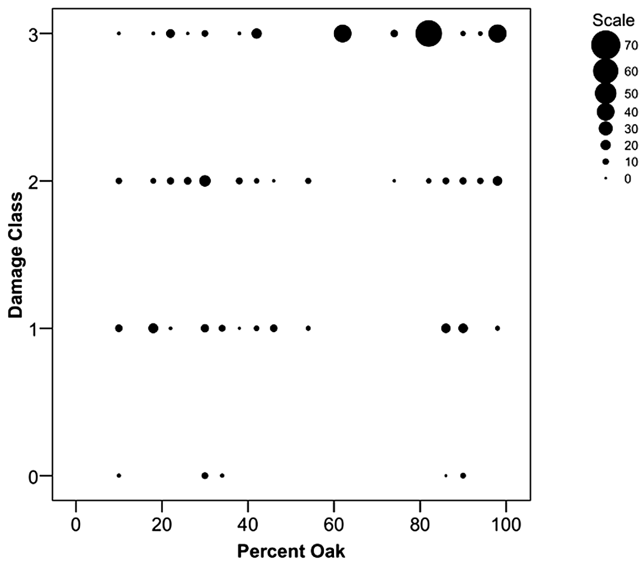

FIGURE 3 Oak trees per infestation class on plots with different percentage of oak trees. Dot size represents number of trees. Plots with oak ≤60% were considered mixed and plots with oak ≥75% were considered pure stands.

use both olfactory and visual cues for locating host trees. Therefore, effects of tree apparency on individual level and of tree species diversity on stand level could be explained (Guyot et al., 2015). In the case of the bark scale, dispersal takes place through passive wind transportation of larvae. Apparency of a host tree is therefore crucial for infestation. *C. arcuata* is believed to disperse locally through a combination of active flight and wind-aided dispersal of adults (Mutun et al., 2009; Zubrik et al., 2019). Therefore, both individual tree apparence and tree diversity at stand level could have an effect. A survey at the leading edge of the invasion front in Austria showed rapid spread from urban oak trees into a mixed riparian forest within 2 years (Hoch, Sallmannshofer, et al., 2023); *C. arcuata* seems to be able to find and establish on new host trees very well. Interestingly, Guyot et al. (2015) refer to the "striking" capability of *D. kuriphilus* to find isolated patches of host trees. Hence, the observed associational resistance found for this species does not prevent infestation of new areas. The fact that percentage of trees in the highest infestation class was lower in plots with lower percentage on oak may indicate that associational resistance could affect *C. arcuata* as well. The mixed stands in our study had three to four tree species admixed to one or two oak species; only four of the sites had only two admixed species. Half of the sites had conifers in the stand (Table S1). Since *C. arcuata* can spill over from oaks to several other broadleaved tree or shrub species (Csóka et al., 2020), the exact species admixed in the oak forests can play a role. Unfortunately, the design of our study does not allow analysis of the effect of tree apparency or tree species diversity and relatedness to the host tree species.

Although the effect of mixed forests on *C. arcuata* infestation intensity was not significant in our study, the presence of oak trees in the landscape acting as stepping stones could influence the expansion of the invaded area. There is wide agreement on the importance of human mediated passive transportation of *C. arcuata* hitchhiking on vehicles or trains (Bernardinelli, 2006; Jurc & Jurc, 2017; Mutun et al., 2009; Sallmannshofer et al., 2021). A recent study showed that on a landscape scale, the oak lace bug was detected in lower altitudes, where more oak trees were present, nearby highways and railways (de Groot et al., 2022). The latter might suggest the importance of these pathways for accidental introduction. The availability of host trees will be crucial for the likelihood of establishment of new satellite populations outside the previous range and consequent spread from these focal areas. However, testing this effect was not the scope of the present study.

The results of our analysis with no significant effect of mixed or pure stand type but with significantly higher proportion of trees in highest

TABLE 3 General linear model with binomial error structure including the proportion of trees in the highest infestation class (class 3).

Variable	Estimate	Std. error	z Value	p (>|z|)
(Intercept)	−3.1176	0.4310	−7.234	4.68e-13
CountryCroatia	0.7408	0.4186	1.770	0.0767
CountryHungary	−0.7427	0.5811	−1.278	0.2012
CountrySerbia	23.1383	1589.574	0.015	0.9884
CountrySlovenia	3.6358	0.4602	7.901	2.77e-15
Factor(stand.type)Pure	1.60020	0.3315	4.827	1.38e-06

infestation class in pure stands do not allow definitive conclusions. A more detailed study including a finer measurement of *C. arcuata* density on the trees than our four-category assessment might detect more subtle differences. However, even if such difference occurred, it would be without major practical impact for preventing establishment of invasive *C. arcuata* populations but might help mitigating the effect of feeding on the oaks. The mechanisms of associational resistance of stands with higher tree diversity are based on resource concentration hypothesis and enemies hypothesis (Root, 1973). In the case of the invasive *C. arcuata*, only mechanisms connected with resource availability, possibly also mediated through host volatiles, should be important since there seem to be no indications currently for significant regulation of *C. arcuata* populations by native natural enemies (Paulin et al., 2020). The support of natural enemies by higher plant diversity (see e.g., Stemmelen et al., 2022) may become relevant when programs to augment parasitoids or pathogens are attempted, such as the inoculative release of native entomopathogenic fungi (Kovač et al., 2021) or releasing imported natural enemies in classical biological programs.

A recent review concluded that there are currently no feasible options to stop or slow the spread of *C. arcuata* or to successfully suppress the populations in forest settings (Williams et al., 2021). The results of our study show that forest tree composition will not prevent severe infestation but may help mitigating the impact of established *C. arcuata* populations. Tree species mix might become important in the case of continuing additive effects of severe damage of oaks by *C. arcuata* in combination with other pests and pathogens, as it will prevent complete deforestation of wide areas should high mortality of oaks occur in the future.

AUTHOR CONTRIBUTIONS

Gernot Hoch: Conceptualization; methodology; investigation; visualization; writing – original draft; writing – review and editing. **Alex Stemmelen:** Conceptualization; methodology; writing – review and editing. **Csaba Béla Eötvös:** Investigation; writing – review and editing. **Werner Hinterstoisser:** Investigation; visualization; writing – review and editing. **Miran Lanšćak:** Investigation; writing – review and editing. **Srđan Stojnić:** Investigation; writing – review and editing. **Máté Tóth:** Investigation; writing – review and editing. **Marjana Westergren:** Writing – review and editing; funding acquisition; project administration. **Simon Zidar:** Investigation; writing – review and editing. **Milica Zlatković:** Investigation; writing – review and editing. **Nikola Zoric:** Investigation; writing – review and editing. **Maarten de Groot:** Conceptualization; methodology; formal analysis; investigation; writing – original draft; writing – review and editing; visualization.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from Zenodo: Hoch, Stemmelen, et al. (2023, https://doi.org/10.5281/zenodo.8324726).

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SUPPORTING INFORMATION

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