

Greater phylogenetic distance from native oaks predicts escape from insect leaf herbivores by non-native oak saplings

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PREMISE: Non-native plant species have been hypothesized to experience lower herbivory in novel environments as a function of their phylogenetic distance from native plant species. Although recent work has found support for this prediction, the plant traits responsible for such patterns have been largely overlooked.

METHODS: In a common garden experiment in northwestern Spain, we tested whether oak species (*Quercus* spp.) not native to this region that are phylogenetically more distantly related to native species exhibit less insect leaf herbivory. In addition, we also investigated plant traits potentially correlated with any such effect of phylogenetic distance.

RESULTS: As expected, phylogenetic distance from native species negatively predicted insect leaf herbivory on non-native oaks. In addition, we found that the leaf traits, namely phosphorus and condensed tannins, were significantly associated with herbivory, suggesting that they are associated with the effect of phylogenetic distance on leaf herbivory on non-native oak species.

CONCLUSIONS: This study contributes to a better understanding of how evolutionary relationships (relatedness) between native and non-native plant species determine the latter's success in novel environments via locally shared enemies, and encourages more work investigating the plant traits that mediate the effects of phylogenetic distance on enemy escape.

KEY WORDS enemy release; Fagaceae; herbivory; nutrients; phenolic compounds; plant defense; *Quercus*; temperate biome.

Non-native plants are introduced either purposefully or accidentally into new areas that have not been historically part of their native range and may, in some cases, become invasive (Prinzing et al., 2002; Maron et al., 2004). The success of non-native plants in novel environments and their propensity to become invasive have been frequently linked to their resistance against native herbivores (Maron and Vilà, 2001; Rogers and Siemann, 2004; Pearse and Altermatt, 2013). The enemy release hypothesis posits that the success of non-native plants is promoted by the absence of co-evolved herbivores in novel sites (Keane and Crawley, 2002). At the same time, native herbivores also feed on non-native plants and can reduce plant colonization success and thus influence population expansion of the introduced plant species (Levine, 2000; Parker et al., 2006; Orians and Ward, 2010; Branco et al., 2015). Accordingly, a robust assessment of the ecological and evolutionary factors that

determine the degree of release of plant species from local herbivores in non-native ranges can provide insight into the mechanisms underlying enemy escape and the invasion potential of introduced non-native plants.

A proposed predictor of enemy escape in non-native species is functional similarity (i.e., redundancy) or phylogenetic relatedness (Funk et al., 2008). According to Darwin's naturalization hypothesis, phylogenetic distance of alien species relative to native residents predicts invasion success (Duncan and Williams, 2002; Feng et al., 2019): the greater the phylogenetic distance, the more likely the success. In the case of plants, evidence is mounting that non-native species are subject to less herbivory in new environments when they are phylogenetically more distant from local native plants (e.g., Pearse and Hipp, 2009, 2014; Hill and Kotanen, 2010; Vialatte et al., 2010; Ness et al., 2011; Yguel et al., 2011). Current empirical work

provides good support for phylogenetic distance as a predictor of enemy escape in non-native plants. For example, Pearse and Hipp (2009) found that mature trees of non-native oak species that were more closely related to local oaks suffered greater damage by leaf-chewing insects at the University of California–Davis Arboretum (see also Pearse and Hipp, 2014). In addition, non-native oaks with leaf traits that had greater overall similarity to those of local oaks also received higher chewing damage (Pearse and Hipp, 2009). Yet, except for these two previous studies, the plant traits underlying the effects of phylogenetic distance from native plants on patterns of enemy attack on non-natives have usually been overlooked.

In this study, we investigated whether phylogenetic distance between native and non-native oak species (*Quercus* spp.) influences patterns of insect leaf herbivory on saplings of non-native oak species. In addition, we further investigated whether leaf chemical defenses (phenolic compounds) and nutritional traits (phosphorus and nitrogen) underlie any such effect of phylogenetic distance. Our study builds from that of Pearse and Hipp (2009) in several ways. First, we include both New World and Old World oak species and thereby provide an extended “inter-continental” test of enemy escape in oaks. Second, we tested for enemy escape using immature oaks (saplings) for which enemy escape patterns may vary relative to adults given differences in size influencing risk of attack and leaf traits affecting palatability. To this end, we tested 3-year-old saplings belonging to four local native oak species and 19 non-native oak species in a common garden field experiment (Fig. 1). By measuring herbivore effects on saplings, a crucial life stage for subsequent plant survival and establishment in trees, we can better understand

how antagonistic interactions shape invasion success of non-native, long-lived plants in novel environments. More broadly, this study provides insights into how evolutionary relationships (relatedness) between native and non-native plants determine the non-natives’ success in novel environments via locally shared herbivores.

MATERIALS AND METHODS

Field experiment

In September 2016, we planted 1-year-old plants (purchased from Planfor nursery, Uchacq-et-Parentis, France) of 23 species of the genus *Quercus* (Fagaceae) in a common garden experiment in northwestern Spain (42°24′20″N, 8°38′51″W). Four of these species [*Quercus robur* L., *Q. petraea* (Matt.) Liebl., *Q. suber* L., and *Q. pyrenaica* Willd.] were local natives found within a 200-km-wide belt in the study region and naturally co-occur in forests of northwestern Spain (Fig. 1). Nineteen of these species were non-native to the study region and distributed in other parts of Europe including Spain (*Q. ilex* L., *Q. faginea* Lam., *Q. pubescens* Willd., *Q. coccifera* L., *Q. frainetto* Ten., and *Q. cerris* L.), North America (*Q. bicolor* Willd., *Q. agrifolia* Née, *Q. macrocarpa* Michx., *Q. coccinea* Münchh., *Q. rubra* L., *Q. shumardii* Buckley, *Q. palustris* Münchh., *Q. nigra* L., *Q. texana* Buckley, *Q. velutina* Lam., and *Q. phellos* L.), or Asia (*Q. serrata* Murray and *Q. phillyraeoides* A.Gray) (Fig. 1). The common garden consisted of a completely randomized design, where we planted 3–8 plants per species (except for *Q. robur* and *Q.*

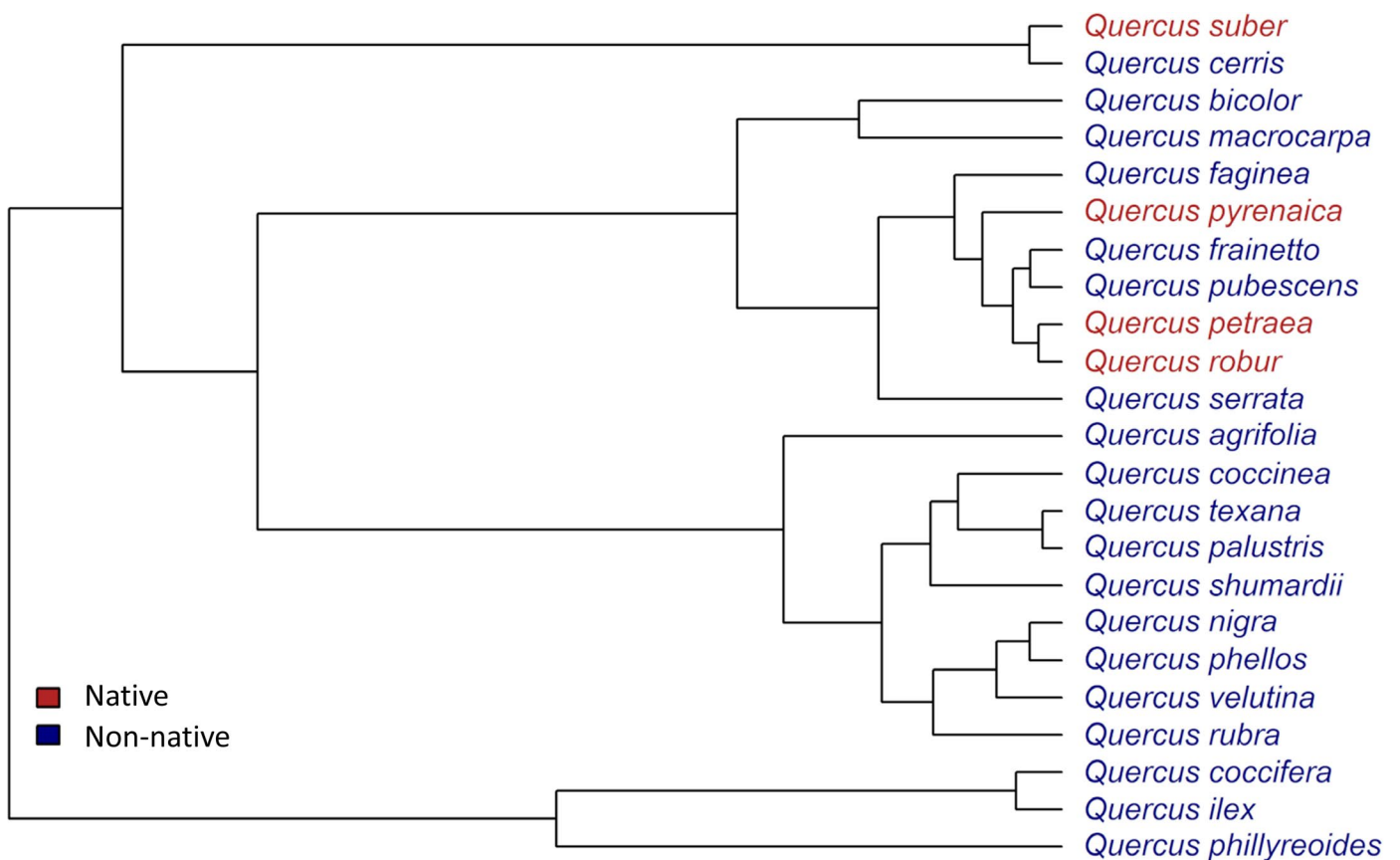


FIGURE 1. Phylogenetic tree of the studied *Quercus* species based on single nucleotide polymorphism matrices generated by ddRAD sequencing.

rubra with 27 and 22 plants, respectively), for a total of 162 plants (Appendix S1). Distance among plants was 2 m. Surrounding vegetation to the common garden was composed mainly of maritime pines (*Pinus pinaster* Aiton), Tasmanian bluegums (*Eucalyptus globulus* Labill.), and pedunculate oaks (*Q. robur* L.).

Description of herbivore species

At our field site, oak species are attacked by several species of native insect leaf chewers such as *Tortrix viridana* L. (Lepidoptera: Tortricidae), *Lymantria dispar* L. (Hemiptera: Lymantridae), *Malacosoma neustria* L. (Lepidoptera: Lasiocampidae), and *Altica quercetorum* Foudras (Coleoptera: Chrysomelidae) (Abdala-Roberts et al., 2016; Moreira et al., 2017, 2018a). The first three species occur locally, but can be found throughout Europe and are reported to attack both local native oaks and European oaks not native to northwestern Spain included in this study (Tack et al., 2010; Giffard et al., 2012). *Altica quercetorum*, on the other hand, is mainly restricted to southwestern Europe (Fernández de Ana et al., 1996); therefore, some of the studied European oaks not native to the study region are not exposed to this herbivore in their native ranges. All these herbivores have negative consequences for oak fitness such as loss of radial growth (Naidoo and Lechowicz, 2001) and reduced acorn production (Selås, 2003).

Measurement of leaf herbivory

At the end of the growing season (September 2018), when average plant height was 73.1 ± 3.8 cm, we estimated the percentage of total leaf area damaged by insect leaf-chewers at the whole-plant level by visually assigning each plant to one of the following categories: 0 = undamaged; 1 = 1–5% damaged; 2 = 6–10% damaged; 3 = 11–25% damaged; 4 = 26–50% damaged; 5 = 51–75% damaged; 6 = >75% damaged (“leaf herbivory” hereafter). To avoid biases in herbivory estimates, the same person (X. Moreira) scored all the plants. In addition, previous to assessing herbivory on all plants, we drew a random sample of leaves for which we visually scored leaf damage and subsequently estimated damage using a digitalization software (ImageJ 1.51j8 software, Wayne Rasband, National Institutes of Health, Bethesda, MD, USA). We found a significant positive correlation between visual and digital estimates ($r = 0.85$, $P < 0.001$, $N = 20$), indicating that the visual estimates were reasonable approximations of actual leaf damage. In addition, we used this subsample to subsequently calibrate our visual estimation of leaf herbivory on all plants. Sampling at the end of the growing season was aimed at minimizing phenological differences in herbivory and plant defensive traits among species and provides an assessment of cumulative leaf damage over most of the growing season. It is important to note that oak phenology (estimated as the date when >5% of buds on a tree had broken and green foliage was visible; Pearse et al., 2015) did not significantly affect herbivory ($F_{1,15} = 1.27$, $P = 0.278$), suggesting that phenological variation among species did not strongly influence our assessment of herbivory.

Leaf sampling

In September 2018, immediately after estimating leaf herbivory, we collected four young, fully expanded undamaged leaves of each plant to quantify phenolic compounds and nutrients. We collected leaves toward the end of the growing season rather than at the

beginning because mechanical damage and leaf tissue removal due to sampling would likely affect growth and defense allocation in young plants, especially for saplings of some of the slow-growing species, which usually only had about 10–12 leaves. Leaves were oven-dried for 48 h at 40°C, ground with liquid nitrogen, and stored at room temperature. As for herbivory, oak phenology (estimated as the date when >5% of buds on a tree had broken and green foliage was visible; Pearse et al., 2015) did not significantly affect plant traits (flavonoids: $F_{1,15} = 2.27$, $P = 0.152$; lignins: $F_{1,15} = 2.66$, $P = 0.124$; condensed tannins: $F_{1,15} = 4.07$, $P = 0.062$; hydrolyzable tannins: $F_{1,15} = 4.21$, $P = 0.058$; phosphorus: $F_{1,15} = 1.40$, $P = 0.255$; nitrogen: $F_{1,15} = 0.04$, $P = 0.843$).

Quantification of phenolic compounds

Phenolic compounds have been reported to confer resistance against insect herbivores in *Quercus* species (e.g., against *Operophtera brumata*: Feeny, 1970; *Dichonia aprilina*, *Catocala spona*, *Acrionicta psi*, and *Amphipyra pyramidea*: Roslin and Salminen, 2008; *L. dispar*: Moreira et al., 2018b and Galmán et al., 2019) and therefore represent a suitable proxy for anti-herbivore chemical defense. Phenolic compounds were extracted from 20 mg of dry leaf tissue with 1 mL of 70% v/v methanol in an ultrasonic bath for 15 min, followed by centrifugation (Moreira et al., 2014). To perform the chromatographic analyses we used an Ultra-High-Performance Liquid-Chromatograph (UHPLC Nexera LC-30AD; Shimadzu Corp., Kyoto, Japan) equipped with a Nexera SIL-30AC injector and one SPD-M20A UV/VIS photodiode array detector (see Moreira et al., 2018a for more details of the chromatographic analyses). We quantified flavonoids as rutin equivalents, condensed tannins as catechin equivalents, hydrolyzable tannins as gallic acid equivalents, and lignins as ferulic acid equivalents (Moreira et al., 2018a) using standard curves at 0.25, 0.5, 1, 2, and 5 $\mu\text{g mL}^{-1}$.

Quantification of nutrients

Previous work has reported positive correlations between leaf herbivory and phosphorus and nitrogen content in leaves for several oak species (e.g., Forkner and Hunter, 2000; Eatough Jones et al., 2008; Moreira et al., 2018a). We therefore considered that these traits were good proxies of leaf nutritional status, which can influence herbivore preference and consumption. To quantify these nutrients, we used colorimetric analyses of nitrogen (indophenol blue method) and phosphorus (molybdenum blue method) concentration using a Bio-Rad 650 Microplate Reader (Bio-Rad, Philadelphia, PA, USA) at 650 nm and 700 nm, respectively (Walinga et al., 1995; Moreira et al., 2012).

Molecular analyses

We used two leaves from three additional plants (not used on this experiment and grown under greenhouse conditions) of each species for molecular analyses. We built a phylogenetic tree of *Quercus* species based on single nucleotide polymorphism (SNP) matrices by double-digestion restriction-site-associated DNA (ddRAD) sequencing (Fig. 1). For this, we extracted DNA using the protocol of Pandey and Tamta (2015), purified it using the Isolate II Plant DNA kit (Bioline, London, UK) and quantified it by fluorimetric methods (see Moreira et al., 2018b for more details of the molecular analyses).

We used RAxML v8 software for the phylogenetic reconstruction of the *Quercus* phylogeny based on SNP matrices that included variable sites. We enabled the ascertainment bias correction for the GTRGAMMA model (-m ASC GTRGAMMA) and tested the two types of corrections (-err-corr=lewis and -asc-corr=felsenstein) described by Leaché et al. (2015). We activated the RAxML option for rapid bootstrapping and the number of bootstraps were automatically determined using the option #- autoMRE. Albeit some exceptions, relationships for New World oak species in our phylogenetic tree were in general terms similar to those reported by Hipp et al. (2018) (see Appendix S2).

Statistical analyses

Effect of phylogenetic distance from native oaks on herbivory on non-native oaks and underlying leaf traits—We ran species-level simple regressions (i.e., using species means) to test for a relationship between phylogenetic distance to native species and leaf herbivory for non-native oaks. Following Pearse and Hipp (2014), we used the minimum phylogenetic distance between each non-native oak species and any one local native estimated as the minimum total branch length between such species (hereafter “phylogenetic distance”) (see Appendix S3). In addition, we also ran regressions separately for each leaf nutrient and group of phenolics to assess whether phylogenetic distance between non-native and native species was correlated with plant traits potentially underlying effects of relatedness on enemy attack (see follow-up analyses in next subsection). Previously to these analyses, we ran a multiple regression model testing for the effect of phylogenetic distance to natives and relative frequency of each non-native species on herbivory on non-natives, as variation in relative species densities may affect patterns of herbivory (e.g., via resource concentration or dilution effects; Underwood et al., 2014). This analysis indicated that species’ relative frequency was not significant, and this factor was therefore excluded from the analyses presented in the Results section. We performed all regressions with PROC REG in SAS 9.4 (SAS Institute, Cary, NC, USA) (Littell et al., 2006).

Leaf traits associated with the effect of phylogenetic distance on non-native oak herbivory—Following from the significant effect of phylogenetic distance on herbivory (based on the aforementioned simple regression; see Results), we ran a species-level multiple regression including the effect of phylogenetic distance to native oak species and leaf traits (phenolic compounds and nutrients) potentially associated with the effect of phylogenetic distance on herbivory on non-native oaks. We expected that if leaf traits account for the effect of phylogenetic distance on herbivory, then a significant main effect in the initial simple regression should turn nonsignificant after including leaf traits. Because some leaf traits were significantly correlated (Appendix S4) and strong colinearity between predictor variables may influence ecological analyses, rather than including all leaf traits at once in the multiple regression, we previously selected relevant traits by running a stepwise backward multiple regression including all leaf traits as predictors of herbivory and based on AIC-based model selection. Leaf traits retained in this model were then individually tested in separate multiple regressions including phylogenetic distance. We caution that our assessment of traits associated with herbivory is by no means exhaustive (i.e., other unmeasured traits could be equally or more important) and that these analyses do not test for a causal association between leaf traits and effects of phylogenetic distance. Rather, we view these analyses as tests of leaf trait correlates of phylogenetic distance effects on herbivory and,

as such, provide a preliminary assessment of candidate traits to be addressed more robustly and in more detail under a phylogenetic framework in subsequent work. We performed all multiple regressions with PROC REG in SAS 9.4 (Littell et al., 2006).

RESULTS

Effect of phylogenetic distance on non-native oak herbivory and underlying leaf traits

Following predictions, results from the simple linear regression indicated a significant negative association between phylogenetic

TABLE 1. Results from simple linear regressions testing for the effect of phylogenetic relatedness of non-native relative to native oak species (measured as the minimum phylogenetic distance from each non-native oak to a native oak species) on insect leaf herbivory and the concentration of leaf chemical defenses (flavonoids, lignins, condensed tannins, and hydrolyzable tannins) and nutrients (phosphorus and nitrogen) in non-native oak saplings ($N = 19$ non-native species). β = slope estimator, R^2 = coefficient of determination. Significant P -values ($P < 0.05$) are highlighted in bold face.

Response	Phylogenetic distance		
	β	R^2	P
Leaf herbivory	-0.025	0.233	0.036
Flavonoids	-0.008	0.023	0.535
Lignins	0.016	0.014	0.631
Condensed tannins	-0.071	0.344	0.008
Hydrolyzable tannins	-0.024	0.256	0.027
Phosphorus	-0.021	0.534	<0.001
Nitrogen	-0.010	0.166	0.083

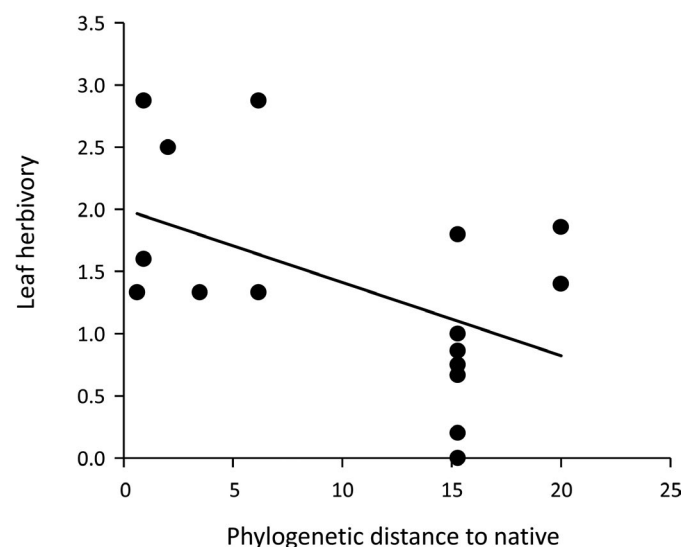


FIGURE 2. Association between minimum phylogenetic distance of non-native oak to native oak species and insect leaf herbivory on non-native oak saplings ($N = 19$ non-native species). Line represents the predicted relationship from the significant ($P < 0.05$) linear regression model (see Table 1 for statistics). Unit for x-axis is pairwise minimum phylogenetic distance between each non-native species and native species (separation $\times 2$).

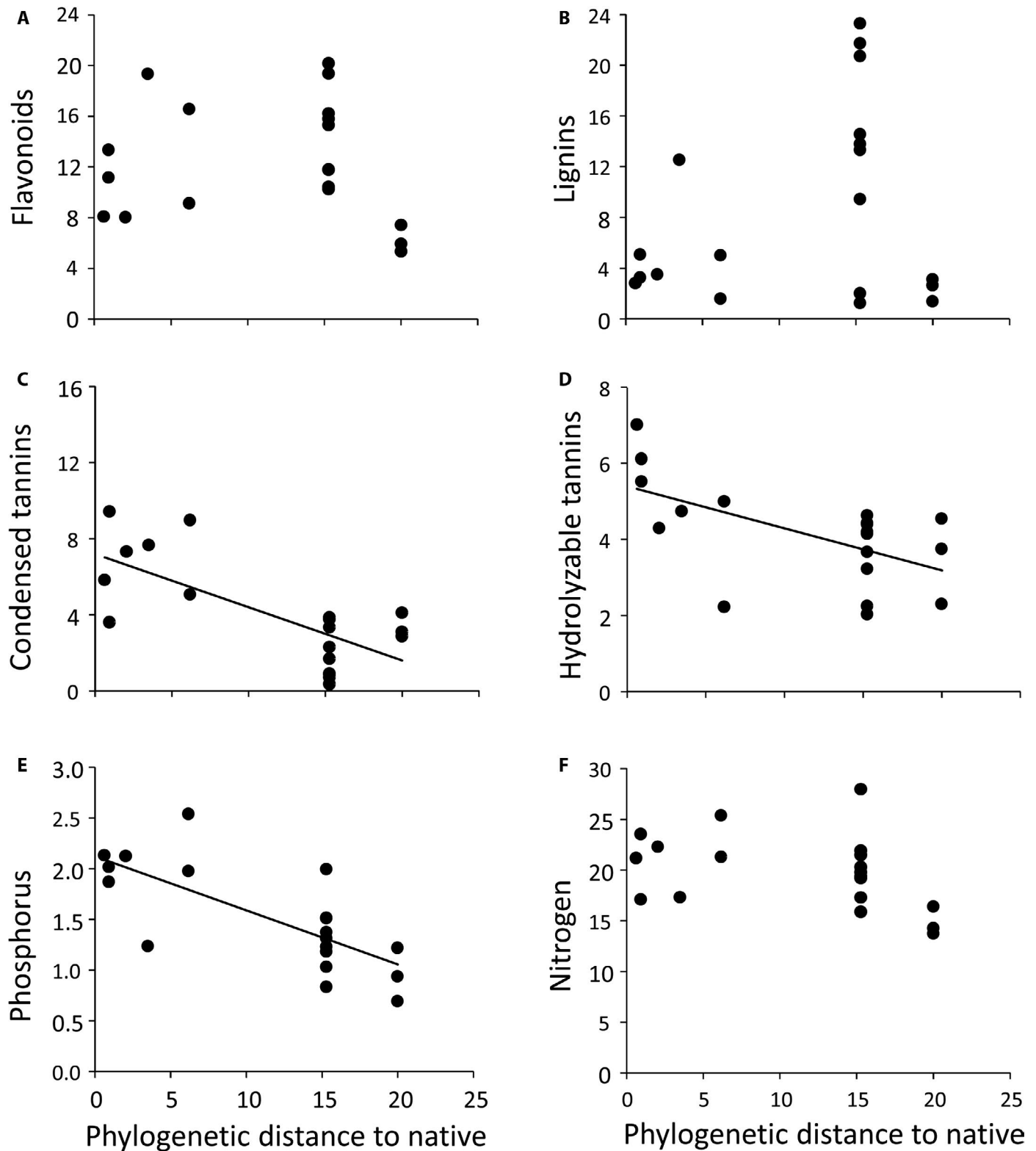


FIGURE 3. Association between minimum phylogenetic distance of non-native oak to native oak species and concentration (in mg g⁻¹ dry mass) of leaf (A) flavonoids, (B) lignins, (C) condensed tannins, (D) hydrolyzable tannins, (E) phosphorus, and (F) nitrogen on non-native oak saplings ($N = 19$ non-native species). Lines represent predicted relationships from significant ($P < 0.05$) linear regression models (see Table 1 for statistics). Unit for x-axis is pairwise minimum phylogenetic distance between each non-native species and native species (separation $\times 2$).

distance to native oaks and non-native oak herbivory (Table 1), i.e., that non-native oaks that are phylogenetically more distant to native species suffered less insect leaf damage (Fig. 2). We found no evidence of spatial autocorrelation (e.g., clustering) of leaf herbivory, but rather leaf damage was homogeneously distributed throughout the study plot (Appendix S5). We also found significant negative associations between non-native to native oak phylogenetic distance and leaf condensed tannins, hydrolyzable tannins, and phosphorus (Table 1, Fig. 3C–E), indicating that non-native oaks that were phylogenetically more distant to natives exhibited lower concentrations of these traits. In contrast, there was no significant association between phylogenetic distance and leaf flavonoids, lignins, or nitrogen (Table 1; Fig. 3A, B, F).

Plant traits associated with the effect of phylogenetic distance on non-native oaks

Leaf flavonoids (slope estimator $\beta = -0.0046 \pm 0.0024$), condensed tannins (slope estimator $\beta = 0.0229 \pm 0.0050$), and phosphorous (slope estimator $\beta = 0.2984 \pm 0.2395$) were retained in the stepwise multiple regression model for herbivory. Follow-up multiple regressions including each trait individually and phylogenetic distance as predictors of herbivory indicated that phylogenetic distance turned nonsignificant after including condensed tannins and also after including phosphorus (Table 2). Both of these leaf traits were positively associated with herbivory, but only condensed tannins had a significant effect in its corresponding model (Table 2).

DISCUSSION

Building from previous work with oaks (see Pearse and Hipp, 2009, 2014), our expanded analyses including both American and European species provided support for the prediction that non-native oaks that are phylogenetically more distantly related to native oak species exhibit lower levels of insect leaf herbivory. In addition, our results also point at plant traits correlated with the effect of phylogenetic distance on insect herbivory on non-native oaks: the effect of phylogenetic distance on herbivory turned nonsignificant after accounting for leaf phosphorus or condensed tannins, suggesting that these traits accounted (at least partly) for the effect of phylogenetic distance on leaf damage. Together, these results point at different underlying traits potentially explaining the effect of phylogenetic distance on enemy escape for the studied non-native oaks.

TABLE 2. Results from multiple regression models testing for the effect of phylogenetic relatedness of non-native relative to native oak species (measured as the minimum phylogenetic distance from each non-native oak to a native oak species) on insect leaf herbivory on non-native oak saplings after including candidate leaf traits presumably underlying such effect (see criteria for trait selection in *statistical analyses*). β = slope estimator, r^2 = partial correlation coefficient. Significant P -values ($P < 0.05$) are highlighted in bold face.

Response	β	r^2	P
Phylogenetic distance	-0.0261	0.286	0.022
Flavonoids	-0.0029	0.150	0.112
Phylogenetic distance	-0.0103	0.060	0.326
Condensed tannins	0.0139	0.588	<0.001
Phylogenetic distance	-0.0093	0.022	0.559
Phosphorus	0.2862	0.101	0.198

Our findings are in line with several previous studies reporting that insect herbivory on non-native plants is a function of their phylogenetic distance to local natives (e.g., Hill and Kotanen, 2010; Ness et al., 2011). In the case of oaks, Pearse and Hipp (2009, 2014) reported that non-native species that are more closely related to a native species received more chewing and mining damage than distantly related oaks in a common garden in the United States. Similarly, Ness et al. (2011) found that herbivore damage decreased with decreasing phylogenetic similarity of focal herbaceous species to native species in two types of communities in North America. Our analyses, however, further point to leaf traits as potentially underlying the effect of phylogenetic distance on non-native oak insect herbivory. Specifically, the effect of phylogenetic distance on herbivory turned nonsignificant after accounting for leaf phosphorus. Although this trait was not significantly associated with herbivory, it has been found to be (positively) associated with herbivory in oaks and other tree species in previous studies (e.g., Zas et al., 2006; Abdala-Roberts et al., 2016). Considering that this trait negatively correlated with phylogenetic distance of non-native to native oaks, our results suggest that leaf phosphorus concentrations underlie the effect of phylogenetic distance on non-native oak insect herbivory. In addition, we also found that the effect of phylogenetic distance on herbivory turned nonsignificant after accounting for leaf condensed tannins. In this case, however, the concentration of these compounds was positively related to insect herbivory suggesting that insect leaf damage drove foliar concentrations of these metabolites (rather than the inverse). Although we took special care to collect leaves with little or no herbivore damage, current or previous damage to other leaves could systemically induce the synthesis of these metabolites and thus explain this positive association. Subsequent work with older plants that are more vigorous and less affected by leaf removal should consider sampling leaves at multiple time points along the growing season (early, mid, and late season) to disentangle the causality of these chemicals in defense–herbivory associations.

Phosphorus concentrations, which are usually present at low concentrations in plant tissue relative to insect nutritional demands (Huberty and Denno, 2006), were recently reported to account for population variation in insect leaf herbivory for *Q. robur* (Abdala-Roberts et al., 2016). Our results therefore suggest that this element could be an important candidate trait to evaluate in further work assessing the influence of plant traits on enemy escape under a phylogenetic framework. Similarly, Pearse and Hipp (2009) reported that leaf physical and chemical defensive traits explained lower damage by chewing (but not mining) insects on non-native American oaks that were phylogenetically more distant to native species. It is important to point out that our results by no means provide evidence for a causal relationship between leaf traits and effects of phylogenetic distance on herbivory. Rather, these tests represent a preliminary assessment of plant traits underlying patterns of enemy escape and point at predictions concerning candidate traits to be tested in future work under a more robust experimental and phylogenetic framework. Including a broader spectrum of plant chemical and physical defenses is also needed in future work to better explain the role of plant traits in mediating phylogenetic distance effects on enemy escape. Finally, while our study provides a more robust experimental design relative to previous studies testing for phylogenetic distance effects on enemy escape in oaks (Pearse and Hipp, 2009, 2014), e.g., by using a randomized design and multiple native species, it is also limited by the use of nursery plants, which may not

be representative of natural variation. Future work should therefore be based on seeds sourced from natural populations and account for intraspecific variation.

Among the non-native oaks to northern Spain that were studied, *Q. rubra* is considered invasive across much of western Europe. Our results therefore provide important information for predicting the success of enemy escape and establishment for this species as well as for other oaks that have already been introduced or in future introductions. Further efforts to measure damage by different insect species or guilds would help to understand how enemy traits and life histories determine enemy escape in present as well as future introductions of non-native oaks. The inclusion of other plant traits associated with other defensive mechanisms such as tolerance (compensatory mechanisms) and induced defenses and tri-trophic interactions (volatiles) is also desirable. In addition, experimental manipulations of the relative effects of different attackers would provide insight into the interactive influences of multiple herbivores. Work addressing the role of species composition and diversity of native plant communities in driving enemy escape would also be valuable, as local patterns may be influenced by associational resistance or susceptibility between native and non-native plants, which ultimately determine invasion success and effects on local native communities. In all of these cases, long-term measurements at multiple sites are necessary to understand how release from herbivores influences seedling establishment, plant growth, and population expansion and, ultimately, invasion dynamics.

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AUTHOR CONTRIBUTIONS

Formulated the idea of the manuscript: X.M. Designed the experiment: X.M., L.A.R. Performed the experiment: X.M., M.E.V. Performed the chemical analyses: X.M., F.C. Contributed reagents/materials/analysis tools: X.M. Analyzed the data: X.M., C.V.G., B.C. Wrote the manuscript: X.M. Contributed critically to the writing: L.A.R., B.C. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

DATA AVAILABILITY

The data used in this study are archived in Appendix S6.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. A 9×24 grid of the common garden field experiment, whereby 3–8 individuals/species were planted in each 2×2 m quadrat.

APPENDIX S2. Comparison between our *Quercus* phylogenetic tree and that of Hipp et al. (2018).

APPENDIX S3. Minimum phylogenetic distance of each non-native oak (*Quercus*) species to each native oak species.

APPENDIX S4. Pearson correlation coefficients from pairwise correlations between leaf traits on non-native oak saplings.

APPENDIX S5. Semivariogram of the residuals after adjusting for main effects in the model for insect leaf herbivory shows the observed semivariance as a function of the distance separating trees.

APPENDIX S6. Dataset used for this study.

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