

HABITAT CREATION AND BIODIVERSITY AT SMALL SCALES: LEAF-TYING CATERPILLARS AS ECOSYSTEM ENGINEERS

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Abstract. Ecosystem engineers are organisms that physically modify the environment, creating, maintaining, modifying, and destroying habitat for other species. Although many species of ecosystem engineers create habitat for many non-engineering species, how large an effect their engineering activities have on biodiversity is largely unknown. For example, leaf-tying caterpillars tie two or more leaves together with silk to create protected habitats in which they feed. However, other arthropods also occupy these leafties when the original caterpillar is present and after the caterpillar has developed and departed. In this project, the effect of leaf-tying on the species richness of leaf-chewing herbivorous insects on red oaks (*Quercus rubra*) was determined using natural and artificial leaf ties. Counts of the number of individuals of each species of leaf-chewing herbivore found in natural and artificial leaf shelters were conducted to distinguish the effects of the leaftier from the effects of the tied leaf structure. Similar counts were conducted for untied pairs of leaves that served as "unengineered" controls. The study examined effects at a number of levels of organization: the patch (a pair of leaves), the habitat type (comprised of artificial tied, natural tied, or untied patches), and the landscape (the combined universe of naturally tied and untied habitat types). Data were used to estimate differences in the species richness of tied and untied habitat types. The species richness of natural and artificial leafties was not significantly different, suggesting that the presence of the physical structure accounts for most of the effects of leafties on species richness. The landscape level species richness of insect herbivores increased by about 50% at the scale of a few trees when these leaf-tying engineers were present. The overall effect was largely due to a low community overlap between the insect herbivores in leafties and those on untied leaves.

INTRODUCTION

Many organisms physically modify the environment through their daily activities, and in the process create habitat for other species. Jones et al. (1997) defined such organisms as physical ecosystem engineers – organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials, thereby modifying, maintaining, or creating habitats.

There are many examples of engineers in the ecological literature (see Jones et al. 1994, 1997; Gutiérrez et al. 2003; and Crooks 2002 for reviews) and while they are not always referred to as engineers, they all alter the environment in ways that affect other species. For example, beaver build dams that create ponds, facilitating the existence of other organisms that cannot build dams themselves, yet are dependent on the pond environment (Pollock et al. 1995). Trees are also engineers. A forest is different from grassland because trees affect the temperature by casting shade, the humidity by evapotranspiration, the structure of the forest floor by dropping leaf litter, and shelter for animals via branches and trunks (Callaway and Walker 1997, Facelli and Pickett 1991). Other engineers modify trees in their search for food or habitat. Woodpeckers drill holes in the trunks, which are later occupied by other organisms (Daily et al. 1993).

Numerous examples of ecosystem engineering exist, yet only a few studies have quantified how much biodiversity in a given ecosystem is due to habitat creation by other organisms (Wright et al. 2002, Lill and Marquis 2003). An engineer could have a positive or negative effect on biodiversity at the patch scale, depending on how it changes the environment and how species respond to that type of environment, but at sufficiently large scales engineers will likely increase the biodiversity by increasing overall habitat diversity (Jones et al. 1997).

How engineers affect biodiversity at various scales needs to be quantified so that the effects of engineers can be compared.

There are at least two reasons why comparative studies of ecosystem engineers across scales are needed. First, ecosystem engineers are everywhere, in every habitat on every part of the globe. There may be common factors influencing the degree to which engineers affect biodiversity at the landscape level that can only emerge from comparisons. Second, it is important to consider engineers in conservation. Conservation efforts concentrate on saving individual species, such as species classified under the Endangered Species Act, and groups of species in biodiversity "hotspots". Since engineers control the availability of habitat for many other species, they can create biodiversity "hotspots", and so conserving engineers can have disproportionately large positive impacts on overall biodiversity conservation. Here, knowing the spatial scale at which an engineer has the maximum effect on biodiversity can facilitate conservation planning.

Leaf-tying caterpillars, which inhabit many species of deciduous trees, are an example of engineers. In early summer, after leaves have fully expanded and hardened, these caterpillars tie two or more overlapping leaves together with silk to make shelters in which they feed and rest. While they make these shelters for their own benefit, other species of arthropods, such as insects and spiders, use these shelters while the caterpillar is present and after the caterpillar has departed (Carroll and Kearby 1978, Carroll et al. 1979, Cappuccino 1993). The shelters reduce dislodgement from wind and rain, provide safety from natural enemies, a favorable microclimate, and perhaps a reduction in antiherbivore defense or increase in food quality (Fukui 2001).

Removing the leaf-ties from a tree reduces the species richness of leaf-chewing herbivorous insects on that tree (Lill and Marquis 2003). The goal of the current study was to quantify the degree to which leaf-tying caterpillars increase the species richness of leaf-chewing herbivorous insects in the forest at different scales, by comparing the presence and abundance of these insects on tied leaf pairs with adjacent untied leaf pairs on red oaks (*Quercus rubra*). Species richness was expected to increase as more leaves were sampled until it reached an asymptote at the point where all of the species that inhabit both tied and untied leaves were found. The asymptotic values for species richness on tied and untied leaves could then be compared. Counts of the number of individuals of each species of leaf-chewing herbivore found in naturally and artificially created leaf shelters were made to separate the effects of the engineer from the effects of the physical structure. Leaf-chewing herbivorous insects were the only inhabitants of tied and untied leaves quantified in this study because time constraints precluded identification of all inhabitants. A biomass equation for red oaks was used to scale the results to the tree level. Information required by the equation included the proportion of tied leaves on accessible branches (branches on which the leaves could be reached without the use of a ladder), the dry mass of the leaves, and the average diameter of the trees at breast height.

This experiment involved measures across several levels of organization: (1) the patch level of a pair of leaves; (2) the habitat type level, comprised of artificial tied, natural tied, or untied patches; (3) the landscape level, comprised of tied and untied habitat types. Sampling of the leaves occurred at the patch level. To test if the engineered structure accounted for the community of inhabitants, artificial and natural tied habitat types were compared. To ascertain the effect of the tied leaves on the species richness of the landscape, species-area curves were constructed.

METHODS

Study Site

The experiment was conducted at the Institute of Ecosystem Studies, Millbrook, NY. Three sites were chosen that had at least twenty-four accessible red oak trees (*Quercus rubra*). Each tree had low branches with at least 176 total leaves to allow the collection of eight leaf-ties per tree along with twenty untied leaves surrounding each tie. The first site, on Cary Drive, had 31 red oaks. The second site, on a dirt road that connects to Cary Drive,

had 26 red oaks. The third site, on the Tea House Hill Road, had 37 red oaks. Since sites were located close enough to each other (within 2 miles), and due to constraints on within-site sample sizes, data sets were pooled for analysis.

Experimental Protocol

During the summer of 2002, as soon as the first naturally tied leaves were observed (June 20), artificial ties were created on 12 red oak trees at each site by using plastic curler clips to fasten pairs of adjacent red oak leaves together (see Lill and Marquis 2003) at a density of 8 ties per tree for a total of 288 ties on 36 trees. Ties were distributed evenly over accessible branches within a tree and between the selected oaks at each site. Leaves selected for artificial ties overlapped naturally, which avoided stress on the petioles, were not already tied by leaf-tying caterpillars, and had less than 5% existing herbivore damage. The remaining red oak trees at each site were used for monitoring the timing of the creation of natural ties and for collecting natural ties.

Fourteen days after constructing artificial ties, leaf censusing began (July 4). At each site, artificial ties, an equal number of natural ties on different trees, and the ten nearest untied leaf pairs for each tie were examined for the presence of leaf-chewing herbivores – Lepidopteran caterpillars, beetles, sawflies, and other insects. Natural and artificial ties were destructively sampled at each site. When it was not known if an insect was an herbivore, the insect was observed in the laboratory to see if it chewed or skeletonized red oak leaves. Insects were identified through the use of field guides (Wagner et al. 1997, Wagner et al. 2001) and through personal communication with John Lill. Adjacent untied leaf pairs were examined *in situ*. The census took place over a week (July 4 – 9), with daily collections in the morning and identification of collected species in the afternoon. Artificial and natural ties were kept in the lab in 16 oz. deli containers for a week to identify any insects that hatched from eggs already laid on the leaves.

Data Analysis

Data were analyzed to answer two questions. 1) Does the presence of the engineered structure account for most of the effect on species richness? 2) What is the size of the effect on species richness as a function of scale? To answer the first question, natural and artificial tied treatments were compared. To answer the second question, natural tied and untied treatments were compared. The tied treatment showed the effect of the engineer on species richness in ties, and the untied treatment represented the species richness of the habitat without the engineer. The combination of the two gave the species richness of the landscape.

Abundances and incidences of each insect species found in both habitat types were compared. The average incidence and abundance of all species was also compared between habitat types. Incidence was defined as the fraction of patches inhabited by a given species, and abundance was defined as the average number of individuals of that species found in a patch. Incidences of the shared species were analyzed using a chi square test, with the null hypothesis that species would have the same incidence in both habitat types. Abundances of shared species were fourth root transformed to normalize the distribution, and compared using a two-tailed t-test. The overall incidences and abundances of habitat types were compared using two-tailed t-tests.

The Morisita-Horn index of similarity was calculated for each comparison of habitat types, using species richness and abundance to derive a similarity score between the two communities. A score of 1.000 indicates complete overlap, while a score of 0.000 indicates no overlap.

Rarefied species richness was estimated using Coleman rarefaction using EstimateS (Colwell 1997). Species-area curves were made to visually represent similarities and differences between habitat types, with rarefied species richness being plotted on the y-axis and cumulative number of patches being plotted on the x-axis. The landscape species-area curve was plotted from resampling of pooled data from natural tied and untied patches, weighted by

the relative abundance of the respective habitat types, again using Coleman rarefaction in EstimateS. The difference between the landscape curve and the untied curve expressed as a percent is the magnitude of the engineering effect of the leaf-tying guild on species richness.

Conversion of Patch to Tree

When analyzed, the data should reveal the degree to which leaf-tying caterpillars increase biodiversity at the patch, habitat, and landscape levels. To convert calculations to the tree level, biomass equations for red oaks were used (Ter-Mikaelian and Korzukhin 1997). These equations are of the form $M = caD^b$, where M is the oven-dry weight of a biomass component of a tree (kg), D is the diameter of the tree at breast height (cm), a and b are regression parameters, and c is a correction factor. For this study M was the total dry mass of the foliage of a red oak tree, $a = 0.0238$, $D = 10.14$ cm, $b = 1.86$, and $c = 1.167$.

At the end the first census, accessible tied and untied leaves were counted on all natural tie trees to estimate the relative numbers of untied and tied patches. Many of the trees were saplings, and all of their leaves could be counted. For the rest of the trees, natural tie distribution was assumed to be uniform, although leaf-ties have been observed to be more common in the understory and on the edges of forests (Carroll and Kearby 1978, Carroll et al. 1979). The diameter at breast height (dbh) was measured for all of the natural tie trees. The dry mass of three pairs of natural tied leaves from each natural tie tree was determined by drying the leaves in an oven after the occupants had been identified, weighing the leaves after they were dry. The dbh and the dry mass per leaf were averaged over the total set of natural tie data.

The average dbh for natural tie trees was inserted into the above equation to determine the total dry mass of the foliage of an average tree. The total dry mass of the leaves was divided by the average mass per leaf to determine the total number of leaves on a tree. This number was divided by two to determine the total number of patches per tree, since a patch was defined as a pair of leaves. To determine the number of tied leaves, the total number of leaves was multiplied by the average proportion of tied leaves to total leaves. This number was divided by two to determine the number of tied patches per tree. The total number of patches per tree was calculated to be 2,160, with 1,965 untied patches and 195 tied patches. Once the number of patches at which leaf-tying caterpillars have the maximum effect on biodiversity was calculated, this number was converted to the number of red oak trees in a forest associated with a given increase in biodiversity of herbivorous insects.

RESULTS

Natural tied vs. artificial tied habitat types

The expectation for this comparison was that there would be no significant differences between the two treatments; the engineered structure would account for all of the effect of leaf-ties on species richness. The same number of leaf-ties were collected for both the artificial and natural treatments ($n = 275$), but 71.6% of the natural ties were inhabited, while only 51.6% of the artificial leaf-ties were inhabited. The total species richness, or total number of species, was similar in each treatment, with 21 species found in the natural ties and 23 species found in the artificial ties. Of the 16 species found in both habitat types, the incidences of only two species and the abundances of only three species were significantly different (Table 1). The incidences of all species found in natural ties compared with all species found in artificial ties did not differ (mean incidence per species ± 1 SD, natural ties: 0.0480 ± 0.540 patches occupied/total patches, artificial ties: 0.0316 ± 0.0380 patches occupied/total patches, t-test, $P = 0.249$). The overall abundance between the two habitat types did not differ either (mean abundance per species ± 1 SD, natural ties: 0.0634 ± 0.100 individuals/patch, artificial ties: 0.0356 ± 0.0462 individuals/patch, t-test, $P = 0.237$). The Morisita-Horn index of similarity between natural and artificial tied treatments was 0.901.

The species-area graphs for the natural and artificial tied treatments are shown in Figure 1. The error bars show the standard deviation for each data point. The curves are very similar to each other, with overlapping standard deviations.

Natural tied vs. natural untied habitat types

Three groups of leaf-chewing herbivorous insects were found inside the tied pairs of leaves: leaf-tying caterpillars, beetles, and inquiline caterpillars. The insects found on the untied leaves included caterpillars, beetles, and other insects that were too large to fit in leaf-ties: katydids, grasshoppers, and walking sticks. The occupation rate of tied leaf pairs was much higher than that of untied leaf pairs: 71.6% of the tied leaf pairs were occupied, while 3.7% of the untied leaf pairs were occupied. The species richness of each habitat type was similar, with 21 species found in natural ties and 26 species found in natural untied patches. Of the 6 species found in both habitat types, four were significantly different in incidence and five were significantly different in abundance (Table 2). The average incidence of species in natural tied patches was 32.7 times higher than the average incidence in natural untied patches (mean incidence per species \pm 1 SD, natural tied: 0.0480 ± 0.540 patches occupied/total patches, natural untied: 0.00147 ± 0.00262 patches occupied/total patches, t-test, $P < 0.001$). The average abundance of species in natural tied patches was 42.3 times higher than the average abundance in natural untied patches (mean abundance per species \pm 1 SD, natural tied: 0.0634 ± 0.100 individuals/patch, natural untied: 0.00150 ± 0.00271 individuals/patch, t-test, $P = 0.003$). The Morisita-Horn index of similarity between natural tied and untied treatments was 0.037.

The species-area graphs for the natural tied and untied treatments are shown in Figure 2. The error bars represent the standard deviation of each data point. The tied curve rises rapidly, while the untied curve rises more slowly, due to the lower incidences of insects on untied leaves. The standard deviations for the landscape curve do not overlap with those of the untied curve. None of the curves reaches an asymptote, so the effect of the leaf-tying caterpillars on species richness was calculated by expressing the difference between the landscape curve and the untied curve as a percentage (Figure 3).

DISCUSSION

The lack of statistically significant differences between the artificial tied and natural tied communities, with respect to incidence and abundance, suggests that the presence of the leaf-tie structure accounts for most of the effects of the leaf-ties on species richness. More natural leaf-ties were inhabited than artificial ties because a leaf-tying caterpillar had to make the structure in the first place, while the artificial leaf-ties were made by the investigator. Some leaf-tying caterpillars will abandon a leaf-tie as the food supply diminishes or once they complete development (Carroll and Kearby 1978, Carroll et al. 1979), which would account for some of the natural leaf-ties being unoccupied at the time of sampling.

There was little overlap between the tied and untied communities, as evidenced by the low Morisita-Horn score for these communities. The untied habitat type had significantly lower abundances and incidences for the species that were common to both habitat types, and for the habitat type as a whole. The higher value of the landscape curve at most scales also indicated low species overlap between habitat types. The engineering guild of leaf-tying caterpillars has the largest effect on species richness at small scales, leveling out to about 50% at the scale of about 3000 patches, or 1.5 trees. The results show that a few oak trees in a forest can dramatically increase the biodiversity of herbivorous insects when leaf-ties are present.

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APPENDIX

TABLE 1. Artificial tied vs. natural tied incidences and abundances by species

| Species | Incidence | | | Abundance | | |
|-----------------------------|------------------|------------------|-----------------------|------------------|------------------|-----------------------|
| | Artificial Tied | Natural Tied | <i>P</i> ^a | Artificial Tied | Natural Tied | <i>P</i> ^b |
| Unidentified leaftier sp. 1 | 0.00727 ± 0.0851 | 0.00727 ± 0.0851 | 1.00 | 0.00727 ± 0.0851 | 0.00727 ± 0.0851 | 1.00 |
| <i>P. quercicella</i> | 0.135 ± 0.342 | 0.193 ± 0.395 | 0.0917 | 0.182 ± 0.563 | 0.451 ± 1.25 | 0.0181 |
| <i>C. rosaceana</i> | 0.0436 ± 0.205 | 0.0545 ± 0.228 | 0.564 | 0.0473 ± 0.229 | 0.0545 ± 0.228 | 0.583 |
| <i>A. cristifasciella</i> | 0.0836 ± 0.277 | 0.120 ± 0.326 | 0.181 | 0.0836 ± 0.277 | 0.131 ± 0.369 | 0.141 |
| Unidentified leaftier sp. 2 | 0.0327 ± 0.178 | 0.0436 ± 0.205 | 0.513 | 0.0327 ± 0.178 | 0.0436 ± 0.205 | 0.505 |
| Unidentified beetle sp. 1 | 0.0291 ± 0.168 | 0.0145 ± 0.120 | 0.248 | 0.0291 ± 0.168 | 0.0145 ± 0.120 | 0.244 |
| <i>A. divisiana</i> | 0.0255 ± 0.158 | 0.0436 ± 0.205 | 0.251 | 0.0255 ± 0.158 | 0.0436 ± 0.205 | 0.244 |
| <i>A. schlaegeri</i> | 0.0218 ± 0.146 | 0.124 ± 0.330 | <0.001 | 0.0218 ± 0.146 | 0.127 ± 0.345 | <0.001 |
| <i>P. reflexella</i> | 0.0545 ± 0.228 | 0.0582 ± 0.235 | 0.857 | 0.0764 ± 0.359 | 0.0836 ± 0.387 | 0.842 |
| <i>Pseudotelphusa</i> sp. | 0.0545 ± 0.228 | 0.109 ± 0.312 | 0.0253 | 0.0545 ± 0.228 | 0.116 ± 0.343 | 0.0178 |
| Unidentified leaftier sp. 3 | 0.00364 ± 0.0603 | 0.00727 ± 0.0851 | 0.564 | 0.00364 ± 0.0603 | 0.00727 ± 0.0851 | 0.563 |
| Unidentified beetle sp. 2 | 0.00727 ± 0.0851 | 0.00364 ± 0.0603 | 0.564 | 0.0109 ± 0.135 | 0.00364 ± 0.0603 | 0.520 |
| <i>Lithophane</i> sp. | 0.00727 ± 0.0851 | 0.00727 ± 0.0851 | 1.00 | 0.00727 ± 0.0851 | 0.00727 ± 0.0851 | 1.00 |
| <i>Pseudotelphusa</i> sp. | 0.124 ± 0.330 | 0.105 ± 0.308 | 0.529 | 0.135 ± 0.373 | 0.120 ± 0.368 | 0.530 |
| <i>C. fuscomaculella</i> | 0.0545 ± 0.228 | 0.0764 ± 0.266 | 0.317 | 0.0582 ± 0.250 | 0.0764 ± 0.266 | 0.320 |
| <i>E. delphinii</i> | 0.00364 ± 0.0603 | 0.00364 ± 0.0603 | 1.00 | 0.00364 ± 0.0603 | 0.00364 ± 0.0603 | 1.00 |

^a The incidence *P* values are based on chi square tests.

^b The abundance *P* values are based on two-tailed t-tests.

Significant *P* values (<0.05) are indicated in **bold**.

TABLE 2. Natural tied vs. natural untied incidences and abundances by species

| Species | Incidence | | | Abundance | | |
|---------------------------|---------------------|----------------------|-----------------------|---------------------|----------------------|-----------------------|
| | Natural Tied | Natural Untied | <i>P</i> ^a | Natural Tied | Natural Untied | <i>P</i> ^b |
| Unidentified beetle sp. 1 | 0.0145 + 0.120 | 0.00764 ± 0.0871 | 0.229 | 0.0145 + 0.120 | 0.00800 ± 0.0931 | 0.00659 |
| <i>A. divisiana</i> | 0.0436 ± 0.205 | 0.00109 ± 0.0330 | <0.001 | 0.0436 ± 0.205 | 0.00109 ± 0.0330 | <0.001 |
| <i>A. schlaegeri</i> | 0.124 ± 0.330 | 0.00109 ± 0.0330 | <0.001 | 0.127 ± 0.345 | 0.00109 ± 0.0330 | <0.001 |
| Unidentified beetle sp. 3 | 0.00364 ± 0.0603 | 0.000364 ± 0.0191 | 0.268 | 0.00364 ± 0.0603 | 0.000364 ± 0.0191 | 0.0596 |
| <i>Lithophane</i> sp. | 0.00727 ± 0.0851 | 0.000364 ± 0.0191 | 0.0442 | 0.00727 ± 0.0851 | 0.000364 ± 0.0191 | 0.00925 |
| <i>M. tentoriferella</i> | 0.00364 ± 0.0603 | 0.00109 ± 0.0330 | 0.000523 | 0.00364 ± 0.0603 | 0.00109 ± 0.0330 | <0.001 |

^a The incidence *P* values are based on chi square tests.

^b The abundance *P* values are based on two-tailed t-tests.

Significant *P* values (<0.05) are indicated in **bold**.

TABLE 3. Appendix of taxonomic groups encountered during the study

| Order | Family | Genus and Species | Herbivore guild ^a |
|-------------|-----------------|--|------------------------------|
| Coleoptera | Curculionidae | <i>Cryptepistemus castaneus</i> | Beetle* |
| Coleoptera | ? | ? | Beetle* |
| Coleoptera | ? | ? | Beetle* |
| Coleoptera | ? | ? | Beetle* |
| Coleoptera | ? | ? | Beetle* |
| Coleoptera | ? | ? | Beetle |
| Coleoptera | ? | ? | Beetle* |
| Hymenoptera | Tenthredinidae | <i>Caliroa</i> sp. | Sawfly |
| Lepidoptera | Bucculatricidae | <i>Bucculatrix</i> nr <i>albertiella</i> | Shelter avoider |
| Lepidoptera | Bucculatricidae | <i>Bucculatrix domicola</i> | Shelter avoider |
| Lepidoptera | Gelechiidae | <i>Arogalea cristifasciella</i> | Leaf-tier |

| | | | |
|-------------|----------------|--------------------------------|-----------------|
| Lepidoptera | Gelechiidae | <i>Trypanisima prudens</i> | Shelter avoider |
| Lepidoptera | Gelechiidae | <i>Pseudotelphusa</i> sp. | Leaftier |
| Lepidoptera | Gelechiidae | <i>Pseudotelphusa</i> sp. | Leaftier |
| Lepidoptera | Gelechiidae | <i>Chinodes fuscomaculella</i> | Leaftier |
| Lepidoptera | Geometridae | <i>Lambdina fervidaria</i> | Shelter avoider |
| Lepidoptera | Geometridae | ? | Shelter avoider |
| Lepidoptera | Geometridae | ? | Shelter avoider |
| Lepidoptera | Geometridae | <i>Anacamptodes defectaria</i> | Inquiline |
| Lepidoptera | Geometridae | ? | Shelter avoider |
| Lepidoptera | Geometridae | ? | Shelter avoider |
| Lepidoptera | Geometridae | <i>Hypomecis umbrosaria</i> | Shelter avoider |
| Lepidoptera | Geometridae | ? | Shelter avoider |
| Lepidoptera | Gracillariidae | <i>Phyllonorycter tcheua</i> | Shelter avoider |
| Lepidoptera | Lasiocampidae | <i>Malacosoma disstria</i> | Shelter avoider |
| Lepidoptera | Limacodidae | <i>Euclea delphinii</i> | Inquiline |
| Lepidoptera | Lymantriidae | <i>Orgyia definita</i> | Shelter avoider |
| Lepidoptera | Noctuidae | <i>Acrionicta haesitata</i> | Shelter avoider |
| Lepidoptera | Noctuidae | <i>Chaetoglea sericea</i> | Shelter avoider |
| Lepidoptera | Noctuidae | <i>Acrionicta lobeliae</i> | Shelter avoider |
| Lepidoptera | Noctuidae | <i>Xystopeplis rufago</i> | Shelter avoider |
| Lepidoptera | Noctuidae | <i>Acatia distincta</i> | Inquiline |
| Lepidoptera | Noctuidae | <i>Lithophane</i> sp. | Inquiline |
| Lepidoptera | Noctuidae | <i>Morrisonia confusa</i> | Leaftier |
| Lepidoptera | Notodontidae | <i>Nadata gibbosa</i> | Inquiline |
| Lepidoptera | Oecophoridae | <i>Psilocorsis quercicella</i> | Leaftier |
| Lepidoptera | Oecophoridae | <i>Anteotricha schlaegeri</i> | Leaftier |
| Lepidoptera | Oecophoridae | <i>Psilocorsis reflexella</i> | Leaftier |
| Lepidoptera | Oecophoridae | <i>Machimia tentoriferella</i> | Inquiline |
| Lepidoptera | Pyralidae | <i>Salebriaria engeli</i> | Leaftier |
| Lepidoptera | Pyralidae | ? | Leaftier |
| Lepidoptera | Tortricidae | <i>Choristoneura rosaceana</i> | Leaftier |
| Lepidoptera | Tortricidae | <i>Anclis divisiana</i> | Leaftier |
| Lepidoptera | ? | ? | Leaftier |
| Lepidoptera | ? | ? | Leaftier |
| Lepidoptera | ? | ? | Shelter avoider |
| Lepidoptera | ? | ? | Shelter avoider |
| Lepidoptera | ? | ? | Shelter avoider |
| Lepidoptera | ? | ? | Shelter avoider |
| Lepidoptera | ? | ? | Shelter avoider |

| | | | |
|--|---------------|-----------------------------|-----------------|
| Lepidoptera | ? | ? | Leaf-tier |
| Lepidoptera | ? | ? | Shelter avoider |
| Lepidoptera | ? | ? | Shelter avoider |
| Orthoptera | Tettigoniidae | <i>Scudderia</i> sp. | Grazer |
| Orthoptera | ? | ? | Grazer |
| Phasmida | Phasmatidae | <i>Diaperomera femorata</i> | Grazer |
| ? | ? | ? | Shelter avoider |
| ? | ? | ? | Grazer* |
| ^a Inquilines are caterpillar species that do not make ties but occupy them on occasion; shelter avoiders are species never found inside shelters. | | | |
| * These non-lepidopteran species also have been found inside leaf-ties. | | | |
| ? The Latin names of these taxonomic groups were not determined. | | | |

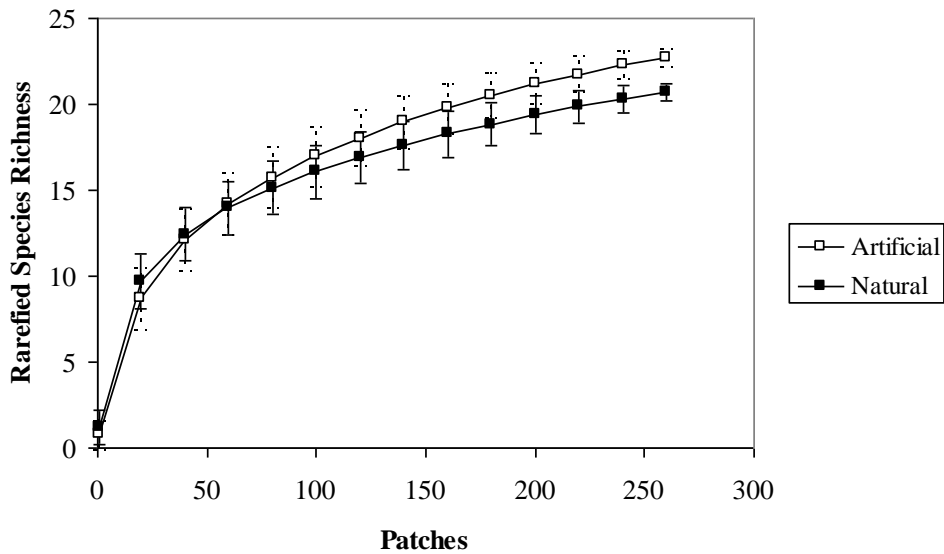


FIGURE 1. Species-area curves (rarefied species richness vs. cumulative patches sampled) for artificial and natural leaf tie habitat types. Species richness was rarefied using the Coleman method. A patch is a pair of tied or untied leaves. Error bars are standard deviations. The data values for every 20 patches only are plotted for clarity.

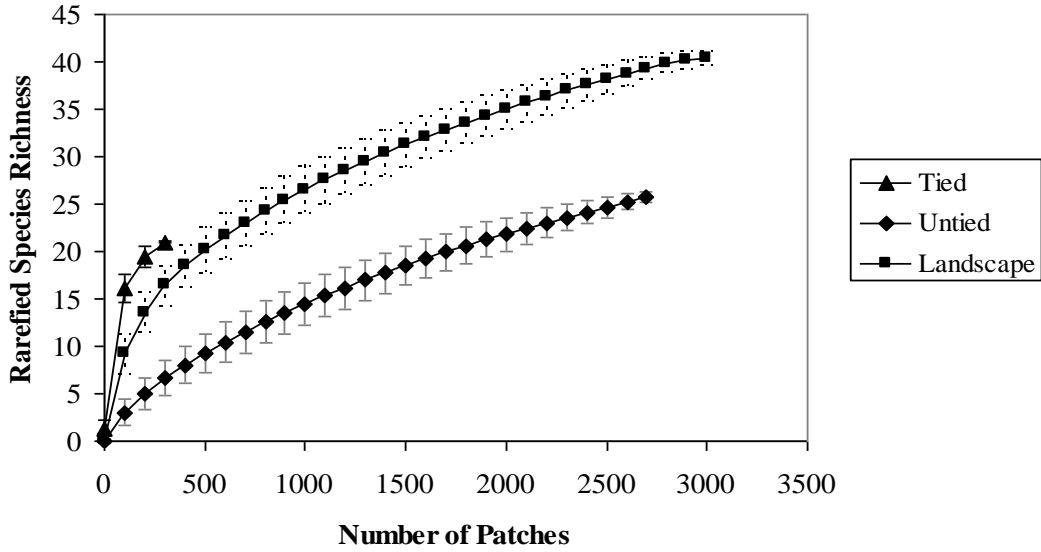


FIGURE 2. Species-area curves (rarefied species richness vs. cumulative patches sampled) for naturally tied and untied leaf habitat types and the landscape resulting from resampling of the habitat types in proportion to their occurrence (10% ties). Species richness was rarefied using the Coleman method. A patch is a pair of tied or untied leaves. The higher value of the landscape curve at most scales indicates low species overlap between habitat types. Error bars are standard deviations. The data values for every 100 patches only are plotted for clarity

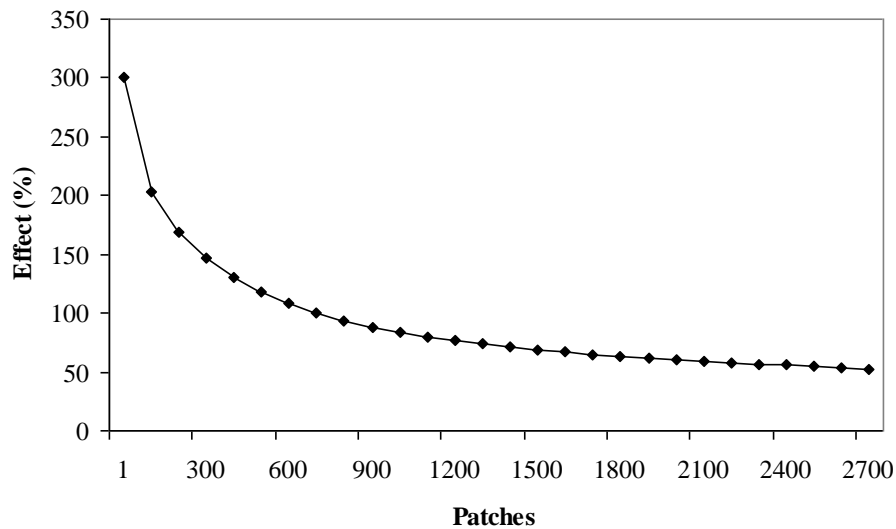


FIGURE 3. The engineering effect on landscape-level species richness, defined as $(\text{landscape species richness} - \text{untied species richness}) / (\text{untied species richness}) \times 100$. In this study, the average red oak tree had 4,320 leaves, or 2,160 patches. The data values for every 100 patches only are plotted for clarity.