ORIGINAL ARTICLE

An intercontinental comparison of insect seed predation between introduced and native oaks

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Abstract

Novel interactions between introduced oaks and their natural enemies across different continents provide an opportunity to test the enemy release hypothesis (ERH) at local and global scales. Based on the ERH, we assessed the impacts of native seed-feeding insects on introduced and native oaks within and among continents. We combined a common-garden experiment in China and biogeographic literature surveys to measure seed predation by insects and the proportion of acorn embryos surviving after insect infestation among 4 oak species with different geographical origins: *Quercus mongolica* origin from China, *Q. robur* and *Q. petraea* from Europe, and *Q. rubra* from North America. Mostly supporting the ERH, oaks in introduced continents escaped seed predation compared to those in native continents and compared to other native oaks in introduced continents. Common-garden comparisons showed that total acorn infestation rate of introduced *Q. rubra* (section *Lobatae*) was considerably lower than that of native oaks (section *Quercus*) in China and Europe, likely because of the differences in seed traits associated with different oak sections. Literature surveys showed that seed predation of introduced oaks was lower in the introduced continent than in the native continent. Embryo survival was higher in introduced *Q. rubra* than native oaks in China and Poland. However, insect seed predation of recently introduced *Q. rubra* in China was similar to that in Europe, which is not consistent with the ERH. Our results suggest that reduced acorn attack by native insects and higher embryo survival after acorn damage could increase the establishment success or invasion risk of introduced oaks in non-native continents.

Key words: acorn performance, common garden, plant–herbivore interactions, species introduction, the enemy release hypothesis

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INTRODUCTION

Many introduced species prosper in their new ranges in part because their natural enemies are absent (Keane & Crawley 2002). This phenomenon, known as the enemy release hypothesis (ERH, Keane & Crawley 2002), is recognized as a major cause of the success of introduced plants through escape from their natural enemies in non-native regions (Liu & Stiling 2006; Jeschke & Heger 2018). Enemy release may allow introduced plants to colonize new ranges (Harvey *et al*. 2013). An implicit assumption of the ERH is that predators and parasites in the introduced range are less likely to consume or infect novel prey species. Both empirical and synthetic studies have been used to evaluate the ERH with introduced (or invasive) plants and native insect herbivores by comparing insect damage and plant performance between native and introduced plants (Liu & Stiling 2006; Bezemer *et al*. 2014; Jeschke & Heger 2018). The debate about scientific evidence for the ERH has raged unabated for over a century, but the ERH, very popular and widely established, has received mixed empirical support (Chun *et al*. 2010). Many introduced plants have been found to experience reduced damage by some herbivores and pathogens in new environments when compared with those co-occurring native species (Liu & Stiling 2006; Jeschke & Heger 2018). In contrast to key predictions from the ERH, however, slow-growing evidence also indicates no support (e.g. Chun *et al*. 2010) or even negative trends (e.g. Cogni 2010; Morrison & Hay 2011). In addition, a recent meta-analysis suggests that enemy release may not always result in greater plant performance (Chun *et al*. 2010). Thus, to what extent the ERH can be used to predict novel interactions between native natural enemies and introduced species, and their consequences for invasiveness, are still open questions (Seebens *et al*. 2017). Therefore, a better understanding novel interactions between alien and native species in novel environments based on the ERH would be critical for species introduction and ecosystem management (Keane & Crawley 2002).

The growing consensus is that enemy release can be an important process in shaping the success of introduced plants. However, the degree of enemy release is context dependent based on biogeographic and local community approaches, and driven by several competing, but not mutually exclusive factors (Bezemer *et al*. 2014; Jeschke & Heger 2018). First, enemy release may depend on the presence or absence of congeners (or phylogenetic distance to native species) because closely related species have similar functional traits and attract the same native enemies (Dawson *et al*. 2009; Pearse & Hipp 2009; Ness *et al*. 2011; Sunny *et al*. 2015). Second, geographical distance between native and introduced ranges may affect enemy release because enemies disperse across space (Kirichenko *et al*. 2013; Kirichenko & Kenis 2016; Tabassum & Leishman 2018). Third, the time since introduction affects enemy release because of the time available for coevolution between introduced plants and native enemies (Brandle *et al*. 2008; Harvey *et al*. 2013; Song *et al*. 2018). Lastly, the type of natural enemies (e.g. specialists vs. generalists) is important for the survival of introduced species because generalized enemies can consume a wide range of plant species whereas specialists cannot (Keane & Crawley 2002; Zhang *et al*. 2018). When plants are introduced into novel environments, specialist and generalist insect herbivores may have different impacts on these alien plants (i.e. a plant species introduced outside its original distribution), though specialist herbivores of these alien plants may be absent beyond their native range (Keane & Crawley 2002; Zhang *et al*. 2018). There are clearly other factors, such as physical and chemical defenses, which can also influence enemy release (Pearse 2011; Zhang *et al*. 2018). Therefore, the ERH is a complex hypothesis (Jescke & Heger 2018), to understand the process of enemy release, it is useful to accumulate multiple lines of evidence at both local and continental scales.

Many oak species (*Quercus*) have been introduced and planted as oak plantations or ornamental trees in botanical gardens and arboretums across the world (Johnson *et al*. 2009; Pearse & Hipp 2014; Nicolescu *et al*. 2020). For example, northern red oak *Quercus rubra* from North America has been planted widely in plantations in most of Europe since the 1700s, and has invaded Central European forests (Nicolescu *et al*. 2020). *Q. rubra* invasion has caused some major negative impacts on native flora and fauna in Central Europe (Woziwoda *et al*. 2014; Nicolescu *et al*. 2020). The major insect seed predators of these oaks, including weevils, acorn moths, and gall wasps, are frequently responsible for heavy or even complete reproductive failure, which have large impacts on the natural regeneration and invasiveness of multiple oak species (Gibson 1982; Crawley & Long 1995; Yu *et al*. 2003; Wang *et al*. 2008; Espelta *et al*. 2009; Perea *et al*. 2011; Xiao *et al*. 2017; Bogdziewicz *et al*. 2018a). Existing studies have documented that enemy release has been observed for *Q. rubra* after introduction into Central Europe. For instance, in the Czech Republic (Krístek 1973), Slovakia (Kelbel 1996), Germany (Goßner & Simon 2005), Hungary (Csóka & Hirka 2006), and Poland (Myczko *et al*. 2017; Bogdziewicz *et al*. 2018a), insect seed predation rate of introduced *Q. rubra* was much lower than that of native oaks. Moreover, introduced *Q. rubra*

had reduced damage by insect seed predators in Central Europe compared to native North America (Bogdziewicz *et al.* 2018a). This is likely because *Q. rubra* acorns have high tannins and thick hulls, which can reduce larval performance, including reduced survival and smaller biomass of *Curculio* weevils (Bogdziewicz *et al.* 2018a). To better understand enemy release and how it influences invasion, there is a need for more extensive geographical comparisons and to examine additional factors that might contribute to enemy release.

In this study, we combined a common-garden experiment in China (Beijing) and a literature survey to measure pre-dispersal seed predation by seed-feeding insects and compare acorn performance measured using embryo survival after insect damage (i.e. the proportion of acorn embryos surviving after insect infestation) among 4 oak species with different geographical origins. The 3 oak species studied in Beijing were *Q. rubra* (native to North America) from section *Lobatae*, and 2 white (*Quercus*) oaks: pedunculate oak (*Q. robur*, Europe) and Mongolian oak (*Q. mongolica*, Asia) (Table 1). All 3 oak species are either native or introduced in each of the 3 continents, Asia, Europe, and North America (https://www.gbif.org). In literature surveys, we were also able to include an additional oak species, *Q. petraea*, as a native species compared with introduced *Q. rubra* in Europe (Goßner & Simon 2005; Bogdziewicz *et al.* 2018a). According to previous studies, these oak species share several major seed-feeding insect groups. However, in their native continents, each oak species is attacked both by different insect species from the same major group occurring in different continents (we call them "worldwide oligophages", e.g. *Curculio* weevils), and also some "regional oligophages" (only occurring in a single continent, e.g. *Cyllorhynchites* weevils in Asia) (Table 1).

Support for the ERH can come from multiple lines of evidence when introduced trees are compared to either trees in native sites or to native relatives in introduced sites (Heger & Jeschke 2014; Jeschke & Heger 2018). Accordingly, we aimed to test the ERH in 4 different ways either within introduced continents with native and introduced species or between introduced and native continents with the same oak species (Table 2):

1. **Measures of enemy or enemy impact**. Support for the ERH may vary depending on the measured response variable (e.g. plant damage, plant fitness, enemy abundance) and the taxonomic identity of insect enemy guilds that predominantly damages a plant (Heger & Jeschke 2014). We evaluated enemy release by comparing (a) total infestation rates of acorns by insects, (b) total infestation rate by particular acorn predators (e.g. *Curculio* weevils, *Cyllorhynchites* weevils, acorn moths), (c) acorn performance measured using embryo survival of acorns following attack, and (d) the differences in enemy release of acorns considering 3 groups of insect seed predators as either worldwide or regional oligophages.

2. **Types of comparison**. Support for the ERH may vary depending on the type of comparison, such as native compared to introduced sites for a single plant species, or native compared to introduced plant species in a single site (Heger & Jeschke 2014). We quantified enemy release of acorns by comparing (a) the same species between native and introduced continents, and (b) comparing native and introduced species within the same continent.

3. **Match to recipient community**. Support for the ERH may vary based on similarity of functional traits (or phylogeny) between an introduced plant and the recipient community because dissimilar introduced plants are unlikely to be colonized by specialist herbivores (Pearse *et al.* 2013). We tested enemy release of introductions of (a) an oak species (*Q. rubra*) that is phylogenetically distinct from oaks in its recipient communities, and (b) an oak species (*Q. robur*) that has oaks that are close phylogenetic relatives in its recipient community.

4. **Time in recipient community**. Support for the ERH may vary based on the length of time that an introduced species has persisted in a recipient community because herbivores slowly adopt it as a host over time (Strong *et al.* 1977; Brändle *et al.* 2008). We tested whether acorn infestation was greater for *Q. rubra* that was introduced into Europe over 200 years ago compared to in China, where *Q. rubra* was introduced within the past 40 years.

MATERIALS AND METHODS

Beijing Botanical Garden

Botanical gardens and arboretums are living flora museums and introduction centers, and collect large numbers of native and alien plant species from different regions across the world. They therefore provide good opportunities for the evaluation of ecological and evolutionary impacts (e.g. invasion risk) of newly introduced plants on native fauna or plant pests (Heywood 2011). Most importantly, botanical gardens and arboretums serve as common gardens for comparisons between alien plants and their native relatives (here congeneric species). We used them to allow comparisons of multiple introduced and

Table 1 Basic information including the origin, key traits, and seed-feeding insects of 3 oak species used in this study: *Quercus mongolica, Q. robur, Q. petraea,* and *Q. rubra*

Basic information	*Quercus mongolica*	*Quercus robur*	*Quercus petraea*	*Quercus rubra*
Oak taxonomy	White oak (Section *Quercus*)	White oak (Section *Quercus*)	White oak (Section *Quercus*)	Red oak (Section *Lobatae*)
Oak origin (continent)				
Native	Asia (China)	Europe	Europe	North America
Introduction (time)	Europe (since 1879) North America (since 1960's)	China (since 1841)[‡] North America (unknown)	North America (unknown)	Europe (since 1724) China (since 1980's)
Beijing Botanical Garden				
Population (individuals)	16	9	No trees	21
DBH (mean ± SD cm)	64.65 ± 36.55	59.80 ± 12.83	—	47.34 ± 24.36
Key oak traits[†] (*N* > 30)				
Acorn mass (± SD g)	2.17 ± 0.70	5.23 ± 1.69	1.26 ± 0.91	5.80 ± 1.29
Hull thickness (± SD mm)	0.29 ± 0.10	0.43 ± 0.09	0.97 ± 0.64	1.12 ± 0.31
Acorn tannins	8.3%	5.2–6.9%	2.65–3.59%	9.8%
Seed-feeding insects				
Regional oligophages (weevil)	Yes, *Cyllorhynchites*	No	No	Yes, *Conotrachelus*
Worldwide oligophages (weevil)	*Curculio*	*Curculio*	*Curculio*	*Curculio*
Acorn moths	Mostly *Cydia*	Mostly *Cydia*	Mostly *Cydia*	Mostly *Cydia*
Other seed-feeding insects	Beetles, etc.	Gallwasps, etc.	Gallwasps, etc.	Gallwasps, etc.

[†]Tannin data of *Q. mongolica* are from Zhishu Xiao (unpublished data) and those of *Q. robur* and *Q. rubra* are from Shimada and Saitoh (2006); the data of *Q. petraea* are from Bogdziewicz *et al.* (2018a). [‡]The introduction of *Q. robur* was much earlier in Xinjiang (China) since 1841 (Teng *et al.* 2016), but not at the Beijing Botanical Garden.

Table 2 An intercontinental comparison of acorn infestation and acorn performance after insect damage among *Quercus mongolica* (QM), *Q. robur* (QRO), *Q. petraea* (QP), and *Q. rubra* (QRU) in their native (N) and introduced (I) regions across Asia (China), Europe, and North America

Indicator	Patterns	Types of enemies	References
Common garden (Beijing, China)			
Seed predation (infestation) (mostly confirmed, see Fig. 1)	QM > QRO > QRU	All insects	This study
	QM > QRO > QRU	*Cyllorhynchites*	This study
	QM > QRO > QRU	*Curculio* weevil	This study
	QM > QRO > QRU	*Cydia* moths	This study
Acorn performance	QM < QRO < QRU	All insects	This study
Common garden (Europe)			
Seed predation (infestation)	QRO/QP > QRU	All insects	Czech Republic (Kristek 1973); Slovakia (Kelbel 1996); Germany (Goßner & Simon 2005); Hungary (Csóka & Hirka 2006); Poland (Bogdziewicz *et al*. 2018a)
	QRO/QP > QRU	*Curculio* weevil	
	Mostly QP > QRU	*Cydia* moths	
Acorn performance	QP > QRU	All insects	Poland (Bogdziewicz *et al*. 2018a)
	QRO = QRU	All insects	Hungary (Csóka & Hirka 2006)
Biogeographic survey			
Seed predation (infestation)	$QRU_N > QRU_I$	All insects	Bogdziewicz *et al*. 2018a; This study
	QRU_I (Europe) = QRU_I (Asia)	All insects	This study with European cases
	$QRO_N > QRO_I$	All insects	This study with European cases

We tested hypotheses using multiple response variables that follow from the enemy release hypothesis to predict the impacts of native seed-feeding insects on introduced and native oaks either within or among continents. #In Germany, QRO data were mixed with another native species (*Q. petraea*) (Goßner & Simon 2005), and in Slovakia (Kelbel 1996) and Poland (Bogdziewicz *et al*. 2018a), *Q. petraea* data were also used.

native tree species and enemy species under standardized conditions (Pearse & Hipp 2009, 2014; Kirichenko *et al*. 2013; Kirichenko & Kenis 2016).

This study was conducted during the fruiting seasons (June–October) during 2016–2018 at the Beijing Botanical Garden, Institute of Botany, Chinese Academy of Sciences, Beijing, China (39.986°N, 116.213°E; 65 m a.s.l.). The Garden has an area of 74 ha and originally consisted of over 10 largely contiguous plantation blocks or compartments planted since the 1950s. Climatically, it is within the warm temperate zone, with an average temperature of −0.7°C for January and +26.1°C in July, and annual precipitation of approx. 640 mm. Over 6000 species, including more than 15 oak species, have been introduced from Asia (China), Europe, and North America at the Beijing Botanical Garden during the 1980s (Tang & Zhang 2003).

Experimental design

Common-garden survey

Based on population size and geographic distribution, *Q. rubra* (origin North America), *Q. robur* (origin Europe), and *Q. mongolica* (origin China) were selected for the common-garden comparison, and 8–10 reproductive individuals of each species were selected to investigate seed production and insect seed predation (Fig. S1, Supporting Information). *Quercus mongolica* came from 2 source populations in Beijing and Hebei provinces in the 1980s, *Q. robur* from 3 source populations from Ireland and China (Shenyang and Qingdao in the 1980s), and *Q. rubra* came from 1 source population from USA in 2001 (Tang & Zhang 2003).

Based on our surveys since 2012, 3 major insect groups attack the acorns of the 3 oak species and other oak

species at the Beijing Botanical Garden, including *Cyllorhynchites ursulus* (hereafter *Cyllorhynchites* weevils), *Curculio* weevils (mainly *Curculio dentipes*), and moths (mainly *Cydia* spp.). *Cyllorhynchites* weevils often lay only one egg on young acorns and then cut the branch, and then larval development occur on the ground; leaving infested acorns containing eggs during the early stage of fruit development (from late June to early August). *Curculio* weevils infest nearly mature acorns and lay 1–11 eggs/larva in each infested acorn from August to the end of fruiting season. Moth infestation occurs throughout the fruiting season. *Curculio* weevils (Coleoptera: Curculionidae) are distributed worldwide and mainly feed on acorns, chestnuts, and other nuts (Gibson 1969; Hughes & Vogler 2004; Wang *et al.* 2008; Peguero *et al.* 2017; Bogdziewicz *et al.* 2018b). In addition, *Cydia* moths (Lepidoptera: Tortricidae) and gallwasps (Hymenoptera: Cynipidae) are also worldwide oligophages feeding on acorns (Gibson 1982; Crawley & Long 1995; Kelbel 1996; Csóka & Hirka 2006; Bogdziewicz *et al.* 2018a). As regional oligophages, *Cyllorhynchites* weevils attack acorns of *Quercus* (including subgenus *Cyclobalanopsis*) and chestnuts (*Castanea*), and most are distributed in Asia (China, Japan, Korea, and Eastern Russia) (Lv *et al.* 2015), while *Conotrachelus* weevils occur only in North America (Gibson 1982).

For each marked tree, we measured DBH (diameter at breast height), height, and canopy area, and placed 3 1 m^2 quadrats randomly before seed fall to measure seed crops for each individual with large canopy area and high seed production; for small red oak trees with low seed production, all fallen acorns were counted and recorded to estimate seed production. We corrected seed production by multiplying canopy area and seed number per 1 m^2 to match the small red oak trees with low seed production. Weekly, we collected 50 fallen acorns if available, or all acorns if less than 50 were available, from each marked tree across the entire July–October fruiting seasons. All acorns (2016, $n = 5207$; 2017, $n = 10\ 524$; 2018, $n = 8051$) were individually deposited in a plastic box for at least 4 weeks to monitor larval development and emergence. Acorns were then dissected and categorized as uninfested or infested with 4 insect groups: *Cyllorhynchites* weevils, *Curculio* weevils, moths, and other insects (e.g. the weevil *Sitophilus oryzae*). Each insect group attacked acorns on the tree, and was easily identified from larvae or damage signs. For insect-damaged acorns, we also examined whether embryos survived despite damage as an indicator of acorn performance.

Biogeographic literature survey

The biogeographic literature survey included all known comparable case studies about insect seed predation between native oaks and introduced oaks (here red oak *Quercus rubra* only) using the following search terms in *Web of Science*: ("*Quercus rubra*" OR "*Q. rubra*" OR "red oak") AND ("seed∗" OR "acorn∗") AND ("infest∗" OR "predat∗" OR "attack∗") AND ("insect∗" OR "weevil∗" OR "*Curculio*") in the title, keywords or abstract. The search resulted in 47 papers. We then removed those papers that were not relevant to the seed predation by insects, which left only 3 papers (i.e. Kelbel 1996; Myczko *et al.* 2017; Bogdziewicz *et al.* 2018a). We also performed additional searches by checking the references within the 3 papers and other related papers with www.scholar.google.com, and then detected 3 additional papers (i.e. Krístek 1973; Goßner & Simon 2005; Csóka & Hirka 2006) related to the ERH theme. In total, we included 5 studies most relevant to test the ERH with native oaks (*Q. robur* and *Q. petrea*) and introduced *Q. rubra* in Central Europe (Czech Republic: Krístek 1973; Slovakia: Kelbel 1996; Germany: Goßner & Simon 2005; Hungary: Csóka & Hirka 2006; Poland: Bogdziewicz *et al.* 2018a), and one recent case with *Q. rubra* in the native range in North America (Bogdziewicz *et al.* 2018a) (Table S1, Supporting Information). Another case with native oaks (*Q. robur*) and *Q. rubra* in Poland (Myczko *et al.* 2017) was not used because the measure of insect infestation was not consistent with the other studies. Among the 5 cases in Central Europe, 2 of them also included data about acorn performance after insect attack (Hungary: Csóka & Hirka 2006; Poland: Bogdziewicz *et al.* 2018a). We extracted data about insect infestation, insect group composition, and acorn performance after insect damage from text, tables, or digitized graphs using WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/).

Data analysis

For the common-garden comparison at the Beijing Botanical Garden, acorn infestation was calculated either for all insects or for each major insect group. We fitted 4 full generalized linear mixed models (GLMMs) with a binomial error distribution and a logit link function to evaluate the effects of oak species on overall infestation rate and the proportion of acorns infested with *Curculio*, *Cyllorhynchites*, and moths. In these GLMMs, we included species and year as fixed factors and tree identity as a random factor. In addition, we fitted GLMMs

with a binomial error distribution and a logit link function to evaluate the effects of oak species on overall infestation rate and the proportion of acorns infested with *Curculio*, *Cyllorhynchites*, and moths for each year (thus 12 GLMMs). In these GLMMs, we included species as fixed factors and tree identity as a random factor. All these 12 GLMMs showed no overdispersion.

We also tested acorn performance after insect damage using the proportion of infested acorns with intact embryos. We estimated the effects of oak species on the probability of embryo survival in infested acorns using a binomial family, logit link GLMM with tree species as a fixed factor, and tree identity as a random factor. In this analysis, we used all data about insect-infested acorns from all 3 years to avoid sample size limitation for infested *Q. rubra* acorns.

Data from literature across the world were compared to our common-garden data to test the generality of whether insect seed predation of introduced oaks was lower in the introduced continent than in the native continent through direct comparison using descriptive statistics without statistical quantitative analysis. We computed the mean of the total infestation rate from the 3 years of data combined at the Beijing Botanical Garden, as well as calculated the mean for each year separately and then calculated mean and the standard error (SE) with site or year as data points for each country for the literature data. We did not perform a quantitative meta-analysis here because of the limited number of publications and the highly heterogeneous data quality for the target oak species.

Data analyses were performed in R 3.4.2 (R Core Team 2017) and all generalized linear mixed models implemented using the lme4 package (Bates *et al*. 2015). The significance of the fixed effects was established via the Anova function of the car package (Fox & Weisberg 2011). We performed post-hoc multiple comparisons among the 3 oak species using the "glht" function of the multcomp package (Hothorn *et al*. 2008). A sequential Bonferroni correction was applied to account for multiple tests.

RESULTS

Insect seed predation between introduced and native oaks in Beijing Botanical Garden

Cyllorhynchites, *Curculio*, and acorn moths were the 3 major insect groups attacking acorns at the Beijing Botan-

ical Garden. The overall proportion of infested acorns and that of each insect group differed significantly among oak species ($\chi^2 = 72.05$, df = 2, $P < 0.001$) and years ($\chi^2 = 956.96$, df = 2, $P < 0.001$, Fig. 1). Specifically, overall infestation was 10 times higher in native *Q. mongolica* (40–49%, depending on the year) than that in introduced *Q. rubra* during the 3 years (4–5%, $Z = 6.54$ in 2016, $Z = 10.59$ in 2017, $Z = 6.39$ in 2018, all $P < 0.001$), and also marginally higher than that in introduced *Q. robur* (18–45%) but only significantly in 2017 ($Z = -3.15$, $P = 0.005$, Fig. 1). Of the 2 introduced oaks, overall infestation of *Q. robur* was higher than that of *Q. rubra* across all 3 years ($Z = 5.32$ in 2016, $Z = 6.99$ in 2017, $Z = 5.66$ in 2018, all $P < 0.001$, Fig. 1).

Infestation by *Cyllorhynchites* weevils was higher in native *Q. mongolica* (13–21%) than in either introduced *Q. rubr*a (0.05–1%) or introduced *Q. robur* (0.6–9%) across all 3 years, but the significance level differed among the 3 years (Table S1, Supporting Information). *Curculio* infestation was higher in native *Q. mongolica* (11–22%) and introduced *Q. robur* (13–18%) than in introduced *Q. rubra* (0.5–4%) across all 3 years (all $Z \geq 3.69$, $P < 0.001$, Fig. 1; Table S1, Supporting Information). However, *Curculio* infestation was non-significantly different between native *Q. mongolica* and introduced *Q. robur* across all 3 years (all $|Z| \leq 0.78$, $P > 0.70$, Fig. 1; Table S1, Supporting Information). Similarly, infestation by moths was higher in native *Q. mongolica* (9–16%) than in both introduced *Q. rubra* (0.2–1.6%) and introduced *Q. robur* (3.5–4%), but the patterns differed among the 3 years (Table S1, Supporting Information).

In Beijing Botanical Garden, the proportions of embryos surviving after infestation differed significantly among the 3 oak species ($\chi^2 = 32.04$, df = 2, $P < 0.01$, Fig. 2a). Proportion of embryos surviving after infestation was much higher in introduced *Q. rubra* (36%) than in either native *Q. mongolica* (16%) or introduced *Q. robur* (23%) ($Z = -5.62$ in comparing with *Q. mongolica*, $Z = -3.98$ in comparing with *Q. roubur*, $P < 0.001$, Fig. 2a), but it was similar for *Q. mongolica* and *Q. robur* ($Z = 1.72$, $P = 0.25$, Fig. 2a).

Insect seed predation of introduced oaks between non-native and native continents

Consistent with our empirical results, the literature survey showed that the total infestation rate of acorns by insects in native oaks was higher than in introduced oaks (Fig. 2b). Total infestation rate of acorns by seed-feeding
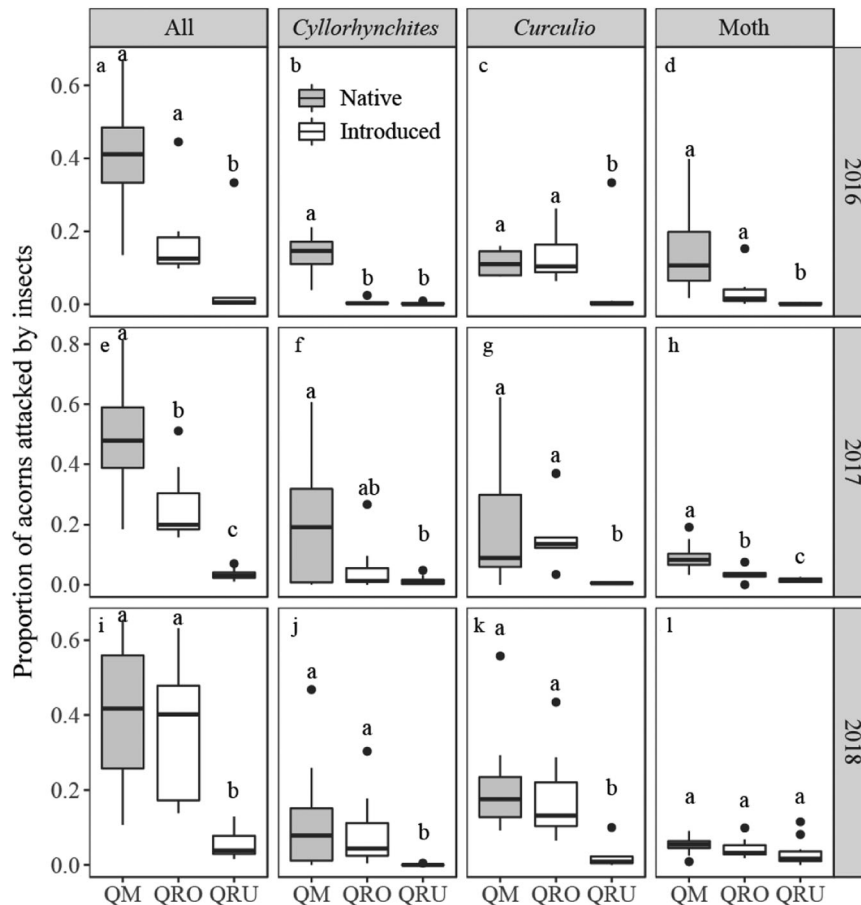
Figure 1 The proportions of acorns of *Quercus mongolica* (QM), *Q. robur* (QRO), and *Q. rubra* (QRU) attacked by all seed-feeding insects (All) and each of the major insect groups (*Curculio*, *Cyllorhynchites*, and moth larvae) at the Beijing Botanical Garden (China) during 2016–2018.

insects in either *Q. rubra* or *Q. robur* was much lower in China than in native continents (North America and/or Europe, Fig. 2b). Moreover, for both *Q. rubra* and *Q. robur*, the infestation by both *Curculio* and acorn moths was also lower when introduced in China than in the native continent (Table S2, Supporting Information). In addition, data from both Europe and China showed that the total infestation rate by insects of *Q. rubra* was lower in the introduced than in the native range (Fig. 2b). By comparison, unlike our results, the proportion of acorns with embryo survival after insect damage was similar between introduced *Q. rubra* and native *Q. robur* in Hungary (Fig. 2a). However, the probability of embryo survival was lower in native sessile *Q. petraea* than in introduced *Q. rubra* (Fig. 2a).

DISCUSSION

To what degree an introduced plant is colonized by native enemies (here insect seed predators) can have large impacts on establishment and invasion success in new regions (Keane & Crawley 2002). Our study provides evidence supporting several hypotheses that are derived from the ERH and help explain ERH at both local and continental scales (Table 2). Common-garden comparisons showed that introduced oaks generally received much lower insect seed predation than native oaks in both China and Europe. Regardless of differences in the major insect groups as oligophages, insect infestation of *Q. rubra* was the lowest among the 3 oak species that we studied. In addition, introduced oaks had lower insect seed
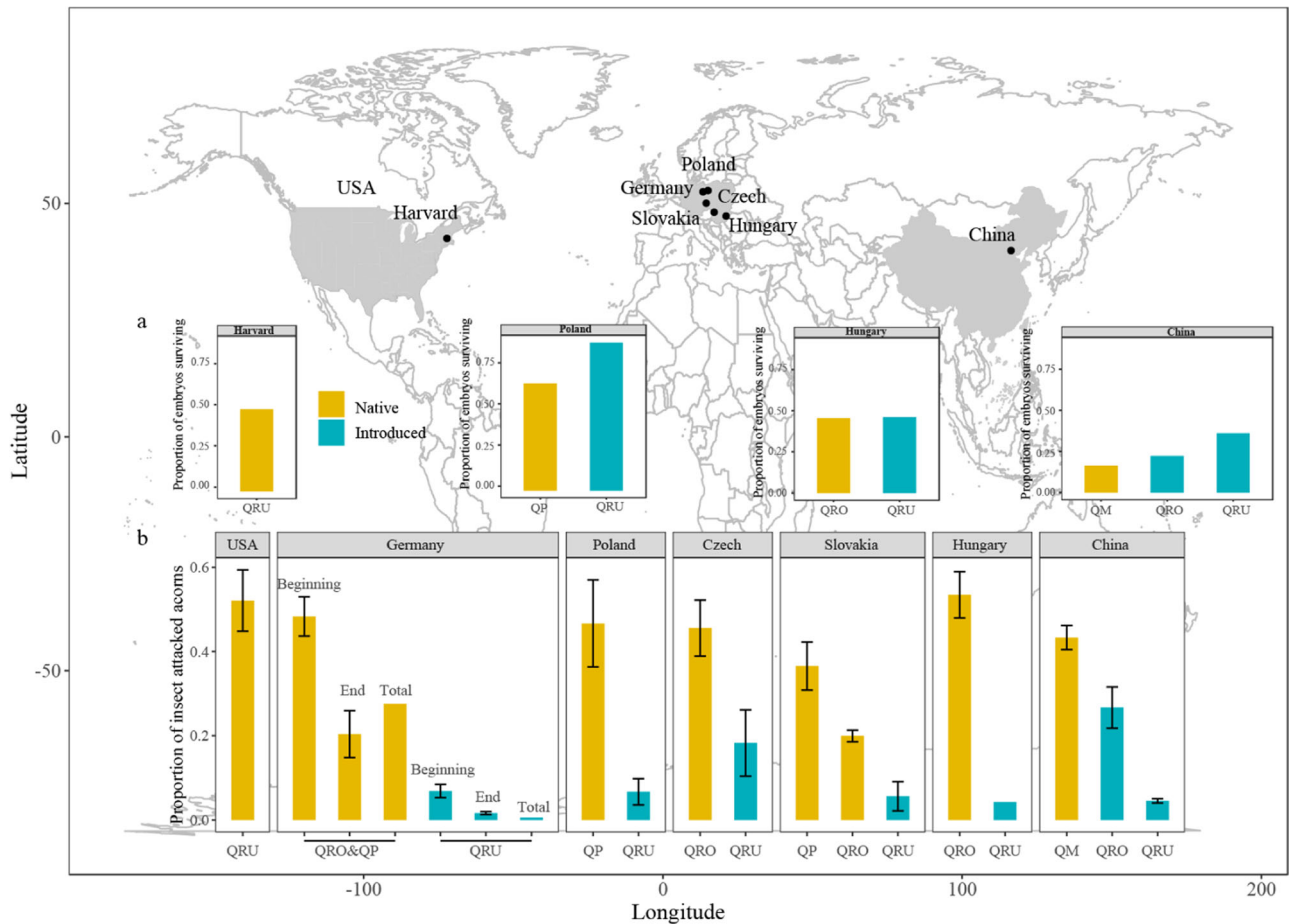
Figure 2 An intercontinental comparison of acorn performance with (a) embryo survival after insect damage (i.e. proportion of infested acorns with intact embryos) and (b) the proportions of acorns attacked by insects (mean ± SE) among *Quercus mongolica* (QM), *Q. robur* (QRO), *Q. petraea* (QP), and *Q. rubra* (QRU) in their native and introduced sites across Asia (China), Europe, and North America. The standard error (SE) was estimated from year and study site combination (i.e. each site in each year as a data point). For the Germany case (Goßner & Simon 2005), "Beginning" and "End" represent at the beginning and end of acorn falling period, respectively, and "Total" is the aggregated data.

predation in the introduced continent than in their native continent. Embryo survival after insect damage was higher in introduced oaks, with more intact embryos of infested acorns in non-native than in native oaks in Beijing but this pattern did not hold in Hungary (Fig. 2). Our continental comparisons with introduced and native oaks indicate that introduced oaks generally received much lower insect seed predation than native oaks and also had higher acorn performance after insect damage. Consequently, introduced oaks may pose a higher invasion risk in non-native continents than in native continents.

Based on our study in China and those in Europe, we found that 2 of 3 insect groups were shared as major seed predators for both introduced and native oaks,

but the composition of major insect groups varied greatly across different oaks and different continents (Table 1; Fig. 2). *Curculio* weevils and *Cydia* moths can attack the acorns of both introduced and native oaks from different continents. Moreover, *Cyllorhynchites* weevils as regional oligophages in China (Asia) can also attack the acorns of both *Q. rubra* from North America and *Q. robur* from Europe. Although some seed-feeding insects may also be introduced species, which could also be "escaping" their natural enemies (such as parasitoids), we did not find any evidence of seed predators belonging to the introduced species at our study site. Our results confirmed that, for the species we were able to examine, all native major insect groups could use acorns with different origins.

One major prediction of the ERH, that introduced oaks have a higher probability to escape natural enemies in non-native continents, was confirmed by our own empirical study in China (Table 2). The common-garden comparison in China and published studies showed that insect seed predation of introduced red oaks was much lower than that of native oaks when comparing the total infestation by all seed-feeding insects or by each major insect group (Table 2; Figs 1, 2). In Central Europe, insect seed predation of native oaks (*Q. robur* or *Q. petraea*) was up to 10 times higher than that of introduced *Q. rubra* (Krístek 1973; Kelbel 1996; Goßner & Simon 2005; Csóka & Hirka 2006; Bogdziewicz *et al*. 2018a). In China, insect seed predation of native *Q. mongolica* (43.3%) was also nearly 10 times higher than that (4.5%) of *Q. rubra*, but insect seed predation (26.7%) of introduced *Q. robur* was intermediate between *Q. rubra* and the native oak, perhaps because *Q. robur* and *Q. mongolica* belong to white oaks (phylogenetic relatedness) and share similar acorn traits (Table 1).

Our data are consistent with another prediction of ERH. Compared to native species, introduced species often show higher performance following enemy damage (Table 2). After insect attack, acorn embryo survival was more frequent for introduced oaks (*Q. rubra* in particular) than for native *Q. mongolica*. Bogdziewicz *et al* (2018a) showed a similar result, that introduced *Q. rubra* in Poland had a higher probability (90%) of embryo survival after infestation than native *Q. petrea* (50%), but the Hungary study showed similar acorn performance after insect attack between introduced *Q. rubra* and native *Q. robur* (Fig. 2; Csóka & Hirka 2006). However, critical evaluation of the ERH requires examining whether the differences in damage, in both seed predation and seed performance after attack, translate into the differences in population and community processes (Keane & Crawley 2002; Chun *et al*. 2010). We should also consider that both embryo survival after insect damage and the extent to which insect-infested acorns germinate and establish as seedlings are essential parts of understanding the advantage of introduced species in escaping natural enemies in non-native regions (Bonal *et al*. 2007; Xiao *et al*. 2007; Perea *et al*. 2011; Bartlow *et al*. 2018). Thus, further studies of the post-seed-attack components of nonnative tree establishment are needed.

Besides the predictions mentioned above, the ERH is relevant to forecasting whether and to what extent introduced species escape from natural enemies in non-native regions in contrast to their native regions. In native North America, total insect predation of *Q. rubra* can be high (up to 35–62%) with 37–48% of weevil infesta-tion of and 2–12% of moth infestation (recent survey from Bogdziewicz *et al*. 2018a; see also Gibson 1982). After introduction to Europe in 1700, insect seed predation of *Q. rubra* was much lower (<12.6%) than in North America, and infestation rate of *Q. rubra* acorns showed the same pattern in China compared to that in North America (Fig. 2b). In this study, insect seed predation of *Q. robur* was much lower after introduced into China than that in its native Europe (Fig. 2b). Therefore, both European and Chinese data mostly confirmed our hypothesis that the total infestation rate of introduced oaks was lower in non-native continents than that in their native continents (Table 2).

In general, ecological similarity, functional similarity and evolutionary history are frequently used to predict the novel interactions between introduced species and native insects (Pearse *et al*. 2013). Closely related (e.g. congeneric or sister species) plant species are often similar in morphology, phenology, biochemistry, and phylogeny, and thus introduced species may be rapidly used as new hosts by native generalists and specialists when congeneric native plants are present (Pearse & Hipp 2009; Ness *et al*. 2011; Bezemer *et al*. 2014; Sunny *et al*. 2015). We found several potential mechanisms based on the ERH that help explain how introduced (invasive) oaks escape seed predation by native insects in non-native continents (Table 2):

1. Shared insect groups and their reduced seed predation in *Q. rubra* after introduction to either Europe or China can likely be predicted by their taxonomy (or phylogenetic relatedness, Pearse & Hipp 2009). Among the 3 oak species used in this study, *Q. rubra* belongs to section *Lobatae* (only occurring in North America), and the other 2 oaks belong to section *Quercus* with a worldwide distribution (Table 1). Several major insect groups such as *Curculio* and *Cydia* have evolved and spread to have a worldwide distribution and have also been shared by all oak groups or species from different continents, and although different oak groups and their insect seed predators may contain quite different species, the plants and insects often have similar traits and life history in different continents (Table 1). In this study, we found that *Cyllorhynchites* weevils, as regional oligophages in China (Asia), can attack the acorns of both *Q. rubra* from North America and *Q. robur* from Europe, which they attack at a lower rate. Conversely, acorn gallwasps (strict specialists either on section *Cerris* or section *Quercus*) in Europe entirely avoid acorns of introduced *Q. rubra* (Csóka & Hirka 2006). Interestingly, acorn predators do not tend to infest acorns of *Q. rubra* and other red

oak species in parts of the world in which these trees are introduced as taxonomic oddities. However, in regions where members of the red oak group are native, many seed predators do not discriminate between red oaks and other oaks (Bonal *et al*. 2016). This may be the key reason that insect infestation of introduced *Q. rubra* was similar between China and Europe though the introduction time is quite longer in Europe.

2. Native insect seed predators in either Europe or China may have different host plant use and result in variation in performance and fitness of acorn during larval development when introduced oaks are used as host plants. Compared to native oaks in Europe and China, introduced *Q. rubra* produce acorns with higher tannin content and thicker hulls (Table 1), which can effectively defend against attack and reduce the performance by *Curculio* weevils (Bogdziewicz *et al*. 2018a). Compared to *Cydia* moths, however, *Curculio* weevils in Europe are found to have a lower larval survival after laying eggs in *Q. rubra* acorns with higher tannins (Goßner & Gruppe 2004; Bogdziewicz *et al*. 2018a). In Europe (Bogdziewicz *et al*. 2018a) and also China (Z. Xiao, unpublished data), *Q. rubra* acorns grow faster and thus have reduced damage from native insects, than in native North America. Myczko *et al*. (2017) found that *Curculio* larvae spent more time emerging from *Q. rubra* acorns. In addition, the emergence probability of mature larvae from *Q. rubra* acorns was lower in Europe (3%) than that in North America (48%) and over 40% in *Q. petraea* (Bogdziewicz *et al*. 2018a). This suggests that *Q. rubra* may act as an ecological trap for *Curculio* weevils in Europe (Bogdziewicz *et al*. 2018a). In China, we also found that larval survival of both *Cyllorhynchites* and *Curculio* weevils was low in *Q. rubra* compared to that in native oaks (personal observation).

3. Embryo survival of introduced oaks may not be reduced after insect damage to the degree that it is in native oaks. In this study, our common-garden survey showed that compared to native *Q. mongolica*, introduced *Q. rubra* acorns had a higher probability of embryo survival after insect infestation, followed by *Q. robur* acorns (Fig. 2a). Both *Q. rubra* and *Q. robur* produce larger acorns than *Q. mongolica* (Table 1) that can tolerate partial consumption, germinate, and emerge as seedlings with a higher probability (Perea *et al*. 2011; Bartlow *et al*. 2018). Therefore, seedling establishment from these partially-damaged acorns could act as another important mechanism for improved regeneration of these introduced oaks in non-native continents (Bartlow *et al*. 2018).

4. Though the time of introduction was earlier (over 200 y) in Central Europe (invaded continent) than in China (approx. 40 y), insect infestation of *Q. rubra* was similar in both continents. This is not consistent with our prediction (Table 2).

CONCLUSIONS

In conclusion, our study showed that on introduced oaks in China and Europe, there is reduced acorn attack by native insects and enhanced acorn performance after insect damage. Our results suggest that reduced insect infestation of introduced oaks may increase the potential for these oak species to invade new regions, for example, introduced *Q. rubra* have become invasive in Central Europe (Woziwoda *et al*. 2014). Though our study extended the intercontinental comparison between introduced and native oaks in Asia (China), our literature survey indicates only 5 matched cases in Europe (but no additional cases in North America, where many oak species have also been introduced, Pearse & Hipp 2009) (Table S2, Supporting Information). Moreover, the research on insect seed predation of alien plants with relatively long time (e.g. several or more years) to produce viable seeds would be further limited when common-garden experiments are performed. Most importantly, our intercontinental study is one key step for highlighting global oak introduction and their consequences in relation to native oaks and native animals after introduced or even invasion into other continents. Since large plantations of introduced oaks occur worldwide, and they share seed predators and dispersal agents with native oaks (Vander Wall 2001; Bogdziewicz *et al*. 2019), other studies are needed to elucidate the invasion risks of alien oak species and their potential impacts on native communities and ecosystems in a non-native world.

CONFLICT OF INTEREST

The authors declare no conflict of interests.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 The distribution of all tree individuals and sampled individuals of *Quercus mongolica*, *Q. robur*, and *Q. rubra* at the Beijing Botanical Garden, China. The numbers in the figure are tree IDs.

Table S1 Summary of post-hoc multiple comparisons between the three oak species *Quercus mongolica* (QM), *Q. robur* (QRO), and *Q. rubra* (QRU) after GLMM test in Beijing Botanical Garden, China

Table S2 Summary of acorn infestations, embryo survival (i.e. proportion of infested acorns with intact embryos) after insect damage in *Quercus mongolica* (QM), *Q. robur* (QRO), *Q. petraea* (QP), and *Q. rubra* (QRU) in their native and introduced sites across Asia (China), Europe and North America (see also Fig. 2)

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