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Materials transfer agreements will be required for the acquisition of the *Wnt5a^{fl/fl}* mice from the National Cancer Institute and the L-WRN cell line from the Washington Univ. Medical School. The data presented in this manuscript are tabulated in the main paper and in the supplementary materials.

Supplementary Materials

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Materials and Methods

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Insect Herbivores Drive Real-Time Ecological and Evolutionary Change in Plant Populations

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Insect herbivores are hypothesized to be major factors affecting the ecology and evolution of plants. We tested this prediction by suppressing insects in replicated field populations of a native plant, *Oenothera biennis*, which reduced seed predation, altered interspecific competitive dynamics, and resulted in rapid evolutionary divergence. Comparative genotyping and phenotyping of nearly 12,000 *O. biennis* individuals revealed that in plots protected from insects, resistance to herbivores declined through time owing to changes in flowering time and lower defensive ellagitannins in fruits, whereas plant competitive ability increased. This independent real-time evolution of plant resistance and competitive ability in the field resulted from the relaxation of direct selective effects of insects on plant defense and through indirect effects due to reduced herbivory on plant competitors.

The ubiquitous consumption of plants by insect herbivores represents one of the dominant species interactions on Earth and has been hypothesized to play a strong role in the diversification of plant species and their traits (1–3). The evolution of plant defense has been studied primarily with either a prospective or retrospective approach. Single-generation prospective approaches measure contemporary natural selection on resistance traits and make predictions about how those traits should evolve given estimates of their heritability (4–6). By contrast, retrospective studies compare populations or species that have diverged over time (7–9) and make inferences about the processes driving evolutionary change. More generally, temporal studies of natural species interactions that influence evolutionary dynamics remain rare, and few have been exper-

imental (9–12). Thus, we lack experimental field studies that quantify how species interactions influence selection on traits and the evolutionary response to this selection. As such, it is not well

established how rapidly plants adapt to selection by herbivores, which traits are most important in the evolution of defense, and whether herbivory drives predictable parallel changes due to selection across populations.

The ecology and evolution of plant-herbivore relationships is, in part, governed by the reciprocal nature of their interaction and the complexity of communities. For example, plant traits and plant community structure are critical for determining insect occurrence and attack rates (1–3). Conversely, insects can directly reduce focal plant abundance (13) or indirectly affect plant abundance through changes in the density of co-occurring competitors (14). Thus, the evolutionary dynamics of a focal plant species might be influenced through direct selection on resistance traits and/or by indirect selection on traits influencing competitive ability (15, 16). Despite this likely scenario, our understanding of how species interactions influence the evolution of constituent community members is surprisingly limited (17).

We conducted a field study of the selective impact of insects and the evolutionary response

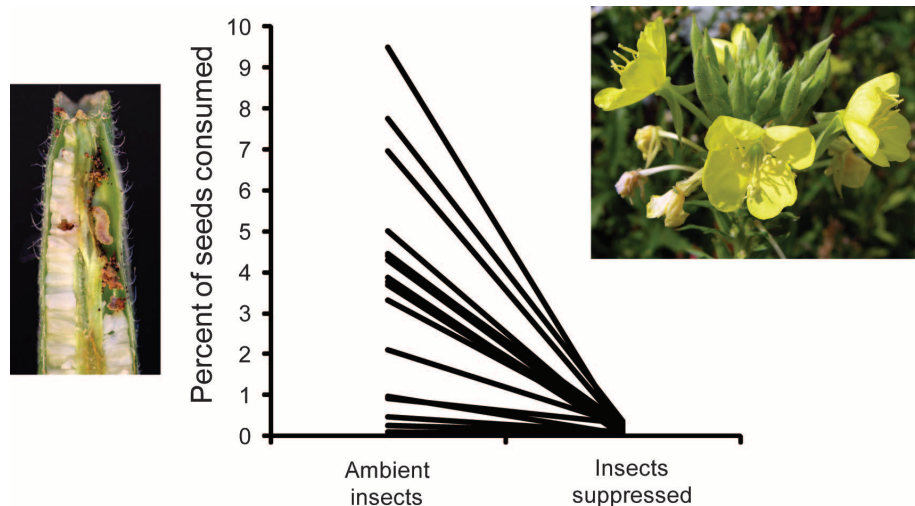


Fig. 1. Fruit loss to seed predator moths (dominated by *M. brevivittella*) in 18 genotypes of *O. biennis* in ambient and insect-suppressed plots (data are from the first generation, 2007–2008, mixed-model analysis of variance, genotype-by-insecticide interaction: $\chi^2 = 57.55$, $P < 0.001$). (Left) an opened fruit with a *M. brevivittella* larvae consuming immature seeds; (right) a flowering *O. biennis*.

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to this selection in the native forb common evening primrose, *Oenothera biennis* (Onagraceae) (18). We established 16 replicate plots planted with 60 individual seedlings of *O. biennis*, containing equivalent frequencies of 18 uniquely identified genotypes (19). Half of the plots were treated biweekly during each growing season with esfenvalerate, a nonsystemic insecticide (insect suppression treatment, supplementary text 2a); the remaining plots received an equivalent amount of water as a control (ambient insect treatment). Because *O. biennis* is annual or biennial, primarily selfing, and has a genetic system that suppresses recombination and segregation of alleles, we could track changes in frequencies of each planted genotype within each replicate population over multiple generations (19). Plots were not further weeded or otherwise manipulated, allowing the natural assembly and early succession of plant species with and without insects (supplementary text 2b). We previously summarized our sampling methods, the effects of flowering phenology on insect attack, and plant life-history evolution in the ambient insect plots (19). Here, we address the effects of experimental insect suppression on ecological and evolutionary change in *O. biennis*, including changes in genotypic composition, defensive chemistry, competitive ability, and flowering time.

Although there were three native species of specialist seed predator moths at our site, fruit

loss in *O. biennis* was dominated by *Mompha brevivittella*, which was >5 times as abundant as *M. stellerella* and *Schinia florida* combined, the other two common specialists. The 18 *O. biennis* genotypes varied substantially in their resistance to these seed predators (Fig. 1), and insect suppression created an environment with potentially large differences in natural selection. Despite increases in *O. biennis* abundance in the first 2 years of the experiment (reaching up to 4000 individuals per plot in 2009), recruitment was substantially lower in the insect suppression plots compared to ambient controls (Fig. 2). This reduction in *O. biennis* density coincided with a rise in the abundance of common dandelion, *Taraxacum officinale* (Asteraceae), an early successional weed that dominated our plots and was twice as abundant in plots where insects were suppressed compared to controls (Fig. 2 and fig. S1).

A specialist seed-feeding beetle of *T. officinale*, *Glocianus punctiger*, was significantly reduced by insect suppression, and a highly abundant generalist moth caterpillar at the site, *Noctua pronuba*, showed a preference for *T. officinale* over *O. biennis* (supplementary text 2c). Thus, we hypothesized that the release of *T. officinale* from its herbivores led to competitive suppression of *O. biennis*. Indeed, populations of *O. biennis* and *T. officinale* showed a negative correlation at the population level (simple correlation, $N = 16$, $r = -0.523$, $P =$

0.038), and an independent field experiment at the same site confirmed that *T. officinale* inhibits early establishment of *O. biennis* (supplementary text 2d). Because *O. biennis* requires light for germination, we hypothesize that *T. officinale* likely affects germination as well as early seedling survival. Therefore, insect suppression substantially affected plant competitors in addition to our focal species.

The net evolutionary consequence of insect suppression was a change in the genetic structure of *O. biennis* populations (Fig. 3, repeated measures canonical correspondence analysis, permutation test, trace = 0.275, $F = 8.511$, $P = 0.020$), with the strongest effect observed in the final year of the experiment (fig. S2). This parallel genetic differentiation among our replicated insect suppression plots in comparison to control plots (Fig. 3) implies that selection by insects, and not genetic drift, drove the observed

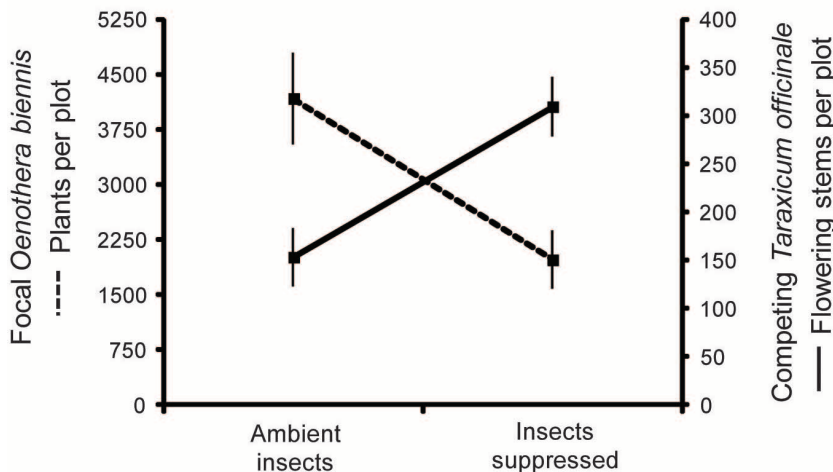


Fig. 2. Effects of insect suppression on the densities of focal *O. biennis* (univariate analysis of variance, $F_{1,14} = 8.97$, $P = 0.010$) and a major colonizing competitor (*T. officinale*, univariate analysis of variance, $F_{1,14} = 12.96$, $P = 0.003$) in 2009 (means \pm SEM); also shown are representative ambient and insect-suppressed plots when *T. officinale* was in peak bloom.

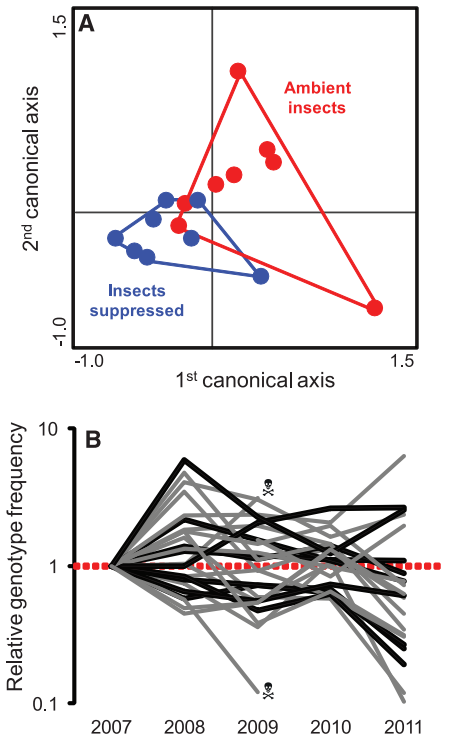


Fig. 3. (A) Results from an unconstrained correspondence analysis on frequencies of all genotypes in 2011. Each dot represents an experimental plot; ambient and suppressed treatments were coded after the analysis. A constrained canonical correspondence analysis revealed substantial genetic differentiation between treatments (data from 2011, permutation test, trace = 0.127, $F = 2.211$, $P = 0.003$). (B) The relative frequency (ambient/suppressed) of each genotype over time. The dashed red line indicates the null hypothesis of no divergence in genotype frequencies between treatments; darker lines highlight genotypes that represented >2% of the plants in 2011. Skull and crossbones indicate two genotypes that went extinct in one treatment. The y axis is on a logarithmic scale to facilitate equal visualization of under- and overrepresented genotype frequencies.

genotypic evolution. At the end of the experiment, 1 of the original 18 genotypes was entirely extirpated, and two additional genotypes were represented only in insect suppression plots (Fig. 3). Only six genotypes consistently maintained a frequency of 2% or higher within the populations. Three novel genotypes, derived from outcrossing events between known parents, each also reached >2% of the populations in 2011 (supplementary text 2e). Thus, across both treatments, nine genotypes dominated all plots (>2% each) at the end of the experiment. Genotypic evenness was >50% higher in insect suppression plots compared to controls (Smith and Wilson's evenness index, E_{var} , univariate analysis of variance, $F_{1,14} = 15.037$, $P = 0.002$), suggesting an erosion of genotypic variance in the presence of insect herbivores. Nonetheless, insect suppression affected neither genotypic richness (univariate analysis of variance, $F_{1,14} = 0.287$, $P = 0.600$) nor diversity (Simpson's index, univariate analysis of variance, $F_{1,14} = 0.377$, $P = 0.549$).

On the basis of annual estimates of genotype frequencies in each plot and genotype-specific means of *M. brevivittella* attack measured in control plots during 2007, we found that experimental suppression of insects resulted in evolution of relaxed plant defense (Fig. 4). We next determined the evolutionary response of traits responsible for this divergence in resistance. We had previously shown that the extent of early-season flowering (number of open or senesced

flowers after 50% of the plants had at least a single open flower) positively correlated with *M. brevivittella* attack in 2 years (19) (i.e., later-flowering plants suffered less damage). There was no difference between treatments in the first year of our study (2007), as early season flowering was not different among the two treatments (univariate analysis of variance, $F_{1,14} = 0.320$, $P = 0.581$); by 2010, there was a significant shift toward earlier flowering in plots with suppressed insects (univariate analysis of variance, $F_{1,14} = 6.105$, $P = 0.027$). This effect was even stronger in 2011 (Fig. 4, univariate analysis of variance, $F_{1,14} = 7.025$, $P = 0.019$) and was predictable on the basis of genotype frequencies and genotype-specific means for early flowering (Fig. 4). Thus, a predicted response to selection was evident in only three to four generations. We found no difference in annual versus biennial phenotypes of *O. biennis* (repeated measures multivariate analysis of variance, $F_{1,14} = 0.935$, $P = 0.350$).

O. biennis produces diverse hydrolyzable tannins, including the largest ellagitannins known from any plant species (20), and these compounds have very high oxidative capacity, negatively affecting insect herbivores (21). One trimer, oenothain A (fig. S3), was the dominant ellagitannin in *O. biennis* fruits (up to 7.8% dry mass). We previously showed that oenothain A is favored by natural selection in *O. biennis* leaves (6), and its production in fruits was negatively genetically correlated with *M. brevivittella* attack in

the current study (simple correlation, $N = 17$, $r = -0.491$, $P = 0.045$) (supplementary text 2f), implicating a role of this compound in defense. Despite a genetic correlation between foliar and fruit ellagitannin chemistry (simple correlation, $N = 18$, $r = 0.848$, $P < 0.001$), only fruit chemistry significantly diverged in our experimental plots (Fig. 4), suggesting that selection was strongest for defense against flower- and fruit-feeding herbivores like *M. brevivittella*. A negative genetic correlation between early-season flowering and the production of oenothain A in fruits (simple correlation, $N = 23$, $r = -0.67$, $P < 0.001$) is consistent with the rapid and joint evolution of these traits (i.e., early flowering with low oenothain A in insect-suppressed plots) (Fig. 4).

Given that insect suppression not only affected herbivory on *O. biennis*, but also resulted in stronger plant competition through larger *T. officinale* populations, we hypothesized that *O. biennis* would evolve greater competitive ability in the absence of insects. We measured the relative competition index (RCI) in total above- and below-ground biomass of different genotypes in an independent experiment (fig. S4). We then used these genotype-specific values of competitive ability to determine if the competitive phenotypes diverged between control and insect-suppressed plots. Insect suppression resulted in the evolution of enhanced competitive ability relative to ambient insect plots (Fig. 4), and because this effect was not genetically correlated with early-season

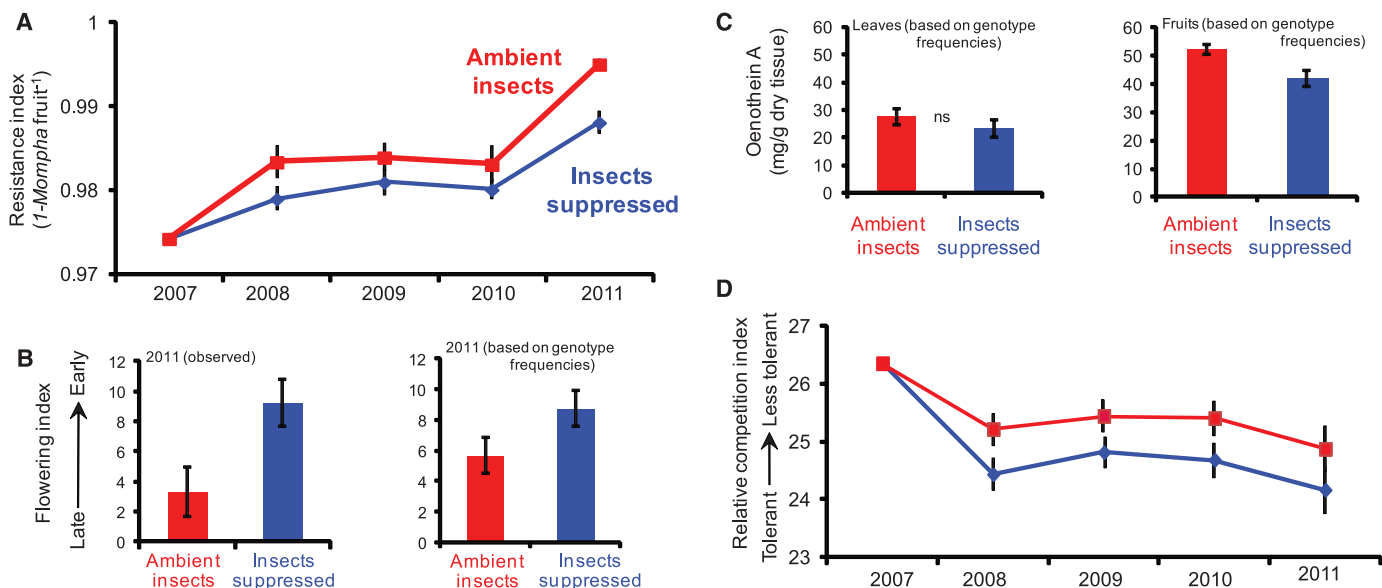


Fig. 4. Phenotypic evolution in *O. biennis* plots. **(A)** In the presence of seed predator insects, higher plant resistance evolved [estimated by multiplying genotype-specific means measured in control (ambient insect) plots by genotype frequencies in each plot] (repeated measures multivariate analysis of variance, $F_{1,14} = 6.322$, $P = 0.025$), and this effect did not vary over time (time-by-treatment interaction, repeated measures multivariate analysis of variance, $F_{3,12} = 1.459$, $P = 0.275$). **(B)** Earlier flowering was observed in the insect suppression plots (univariate analysis of variance, $F_{1,14} = 7.025$, $P = 0.019$). We confirmed that this was an evolutionary response by multiplying genotype-specific means by genotype frequencies (univariate analysis of variance, $F_{1,14} = 4.530$, $P = 0.050$); the former field assessment includes the possible effects of

phenotypic plasticity, whereas the latter is based on genotypic values. **(C)** Leaf defensive chemistry did not diverge (univariate analysis of variance, $F_{1,14} = 1.716$, $P = 0.211$) but fruit chemistry changed (univariate analysis of variance, $F_{1,14} = 8.917$, $P = 0.010$) as predicted by genotypic means and genotype frequencies. **(D)** Competitive ability of *O. biennis* when grown with *T. officinale*; plants in the insect-suppressed plots evolved a greater ability to maintain above- and belowground biomass (relative competition index) when grown with a competitor than when grown alone (repeated measures multivariate analysis of variance, $F_{1,14} = 5.189$, $P = 0.038$); this effect did not vary over time (repeated measures multivariate analysis of variance, time-by-treatment interaction ($F_{3,12} = 0.072$, $P = 0.974$)). All panels show means \pm SEM; ns, not significant.

flowering (simple correlation, $N = 23$, $r = -0.157$, $P = 0.474$), the production of oenothien A (simple correlation, $N = 23$, $r = 0.035$, $P = 0.871$), or resistance to *M. brevivittella* (simple correlation, $N = 17$, $r = -0.255$, $P = 0.241$), responses to natural selection were unconstrained by genetic correlations. The evolution of increased susceptibility to herbivores and enhanced competitive ability was jointly favored by the suppression of insects.

Concurrent evolution of herbivore resistance and competitive ability was only partially predictable from annual measures of natural selection. We correlated trait values against lifetime seed production in each year, hypothesizing that we would observe divergent slopes concordant with the divergent evolutionary change that we observed between our two treatments. Although we found significantly divergent natural selection between ambient and insect suppression plots for the two resistance traits, this effect was observed in only 1 of 4 years (fig. S5). Nonetheless, when differences in natural selection were observed, they were in the predicted direction on the basis of the observed evolutionary change (table S1). Thus, annual measures of natural selection predicted from fecundity were not strong predictors of evolutionary change, which suggests that selection on other components of fitness contribute to observed evolutionary responses (19).

Our study provides definitive evidence for the rapid evolution of insect-mediated plant resistance traits in real time, supporting current interest in reciprocal feedbacks between evolutionary change and ecological dynamics (17, 19, 22, 23). We highlight how biotic environmental factors simultaneously alter ecological and evolutionary dynamics. Specifically, our finding that multiple

herbivores attacking co-occurring host plants can alter competitive interactions is likely quite general in natural ecosystems (14, 24, 25), and the rapid evolutionary responses observed confirm predicted interactive effects of herbivory and competition on plant evolution (15, 16). Given that *O. biennis* is a poor competitor, we predict that evolutionary shifts in resistance and competitive ability allow this species to persist for longer periods of time during succession.

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Supplementary Materials

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Natural Enemies Drive Geographic Variation in Plant Defenses

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Plants defend themselves against attack by natural enemies, and these defenses vary widely across populations. However, whether communities of natural enemies are a sufficiently potent force to maintain polymorphisms in defensive traits is largely unknown. Here, we exploit the genetic resources of *Arabidopsis thaliana*, coupled with 39 years of field data on aphid abundance, to (i) demonstrate that geographic patterns in a polymorphic defense locus (*GS-ELONG*) are strongly correlated with changes in the relative abundance of two specialist aphids; and (ii) demonstrate differential selection by the two aphids on *GS-ELONG*, using a multigeneration selection experiment. We thereby show a causal link between variation in abundance of the two specialist aphids and the geographic pattern at *GS-ELONG*, which highlights the potency of natural enemies as selective forces.

Intraspecific genetic variation is essential in enabling species to respond rapidly to evolutionary challenges such as changing environ-

mental conditions (1) or the emergence of novel pests and pathogens (2). This diversity often reflects the balance between the strength of local

selection and the current and historical levels of population substructure and gene flow (3, 4). Geographic analyses of genetic variation in several plant species have revealed clear genetic signals of local adaptation (5), caused by differences in the selective regime among locations. These analyses are further supported by reciprocal transplant experiments, in which home genotypes generally outperform those transplanted from other populations (6, 7). Although the drivers of local adaptation often remain unidentified, there

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