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# Both host plant and ecosystem engineer identity influence leaf-tie impacts on the arthropod community of *Quercus*

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**Abstract.** Many insect herbivores build shelters on plants, which are then colonized by other arthropod species. To understand the impacts of such ecosystem engineering on associated species, the contributions of ecosystem engineer and host-plant identities must be understood. We investigated these contingencies at the patch scale using two species of leaf-tying caterpillars, which vary in size and tie construction mode, on eight species of oak (*Quercus*) trees, which vary in leaf size and leaf chemistry. We created three types of artificial leaf ties by clipping together pairs of adjacent leaves using metal hair clips. We left the first type of leaf tie empty while adding individuals of the leaf-tying caterpillars of either *Pseudotelphusa quercinigracella* or *Psilocorsis cryptolechiella* to the other two. We also created a control treatment of untied leaves by affixing clips to single leaves. Leaf ties increased occupancy in the early season and arthropod  $\alpha$  diversity throughout the experiment, on average fourfold. Furthermore, the presence of leaf ties increased arthropod species density on average three times and abundance 10–35 times, depending on the plant species. The mean phenolic content of the leaves of each oak species was positively correlated with the leaf-tie effect on abundance and negatively correlated with the leaf-tie effect on species diversity. Species diversity, but not abundance, was affected by the identity of the tie-maker. Arthropod species composition differed between untied leaves and artificial leaf ties, and between ties made by the two leaf-tier species. Our results demonstrate that the presence of leaf ties adds to habitat diversity within the oak–herbivore system, not only by creating a new kind of microhabitat (the leaf tie) within trees, but also by exacerbating differences among the eight oak species in apparent habitat quality. The identity of the leaf-tying caterpillar adds to this heterogeneity by creating leaf ties of different size, thus influencing subsequent colonization by other leaf-tying caterpillars of different sizes.

**Key words:** context dependency; ecosystem engineering; leaf-tying caterpillar; patch scale; species density; species diversity; species richness.

## INTRODUCTION

Physical ecosystem engineering is the modification of habitats by an organism, changing resource availability for other organisms in the community (Jones et al. 1997, Wright et al. 2003, 2006). There is increasing evidence that the outcome of ecosystem engineering depends on the identity of both the affected organism and the engineer itself, as well as modifying abiotic factors (Wright et al. 2002, 2003, 2006, Rosell et al. 2005, Padilla 2010). Ecosystem engineering by insect herbivores, in the form of shelter-building, has generally been overlooked as a factor that influences arthropod structure on plants (Strong et al. 1984, Marquis and Lill 2006). Shelter-building caterpillars manipulate microhabitats by constructing shelters using their food plants (Fukui 2001, Lill and Marquis 2004, 2007). Such shelters are often utilized by arthropods in the commu-

nity, both concurrently and following the departure of the original shelter-maker (Fukui 2001, Lill and Marquis 2003, 2007).

Leaf shelters can increase arthropod abundance and/or species richness on various host-plant species (Cappuccino and Martin 1994, Martinsen et al. 2000, Lill and Marquis 2003). Protection from predation and parasitism (Loeffler 1996), increased leaf quality (Sagers 1992), increased resources in the form of frass and insect parts, and amelioration of stressful abiotic environment (Hunter and Willmer 1989) are possible benefits. These results suggest that the effects on associated species are mostly positive, but species that avoid shelters may be negatively affected (Lill and Marquis 2003, Nakamura and Ohgushi 2003). Few studies have examined the context influencing the directions and magnitudes of the engineering outcomes of leaf shelters.

At our study site in eastern Missouri, USA, 15 species of caterpillars, belonging to six families, create shelters by tying together leaves or portions of leaves of oak trees (*Quercus* spp.) with silk (Lill and Marquis 2003, 2004). The presence of numerous engineering species allows comparison of the effects of engineers that build

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constructs of different sizes and duration, an advantage not available in other systems, particularly those involving vertebrates (e.g., Wright et al. 2002). Lill and Marquis (2003) demonstrated that leaf ties constructed by mostly one species of caterpillar on one species of *Quercus* significantly increased insect herbivore species richness at the whole plant level (i.e., at the landscape level encompassing both tied and non-tied leaves). However, individual leaf-tie species differ in body size, the size of the leaf ties they build, the accessibility of the tie, and the amount of frass they leave in the tie (R. J. Marquis, *personal observation*). The leaf-tying caterpillars colonize several species of *Quercus*, which differ in leaf quality, texture, and size, and in plant architecture (Marquis and Lill 2010). Differences among host-plant species and among the engineers themselves may generate discrepancies in the outcome of the engineering effects of these caterpillars and their influence on the arthropod community dynamics at the patch level (i.e., leaf ties vs. non-tied leaves).

We examined the ecosystem engineering effects of two sympatric species of leaf-tying caterpillars, *Psilocorsis cryptolechiella* Chambers (Oecophoridae) and *Pseudotelphusa quercinigracella* Chambers (Gelichiidae). We focused on the patch scale instead of the whole plant (i.e., landscape) level as in Lill and Marquis (2003), acknowledging that the effects of an ecosystem engineer can differ between the two scales (Jones et al. 1997). *Psilocorsis* individuals on average are twice as large in body size and generally build larger ties than *Pseudotelphusa* individuals (R. J. Marquis, *personal observation*). Larger engineer-modified habitats allow greater accumulation of species relative to smaller ones, particularly at smaller spatial scales (Wright et al. 2006). In addition, larger leaf ties can contain higher amounts of other resources, such as caterpillar frass.

We assessed the context dependency of these engineering effects across a habitat quality gradient of eight species of host trees, which also differ in leaf size and morphology. Here we equate lower host quality with decreasing habitat quality, particularly for those arthropod species using the leaves as a food resource. We used leaf phenolics as a proxy for habitat quality. Leaf phenolics have been demonstrated to negatively impact arthropod abundance on oak trees (Forkner et al. 2004). Plants with lower phenolic defenses represent higher quality habitat for herbivores, and therefore likely attract more arthropods, potentially amplifying the engineering effect of leaf ties. Furthermore, tree species with larger leaves provide greater habitat size, potentially allowing greater species accumulation.

We examined the arthropod communities associated with the shelters constructed by the two species of caterpillars on eight species of oak trees. Specifically, we assessed whether (1) the presence of leaf ties positively affected occupancy, species richness, species density, and abundance of arthropods at the patch level, (2) these engineering effects varied between the two species of

leaf-tiers, and (3) the effect of leaf ties on arthropod species diversity and composition varied by host tree species. We hypothesized that (1) occupancy, species richness, species density, diversity, and abundance of arthropods would increase in leaf ties compared to untied leaves on oak trees (i.e., same as the observation at the larger, whole tree level), (2) leaf ties built by *Psilocorsis* would have a greater effect on secondary user abundance and species richness than leaf ties of the smaller *Pseudotelphusa*, and (3) the engineering effects of these caterpillars on inquiline diversity and abundance would be greatest on plant species of the highest quality and with the largest leaves. To our knowledge, this is the first study to both manipulate the engineer and the environmental context in which ecosystem engineering is taking place.

## METHODS

### *Study system and site*

We conducted the experiment from July to October 2008 at Cuivre River State Park (CRSP) near Troy, Missouri, USA. The park contains second-growth mixed oak-hickory forest. The oak trees used in our study represent the eight most common species of oaks at CRSP, including white (*Quercus alba*), post (*Q. stellata*), chinkapin (*Q. muehlenbergii*), and burr (*Q. macrocarpa*) oaks, all of the white oak *Leucobalanus* subgenus, and black (*Q. velutina*), blackjack (*Q. marilandica*), shingle (*Q. imbricaria*), and northern red (*Q. rubra*) oaks, of the red oak *Erythrobalanus* subgenus. All species co-occur at our study site except *Q. macrocarpa*, found in alluvial forest, and *Q. marilandica*, found in dry open forest and forest edges.

The leaf-tying caterpillars at our study site use their engineered habitat (i.e., tied oak leaves) as both a shelter and a source of food. Leaf ties, once made, can last until leaf fall in late autumn (H. G. Wang, *personal observation*). Secondary users, including herbivores, predators, scavengers, and other species of leaf-tying lepidopterans, often start colonizing the leaf ties while the primary engineer is still present, and continue to occupy the shelters throughout the season (Lill 2004). The two species of caterpillars used in our study (*Pseudotelphusa quercinigracella* and *Psilocorsis cryptolechiella*) were the two most common species of leaf-tiers at CRSP at the time of the study, and in general, with densities of >2 individuals per 100 leaves on *Q. alba* (Lill 2004). While *Q. alba* is the most common host species for these caterpillars, they also naturally occur on all the other species of oaks used in our study (R. J. Marquis, *personal observation*). A small percentage of the caterpillars that we identified as *Psilocorsis cryptolechiella* may have been *P. reflexella*, as these two species are impossible to tell apart morphologically in their early instars. Regardless, the majority of caterpillars used in this experiment were of mid-instar, collected from non-experimental trees (mostly *Q. alba* and *Q. velutina*) at least 200 m from our experimental site.

### Artificial leaf-tie experiment

We selected 80 small oak trees, 2–5 m in height ( $N = 10$  per species), in early summer of 2008. Leaf samples were collected from each tree for chemical characterization and the number of leaves was counted per tree. We set up the experiment in mid-July 2008, which was relatively late due to the late emergence of leaf-tying caterpillars that year, with the first generation not appearing until mid-June 2008. Thirty-six leaves were selected haphazardly on each tree and assigned to one of four treatments, with all four treatments on each tree. Lightweight metal hair clips (Brentwood Beauty Labs International, Hillside, Illinois, USA) were used to clip two leaves together, upper surface of the lower leaf flat against the lower surface of the upper leaf (Marquis and Lill 2010), to form artificial leaf ties in three of the four treatments (see Plate 1). In so doing, we controlled for differences among trees and among tree species in architecture (Marquis et al. 2002, Marquis and Lill 2010), while providing a starting point for establishment of a tie when a leaf-tying caterpillar was provided. In the untied leaf treatment (NO TIE), we affixed 18 clips on 18 individual leaves (one clip per leaf) in each tree. These leaves served as controls for the other three treatments. In the first leaf-tie treatment (TIE ONLY), we established three artificial leaf ties. For the second leaf-tie treatment (TIE + SM SP), we created three artificial leaf ties as in the TIE ONLY treatment and placed one mid-instar *Pseudotelphusa quercinigracella* (small caterpillar species) individual in each leaf tie. The third leaf-tie treatment (TIE + LG SP) was identical to the TIE + SM SP treatment except that we placed one mid-instar individual of *Psilocorsis cryptolechiella* (large caterpillar species) in each artificial tie.

Although we did not explicitly monitor these caterpillars after the transplant, previous studies have demonstrated that >90% of leaf-tiers establish in the artificial ties in which they are placed (Lill and Marquis 2001). We conducted two censuses, one at one month (26–29 August 2008) and the other at two months (23 September–1 October 2008) after establishing the artificial ties. At each census, we recorded the number and morphospecies (hereafter species) of all arthropods on clipped leaves. In the TIE ONLY, TIE + SM SP, and TIE + LG SP treatments, the ties were opened for the census and subsequently re-clipped. While we recognize the sacrifice in sample independence by placing all four treatments on every tree, we did this to minimize the potential effect of genetic variability among individual trees, and to facilitate the examination of engineering effects at the patch level. Differences in response variables between TIE + SM SP and TIE + LG SP treatments would be due to differences in the identity of leaf-tying caterpillar. Any differences between TIE ONLY vs. TIE + SM SP and TIE + LG SP treatments would be due to the presence of a leaf-tying caterpillar, regardless of caterpillar identity.

### Leaf size and quality

We quantified leaf size by determining the mean leaf width for each experimental tree, based on 12 leaves used in our artificial leaf-tie experiment on each tree (Appendix A). Leaf width was used because wider leaves represent greater habitat structure for leaf-tie construction. We assessed leaf chemical quality at the individual plant level by measuring the total phenolic concentration of each tree (Appendix B).

### Data analysis

We compared occupancy by all arthropods across leaf-tie treatments, host tree species, and the two census periods using generalized linear mixed models (GLMMs), with individual trees as replicates. The models were fit by the Laplace approximation using the glmer function of the lme4 package of R 2.12.1 (R Development Core Team 2010). See Appendix C for detailed explanations of the model construction and selection processes.

We compared  $\alpha$  diversity of all arthropods across leaf-tie treatments, host tree species, and the two censuses using GLMMs. Individual trees were considered replicates, and the models were fit using methods described in Appendix D. We also used sample-based rarefaction curves (Gotelli and Colwell 2001) to assess our sampling effort for the different species of host trees, with each individual tree as a sampling unit, and all leaves in the same leaf-tie treatment on each tree as a sample. We pooled data over the two censuses and over all eight oak species because most separate rarefaction curves for the eight host tree species approached asymptote instead of reaching it (Appendix E: Fig. E1). All rarefaction curves were calculated using EstimateS 8.2 (Colwell 2009). A detailed description of the calculation process is given in Appendix E.

We used linear mixed-effects models (LMMs) to compare two additional variables, the reciprocal of Simpson's diversity index ( $1/D$ ) (Appendix F) and the overall abundance of arthropods (Appendix G), across tree species and leaf-tie treatments, with individual trees as replicates and data pooled over the two censuses. We fit the LMMs by maximum likelihood using the lmer function of the lme4 package of R 2.12.1 (R Development Core Team 2010).

We correlated (Pearson product-moment  $r$ ) the sample effect sizes of  $1/D$  and overall abundance with leaf width and total phenolics of the host trees. We calculated the effect sizes of the two metrics using the formula  $\ln(x/y)$ , where  $x$  is either the  $1/D$  or the number of individuals per leaf, pooled across the artificial leaf ties (TIE ONLY, TIE + SM SP, and TIE + LG SP), and  $y$  is the respective value of untied leaves (NO TIE) of the same tree. A value of one (of a dummy species) was added to each sample of abundance for this analysis.

To compare species composition among leaf-tie treatments and across host tree species, we used the permutational multivariate analysis of variance (PER-

MANOVA), a distribution-free multivariate method that can be based on any type of distance or dissimilarity measure (Anderson 2001, McArdle and Anderson 2001). We pooled data over the two censuses and tested for significance of leaf-tie treatments, host tree species identity, and their interaction. We performed the tests on the entire data set of all arthropods, then separately on two subsets of our data, one of all leaf-tying caterpillars minus the original tiers we inserted into the artificial leaf ties, and another one of all non-tying arthropods. These tests were performed using the *adonis* function of the *vegan* package of R 2.12.1 (R Development Core Team 2010), using the Bray–Curtis dissimilarity distance and 9999 permutations. Because each individual tree was a sampling unit, we stratified the permutations by each tree to account for possible correlations among the leaf-tie treatments. We then used canonical analysis of principal coordinates (CAP; Anderson and Robinson 2003, Anderson and Willis 2003) to visualize and discriminate the significant treatment differences in species compositions identified by PERMANOVA. We performed this analysis with the FORTRAN program CAP (Anderson 2004), using the Bray–Curtis dissimilarity distance. The factors of leaf-tie treatment and host tree species were analyzed in separate single factor analyses. The number of unconstrained principal coordinate axes was chosen to maximize the proportion of variability explained by the axes without exceeding 100% of the total variability of the dissimilarity matrix (Anderson and Willis 2003). We also checked the goodness of fit of the matrix to the principal coordinate axes by calculating the proportion of misclassified observations using the “leave-one-out” cross-validation method. Arthropod data were  $\ln(x + 1)$  transformed for the host-species analysis; this approach yielded the highest correct sample classification. In addition, we computed the correlation of each species to the first two canonical axes to assess their contribution to variability (Anderson and Willis 2003). A species was considered to have strong association with the variations along the two axes if its  $|r|$  was  $\geq 0.30$ .

## RESULTS

### *Occupancy across treatments and census periods*

Consistent with hypothesis 1, occupancies of artificial leaf ties in the August census (TIE ONLY, 88.5%; TIE + SM SP, 98.7%; TIE + LG SP, 98.7%) were higher than that of untied leaves (NO TIE, 57.7%). This did not hold true for the September census (NO TIE, 85.9%; TIE ONLY, 92.3%; TIE + SM SP, 98.7%; TIE + LG SP, 100%). The four top-ranked models, essentially equally valid (all  $\Delta\text{AIC} < 3$ ), included the effect of leaf-tie treatment, census period, and individual tree (random intercept only), and two of these models also included a tree species effect. The second ranked model ( $\Delta\text{AIC} = 2.0$ ) included a leaf-tie treatment  $\times$  census interaction (Appendix C: Table C2).

### *Species richness and density across treatments and host tree species*

We recorded 5469 individuals representing 76 morphospecies of arthropods. Alpha diversity on untied leaves (NO TIE) was significantly lower than that in artificial leaf-ties (TIE ONLY, TIE + SM SP, and TIE + LG SP) in both census periods for most species of oak trees (Fig. 1A). This is consistent with our hypothesis 1 and was confirmed by the GLMM we selected. The best model included a scalar (intercept-only) random effect of individual tree, the additive fixed effect of host tree species, and the interacting fixed effects of leaf-tie treatment  $\times$  census (Appendix D: Table D2). All three types of artificial leaf ties had positive effects on arthropod  $\alpha$  diversity ( $\beta \pm \text{SE}$  for TIE ONLY,  $1.3 \pm 0.1$ ; TIE + SM SP,  $1.6 \pm 0.1$ ; TIE + LG SP,  $1.8 \pm 0.1$ ), and there was no significant difference between the two censuses in each of these leaf ties. However,  $\alpha$  diversity on untied leaves (NO TIE) in the September census was significantly higher than in the August census. Furthermore,  $\alpha$  diversity in leaf ties inoculated with caterpillars (TIE + SM SP and TIE + LG SP) was significantly higher than in uninoculated leaf ties (TIE ONLY) in the August census (Fig. 1A). Overall  $\alpha$  diversity on *Q. macrocarpa* was lower than that on the other seven species of host trees (Appendix D: Fig. D1). There was no support for any other model for  $\alpha$  diversity (all  $\Delta\text{AIC} > 10$ ).

Untied leaves (NO TIE) had significantly lower species density (Mao Tau scaled by number of samples; Fig. 1B) but not species richness (Mao Tau scaled by number of individuals; Fig. 1C) than artificial leaf ties (TIE ONLY, TIE + SM SP, and TIE + LG SP), regardless of the presence or species identity of leaf-tying caterpillars. Adding artificial leaf ties doubled species density, averaged across the eight tree species and the two caterpillar species. All rarefaction curves for the leaf-tie treatments pooled across tree species reached an asymptote, indicating sufficient sampling efforts for all treatments (Figs. 1B and C).

### *Species diversity across treatments and host tree species*

Consistent with our first hypothesis, artificial leaf ties had higher  $1/D$  than untied leaves in six of the eight oak species (Fig. 2A). The two exceptions were artificial ties on *Quercus marilandica* and *Q. stellata*, each having lower diversity (but higher abundance) than untied leaves. In both oak species, the leaf-tie faunas were dominated by psocids (order Psocoptera) and caterpillars of *Anteotricha humilis* (see results of species composition across host tree species in Appendix 1). The two highest ranking LMMs (both  $\Delta\text{AIC} \leq 2.0$ ) included the interaction term of leaf-tie treatment  $\times$  host-tree species (Appendix F: Table F1), consistent with the idea that the effects of leaf-tie treatments on diversity varied by tree species. There was some suggestion that treatment effects depended on initial diversity of untied leaves (the highest ranked model

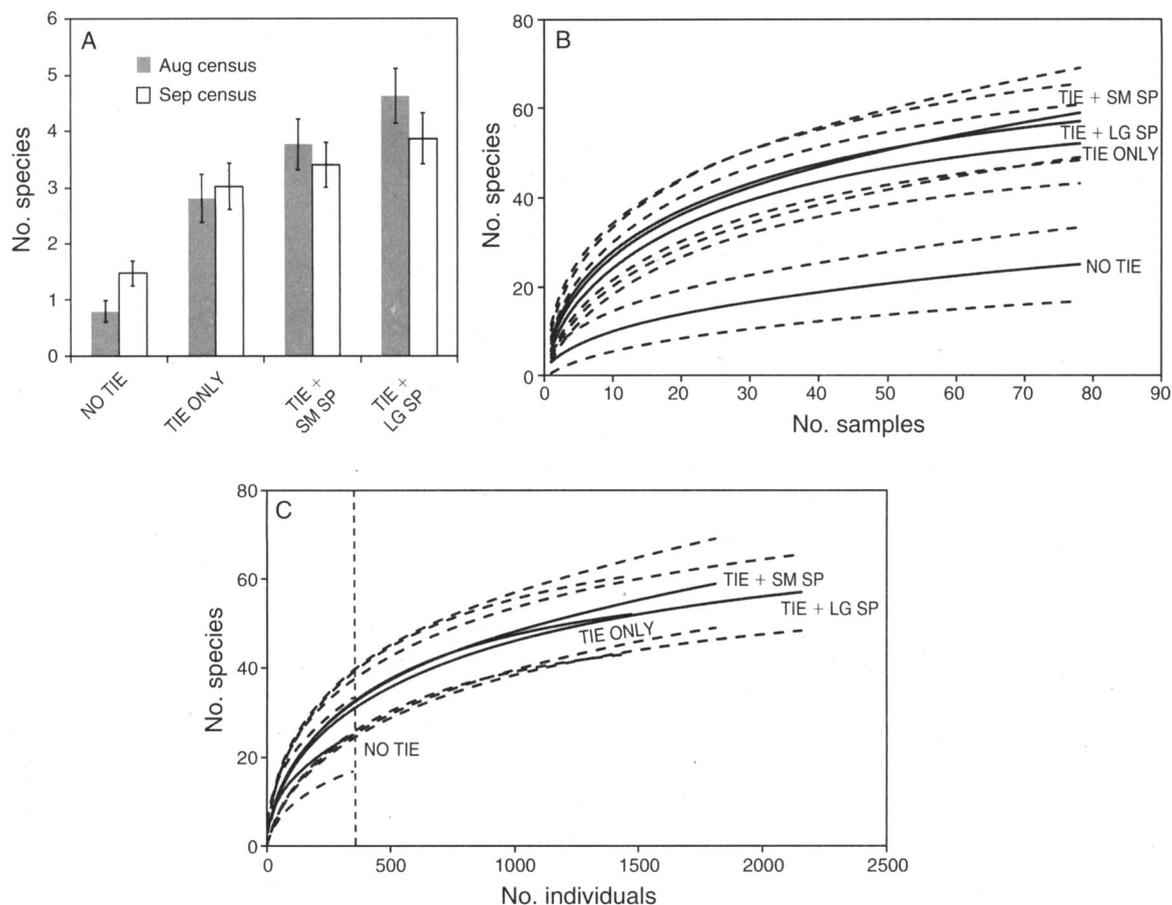


FIG. 1. (A) Average  $\alpha$  diversity of all arthropods of the four leaf-tie treatments, pooled over eight host tree species, across two censuses. The error bars represent 95% confidence intervals. (B, C) Sample-based rarefaction curves of combined richness of eight species of oaks scaled by the number of samples, representing (B) species density, and scaled by the number of individuals, representing (C) species richness, of the four artificial leaf-tie treatments. Solid lines represent the estimated number of species (Mao Tau) of each treatment, and each pair of dashed lines represents the corresponding upper and lower 95% confidence intervals. The vertical dashed line in panel (C) represents the rarefied number of arthropod individuals at which species richness was compared among treatments. The four treatments are untied leaves (NO TIE), ties only (TIE ONLY), leaf ties plus one mid-instar *Pseudotelphusa quercinigracella* (small caterpillar species; TIE + SM SP), and leaf ties plus one mid-instar individual of *Psilocorsis cryptolechiella* (large caterpillar species; TIE + LG SP).

included a correlated intercept and slope effect for individual trees; Appendix F: Table F1); however, these within-tree correlations were low ( $|r| \leq 0.25$ ) for all three leaf-tie treatments.

Overall, all three types of artificial leaf ties had positive effects on arthropod species diversity, increasing it by as much as 100% ( $\beta \pm SE$  for TIE ONLY,  $1.8 \pm 0.3$ ; TIE + SM SP,  $1.9 \pm 0.2$ ; TIE + LG SP,  $1.3 \pm 0.2$ ). There were two exceptions to these general positive effects. First, all three types of artificial leaf ties on *Q. marilandica* had negative effects on arthropod species diversity (TIE ONLY,  $-4.8 \pm 0.4$ ; TIE + SM SP,  $-4.7 \pm 0.3$ ; TIE + LG SP,  $-4.1 \pm 0.3$ ). Second, leaf ties inoculated with caterpillars on *Q. stellata* had lower arthropod diversity (TIE + SM SP,  $-2.9 \pm 0.3$ ; TIE + LG SP,  $-2.2 \pm 0.3$ ) than untied leaves (Fig. 2A). Effect sizes for Simpson's index reciprocals were not correlated with mean leaf width ( $r = -0.14$ ,  $P = 0.22$ ) but were

negatively correlated with foliar total phenolics ( $r = -0.27$ ,  $P = 0.02$ ), consistent with part of our prediction for hypothesis 3.

#### Arthropod abundance across treatments and host tree species

Artificial leaf ties had positive effects on overall arthropod abundance in all eight species of host trees, but these effects varied by tree species. Similar to the model set of species diversity, the three arthropod abundance models containing the interaction term of leaf-tie treatment  $\times$  host tree species in the fixed effects ranked the highest (Appendix G: Table G1). The highest ranking LMM included random slope of leaf-tie treatment within individual trees with correlated random intercept. The only strong correlation in this model was between the random intercept (NO TIE) and the random slope of the TIE + LG SP treatment ( $r = 0.31$ ),

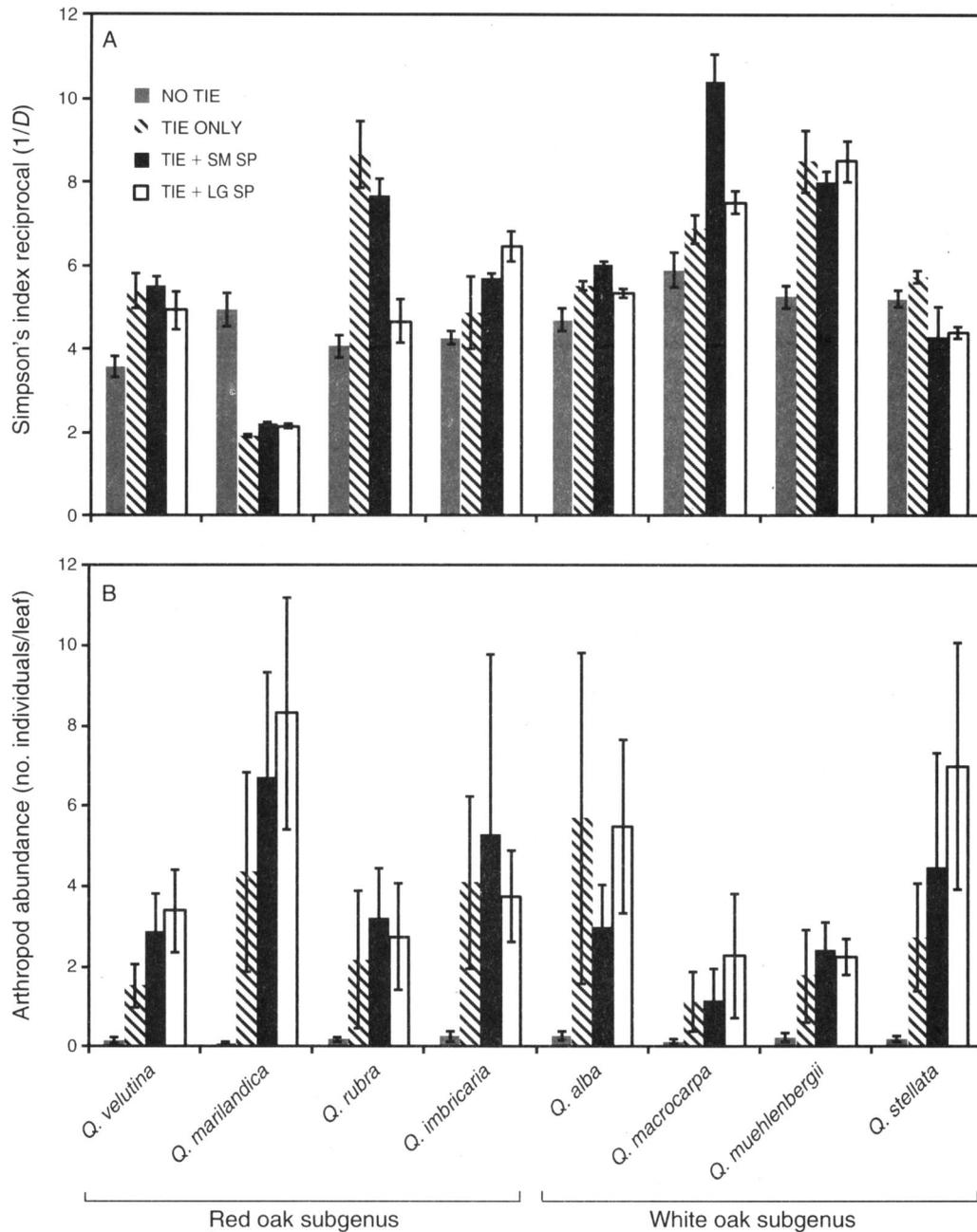


FIG. 2. (A) Average Simpson's diversity index reciprocal (1/D), pooled over two census periods, by leaf-tie treatments and host tree species. (B) Average number of arthropod individuals per leaf by leaf-tie treatments and host tree species (all genus *Quercus*). Error bars show 95% CI.

suggesting that arthropod abundance increase in leaf ties inoculated with *Psilocorsis cryptolechiella* was more pronounced on trees with higher arthropod abundance on untied leaves.

The average abundance of arthropods on untied leaves was the same across all eight species of oaks (Fig. 2B). Arthropod abundance was positively affected by all three types of artificial leaf ties, increasing abundance 10–35 times over non-tied leaves, with the

two inoculated with caterpillars ( $\beta \pm SE$  for TIE + SM SP,  $2.7 \pm 1.2$ ; TIE + LG SP,  $3.2 \pm 1.0$ ) having stronger effects than the initially unoccupied one (TIE ONLY,  $1.4 \pm 1.1$ ). While host-tree species identity had no independent effect on arthropod abundance, there was a significant tree-species  $\times$  leaf-tie treatment interaction. TIE + SM SP ( $\beta \pm SE$ ,  $3.9 \pm 1.7$ ) and TIE + LG SP ( $5.0 \pm 1.4$ ) treatments on *Q. marilandica* had higher arthropod abundance than untied leaves, as did TIE

ONLY on *Q. alba* ( $4.1 \pm 1.6$ ) and TIE + LG SP on *Q. stellata* ( $3.6 \pm 1.4$ ) (Fig. 2B). There was no correlation between abundance effect size and leaf width ( $r = 0.17$ ,  $P = 0.15$ ) and a marginally significant positive correlation between abundance effect size and total phenolics ( $r = 0.20$ ,  $P = 0.08$ ), contradicting hypothesis 3.

#### Species composition across treatments and host tree species

Species composition of all arthropods was most strongly affected by leaf-tie treatment and less so by host tree species identity (PERMANOVA analysis; Appendix H: Table H1). Similarly, leaf-tie treatment was a stronger factor than host species for leaf-tier (Appendix H: Table H2) and nontier (Appendix H: Table H3) species compositions when analyzed separately. For leaf-tie treatment effects, the constrained ordination of all arthropods showed the most distinct grouping of samples, and we focus on the result of this analysis. In this ordination, 19 principal coordinate axes were used, with the first two axes explaining 22.8% and 13.3% of the dissimilarity matrix variability, respectively. This model yielded 60.6% correct allocation of observations. Axis 1 represented the difference between untied leaves and artificial leaf ties, while axis 2 separated TIE + LG SP treatment from TIE ONLY and TIE + SM SP treatments (Fig. 3A), with no significant difference between TIE ONLY and TIE + SM SP treatments. Based on correlations of individual species with canonical axis 1, spiders ( $r = -0.56$ ) were the only arthropods associated with untied leaves, whereas psocids ( $r = 0.32$ ) were associated with artificial leaf ties (Fig. 3B). *Psilocorsis cryptolechiella*, *P. quercicella*, and *Pseudotelphusa quercinigracella* had strong positive correlations with axis 1 (all  $r > 0.35$ ) but weak correlations with axis 2 (all  $|r| < 0.25$ ), indicating that individuals of these three species were evenly distributed among leaf ties of TIE ONLY, TIE + SM SP, and TIE + LG SP treatments (Fig. 3B). In contrast, *Psilocorsis reflexella* was associated only with leaf ties of TIE + LG SP ( $r = 0.68$  for axis 2; Fig. 3B). Results of the ordination for host tree species effect indicated that arthropod communities on *Q. muehlenbergii* and *Q. macrocarpa* separated from those on *Q. marilandica* and *Q. stellata* (Appendix I).

#### DISCUSSION

Our understanding of the context dependency and magnitude of the effects of leaf shelters on arthropod communities on plants is in its infancy. This is the first study to consider simultaneously both the role of the host plant (Marquis and Lill 2010) and the identity of the shelter-maker. We show that the presence of leaf ties, and thus the caterpillars as ecosystem engineers, affected arthropod abundance,  $\alpha$  diversity, species density, diversity, composition, and occupancy at the patch scale on each of the eight species of oak trees of the study (hypothesis 1). On average, across the eight host plants

and two species of leaf-tying caterpillars, the species density,  $\alpha$  diversity, and abundance of arthropods were higher in the artificial leaf ties (TIE ONLY, TIE + SM SP, and TIE + LG SP) than on untied leaves (NO TIE), as much as 35 times greater depending on the variable (Fig. 2).

These impacts, however, depended both on the identity of the caterpillar species making the leaf tie (hypothesis 2) and on the host-plant species on which the tie was made (hypothesis 3). The number of species and diversity of arthropods on untied leaves were relatively consistent across the host tree species, whereas their values were more varied in the artificial leaf ties (Fig. 2). This demonstrates that the magnitude of the engineering effect was contingent upon the host tree species identity. Furthermore, these values varied between TIE + SM SP (*Pseudotelphusa quercinigracella*) and TIE + LG SP (*Psilocorsis cryptolechiella*) treatments, demonstrating an engineer species identity effect.

#### Hypothesis 1: effect of leaf ties on arthropod species richness, density, diversity, and occupancy

The artificial leaf ties increased both arthropod  $\alpha$  diversity and occupancy at the patch level on oak trees. However, the GLMMs indicated that the effects of leaf-tie treatments on both metrics differed between the two censuses, suggesting a temporal difference in these effects. Both  $\alpha$  diversity and occupancy on untied leaves (NO TIE) were higher in September than in August, but these values did not differ between the two censuses for any of the three types of artificial leaf ties. Leaf ties appear to maintain a relatively constant arthropod community composition while the external community fluctuates temporally.

Using sample-based rarefaction curves, we demonstrated that leaf-tying caterpillars increased species densities of arthropods in their modified habitat patch. Leaf ties had significantly higher arthropod abundance than untied leaves, therefore it is reasonable to expect the number of species to increase because more individuals were present in the samples from leaf ties (Gotelli and Colwell 2001). While we observed higher arthropod  $\alpha$  diversity in leaf ties than on untied leaves, this difference in species richness disappeared when we adjusted for arthropod abundance differences between the two habitat types. This result suggests that leaf shelters affected  $\alpha$  diversity mainly by increasing the number of individuals sampled. A similar mechanism may also have led to earlier findings of leaf shelters increasing arthropod species richness (e.g., Martinsen et al. 2000, Lill and Marquis 2003).

While the process of ecosystem engineering may increase species richness at the landscape scale, engineer-modified habitat per se (i.e., at the patch scale) does not necessarily contain higher or lower numbers of species than unmodified habitat (Jones et al. 1997, Wright et al. 2002). An engineer can create suitable habitat for certain species while destroying habitat for

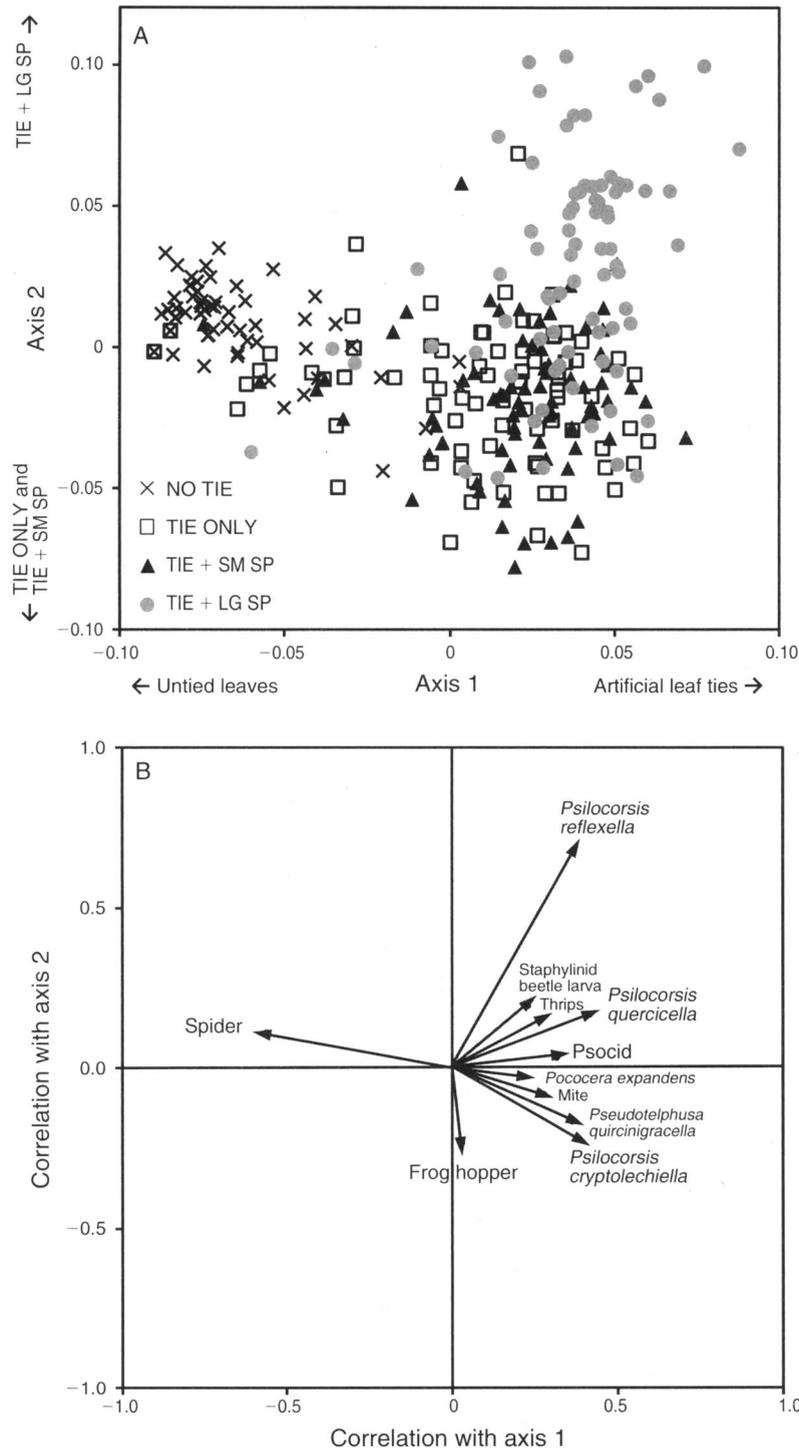


FIG. 3. (A) Constrained ordinations (CAP) of arthropod communities grouped by leaf-tie treatments. (B) Biplot showing correlations of arthropod species with the first two canonical axes of the leaf-tie treatment effect. Only species (morphospecies) with  $|r| \geq 0.20$  on at least one axis are included in the plot.

others. This phenomenon has been observed for leaf ties on *Quercus* in that some species of arthropods are “shelter avoiders” (Lill and Marquis 2003). Spiders appear to fit this category in this study. Results of the

multivariate analysis of variance suggest that species composition of leaf ties differed from that of untied leaves. When all arthropods were analyzed, several common species of leaf-tying caterpillars (*Psilocorsis*

*cryptolechiella*, *P. reflexella*, *P. quercicella*, and *Pseudotelphusa quercinigracella*) and psocids were strongly associated with leaf ties (all  $r \geq 0.30$  for axis 1). While the ordination of non-tying arthropods did exhibit separation between non-tied leaf and leaf-tie samples, most of these arthropod species appeared to be habitat generalists or have weak associations with either tied or non-tied leaves ( $|r| < 0.30$ ), demonstrating that the species composition difference between the two types of habitats in the current experiment was largely driven by the four species of leaf-tiers.

On Missouri oaks, leaf ties provide shelter for predators, herbivores, and scavengers (Lill and Marquis 2004). Because spiders in our study were strongly associated with untied leaves on oak trees, leaf ties may serve as enemy-free space (Berdegue et al. 1996) for some arthropods. Crutsinger and Sanders (2005) observed that aphid-tending ants around leaf rolls on *Salix hookeriana* possibly reduced herbivore abundance outside the shelters and drove them into the leaf rolls. We found no effect of leaf-tie presence on any other predators, such as Coccinellidae beetles, but this was likely due to their low abundance on our experimental trees. Leaf ties may also offer protection from parasitoids. Le Corff et al. (2000) reported 50% lower attack rates by parasitoids on leaf-tiers than external feeders on Missouri oaks in two of the three years of their study. Further manipulative studies of tritrophic interactions around leaf ties and the potential of leaf ties in providing enemy-free space are warranted, particularly regarding the role of parasitoids.

*Hypothesis 2: effect of leaf-tier species identity on its engineering performance*

There was no significant difference in arthropod species richness, density, or occupancy among the three different types of artificial leaf ties in our experiment. Initially unoccupied leaf ties (TIE ONLY) contained comparable overall abundance and number of species as leaf ties inoculated with *Pseudotelphusa quercinigracella* (TIE + SM SP) or *Psilocorsis cryptolechiella* (TIE + LG SP) individuals, suggesting that inquiline species respond primarily to the habitat structure (i.e., engineered habitat) rather than to the presence of the caterpillars. This also was supported by the ordination of non-tying arthropods, for which the three types of artificial leaf ties displayed no distinct grouping.

On the other hand, leaf-tier species diversity varied among the three types of leaf ties. The leaf-tier *Psilocorsis reflexella* was strongly associated with leaf ties inoculated with the congeneric caterpillar *P. cryptolechiella*. Among the three species of caterpillars, individuals of *Psilocorsis reflexella* have the highest average body mass, while individuals of *Pseudotelphusa quercinigracella* are the smallest, and individuals of *Psilocorsis cryptolechiella* are intermediate (R. J. Marquis, *personal observation*). It is possible that leaf ties constructed by *Pseudotelphusa quercinigracella* are not

sufficiently large for colonization by *Psilocorsis reflexella*. This indicates that the engineering effects of different species of leaf-tying caterpillars can differ as a result of the size discrepancies between engineers (for a contrasting example in beavers, see Collen and Gibson 2001, Rosell et al. 2005). Furthermore, *P. quercinigracella* makes a looser tie, tying together only the edges of the overlapping portions of the leaves with silk "guywires," while *P. cryptolechiella* builds, in addition to guywires, a silk tunnel through which it moves, resulting in an apparently more strongly sealed tie (R. J. Marquis, *personal observation*). These morphological and behavioral differences among engineer species, as well as size, may be mechanisms that generate engineering effect differences. Frass accumulation in ties is also likely to be important as ties made by species of leaf-tying caterpillars on Missouri oaks who keep a frass-free tie have few if any inquilines (R. J. Marquis, *personal observation*). Because many leaf-tying caterpillars frequently share and perpetuate leaf shelters of heterospecific leaf-tiers (Lill et al. 2007), such interspecific associations between leaf-tiers can have implications for community dynamics. For instance, an outbreak of the small-bodied *Pseudotelphusa quercinigracella* may facilitate other species of small leaf-tiers but not the larger *Psilocorsis reflexella*.

*Hypothesis 3: effect of host-plant species identity on leaf-tier engineering performance*

The LMMs including the leaf-tie treatment  $\times$  host-tree species interaction term ranked the highest in both the Simpson's index and abundance sets, suggesting that leaf-tie effects were contingent upon host species identity. On the whole, leaf ties had positive effects on the abundance and species diversity of arthropods on oaks; however, these effects were stronger in some host species than others. Arthropod species diversity ( $1/D$ ) on untied leaves (NO TIE) was largely constant across all eight species of host trees. While arthropod species diversity was higher in leaf ties than on untied leaves for most oak species, two exceptions occurred (Fig. 2A). First, species diversity was lower in leaf ties than on untied leaves of *Quercus marilandica*. Second, inoculation of clipped leaves with *Pseudotelphusa quercinigracella* (TIE + SM SP) and *Psilocorsis cryptolechiella* (TIE + LG SP) on *Q. stellata* decreased arthropod species diversity relative to non-inoculated artificial ties (TIE ONLY). Artificial leaf ties on these two oak species also had relatively large positive effects on arthropod abundance compared to all other oaks other than *Q. alba* (Fig. 2B), but added individuals were of relatively few species on *Q. marilandica* and *Q. stellata* (mostly psocids and *Anteotricha humilis*), resulting in lower diversity. The similarity in the community responses to leaf ties on these two species of trees was also reflected by their proximity in the constrained ordination plot (Appendix I: Fig. I1).



PLATE 1. Artificial leaf-tie (two leaves clipped together with a spring-loaded hair clip) on *Quercus alba*, with skeletonization damage caused by *Arogalea cristifaciella* (Gelechiidae). Photo credit: R. J. Marquis.

Although the eight species of host trees differed significantly in both leaf width (Appendix A) and foliar total phenolics (Appendix B), the discrepancies in arthropod responses to leaf-tie presence in the present study appeared to be more strongly associated with the leaf tissue content and tie construction than with leaf size. While arthropod diversity and abundance in artificial leaf ties had opposite correlations with foliar total phenolics contents (negative for  $1/D$  and positive for abundance), neither measurement was correlated with leaf width. This is consistent with the findings of Marquis and Lill (2010), where natural leaf-tie formation was demonstrated to be correlated with foliar chemical traits including nitrogen availability and protein-binding capacity, but not physical traits such as leaf toughness and specific leaf area. These chemical traits contributed significantly to different natural leaf-tie densities among five species of oaks (*Q. alba*, *Q. muehlenbergii*, *Q. stellata*, *Q. velutina*, and *Q. rubra*) (Marquis and Lill 2010), potentially affecting inquiline arthropod abundance and richness on these trees. While the role of secondary compounds in herbivory defense is sometimes questioned (Carmona et al. 2011), our results and those of earlier studies (Forkner et al. 2004, Marquis and Lill 2010) suggest that foliar chemicals are important factors in structuring arthropod communities in the oak-leaf-tie system.

Our finding of interspecific host-plant variation in herbivore ecosystem engineering effects echoes that of Crutsinger et al. (2009) on intraspecific variation of *Solidago altissima*, which suggests that genetic variation

of this host-plant contributed to inquiline diversity differences in leaf rosette galls created by the rosette-galling midge (*Rhopalomyia solidaginis*). In that study, size and quality of the galls, both genetically variable traits, were shown to be correlated with herbivore diversity. The implication is that the host-plant species identity effect in our study is ultimately attributable to genetically variable traits among the oak species.

#### *Patch- vs. landscape-level effects of leaf-tie ecosystem engineering*

We emphasize that our results apply to the scale of individual leaves and individual leaf ties (i.e., the patch level), and not necessarily to the whole plant level, as we did not conduct whole plant manipulations. When Lill and Marquis (2003) conducted manipulations at the whole plant level on *Q. alba*, they found that both arthropod composition and species richness were affected. Additional experiments corroborate that much colonization is coming from direct oviposition into leaf ties (Lill and Marquis 2004). This indicates that differences in composition between tied and non-tied leaves are due to colonization of the tree and not just shifting of individuals within a tree. We believe that much the same process occurred in the current study, especially for obligate leaf-tying caterpillars. Their higher abundance in ties must have resulted from oviposition subsequent to the start of the experiment, the oviposition choice based in part on the identity of the host plant and that of the leaf-tie. Whole-plant experiments will be required to further distinguish

between patch-level and landscape-level effects with regard to ecosystem engineering context dependency.

#### CONCLUSION

Our results support previous findings (Lill and Marquis 2003, Marquis and Lill 2010) that shelter-building arthropods can highly modify the structure of arthropod communities on plants through their engineering effect. Not only does our experiment demonstrate that leaf ties provide a new kind of microhabitat that changes many metrics of arthropod community structure within trees, it also shows that leaf ties exacerbate differences among the eight oak species in perceived habitat quality (Fig. 2, the other three tie treatments). In contrast, although the eight oak species vary greatly in leaf architecture and quality (Appendices A and B; Marquis and Lill 2010), the arthropod fauna perceives untied leaves (NO TIE) of the eight oak species as relatively equal (Fig. 2), at least for the time of year of this study. The result is that leaf ties create a more heterogeneous habitat both within individual trees and among tree species for the arthropods that utilize oak trees. This is consistent with studies of beaver engineering effects, which suggest that the impact strength of beavers as engineers is affected by the location and habitat type of the site of the construct (Rosell et al. 2005). Our study also suggests that engineer identity contributes to this heterogeneity effect. Our finding of the relationship of tie sharing between different sized leaf-tier species is particularly useful for other types of ecosystem engineers living commensally, such as fossorial mammal species that share burrows. The overall implication of our study is that one must understand the relationships between habitat quality, engineering construct formation, engineer identity, and habitat type in order to understand the factors that influence ecosystem engineering outcomes.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

Methodology of leaf width measurement (*Ecological Archives* E093-207-A1).

##### Appendix B

Methodology of total phenolic measurement (*Ecological Archives* E093-207-A2).

##### Appendix C

GLMMs for occupancy comparison (*Ecological Archives* E093-207-A3).

##### Appendix D

GLMMs for  $\alpha$  diversity comparison (*Ecological Archives* E093-207-A4).

##### Appendix E

Calculation of the sample-based rarefaction curves (*Ecological Archives* E093-207-A5).

##### Appendix F

LMMs for Simpson's diversity index reciprocal ( $1/D$ ) comparison (*Ecological Archives* E093-207-A6).

##### Appendix G

LMMs for arthropod abundance comparison (*Ecological Archives* E093-207-A7).

##### Appendix H

PERMANOVA results of species composition (*Ecological Archives* E093-207-A8).

##### Appendix I

CAP result for host tree species effect on arthropod community composition (*Ecological Archives* E093-207-A9).