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Native plant diversity increases herbivory to non-natives

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There is often an inverse relationship between the diversity of a plant community and the invasibility of that community by non-native plants. Native herbivores that colonize novel plants may contribute to diversity–invasibility relationships by limiting the relative success of non-native plants. Here, we show that, in large collections of non-native oak trees at sites across the USA, non-native oaks introduced to regions with greater oak species richness accumulated greater leaf damage than in regions with low oak richness. Underlying this trend was the ability of herbivores to exploit non-native plants that were close relatives to their native host. In diverse oak communities, non-native trees were on average more closely related to native trees and received greater leaf damage than those in depauperate oak communities. Because insect herbivores colonize non-native plants that are similar to their native hosts, in communities with greater native plant diversity, non-natives experience greater herbivory.

1. Introduction

Non-native plants are becoming a common component of most of the world’s ecosystems. One major factor that affects a non-native plant’s success and invasiveness is the degree to which that plant is colonized by native herbivores [1–3]. The enemy release hypothesis states that non-native plants escape their co-evolved herbivores when they are introduced into a new geographical region [4]. Herbivores native to the new range also colonize non-native plants to varying degrees [3,5–7], and their damage may in some cases reduce the fitness of non-native hosts and negate the effects of enemy release [2,8].

The colonization of a non-native plant by local herbivores is a function of the match between local herbivores and potential non-native hosts [3,6]. One strong indicator of the suitability of a non-native plant for native herbivores is the phylogenetic relationship between the non-native plant and local plants that already host herbivores [5]. In several documented cases, this leads to a trend where non-native plants that are more distantly related to native flora tend to escape herbivory from native insects [9–12]. In other cases, especially when herbivory caused by generalist herbivores is assayed, particular plant traits affect herbivory to the non-native plant more than phylogenetic relatedness to a native plant [13]. Replicated studies that survey herbivory to non-native plants in the context of different native plant and herbivore communities are necessary to understand the variation in the relationship between non-native plant phylogenetic position and herbivory.

While herbivores are one aspect of biological communities that may impart resistance to plant invasions, plant diversity is another [1]. For example, in grassland systems, both the species richness and evenness of native plant communities can limit the success of the most aggressive invasive plants [14,15]. Mechanistically, competition for limited resources, niche-filling and pathogen load are typically presumed to be the mechanisms linking diversity to invasion resistance in plant communities [16–18]. Herbivory could also link plant diversity to invasion resistance because diverse plant communities contain more types of herbivores [19]; however, this mechanism is poorly explored.
We investigated the relationship between plant phylogenetic relatedness, native plant diversity and herbivore damage to non-native plants by surveying non-native oaks (*Quercus* and *Notholithocarpus*) in arboreta replicated across the USA as a biogeographically replicated experiment (figure 1a). Each arboretum served as a common garden containing a unique composition of non-native oak species from around the Northern Hemisphere, ranging from 18 to 55 non-native oak species. The region surrounding each garden likewise contained a unique composition and species richness of native oak species (figure 1b). We estimated the phylogenetic relationships between native and non-native oak species in this study using a supertree (figure 1b) based largely on a recent, well-supported oak phylogeny [9] and used this phylogeny to conduct comparisons of damage to oak species. Our hypotheses were that: (i) non-native oak species with close native relatives would experience higher levels of herbivory, and (ii) non-native oaks would experience higher levels of herbivory in regions with greater native oak species richness.

### 2. Material and methods

**(a) Sites, natural history and damage surveys**

Oak species are commonly planted outside of their ranges for horticultural purposes, especially in taxonomic collections at arboreta. We selected eight arboreta across the USA based on the size of their collections, the maturity of trees, semi-natural settings and unique geographical locality (electronic supplementary material, table S1). None of the oak collections had been treated for herbivores within the institutional memory of employees at each site, corresponding to at least 5 years prior to the survey. Mean annual temperature and rainfall for each site were estimated as 10-year averages from the nearest weather station (electronic supplementary material, table S1). Water balance was estimated for each site as precipitation (mm) — potential evapotranspiration (mm), derived from Thornthwaite’s equation [20]. The number and identity of native oaks with a 20 km of each site was determined from range maps of North American oak trees [21,22] and assembled locality records [23]. The number and identity of native non-oak trees was estimated from county records using the USDA PLANTS database [22]. Presence of a non-oak tree was recorded if the tree occurred within the county of the arboretum site, except for two sites (UWBG and SA), which occur in small, urban counties. In these cases, surrounding counties were used. Subspecies and hybrids were excluded from these estimates and from oak surveys, owing to inconsistencies in their reporting in the literature. We could not be sure of the age of each tree in the survey, but all trees were at the sapling or adult (acorn-bearing) stage. At each site, an oak species was represented by one to six individual trees. Both native and non-native oak species were sampled at each arboretum. Each arboretum contained representatives of its local natives.

We estimated the per cent leaf damage of 20 randomly chosen leaves on each tree according to Pearse & Hipp [9]. Leaves were selected at a height of 1.5–6 m in the canopy, except in a few shrubby oak species/individuals that were under 1.5 m in height. We selected leaves by standing at five locations around the base of the tree and sighting along a haphazardly aimed fixed point four times. The first leaf visually intersecting that point was chosen. Per cent area removed from each leaf was estimated and recorded. Per cent leaf damage was averaged by tree and then by tree species at each site.

**Figure 1. A description of non-native oak sites. (a) Leaf damage was surveyed on oaks at eight sites across the USA. (b) Each site contained 27–57 oak species, where 1–11 of those oak species were native (blue lines) and the remainder were non-native (red lines). We estimated the evolutionary relationships among these oak species using a supertree based on a recent oak phylogeny [9].** (Online version in colour.)

**(b) Oak phylogeny**

The phylogeny used in this study uses the amplified fragment length polymorphism (AFLP) phylogeny of Pearse & Hipp [9] as a starting tree. Because of the tendency for AFLP phylogenies to exhibit long terminal branches, the minimum evolution tree used in that paper back to the most recent common ancestor for each species that possessed at least two individuals per tip. For species with only a single exemplar per tip, tips were pruned to 50% of their original length. The resulting tree was ultrametricized using penalized likelihood with the smoothing parameter set at 0.1 [23]. Taxa for which we did not have AFLP data were attached to this tree as explained in the appendix (electronic supplementary material, table S1). The minimum phylogenetic distance between each non-native tree and any local native was estimated as minimum total branch length between those individuals.

Because the evidence for our supertree phylogeny (Tree 1) was incomplete, we estimated minimum phylogenetic distance to a local native using four alternate phylogenies representing alternate hypotheses of oak relationships. Tree 2 moved the Old World white oaks to an internal node within the white oak section, as suggested by Hipp et al. [24]. Tree 3 collapsed all nodes internal to well-accepted sectional groupings into polytomies. Tree 4 used the previous highly polytomous phylogeny, but set all terminal branches to approximately half the total tree distance, so that all distances within strongly supported clades were approximately the same. Tree 5 simply removed all species not present in the core phylogeny [9].
In an initial analysis, we asked whether oak species native to a given site experienced greater herbivore damage than non-native oak species. For this, we constructed a linear mixed effects model with site as a random factor and ‘nativeness’ as a fixed predictor of species-level leaf damage estimates. Next, we analysed the relationship between phylogenetic relatedness (minimum phylogenetic distance between a non-native and a local native) and leaf damage to each non-native oak species at each site using a mixed effects model with arboreturn as a random effect. In a separate fixed-effects model, we tested for the significance of an interaction term between site and minimum phylogenetic distance. The interaction between arboretum and phylogenetic relatedness was significant, so we also analysed the relationship between phylogenetic relatedness and leaf damage at each site. Using the four alternate phylogenies described above, we modelled the relationship between minimum phylogenetic distance to a native species and herbivory suffered by each non-native species. The relationship between phylogenetic distance and herbivory was consistent using each phylogeny, so our analyses are robust to inaccuracies in our estimation of oak phylogenetic relationships. Moreover, the fact that our third and fourth alternative trees collapse all well-supported clades suggests that much of the phylogenetic effect we observe in this paper is owing to differences across the deepest divergences in the oak phylogeny. At the arboreturn scale, we calculated the mean leaf damage to all non-native oaks and explored whether that related to the number of oaks at a site, the mean phylogenetic relatedness of non-native oaks to local natives, native tree species richness, phylogenetic diversity (Faith’s) of all oaks (native + non-native), latitude and climate. We calculated Pearson’s correlations between each of these predictors and chewing damage. The number of sites (eight) was too small to assess these correlations in multiple regression framework, so simple correlations are reported. All statistical and phylogenetic analyses were conducted in R v. 3.1.0 using packages ape v. 3.1, nlme v. 3.1 and picante v. 1.6 [25–28].

(c) Statistical analysis

Analyses were conducted at two scales: tree species and arboreturn. At the tree species scale, leaf damage estimates were square-root transformed to meet assumptions of normality. In an initial analysis, we asked whether oak species native to a given site experienced greater herbivore damage than non-native oak species. For this, we constructed a linear mixed effects model with site as a random factor and ‘nativeness’ as a fixed predictor of species-level leaf damage. The inter-effects, we tested for the significance of an interaction term between site and minimum phylogenetic distance. The inter-effects, we tested for the significance of an interaction term with site and minimum phylogenetic distance as fixed effects, we tested for the significance of an interaction term between site and minimum phylogenetic distance. The interaction between arboreturn and phylogenetic relatedness was significant, so we also analysed the relationship between phylogenetic relatedness and leaf damage at each site. Using the four alternate phylogenies described above, we modelled the relationship between minimum phylogenetic distance to a native species and herbivory suffered by each non-native species. The relationship between phylogenetic distance and herbivory was consistent using each phylogeny, so our analyses are robust to inaccuracies in our estimation of oak phylogenetic relationships. Moreover, the fact that our third and fourth alternative trees collapse all well-supported clades suggests that much of the phylogenetic effect we observe in this paper is owing to differences across the deepest divergences in the oak phylogeny. At the arboreturn scale, we calculated the mean leaf damage to all non-native oaks and explored whether that related to the number of oaks at a site, the mean phylogenetic relatedness of non-native oaks to local natives, native tree species richness, phylogenetic diversity (Faith’s) of all oaks (native + non-native), latitude and climate. We calculated Pearson’s correlations between each of these predictors and chewing damage. The number of sites (eight) was too small to assess these correlations in multiple regression framework, so simple correlations are reported. All statistical and phylogenetic analyses were conducted in R v. 3.1.0 using packages ape v. 3.1, nlme v. 3.1 and picante v. 1.6 [25–28].

3. Results

In general, non-native oak species accumulated less herbivore damage than native oak species (14.6 ± 1.1% damage native, 6.3 ± 0.3% damage non-native, F = 39.44, p < 0.001), and non-native oak species that were close relatives to local native oaks experienced greater leaf damage than oak species that were distant relatives from any local native (F = 29.65, p < 0.001; figure 2). The strength of the relationship between phylogenetic relatedness and damage depended on the locality in question (F = 2.57, p = 0.014). A negative trend between phylogenetic dissimilarity of natives and non-natives and herbivore damage was apparent at five of the eight gardens that were surveyed, but not in Washington, Colorado, or North Carolina (figure 2; electronic supplementary material, table S3). The relationship between phylogenetic relatedness and herbivory did not depend on the number of non-native oaks in a given garden (F = 0.31, p = 0.575), suggesting that differences among gardens were not due to a difference in statistical power among sites. The relationship between phylogenetic relatedness and herbivory was unaffected by alternative plausible resolutions of the oak phylogeny, suggesting that our results are robust to phylogenetic uncertainty (electronic supplementary material, table S4).

We used the differences in native oak communities at our sites across the USA to test whether there was a relationship between the species richness of a native plant clade and herbivore pressure to non-native plants of the same clade (figure 3a). We found that in regions with higher oak species richness, the overall damage to non-native oaks was greater than in areas with lower oak species richness (figure 3b). As a cause of this, we hypothesized that the effect of plant species richness on herbivore pressure to non-natives was mediated by plant phylogenetic relationships (figure 3a). In a diverse plant community, a given non-native plant will be more likely to be a close relative of a local native than the same plant would be in a depauperate native plant community. In support of this hypothesis, we found that the average
Figure 3. Relationship between native species richness and damage to non-native oak species. (a) The hypothesized connection between oak richness and herbivore damage. (b)(i) A positive correlation between native oak richness and herbivore damage to non-native oaks at eight sites across North America. (ii) A negative correlation between the mean phylogenetic distance between the native oaks and non-native oaks at each site and the herbivore damage at that site. Bars (vertical and horizontal) are mean ± s.e. (Online version in colour.)

4. Discussion

Our study demonstrates that phylogenetic distance between native and non-native plants influences two important components of herbivory experienced by non-native plants: (i) how herbivores interact with non-native tree species at a local site, and (ii) at a larger scale, how plant diversity relates to levels of herbivory to non-native plants. Several studies at single sites or regions have found that phylogenetic distance from a local native is a strong predictor of damage to a non-native plant [9–12]. This study shows that over many sites, there is generally a relationship between phylogenetic distance from a native and herbivory. However, at some localities, this relationship was not found. This is expected if there is variation in the composition of herbivore communities such that some communities are dominated by specialist feeders that have a strong phylogenetically defined host breadth, and other herbivore communities are dominated by generalist herbivores that may not strongly discriminate between plants within the same genus or family. Alternatively, the relative abundance of native hosts could be an important factor in predicting damage to non-natives, especially at sites like North Carolina with many native species. In these cases, most non-natives tend to have a close native relative, but rare native relatives may contribute fewer herbivores than abundant native relatives. In general, our results may help to explain observed patterns in native oak communities that exhibit phylogenetic evenness, a pattern where close relatives rarely co-occur [29].

We suggest that the relationship between tree diversity and herbivore pressure may be determined by the overlap between host-breadths of herbivores, such that diverse host plant communities are likely to contain more herbivores that could consume a novel plant. Our study shows that in plant communities with high oak diversity, non-native oaks experienced greater herbivore damage than in more...
If the relationship between plant diversity and invasibility is mediated by herbivores, non-native plants must experience greater herbivore damage when introduced into diverse plant communities, and this damage must translate into substantial population-level fitness costs to the non-natives. Our study suggests that in oak communities, the first of these conditions is met, and herbivores may in part mediate diversity–invasibility correlations. While relatively low levels of leaf-feeding insects can negatively affect fitness in at least some native oak species [30–32], it is unclear to what degree herbivores limit the fitness of non-native oaks.

In native plant communities, the diversity of non-hosts can have opposing effects on herbivore pressure. For example, when the overall phylogenetic diversity of plant communities was considered, the presence of non-hosts in a community (which also increases overall plant diversity) decreased herbivore outbreaks on a focal plant species [33], probably because the presence of non-host odours or visual cues made it harder for herbivores to locate their hosts [34]. In our study, the total tree species richness, beyond oaks, communities was considered, the presence of non-hosts in a community (which also increases overall plant diversity) decreased herbivore outbreaks on a focal plant species [33], probably because the presence of non-host odours or visual cues made it harder for herbivores to locate their hosts [34].

As non-native plants become an ever greater component of the world’s ecosystems, it is increasingly important to understand how non-native plants fit into existing communities. The ability of native herbivores to consume a non-native plant is one large determinant of that plant’s success and its consequences for the novel community [1,3,35]. We show that evolutionary relationships between native and non-native plants shape not only the herbivory experienced by a non-native plant, but also the relationship between plant diversity and damage to non-natives, which may lead to differences in invasibility. These findings implicate herbivores as one important driver of diversity–invasibility relationships and may help to explain why some plant communities resist invaders while others are easily dominated by them.

Data accessibility. All ecological data in this study as well as R analytical code is available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.5b6t7.


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