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Invasive oaks escape pre-dispersal insect seed predation and trap enemies in their seeds

Running Head: Invasive oaks escape seed predation

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Abstract

Species introduced to habitats outside their native range often escape control by their natural enemies. Besides competing with native species, an alien species might also affect the native herbivores by introducing a new source of different quality food. Here, we describe the case of northern red oak (*Quercus rubra*) invasion in Europe. We collected data on insect (moth *Cydia* spp. and weevil *Curculio* spp.) seed predation of northern red oak in its native (USA, North America) and invasive (Poland, Europe) range, as well as for sessile oaks (*Q. petrea*) in Europe. We also evaluated the quality of acorns as hosts for weevil larvae by collecting infested acorns and measuring weevil developmental success, and quantifying acorn traits such as seed mass, tannins, lipids, and protein concentration. We used DNA barcoding to identify insects to the species level. The predation by moths was similar and very low in both species and in both ranges. However, red oaks escape pre-dispersal seed predation by weevils in Europe. Weevil infestation rates of northern red oak acorns in their invasive range were 10 times lower than that of sessile oaks, and also 10 times lower than that of red oaks in N. America. Furthermore, even when weevils oviposited into northern red oaks, the larvae failed to develop, suggesting that the exotic host created a trap for the insect. This phenomenon might gradually decrease the local abundance of the seed predator, and further aid the invasion.

Key-words: biotic invasions, ecological trap, enemy release hypothesis, seed predation, weevils

Introduction

Species introduced to habitats outside their native range (i.e. alien species) frequently escape control by their natural enemies (Keane & Crawley 2002, Torchin *et al.* 2003, Liu & Stiling 2006). Capitalization on predation release often allows the survival rate, recruitment, and growth to be higher in the introduced than in the native range, which gives invaders an advantage over native competitors (Siemann & Rogers 2001, Wolfe 2002, Colautti *et al.* 2004, Muller-Scharer *et al.* 2004). These changes cause or contribute to the troublesome success of many alien species.

Furthermore, in some situations, natural enemies may not only fail to control the population of an invader, but may suffer themselves in the interaction (Keeler and Chew 2008, Harvey *et al.* 2010, Yoon & Read 2016). For example, lepidopterans that oviposit on and consume host plants, do not show strong preference towards native hosts as compared to exotics, despite lower performance on the latter (Yoon & Read 2016). On the other hand, the presence of non-native prey may increase food availability, which ultimately translates into higher survival rates of the predator (Cattau *et al.* 2010, Brown *et al.* 2016, Cattau *et al.* 2016). Thus, depending on the quality of the exotic prey for the native enemy, it can reduce or boost the predator population (Pearse *et al.* 2013, Brown *et al.* 2016, Yoon & Read 2016). If the exotic species harm the populations of native predators or herbivores, it can further accelerate the invasion of the exotic species, as the natural enemy is gradually removed from the local habitat (Pearse *et al.* 2013). Yet there are still few studies that, beyond the existence of "predator release effects", have provided the evaluation of the effects of the invasive plant on the local enemy (but see e.g. Keeler and Chew 2008, Harvey *et al.* 2010, Brown *et al.* 2016).

In this study, we describe a case of a northern red oak (*Quercus rubra*) invasion in Europe, in which the plant not only escapes seed predation but also may harm natural enemies by trapping them in its acorns. The northern red oak was introduced to European forests from North America in the 17th century as an ornamental species, and started to be commercially planted at the end of 18th century (Woziwoda *et al.* 2014b). Nowadays, it is one of the most frequent foreign deciduous species in Central European forests (Woziwoda *et al.* 2014b). Northern red oaks are considered invasive and their abundance correlates negatively with abundance and richness of numerous native species (Chmura 2013, Woziwoda *et al.* 2014a). The invasion will likely further accelerate as northern red oaks have a great recruitment potential in Central Europe: at some sites, their density of regeneration exceeds all other tree species combined (Major *et al.* 2013, Myczko *et al.* 2014). Dense seedling banks beneath the canopies suggest that low seed predation may contribute to the regeneration advantage of red oaks over other local oaks (Major *et al.* 2013). Nonetheless, whether northern red oaks escape seed predation by weevils in their invasive range is unknown (but see Myczko *et al.* 2017).

Weevil larvae (Coleoptera: Curculionidae) and moth caterpillars (Lepidoptera: Tortricidae) represent the most important groups of oak acorn predators, although weevils are responsible for majority of seed loses (Crawley & Long 1995, Branco *et al.* 2002, Bonal *et al.* 2007, Espelta *et al.* 2009). Weevil pre-dispersal predation shapes recruitment potential of trees (Crawley & Long 1995, Espelta *et al.* 2009, Bogdziewicz *et al.* 2017), and severely destroys crops of northern red oaks in their native range (Lombardo & McCarthy 2008, Bogdziewicz *et al.* 2017). While less is known about moth feeding ecology, weevils are feeding specialists with particular species best adapted to exploit particular hosts (Bonal *et al.* 2011, Govindan *et al.* 2012, Muñoz *et al.* 2014, Peguero *et al.* 2017). Concerning predation upon red and European white oaks, differences may arise because red oaks acorns have higher tannin concentration, as well as thicker shells than European white oaks (Shimada & Saitoh 2006, Steele 2008, but see Łuczaj *et al.* 2014). In fact, differences in the communities of endosymbiont bacteria associated with weevils are correlated with the use of different host plants (Toju & Fukatsu 2011, Merville *et al.* 2013). Therefore, since European weevils have a relatively short history of co-occurrence with red oaks, we could expect a lower adaptation to this alien host and

thus reduced acorn predation rates compared to native white oaks. Moreover, European oaks belong to the white oaks (section *Quercus*), while northern red oaks belong to the section *Lobatae*. This has been observed in some previous studies to be a factor for the specialization of acorn weevils (Peguero *et al.* 2017, but see Bonal *et al.* 2016). Host specialization could, however, differ between native predators, thus conditioning their abilities to exploit alien plant species.

In this study, we evaluated insect pre-dispersal predation on northern red oak in North America and Europe as well as on sessile oak (*Quercus petrea*), which is the dominant native oak in Central European forests. We predicted that weevils will destroy a higher proportion of northern red oak acorns in N. America than in Europe, and a higher proportion of sessile than northern red oak acorns in Europe. Based on the acorn quality data from past studies (Shimada & Saitoh 2006, Steele 2008), and in particular on high tannin concentrations and thick shells of red oaks acorns, we predict that the red oak is a lower quality host for European weevils than is the sessile oak, and this results in lower predation rates on the former species. To evaluate these predictions, we measured weevil prevalence in acorns of northern red oaks (in Europe and N. America) and of sessile oaks. Moreover, we evaluated quality of acorns as hosts for weevil larvae by collecting infested acorns and measuring weevil developmental success, and quantifying acorn traits such as seed mass and shell thickness, and tannins, lipids, and protein concentration. Finally, we assessed whether the ability to exploit alien host seeds differed among pre-dispersal insect predators, using DNA barcoding to identify weevil larvae and moth caterpillars to the species level.

Materials and Methods

Study site

The study was conducted over the course of three years in Europe (2014-2016) and North America (2013-2015). In Europe, we conducted research in Gorzowska Forest (52° 47' 1.71" N, 15° 3' 21.87" E), situated in western Poland at an altitude of 60–80 m. Gorzowska Forest is located in the temperate climate zone, with average annual precipitation of 523 mm and average annual temperature of 8°C (Zwolak *et al.* 2016). For the study, we selected two sites in mixed sessile-northern red oak stands. In USA, two sites were established in northern red oak-dominated stands in Harvard Forest (42° 31' 53.28" N, 72° 11' 23.78" W), Massachusetts, which is located in the temperate climate zone, with average annual precipitation of 1100 mm and average annual temperature of 10°C. In both regions, the study sites were spaced over 1 km from each other.

Field sampling and laboratory procedures

Each year, we collected acorns under haphazardly chosen trees (i.e. first trees that we encountered once entering the stand that shed acorns): 13 red and 12 sessile oaks in Poland, and 30 northern red oaks in USA (half of that number of the trees per site, red oaks in Europe 6 and 7 trees per site). In Poland, we collected samples from the ground beneath each tree in 0.5×0.5 m-squares placed 1-m from each tree trunk in the four cardinal directions, and in a 2-m-radius circle centered at each tree trunk in the USA. Acorns were collected at the beginning of October, bagged separately according to the tree of origin, transported to the laboratory and refrigerated (4 °C) until further processing. The phenology of acorn fall is similar in red and sessile oaks in Poland, therefore bias due to any phenological difference is unlikely (Bogdziewicz *et al.* personal observation, see also Myczko *et al.* 2017). The number of acorns collected in the samples was used as an index of individual tree acorn production.

In the laboratory, we weighed, measured (width and length) and assessed insect infestation for individual acorns from each treatment (Poland: northern red oaks = 981 acorns, sessile oaks = 1203;

USA: northern red oaks = 1219). Previous studies provided evidence for chemical gradients in acorns that promote consumption of the basal end of the acorns (i.e. avoidance of the apical end) by seed predators (Steele *et al.* 1993, Bogdziewicz *et al.* 2017). Therefore, we cut each acorn transversely into a top (basal) and bottom half (apical) and counted all insect larvae in each half (following earlier protocols, see Steele *et al.* 1993).

Another sample of acorns was collected to estimate the probability of successful weevil emergence, the total number of larvae per infested acorn, and the probability that the larvae depredated an acorn embryo. This sample consisted only of acorns with oviposition scars but without emergence holes (i.e., acorns that still had all larvae inside). We collected the acorns from the soil at 20 haphazardly chosen northern red oaks in USA (in 2015), and 10 red and 10 sessile oaks in Poland (in 2016) at the same sites as described above (Poland: northern red oak = 237 acorns, sessile oak = 296; USA: northern red oak = 352). In the laboratory, we placed the acorns in separate open plastic vials. Each day we checked acorns to register emerged larvae. Once all larvae had emerged (i.e. no emergence was recorded for 3 weeks), we dissected acorns to further check whether the acorn embryo had been predated and whether there were non-emerged larvae inside (following earlier protocols e.g. Bonal and Muñoz 2008, Muñoz *et al.* 2014).

DNA barcoding and larval identification

Larval identification is necessary to establish unequivocal trophic relationships between insects and their host plants, and the lack of morphological keys makes the use of molecular techniques necessary. For DNA-based species identification we selected a random sample of larvae collected from northern red oak acorns (North America, N = 24, and Europe, N = 16) and from sessile oak acorns (Europe, N = 24). We did not pre-determine whether larvae were moths or beetles. DNA was from tissue and extracted following the salt extraction protocol (Aljanabi & Martínez 1997). In the case of weevil larvae, we sequenced a fragment (826 bp) of the mitochondrial cytochrome oxidase subunit 1 (cox1) using primers Pat and Jerry following methods described previously (Hughes and Vogler 2004a). We chose this fragment of cox1 due to the availability of many reference sequences of European and North American *Curculio spp.* to compare with (Hughes and Vogler 2004a). In the case of *Cydia spp.* caterpillars we amplified a different fragment (625 base pairs long) of the same mitochondrial gene (cytochrome oxidase I) using the universal primers pair LCOI1490/HCOI2198, common in DNA barcoding (see Folmer *et al.* 1994 for details on the primer sequences and PCR protocols). Sequencing was performed using Big-Dye (Perkin-Elmer) technology and an ABI3700 sequencer. Sequence chromatograms were assembled and edited using Sequencher 4.6 (Gene Codes Corp., Ann Arbor, MI, USA).

Two alignments (one for weevil larvae and another for caterpillar moths) were created using CLUSTALW supplied via http://align.genome.jp, with default gap open and gap extension penalties. The alignment sets were collapsed into unique haplotypes and each of this compared to the reference sequences available at GenBank (for weevil larvae) or the Barcoding of Life Datasystem (for moth caterpillars). We applied the most conservative limit used in DNA barcoding, that states a maximum genetic divergence of 1% with the reference sequence for an unambiguous identification to the species level (Ratnasingham & Herbert 2007). In the case of acorn weevils, we additionally built a Neighbor Joining gene tree based on Kimura 2 Parameter model genetic distances (2KP, Kimura 1980). The objective was to further assess whether the haplotypes corresponding to the individuals classified as the same species clustered together forming discrete groups separated from the others by significant genetic discontinuities (branch lengths). This gene tree was built pooling together the haplotypes of the individuals sequenced at our study sites with reference sequences of the Holarctic species of *Curculio spp.* available at GenBank from Hughes & Vogler (2004a). The gall-feeding *C. pyrrhoceras* was used as an outgroup.

Lipid, tannin, and protein concentration in acorns

Previous studies provided evidence for chemical gradients in acorns that promote consumption of the basal end of the acorns (i.e. avoidance of the apical end) by seed predators (Steele *et al.* 1993). Therefore, we cut each acorn transversely into a top (basal) and bottom half (apical), and analyzed the halves separately. We used only non-infested acorns, and measured the concentration of each compound based on 10 replicates per oak species. Each sample consisted of 5-6g of chopped cotyledons originated from different trees. The detailed description of procedures is presented in the Online Appendix.

Data analysis

We analyzed data in R using the generalized linear mixed models (GLMMs) implemented via lme4 package (Bates *et al.* 2015). Each below-described model was run separately for European and N. American data. For the European comparison, we did not include seed mass as a covariate because acorn mass and species were strongly confounded: northern red oak acorns were on average twice heavier than sessile oak acorns (Table 1). We estimated the proportion of acorns infested with weevil and moth larvae separately, as well as overall infestation rate, each with a separate model. We built a binomial family, logit link GLMMs (one per continent) with tree ID as a random effect. Fixed effects included year, crop size index, oak species, and oak species by crop size interaction term. Species and interaction terms were only included in the 'European' model. We used the total number of acorns collected under each tree as an index of individual crop size.

We estimated the probability of successful emergence from the infested acorn with binomial family, logit link GLMM, with tree ID included as random effect. In this analysis, the response variable was binomial with failure (0) indicating oviposition mark on the acorn but no larvae emergence, and success (1) indicated acorn with both oviposition mark and emerged larvae. We used oak species as fixed effect, again, only in the 'European' model. We also tested for differences in probability of acorn embryo survival in weevil-infested acorns using binomial family, logit link GLMM, with tree ID as random effect. Species was included as a fixed effect in 'European' models, while 'American' models were fitted with the intercept only.

Results

In the models fitted to European data, the estimated overall proportion of infested acorns was higher in sessile (33-67%, depending on the year) than in northern red oaks (3-13%; $\chi 2 = 254.53$, d.f. = 1, p < 0.001, Fig. 1). The difference was driven by the decrease in weevil infestation in red oak (3-10%) as compared to sessile oak (31-64%, $\chi 2 = 256.71$, d.f. = 1, p < 0.001). Infestation by *Cydia* sp. did not differ between species ($\chi 2 = 0.03$, d.f. = 1, p = 0.86), and ranged 1-5% depending on the year. In the 'N. American' model, the estimated overall proportion of infested northern red oak acorns ranged 35-62% depending on the year (Fig. 1). Weevil infestation ranged 37-48%, while moth infestation ranged 2-12%. In all models, infestation rates also differed significantly among years (p < 0.001, Fig. 1), but individual tree acorn production did not have an effect (p < 0.40).

In Europe, the probability of successful weevil larvae emergence from an infested acorn was over 20 times higher in sessile oaks than in northern red oaks (~40% vs. ~2%, z = 6.13, p < 0.001; Fig. 2). In contrast, the probability of emergence of weevils from northern red oak acorns in USA was similar to the probability of emergence of weevils from sessile oak acorns in Europe (Fig. 2).

When the acorns infested by any type of insect (either weevil or moth caterpillar) were pooled, the probability of embryo survival after infestation also differed among oak species. In Europe, this probability was lower in sessile than in northern red oaks (65% vs. 90%, Fig. 3, z = -4.40, p < 0.001), and was the lowest (50%) in northern red oaks in N. America.

Using DNA barcoding we successfully identified 21 out of 24 larvae collected from red oaks in N. America, 16 out of 16 collected from red oaks in Europe, and 17 out of 24 from sessile oaks. We identified two acorn weevil species in North America: *Curculio proboscideus* (12 sequences, 7 haplotypes) and *Curculio nasicus* (4 sequences, 2 haplotypes), all of them feeding on northern red oak acorns. In Europe we identified only one, namely *Curculio venosus* (8 sequences, 2 haplotypes) and weevil larvae were found both in red and white oaks. The comparison with reference sequences retrieved a divergence below 1% in all cases. Moreover, the Neighbor Joining tree showed that the distinct haplotypes clustered with their respective reference sequences, being separated from the rest of the species in the phylogeny by longer branches (Fig. 3). Although not identified in our study, the other potential species present at our site are *C. glandium*, *C. pellitus*, and *C. elephas* (Burakowski *et al.* 1995). In the case of moth caterpillars, two species were identified in Europe: *Cydia amplana* (6 sequences, 1 haplotype) and *Cydia splendana* (4 sequences, 2 haplotypes); both species were collected from northern red oak and sessile oak acorns.

The concentration of tannins was similar in northern red and sessile oaks in Europe (Table 1), although red oak acorns in Europe had almost two times lower tannin concentration than that reported for N. America populations. Lipid concentration was almost three times higher in northern red than in sessile oaks in Europe. Protein concentration was also higher in northern red than in sessile oaks (Table 1). The mass of northern red oak acorns in Europe was almost twice lower than in their native range. Nonetheless, acorns of northern red oaks in Europe were almost twice heavier than those of sessile oaks. Acorn shell was thicker in northern red oaks than in sessile oaks (Table 1).

Discussion

Northern red oaks escape pre-dispersal seed predation by weevils in Europe. The predation by moths was similar in both species and in both ranges, but the proportion of seeds infested by *Cydia sp.* was low compared to that predated by weevils (see Myczko *et al.* 2017 for more detailed analyses of *Cydia* infestation in northern red and sessile oaks in Poland). The lower prevalence of *Cydia spp.* compared to weevils is common in temperate oak forests (see e.g. Bonal *et al.* 2007 for a similar result). The weevil infestation rates of northern red oak acorns in their invasive range were 10 times lower than that of sessile oaks, and also 10 times lower than that of red oaks in N. America. Plant species with large seeds, like oaks, are particularly likely to be seed-limited (Moles & Westoby 2002, Clark *et al.* 2007). Thus, the drastically reduced pre-dispersal seed predation of northern red oaks in their exotic range is likely to favor their recruitment and accelerate their invasion in European forests. Furthermore, even when weevils, the main pre-dispersal insect predators of oaks, oviposit into northern red oaks, the larvae fail to develop. Thus, the exotic host apparently creates a "trap" for the insect (Schlaepfer *et al.* 2002).

The enemy release hypothesis (ERH) makes three predictions about the effects of natural enemies on alien plants (Keane & Crawley 2002), and even though our study was not designed to test them, several lines of evidence suggest that the escape from seed predation in exotic range may aid the spread of northern red oaks. First, ERH assumes that enemies are important regulators of plant populations. Although we have not determined whether oaks at our sites are seed-limited, seed predation commonly limits recruitment in oaks (Crawley & Long 1995, Haas & Heske 2005, Espelta *et al.* 2009, Bogdziwicz *et al.* 2017). Second, according to the ERH, enemies should have greater impact on native than on alien plants. Our results show that the magnitude of pre-dispersal seed predation by weevils is almost 10 times higher on sessile oaks than on northern red oaks, and a similar study by Myczko *et al.* (2017) reported even greater differences. Assuming that these populations are seed-limited, we can tentatively conclude that the impact of weevil predation on populations of sessile oaks is greater than on northern red oaks. Finally, according to the ERH, alien species should be able to capitalize on the enemy release and increase in abundance (Keane & Crawley 2002). Northern red

oaks have a large recruitment advantage over native oaks in Central Europe (Major *et al.* 2013, Myczko *et al.* 2014), but the mechanism is unknown. Our results suggest that the release from pre-dispersal seed predation might be an important driver.

Northern red oaks not only escape seed predation by weevils but also seem to effectively trap insects in their acorns. In Europe, the probability of successful larvae emergence from a northern red oak acorn with an oviposition scar was lower than 3%, compared to 48% in red oaks in N. America and over 40% in sessile oaks. This low success could be the result of larval development failure due to the lack of trophic adaptation to feed on the alien host tree. Recent studies stressed the importance of endosymbiont bacteria associated with acorn weevils in the adaptation to different trophic sources. The community of these bacteria not only changes among weevil species, but also within species between populations feeding on different host plants (Toju & Fukatsu 2011, Merville *et al.* 2013). The species feeding on red oak acorns in North America (*C. proboscideus* and *C. nasicus*) were different from that recorded in Europe (*C. venosus*). In fact, there is not a single acorn weevil species found in both continents (Hughes & Vogler 2004b). Thus, along its evolutionary history, European species like *C. venosus* have not faced any red oak species, as red oaks (section *Lobatae*) are exclusive to America. This might have prevented associations with endosymbiont bacteria that would allow insects to feed on seeds with a different chemical composition.

One caveat to the argument of the lack of trophic adaptation in acorn weevils is that it is not possible to distinguish whether females laid eggs, but the larvae development was stopped at early stages, or that females drilled an oviposition hole but failed to lay eggs. Which scenario is more likely? On one hand, red oaks have a shell that is twice the thickness of that of sessile oaks, and the weevil rostrum size correlates positively with size of the acorn host (Hughes and Voegler 2004b). Therefore, European weevils may be less successful at drilling oviposition holes in red oak acorns. In such a scenario, the oviposition scars we observed on red oak acorns may not always result in egg laying. However, recent studies suggest that rostrum length of weevils is not critical for exploiting seeds (Bonal *et al.* 2011). Furthermore, *C. venosus* lays eggs very early in the season, before the acorn shell is fully developed (Venner *et al.* 2011, Pélisson *et al.* 2013).

The alternative scenario is that female weevils fail to perceive northern red oak acorns as lethal hosts for their larvae. Weevils generally seem to concentrate ovipositioning in seeds of higher quality, although the host-selection process is not clear (Desouhant 1998, Espelta *et al.* 2009, Bonal *et al.* 2011, Muñoz *et al.* 2014). In our population, northern red oaks have similar tannin concentration to sessile oaks (although the level of non-tannin phenolics is much higher in red than in sessile oaks in Poland: Łuczaj *et al.* 2014), but much higher lipid and protein concentration. Therefore, a mismatch between perceived and real quality of the host seems to take place, suggesting an ecological trap (Schlaepfer *et al.* 2002). If true, northern red oaks will function as sink habitats for weevils across the landscape (Govindan *et al.* 2012). The process would slowly result in gradual removal of insects from local habitats, which will further decrease predation and accelerate northern red oak invasion. As a caveat, we have not measured the preference of weevils to oviposit in red vs. sessile oaks in Europe. Thus, further studies are required to test whether red oaks create true ecological traps for weevils (i.e. are preferred and lethal host, cf. Schlaepfer *et al.* 2002), or are just lethal hosts that are nevertheless exploited.

To conclude, our study shows that northern red oaks almost completely avoid pre-dispersal seed predation in their exotic range in contrast to their native range, and in contrast to sessile oaks. Furthermore, European weevils oviposit in the red oaks, but the probability of larval emergence from acorns with oviposition scars is less than 3%. Moreover, even infested northern red oak acorns have a 90% chance that their embryo survives, and that these acorns will germinate and produce viable seedlings (Bonal *et al.* 2007, Xiao *et al.* 2007, Muñoz *et al.* 2014). We suggest that the mechanisms described in our study might contribute to the invasion of the northern red oak across Central

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European forests. The next important step towards testing this hypothesis would be to confirm demographic impacts of reduced pre-dispersal seed predation in the northern red oak.

Acknowledgments

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SUPPLEMENTARY MATERIALS

Lipid, tannin, and protein concentration in acorns

Table 1 Traits of northern red oak (in Europe and N. America) and sessile oak acorns. Tannins and lipids are expressed as a percent of acorns dry mas, and proteins in g per dry mass. Values in brackets represent standard deviations from the mean. Proteins were only measured in the European sample.

Trait	Sessile oak		Red oak (Europe)		Red oak (N. America)	
	Apical	Basal	Apical	Basal	Apical	Basal
Tannins	3.59 (1.05)	2.65 (0.85)	3.75 (0.81)	3.72 (0.62)	9.8*	-*
Lipids	5.14 (0.39)	5.60 (0.73)	14.10 (1.46)	16.49 (1.95)	15.36 (2.75)	18.15 (3.46)
Proteins	0.36 (0.02)	0.28 (0.02)	0.49 (0.03)	0.46 (0.04)	-	-
Mass (g)	1.26 (0.91)		2.85 (1.19)		4.81 (1.48)	
Shell thickness (mm)	0.97 (0.64)		1.71 (0.60)		1.49 (0.54)	

*data on tannin concentration in northern red oak acorns in N. America following Shimada and Saitoh (2006), measured for the whole acorn.

Figure 1 Estimates of the pre-dispersal predation rates (combined, weevils and moths) of sessile oaks (SO) and northern red oaks (RO, in Europe and N. America) across three years of the study. Estimates are based on binomial GLMMs, whiskers represent standard deviations. Dots represent different years of data collection.
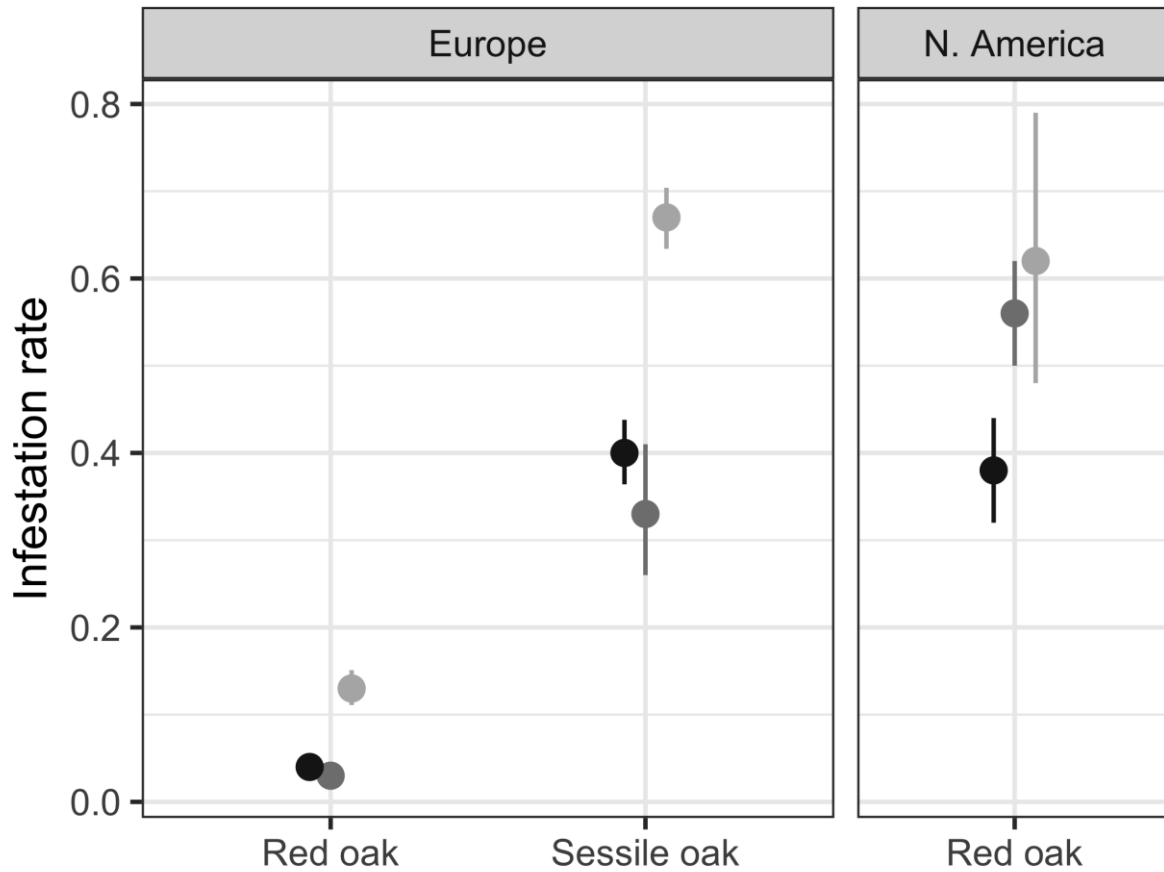
Figure 2 Probability of successful emergence of weevil larvae from infested northern red (in Europe and N. America) and sessile oak acorns. Estimates are based on the binomial GLMMs (see Methods for details), whiskers represent standard deviations.
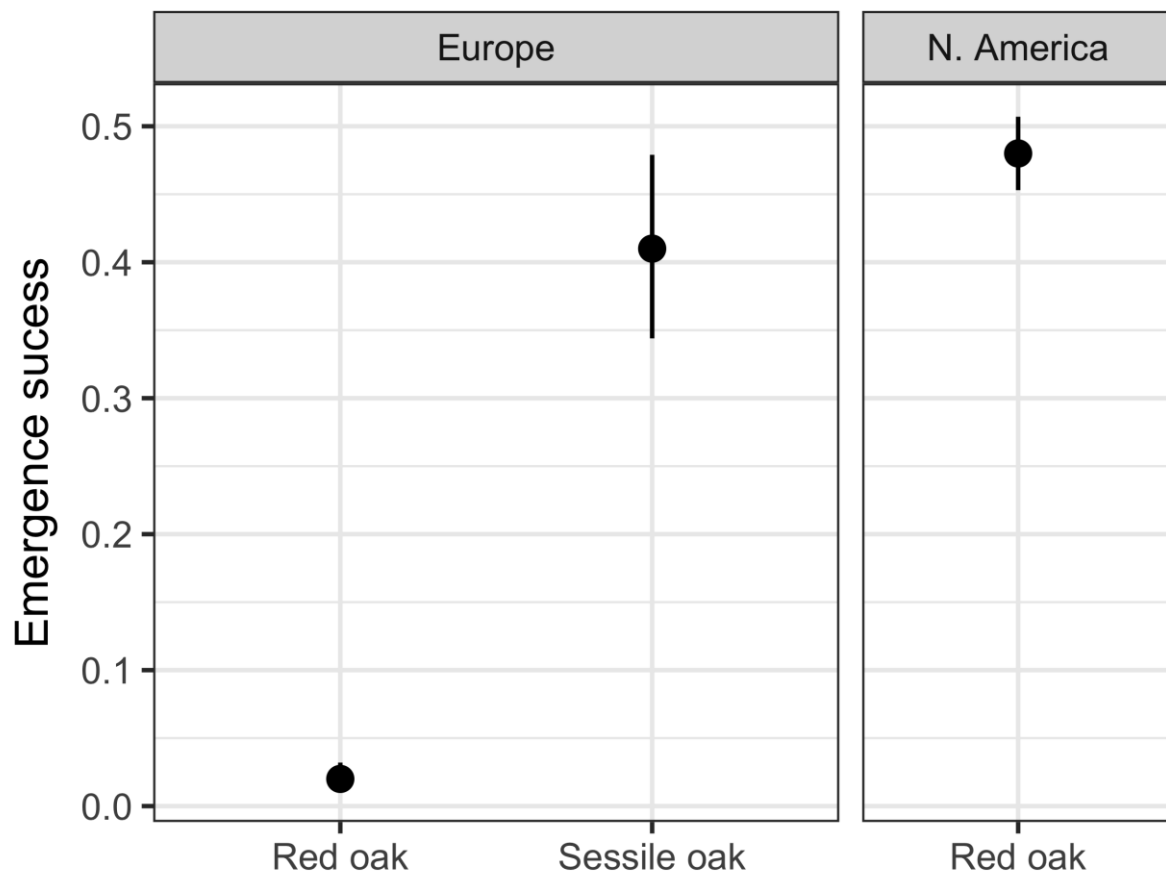
Figure 3 Neighbour Joining tree based on the mitochondrial gene citochrome oxidase I showing the positions of the 11 haplotypes obtained from the weevil larvae at the study sites and published reference sequences from Holartic Curculio spp. Sequences correspond to the distinct haplotypes, the evolutionary distances were computed using the Kimura 2-parameter method. The gall-feeding *C. pyrrhoceras* was the outgroup. We identified *C. proboscideus* and *C. nasicus* in North American, and *C. venosus* in the European sample.