

Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees

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Abstract. Ecosystem engineers, organisms that modify the physical environment, are generally thought to increase diversity by facilitating species that benefit from engineered habitats. Recent theoretical work, however, suggests that ecosystem engineering could initiate cascades of trophic interactions that shape community structure in unexpected ways, potentially having negative indirect effects on abundance and diversity in components of the community that do not directly interact with the habitat modifications. We tested the indirect effects of a gall-forming wasp on arthropod communities in surrounding unmodified foliage. We experimentally removed all senesced galls from entire trees during winter and sampled the arthropod community on foliage after budburst. Gall removal resulted in 59% greater herbivore density, 26% greater herbivore richness, and 27% greater arthropod density five weeks after budburst. Gall removal also reduced the differences in community composition among trees (i.e., reduced beta diversity), even when accounting for differences in richness. The community inside galls during winter and through the growing season was dominated by jumping spiders (Salticidae; 0.87 ± 0.12 spiders per gall). We suggest that senesced galls provided habitat for spiders, which suppressed herbivorous arthropods and increased beta diversity by facilitating assembly of unusual arthropod communities. Our results demonstrate that the effects of habitat modification by ecosystem engineers can extend beyond merely providing habitat for specialists; the effects can propagate far enough to influence the structure of communities that do not directly interact with habitat modifications.

Key words: ecosystem engineer; gall wasp; habitat engineering; indirect interaction; *Quercus lobata*; trait-mediated interaction.

INTRODUCTION

Organisms that create or modify physical habitats can have disproportionately large effects on the diversity and structure of biological communities (Jones et al. 1994, 1997). These ecosystem engineers are generally thought to increase diversity by facilitating species that directly benefit from the habitat modifications (Lill and Marquis 2003, Wright and Jones 2006, Gribben et al. 2009, Meadows et al. 2012). For example, beavers facilitate wetland plants by building dams that create wetlands (Wright et al. 2002), and seagrasses form meadows in soft sediments that support communities

unique to these shallow marine systems (Orth et al. 2006). Most studies on the consequences of ecosystem engineering have focused on the diversity of species that rely on habitats created by engineers. Indeed, one recent study predicts the effects of engineering on landscape-level diversity by looking at the proportion of the landscape that is modified by engineers (Wright 2009). Recent theoretical work, however, suggests that ecosystem engineering could initiate cascades of trophic interactions that shape community structure in unexpected ways, potentially having negative indirect effects on abundance and diversity in components of the community that do not directly interact with the habitat modifications (Sanders et al. 2014). If we are to develop a holistic understanding of species interactions, one that combines trophic and non-trophic interactions (Bascompte 2010, Kefi et al. 2012), we need more empirical work that examines the indirect effects of habitat modification on the composition and structure of ecological communities.

There is increasing evidence indicating that engineering can have negative indirect effects on species that do not physically interact with the engineered

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modifications. For example, agricultural lands formed by human ecosystem engineers indirectly increase the risk of predation for songbird nests in adjacent forest patches by facilitating mammalian predators, like raccoons (Andrén and Angelstam 1988). On a smaller spatial scale, herbivorous leaf beetles disappeared at a faster rate when experimentally placed on leaves near leaf shelters built by leaf-rolling caterpillars than when placed on leaves far from shelters, mostly likely because they were removed by ants tending aphids that had colonized the shelters (Nakamura and Ohgushi 2003). These studies show that engineering can have surprising negative indirect effects, but such studies have been at too fine a scale to show how these effects scale up to the entire community.

Recent work has begun to examine the effects of habitat engineering at community scales that encompass species that do and do not interact directly with the habitat modifications. For example, leaf shelters formed by leaf-tying caterpillars increase diversity of arthropods at the scale of entire trees, which themselves are mosaics of engineered leaf shelters and unmodified foliage (Lill and Marquis 2003, Baer and Marquis 2014). This increased diversity, however, is limited to the recruitment of leaf shelter specialists to leaf shelters, with no consistent effects of leaf shelters on the arthropod community that uses unmodified leaves. The lack of an effect on the community beyond leaf shelters may be unsurprising in this system, however, because leaf shelters are used primarily by leaf-shelter specialists, which are mostly isolated from the arthropod community on the surrounding unmodified foliage (Lill and Marquis 2003). Further, leaf shelters are ephemeral habitats that are built each summer after leaves reach maturity, require maintenance because silk degrades, and fall from trees at the end of the growing season; consequently, these structures seem to have little effect on the broader plant-associated arthropod community (Marquis and Lill 2007).

Organisms that create long-lasting habitat structures likely have higher potential to initiate community-wide indirect effects than do organisms forming short-lived structures (Hastings et al. 2007). One reason for this is simply that persistent structures continue to exert effects after the engineer has died (Jones et al. 1997). A less commonly recognized reason persistent structures could have greater effects is habitat structures persisting through multiple seasons could serve as a refuge during unfavorable seasons and lead to elevated densities of refuge specialists at the beginning of the growing season. This temporally dependent facilitation could initiate priority effects that would influence seasonal assembly trajectories, potentially altering density, richness, and even beta diversity of entire communities assembling following an unfavorable season (Robinson and Dickerson 1987). Recent work has shown that engineered habitats can provide refuge during unfavorable conditions. Woodland salamanders have higher overwintering survival when they reside in earthworm tunnels (Ransom 2010). Gopher tortoise burrows

are used by more than 50 vertebrates and 300 invertebrates, and can serve as thermal refuges during wildfires or other high or low temperature extremes (Pike and Mitchell 2013). Despite our growing appreciation of the positive effects of ecosystem engineers on species persistence during unfavorable conditions, we have a relatively poor understanding of the consequences of long-lasting engineered structures for community assembly in seasonal environments.

We examined the effects of senesced oak apple galls, engineered habitat formed by the California gall wasp (*Andricus quercuscalifornicus*), on the seasonal assembly of arthropod communities on valley oak (*Quercus lobata*), a deciduous tree. Galls are well documented to be microhabitats that support diverse communities of specialized arthropods that are distinct from foliage-dwelling communities (Sanver and Hawkins 2000). Oak apple galls persist on oak branches for many years after they senesce and are abandoned by gall wasps, and the emergence tunnels left behind by eclosing gall wasps are colonized by several species of secondary inhabitants (Fig. 1; Russo 2006, Joseph et al. 2011). In the autumn prior to this study, we observed that many senesced galls contained jumping spiders (Salticidae), generalist predators of herbivorous arthropods. This observation led us to hypothesize (1) that gall wasps would indirectly, via the changes they induce in host-plant structure, suppress density and diversity of herbivores on oak foliage and (2) that these effects would interact with the seasonal community assembly that takes place on oaks each spring. To test for these indirect, trait-mediated interactions, we experimentally removed all senesced galls from entire trees during winter and sampled foliage-dwelling arthropods through community assembly in spring. Our study addressed two main questions: (1) How does persistent habitat engineering indirectly influence the portion of a community that does not directly interact with the habitat modification? (2) How does persistent habitat engineering influence the seasonal community assembly process?

METHODS

Study system

We worked at the University of California, Davis Putah Creek Riparian Reserve (Davis, California, USA; 38.54° N, 121.87° W). Our study site was an oak savanna that recolonized a kiwi orchard abandoned in the late 1970s with an area of approximately 0.17 km². The California gall wasp (*Andricus quercuscalifornicus*) oviposits in valley oak (*Quercus lobata*) twigs in the fall; the eggs overwinter; and larvae eclose and elicit the development of spherical, multi-chambered galls (5–250 cm³) by the host plant in the late spring or summer (Rosenthal and Koehler 1971, Joseph et al. 2011). Galls desiccate, senesce,



FIG. 1. (Clockwise from top left) A valley oak (*Quercus lobata*) during winter with thousands of senesced oak apple galls initiated and abandoned in previous growing seasons by the California gall wasp (*Andricus quercuscalifornicus*), a valley oak without oak apple galls, a senesced oak apple gall showing an emergence tunnel left behind by a California gall wasp, a dissected senesced oak apple gall showing spider silk in several chambers. Photo credits: oaks by R. M. Screen, galls by W. C. Wetzel.

and become woody by the fall, and adults tunnel out soon thereafter. Galls can stay on their hosts for three or more years after being abandoned by *A. quercuscalifornicus* (Russo 2006); these senesced, woody galls are the only galls present on trees during the winter and were the focus of our study. Arthropod community assembly begins with budburst, which was 29 March–2 April in 2013.

Gall removal experiment

In March 2013, we counted oak apple galls on all of the 137 valley oaks at the study site with a height <7 m, the highest we could reach with telescoping poles (20% of valley oaks at the study site). Of those trees, 102 had at least 10 galls: we randomly assigned these trees to a control or gall-removal treatment, stratifying the randomization by gall density to ensure equal representation of treatments across the natural

range of gall density. We also randomly selected 12 of the 35 trees that naturally had zero galls to serve as a naturally gall-free comparison to the experimental gall-removal treatment.

From 16 to 21 March 2013, we sampled the pre-treatment arthropod community on all control trees, removal trees, and naturally gall-free trees using sweep nets and beat sticks with trays. We swept foliage with four sweeps on opposite sides of each tree using 38.1-cm diameter sweep nets. We beat branches on the remaining two sides to collect arthropods into white plastic trays (1235-cm² surface area) with four taps. We collected all arthropods from sweep nets and trays using aspirators and combined them into one sample per tree (hereafter: sweep samples). We also sampled using one sticky trap (120-cm² sticky area) hung from a branch on each tree for 48 h from 15 to 17 March.

From 26 to 29 March, shortly before budburst, we removed all 5026 oak apple galls from the 52 removal

trees using plastic bats and 4-m telescoping poles. All galls on trees at this time of year were initiated, used, and abandoned by gall wasps in a previous summer, making them at least 11 months old at the time of removal. Because our treatment only involved senesced galls, our study isolated the effects of galls as structures from the direct trophic effects of the engineer. In addition, the gall-removal treatment was unlikely to have influenced plant chemistry or physiology because senesced galls are dead tissue. We controlled for the physical disturbance required to remove galls from removal trees by disturbing control and gall-free trees with poles for 1–10 min (1 min per 10 galls) without actually removing galls. We preserved two galls from each removal tree, dissected them under a stereomicroscope, and identified gall inhabitants and evidence of inhabitants, such as spider silk. The rest of the galls were disposed of >5 km off-site. We sampled arthropods on all trees again 2 and 5 weeks following the treatment using both the sweep and sticky trap methods described above (11–14 April 2013 and 2–7 May 2013). We grouped the 6998 arthropod specimens from sweep samples into 238 morphospecies and subsequently identified them to the lowest feasible taxonomic resolution (mainly genus). We identified the 8341 arthropod specimens from sticky trap samples to order.

Finally, we assessed whether the pre-budburst arthropod community within galls continued to use galls throughout the growing season, or if they moved out of galls and onto foliage and stems. We did this by sampling arthropods from branches on 16 May 2015 from 16 randomly selected trees with galls and 16 without galls. We chose one branch (approximately 1 m long) per tree, placed a sheet underneath, carefully bagged and removed each gall on the branch, and then tapped the branch until no additional arthropods fell into the sheet. We collected arthropods from the sheet, cut the branch off the tree, and searched the branch for additional arthropods, which we collected. We dissected all galls and identified arthropods from galls and branches. These data gave us a detailed picture of the composition of the arthropod communities within galls vs. on stems and foliage during the growing season.

Statistical analysis

We addressed our question about the effects of engineering on the part of the community that does not physically interact with the habitat modification (question 1) by asking how removal of galls from a tree influences the foliage-dwelling community. To answer this, we decided a priori to examine the following response variables: density and richness of all arthropods, herbivores, predators, and parasitoids; mean multivariate community composition; and beta diversity (multivariate dispersion). If trees from which we removed galls supported a higher abundance and

diversity of leaf herbivores, it would support our hypothesis that galls indirectly suppressed that group. We addressed our question about the interaction between engineering and seasonal community assembly (question 2) by asking how the effects of gall removal vary through the growing season. If the effects of gall-removal depended on sampling period, it would suggest that the effects of galls interact with the seasonal community assembly process.

Finally, the observation that some trees lacked oak apple galls led us to ask if removal of galls from a tree would make its arthropod community more similar to those on naturally gall-free trees, or if trees that can support galls also support fundamentally different arthropod communities regardless of the actual presence of galls. If the former were true, it would suggest the main difference between these trees for arthropods is the presence of gall habitat. If the latter were true, it would suggest that trees that support galls are inherently different, as hosts for gall-makers and other arthropods, from trees without galls, indicating that the engineering pathway may depend on host-plant quality.

We analyzed sweep and sticky trap data separately because they represent separate parts of the broader oak savanna arthropod community. Sweep sampling captured primarily less mobile, foliage-dwelling organisms that complete development primarily on one oak, whereas the sticky trap sampling captured primarily flying organisms that probably forage at scales larger than single trees. We did not use sticky trap data to answer questions about mean community composition or beta diversity because order-level identifications were too taxonomically coarse for multivariate community analyses. For analysis of sticky trap data, we grouped Araneae, Formicidae, Opiliones, and Hymenoptera excluding bees into a natural enemy category and the rest of the specimens into a potential prey category. These categories are best treated as rough groupings, but it is likely the groupings are accurate for the majority of specimens from each order.

We tested for an effect of gall removal on density and richness of all arthropods, herbivores, parasitoids, and predators using negative binomial generalized linear mixed models (GLMM). The negative binomial distribution accounts for overdispersion inherent to ecological count data (Ver Hoef and Boveng 2007). We analyzed pre-treatment data alone to determine whether treatment groups differed before the experiment. We analyzed the two post-treatment samples simultaneously in models with a fixed effect for time period. We used likelihood ratio tests (Bolker et al. 2009) to test for differences in density and richness between the removal and control groups (question 1), to test for an interaction between removal treatment and sampling period (question 2), and to test for differences between removal and naturally gall-free trees. For response variables with significant removal \times time interactions, we conducted additional GLMMs separately for each sampling

period to test for differences between the removal and control groups within sampling period.

Each post-treatment model had a random effect for tree identity to account for the non-independence of trees re-sampled through time. We also included initial gall density as a covariate in all univariate models, because we hypothesized that the effect of gall removal would increase with the number of galls present before removal. Thus we also included an interaction between gall removal and initial gall density in all models with an effect of gall removal. Finally, we used a random effect for sampling date because we hypothesized conditions on any particular day could influence capture rates. Random effect structures were set by our experimental design, and therefore we did not test their significance. The details of each model and likelihood ratio test can be found in Appendix S1. We fit all univariate models using maximum likelihood with the R packages *glmmADMB* and *bbmle* (Bolker 2008, 2012, Fournier et al. 2012, Skaug et al. 2013, R Core Team 2014).

We used a permutational multivariate analysis of variance with distance matrices to test whether mean multivariate community composition differed between treatments and used nonmetric multidimensional scaling to visualize differences (Oksanen et al. 2013). We tested for differences in beta diversity between treatments by testing for multivariate homogeneity of group dispersions (Anderson 2005, Anderson et al. 2006, 2010, Oksanen et al. 2013). We used a null model approach to disentangle beta diversity and richness to determine if the observed differences in beta diversity between groups were simply a product of differences in species richness (Fukami 2004). To do this, we compared the observed differences in beta diversity to the distribution of differences obtained by permuting the community density matrix while holding richness per tree and density per tree constant. We also repeated this analysis with a community presence-absence matrix and held both richness per tree and species prevalence constant (Anderson et al. 2010). If an observed difference in beta diversity fell outside the 95% confidence interval of these null models, the difference would be considered unlikely to have arisen solely through differences in richness. We excluded naturally gall-free trees from all multivariate analyses because these methods can be sensitive to differences in sample size.

RESULTS

Pre-treatment community

Sweep samples.—Before gall removal, sweep samples on the control and removal trees had similar density and richness of all arthropods, herbivores, parasitoids, and predators (16–21 March in Figs. 2 and 3). Sweep samples from naturally gall-free trees, however, yielded on average 42.3% fewer individual arthropods

($\chi^2_1 = 6.0$, $P = 0.014$) and 36.7% lower arthropod richness ($\chi^2_1 = 5.9$, $P = 0.015$) than samples from removal trees. There were no significant pre-treatment differences in herbivore, parasitoid, or predator density or richness between gall-free and removal trees (see Appendix S1 for parameter estimates and likelihood ratio tests). Neither mean community composition ($F_{2,105} = 1.6$, $P > 0.05$) nor beta diversity (multivariate dispersion: $F_{1,97} = 0.43$, $P > 0.05$) varied significantly between pre-treatment control and removal trees (Fig. 4a). Despite their prevalence inside galls (see below), we caught no jumping spiders in pre-treatment sweep samples.

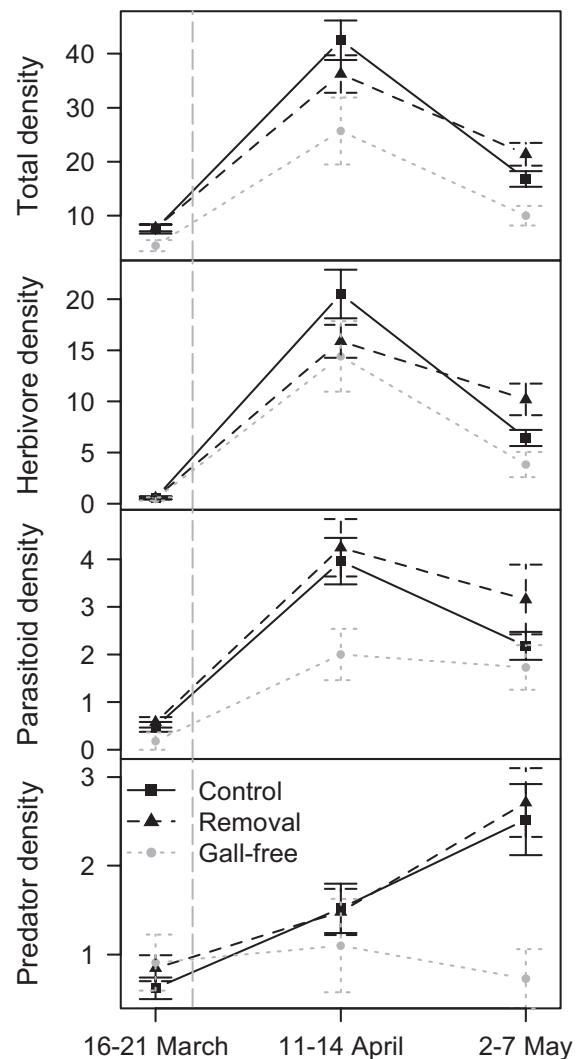


FIG. 2. Mean number of all arthropods, herbivores, parasitoids, and predators in sweep samples by treatment and time. Control trees are squares with solid lines, removal trees are triangles with dashed lines, and naturally gall-free trees are circles with gray dotted lines. Error bars are \pm SE. Vertical, gray dashes separate the pre-treatment/pre-budburst sample from the post-treatment/post-budburst samples.

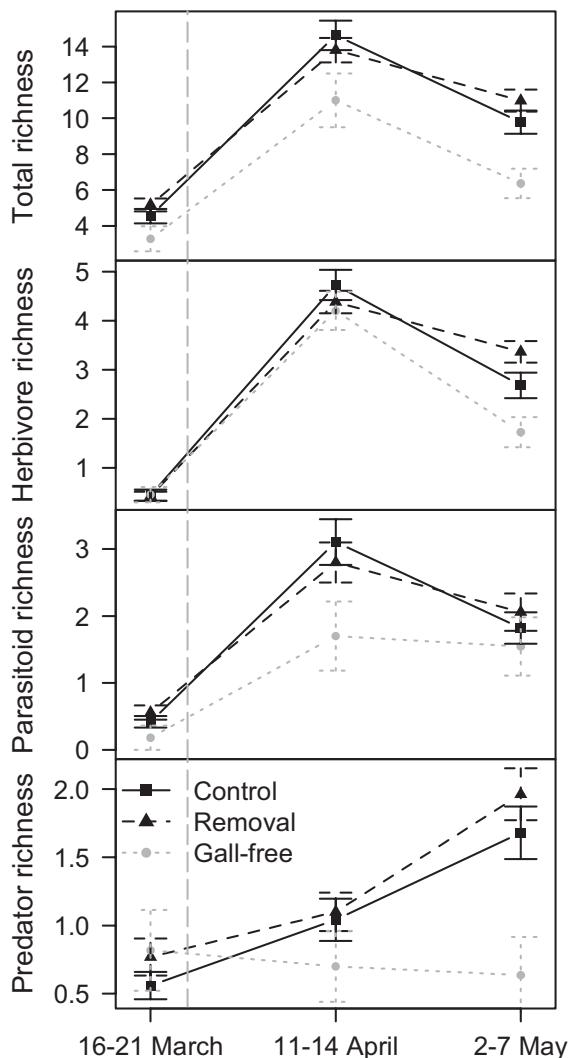


FIG. 3. Mean arthropod, herbivore, parasitoid, and predator morphospecies richness in sweep samples by treatment and time. Control trees are squares with solid lines, removal trees are triangles with dashed lines, and naturally gall-free trees are circles with gray dotted lines. Error bars are \pm SE. Vertical, gray dashes separate the pre-treatment/pre-budburst sample from the post-treatment/post-budburst sample.

Sticky-trap samples.—Before gall removal, sticky trap samples on the removal, control, and gall-free trees had similar numbers of all arthropods, prey, and natural enemies (Fig. 5; Appendix S1).

Overwintering gall inhabitants

Jumping spiders (Salticidae) were the dominant group we found overwintering in oak apple galls during late March. One or more adult jumping spider was found in 49.5% of galls dissected, yielding an average of 0.87 ± 0.12 (SE) spiders per gall. These are likely underestimates, because some spiders probably escaped during collection. Indeed, we found evidence of spider

activity, including egg sacs and silk, in 66.4% of galls. The second most common overwintering inhabitant was *Ozognathus cornutus* (Anobiidae), a detritivorous beetle present in 37.4% of galls, and which feeds on woody gall material and probably goes through multiple generations within single galls (Joseph et al. 2011). We found Hymenoptera larvae or pupae in 24.3% of galls. These were probably overwintering parasitoids of the gall-former. Psocoptera were present in 11.2% of galls and probably also feed on decaying woody gall material. The rest of the species in the gall community were relatively rare (e.g., earwigs [Dermaptera] found in 2.8% of galls or ant lions [Myrmeleontidae] found in 0.9%).

Post-treatment community

Sweep samples.—Overall arthropod abundance and richness in sweep samples increased 419.1% and 195.4% from the first (pre-treatment) sample to the second (post-treatment) sample and then declined 52.0% and 28.1% from the second to the third sample, 3 weeks later (Figs. 2 and 3). The GLMM parameter estimates for these declines had 95% confidence intervals that did not overlap zero (-0.86 ± 0.3 and -0.38 ± 0.18), indicating that the declines were meaningful. This temporal pattern was similar on control, removal, and naturally gall-free trees, suggesting this result was the product of a strong seasonal effect that did not depend on treatment or natural gall presence. The density and richness of herbivores and parasitoids on control, removal, and naturally gall-free trees generally followed this pattern (Figs. 2 and 3). Predator density and richness, on the other hand, steadily increased through the season on control and removal trees and stayed relatively constant on naturally gall-free trees.

Given the strong seasonal effect, it is unsurprising that the main effects of gall removal across both post-treatment samples were nonsignificant for all density and richness response variables (Figs. 2 and 3; Appendix S1). However, there were significant interactions between time and removal treatment for total density ($\chi^2_1 = 7.3$, $P = 0.007$), herbivore density ($\chi^2_1 = 8.8$, $P = 0.003$), and herbivore richness ($\chi^2_1 = 4.5$, $P = 0.035$), and a moderate but nonsignificant removal \times time interaction for total richness ($\chi^2_1 = 3.6$, $P = 0.058$; Figs. 2 and 3). In other words, density and richness of all arthropods and herbivores decreased on both removal and control trees from the second to the third sampling, but the drop was significantly greater on control trees.

For each significant removal \times time interaction, we did separate negative binomial regressions for each sampling period. None of the differences in density and richness between the removal and control trees were significant in the second sampling. However in the third sampling, there were 27.3% more arthropods ($\chi^2_1 = 4.0$, $P = 0.046$), 58.8% more herbivores ($\chi^2_1 = 6.0$, $P = 0.014$), and 25.6% greater herbivore richness ($\chi^2_1 = 3.7$,

$P = 0.055$) on removal trees than on control trees. These results indicate that gall removal had a positive effect on herbivore density and richness, but that the effect did not emerge until after the first several weeks after budburst and gall removal treatment.

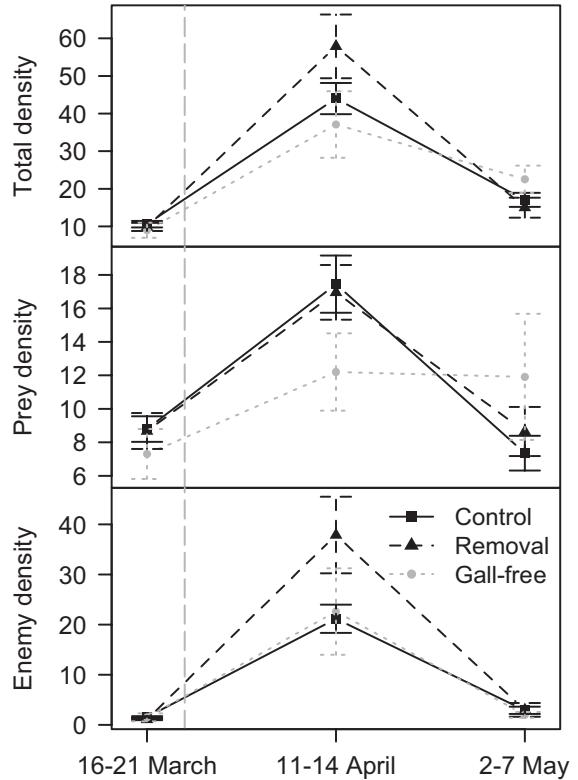
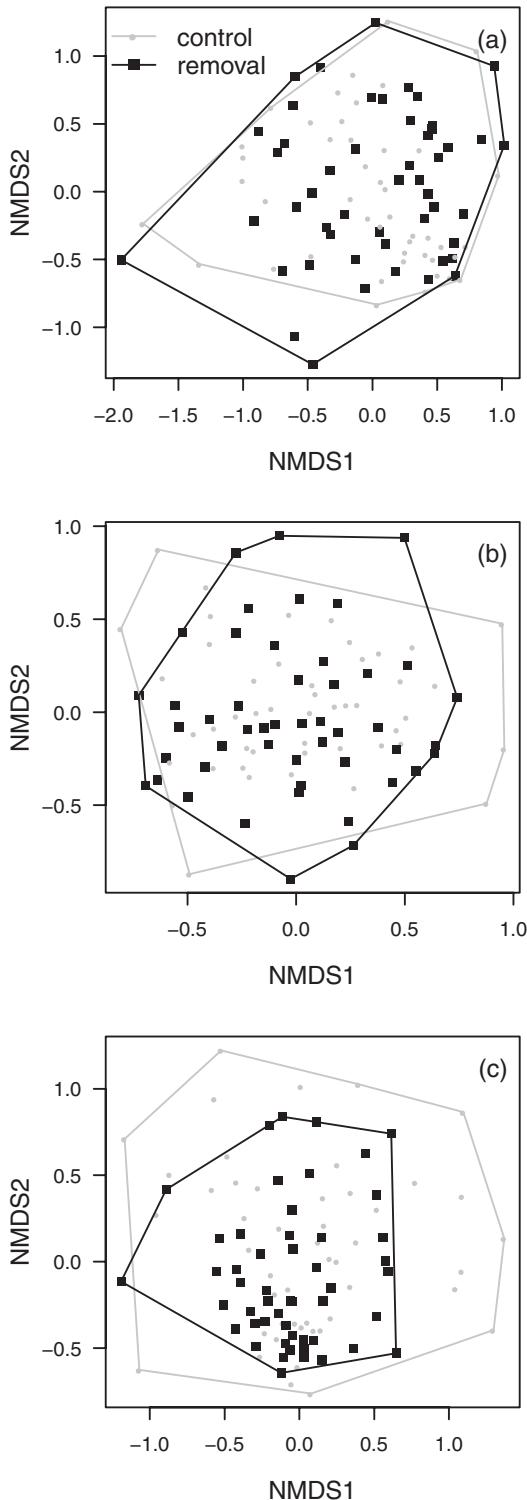


FIG. 5. Mean number of all arthropods, prey, and natural enemies (predators and parasitoids) on sticky traps by treatment and time. Control trees are squares with solid lines, removal trees are triangles with dashed lines, and naturally gall-free trees are circles with gray dotted lines. Error bars are \pm SE. Vertical, gray dashes separate the pre-treatment/pre-budburst sample from the post-treatment/post-budburst samples.

The results for parasitoid and predator density and richness mirrored those for total and herbivore density and richness, though the effects were relatively weak and nonsignificant: parasitoids and predators had 44.7% and 7.6% higher densities and 13.1% and 16.8% higher richness on removal trees than on control trees, respectively, in the third sampling (for all comparisons $P > 0.05$, Figs. 2 and 3). Moreover, parasitoids and predators had declined less from the second to the third sample on removal trees than on control trees, as was the case for total and herbivore density and richness. We caught too

FIG. 4. Nonmetric multidimensional scaling ordinations for arthropod communities on the removal and control trees in the (a) pre-treatment sampling and in the samplings (b) two and (c) five weeks post-treatment. Mean community composition did not differ between treatments in any sampling. In the third sample (c), control trees had significantly higher beta diversity (multivariate dispersion) than did removal trees. Three trees with communities >2 standard deviations from the mean were held out of each figure because those communities were so different they obscured variation among the rest of the communities. Inclusion or exclusion of these communities did not influence the outcome of analyses. Stress is 0.19, 0.25, and 0.23, respectively.

few jumping spiders (11 in total across all sweep samples) to analyze differences among treatment groups.

Beta diversity, measured as mean multivariate dispersion, was significantly higher among control trees than among removal trees in the third sample ($F_{1,100} = 4.1$, $P = 0.046$) but not in the second ($F_{1,96} = 0.01$, $P = 0.92$; Fig. 4). Samples from control trees were on average 5.9% farther in Bray-Curtis multivariate distance and 29.2% farther in NMDS distance from the mean community composition than samples from control trees were from their mean (Fig. 4). The difference in beta diversity between the removal and control trees in the third sample was not simply a product of differences in richness: the observed difference in beta diversity fell outside the 95% confidence interval of the differences generated by both a density null model that held richness and density per tree constant ($P = 0.001$) and a presence-absence null model that held richness and species prevalence constant ($P = 0.037$), thereby indicating that gall removal reduced the variability of community composition in the removal group relative to the control group.

Mean multivariate community composition, however, did not differ significantly between control and removal trees in either the second sample ($F_{2,104} = 1.3$, $P = 0.082$) or the third ($F_{2,109} = 1.05$, $P = 0.34$; Fig. 4; Appendix S1). This suggests the significant differences in overall herbivore density and richness on removal and control trees were not enough to drive differences in mean composition across all arthropod morphospecies.

There was no support for the hypothesis that gall removal would make the density and richness of arthropods closer to those on trees naturally free of galls. Density and richness of all arthropods, herbivores, and predators on naturally gall-free trees was significantly lower than that on removal trees across both post-treatment samples (Figs. 2 and 3). There were 39.0% fewer arthropods ($\chi^2_2 = 8.1$, $P = 0.018$), 31.8% fewer herbivores ($\chi^2_1 = 9.1$, $P = 0.011$), 57.1% fewer predators ($\chi^2_1 = 9.9$, $P = 0.007$), 30.7% lower arthropod richness ($\chi^2_1 = 10.8$, $P = 0.005$), 24.8% lower herbivore richness ($\chi^2_1 = 7.3$, $P = 0.026$), and 56.7% lower predator richness ($\chi^2_1 = 11.3$, $P = 0.004$) on naturally gall-free trees than on removal trees across both post-treatment samples (Appendix S1). Density and richness of parasitoids on naturally gall-free trees were 49.6% ($\chi^2_2 = 4.0$, $P = 0.13$) and 33.1% ($\chi^2_2 = 3.0$, $P = 0.23$) lower than on removal trees in the third sample, though these differences were not significant. In general, numbers on removal trees were closer to those of control trees than they were to naturally gall-free trees (Figs. 2 and 3). These results suggest that, as hosts for arthropods, naturally gall-free trees differ from trees with galls in more ways than gall presence.

We had hypothesized that the effect of gall removal would be greater on trees with a higher initial density of galls, but this was not supported by the data. All of the parameter estimates for the interaction between initial gall density and gall removal had 95% confidence intervals that overlapped zero (Appendix S1).

Sticky-trap samples.—In contrast to the patterns for the sweep community, the community sampled by sticky traps was not significantly influenced by gall removal. There were no significant interactions between removal and time; nor were there significant main effects of removal (Fig. 5; Appendix). More similarly to sweep results, sticky trap samples from naturally gall-free trees tended to have lower density than did removal trees (Fig. 5). Total arthropod density ($X^2_2 = 8.9$, $P = 0.012$) was significantly different on removal and naturally gall-free trees across the two post-treatment samples. As expected, we caught no jumping spiders in sticky traps.

Growing-season gall inhabitants

Jumping spiders were also the dominant group inside oak apple galls during the late May sampling, indicating that galls were important refuges for these spiders not just during the winter but also during the growing season. We found 44 jumping spiders on the 16 branches with galls, 41 of which were inside galls, for a mean of 0.40 ± 0.13 (SE) jumping spiders per gall. Of all the arthropods we found inside galls, 66% were jumping spiders, 19% were Hymenoptera larvae or pupae, 11% were Dermaptera, and 3% were Hymenoptera adults. In contrast, we found just two jumping spiders on the 16 branches that were naturally lacking galls.

DISCUSSION

Our gall removal treatment had widespread effects on the foliage-dwelling arthropod community on valley oak. During winter, oak apple galls, vacant of gall wasps for at least several months, contained a community of overwintering inhabitants dominated by jumping spiders. These spiders persisted in galls throughout the growing season. We removed those galls and their inhabitants from trees before the seasonal assembly of the arthropod community. Then, by two weeks after budburst, the arthropod community in oak foliage had increased in density and richness by factors of four and two on both the removal and control trees with no detectable effect of gall removal. By five weeks after budburst, however, the removal trees had nearly 60% more herbivores, nearly 30% more arthropods, and about 25% greater herbivore richness than did control trees (Figs. 2 and 3). In addition, the control trees had greater beta diversity, measured as mean differences among communities in multivariate composition, than did removal trees. Finally, arthropod density and richness were consistently lower on trees naturally free of galls than on control and removal trees. These results indicate that the California gall wasp has important effects on the arthropod community that dwells on oak foliage. These effects are initiated indirectly via habitat modification, are temporally delayed and long lasting, interact with seasonal community assembly, depend on host-plant quality, and influence the foliage-dwelling

arthropod community at the scale of entire trees, including species that do not interact directly with the habitat modifications themselves.

Ecologists have long recognized habitat engineering as a major pathway by which single species can influence communities (Jones et al. 1997). Indeed, recent studies conducted at the scale of mosaics including both engineered and unmodified habitat confirm that ecosystem engineers can significantly increase regional diversity by facilitating specialists of engineered habitats (Wright et al. 2002, Lill and Marquis 2003, Castilla et al. 2004, Badano et al. 2006). Much less attention has been paid to the indirect effects of ecosystem engineers on the portion of a community that does not directly interact with modified habitats (Miyashita and Takada 2007). Our study demonstrates that indirect effects, initiated by ecosystem engineering, can shape patterns of abundance and diversity at the community level. Habitat engineering by the California gall wasp goes beyond merely providing habitat for gall specialists. By engineering galls in the summer, the California gall wasp influences the community of arthropods overwintering on oak trees and ultimately changes the foliage-dwelling arthropod community in future summers. This means if we are to predict the effects of ecosystem engineering on regional diversity, it may not be enough to know what proportion of a landscape is engineered and unmodified: it may be necessary to look for indirect interactions that reverberate through resident communities.

Indirect interactions that propagate to community scales may have been especially likely in the oak apple gall system because the galls persist on trees for at least several years after their engineers die (Russo 2006). This prolongs the effects of a gall-maker on the arthropod community well beyond its lifetime, but it also means that the galls are present through seasonal transitions. Oak apple galls are abandoned by gall wasps near the end of a growing season, and are present through the winter into the following growing season and beyond. Therefore, they provide refuge habitat for jumping spiders and other secondary inhabitants through the winter. In the spring at budburst, trees with galls had much higher starting densities of these species than did trees without galls, potentially altering the trajectory of the seasonal assembly process. The effects of the altered assembly trajectory, however, did not manifest until after more than three weeks into the growing season, indicating an interaction between habitat engineering and timing of seasonal assembly. This delay could have occurred because the effect of gall removal was obscured by the dramatic increases in arthropod density on all trees at the beginning of the growing season, or perhaps because community assembly trajectories in the presence or absence of galls take time to diverge. The temporal persistence of oak apple galls contrasts with that of leaf shelters, which are the focus of the majority of

work on the effects of arthropod engineers on plant-associated arthropod communities: leaf shelters fall apart without frequent maintenance by leaf-tying arthropods and tend to have little to no effect on the arthropod community beyond leaf shelters and their specialists (Martinsen et al. 2000, Lill and Marquis 2003, Marquis and Lill 2007).

The difference in herbivore density between trees that are naturally gall-free and trees with galls removed suggests that top-down and bottom-up forces simultaneously play roles in the effects of gall-wasp habitat engineering on the community of folivorous herbivores. The increase in herbivore densities following gall removal suggests that top-down predation, likely from jumping spiders that take refuge in galls, plays an important role in community dynamics. However, we would have expected similar densities of herbivores on naturally gall-free trees and experimental gall-removal trees had community dynamics been primarily controlled by such top-down forces; to the contrary, sweep samples from trees naturally free of galls had consistently low densities of herbivores and all arthropods, lower even than those on control trees (Figs. 2 and 3). Even on sticky traps, abundance from removal trees was consistently closer to that of control trees than naturally gall-free trees (Fig. 5). These results suggest that naturally gall-free trees (14.6% of trees at our study site) were very poor quality as hosts for both the California gall wasp and other herbivorous arthropods, perhaps because these trees were chemically defended against herbivory, had lower nutrient concentrations, or both. Indeed, a large body of work on oak gall wasps suggests host-plant quality is more important than predation as a determinant of the distribution of galls among individual trees (reviewed in Stone et al. 2002). These patterns suggest the negative effects of galls on foliage-dwelling herbivores are possible only when plant quality is sufficiently high.

Observed patterns of predator and parasitoid density also suggest bottom-up forces were important. Predators and parasitoids followed the herbivore trend by increasing on gall-removal trees, though weakly and nonsignificantly. These patterns suggest that the increase in herbivore density following gall removal may have subsidized foliage-dwelling predators and parasitoids. These results are consistent with the notion that heterogeneity in bottom-up forces (e.g., plant quality) is the template upon which top-down forces act (Hunter and Price 1992), and also with the ecosystem exploitation hypothesis (Oksanen et al. 1981), which states that productivity should influence the relative importance of top-down and bottom-up forces at each trophic level. An added complexity in this system is that the indirect effects propagate via both trait-mediated and density-mediated effects that are initiated by an organism that is itself dependent on resource quality.

Most work on the effect of ecosystem engineers on beta diversity has focused on differences in community

composition between engineered and unmodified habitat (Hewitt et al. 2005, Bangert and Slobodchikoff 2006). Our work, however, shows that habitat engineering can also influence beta diversity at a larger scale: engineering can lead to differences in community composition among patches (trees) that encompass both engineered microhabitat (galls) and unmodified microhabitat (leaves). Control trees with intact galls had higher beta diversity (differences in community composition among trees), suggesting that galls increased variability in the seasonal assembly of the foliage-dwelling community. Theoretical work shows that beta diversity can increase as local community size declines relative to the size of the regional species pool merely because of a statistical sampling effect (Fukami 2004). However, the control trees in our study still had significantly higher beta diversity than removal trees even when we used a null model that accounted for differences in local community size (Anderson et al. 2010). This indicates that galls and their secondary inhabitants facilitated the assembly of unusual communities more than by simply reducing local community size. This would be possible if spiders that overwintered in galls suppressed herbivore richness and density, and historically contingent species interactions led to diverging assembly trajectories that produced unusual communities. Alternatively, galls and their secondary inhabitants might provide additional axes of variation that increase among-tree variation and consequently increase beta diversity deterministically. These results suggest habitat engineering can influence community assembly in ways that increase diversity at scales larger than previously examined.

Although our study was focused on broad community patterns and not on mechanisms, we hypothesize the most likely mechanism was that galls provided refuges for jumping spiders, both during the winter and through the growing season, leading to higher spider densities, which then suppressed herbivore richness and density and promoted variation in community composition among trees. The apparently low densities of jumping spiders on stems or leaves, despite their surprisingly high densities inside galls, is likely because they mainly leave galls only for foraging. It is unlikely that secondary inhabitants other than spiders were responsible for effects on the foliage-dwelling community for four reasons: (1) Galls overwhelmingly contained spiders or evidence of spider use, such as egg sacs, from the end of winter throughout the course of our experiment. (2) The second most common inhabitant of galls was a detritivorous beetle (*O. cornutus*) that specializes on oak apple galls and is unlikely to interact with folivorous arthropods (Joseph et al. 2011). (3) The third most common secondary inhabitants were parasitoid pupae and larvae that probably specialized on the gall-former and did not interact with folivorous arthropods (Joseph et al. 2011). (4) The remaining inhabitants were either detritivorous psocopteran nymphs, also unlikely to influence the arthropod community outside galls, or rare (present in <3% of galls).

The structure of the galls themselves may have influenced the foliage-dwelling herbivore community, but this is unlikely for three reasons: (1) We found very little overlap between the foliage-dwelling community and the secondary gall-inhabitant community; in particular, no herbivores were found in galls. (2) Green foliage, from which we sampled the arthropod community, is typically distal to old oak apple galls on valley oaks, suggesting that the galls were unlikely to have influenced environmental conditions on leaves in a way that would significantly influence foliage-dwelling herbivores. (3) There was no relationship between gall density and any of our community response variables, suggesting that the structure of galls themselves was not important for the treatment effect.

CONCLUSIONS

This work shows that the California gall wasp influences the annual assembly of the foliage-dwelling arthropod community on valley oak. The effects are initiated indirectly via formation of woody galls, propagate to a component of the community that does not interact directly with the engineered structures, do not begin until several months after the death of the gall-maker, and last as long as the galls remain adhered to the tree, which can be at least several years. Further, these indirect effects appear to occur only on trees of sufficient host-plant quality to support gall wasps and a rich foliage-dwelling community. The work presented here differs from previous work on habitat engineering because it demonstrates that the effects of habitat engineering can go beyond merely providing habitat for specialists that colonize engineered habitat; they can propagate through the community far enough to have negative effects on density and richness of resident species that do not interact directly with the engineered structures. Taken together, our results provide a glimpse of the intersection between phenomena typically studied in isolation: habitat engineering, phenological timing, and trophic control. The picture that emerges illustrates that habitat engineering, in the form of trait-mediated indirect interactions, can interact with phenological timing to influence heterogeneity in trophic control at the community scale.

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