

## ECOSYSTEM ENGINEERING BY CATERPILLARS INCREASES INSECT HERBIVORE DIVERSITY ON WHITE OAK

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**Abstract.** By creating or modifying habitats used by other organisms, physical ecosystem engineers can influence local patterns of biological diversity. However, there have been very few empirical studies quantifying engineering effects in different biological systems. In this study, we examined the effect of shelter-building caterpillars on the species richness and guild structure of leaf-chewing herbivores occupying individual white oak (*Quercus alba*) saplings. For each of two years, we disrupted leaf-tie formation on 93 white oak saplings during a three-week period in early summer that coincided with the peak in leaf-tie construction by the most common leaf-tying caterpillar, *Pseudotelphusa* sp. (Gelechiidae). We then created artificial leaf ties on 62 of these saplings by clipping together adjacent pairs of leaves (10% of the foliage) on each tree. For 31 of these trees, we also placed a single *Pseudotelphusa* caterpillar into each artificial tie to examine possible non-engineering effects associated with the caterpillar in addition to its shelter-building activity. One month later, removal of leaf ties had reduced the average density of leaf ties present on a tree by 61% (1999) and 54% (2000). This effect persisted throughout the season, indicating that no species assumed the engineering role of *Pseudotelphusa* sp. once it was removed. The decrease in shelter availability significantly decreased mean cumulative species richness of leaf-chewing insects by 38% (1999) and 14% (2000) compared to the two artificial tie treatments (with and without caterpillars initially), which did not differ from one another. Herbivore community composition also differed significantly between the removal and artificial tie treatments in both years, due to increased species richness of leaf-tying caterpillars (1999 and 2000), sawflies (1999 only), and beetles (2000 only) on trees with artificial ties. By creating leaf shelters early in the season, *Pseudotelphusa* sp. caterpillars have large and persistent effects on seasonal patterns of herbivore recruitment to and/or retention by white oak trees.

**Key words:** ecosystem engineering; leaf shelter; Lepidoptera; oak herbivore community; Ozark plateau, Missouri; *Quercus alba*; species richness; white oak.

### INTRODUCTION

The diversity of organisms comprising biological communities is often influenced by interactions among species. The most frequently studied of these biotic interactions are competition, predation, parasitism, and mutualism (Paine 1966, Lawton and Strong 1981, Bronstein 1993, Begon et al. 1996). Organisms, however, can also influence the diversity of their associated communities through their role as ecosystem engineers. Ecosystem engineers influence resource availability by modifying, maintaining, and/or creating new habitats that are subsequently used by other organisms (Jones et al. 1994, 1997). The dam-building activity of beavers (*Castor canadensis*), for example, creates wetland habitat that is colonized by an astounding diversity of plants and animals not associated with free-flowing streams (Naiman et al. 1988, Wright et al. 2002). Similarly, earthen mounds created by burrowing rodents

influence the structure of plant communities (Reichman and Seabloom 2002), and the excavations of sediment-burrowing tilefish and grouper provide habitat refuges for suites of fish and invertebrates (Coleman and Williams 2002). While it has long been recognized that organisms can have major effects on species assemblages by creating or maintaining habitats, studies that separate an organism's engineering impacts from its other biotic effects (e.g., as a competitor, predator, mutualist, or parasite) are currently lacking.

Shelter-building caterpillars also engineer their environment. In constructing leaf shelters (e.g., leaf rolls, ties, folds, and tents), these caterpillars create new habitats on plants that are often used concurrently or subsequently by other insect species (Carroll and Kearby 1978, Carroll et al. 1979, Cappuccino 1993, Cappuccino and Martin 1994). Because leaf shelters increase the structural complexity of the plant, a factor that has been shown to positively influence the diversity of herbivorous insects (Lawton and Strong 1981, Lawton 1983), the presence and/or abundance of shelters on a particular plant may influence the richness of its associated herbivore fauna. While previous studies have shown that artificially constructed leaf shelters, like

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naturally built shelters, are readily colonized by both herbivores and non-herbivores (Cappuccino 1993, Cappuccino and Martin 1994, Larsson et al. 1997, Martinsen et al. 2000), studies examining the effects of leaf shelters on herbivore communities at the whole-plant level are currently lacking.

#### *Study system*

There are at least 40 species of shelter-building Lepidoptera on oaks (*Quercus* spp.) in Missouri (R. J. Marquis et al., *unpublished manuscript*). These include leaf-rollers, leaf-tiers, leaf-webbers, and leaf-folders in the families Gelechiidae, Hesperiiidae, Incurvariidae, Noctuidae, Oecophoridae, Pyralidae, and Tortricidae. The shelters are created using silk produced in specialized exocrine glands and spun from structures called spinnerets (Berenbaum 1999). Upon completing construction, most of the species feed within their shelters, wherein they typically complete development (some of the larger species must build multiple shelters and/or add leaves once food resources have been exhausted; Carroll 1977). The use of oak leaf shelters by other caterpillar species (both concurrently and through time) has been previously described (Carroll and Kearby 1978, Lill 1999). The colonists of previously constructed shelters include both shelter-building and non-shelter-building arthropods from a variety of taxa (J. T. Lill, *unpublished manuscript*). Our previous studies of the herbivores of white oak (*Quercus alba* L.) in Missouri suggested that many of the leaf-tying caterpillar species (i.e., those shelter-builders that create "leaf sandwiches" by binding together overlapping leaves) preferentially take up residence in existing leaf ties, if available, in lieu of constructing them de novo. Leaf-tie formation on oaks at our study site begins in late spring. Subsequent to this, previously constructed ties are available for colonization.

At our study site, one particularly abundant caterpillar in the genus *Pseudotelphusa* (Gelechiidae: currently not described; henceforth referred to as *Pseudotelphusa*) is largely responsible for creating the first set of leaf ties during late spring. Beginning in early June, once the oak leaves have fully expanded and hardened, *Pseudotelphusa* females oviposit, and the resulting caterpillars bind pairs of naturally overlapping leaves into leaf ties. These caterpillars feed by skeletonizing the leaf surfaces of the leaf-tie interior and develop for ~2 wk within these ties, after which they drop to the leaf litter to pupate. Leaf ties made by *Pseudotelphusa* typically contain 1–3 conspecific caterpillars, which in their final instar are <1 cm in length. Despite its small size and inconspicuous nature, *Pseudotelphusa* is one of the most abundant insect herbivores found on white oak in Missouri. Once created by *Pseudotelphusa*, leaf ties provide a habitat that is colonized by a succession of other species (both leaf-tying and non-leaf-tying) throughout the season. By maintaining the leaf ties that would otherwise come apart

when the silk degrades, these secondary colonists maintain the habitat, which in turn is available for subsequent colonization events by other caterpillar species. Colonization, maintenance, and subsequent abandonment can continue to occur long after the original tie-maker has left. Over the course of a single season, we have recorded up to nine different species of leaf-chewing insects within a single leaf tie (J. T. Lill, *unpublished manuscript*). In laboratory rearings of *Pseudotelphusa* from egg hatch to pupation, larvae skeletonized an average of  $9.55 \pm 0.65$  cm<sup>2</sup> ( $\pm 1$  SE) of white oak foliage during their entire development (J. T. Lill and R. J. Marquis, *unpublished data*); this represents ~25% of the tied area of an average pair of leaves (80 cm<sup>2</sup>) that overlap by 50% (the degree of overlap of leaves incorporated into ties is highly variable). Thus, in the majority of leaf ties there is a large amount of remaining leaf tissue following occupation by *Pseudotelphusa*.

Here, we describe a field experiment designed to quantify the relative impact of engineering vs. non-engineering effects of *Pseudotelphusa* on the community of insect herbivores occupying individual white oak saplings over the course of two years. Our study is unique in that we examined the influence of both the shelter and the shelter-builder on the herbivore community, and we did so at the scale of whole plants, the canopies of which are mosaics of engineered and non-engineered habitats.

#### *Study site*

This experiment was conducted at Cuivre River State Park, located near Troy, Missouri. The 2500-ha park is located in the Lincoln Hills region of east-central Missouri. This second growth forest is typical of that found on the Ozark plateau, with an overstory consisting mostly of white oak (*Quercus alba* L.), black oak (*Q. velutina*), and hickory (*Carya* spp.), and an understory of flowering dogwood (*Cornus florida* L.), sassafras (*Sassafras albidum* Nees), sugar maple (*Acer saccharum* Marsh), redbud (*Cercis canadensis* L.), and various oak saplings. The park is surrounded mostly by agricultural land.

#### METHODS

During the spring of 1999, we marked 124 small white oak trees (1–4 m in height) at the study site and randomly assigned them to one of four experimental treatments ( $N = 31$  trees/treatment: leaf-tie removal [R], removal plus artificial ties [R+T], removal plus artificial ties with caterpillars [R+T+C], and control). We removed the leaf-tying caterpillars and separated tied leaves on all trees ( $N = 93$ ) in the three manipulation treatments on 1, 3, 7, 11, 15, and 19 June 1999 and 1, 5, 8, 12, 15, and 19 June 2000. This 3-wk period coincided with the peak of *Pseudotelphusa* shelter-building in both years. Following the removal period, we then created artificial leaf ties on saplings in the

R+T and R+T+C treatments by clipping pairs of adjacent leaves together (10% of the leaves on each tree) using lightweight plastic hair curler clips (Brentwood Beauty Labs International, Hillside, Illinois). This is well within the natural range of leaf-tie densities we have observed previously in the field. Finally, for saplings in the R+T+C treatment, a single early-instar *Pseudotelphusa* caterpillar (collected from non-study trees at the study site) was also placed into each artificial leaf tie at the time it was created. While the fate of these caterpillars was not explicitly monitored, previous experiments have shown that establishment in artificial shelters is very high, on the order of 80–90% (Lill and Marquis 2001). By creating artificial ties with and without *Pseudotelphusa* caterpillars (R+T+C and R+T, respectively), we were able to compare the effects of providing initially unoccupied shelters (engineering effects alone) with initially occupied shelters (engineering + nonengineering effects) on the herbivore community associated with a particular tree. The remaining 31 nonmanipulated saplings (control treatment) provided baseline data on the natural density of leaf ties at the study site.

During three monthly censuses beginning 1 mo after establishing the artificial ties, we searched all leaves on each noncontrol tree (both tied and non-tied leaves), recording the species of each leaf-chewing insect encountered without removal. More than a decade of collecting, photographing, and rearing oak herbivores by R. J. Marquis made possible the in situ species identifications, which were based on larval morphology and natural history. An illustrated field guide to the immature lepidopteran fauna of oaks of Missouri is currently in preparation (R. J. Marquis et al., *unpublished manuscript*). Leaf ties (both artificial and naturally occurring) were opened briefly during each census to record the occupants and then clipped back together. All clips on natural ties were removed 3 d following each census (to allow the occupants to retie the leaves). The total number of ties (and all externally feeding herbivores) was counted on control trees. This experiment was then repeated in its entirety the following year (2000), using the same trees and treatment assignments, excluding trees that had died ( $N = 13$ ) in 1999.

#### Data analysis

The total number of leaf-chewing herbivore species found on each tree was accumulated over the three censuses in each year. Differences in the sizes of trees required that we standardize species richness by a measure of foliage biomass on each tree. Exploratory plots of cumulative species richness on leaf number indicated that this relationship was nonlinear (i.e., the rate of species accumulation decreased with increasing leaf number); as a consequence, we divided species richness values by the cube root of leaf number for each tree, which produced a linear relationship. Repeated-measures ANOVA was used to examine the effect of the

treatments on species richness, with treatment as the between subjects factor and census and year (and their interactions with treatment) as within subject factors. Two a priori contrasts were also made to examine the engineering effects (R vs. the two R+T treatments) and to distinguish the additional nonengineering effects of caterpillar presence (R+T+C) from the engineering effects alone (R+T). *F* statistics for the between subjects effects were based on Wilks' lambda. Only trees that were alive throughout the entire experiment ( $N = 111$ ) were included in the analysis.

To examine the effects of the treatments on herbivore community structure (within each year), we calculated the number of herbivore species per tree (summing over all three censuses) for each of six functional groups: leaf-tying caterpillars, inquiline caterpillars (species that do not construct leaf shelters but occupy them on occasion), shelter-avoiding caterpillars (never found in shelters), beetles, larval sawflies, and grazers (mobile orthopterans) (see Appendix for guild assignments). Canonical discriminant analysis ([CDA], Proc CANDISC; SAS Institute 1989) was used to examine the effects of the treatments on the composite guild structure, using the number of species/leaf<sup>0.33</sup> in each guild as the response variable. Canonical discriminant analysis is useful for analyzing community data collected from field experiments because it reduces the dimensionality of multivariate data by deriving canonical variables (linear combinations of the response variables) that summarize between-treatment variation (SAS Institute 1989) and permits hypothesis testing. Species richness data were  $\log_{10}(x+1)$  transformed prior to analysis to achieve an approximate multivariate normal distribution within each treatment. When the treatment effect was significant in the multivariate main effects model, treatment means were compared with pairwise *F* tests based on Mahalanobis distances (pairwise squared distances between treatment means based on the pooled within-treatment covariance matrix; SAS Institute 1989).

#### RESULTS

A total of 469 and 588 caterpillars were removed from the experimental trees during the removal periods of 1999 and 2000, respectively. As anticipated, the most common species removed was *Pseudotelphusa* sp. (Table 1); the remaining individuals were leaf-tying species typically more abundant later in the season.

Removing the early wave of leaf-tiers (treatment R) significantly reduced the density of leaf ties 1 mo later by an average of 61% (1999) and 54% (2000) compared to control trees. As a result, leaf-tie densities remained significantly reduced throughout the season in both years (Fig. 1). This season-long reduction in tie density occurred despite the fact that the removal treatment ended after 3 wk.

The density of artificial ties added to trees in the R+T and R+T+C treatments was very similar to the

TABLE 1. Summary of leaf-tie experiment to quantify the impact of *Pseudotelphusa* on insect herbivores occupying white oak.

Variable	1999	2000
Total number of trees	123	111
Leaves per tree (mean ± 1 SE)	248.6 ± 10.7	252.9 ± 11.4
Total leaf-tying caterpillars removed during 3-wk period (% that were <i>Pseudotelphusa</i> )	469 (75)	588 (54)
Artificial ties created (range for individual trees)	799 (5–45)	897 (4–60)
Total leaf-chewing herbivore species recorded on experimental trees (range for individual trees)	71 (7–32)	78 (8–34)

natural tie density on control trees: the fixed density of artificial ties, 5.0 ties/100 leaves, fell well within the 95% CI for control means for all censuses in both years. However, because natural ties were also formed in these treatments, the mean (± 1 SE) total leaf-tie density (averaged across the three censuses) in these

two treatments was significantly increased (relative to controls) by 18.4 ± 5.4% (1999) and 46.6 ± 5.7% (2000) in the R+T treatment and by 31.1 ± 3.2% (1999) and 49.6 ± 6.5% (2000) in the R+T+C treatment. The density of leaf ties on individual trees in the artificial tie treatments, however, never exceeded the maximum tie density found in the control treatment.

Over the course of the three censuses, 71 (1999) and 78 (2000) species of leaf-chewing insects (plus one snail) were recorded on the experimental trees. Control trees were not included in this tally because only non-shelter-inhabiting herbivores were recorded for these trees (leaf shelters were left undisturbed all season, and thus the occupants were unknown). The community of herbivores found on the experimental trees was very similar between years (64 species were found in both years; Sorenson's similarity index = 0.872), and ~30%

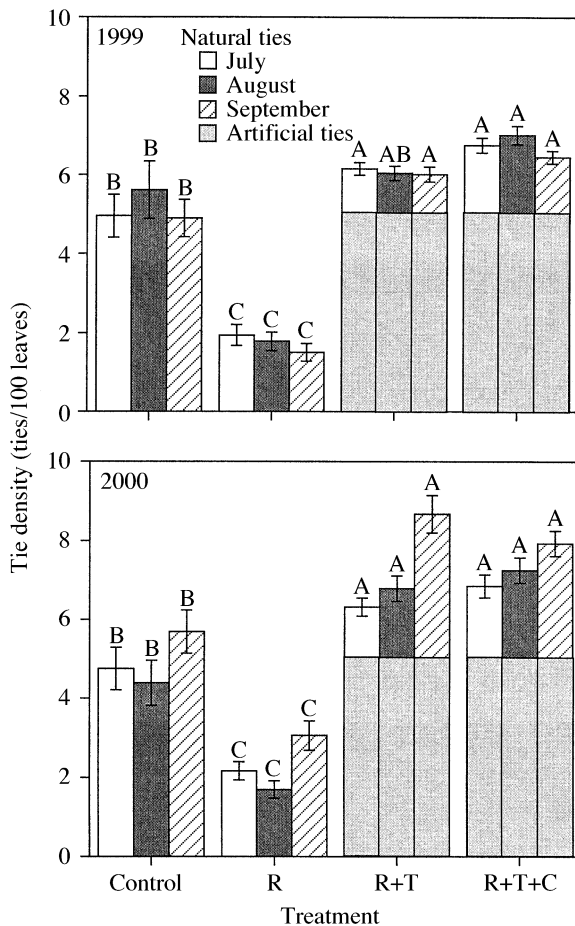


FIG. 1. Average leaf-tie density on white oak trees over the course of the season during two consecutive years (R, removal; T, artificial ties added; C, caterpillars added to artificial ties). Error bars are ± 1 SE. Within a census, means with the same letter are not significantly different by Fisher's LSD test. The density of artificial ties in the +T treatments was fixed at 5.0 leaf ties/100 leaves throughout the experiment (additional leaf ties were those naturally occurring).

TABLE 2. Leaf-tying/webbing caterpillars recorded on experimental white oak trees.

Family	Species
Gelechiidae	<i>Arogalea cristifasciella</i> (Cham.)
	<i>Chionodes fuscomaculella</i> (Cham.)
	<i>Coleotechnites quercivorella</i> (Cham.)†
	<i>Pseudotelphusa</i> sp. nov.
Hesperiidae	<i>Erynnis juvenalis</i> (F.)‡
	<i>Erynnis brizo</i> (Bdv. & Leconte)‡
Noctuidae	<i>Morrisonia confusa</i> (Hbn.)
	<i>Charada deridens</i> (Gn.)§
Oecophoridae	<i>Antaeotricha humilis</i> (Zell.)
	<i>Antaeotricha osseella</i> (Wlsm.)
	<i>Antaeotricha schlaegeri</i> (Zell.)
	<i>Psilocorsis cryptolechiella</i> (Cham.)
	<i>Psilocorsis quercicella</i> (Clem.)
	<i>Psilocorsis reflexella</i> (Clem.)
Pyralidae	<i>Setiostoma xanthobasis</i> (Zell.)
	<i>Oneida lunulalis</i> (Hulst)
	<i>Salebriaria engeli</i> (Dyar)
	<i>Salebriaria tenebrosella</i> (Hulst)
Tortricidae	<i>Tetralopha expansens</i> (Wlk.)
	<i>Anclis divisana</i> (Wlk.)
	<i>Choristoneura rosaceana</i> (Harr.)
	<i>Pandemis limitata</i> (Rob.)

Note: Nomenclature and authors follow Hodges (1983).  
 † Recorded only in 2000.  
 ‡ In the field, we were not able to discriminate between these two species until 2000.  
 § Recorded only in 1999.

TABLE 3. Repeated-measures AVOVA for cumulative species richness of leaf-chewing herbivore on white oak during three censuses over two years.

Source	df	F	P
Between subjects			
Treatment	2, 79	12.94	0.0001
Contrasts			
Removal vs. artificial ties	1, 79	25.26	0.0001
Ties empty vs. ties occupied	1, 79	0.53	0.4674
Within subjects			
Year	1, 79	4.96	0.0288
Year $\times$ Treatment	2, 79	5.55	0.0056
Census	2, 78	669.27	0.0001
Census $\times$ Treatment	4, 156	0.78	0.5401
Year $\times$ Census	2, 78	19.64	0.0001
Year $\times$ Census $\times$ Treatment	4, 156	0.36	0.8338

of the species in both years made leaf shelters by tying together nearby leaves (Table 2).

Treatment had a highly significant effect on species richness (Table 3), with trees in the removal treatment supporting fewer species than trees with artificial ties. Averaged over the three censuses, trees in the removal treatment had 38% (1999) and 14% (2000) fewer herbivore species than trees in the two artificial tie treatments (Table 3; Fig. 2). The significant year  $\times$  treatment interaction reflects this difference in the magnitude of the treatment effects in the two years. The pre-planned contrasts show that the treatment effect was due to the difference between the removal treatment (R) and the two artificial tie treatments (R+T and R+T+C). Although mean species richness was slightly higher in 1999 in the R+T+C treatment compared to the R+T treatment, the two treatments did not differ significantly during any of the census periods in either year. The significant census effect reflects the seasonal turnover in the oak herbivore community (which is essentially linear in all years and treatments). The slopes of the accumulation curves were steeper in 2000 than in 1999 yielding a significant year  $\times$  census interaction term.

While there was considerable overlap in the insect communities found in the three treatments (all three shared 41/71 [1999] and 50/78 [2000] species), several species were found exclusively on trees in the two artificial tie treatments. Excluding species represented by a single individual (singletons), 10 species were unique to the R+T and R+T+C treatments. Of these, five species were restricted to the artificial tie treatments in both years and five were restricted in one year and absent (from all treatments) in the other. The former included three caterpillars (*Antaeotricha humilis*, *Setiostoma xanthobasis* [both Oecophoridae], and *Adoneta spinuloides* [Limacodidae]) and two orthopterans (unidentified species in the genera *Melanoplus* [Acrididae] and *Scudderia* [Tettigoniidae]), all of which are either obligate or facultative occupants of leaf shelters (except for *A. spinuloides*, which is a shelter-avoider).

By contrast, trees in the removal treatment contained no species (excluding singletons) that were not also found on trees in the artificial tie treatments in one or both years.

The means of the first canonical variable (CAN1) differed significantly among the treatments in both years ( $F_{12,168} = 6.16$ ,  $P = 0.0001$  [1999];  $F_{12,148} = 2.63$ ,  $P = 0.0033$  [2000]; Fig. 3) and the  $R^2$  between CAN1 and treatment was 0.50 in 1999 and 0.30 in 2000. By contrast, CAN2 did not significantly separate treatment means in either year ( $F_{5,85} = 0.80$ ,  $P = 0.56$  [1999];  $F_{5,75} = 0.55$ ,  $P = 0.74$  [2000]). In both years, analysis of the Mahalanobis distances indicated that the removal treatment differed significantly from each of the two artificial tie treatments, which did not differ from one another. The leaf-tying guild made the largest positive contribution to CAN1 in both years, with sawflies and beetles also making positive contributions in 1999 and 2000, respectively (Fig. 4). The remaining guilds made relatively small contributions to CAN1 (either positive or negative) in each year and generally had a greater association with CAN2. Univariate ANOVAs (not reported) testing the treatment effect on the log-transformed richness of each of the eight herbivore guilds strongly support these multivariate results, indicating

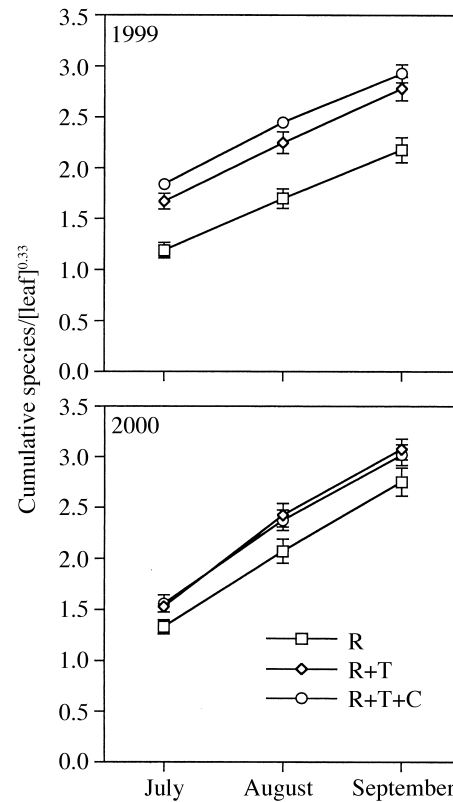


FIG. 2. Mean cumulative species richness of leaf-chewing herbivores over the season in three experimental treatments (R, removal; T, artificial ties added; C, caterpillars added to artificial ties). Error bars are  $\pm 1$  SE.

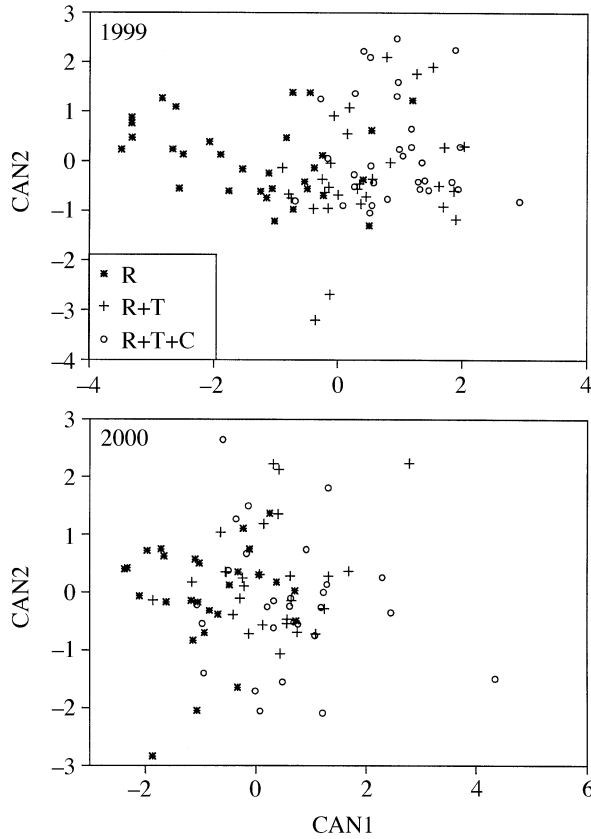


FIG. 3. Scatter plot of two canonical variables (CAN1 and CAN2) depicting the composite responses of six herbivore guilds to three experimental treatments (R, removal; T, artificial ties added; C, caterpillars added to artificial ties). Significant treatment effects were detected in both years ( $F_{12,168} = 6.16, P = 0.0001$  [1999];  $F_{12,148} = 2.63, P = 0.0033$  [2000]).

that trees with artificial ties had significantly increased species richness of leaf-tying caterpillars in both years and increased richness of sawflies and beetles in 1999 and 2000, respectively. There were no significant treatment effects for the other guilds in either year.

DISCUSSION

These results demonstrate that the availability of leaf shelters within a tree's canopy can be an important organizing factor and determinant of species richness for the associated insect herbivore community. By creating and/or maintaining these structures, leaf-tying caterpillars provide a limiting resource (Jones et al. 1997) and in so doing, influence the number of species of leaf-chewing herbivores attacking individual trees throughout the season. The possible resources that leaf shelters provide include a favorable microclimate for desiccation-prone Lepidoptera larvae, increased food quality, shelter from the elements (rain, dislodgement, temperature extremes), and protection from natural enemies (Fukui 2001). We are currently investigating

which of these possible benefits are enjoyed by common leaf-tie occupants of *Q. alba*.

While leaf shelters have been shown previously to have strong local effects on arthropod diversity (Martinsen et al. 2000), this experiment is the first to document these effects for entire plants. When experiments are conducted at the branch level (e.g., Martinsen et al. 2000), increased diversity in branches with leaf shelters compared to branches without could reflect the spatial redistribution of individuals already present on a particular plant. In contrast, the increased richness in the artificial tie treatments shown here suggests that herbivores are actively recruiting to and/or remaining longer on plants with increased densities of leaf shelters. Thus, our results strongly suggest that trees with differing numbers of ties represent very different resources.

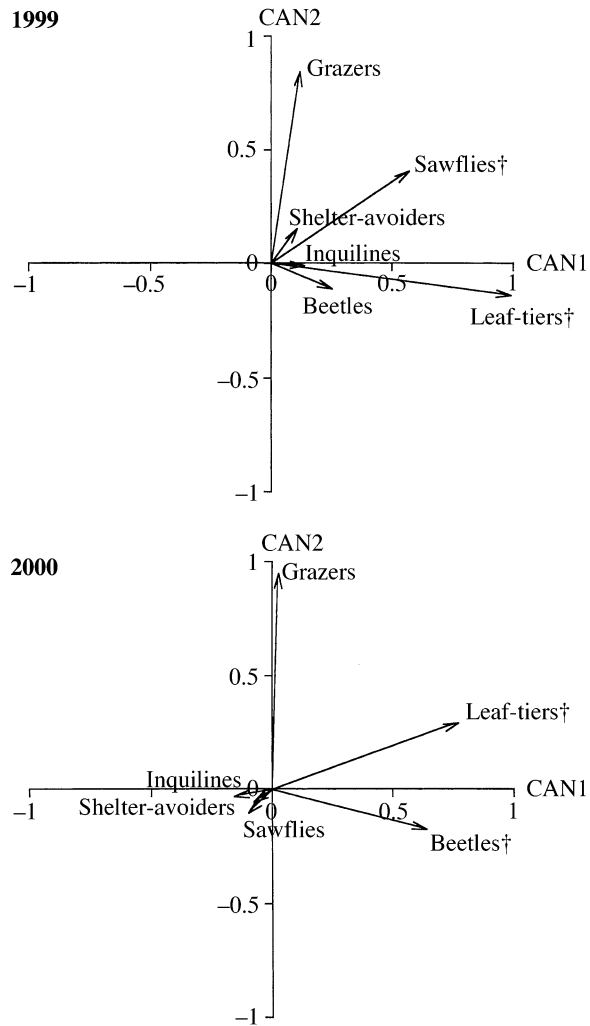


FIG. 4. Total canonical structure depicting contributions of each of six herbivore guilds to the canonical coefficients CAN1 and CAN2 in both years. Dagger symbols indicate guilds in which the species richness varied significantly among treatments in univariate ANOVAs.

A combination of observational and experimental evidence indicates that leaf shelters serve as oviposition sites for a variety of herbivore species (including both shelter-builders and non-shelter-builders; Carroll and Kearby 1978, Cappuccino 1993) lending support to the "active recruitment" hypothesis. In our oak system, we have found that the rate of oviposition by all arthropods inside tied leaves was 4–5 times higher than on non-tied leaves (J. T. Lill and R. J. Marquis, *unpublished data*). It is also possible, however, that the shelter effect on oak herbivore species richness is due in part to increased survival (resulting from decreased predation, parasitism, or desiccation; Fukui 2001) or increased fidelity on plants with increased shelter density. Further experiments are needed that quantify the rates of oviposition, mortality, and larval dispersal on trees with varying shelter densities. Even though roughly one-third of the 80+ herbivore species encountered in the study are capable of constructing leaf shelters, we consider *Pseudotelphusa* to be the most important ecosystem engineer in our system. Because it constructs the majority of the early season leaf shelters on white oak, we attribute the bulk of the treatment effects on species richness to *Pseudotelphusa*. Because we did not find any significant differences between the artificial tie treatments (with and without a *Pseudotelphusa* caterpillar initially present), we conclude that the construction of leaf shelters is the principal mode of interaction between *Pseudotelphusa* and the complex of other insect herbivore species found on white oak. This ecosystem engineering effect superceded all nonengineering effects stemming from conventional trophic interactions, such as competition (both direct and indirect) for food, living space, and enemy-free space (Karban 1989, Strauss 1991, Damman 1993, Wootton 1994). To our knowledge, this is the first study to experimentally quantify both the engineering and nonengineering effects of ecosystem engineers on local biodiversity. However, because virtually all of the initially empty shelters created in the R+T treatment had been colonized by the end of each season and thus presented similar visual and olfactory cues to potential colonists, our ability to assess nonengineering effects (e.g., due to the presence of the caterpillar within the shelter) was compromised as the season progressed.

Two additional lines of evidence suggest that the early wave of shelters built by *Pseudotelphusa* plays a pivotal role in this system. First, the canonical discriminant analysis indicated that the herbivore guild most affected by the removal of these early shelters was the leaf-tiers. Subsequent species of leaf-tiers (after *Pseudotelphusa*) appear to have greater success colonizing trees with preexisting shelters, despite potential competitive effects (direct and indirect) of occupying previously and/or currently occupied shelters (Zwofler 1979, Heinrich and Collins 1983, Steiner 1984, Pallini et al. 1998). Second, the lack of colonization of trees in the removal treatment for the entirety of the season

indicates that the early shelters created by *Pseudotelphusa* are not readily replaced by later colonizing species. If leaf-tier colonization occurs by random oviposition or by passive dispersal (e.g., by larval ballooning), we would expect that the density of leaf ties would increase in each successive census. The fact that it does not suggests that cues used by the first generation of *Pseudotelphusa* in selecting colonization sites differ from those used by subsequent colonists (including the second generation of *Pseudotelphusa*). As a group, the leaf-tiers appear to prefer preexisting shelters when they are available; since *Pseudotelphusa* is largely responsible for creating the initial shelters, our data suggest that trees not colonized by *Pseudotelphusa* during the early season may enjoy a measure of protection from this leaf-tying guild. One factor that is likely to influence early colonization is plant architecture: white oak trees with fewer touching leaves are less likely to be colonized by leaf-tiers than those with more touching leaves (Marquis et al., *in press*).

Two other guilds of herbivores, sawflies and beetles, also responded to the treatments, but their effects were smaller than the leaf-tiers and differed between years. These guilds are composed of only a few species each (three species and six species for sawflies and beetles, respectively), so interannual variation in the population of one or a few species may have had a large effect on species richness of the entire guild. Indeed, the mean densities of the two most common beetle species (a case-bearing beetle in the genus *Pachybrachis* and the introduced asiatic oak weevil *Cryptepistomus castaneus*) were respectively 100% and 1000% greater in 1999 than in 2000. Similarly, the most common sawfly (a gregarious species of *Caliroa*) was ~40% greater in 2000 than 1999. Collectively, these three species are among the most common secondary inhabitants of leaf shelters, so when their populations are reduced, they are likely to be found exclusively on trees with high densities of shelters. For this reason, the contribution of these two guilds to the treatment effect was only detected in the year they were low in abundance. In contrast, when they were abundant, they were found on all trees and thus contributed little to treatment effects on community composition. This result suggests that leaf ties may serve as important safe sites for these species during population lows.

The species richness values of the other three herbivore guilds (inquiline caterpillars, shelter-avoiding caterpillars, and grazers) were unaffected by the treatments. This indicates that the density of leaf ties on a tree had little effect on the recruitment, survival, or retention of non-shelter-building caterpillars and mobile orthopterans (almost all of which occupy leaf shelters on occasion) and did not repel species from experimental trees. Our finding that leaf shelters influenced some herbivore guilds but not others is consistent with the pattern of guild dependency reported by Damman (1993) in his analysis of the mechanisms and di-

rections (positive or negative) of herbivore–herbivore interactions reported in the literature.

Shelter-building is just one means by which herbivores may have positive effects on each other. Other pathways include feeding-related changes in plant quality (induced susceptibility of the plant; Karban and Baldwin 1997: Table 4.2) and associational resistance against natural enemies (e.g., Fritz 1983, Smiley et al. 1988). In the case of leaf-tiers on oaks, experiments are needed to clarify the potential benefits received by secondary occupants of leaf ties, whether they be resource-based, enemy-based, or some combination of the two (see Damman 1993).

As ecosystem engineers, shelter-building caterpillars may influence both local (i.e., tree-level) and regional (e.g., habitat-level) patterns of arthropod diversity, due to their high densities and broad distributions (Jones et al. 1994). Although the structures are small and somewhat ephemeral (lasting one season at most), they are used by a large number of insect species, most of which have relatively short life spans relative to the duration of a typical leaf tie (6–8 wk; J. T. Lill and R. J. Marquis, *unpublished data*). Inasmuch as the results of this study are typical for white oak, shelter-building caterpillars may play an important role in structuring forest insect communities through much of eastern North America, where white oak is commonly a dominant canopy species (Burns and Honkala 1990). Moreover, because shelter-building caterpillars comprise a significant component of many regional herbivore faunas (35% of the 1100+ species of British microlepidoptera and >50% of the Canadian tree-feeding microlepidoptera; McGugan 1958, Prentice 1962, 1963, 1965, Gaston et al. 1992), their collective constructions may influence regional patterns of insect herbivore diversity throughout much of the broad-leaved forests of Europe and North America.

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#### LITERATURE CITED

- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology. Individuals, populations, and communities*. Second edition. Blackwell Scientific, Boston, Massachusetts, USA.
- Berenbaum, M. 1999. Shelter-making caterpillars: rolling their own. *Wings* **22**:7–10.
- Bronstein, J. L. 1993. Our current understanding of mutualism. *Quarterly Review of Biology* **69**:31–51.
- Burns, R. M., and B. H. Honkala. 1990. *Silvics of North America 2. Hardwoods*. Agriculture Handbook 654, Volume 2. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.
- Cappuccino, N. 1993. Mutual use of leaf-shelters by lepidopteran larvae on paper birch. *Ecological Entomology* **18**:287–292.
- Cappuccino, N., and M.-A. Martin. 1994. Eliminating early-season leaf-tiers of paper birch reduces abundance of mid-summer species. *Ecological Entomology* **19**:399–401.
- Carroll, M. R. 1977. Observations on microlepidopterous oak leaf tiers (Lepidoptera: Gelechioidea) in central Missouri. Thesis. University of Missouri, Columbia, Missouri, USA.
- Carroll, M. R., and W. H. Kearby. 1978. Microlepidopterous leaf tiers (Lepidoptera: Gelechioidea) in central Missouri. *Journal of the Kansas Entomological Society* **51**:457–471.
- Carroll, M. R., M. T. Wooster, W. H. Kearby, and D. C. Allen. 1979. Biological observations on three oak leaf-tiers: *Psilocorsis quercicella*, *P. reflexella*, and *P. cryptolechiella* in Massachusetts and Missouri. *Annals of the Entomological Society of America* **72**:441–447.
- Coleman, F. C., and S. L. Williams. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology and Evolution* **17**:40–44.
- Damman, H. 1993. Patterns of interaction among herbivore species. Pages 132–169 in N. E. Stamp and T. M. Casey, editors. *Caterpillars: ecological and evolutionary constraints on foraging*. Chapman and Hall, New York, New York, USA.
- Fritz, R. S. 1983. Ant protection of host plant's defoliator: consequence of an ant–membracid mutualism. *Ecology* **64**:789–797.
- Fukui, A. 2001. Indirect interactions mediated by leaf shelters in animal–plant communities. *Population Ecology* **43**:31–40.
- Gaston, K. J., D. Reavey, and G. R. Valladares. 1992. Intimacy and fidelity: internal and external feeding by the British microlepidoptera. *Ecological Entomology* **17**:86–88.
- Heinrich, B., and S. L. Collins. 1983. Caterpillar leaf damage, and the game of hide-and-seek with birds. *Ecology* **64**:592–602.
- Hodges, R. W. 1983. *Checklist of the Lepidoptera of America north of Mexico*. Wedge Entomological Foundation, London, UK.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* **69**:373–386.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as ecosystem engineers. *Ecology* **78**:1946–1957.
- Karban, R. 1989. Community organization of *Erigeron glaucus* folivores: effects of competition, predation, and host plant. *Ecology* **70**:1028–1039.
- Karban, R., and I. T. Baldwin. 1997. *Induced responses to herbivory*. Chicago Press, Chicago, Illinois, USA.
- Larsson, S., H. E. Haggström, and R. F. Denno. 1997. Preference for protected feeding sites by larvae of the willow-feeding leaf beetle *Galerucella lineola*. *Ecological Entomology* **22**:445–452.
- Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* **28**:23–39.
- Lawton, J. H., and D. R. Strong. 1981. Community patterns and competition in folivorous insects. *American Naturalist* **118**:317–338.
- Lill, J. T. 1999. *The influence of adjacent trophic levels on life history of Psilocorsis quercicella*. Dissertation. University of Missouri, St. Louis, Missouri, USA.
- Lill, J. T., and R. J. Marquis. 2001. The effects of leaf quality on herbivore performance and attack from natural enemies. *Oecologia* **126**:418–428.
- Marquis, R. J., J. T. Lill, and A. Piccinni. *In press*. Effect of plant architecture on colonization and damage by leaf-tying caterpillars of *Quercus alba*. *Oikos*.



- Martinsen, G. D., K. D. Floate, A. M. Waltz, G. M. Wimp, and T. G. Whitham. 2000. Positive interactions between leafrollers and other arthropods enhance biodiversity on hybrid cottonwoods. *Oecologia* **123**:82–89.
- McGugan, B. M. 1958. Forest Lepidoptera of Canada. Volume 1. Papilionidae to Arctiidae. Bulletin number 128. Department of Forestry of Canada, Ottawa, Canada.
- Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. *BioScience* **38**:753–762.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- Pallini, A., A. Janssen, and M. W. Sabelis. 1998. Predators induce interspecific competition for food in refuge space. *Ecology Letters* **1**:171–177.
- Prentice, R. M. 1962. Forest Lepidoptera of Canada. Volume 2. Nycteolidae, Notodontidae, Noctuidae, Liparidae. Bulletin number 1013. Department of Forestry of Canada, Ottawa, Canada.
- Prentice, R. M. 1963. Forest Lepidoptera of Canada. Volume 3. Lasiocampidae, Drepanidae, Thyatiridae, Geometridae. Bulletin number 1034. Department of Forestry of Canada, Ottawa, Canada.
- Prentice, R. M. 1965. Forest Lepidoptera of Canada. Volume 4. Microlepidoptera. Bulletin number 1142. Department of Forestry of Canada, Ottawa, Canada.
- Reichman, O. J., and E. W. Seabloom. 2002. The role of pocket gophers as subterranean ecosystem engineers. *Trends in Ecology and Evolution* **17**:44–49.
- SAS Institute. 1989. SAS/STAT user's guide, version 6. Fourth edition, Volume 1. SAS Institute, Cary, North Carolina, USA.
- Smiley, J. T., P. R. Atsatt, and N. E. Pierce. 1988. Local distribution of the lycaenid butterfly, *Jalmenus evagorus*, in response to host ants and plants. *Oecologia* **76**:416–422.
- Steiner, A. L. 1984. Observations on the possible use of habitat cues and token stimuli by caterpillar-hunting wasps: *Eudynerus foraminatus* (Hymenoptera: Eumenidae). *Quaestiones Entomologicae* **20**:25–34.
- Strauss, S. Y. 1991. Indirect effects in community ecology: their definition, study, and importance. *Trends in Ecology and Evolution* **6**:206–210.
- Wootton, J. T. 1994. The nature and consequence of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**:443–466.
- Wright, J. P., C. G. Jones, and A. S. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* **132**:96–101.
- Zwölfer, H. 1979. Strategies and counterstrategies in insect population systems competing for space and food in flower heads and plant galls. *Fortschritte der Zoologie* **25**:331–353.

#### APPENDIX

A table with a list of leaf-chewing herbivores recorded in the study with guild assignments is available in ESA's Electronic Data Archive: Ecological Archives E084-014-A1.