

UC Davis

UC Davis Previously Published Works

Title

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

Permalink

<https://escholarship.org/uc/item/1vw8j252>

Journal

Ecology, 97(2)

ISSN

0012-9658

Authors

Wetzel, William C
Screen, Robyn M
Li, Ivana
[et al.](#)

Publication Date

2016-02-01

DOI

10.1890/15-1347.1

Peer reviewed

1 Running head: Ecosystem engineering on valley oaks

2

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

5

6 William C. Wetzel^{1,4,5}, Robyn M. Screen^{1,6}, Ivana Li², Jennifer McKenzie^{3,7}, Kyle A. Phillips^{1,3},
7 Melissa Cruz², Wenbo Zhang¹, Austin Greene¹, Esther Lee¹, Nuray Singh¹, Carolyn Tran¹, and
8 Louie H. Yang²

9

10 ¹Department of Evolution and Ecology, University of California, Davis, One Shields Avenue,
11 Davis, California, 95616, USA

12 ²Department of Entomology and Nematology, University of California, Davis, One Shields
13 Avenue, Davis, California, 95616, USA

14 ³Department of Wildlife, Fish, and Conservation Biology, University of California, One Shields
15 Avenue, Davis, California, 95616, USA

16

17 ⁴Corresponding author e-mail: wcwetz@cornell.edu

18 ⁵Present address: Department of Entomology, Cornell University, Comstock Hall, Ithaca, NY,
19 14853, USA

20 ⁶Present address: Department of Biology, University of Hawaii at Manoa, 2500 Campus Rd,
21 Honolulu, HI, 96822, USA

22 ⁷Present address: Department of Forestry, University of Kentucky, Lexington, KY, 40546, USA

23

24 **Abstract**

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

44

45 **Key words:** Ecosystem engineer, habitat engineering, indirect interaction, trait-mediated
46 interaction, *Quercus lobata*, gall wasp

47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69

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 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

70 raccoons (Andrén and Angelstam 1988). On a smaller spatial scale, herbivorous leaf beetles
71 disappeared at a faster rate when experimentally placed on leaves near leaf shelters built by leaf-
72 rolling caterpillars than when placed on leaves far from shelters, mostly likely because they were
73 removed by ants tending aphids that had colonized the shelters (Nakamura and Ohgushi 2003).
74 These studies show that engineering can have surprising negative indirect effects, but such
75 studies have been at too fine a scale to show how these effects scale up to the entire community.

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

90 Organisms that create long-lasting habitat structures likely have higher potential to
91 initiate community-wide indirect effects than do organisms forming short-lived structures
92 (Hastings et al. 2007). One reason for this is simply that persistent structures continue to exert

93 effects after the engineer has died (Jones et al. 1997). A less commonly recognized reason
94 persistent structures could have greater effects is habitat structures persisting through multiple
95 seasons could serve as a refuge during unfavorable seasons and lead to elevated densities of
96 refuge specialists at the beginning of the growing season. This temporally dependent facilitation
97 could initiate priority effects that would influence seasonal assembly trajectories, potentially
98 altering density, richness, and even beta diversity of entire communities assembling following an
99 unfavorable season (Robinson and Dickerson 1987). Recent work has shown that engineered
100 habitats can provide refuge during unfavorable conditions. Woodland salamanders have higher
101 overwintering survival when they reside in earthworm tunnels (Ransom 2010). Gopher tortoise
102 burrows are used by more than 50 vertebrates and 300 invertebrates, and can serve as thermal
103 refuges during wildfires or other high or low temperature extremes (Pike and Mitchell 2013).
104 Despite our growing appreciation of the positive effects of ecosystem engineers on species
105 persistence during unfavorable conditions, we have a relatively poor understanding of the
106 consequences of long-lasting engineered structures for community assembly in seasonal
107 environments.

108 We examined the effects of senesced oak apple galls, engineered habitat formed by the
109 California gall wasp (*Andricus quercuscalifornicus*), on the seasonal assembly of arthropod
110 communities on valley oak (*Quercus lobata*), a deciduous tree. Galls are well-documented to be
111 microhabitats that support diverse communities of specialized arthropods that are distinct from
112 foliage-dwelling communities (Sanver and Hawkins 2000). Oak apple galls persist on oak
113 branches for many years after they senesce and are abandoned by gall wasps, and the emergence
114 tunnels left behind by eclosing gall wasps are colonized by several species of secondary
115 inhabitants (Fig. 1; Russo 2006, Joseph et al. 2010). In the winter prior to this study, we observed

116 that many senesced galls contained jumping spiders (Salticidae), generalist predators of
117 herbivorous arthropods. This observation led us to hypothesize (1) that gall wasps would
118 indirectly—via the changes they induce in host-plant structure—suppress density and diversity
119 of herbivores on oak foliage, and (2) that these effects would interact with the seasonal
120 community assembly that takes place on oaks each spring. To test for these indirect, trait-
121 mediated interactions, we experimentally removed all senesced galls from entire trees during
122 winter and sampled foliage-dwelling arthropods through community assembly in spring. Our
123 study addressed two main questions: (1) How does persistent habitat engineering indirectly
124 influence the portion of a community that does not directly interact with the habitat
125 modification? (2) How does persistent habitat engineering influence the seasonal community
126 assembly process?

127

128

Methods

129

Study system

130

131

132

133

134

135

136

137

138

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. 2010). Galls desiccate, senesce, 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

139 galls present on trees during the winter and were the focus of our study. Arthropod community
140 assembly begins with budburst, which was 29 March – 2 April in 2013.

141 *Gall removal experiment*

142 In March 2013, we counted oak apple galls on all of the 137 valley oaks at the study site
143 with a height less than 7 m, the highest we could reach with telescoping poles (20% of valley
144 oaks at the study site). Of those trees, 102 had at least 10 galls: we randomly assigned these trees
145 to a control or gall-removal treatment, stratifying the randomization by gall density to ensure
146 equal representation of treatments across the natural range of gall density. We also randomly
147 selected 12 of the 35 trees that naturally had zero galls to serve as a naturally gall-free
148 comparison to the experimental gall-removal treatment.

149 From 16-21 March 2013, we sampled the pre-treatment arthropod community on all
150 control trees, removal trees, and naturally gall-free trees using sweep nets and beat sticks with
151 trays. We swept foliage with four sweeps on opposite sides of each tree using 38.1-cm diameter
152 sweep nets. We beat branches on the remaining two sides to collect arthropods into white plastic
153 trays (1,235-cm² surface area) with four taps. We collected all arthropods from sweep nets and
154 trays using aspirators and combined them into one sample per tree (hereafter: sweep samples).
155 We also sampled using one sticky trap (120-cm² sticky area) hung from a branch on each tree for
156 48 hours from 15-17 March.

157 From 26-29 March, shortly before budburst, we removed all 5,026 oak apple galls from
158 the 52 removal trees using plastic bats and 4-m telescoping poles. All galls on trees at this time
159 of year were initiated, used, and abandoned by gall wasps in a previous summer, making them at
160 least 11 months old at the time of removal. Because our treatment only involved senesced galls,
161 our study isolated the effects of galls as structures from the direct trophic effects of the engineer.

162 In addition, the gall-removal treatment was unlikely to have influenced plant chemistry or
163 physiology because senesced galls are dead tissue. We controlled for the physical disturbance
164 required to remove galls from removal trees by disturbing control and gall-free trees with poles
165 for 1-10 minutes (1 minute per 10 galls) without actually removing galls. We preserved two galls
166 from each removal tree, dissected them under a stereomicroscope, and identified gall inhabitants
167 and evidence of inhabitants, such as spider silk. The rest of the galls were disposed of > 5 km
168 off-site. We sampled arthropods on all trees again two and five weeks following the treatment
169 using both the sweep and sticky trap methods described above (11-14 April 2013 and 2-7 May
170 2013). We grouped the 6,998 arthropod specimens from sweep samples into 238 morphospecies
171 and subsequently identified them to the lowest feasible taxonomic resolution (mainly genus). We
172 identified the 8,341 arthropod specimens from sticky trap samples to order.

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

183 *Statistical analysis*

184 We addressed our question about the effects of engineering on the part of the community
185 that does not physically interact with the habitat modification (question 1) by asking how
186 removal of galls from a tree influences the foliage-dwelling community. To answer this, we
187 decided *a priori* to examine the following response variables: density and richness of all
188 arthropods, herbivores, predators, and parasitoids; mean multivariate community composition;
189 and beta diversity (multivariate dispersion). If trees from which we removed galls supported a
190 higher abundance and diversity of leaf herbivores, it would support our hypothesis that galls
191 indirectly suppressed that group. We addressed our question about the interaction between
192 engineering and seasonal community assembly (question 2) by asking how the effects of gall
193 removal vary through the growing season. If the effects of gall-removal depended on sampling
194 period, it would suggest that the effects of galls interact with the seasonal community assembly
195 process.

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

204 We analyzed sweep and sticky trap data separately because they represent separate parts
205 of the broader oak savanna arthropod community. Sweep sampling captured primarily less
206 mobile, foliage-dwelling organisms that complete development primarily on one oak, whereas

207 the sticky trap sampling captured primarily flying organisms that probably forage at scales larger
208 than single trees. We did not use sticky trap data to answer questions about mean community
209 composition or beta diversity because order-level identifications were too taxonomically coarse
210 for multivariate community analyses. For analysis of sticky trap data, we grouped Araneae,
211 Formicidae, Opiliones, and Hymenoptera excluding bees into a natural enemy category and the
212 rest of the specimens into a potential prey category. These categories are best treated as rough
213 groupings, but it is likely the groupings are accurate for the majority of specimens from each
214 order.

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

227 Each post-treatment model had a random effect for tree identity to account for the non-
228 independence of trees re-sampled through time. We also included initial gall density as a
229 covariate in all univariate models, because we hypothesized that the effect of gall removal would

230 increase with the number of galls present before removal. Thus we also included an interaction
231 between gall removal and initial gall density in all models with an effect of gall removal. Finally,
232 we used a random effect for sampling date because we hypothesized conditions on any particular
233 day could influence capture rates. Random effect structures were set by our experimental design,
234 and therefore we did not test their significance. The details of each model and likelihood ratio
235 test can be found in Appendix A in the online supplemental material. We fit all univariate
236 models using maximum likelihood with the R packages glmmADMB and bbmle (Bolker 2008,
237 2012, Fournier et al. 2012, Skaug et al. 2013, R Core Team 2014).

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

253

254

Results

255

Pre-treatment community

256

257

258

259

260

261

262

263

264

265

266

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 ($X^2_1 = 6.0$, $P = 0.014$) and 36.7% lower arthropod richness ($X^2_1 = 5.9$, $P = 0.015$) 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 A in online supplemental material 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.

267

268

269

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 A).

270

Overwintering gall inhabitants

271

272

273

274

275

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

276 inhabitant was *Ozognathus cornutus* (Anobiidae), a detritivorous beetle present in 37.4% of galls,
277 and which feeds on woody gall material and probably goes through multiple generations within
278 single galls (Joseph et al. 2010). We found Hymenoptera larvae or pupae in 24.3% of galls.
279 These were probably overwintering parasitoids of the gall-former. Psocoptera were present in
280 11.2% of galls and probably also feed on decaying woody gall material. The rest of the species in
281 the gall community were relatively rare (e.g., earwigs [Dermaptera] found in 2.8% of galls or ant
282 lions [Myrmeleontidae] found in 0.9%).

283 *Post-treatment community*

284 *Sweep samples.*—Overall arthropod abundance and richness in sweep samples increased
285 419.1% and 195.4% from the first (pre-treatment) sample to the second (post-treatment) sample
286 and then declined 52.0% and 28.1% from the second to the third sample, three weeks later (Figs.
287 2 and 3). The GLMM parameter estimates for these declines had 95% confidence intervals that
288 did not overlap zero (-0.86 ± 0.3 and -0.38 ± 0.18), indicating that the declines were meaningful.
289 This temporal pattern was similar on control, removal, and naturally gall-free trees, suggesting
290 this result was the product of a strong seasonal effect that did not depend on treatment or natural
291 gall presence. The density and richness of herbivores and parasitoids on control, removal, and
292 naturally gall-free trees generally followed this pattern (Figs. 2 and 3). Predator density and
293 richness, on the other hand, steadily increased through the season on control and removal trees
294 and stayed relatively constant on naturally gall-free trees.

295 Given the strong seasonal effect, it is unsurprising that the main effects of gall removal
296 across both post-treatment samples were non-significant for all density and richness response
297 variables (Figs. 2 and 3; Appendix A). However, there were significant interactions between time
298 and removal treatment for total density ($X^2_1 = 7.3$, $P = 0.007$), herbivore density ($X^2_1 = 8.8$, $P =$

299 0.003), and herbivore richness ($X^2_1 = 4.5, P = 0.035$), and a moderate but non-significant
300 removal \times interaction for total richness ($X^2_1 = 3.6, P = 0.058$; Figs. 2 and 3). In other words,
301 density and richness of all arthropods and herbivores decreased on both removal and control
302 trees from the second to the third sampling, but the drop was significantly greater on control
303 trees.

304 For each significant removal \times time interaction, we did separate negative binomial
305 regressions for each sampling period. None of the differences in density and richness between
306 the removal and control trees were significant in the second sampling. However in the third
307 sampling, there were 27.3% more arthropods ($X^2_1 = 4.0, P = 0.046$), 58.8% more herbivores (X^2_1
308 $= 6.0, P = 0.014$), and 25.6% greater herbivore richness ($X^2_1 = 3.7, P = 0.055$) on removal trees
309 than on control trees. These results indicate that gall removal had a positive effect on herbivore
310 density and richness, but that the effect did not emerge until after the first several weeks after
311 budburst and gall removal treatment.

312 The results for parasitoid and predator density and richness mirrored those for total and
313 herbivore density and richness, though the effects were relatively weak and non-significant:
314 parasitoids and predators had 44.7% and 7.6% higher densities and 13.1% and 16.8% higher
315 richness on removal trees than on control trees respectively in the third sampling (for all
316 comparisons $P > 0.05$, Figs. 2 and 3). Moreover, parasitoids and predators had declined less from
317 the second to the third sample on removal trees than on control trees, as was the case for total
318 and herbivore density and richness. We caught too few jumping spiders (11 in total across all
319 sweep samples) to analyze differences among treatment groups.

320 Beta-diversity, measured as mean multivariate dispersion, was significantly higher
321 among control trees than among removal trees in the third sample ($F_{1,100} = 4.1, P = 0.046$) but

322 not in the second ($F_{1,96} = 0.01$, $P = 0.92$; Fig. 4). Samples from control trees were on average
323 5.9% farther in Bray-Curtis multivariate distance and 29.2% farther in NMDS distance from the
324 mean community composition than samples from control trees were from their mean (Fig. 4).
325 The difference in beta diversity between the removal and control trees in the third sample was
326 not simply a product of differences in richness: the observed difference in beta diversity fell
327 outside the 95% confidence interval of the differences generated by both an density null model
328 that held richness and density per tree constant ($P = 0.001$) and a presence-absence null model
329 that held richness and species prevalence constant ($P = 0.037$), thereby indicating that gall
330 removal reduced the variability of community composition in the removal group relative to the
331 control group.

332 Mean multivariate community composition, however, did not differ significantly between
333 control and removal trees in either the second sample ($F_{2,104} = 1.3$, $P = 0.082$) or the third ($F_{2,109}$
334 $= 1.05$, $P = 0.34$; Fig. 4; Appendix A). This suggests the significant differences in overall
335 herbivore density and richness on removal and control trees were not enough to drive differences
336 in mean composition across all arthropod morphospecies.

337 There was no support for the hypothesis that gall removal would make the density and
338 richness of arthropods closer to those on trees naturally free of galls. Density and richness of all
339 arthropods, herbivores, and predators on naturally gall-free trees was significantly lower than
340 that on removal trees across both post-treatment samples (Figs. 2 and 3). There were 39.0%
341 fewer arthropods ($X^2_2 = 8.1$, $P = 0.018$), 31.8% fewer herbivores ($X^2_1 = 9.1$, $P = 0.011$), 57.1%
342 fewer predators ($X^2_1 = 9.9$, $P = 0.007$), 30.7% lower arthropod richness ($X^2_1 = 10.8$, $P = 0.005$),
343 24.8% lower herbivore richness ($X^2_1 = 7.3$, $P = 0.026$), and 56.7% lower predator richness ($X^2_1 =$
344 11.3 , $P = 0.004$) on naturally gall-free trees than on removal trees across both post-treatment

345 samples (Appendix A). Density and richness of parasitoids on naturally gall-free trees were
346 49.6% ($X^2_2 = 4.0$, $P = 0.13$) and 33.1% ($X^2_2 = 3.0$, $P = 0.23$) lower than on removal trees in the
347 third sample, though these differences were not significant. In general, numbers on removal trees
348 were closer to those of control trees than they were to naturally gall-free trees (Figs. 2 and 3).
349 These results suggest that, as hosts for arthropods, naturally gall-free trees differ from trees with
350 galls in more ways than gall presence.

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

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

363 *Growing-season gall inhabitants*

364 Jumping spiders were also the dominant group inside oak apple galls during the late May
365 sampling, indicating that galls were important refuges for these spiders not just during the winter
366 but also during the growing season. We found 44 jumping spiders on the 16 branches with galls,
367 41 of which were inside galls, for a mean of 0.40 ± 0.13 (SE) jumping spiders per gall. Of all the

368 arthropods we found inside galls, 66% were jumping spiders, 19% were Hymenoptera larvae or
369 pupae, 11% were Dermaptera, and 3% were Hymenoptera adults. In contrast, we found just two
370 jumping spiders on the 16 branches that were naturally lacking galls.

371

372

Discussion

373 Our gall removal treatment had widespread effects on the foliage-dwelling arthropod
374 community on valley oak. During winter, oak apple galls, vacant of gall wasps for at least
375 several months, contained a community of overwintering inhabitants dominated by jumping
376 spiders. These spiders persisted in galls throughout the growing season. We removed those galls
377 and their inhabitants from trees before the seasonal assembly of the arthropod community. Then
378 by two weeks after budburst, the arthropod community in oak foliage had increased in density
379 and richness by factors of four and two on both the removal and control trees with no detectable
380 effect of gall removal. By five weeks after budburst, however, the removal trees had nearly 60%
381 more herbivores, nearly 30% more arthropods, and about 25% greater herbivore richness than
382 did control trees (Figs. 2 and 3). In addition, the control trees had greater beta diversity,
383 measured as mean differences among communities in multivariate composition, than did removal
384 trees. Finally, arthropod density and richness were consistently lower on trees naturally free of
385 galls than on control and removal trees. These results indicate that the California gall wasp has
386 important effects on the arthropod community that dwells on oak foliage. These effects are
387 initiated indirectly via habitat modification, are temporally delayed and long lasting, interact with
388 seasonal community assembly, depend on host-plant quality, and influence the foliage-dwelling
389 arthropod community at the scale of entire trees, including species that do not interact directly
390 with the habitat modifications themselves.

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

407 Indirect interactions that propagate to community scales may have been especially likely
408 in the oak apple gall system because the galls persist on trees for at least several years after their
409 engineers die (Russo 2006). This prolongs the effects of a gall-maker on the arthropod
410 community well beyond its lifetime, but it also means that the galls are present through seasonal
411 transitions. Oak apple galls are abandoned by gall wasps near the end of a growing season, and
412 are present through the winter into the following growing season and beyond. Therefore, they
413 provide refuge habitat for jumping spiders and other secondary inhabitants through the winter. In

414 the spring at budburst, trees with galls had much higher starting densities of these species than
415 did trees without galls, potentially altering the trajectory of the seasonal assembly process. The
416 effects of the altered assembly trajectory, however, did not manifest until after more than three
417 weeks into the growing season, indicating an interaction between habitat engineering and timing
418 of seasonal assembly. This delay could have occurred because the effect of gall removal was
419 obscured by the dramatic increases in arthropod density on all trees at the beginning of the
420 growing season, or perhaps because community assembly trajectories in the presence or absence
421 of galls take time to diverge. The temporal persistence of oak apple galls contrasts with that of
422 leaf shelters, which are the focus of the majority of work on the effects of arthropod engineers on
423 plant-associated arthropod communities: leaf shelters fall apart without frequent maintenance by
424 leaf-tying arthropods and tend to have little to no effect on the arthropod community beyond leaf
425 shelters and their specialists (Martinsen et al. 2000, Lill and Marquis 2003, Marquis and Lill
426 2007).

427 The difference in herbivore density between trees which are naturally gall-free and trees
428 with galls removed suggests that top-down and bottom-up forces simultaneously play roles in the
429 effects of gall-wasp habitat engineering on the community of folivorous herbivores. The increase
430 in herbivore densities following gall removal suggests that top-down predation—likely from
431 jumping spiders that take refuge in galls—plays an important role in community dynamics.
432 However, we would have expected similar densities of herbivores on naturally gall-free trees and
433 experimental gall-removal trees had community dynamics been primarily controlled by such top-
434 down forces; to the contrary, sweep samples from trees naturally free of galls had consistently
435 low densities of herbivores and all arthropods—lower even than those on control trees (Figs. 2
436 and 3). Even on sticky traps, abundance from removal trees was consistently closer to that of

437 control trees than naturally gall-free trees (Fig. 5). These results suggest that naturally gall-free
438 trees (14.6% of trees at our study site) were very poor quality as hosts for both the California gall
439 wasp and other herbivorous arthropods, perhaps because these trees were chemically defended
440 against herbivory, had lower nutrient concentrations, or both. Indeed, a large body of work on
441 oak gall wasps suggests host-plant quality is more important than predation as a determinant of
442 the distribution of galls among individual trees (reviewed in Stone et al. 2002). These patterns
443 suggest the negative effects of galls on foliage-dwelling herbivores are possible only when plant
444 quality is sufficiently high.

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

456 Most work on the effect of ecosystem engineers on beta diversity has focused on
457 differences in community composition between engineered and unmodified habitat (Hewitt et al.
458 2005, Bangert and Slobodchikoff 2006). Our work, however, shows that habitat engineering can
459 also influence beta diversity at a larger scale: engineering can lead to differences in community

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

476 Although our study was focused on broad community patterns and not on mechanisms,
477 we hypothesize the most likely mechanism was that galls provided refuges for jumping spiders,
478 both during the winter and through the growing season, leading to higher spider densities, which
479 then suppressed herbivore richness and density and promoted variation in community
480 composition among trees. The apparently low densities of jumping spiders on stems or leaves,
481 despite their surprisingly high densities inside galls, is likely because they mainly leave galls
482 only for foraging. It is unlikely that secondary inhabitants other than spiders were responsible for

506 gall-maker, and last as long as the galls remain adhered to the tree, which can be at least several
507 years. Further, these indirect effects appear to occur only on trees of sufficient host-plant quality
508 to support gall wasps and a rich foliage-dwelling community. The work presented here differs
509 from previous work on habitat engineering because it demonstrates that the effects of habitat
510 engineering can go beyond merely providing habitat for specialists that colonize engineered
511 habitat; they can propagate through the community far enough to have negative effects on
512 density and richness of resident species that do not interact directly with the engineered
513 structures. Taken together, our results provide a glimpse of the intersection between phenomena
514 typically studied in isolation: habitat engineering, phenological timing, and trophic control. The
515 picture that emerges illustrates that habitat engineering—in the form of a trait-mediated indirect
516 interactions—can interact with phenological timing to influence heterogeneity in trophic control
517 at the community scale.

518

519

Acknowledgments

520 We thank I. Pearse for insights into the oak gall system, S. Heydon for help with
521 taxonomy, and B. Hammock for help in the field. P. Grof-Tisza, B. Hammock, I. Pearse, D.
522 Strong, R. Karban, J. Rosenheim, M. Meek, and M. Bogan provided feedback and advice. We
523 thank the editor and two anonymous reviewers for helpful comments and for encouraging us to
524 collect additional field data that greatly improved the manuscript. We are grateful to A. Fulks
525 and J.P. Marie of the UC Davis Putah Creek Riparian Reserve. This project was performed by
526 the undergraduate class EVE/ENT 180 Experimental Ecology and Evolution in the Field at the
527 University of California, Davis. The UC Davis departments of Evolution & Ecology and

528 Entomology & Nematology provided funding. WW was supported by NSF DEB 081430, the
529 REACH IGERT at UC Davis.

530

531 **Literature Cited**

532 Anderson, M. J. 2005. Distance-Based Tests for Homogeneity of Multivariate Dispersions.
533 *Biometrics* 62:245–253.

534 Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure
535 of beta diversity. *Ecology Letters* 9:683–693.

536 Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J.
537 Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C.
538 Stegen, and N. G. Swenson. 2010. Navigating the multiple meanings of β diversity: a
539 roadmap for the practicing ecologist. *Ecology Letters* 14:19–28.

540 Andrén, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands:
541 experimental evidence. *Ecology* 69:544–547.

542 Badano, E. I., C. G Jones, L. A Cavieres, and J. P Wright. 2006. Assessing impacts of ecosystem
543 engineers on community organization: a general approach illustrated by effects of a high-
544 Andean cushion plant. *Oikos* 115:369–385.

545 Baer, C. S., and R. J. Marquis. 2014. Native leaf-tying caterpillars influence host plant use by the
546 invasive Asiatic oak weevil through ecosystem engineering. *Ecology* 95:1472–1478.

547 Bangert, R. K., and C. N. Slobodchikoff. 2006. Conservation of prairie dog ecosystem
548 engineering may support arthropod beta and gamma diversity. *Journal of Arid Environments*
549 67:100–115.

550 Bascompte, J. 2010. Structure and dynamics of ecological networks. *Science* 329: 765-766.

551 Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press, Princeton, NJ.

552 Bolker, B. M. 2012. bbmle: Tools for general maximum likelihood estimation. R Development
553 Core Team.

554 Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-
555 S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and
556 evolution. *Trends In Ecology & Evolution* 24:127–135.

557 Castilla, J. C., N. A. Lagos, and M. Cerda. 2004. Marine ecosystem engineering by the alien
558 ascidian *Pyura praeputialis* on a mid-intertidal rocky shore. *Marine Ecology Progress Series*
559 268:119–130.

560 Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. Maunder, A. Nielsen, and
561 J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of
562 highly parameterized complex nonlinear models. *Optimization Methods and Software*
563 27:233–249.

564 Fukami, T. 2004. Assembly history interacts with ecosystem size to influence species diversity.
565 *Ecology* 85:3234–3242.

566 Gribben, P. E., J. E. Byers, M. Clements, L. A. McKenzie, P. D. Steinberg, and J. T. Wright.
567 2009. Behavioural interactions between ecosystem engineers control community species
568 richness. *Ecology Letters* 12:1127–1136.

569 Hastings, A., J. E. Byers, J. A. Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, T. S.
570 Talley, and W. G. Wilson. 2007. Ecosystem engineering in space and time. *Ecology Letters*
571 10:153–164.

572 Hewitt, J. E., S. F. Thrush, J. Halliday, and C. Duffy. 2005. The importance of small-scale
573 habitat structure for maintaining beta diversity. *Ecology* 86:1619–1626.

574 Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative
575 roles of bottom-up and top-down forces in natural communities. *Ecology* 73:723–732.

576 Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers.
577 *Oikos*:373–386.

578 Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as
579 physical ecosystem engineers. *Ecology* 78:1946–1957.

580 Joseph, M. B., M. Gentles, and I. S. Pearse. 2010. The parasitoid community of *Andricus*
581 *quercuscalifornicus* and its association with gall size, phenology, and location. *Biodiversity*
582 *and Conservation* 20:203–216.

583 Kefi, S., E. L. Berlow, E. A. Wieters, S. A. Navarrete, O. L. Petchey, S. A. Wood, A. Boit, L. N.
584 Joppa, K. D. Lafferty, R. J. Williams, N. D. Martinez, B. A. Menge, C. A. Blanchette, A. C.
585 Iles, and U. Brose. 2012. More than a meal... integrating non-feeding interactions into food
586 webs. *Ecology Letters* 15: 291-300.

587 Lill, J. T., and R. J. Marquis. 2003. Ecosystem engineering by caterpillars increases insect
588 herbivore diversity on white oak. *Ecology* 84:682–690.

589 Marquis, R. J., and J. T. Lill. 2007. Effects of arthropods as physical ecosystem engineers on
590 plant-based trophic interaction webs. *in* T. Ohgushi, T. P. Craig, and P. W. Price, editors.
591 *Ecological communities: Plant mediation in indirect interaction webs*. Cambridge University
592 Press, New York.

593 Martinsen, G. D., K. D. Floate, A. M. Waltz, G. M. Wimp, and T. G. Whitham. 2000. Positive
594 interactions between leafrollers and other arthropods enhance biodiversity on hybrid
595 cottonwoods. *Oecologia* 123:82–89.

596 Meadows, P. S., A. Meadows, and J. M. Murray. 2012. Biological modifiers of marine benthic

597 seascapes: Their role as ecosystem engineers. *Geomorphology* 157:31–48.

598 Miyashita, T., and M. Takada. 2007. Habitat provisioning for aboveground predators decreases
599 detritivores. *Ecology* 88:2803–2809.

600 Nakamura, M., and T. Ohgushi. 2003. Positive and negative effects of leaf shelters on
601 herbivorous insects: linking multiple herbivore species on a willow. *Oecologia* 136:445–449.

602 Oksanen, L., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O’Hara, G. L. Simpson,
603 P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. *vegan*: Community ecology package.

604 Oksanen, L., S. Fretwell, J. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients
605 of primary productivity. *The American Naturalist* 118:240–261.

606 Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, A.
607 R. Hughes, G. Kendrick, W. J. Kenworthy, S. Olyarnik, F. T. Short, M. Waycott, and S. L.
608 Williams. 2006. A Global Crisis for Seagrass Ecosystems. *BioScience* 56:987.

609 Pike, D. A., and J. C. Mitchell. 2013. Burrow-dwelling ecosystem engineers provide thermal
610 refugia throughout the landscape. *Animal Conservation* 16:694–703.

611 R Core Team. 2014. *R: A Language and Environment for Statistical Computing*. R Foundation
612 for Statistical Computing, Vienna, Austria.

613 Ransom, T. S. 2010. Earthworms, as ecosystem engineers, influence multiple aspects of a
614 salamander’s ecology. *Oecologia* 165:745–754.

615 Robinson, J. F., and J. E. Dickerson. 1987. Does invasion sequence affect community structure?
616 *Ecology*:587–595.

617 Rosenthal, S. S., and C. S. Koehler. 1971. Intertree distributions of some Cynipid (Hymenoptera)
618 galls on *Quercus lobata*. *Annals of the Entomological Society of America* 64:571–574.

619 Russo, R. 2006. *Field guide to plant galls of California and other western states*. University of

620 California Press, Berkeley.

621 Sanders, D., C. G. Jones, E. Thebault, T. J. Bouma, T. van der Heide, J. van Belzen, and S. Barot.
622 2014. Integrating ecosystem engineering and food webs. *Oikos* 123: 513-524.

623 Sanver, D., and B. A. Hawkins. 2000. Galls as habitats: the inquiline communities of insect galls.
624 *Basic And Applied Ecology* 1:3–11.

625 Skaug, H. J., D. A. Fournier, A. Nielsen, A. Magnusson, and B. M. Bolker. 2013. Generalized
626 Linear Mixed Models using AD Model Builder.

627 Stone, G. N., K. Schönrogge, R. J. Atkinson, D. Bellido, and J. Pujade-Villar. 2002. The
628 population biology of oak gall wasps (Hymenoptera: Cynipidae). *Annual Review of*
629 *Entomology* 47:633–668.

630 Ver Hoef, J. M., and P. L. Boveng. 2007. Quasi-Poisson vs. negative binomial regression: how
631 should we model overdispersed count data? *Ecology* 88:2766–2772.

632 Wright, J. P. 2009. Linking populations to landscapes: richness scenarios resulting from changes
633 in the dynamics of an ecosystem engineer. *Ecology* 90:3418–3429.

634 Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years
635 on: Progress, limitations, and challenges. *BioScience* 56:203–209.

636 Wright, J. P., C. G. Jones, and A. S. Flecker. 2002. An ecosystem engineer, the beaver, increases
637 species richness at the landscape scale. *Oecologia* 132:96–101.

638

639

Supplemental Material

640

Appendix A: Tables of parameter estimates and likelihood ratio test statistics

641

642

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

649
650 Fig. 2. Mean number of all arthropods, herbivores, parasitoids, and predators in sweep samples
651 by treatment and time. Control trees are squares with solid lines, removal trees are triangles with
652 dashed lines, and naturally gall-free trees are circles with grey dotted lines. Error bars are ± 1 SE.
653 Vertical, grey dashes separate the pre-treatment/pre-budburst sample from the post-
654 treatment/post-budburst samples.

655
656 Fig. 3. Mean arthropod, herbivore, parasitoid, and predator morphospecies richness in sweep
657 samples by treatment and time. Control trees are squares with solid lines, removal trees are
658 triangles with dashed lines, and naturally gall-free trees are circles with grey dotted lines. Error
659 bars are ± 1 SE. Vertical, grey dashes separate the pre-treatment/pre-budburst sample from the
660 post-treatment/post-budburst sample.

661
662 Fig. 4. Non-metric multidimensional scaling ordinations for arthropod communities on the
663 removal and control trees in the (a) pre-treatment sampling and in the samplings (b) two and (c)
664 five weeks post-treatment. Mean community composition did not differ between treatments in
665 any sampling. In the third sample (c), control trees had significantly higher beta diversity

666 (multivariate dispersion) than did removal trees. Three trees with communities > 2 standard
667 deviations from the mean were held out of each figure because those communities were so
668 different they obscured variation among the rest of the communities. Inclusion or exclusion of
669 these communities did not influence the outcome of analyses. Stress is 0.19, 0.25, and 0.23,
670 respectively.

671

672 Fig. 5. Mean number of all arthropods, prey, and natural enemies (predators and parasitoids) on
673 sticky traps by treatment and time. Control trees are squares with solid lines, removal trees are
674 triangles with dashed lines, and naturally gall-free trees are circles with grey dotted lines. Error
675 bars are ± 1 SE. Vertical, grey dashes separate the pre-treatment/pre-budburst sample from the
676 post-treatment/post-budburst samples.

677

678

679

680

681

682

683

684

685

686

687

688

689



690



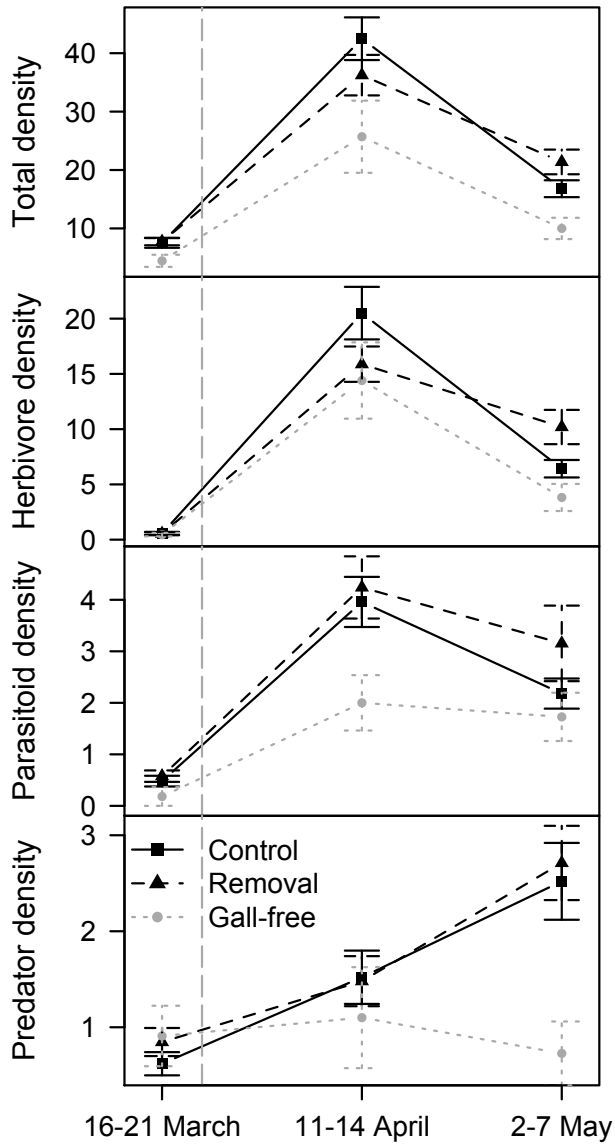
691

692 Fig. 1.

693

694

695

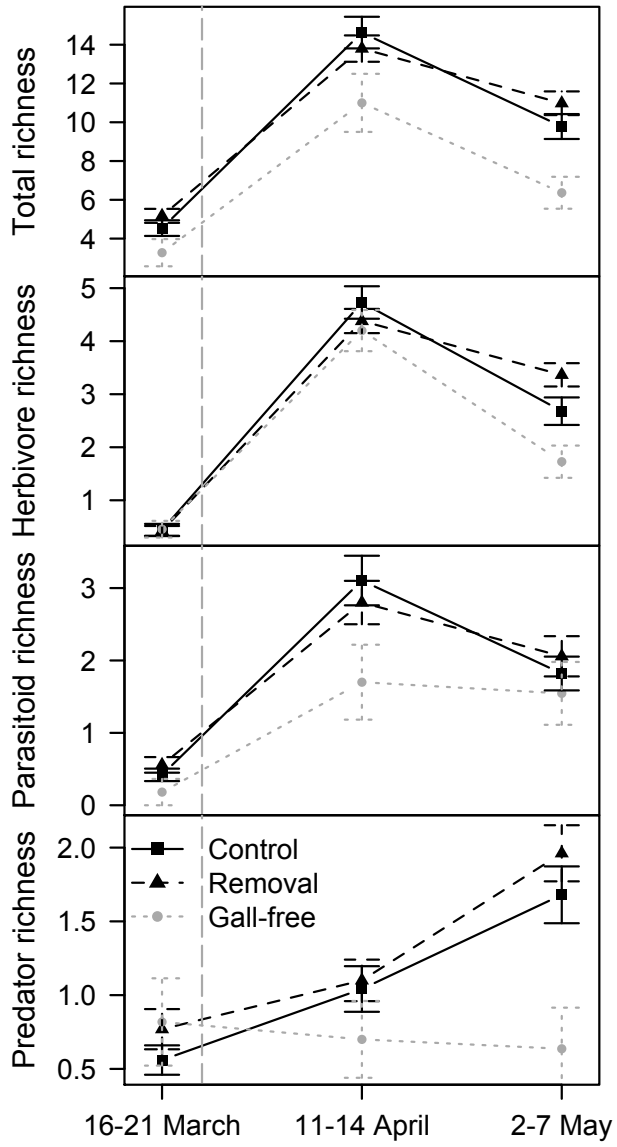


697

698 Fig. 2.

699

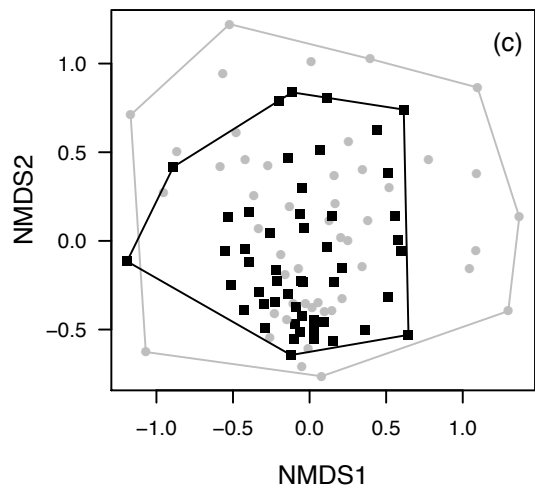
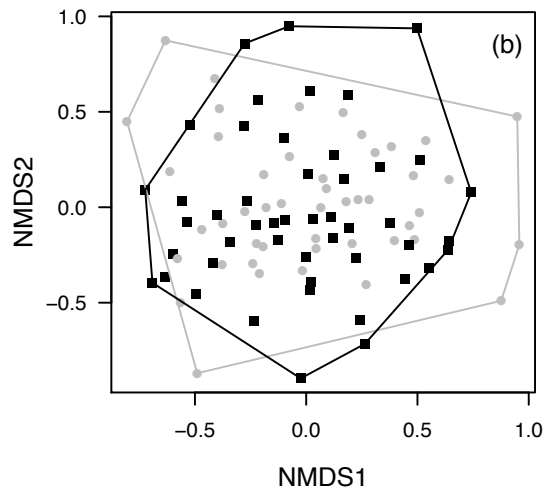
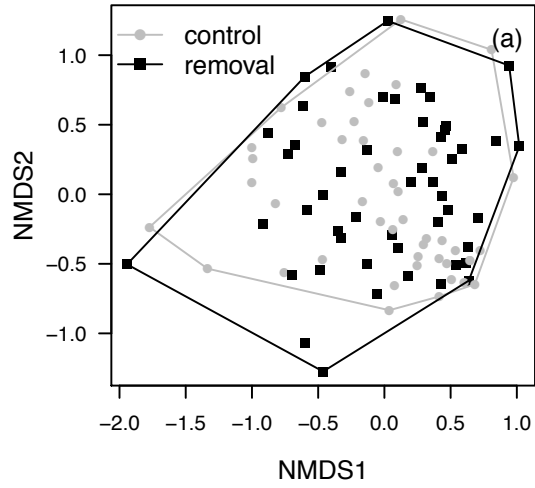
700



701

702 Fig. 3.

703

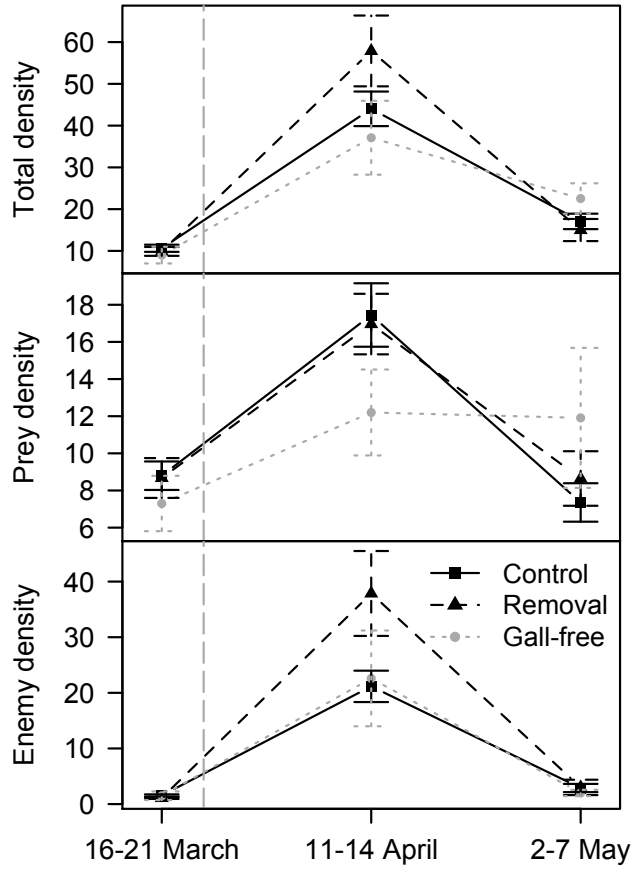


704

705 Fig. 4.

706

707



708

709 Fig. 5.

710

711

712

713

714

715

716

Online supplemental material

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

Appendix A: Parameter estimates and likelihood ratio test statistics

1. Variable name definitions
2. Pre-treatment univariate sweep/beat data
3. Pre-treatment multivariate sweep/beat data
4. Pre-treatment sticky trap data
5. Post-treatment univariate sweep/beat data
6. Post-treatment multivariate sweep/beat data
7. Post-treatment sticky trap data

1. Variable name definitions

control: control group indicator variable
enemy.count: natural enemy abundance in sticky traps
gph: galls per meter height of tree
H: herbivore abundance in sweep samples
Hrich: herbivore morphospecies richness in sweep samples
K: predator abundance in sweep samples
Krich: predator morphospecies richness in sweep samples
P: parasitoid abundance in sweep samples
prey.count: prey abundance in sticky traps
Prich: parasitoid morphospecies richness in sweep samples
removal: gall-removal treatment indicator variable
richness: total arthropod morphospecies richness in sweep samples
s.factor3: sampling period 3 indicator variable
tot: total arthropod abundance in sweep samples
total.count: total arthropod abundance in sticky traps
zero: naturally gall-free indicator variable

2. Pre-treatment univariate sweep/beat data

Total abundances

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	1.91679	0.17143	11.18	<2e-16	1.581	2.253
gph	0.00456	0.00239	1.91	0.057	0	0.009
removal	0.00926	0.13036	0.07	0.943	-0.246	0.265
zero	-0.58817	0.23769	-2.47	0.013	-1.054	-0.122

Removal vs control likelihood ratio test (LRT)

Model 1: tot ~ gph + zero

Model 2: tot ~ gph + removal + zero

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-322.21			
2	6	-322.20	1	0.004	0.9496

Removal vs gall-free trees LRT

Model 1: tot ~ gph + control

Model 2: tot ~ gph + removal + zero

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-325.24			
2	6	-322.20	1	6.074	0.01372

Herbivore abundances

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	-0.72146	0.35117	-2.05	0.04	-1.41	-0.033
gph	-0.00293	0.00738	-0.40	0.69	-0.017	0.012
removal	-0.18985	0.34094	-0.56	0.58	-0.858	0.478
zero	-0.47730	0.59971	-0.80	0.43	-1.653	0.698

Removal vs control LRT

Model 1: $H \sim \text{gph} + \text{zero}$

Model 2: $H \sim \text{gph} + \text{removal} + \text{zero}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-109.96			
2	6	-109.80	1	0.31	0.5777

Removal vs gall-free trees LRT

Model 1: $H \sim \text{gph} + \text{control}$

Model 2: $H \sim \text{gph} + \text{removal} + \text{zero}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-109.92			
2	6	-109.80	1	0.236	0.6271

Parasitoid abundances

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	-0.76604	0.24023	-3.19	0.0014	-1.237	-0.295
gph	0.00545	0.00375	1.45	0.1464	-0.002	0.013
removal	0.20224	0.29240	0.69	0.4892	-0.371	0.775
zero	-0.80706	0.75748	-1.07	0.2867	-2.292	0.678

Removal vs control LRT

Model 1: $P \sim \text{gph} + \text{zero}$

Model 2: $P \sim \text{gph} + \text{removal} + \text{zero}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-103.78			
2	6	-103.54	1	0.478	0.4893

Removal vs gall-free trees LRT

Model 1: $P \sim \text{gph} + \text{control}$

Model 2: $P \sim \text{gph} + \text{removal} + \text{zero}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-104.72			
2	6	-103.54	1	2.344	0.1258

Predator abundances

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	-0.62245	0.26325	-2.36	0.0181	-1.138	-0.106
gph	0.00878	0.00333	2.64	0.0083	0.002	0.015
removal	0.28982	0.25483	1.14	0.2554	-0.21	0.789
zero	0.45965	0.40132	1.15	0.2521	-0.327	1.246

Removal vs control LRT

Model 1: $K \sim \text{gph} + \text{zero}$

Model 2: $K \sim \text{gph} + \text{removal} + \text{zero}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-129.88			
2	6	-129.24	1	1.286	0.2568

Removal vs gall-free trees LRT

Model 1: $K \sim \text{gph} + \text{control}$

Model 2: $K \sim \text{gph} + \text{removal} + \text{zero}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-129.33			
2	6	-129.24	1	0.19	0.6629

Total richness

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	1.44861	0.13476	10.75	<2e-16	1.184	1.713
gph	0.00377	0.00165	2.28	0.023	0.001	0.007
removal	0.09297	0.10420	0.89	0.372	-0.111	0.297
zero	-0.37441	0.19951	-1.88	0.061	-0.765	0.017

Removal vs control LRT

Model 1: richness $\sim \text{gph} + \text{control}$

Model 2: richness $\sim \text{gph} + \text{removal} + \text{zero}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-104.72			
2	6	-103.54	1	2.344	0.1258

Removal vs gall-free trees LRT

Model 1: richness $\sim \text{gph} + \text{control}$

Model 2: richness $\sim \text{gph} + \text{removal} + \text{zero}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-260.55			
2	6	-257.59	1	5.924	0.01494

Herbivore richness

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	-0.94296	0.32844	-2.87	0.0041	-1.587	-0.299
gph	-0.00434	0.00782	-0.55	0.5794	-0.02	0.011
removal	-0.17709	0.32290	-0.55	0.5834	-0.81	0.456
zero	-0.24564	0.53043	-0.46	0.6433	-1.285	0.794

Removal vs control LRT

Model 1: Hrich $\sim \text{gph} + \text{zero}$

Model 2: Hrich $\sim \text{gph} + \text{removal} + \text{zero}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-95.823			
2	6	-95.672	1	0.3002	0.5838

Removal vs gall-free trees LRT

Model 1: Hrich $\sim \text{gph} + \text{control}$

Model 2: Hrich $\sim \text{gph} + \text{removal} + \text{zero}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-95.681			
2	6	-95.672	1	0.0172	0.8957

Parasitoid richness

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	-0.87709	0.24921	-3.52	0.00043	-1.366	-0.389
gph	0.00376	0.00381	0.99	0.32429	-0.004	0.011
removal	0.28224	0.29405	0.96	0.33715	-0.294	0.859
zero	-0.72027	0.74829	-0.96	0.33577	-2.187	0.746

Removal vs control LRT

Model 1: Prich ~ gph + zero

Model 2: Prich ~ gph + removal + zero

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-98.823			
2	6	-98.361	1	0.9256	0.336

Removal vs gall-free trees LRT

Model 1: Prich ~ gph + control

Model 2: Prich ~ gph + removal + zero

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-99.592			
2	6	-98.361	1	2.4622	0.1166

Predator richness

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	-0.71222	0.24838	-2.87	0.0041	-1.199	-0.225
gph	0.00838	0.00289	2.90	0.0037	0.003	0.014
removal	0.31735	0.25185	1.26	0.2076	-0.176	0.811
zero	0.47435	0.39696	1.19	0.2321	-0.304	1.252

Removal vs control LRT

Model 1: Krich ~ gph + zero

Model 2: Krich ~ gph + removal + zero

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-121.44			
2	6	-120.64	1	1.592	0.207

Removal vs gall-free trees LRT

Model 1: Krich ~ gph + control

Model 2: Krich ~ gph + removal + zero

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-120.73			
2	6	-120.64	1	0.17	0.6801

3. Pre-treatment multivariate sweep/beat data

Multivariate community composition (permutational ANOVA)

Component	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
td1.nz\$trtz	2	1.185	0.59246	1.56668	0.02876	0.06051
td1.nz\$gphd	1	0.313	0.31261	0.82665	0.00759	0.87346
Residuals	105	39.707	0.37816		0.96366	
Total	108	41.204			1.00000	

Beta-diversity

Multivariate homogeneity of group dispersions

Component	Df	SumSq	MeanSq	F-value	Pr(>F)
Groups	1	0.00335	0.0033521	0.4349	0.5112
Residuals	97	0.74763	0.0077075		

Presence-absence community matrix null model holding row and column sums constant: P = 0.501

Abundance community matrix null model holding row sums constant: P = 0.329

4. Pre-treatment sticky trap data

Total abundance

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)
(Intercept)	2.364465	0.089037	26.56	<2e-16
gph	-0.000411	0.002109	-0.19	0.85
trtz.factorremoval	-0.072888	0.124570	-0.59	0.56
trtz.factorzero	-0.173695	0.223000	-0.78	0.44

Removal vs control LRT

Model 1: total.count ~ gph + zero

Model 2: total.count ~ gph + trtz.factor

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-349.47			
2	6	-349.30	1	0.342	0.5587

Removal vs gall-free tree LRT

Model 1: total.count ~ gph + control

Model 2: total.count ~ gph + trtz.factor

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-349.4			
2	6	-349.3	1	0.202	0.6531

Prey abundance

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)
(Intercept)	2.174671	0.097363	22.34	<2e-16
gph	-0.000336	0.002310	-0.15	0.88
trtz.factorremoval	-0.013885	0.135750	-0.10	0.92
trtz.factorzero	-0.192081	0.244420	-0.79	0.43

Removal vs control LRT

Model 1: prey.count ~ gph + zero

Model 2: prey.count ~ gph + trtz.factor

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5				
2	6		1		

1	5	-337.95			
2	6	-337.95	1	0.01	0.9203

Removal vs gall-free tree LRT

Model 1: prey.count ~ gph + control

Model 2: prey.count ~ gph + trtz.factor

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-338.21			
2	6	-337.95	1	0.526	0.4683

Natural enemy abundance

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)
(Intercept)	0.44162	0.13785	3.20	0.0014
gph	-0.00152	0.00359	-0.42	0.6716
trtz.factorremoval	-0.34965	0.20501	-1.71	0.0881
trtz.factorzero	-0.06007	0.34333	-0.17	0.8611

Removal vs control LRT

Model 1: enemy.count ~ gph + zero

Model 2: enemy.count ~ gph + trtz.factor

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-171.68			
2	6	-170.23	1	2.892	0.08902

Removal vs gall-free tree LRT

Model 1: enemy.count ~ gph + control

Model 2: enemy.count ~ gph + trtz.factor

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	5	-170.57			
2	6	-170.23	1	0.672	0.4124

5. Post-treatment univariate sweep/beat data

Total abundance

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5% CI	97.5% CI
(Intercept)	3.60377	0.12837	28.07	<2e-16	3.352	3.855
s.factor3	-0.86290	0.15498	-5.57	2.6e-08	-1.167	-0.559
gph	0.00246	0.00214	1.15	0.2494	-0.002	0.007
removal	-0.15050	0.12199	-1.23	0.2173	-0.390	0.089
zero	-0.46116	0.21844	-2.11	0.0348	-0.889	-0.033
s.factor3:removal	0.36671	0.13435	2.73	0.0063	0.103	0.630
s.factor3:zero	-0.02148	0.24300	-0.09	0.9296	-0.498	0.455
gph:removal	0.00337	0.00367	0.92	0.3577	-0.004	0.011

Removal vs control LRT

Model 1: tot ~ s.factor + gph + zero + s.factor:zero

Model 2: tot ~ s.factor + gph + removal + zero + s.factor:zero + removal:gph

Model 3: tot ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-886.25			

2	10	-885.78	2	0.958	0.619402
3	11	-882.14	1	7.270	0.007012

Removal vs gall-free tree LRT

Model 1: tot ~ s.factor + gph + removal.zero + s.factor:removal.zero + removal.zero:gph

Model 2: tot ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-886.16			
2	11	-882.14	2	8.048	0.01788

Herbivore abundance

Full model

	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	2.883281	0.211750	13.62	<2e-16	2.468	3.298
s.factor3	-1.184399	0.274820	-4.31	1.6e-05	-1.723	-0.646
gph	0.000783	0.002943	0.27	0.7902	-0.005	0.007
removal	-0.202037	0.169090	-1.19	0.2321	-0.533	0.129
zero	-0.238519	0.299970	-0.80	0.4265	-0.826	0.349
s.factor3:removal	0.601981	0.200900	3.00	0.0027	0.208	0.996
s.factor3:zero	-0.340894	0.367400	-0.93	0.3535	-1.061	0.379
gph:removal	0.003150	0.004958	0.64	0.5253	-0.007	0.013

Removal vs control LRT

Model 1: H ~ s.factor + gph + zero + s.factor:zero

Model 2: H ~ s.factor + gph + removal + zero + s.factor:zero + removal:gph

Model 3: H ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-755.37			
2	10	-754.98	2	0.766	0.681813
3	11	-750.57	1	8.816	0.002986

Removal vs gall-free tree LRT

Model 1: H ~ s.factor + gph + removal.zero + s.factor:removal.zero + removal.zero:gph

Model 2: H ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-755.11			
2	11	-750.57	2	9.07	0.01073

Parasitoid abundance

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	1.20919	0.19850	6.09	1.1e-09	0.82	1.598
s.factor3	-0.50251	0.25067	-2.00	0.045	-0.994	-0.011
gph	0.00700	0.00294	2.38	0.017	0.001	0.013
removal	0.05676	0.18471	0.31	0.759	-0.305	0.419
zero	-0.49644	0.36105	-1.37	0.169	-1.204	0.211
s.factor3:removal	0.16582	0.22484	0.74	0.461	-0.275	0.607
s.factor3:zero	0.40435	0.43518	0.93	0.353	-0.449	1.257
gph:removal	-0.00818	0.00544	-1.50	0.133	-0.019	0.002

Removal vs control LRT

Model 1: P ~ s.factor + gph + zero + s.factor:zero

Model 2: P ~ s.factor + gph + removal + zero + s.factor:zero + removal:gph

Model 3: $P \sim \text{s.factor} + \text{gph} + \text{removal} + \text{zero} + \text{s.factor:removal} + \text{s.factor:zero} + \text{removal:gph}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-487.99			
2	10	-486.64	2	2.708	0.2582
3	11	-486.37	1	0.544	0.4608

Removal vs gall-free tree LRT

Model 1: $P \sim \text{s.factor} + \text{gph} + \text{removal.zero} + \text{s.factor:removal.zero} + \text{removal.zero:gph}$

Model 2: $P \sim \text{s.factor} + \text{gph} + \text{removal} + \text{zero} + \text{s.factor:removal} + \text{s.factor:zero} + \text{removal:gph}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-488.39			
2	11	-486.37	2	4.046	0.1323

Predator abundance

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	0.10815	0.27725	0.39	0.696	-0.435	0.652
s.factor3	0.53211	0.34646	1.54	0.125	-0.147	1.211
gph	0.00523	0.00282	1.85	0.064	0.000	0.011
removal	0.03652	0.22971	0.16	0.874	-0.414	0.487
zero	-0.17418	0.43639	-0.40	0.690	-1.029	0.681
s.factor3:removal	0.06595	0.27540	0.24	0.811	-0.474	0.606
s.factor3:zero	-1.00488	0.58384	-1.72	0.085	-2.149	0.139
gph:removal	-0.00269	0.00532	-0.50	0.614	-0.013	0.008

Removal vs control LRT

Model 1: $K \sim \text{s.factor} + \text{gph} + \text{zero} + \text{s.factor:zero}$

Model 2: $K \sim \text{s.factor} + \text{gph} + \text{removal} + \text{zero} + \text{s.factor:zero} + \text{removal:gph}$

Model 3: $K \sim \text{s.factor} + \text{gph} + \text{removal} + \text{zero} + \text{s.factor:removal} + \text{s.factor:zero} + \text{removal:gph}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-397.58			
2	10	-397.36	2	0.446	0.8001
3	11	-397.33	1	0.058	0.8097

Removal vs gall-free tree LRT

Model 1: $K \sim \text{s.factor} + \text{gph} + \text{removal.zero} + \text{s.factor:removal.zero} + \text{removal.zero:gph}$

Model 2: $K \sim \text{s.factor} + \text{gph} + \text{removal} + \text{zero} + \text{s.factor:removal} + \text{s.factor:zero} + \text{removal:gph}$

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-402.26			
2	11	-397.33	2	9.85	0.007263

Total richness

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	2.621783	0.071891	36.47	<2e-16	2.481	2.763
s.factor3	-0.382369	0.090695	-4.22	2.5e-05	-0.56	-0.205
gph	0.002084	0.001232	1.69	0.091	0.000	0.004
removal	-0.048335	0.074020	-0.65	0.514	-0.193	0.097
zero	-0.237760	0.138190	-1.72	0.085	-0.509	0.033
s.factor3:removal	0.169060	0.088477	1.91	0.056	-0.004	0.342
s.factor3:zero	-0.152694	0.175670	-0.87	0.385	-0.497	0.192
gph:removal	0.000843	0.002140	0.39	0.694	-0.003	0.005

Removal vs control LRT

Model 1: richness ~ s.factor + gph + zero + s.factor:zero

Model 2: richness ~ s.factor + gph + removal + zero + s.factor:zero + removal:gph

Model 3: richness ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-639.90			
2	10	-639.71	2	0.388	0.82366
3	11	-637.91	1	3.586	0.05827

Removal vs gall-free tree LRT

Model 1: richness ~ s.factor + gph + removal.zero + s.factor:removal.zero + removal.zero:gph

Model 2: richness ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-643.30			
2	11	-637.91	2	10.776	0.004571

Herbivore richness

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	1.554815	0.100700	15.44	<2e-16	1.357	1.752
s.factor3	-0.623890	0.157870	-3.95	7.8e-05	-0.933	-0.314
gph	0.000145	0.001510	0.10	0.924	-0.003	0.003
removal	-0.091562	0.096113	-0.95	0.341	-0.28	0.097
zero	-0.111724	0.174140	-0.64	0.521	-0.453	0.23
s.factor3:removal	0.315977	0.149990	2.11	0.035	0.022	0.61
s.factor3:zero	-0.330142	0.300100	-1.10	0.271	-0.918	0.258
gph:removal	0.003578	0.002423	1.48	0.140	-0.001	0.008

Removal vs control LRT

Model 1: Hrich ~ s.factor + gph + zero + s.factor:zero

Model 2: Hrich ~ s.factor + gph + removal + zero + s.factor:zero + removal:gph

Model 3: Hrich ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-429.48			
2	10	-428.19	2	2.584	0.27472
3	11	-425.96	1	4.456	0.03478

Removal vs gall-free tree LRT

Model 1: Hrich ~ s.factor + gph + removal.zero + s.factor:removal.zero + removal.zero:gph

Model 2: Hrich ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-429.61			
2	11	-425.96	2	7.302	0.02597

Parasitoid richness

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	1.02340	0.14951	6.85	7.6e-12	0.73	1.316
s.factor3	-0.46479	0.20604	-2.26	0.0241	-0.869	-0.061
gph	0.00576	0.00215	2.69	0.0072	0.002	0.01
removal	-0.06253	0.15310	-0.41	0.6829	-0.363	0.238
zero	-0.45639	0.31210	-1.46	0.1437	-1.068	0.155
s.factor3:removal	0.19404	0.20967	0.93	0.3547	-0.217	0.605

s.factor3:zero	0.41208	0.40593	1.02	0.3100	-0.384	1.208
gph:removal	-0.00634	0.00425	-1.49	0.1359	-0.015	0.002

Removal vs control LRT

Model 1: Prich ~ s.factor + gph + zero + s.factor:zero

Model 2: Prich ~ s.factor + gph + removal + zero + s.factor:zero + removal:gph

Model 3: Prich ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-422.09			
2	10	-420.98	2	2.222	0.3292
3	11	-420.55	1	0.858	0.3543

Removal vs gall-free tree LRT

Model 1: Prich ~ s.factor + gph + removal.zero + s.factor:removal.zero + removal.zero:gph

Model 2: Prich ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-422.04			
2	11	-420.55	2	2.968	0.2267

Predator richness

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)	2.5%	97.5%
(Intercept)	-0.034807	0.187220	-0.19	0.853	-0.402	0.332
s.factor3	0.479553	0.235480	2.04	0.042	0.018	0.941
gph	0.002621	0.001974	1.33	0.184	-0.001	0.006
removal	0.070164	0.197040	0.36	0.722	-0.316	0.456
zero	-0.287732	0.410860	-0.70	0.484	-1.093	0.518
s.factor3:removal	0.103103	0.245710	0.42	0.675	-0.378	0.585
s.factor3:zero	-0.636355	0.568140	-1.12	0.263	-1.75	0.477
gph:removal	-0.000351	0.003784	-0.09	0.926	-0.008	0.007

Removal vs control LRT

Model 1: Krich ~ s.factor + gph + zero + s.factor:zero

Model 2: Krich ~ s.factor + gph + removal + zero + s.factor:zero + removal:gph

Model 3: Krich ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-321.58			
2	10	-320.93	2	1.306	0.5205
3	11	-320.84	1	0.176	0.6748

Removal vs gall-free tree LRT

Model 1: Krich ~ s.factor + gph + removal.zero + s.factor:removal.zero + removal.zero:gph

Model 2: Krich ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-326.47			
2	11	-320.84	2	11.26	0.003589

6. Post-treatment multivariate sweep/beat data

Multivariate community composition (permutational ANOVA)

First post-treatment sample:

Component	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
-----------	----	-----------	---------	---------	----	--------

td2.nz\$trtz	2	0.7206	0.36029	1.33087	0.02473	0.082
td2.nz\$gphd	1	0.2643	0.26427	0.97617	0.00907	0.483
Residuals	104	28.1549	0.27072		0.96620	
Total	107	29.1397			1.00000	

Second post-treatment sample:

Component	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
td3.nz\$trtz	2	0.784	0.39177	1.0457	0.01862	0.338
td3.nz\$gphd	1	0.468	0.46810	1.2494	0.01112	0.267
Residuals	109	40.836	0.37464		0.97026	
Total	112	42.088			1.00000	

Beta-diversity

First post-treatment sample:

Multivariate homogeneity of group dispersions

Component	Df	SumSq	MeanSq	F-value	Pr(>F)
Groups	1	0.00009	0.0000949	0.0105	0.9186
Residuals	96	0.86740	0.0090354		

Presence-absence community matrix null model holding row and column sums constant: P = 0.866

Abundance community matrix null model holding row sums constant: P = 0.871

Second post-treatment sample:

Multivariate homogeneity of group dispersions

Component	Df	SumSq	MeanSq	F-value	Pr(>F)
Groups	1	0.02604	0.026043	4.0884	0.04585
Residuals	100	0.63700	0.006370		

Presence-absence community matrix null model holding row and column sums constant: P = 0.0367

Abundance community matrix null model holding row sums constant: P = 0.0012

7. Post-treatment sticky trap data

Total abundance

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)
(Intercept)	3.739863	0.111160	33.64	<2e-16
s.factor3	-0.921128	0.143850	-6.40	1.5e-10
gph	-0.000873	0.005632	-0.16	0.877
removal	0.188345	0.157800	1.19	0.233
zero	-0.152941	0.268920	-0.57	0.570
s.factor3:removal	-0.387611	0.203000	-1.91	0.056
s.factor3:zero	0.540875	0.332800	1.63	0.104
gph:removal	0.004768	0.006552	0.73	0.467

Removal vs control LRT

Model 1: total.count ~ s.factor + gph + zero + s.factor:zero

Model 2: total.count ~ s.factor + gph + removal + zero + s.factor:zero + removal:gph

Model 3: total.count ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-859.31			
2	10	-858.99	2	0.636	0.72760
3	11	-857.18	1	3.626	0.05688

Removal vs gall-free tree LRT

Model 1: total.count ~ s.factor + gph + removal.zero + s.factor:removal.zero + removal.zero:gph

Model 2: total.count ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-861.61			
2	11	-857.18	2	8.866	0.01188

Prey abundance

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)
(Intercept)	2.93154	0.18173	16.13	<2e-16
s.factor3	-0.90180	0.16409	-5.50	3.9e-08
gph	0.00309	0.00557	0.55	0.579
removal	-0.19158	0.16711	-1.15	0.252
zero	-0.44391	0.29277	-1.52	0.129
s.factor3:removal	0.23700	0.22783	1.04	0.298
s.factor3:zero	0.94191	0.37863	2.49	0.013
gph:removal	0.00265	0.00646	0.41	0.682

Removal vs control LRT

Model 1: prey.count ~ s.factor + gph + zero + s.factor:zero

Model 2: prey.count ~ s.factor + gph + removal + zero + s.factor:zero + removal:gph

Model 3: prey.count ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-690.38			
2	10	-690.13	2	0.498	0.7796
3	11	-689.59	1	1.084	0.2978

Removal vs gall-free tree LRT

Model 1: prey.count ~ s.factor + gph + removal.zero + s.factor:removal.zero + removal.zero:gph

Model 2: prey.count ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-691.63			
2	11	-689.59	2	4.094	0.1291

Natural enemy abundance

Full model

Parameter	Estimate	Std.Error	z-value	Pr(> z)
(Intercept)	2.9966	0.1854	16.16	<2e-16
s.factor3	-2.2126	0.2481	-8.92	<2e-16
gph	-0.0135	0.0101	-1.35	0.178
removal	0.3884	0.2618	1.48	0.138
zero	-0.1323	0.4512	-0.29	0.769
s.factor3:removal	-0.5431	0.3493	-1.56	0.120
s.factor3:zero	-0.0888	0.5838	-0.15	0.879
gph:removal	0.0195	0.0116	1.68	0.093

Removal vs control LRT

Model 1: enemy.count ~ s.factor + gph + zero + s.factor:zero

Model 2: enemy.count ~ s.factor + gph + removal + zero + s.factor:zero + removal:gph

Model 3: enemy.count ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	8	-653.81			

2	10	-652.14	2	3.324	0.1898
3	11	-650.94	1	2.404	0.1210

Removal vs gall-free tree LRT

Model 1: enemy.count ~ s.factor + gph + removal.zero + s.factor:removal.zero + removal.zero:gph

Model 2: enemy.count ~ s.factor + gph + removal + zero + s.factor:removal + s.factor:zero + removal:gph

Model	NoPar	LogLik	Df	Deviance	Pr(>Chi)
1	9	-651.25			
2	11	-650.94	2	0.608	0.7379