

Native leaf-tying caterpillars influence host plant use by the invasive Asiatic oak weevil through ecosystem engineering

CHRISTINA S. BAER AND ROBERT J. MARQUIS¹

Department of Biology, University of Missouri, One University Boulevard, St. Louis, Missouri 63121-4499 USA

Abstract. We tested the effect of leaf-tying caterpillars, native ecosystem engineers, on the abundance and host feeding of an invasive insect, the Asiatic oak weevil, *Cyrtopistomus castaneus* (Roelofs). Leaf quality was previously thought to be the sole factor determining host use by *C. castaneus*, but adult weevils congregate in leaf ties made by lepidopteran larvae (caterpillars). Adult weevil abundance was naturally higher on *Quercus alba* and *Q. velutina* compared to four other tree species tested (*Acer rubrum*, *Carya ovata*, *Cornus florida*, and *Sassafras albidum*). These differences were associated with more natural leaf ties on the two *Quercus* species. In the laboratory, weevils fed on all six species but again preferred *Q. alba* and *Q. velutina*. When artificial ties were added to all six tree species, controlling for differences in leaf-tie density, adult weevil density increased on all six tree species, damage increased on all species but *A. rubrum*, and host ranking changed based on both abundance and damage. We conclude that leaf ties increase the local abundance of *C. castaneus* adults and their feeding. Thus, these native leaf-tying caterpillars engender the success of an invasive species via structural modification of potential host plants, the first described example of this phenomenon.

Key words: *Cyrtopistomus castaneus*; deciduous tree host species; ecosystem engineering; invasive species; leaf-tying caterpillars; Ozark Plateau, Missouri, USA; *Quercus*.

INTRODUCTION

The contingencies that determine the success of species in their invaded habitat are many (Pysek and Richardson 2010). Both positive (e.g., mutualism; Richardson et al. 2000) and negative (e.g., predator–prey [Parker et al. 2006]) interactions between native and invasive species are well documented. In contrast, whether ecosystem engineering positively or negatively affects the success of invasive species is largely unexplored (Bulleri et al. 2008). On the one hand, invading ecosystem engineers frequently foster their own success through habitat modification (Jordan et al. 2008, Tsai et al. 2010). On the other hand, native ecosystem engineers can facilitate the invasion and spread of invasive species through their engineering activities (Maron and Connors 1996, Altieri et al. 2010). Understanding these positive effects of ecosystem engineers may help mitigate the spread and resultant impacts of invasive species (Bulleri et al. 2008, Pearse and Altermatt 2013). Despite the prevalence of insects, there are only two published studies of native insect species (both ants) influencing the abundance of nonnative species (both nonnative plants) through ecosystem engineering (Farji-Brener et al. 2010, Berg-Binder and Suarez 2012).

The leaf- and root-feeding invasive species the Asiatic oak weevil, *Cyrtopistomus castaneus* (Roelofs) (Curculionidae: Coleoptera), is one of the most abundant leaf-chewing insect species on oaks in Missouri, USA (Forkner et al. 2006), and in much of eastern North America (Frederick and Gering 2006). Larval and adult *C. castaneus* feed on numerous deciduous tree species, both oak and non-oak species (Frederick and Gering 2006), with larvae on roots and adults on leaves. Our initial investigation has shown that leaf ties are major congregation sites for adult *C. castaneus* on *Quercus alba*. Leaf ties are leaves tied together with silk to form flat, overlapping surfaces (Wang et al. 2012). In making ties that are then used by *C. castaneus* and other arthropod species (Lill and Marquis 2003, Wang et al. 2012), the leaf-tying caterpillars act as ecosystem engineers (Jones et al. 1997). Adult *C. castaneus* feed in leaf ties and apparently use them as shelter from predators and the abiotic environment, often inhabiting the ties with the original tie-makers (Lill and Marquis 2003). *Cyrtopistomus castaneus* abundance on *Q. alba* at the whole-plant level is positively affected by the number of leaf ties made by caterpillars (Lill and Marquis 2003).

Multiple factors could determine host plant use by adult *C. castaneus*. First, emerging adults from the ground could simply colonize the nearest tree, i.e., their larval host tree. In that case, interspecific patterns of host use by feeding adults would match those of adults emerging from the ground. Second, host use by feeding adults could be determined by leaf quality differences

Manuscript received 4 September 2013; revised 6 January 2014; accepted 12 February 2014. Corresponding Editor: M. D. Eubanks.

¹ Corresponding author.
E-mail: robert_marquis@umsl.edu

among available tree species, as hypothesized by Ferguson et al. (1991, 1992) and Frederick and Gering (2006). Finally, given that this weevil is found preferentially in leaf ties on *Q. alba* relative to single leaves within the same tree (Lill and Marquis 2003), *C. castaneus* may choose among host plant species based on leaf-tie abundance on those trees. In this way, the engineering effects of leaf-tying caterpillars may contribute to host plant choice by this invasive species, its overall abundance, and thus its success as an invader.

This study was designed to disentangle the effects of larval host plant, and leaf quality and leaf ties on the distribution of *C. castaneus* adults on six common tree species. We asked four questions: (1) How are abundances of emerging adults related to the identity of the tree species under which they first appear? (2) What are the feeding preferences of adults in the laboratory? Feeding trials in the laboratory measured host use by adults in the absence of leaf ties. (3) What is the natural abundance of adults on the six tree species, both in natural ties and on single leaves? (4) How do artificial leaf ties influence adult abundance on the six plant species? To answer this last question, we manipulated tree architecture to create equal numbers of artificial leaf ties on the six tree species. If leaf quality alone determines host use by adult weevils, then the experimental addition of leaf ties would not change the distribution and feeding of weevils across the six species. In contrast, if leaf ties affect host use in addition to leaf quality, then adding leaf ties in equal abundances to all six tree species should increase the local abundance of, and feeding by, weevils.

METHODS

Study site and study species

The study was conducted in the North Woods Conservation Area of Cuivre River State Park, located near Troy, Missouri, USA, during the summer of 2009. The area is a northern extension of the Ozark Plateau and supports a secondary oak–hickory forest. In addition to these two major tree taxa, the canopy includes stands of maples. The understory is primarily composed of dogwood, sassafras, ironwood, and canopy saplings. We used six of the most common species at the study site as study species: white oak (*Quercus alba*) and black oak (*Q. velutina*) (both Fagaceae), red maple (*Acer rubrum*, Sapindaceae), flowering dogwood (*Cornus florida*, Cornaceae), sassafras (*Sassafras albidum*, Lauraceae), and shagbark hickory (*Carya ovata*, Juglandaceae). All five genera have representatives in China (eFloras 2008), part of the weevil's natural range. The specific area where the sampling and experiments were conducted is ~4 ha in area, and exemplifies upland forest in the park and the northern Missouri Ozark deciduous forest.

The Asiatic oak weevil *Cyrtopistomus castaneus* (Coleoptera: Curculionidae) (Appendix: Fig. A1A) is native to Japan, China, and Korea, where it feeds on

Quercus serrata and *Q. acutissima* (Morimoto et al. 2006). Apparently nothing else is known of its biology in its native range (T. Ohgushi, *personal communication*) except that it is parthenogenetic (Morimoto et al. 2006). First introduced to the United States in 1933 in New Jersey (Frederick and Gering 2006), it now occurs throughout the eastern United States and adjacent Canada. Because it is abundant and consumes large quantities of root hairs as a larva (Roling 1979) and up to 20% of the understory oak foliage as an adult (Gass and Phillips 1979), it has the potential to influence forest composition. In the forests of eastern Missouri, adults appear in mid-June to early July, with abundances dropping off dramatically by late August (Roling 1979). Adults are frequently gregarious (Roling 1979), and are of equal or greater abundance in the understory than in the canopy (Le Corff and Marquis 1999).

Abundance of emerging adults

Emergence traps were used in the field to determine emerging adult abundance so that we could relate it to the distribution of feeding adults among the six tree species. Two traps each were placed under 60 trees (10 trees per tree species) within 2 m of the trunk of the focal tree. Traps (Appendix: Fig. A1B) were constructed as in Roling (1979), and were erected 17–30 June 2009. Adult *C. castaneus* were collected every 7–14 days until fewer than 10 individuals across all traps were encountered. Emerging adults were dried and weighed.

Adult feeding preference: laboratory feeding trials

Feeding trials in the laboratory were conducted to determine host use of adult weevils in the absence of leaf ties. Two trials were conducted to determine if host preferences were consistent across time. On the first day of each trial (Trial 1, 10 July; Trial 2, 20 July), adult *C. castaneus* were collected from non-study *Quercus alba* saplings. Sprigs of leaves from each tree species were collected and maintained in water. In the laboratory, sprigs of each species were placed together in a 32 ounce [0.338 fluid ounce = 0.01 L] clear plastic delicatesse container with 10 live *C. castaneus* and covered. After 5–7 days leaf damage was measured. Damage by *C. castaneus* consists of distinctive linear channels emanating from leaf margins or previous damage (Appendix: Fig. A1C). Damage was visually estimated at the whole-leaf level using 10 approximately equal categories of percentage area damaged from 0% to 100%. More leaf area remained than that eaten for all containers and all species ($P < 0.0052$).

Natural tie density and adult abundance

Natural abundances of leaf ties and weevils were measured on five unmanipulated individuals (2–5 m tall) of each of the study tree species, selected within the same area as the trees used for the emergence traps. We counted the number of leaves on each tree to estimate tree size. Approximately 300 leaves on each tree were

selected on 1–2 neighboring branches and censused for weevil (29–30 July and 9 September) and leaf-tie abundance (9 September).

Effect of ecosystem engineering on adult abundance and leaf damage

We created equal numbers of artificial leaf ties on another 10 individuals of each tree species (2–5 m tall, again in the same area as the emergence traps) (Wang et al. 2012). On 7–8 July we clipped together 20 pairs of leaves with metal hair clips (Sally's Beauty Supplies, Denton, Texas, USA) to simulate leaf ties, while placing clips on 40 single leaves to control for the effect of placing clips on leaves. Clipped and control leaves were scattered throughout the canopy, with leaves chosen showing little or no damage by herbivores. We removed all natural leaf ties and leaf-tying caterpillars found on the trees. We censused weevil abundance on 27–29 July and 26 August–16 September. We collected all clipped leaves after the second census and visually assessed them for damage by leaf-tying caterpillars (skeletonization, with the upper or lower epidermis remaining), *C. castaneus* (damage as described above), and unscrubbed sources.

Statistical analysis

All analyses were conducted with SAS 9.3 for Windows (SAS 2002–2010). Abundances of emerging adults in traps were tested using repeated measures against a negative binomial distribution (PROC GLIMMIX) for the effect of tree species, with tree as the repeated factor, and the slice option for testing differences among means. We assumed that an adult's larval host tree was the tree under which it emerged, as a tree's roots are concentrated under its crown (Yanai et al. 2006). The effect of census and host species on the dry body mass of emerging adults was tested with an ANOVA of ranked data (PROC GLM) because residuals from the ANOVA of the original data were not normally distributed, and data could not be transformed to conform to a parametric distribution. We treated each weevil as an independent estimate of the effect of host tree and census on body mass as we did not track from which specific trap each emerged. A post hoc Tukey test was conducted to test for differences in mass by tree species.

In the feeding trials, effects of tree species, container (random blocking factor), and trial (also random) on leaf area eaten per day were tested with ANOVA after calculating the area lost, and log₁₀-transforming the data to equalize variances among host species (PROC MIXED). Percentage-of-area-damaged categories were converted to the midpoint percentage of each category and were then multiplied by the mean leaf size for the respective tree species to estimate the leaf area eaten from each leaf in a trial. We calculated mean leaf areas by scanning 100 undamaged leaves per species, using SigmaScan Pro 5.0 (SPSS 1999) to estimate their areas.

We tested whether and leaf-tie density (leaf ties/leaves censused) and *C. castaneus* density (weevils/leaf area censused) varied significantly by tree species on the five unmanipulated trees (July census only as the August census individuals were likely a subset of those counted in July because there is a single generation each year and emergence had all but stopped by late August; Appendix: Fig. A2). This also allowed us to determine whether *C. castaneus* was more likely to occur in natural ties than on single leaves, all using ANOVA. Weevil density was tested using a split-plot design against a Poisson distribution, with tree species as the whole-plot factor and leaf type (tied or not) as the subplot factor (PROC GLIMMIX). Trees with no natural ties were omitted from the analysis.

We also used a generalized linear mixed model (PROC GLIMMIX) based on a Poisson distribution to test the effect of artificial ties on *C. castaneus* abundance by comparing their number on control leaves and in artificial leaf ties. We analyzed the design as a split plot, with tree species as the whole-plot factor and leaf type as the subplot factor. Neither total leaf number, as an estimate of total leaf area, nor the cube root of leaf number, as a measure of tree volume, was correlated with *C. castaneus* abundance on a tree, so we excluded these two variables as covariates in the model. Finally, to estimate the effects of clip type and tree species on leaf area eaten from manipulated trees, we used PROC MIXED, again considering the design to be a split plot, with tree species as the whole factor and leaf position and type (top leaf vs. bottom leaf of an artificial tie and control leaf) as the subplot factor. Initial estimates have shown the damage caused by leaf-tying caterpillars varies between the top and bottom leaf of a leaf tie, so we maintained this distinction for estimating *C. castaneus* damage.

RESULTS

Emerging adult abundance and performance

The species identity of the tree overhead significantly affected *Cyrtopistomus castaneus* abundance in emergence traps. Emergence was highest under *Quercus velutina*, *Acer rubrum*, and *Q. alba*, followed by *Cornus florida*, *Carya ovata*, and *Sassafras albidum* ($F_{5,36} = 4.40$, $P < 0.0031$) (Fig. 1A; Appendix: Fig. A2). Mass of emerging adults was also affected by tree species ($F_{5,577} = 6.59$, $P < 0.0001$) (Appendix: Fig. A3), census ($F_{5,577} = 8.54$, $P < 0.0001$), and the census \times species interaction ($F_{23,577} = 2.47$, $P = 0.0002$).

Adult preference: laboratory feeding trials

In feeding trials, in the absence of leaf ties, adult *C. castaneus* ate leaves from all six tree species, the amount eaten significantly affected by tree species ($F_{5,70} = 9.61$, $P < 0.0001$) (Fig. 1B). On average, weevils ate most from *Q. alba* and *Q. velutina*, followed by *S. albidum*, *C. ovata*, *A. rubrum*, and *C. florida*. The trial effect was not significant ($P = 0.8948$).

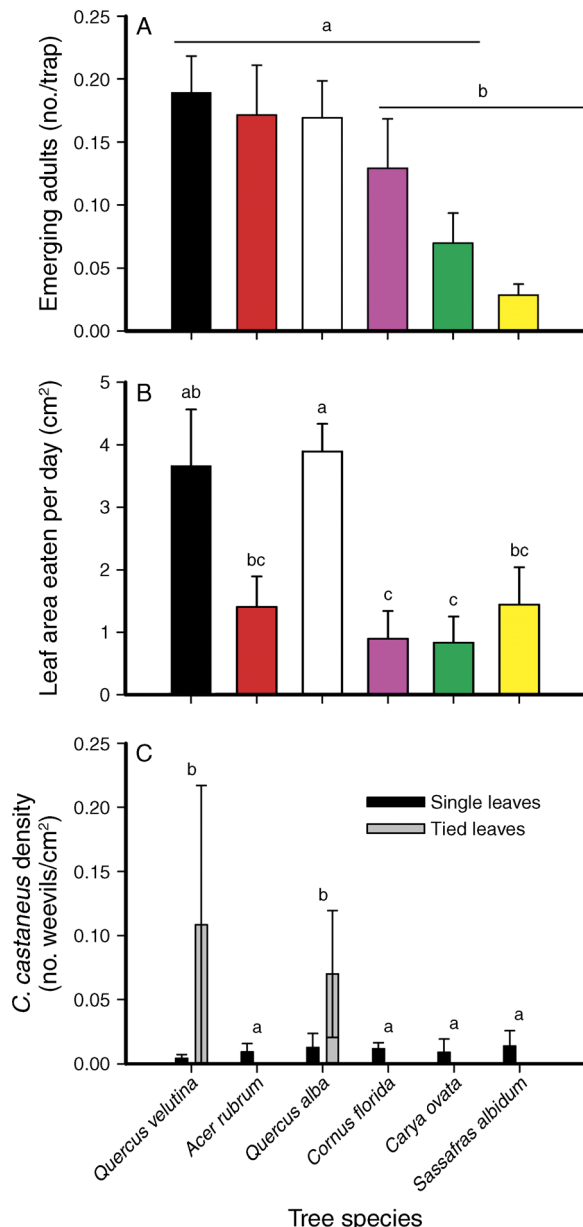


FIG. 1. (A) The number (mean + SE) of *Cyrtopistomus castaneus* (Asiatic oak weevil) adults captured per trap day under the canopy of the six study tree species. (B) The amount of leaf area (mean + SE) eaten by 10 *C. castaneus* adults per feeding chamber when provided with excess leaf material from the six study tree species. (C) *C. castaneus* adult density on unmanipulated trees. Lines and letters above the bars indicate groups of statistically similar tree species ($P < 0.05$).

Natural tie density and adult abundance

Natural tie density varied significantly by species, and this difference was associated with differences in weevil abundance by tree species. *Quercus alba* and *Q. velutina* had 10 times as many natural ties as *C. ovata*, *S. albidum*, and *A. rubrum* ($F_{5,52} = 22.25$, $P < 0.0001$). We found no natural ties on the five *C. florida* trees (Appendix: Fig. A4).

Natural weevil density varied marginally with tree species and the species \times tie status interaction ($F_{4,13} = 3.06$, $P = 0.0558$, and $F_{4,13} = 3.17$, $P = 0.0505$, respectively; tie status, $P = 0.091$). Differences in abundance between tied and single leaves were found for *Q. alba* ($P = 0.0022$) and *Q. velutina* ($P = 0.0024$), but not for the other species ($P > 0.594$) (Fig. 1C). On average on a leaf-area basis there were four times as many weevils in natural ties as on single leaves ($8.4 \pm 2.8 \times 10^{-4}$ weevils/cm² vs. $2.0 \pm 0.5 \times 10^{-4}$ weevils/cm², respectively).

Natural weevil density was correlated with tie density at both the tree level ($r = 0.387$, $P = 0.0027$) (Fig. 2A) and the species level ($r = 0.875$, $P = 0.0225$) (Appendix: Fig. A5). Furthermore, weevil density in natural ties was correlated with the density of those ties ($r = 0.622$, $P = 0.0003$, $n = 28$), while weevil density on single leaves was not ($r = -0.068$, $P = 0.7255$) (Fig. 2B). These correlations suggest that weevils colonize trees with more ties, and then enter those ties.

Effect of ecosystem engineering on adult abundance and leaf damage

Creating leaf ties changed rankings of host species use, whether based on abundance or feeding. Across all tree species, there were 3.5 times as many *C. castaneus* found in artificial leaf ties as on single leaves (effect of leaf type on weevil abundance: 5.2 ± 0.6 vs. 1.8 ± 0.4

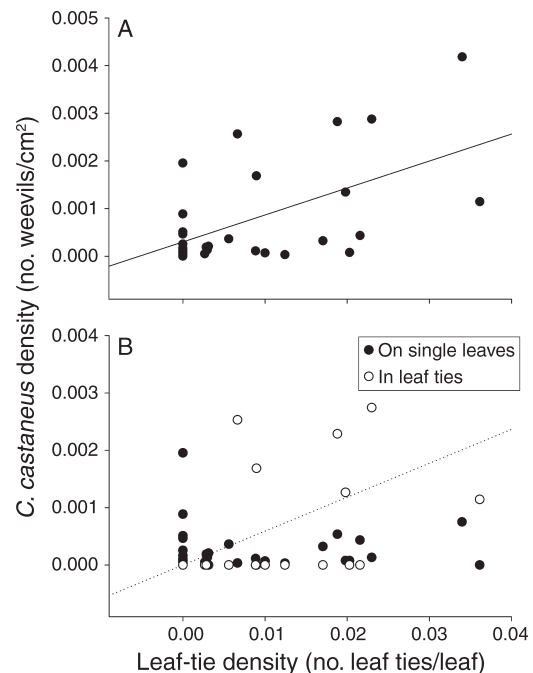


FIG. 2. (A) Relationship between *C. castaneus* adult density and leaf-tie density on unmanipulated trees. (B) Relationships between *C. castaneus* adult density (in leaf ties and on single leaves) and leaf-tie density on unmanipulated trees. The dotted line is the regression for weevil density in leaf ties on density of leaf ties. Circles represent individual trees in both panels.

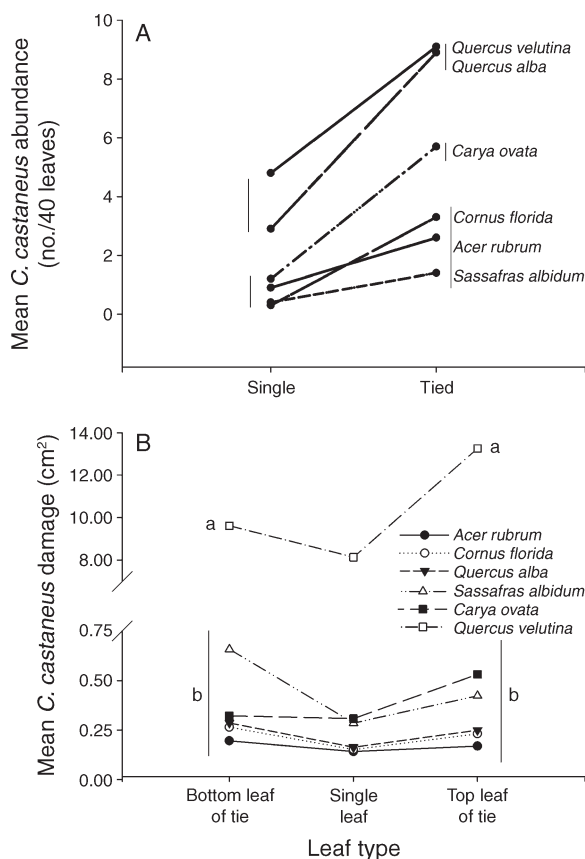


FIG. 3. The effect of adding artificial leaf clips (two adjacent leaves clipped together with a hair clip) to each of the six study tree species on (A) the mean abundance of *C. castaneus* adults per 40 leaves, and (B) *C. castaneus* damage (leaf area missing [cm²]). Single leaves had a hair clip attached to each as a control for the presence of the clip itself. Thin vertical lines indicate significantly different means within each treatment ($P < 0.05$). Significant differences among leaf types are described in Results: Effects of ecosystem engineering on adult abundance and leaf damage.

individuals/40 leaves; $F_{1,3524} = 141.01$, $P < 0.0001$). *Quercus velutina* and *Q. alba* had the most weevils, followed by *C. ovata*, with *C. florida*, *A. rubrum*, and *S. albidum* having the least (species effect: $F_{5,55} = 11.49$, $P < 0.0001$) (Fig. 3A). The extent to which ties increased weevil abundance varied by tree species (clip type \times species interaction: $F_{5,3524} = 3.1$, $P = 0.0085$). As a result, the relative rankings of host use based on abundance changed. Abundance on *Q. alba* became equal to that of *Q. velutina*, while *C. florida* and *A. rubrum* switched ranks (Fig. 3A).

Cyrtopistomus castaneus damage differed significantly with leaf type (top vs. bottom leaf in artificial tie vs. control leaf) (leaf area missing = 2.4 ± 0.2 cm², 1.9 ± 0.1 cm², and 1.5 ± 0.1 cm², respectively; $F_{2,4600} = 26.06$, $P < 0.0001$). In addition, there was a significant species effect ($F_{5,55} = 41.58$, $P < 0.0001$), with *Q. velutina* having significantly more damage than all other species (Fig.

3B). Ties increased damage over single leaves in all species ($P < 0.043$) but *A. rubrum* ($P > 0.08$). As a result, rankings of host use based on damage also changed. *Quercus velutina* was still the most preferred, but *C. ovata* and *S. albidum* were no longer equally preferred, and *C. florida* and *Q. alba* were equally preferred but more so than *A. rubrum* (Fig. 3B).

DISCUSSION

Our results demonstrate that native insect ecosystem engineers can increase the local abundance of an invasive insect species and change host rankings, measured by both abundance and damage. First, differences between numbers of emerging adults (Fig. 1A) and adults on trees (Fig. 1C) demonstrate that aboveground abundance is not simply a result of adults occupying their larval host trees. Furthermore, we show that weevil abundance is greater in natural leaf ties than on single leaves for two tree species (Fig. 1C), and greater in artificial ties than on single leaves for all six tree species (Fig. 3A). Finally, damage to artificial leaf ties was greater than to single leaves in all but *Acer rubrum* (Fig. 3B). Because the weevil is established in our region, we cannot verify that leaf-tying caterpillars facilitated the invasion of *Cyrtopistomus castaneus*. We can conclude, however, that leaf ties increase local weevil abundance.

Almost invariably, host plant choice is considered to be a consequence of the combined effects of host tissue quality and enemy-free space (Mooney et al. 2012). For the generalist *C. castaneus*, host breadth is influenced not just by leaf quality, as previously concluded (Frederick and Gering 2006), but by a third factor, the presence of leaf ties. For *C. castaneus*, and possibly other generalists, such engineered shelters can alter the distribution of insect abundance or feeding among multiple host species. *Cyrtopistomus castaneus* abundance was significantly greater in artificial leaf ties than in single, control leaves for all six tree species (Fig. 3A), and there was a significant between-tree correlation (Fig. 2A) and a significant between-species correlation between leaf-tie density and weevil density (Fig. A5). These results suggest that leaf ties can increase weevil abundance on single plants and across species. In a previous experiment, Lill and Marquis (2003) showed that removal of leaf ties from entire trees of *Quercus alba* reduced *C. castaneus* abundance. Similar experiments are needed for the other five species studied here to establish whether effects at the branch level could be extrapolated to the whole plant. However, the fact that we did not find a significant negative correlation between the number of leaf ties and the number of weevils on single leaves suggests that leaf ties are not simply causing a redistribution of weevils within trees, but drawing them in from the surrounding environment.

The natural abundance of weevils in leaf ties was correlated with tie abundance, but abundance on single leaves was not. These results suggest that weevils are

attracted to trees with more leaf ties, and once they arrive on a tree, they go into those ties. Leaf quality is also likely important, as adult weevils preferentially fed on *Q. alba* and *Q. velutina*, both in the laboratory and in the field experiment. The presence of leaf ties changed the relative ranking of species, but the two oak species were always the most preferred species (Fig. 3).

We have not yet determined the benefit weevils gain from congregating in leaf ties, although protection from predation and the abiotic environment are both possibilities. A change in leaf quality may not be important, as leaves were already mature at the beginning of the experiment. No parasitism of *C. castaneus* has been observed by us or reported in the literature, although protection against parasitism is often a function of leaf shelters (e.g., LoPresti and Morse 2013). Ants facilitate the abundance of nonnative plant species by providing establishment sites of reduced competition (Farji-Brener et al. 2010, Berg-Binder and Suarez 2012), but just the opposite may be the case in our system if multiple species use the same shelters, increasing competition (Sliwinski and Sigmon 2013) or parasitism (Lill et al. 2007).

Leaf quality, in addition to directly affecting weevil abundance, is also likely to indirectly influence *C. castaneus* through its effects on leaf-tie abundance. For example, the abundance of the leaf-tying caterpillar *Pseudotelphusa quercinigracella* on white oak saplings is positively correlated with tannin concentration (R. J. Marquis, *personal observation*). Similarly, plant architecture may affect leaf tie and *C. castaneus* abundance. Plants of *Q. alba* with more touching leaves are more heavily attacked by leaf-tying caterpillars (Marquis et al. 2002), while we found no natural ties on *Cornus florida*, which has small, opposite, and rarely touching leaves.

Previous research has shown that native insects can interact positively with invasive insect species (Lach 2007, Brightwell and Silverman 2010, Styrksy and Eubanks 2010.), but ours is the first to show that local abundance of invasive insect species is influenced by the engineering effects of a native insect species. These findings demonstrate that native insect ecosystem engineers can play an important role in the success of invasive insects, in this case by potentially increasing the invasibility of the forest habitat. Not only would tree species composition be important in the yet-to-be invaded forest, as some tree species are preferred over others based on the nutritive quality of the plant tissue, but—as this study shows—the presence of shelter-building insects would also be a contributing factor. Because shelters built by insects (including leaf structures, cavities produced by stem-boring beetles, web nests built by Lepidoptera, and galls) are common, and are commonly used by non-shelter-building arthropods (Fukui 2001), the positive effects of ecosystem-engineering insects on invasive species are likely underestimated. In our case, the relevant construct is built not by a single species but by a local guild of species, meaning that

multiple engineering species contribute to the positive effect on the invader, and that the effects on the invader are likely buffered against the loss of any one engineering species. An important question that remains is the degree to which native engineers in this and other systems might actually facilitate the initial invasion of exotic species. For invasive arthropods that use engineered plant parts, invasibility is likely a consequence of the interplay of host preference and host abundance for herbivorous arthropods, natural enemy attack, and the modifying effects of engineered constructs.

ACKNOWLEDGMENTS

We thank K. Barnett, J. Reinhardt, A. Duckwell, and C. Welker for help with field work, V. Kuczynska, D. Simberloff, D. Salazar, and two anonymous reviewers for comments on the manuscript, R. Ricklefs for encouragement, B. Schuette and MO-DNR for access to Cuivre River State Park, and T. Ohgushi and C. O'Brien for background information. Funding came from NSF DEB 0614397.

LITERATURE CITED

- Altieri, A. H., B. K. van Wesenbeeck, M. D. Bertness, and B. R. Silliman. 2010. Facilitation cascade drives positive relationship between native biodiversity and invasion success. *Ecology* 91:1269–1275.
- Berg-Binder, M. C., and A. V. Suarez. 2012. Testing the directed dispersal hypothesis: Are native ant mounds (*Formica* sp.) favorable microhabitats for an invasive plant? *Oecologia* 169:763–772.
- Brightwell, R. J., and J. Silverman. 2010. Invasive Argentine ants reduce fitness of red maple via a mutualism with an endemic coccid. *Biological Invasions* 12:2051–2057.
- Bulleri, F., J. Bruno, and L. Benedetti-Cecchi. 2008. Beyond competition: incorporating positive interactions between species to predict ecosystem invasibility. *PLoS Biology* 6: 11136–11140.
- eFloras. 2008. Volumes 4 (*Carya*, *Quercus*), 7 (*Sassafras*), 11 (*Acer*), and 14 (*Cornus*). Missouri Botanical Garden, St. Louis, Missouri, USA. www.efloras.org/index.aspx
- Farji-Brener, A. G., N. Lescan, and L. Ghermandi. 2010. Ecological engineering by a native leaf-cutting ant increases the performance of exotic plant species. *Oecologia* 163:163–169.
- Ferguson, C. S., M. J. Linit, and G. Krause. 1991. Host plant preference of the Asiatic oak weevil (Coleoptera: Curculionidae). *Environmental Entomology* 20:1427–1432.
- Ferguson, C. S., M. J. Linit, and G. Krause. 1992. Dispersion and density of Asiatic oak weevil (Coleoptera: Curculionidae) relative to oak density. *Environmental Entomology* 21: 247–252.
- Forkner, R. E., R. J. Marquis, J. T. Lill, and J. Le Corff. 2006. Impacts of alternative timber harvest practices on leaf-chewing herbivores of oak. *Conservation Biology* 20:429–440.
- Frederick, K. H., and J. C. Gering. 2006. A field study of host tree associations of an exotic species, the Asiatic oak weevil [*Crytepisonomus castaneus* (Roelofs 1873), Coleoptera: Curculionidae]. *American Midland Naturalist* 155:11–18.
- Fukui, A. 2001. Indirect interactions mediated by leaf shelters in animal-plant communities. *Population Ecology* 43:31–40.
- Gass, R. D., and S. O. Phillips. 1979. Missouri pest report. Forestry Division, Missouri Department of Conservation, Jefferson City, Missouri, USA.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957.

- Jordan, N. R., D. L. Larson, and S. C. Huerd. 2008. Soil modification by invasive plants: effects on native and invasive species of mixed-grass prairies. *Biological Invasions* 10:177–190.
- Lach, L. 2007. A mutualism with a native membracid facilitates pollinator displacement by Argentine ants. *Ecology* 88:1994–2004.
- Le Corff, J., and R. J. Marquis. 1999. Understorey and canopy differences in herbivore composition and leaf quality for two oak species in Missouri. *Ecological Entomology* 24:46–58.
- Lill, J. T., and R. J. Marquis. 2003. Ecosystem engineering by caterpillars increases insect herbivore density on white oak. *Ecology* 84:682–690.
- Lill, J. T., R. M. Marquis, M. A. Walker, and L. Peterson. 2007. Ecological consequences of shelter sharing by leaf-tying caterpillars. *Entomologia Experimentalis et Applicata* 124:45–53.
- LoPresti, E. F., and D. H. Morse. 2013. Costly leaf shelters protect moth pupae from parasitoids. *Arthropod-Plant Interactions* 7:445–453.
- Maron, J., and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105:302–312.
- Marquis, R. J., J. T. Lill, and A. Piccinni. 2002. Effect of plant architecture on colonization and damage by leaf-tying caterpillars of *Quercus alba*. *Oikos* 99:531–537.
- Mooney, K. A., R. T. Pratt, and M. S. Singer. 2012. The tri-trophic interactions hypothesis: interactive effects of host plant quality, diet breadth and natural enemies on herbivores. *PLoS ONE* 7(4):e34403.
- Morimoto, K., H. Kojima, and S. Miyakawa. 2006. The insects of Japan, volume 3: Curculionioidea: general introduction and Curculionidae: Entiminae (part 1). Phyllobiini, Polydrusini and Cyphicerini (Coleoptera). Touka Shobo Company, Fukuoka, Japan.
- Parker, J. D., D. E. Burkpile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasives. *Science* 311:1459–1461.
- Pearse, I. S., and F. Altermatt. 2013. Predicting novel trophic interactions in a non-native world. *Ecology Letters* 16:1088–1094.
- Pysek, P., and D. M. Richardson. 2010. Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources* 35:25–55.
- Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmanek. 2000. Plant invasions—the role of mutualisms. *Biological Reviews* 75:65–93.
- Roling, M. 1979. Biology of the Asiatic oak weevil in central Missouri. Dissertation. University of Missouri, Columbia, Missouri, USA.
- SAS. 2002–2010. Statistical analysis software. SAS Institute, Cary, North Carolina, USA.
- Sliwinsky, M., and E. Sigmon. 2013. Why do leaf-tying caterpillars abandon their leaf ties? *PeerJ* 1:e173.
- SPSS. 1999. SigmaScan Pro 5.0. SPSS, Chicago, Illinois, USA.
- Styrsky, J. D., and M. D. Eubanks. 2010. A facultative mutualism between aphids and an invasive ant increases plant reproduction. *Ecological Entomology* 35:190–199.
- Tsai, C., S. Yang, A. C. Trimble, and J. L. Ruesink. 2010. Interactions between two introduced species: *Zostera japonica* (dwarf eelgrass) facilitates itself and reduces competition of *Ruditapes philippinarum* (Manila clam) on intertidal flats. *Marine Biology* 157:1929–1936.
- Wang, H. G., R. J. Marquis, and C. S. Baer. 2012. Both host plant and ecosystem engineer identity influence leaf-tie impacts on the arthropod community of *Quercus*. *Ecology* 93:2186–2197.
- Yanai, R. D., B. Park, and S. P. Hamburg. 2006. The vertical and horizontal distribution of roots in northern hardwood stands of varying age. *Canadian Journal of Forest Research* 36:450–459.

SUPPLEMENTAL MATERIAL

Appendix

Leaf ties and the invasive Asiatic oak weevil: photodocumentation. (Fig. A1, adult weevil, weevil emergence trap, and weevil damage) and figures showing seasonal emergence and mass of adults, density of leaf ties by tree species, and correlation of leaf-tie abundance and weevil abundance by tree species ([Ecological Archives E095-130-A1](#)).