

Arthropod Associations Show Naturalization with Non-Native *Quercus* Species in the Georgia Piedmont¹

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Abstract Native plants may coevolve with native arthropods and may be associated with greater arthropod diversity than non-native plants. Thompson Mills Forest, a state arboretum owned by the University of Georgia and located in Braselton, GA, is home to a variety of oak (*Quercus* L., Fagaceae) species, both native and non-native to Georgia. Arthropods were sampled from 20 trees belonging to 12 species, 8 native and 4 non-native, using beat sheets for 10 consecutive weeks in 2018. More than 500 arthropods were collected, with Coleoptera, Araneae, and Psocodea comprising more than 70% of the arthropods collected. Neither abundance nor Shannon index varied among trees of native or non-native origin or among tree species, although both variables peaked during the middle of the sampling period. Multivariate analyses showed similar arthropod communities were associated with native and non-native oaks. The results suggest that non-native plants may naturalize and, if so, may interact with arthropod communities in similar ways as native congeners. Further research into the long-term ecological interactions with non-native plants is recommended.

Key Words community ecology, exotic species, herbivory, naturalize, oak

Native plants, for example, those that have evolved in an area and existed there for thousands of years, have coevolved with the communities around them and play vital roles in their ecosystems. Non-native plants, those that have established more recently, have often established as a result of human activities (Vitousek et al. 1997). Non-native plants may be associated with reduced biodiversity and population sizes of not only plants but also the communities that rely on plants either directly or indirectly (Mooney and Cleland 2001, Narango et al. 2018, Schlaepfer et al. 2005). Non-native species that have a detrimental effect on their surrounding communities and ecosystems are defined as invasive species (NISIC 1999). Invasive species are considered the second-most important threat to biodiversity, following habitat loss (Bellard et al. 2016, Wilcove et al. 1998).

Generally, native plants are associated with greater values of ecosystem services (Stein et al. 2014). Much literature has clearly associated native plant diversity with arthropod diversity and ecosystem services in a variety of terrestrial habitats such as agroecosystems (Fiedler and Landis 2007, Isaacs et al. 2008), forests (Fickensher et al. 2014), and urban ecosystems (Ballard et al. 2013). Native plants function as food sources, habitats, and pollination partners for arthropods

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(Sunny et al. 2015). Conversely, non-native plants may provide fewer services for arthropods and thus may be less supportive of arthropod diversity (Bezemer et al. 2014, Cappuccino and Carpenter 2005, Grunzweig et al. 2015, Hanula and Horn 2011, Litt et al. 2014, Spafford et al. 2013, Southwood et al. 1982, Vila et al. 2011). Non-native plants may, however, support arthropods more as they naturalize over time (Harvey et al. 2013, Keeler and Chew 2008).

Oaks, *Quercus* spp. L., are known to be exceptionally supportive of arthropod diversity (Southwood et al. 2005, Tovar-Sanchez 2009), with North American native species alone supporting more than 550 lepidopteran species (Tallamy and Shropshire 2009). Because oaks are popular ornamental trees, several exotic species are cultivated in the United States, some of which have escaped cultivation (Coblentz 1981). These non-native species may associate with arthropods in unknown ways. Previous research has demonstrated that herbivorous arthropods may be more abundant on native oak species compared with exotic oak species (Southwood et al. 2004, 2005). The ecology and evolution of oak trees and arthropods is also of interest because of the extensive hybridization and introgression in the genus *Quercus* (Curtu et al. 2007, McVay et al. 2007).

Here, our objective was to determine whether abundance and diversity of arthropod component communities associated with oak trees were influenced by native or non-native origin of those trees. We hypothesized that oak species native to the southeastern U.S. Piedmont ecoregion coevolved with local arthropods and were able to support greater arthropod populations and diversity. We predicted that more arthropods would be collected from trees belonging to native species compared to non-native species and that arthropod diversity indices would be greater for component communities collected from native oak species.

Materials and Methods

Study site. Thompson Mills Forest (TMF), located in Jackson Co., Georgia, USA, is the State Arboretum of Georgia. The TMF arboretum is located near the ecotones of the Inner Piedmont, which is dominated by oak-pine and oak-hickory forests, and the Outer Piedmont, which is dominated by loblolly-shortleaf pine forests. The TMF arboretum is surrounded by 133.5 ha of forests and cattle-grazed grasslands, mostly owned by the University of Georgia and a private owner. More than 20 *Quercus* spp., both native and non-native to the Georgia Piedmont, are planted at TMF. Twenty trees were identified, 9 of which belonged to 6 non-native species and 11 of which belonged to 6 native species (Table 1). Based on the location of the TMF arboretum, we defined “native” as trees with a geographic range that included the Georgia Piedmont according to the U.S. Department of Agriculture PLANTS database (<https://plants.sc.egov.usda.gov/java/>; accessed 10 September 2021), and “non-native” as any tree that is not found naturally in the Georgia Piedmont. By this definition, two species that are found in other Georgia ecoregions (*Q. virginiana* Miller and *Q. myrtifolia* Willdenow, both found in coastal plains) were considered non-native. The only species listed by the Georgia Exotic Pest Council (<https://www.gaeppc.org/list/>; accessed 10 September 2021) was *Q. acutissima* Carruthers, which is considered Category 4: exotic, naturalized plant generally not considered a pest.

Table 1. List of tree species growing in the Georgia State Arboretum that were sampled.

Species	Origin	Range	Number of Trees
<i>Quercus georgiana</i>	Native	Georgia, Alabama, South Carolina Piedmont	2
<i>Q. lyrata</i>	Native	Southeastern United States, widespread	2
<i>Q. michauxii</i>	Native	Southeastern United States, widespread	2
<i>Q. montana</i>	Native	Eastern United States	2
<i>Q. muehlenbergii</i>	Native	Eastern-Central United States	1
<i>Q. oglethorpensis</i>	Native	Georgia, South Carolina Piedmont	2
<i>Q. acutissima</i>	Non-native	China, Korea, Japan	2
<i>Q. macrocarpa</i>	Non-native	Central United States	2
<i>Q. myrtifolia</i>	Non-native	Southeastern United States, coastal	1
<i>Q. palustris</i>	Non-native	Central United States	2
<i>Q. robur</i>	Non-native	Western Europe	1
<i>Q. virginiana</i>	Non-native	Southeastern United States, coastal	1

Quercus myrtifolia and *Q. virginiana*, both found in Georgia, were treated as non-native because both are found in naturally in coastal ecosystems that differ substantially from those in the Piedmont ecoregion where sampling occurred. Each tree was sampled for 10 consecutive weeks.

Sampling. Arboreal arthropods were sampled from the 20 *Quercus* spp. trees for 10 consecutive weeks, from May to July 2018. Samples were collected starting at 0900 hours each Monday. Four limbs from each tree were sampled by striking the limbs four times and catching arthropods with beating sheets (#2840C, BioQuip Products, Inc., Rancho Dominguez, CA), and all arthropods on the sheets were removed with aspirators or forceps and preserved in 70% ethanol. Arthropods were counted and identified to order in the laboratory. Shannon index, using the taxonomic resolution of order, was calculated for each of the 200 samples and calculated using the pooled data for each tree species.

Analysis. The mean number of arthropods collected from each tree was compared between native and non-native trees using a repeated measures general linear model (Quinn and Keough 2002), in which weeks were the repeated measure and origin was the between-subjects factor. The assumption of sphericity was tested using Mauchly's test, and, if violated, we used a Greenhouse-Geisser correction. The repeated-measures general linear model procedure of SPSS v. 23.0

Table 2. Mean (\pm SEM) numbers of arthropods collecting from each sampling bout.

Order	Number	Average per Native <i>Quercus</i> Tree ($n = 11$)	Average per Non-native <i>Quercus</i> Tree ($n = 9$)
Araneae	79	0.47 \pm 0.06	0.30 \pm 0.08
Opiliones	13	0.05 \pm 0.02	0.08 \pm 0.03
Orthoptera	16	0.10 \pm 0.03	0.06 \pm 0.02
Hemiptera	13	0.06 \pm 0.02	0.07 \pm 0.03
Psocodea	48	0.20 \pm 0.05	0.29 \pm 0.06
Coleoptera	268	1.28 \pm 0.17	1.41 \pm 0.22
Lepidoptera	30	0.15 \pm 0.05	0.16 \pm 0.04
Diptera	5	0.03 \pm 0.01	0.02 \pm 0.01
Hymenoptera	37	0.17 \pm 0.05	0.20 \pm 0.07
Total	513	2.55 \pm 0.08	2.58 \pm 0.22

Each tree was sampled for 10 consecutive weeks.

(IBM, Armonk, NY) was used for these analyses. The mean abundance of any arthropod order found on all 12 tree species was compared between native and non-native trees using two-tailed, independent sample *t* tests.

Variation in arthropod abundance and Shannon diversity of each sample were both analyzed using generalized linear models (Quinn and Keough 2002). The distributions of both variables were visualized with frequency histograms to determine how to build models. Abundance was analyzed using a log-linked negative binomial model, and Shannon index was analyzed using a linear distribution. Full factorial models were built in which tree species and week were included. The generalized linear model procedure of SPSS v. 23.0 (IBM) was used for these analyses.

The arthropod community compositions also were compared among the 20 trees. The 10 sets of counts for each of nine arthropod orders were combined and used for a multivariate analysis. Count data were standardized and square-root transformed, and resemblance among tree species was calculated using Bray-Curtis similarity. Resemblance data were analyzed with cluster analysis and nonmetric multidimensional scaling (nMDS) (Gotelli and Ellison 2004). Scatterplots resulting from nMDS were visualized in three dimensions, which reduced stress values by 0.04–0.11. PRIMER 7 (PRIMER-e, Quest Research Limited, Auckland, NZ) was used for this analysis.

Results

A total of 513 arthropods was collected. The three most common orders collected were Coleoptera, Araneae, and Psocodea, which accounted for more than 75% of the arthropods identified (Table 2). The assumption of sphericity was

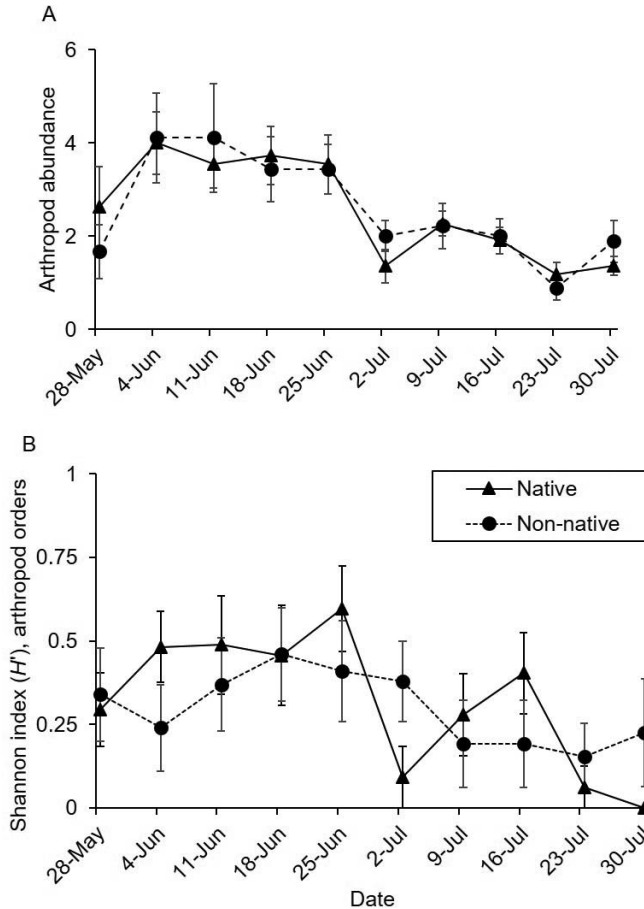


Fig. 1. Mean (\pm SEM) abundance (A) and Shannon diversity (B) of arthropods sampled from native ($n = 11$) and non-native ($n = 9$) *Quercus* trees.

violated ($P < 0.0001$), so the Greenhouse-Geisser correction was applied. The repeated measure of week was significant ($F = 7.34$, $df = 9$, $P < 0.001$), indicating that the mean number of arthropods collected varied from week to week. The factor of origin was not significant ($F = 0.58$, $df = 1$, $P = 0.70$), indicating that the mean number of arthropods collected did not differ between native and non-native tree species. The mean abundance did not differ significantly for any of the nine arthropod orders ($P > 0.05$ for each; Table 2).

Arthropod abundance varied by collection week (Wald $\chi^2 = 24.87$, $df = 9$, $P = 0.003$) but not by tree species (Wald $\chi^2 = 8.96$, $df = 11$, $P = 0.63$). Abundance was higher during the second through fifth weeks (Fig. 1A). Arthropod Shannon diversity varied by collection week (Wald $\chi^2 = 27.53$, $df = 9$, $P = 0.001$) but not by tree species (Wald $\chi^2 = 16.67$, $df = 11$, $P = 0.12$). Shannon diversity was higher during the second through fifth weeks (Fig. 1B).

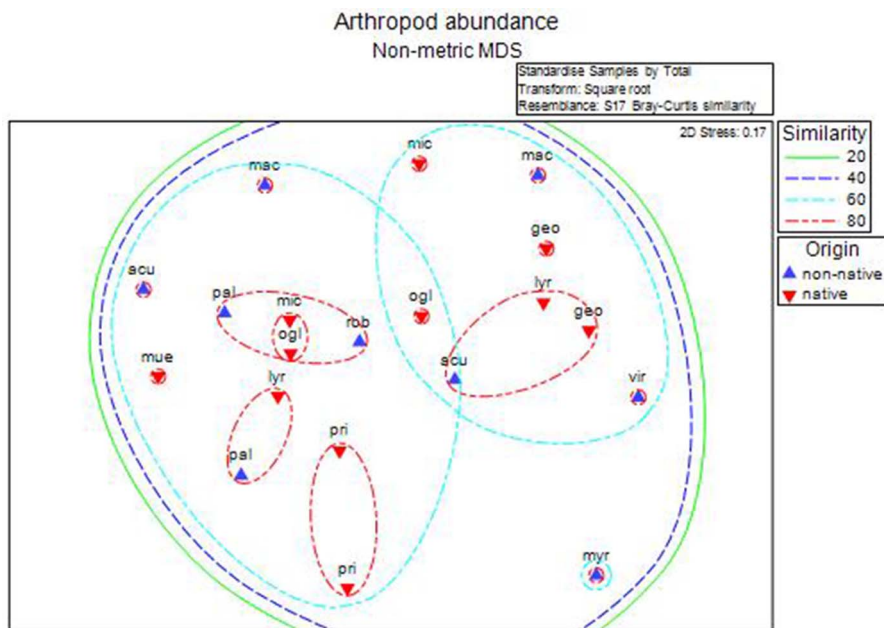


Fig. 2. nMDS comparison of abundance of nine arthropod orders collected from 20 *Quercus* trees, 6 of which are native species and 6 of which are non-native species. acu., *Q. acutissima*; geo, *Q. georgiana*; lyr, *Q. lyrata*; mac, *Q. macrocarpa*; mic, *Q. michauxii*; mue, *Q. muehlenbergii*; myr, *Q. myrtifolia*; pal, *Q. palustris*; ogl, *Q. oglethorpensis*; pri, *Q. prinus*; rob, *Q. robur*; vir, *Q. virginiana*.

Bray-Curtis similarity ranged from 37.11 (non-native *Q. macrocarpa* Michaux and native *Q. prinus* L.) to 92.00 (native *Q. oglethorpensis* Duncan and native *Q. michauxii* Nuttall). The cluster analysis revealed three main clusters, one consisting of *Q. myrtifolia* alone and the other two consisting of 12 and 7 species, respectively. The two large clusters included both native and non-native species. Only once did two non-native trees resolve together as sisters, in the *Q. robur* L. tree and one of the *Q. macrocarpa* trees. Two trees were sampled from 8 of the 12 species, and in only one species were the two individuals clustered together (*Q. prinus*). Overall, there was no consistent similarity observed in arthropod communities sampled in native and non-native trees (Fig. 2). Moreover, when trees were analyzed by section (*Quercus*, *Cerris*, and *Lobatae*), trees failed to cluster by section.

Discussion

Native plants may coevolve with other organisms, and the increased associations among native plants and their surrounding communities may lead to more abundance and diversity within those communities (Bezemer et al. 2014, Štrobl et al. 2019). We were not able to find support for the hypothesis that native

oak species were associated with greater arthropod abundance and diversity compared with non-native species. Although the abundance and diversity both peaked in June and declined in late July, neither abundance nor diversity differed between native and non-native species. This was the case when comparing both individual species and when comparing native and non-native species as groups. Furthermore, although our diversity data were limited because of identification only to the rank of order, our data still suggested that similar communities of arthropods were found on all oak trees, regardless of origins.

Non-native plants have been demonstrated to naturalize to their new habitats (Richardson et al. 2001). As plants naturalize, it is possible that arthropod component communities form with naturalizing plants over time that are similar to those associated with native plants (Branco et al. 2015). In the case of oaks, local arthropods may be able to transition to tree species that belong to the same section or genus as native host plants (Branco et al. 2015, Connor et al. 1980, Kirichenko and Kenis 2016). The lower values of arthropod abundance in native and non-native plants seem to be dampened if the non-native plants are congeners of native plants (Grandez-Rios et al. 2015). The trees that we sampled were mostly 30 years or older (Bill Lott, University of Georgia, pers. comm.), and species like *Q. acutissima* have been grown locally since the early 20th century (Hopkins and Huntley 1979). Arthropods could have transitioned after hundreds of generations to the non-native species we sampled.

Two of the three most abundant arthropod groups, Coleoptera and Psocodea, that were collected were phytophagous. Native phytophagous arthropods may be more likely to associate with native plants than nonphytophages (Southwood et al. 2005). Most of the coleopterans that were collected were in the phytophagous families Curculionidae and Chrysomelidae, and coleopteran abundance was higher in the non-native trees. Although coleopterans were not identified to species, it is possible that the individuals collected may have been exotic species themselves. Alternatively, many chrysomelids are polyphagous or oligophagous (Jovliet and Hawkeswood 1995, Kishimoto-Yamada et al. 2013), and generalist species with broader diet breadth may have established on non-native trees. Conversely, more specialized coleopterans may have been able to establish on non-native congeners of their host plants because of adaptations to plant traits broadly distributed through the genus *Quercus* (Grandez-Rios et al. 2015). Investigation of the diet breadth of phytophagous coleopterans would allow future researchers to distinguish between these explanations. Coleopterans were abundant on each of the non-native oak species sampled, with at least 20 individuals collected in each tree. Defoliating species, like the chrysomelids we collected, may be better able to transition to non-native plants compared with other guilds such as borers and root feeders (Branco et al. 2015). Another abundant group of phytophages, Psocodea, did not differ in abundance between native and non-native trees. Previous research suggests Psocodea may be abundant on trees irrespective of origin, potentially because they are feeding on lichens and mosses rather than the oak foliage itself (Southwood et al. 2005). In all cases, chewing phytophagous arthropods were more likely to be collected than piercing-sucking phytophagous arthropods.

Araneae, for example, spiders, were the second-most abundant arthropod group, and their abundance did not differ between native and non-native trees. Carnivorous arthropods often associate indirectly with trees rather than directly, and

thus their abundance may “track” the abundance of prey species (Litt et al. 2014). Carnivorous arthropods may be less likely to be influenced by tree origin compared with phytophagous arthropods (Southwood et al. 2005). Future investigation of trophic links and abundance within different trophic levels can yield insights about how tree origin influences arthropod food webs.

Further sampling is required to conclusively determine that native and non-native oak trees did not differ in arthropod community composition. Beat sheets sample primarily specific guilds such as foliar feeders (Ozanne 2015), and guilds such as leaf miners, stem feeders, and gall formers may not have been adequately sampled (Valencia-Cuevas and Tovar-Sánchez 2015). Methods such as knockdown sampling and sampling leaves themselves may reveal if there are differences in diversity and abundance in these guilds. Furthermore, a sample period that lasts one or more full oak growing seasons may reveal other trends. Additional locations within or outside of the Piedmont ecoregion can also be sampled to determine how widespread naturalization can be. Last, because oaks from different sections differ chemically and may harbor different specialist herbivores (Abrahamson et al. 1998), further research may compare native and non-native oaks specifically within a single section.

In conclusion, this study failed to discover increased abundance and diversity of arthropods on native oaks compared to non-native oaks. Non-native oaks have been introduced into North America and are common ornamental plants. Communities of arthropods may be able to transition to close relatives of their native host plants. In the case of oaks, non-native congeners of native species may provide similar ecosystem services to native species, and this possibility should be investigated. More research is required to determine whether non-native oaks can establish and support arthropod diversity in forest ecosystems.

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