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Covariation and composition of arthropod species across plant genotypes of evening primrose, *Oenothera biennis*

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Genetic variation in plants has broad implications for both the ecology and evolution of species interactions. We addressed how a diverse community of arthropod species covary in abundance among plant genotypes of a native herbaceous plant (*Oenothera biennis*), and if these effects scale-up to shape the composition, diversity, and total abundance of arthropods over the entire lifetime of plants (two years). In a field experiment, we replicated 14 plant genotypes of *O. biennis* across five field habitats and studied the arthropod communities that naturally colonized plants. Genetic variation in *O. biennis* affected the abundance of 45% of the eleven common species in 2002, and 75% of sixteen common species in 2003. We examined the strength of correlations in mean abundance of arthropod species among plant genotypes and found that species responded independently to variation among genotypes in the first year of the study, whereas species formed positively covarying clusters of taxa in the second year ($r_{mean} = 0.35$). The strength of these correlations did not consistently correspond to either taxonomy or functional attributes of the different species. The effects of plant genetic variation on the abundance and covariation of multiple arthropod species was associated with cascading effects on higher levels of community organization, as plant genotype and habitat interacted to affect the species composition, diversity, and total abundance of arthropods in both 2002 and 2003, though the specific effects varied across years. Our results suggest that plants may employ generalized resistance strategies effective against multiple herbivores, but such strategies are unlikely to be effective against entire functional groups of species. Moreover, we show that genotypic variation in plants is an important ecological factor that affects multiple levels of community organization, but the effects of plant genotype vary in both space and time.

It is increasingly recognized that there is a dynamic interplay between ecological and evolutionary processes within communities (Price 1983, Antonovics 1992, Vellend and Geber 2005, Johnson and Stinchcombe 2007), and the study of plant–arthropod interactions has played a central role in this realization (Denno and McClure 1983, Strong et al. 1984, Fritz and Simms 1992, Whitham et al. 2006). Herbivorous and predaceous arthropods frequently select on genetic variation in plant traits that affect the preference or performance of arthropods on plants (Price et al. 1980, Marquis 1984, Rausher and Simms 1989, Simms and Rausher 1989, Hare 2002). As plant populations evolve in response to this selection, changes in the genetic composition of plant populations can feed-back to affect the abundance of individual arthropod species, interspecific interactions among species, as well as the composition of entire arthropod assemblages (Whitham et al. 2003). In this paper, we address components of this interplay by examining the response of individual arthropod populations and communities to genetic variation in a native plant species.

Whether or not arthropod species covary in response to genetic variation in plants, bears directly on the issue of specificity in insect–plant relationships and the potential for pair-wise vs diffuse selection and (co)evolution (Janzen 1980, Fox 1981, Iwao and Rausher 1997). A necessary condition for pair-wise co-evolution is that different arthropods must exhibit uncorrelated susceptibilities to genetic variation in plant traits

(Iwao and Rausher 1997, Stinchcombe and Rausher 2001, Strauss et al. 2005). Susceptibility is often measured as either arthropod abundance (Maddox and Root 1987, Roche and Fritz 1997) or herbivory damage (Marquis 1984, Simms and Rausher 1989), where the inverse of these measures correspond to the degree of resistance exhibited by a plant (Leimu and Koricheva 2006). When two or more arthropod species exhibit correlated susceptibilities to genetic variation in a plant population, selection by arthropods on the plant population is likely to be diffuse, provided that arthropods impact plant fitness. Few field studies have examined how genetic variation within plant populations shapes the covariation and assembly of arthropod communities on plants (Maddox and Root 1990, Roche and Fritz 1997, Wimp et al. 2005, Leimu and Koricheva 2006). The lack of studies on this topic leaves a critical gap in our understanding of the degree to which plants exhibit generalized vs specific plant resistance against arthropods.

If plants exhibit genetically based tradeoffs in resistance to different natural enemies, we expect to observe negative genetic correlations in the damage or abundance of different arthropod species among plant genotypes (Simms and Rausher 1989, Fritz 1992, Leimu and Koricheva 2006). Alternatively, arthropod species are predicted to positively covary across plant genotypes when they share similar traits that relate to how they use a plant, or when plants have evolved generalized defenses effective against a diverse array of enemies (Fritz 1992). This prediction was first tested using the plant *Solidago altissima*, which hosts a large and diverse community of arthropods (Maddox and Root 1987, 1990). Genetic variation in *S. altissima* affected the abundance of multiple arthropod species, and groups of species covaried in abundance across plant genotypes, but the composition of these groups was unrelated to taxonomic or functional relationships between arthropod species. Similar results were also reported for a diverse community of arthropods associated with a native shrub (Roche and Fritz 1997).

A recent meta-analysis builds on these findings by reviewing 29 studies that examined genetic variation in plant resistance to natural enemies (mammalian herbivores, arthropod herbivores and pathogens) (Leimu and Koricheva 2006). Most studies included in the review measured covariation in damage or abundance among a small number of enemies (<5 species), or reported the effects of genetic variation in plants to multiple enemies, but did not examine covariation among enemies across plant genotypes. Leimu and Koricheva (2006) conclude that generalist species (i.e. enemies that attack multiple plant families) positively correlated with one another in their abundance or degree of damage across plant genotypes, as did specialists (i.e. enemies that attack a single plant family), but there was no association between generalists and specialists. These results suggest that 1) plants employ different yet complimentary defenses against generalist and specialist enemies, and 2) support the hypothesis that functional associations between arthropod consumers (e.g. generalist vs specialist) can be used to predict how species will respond to genetic variation in plants.

In addition to the evolutionary significance of plant–arthropod interactions, genetic variation in plant populations that affects the abundance and covariation among arthropod species is predicted to have cascading ecological effects on higher orders of community organization, such as the composition and diversity of arthropod communities (Whitham et al. 2003). The spatial and temporal consistency of these genetic effects, however, are poorly understood. For example, genetic variation in the plant *Oenothera biennis* explained as much as 41% of the variation in arthropod diversity, but the effects of plant genotype varied dramatically between environments (Johnson and Agrawal 2005). In contrast, different plant genotypes within hybridizing shrubs and trees can have qualitatively consistent effects on arthropod communities across large spatial scales (Bangert et al. 2006, Tovar-Sánchez and Oyama 2006). Temporal consistency in the community-level consequences of genetic effects have also been shown in a handful of systems (Maddox and Root 1987, Fritz and Price 1988, Bangert et al. 2005), but such consistency is not universal (Roche and Fritz 1997).

The present study addresses several novel questions that expand on our previous work (Johnson and Agrawal 2005). We showed that over a single growing season, plant genotype and habitat interacted to affect the diversity, total abundance and total biomass of arthropods found on *Oenothera biennis* (Johnson and Agrawal 2005). Genotypic differences had their strongest effects on herbivore and omnivore richness and abundance, whereas there was no effect on predator richness and a relatively weak effect on predator abundance. Genetic variation in life-history strategy (annual vs biennial reproduction), and traits associated with plant size and morphology were most strongly correlated with variation in the arthropod community (Johnson and Agrawal 2005). There was also a feedback onto plant fitness, where arthropods reduced lifetime fecundity of *O. biennis* plants by 13% (Johnson and Agrawal 2005).

Here we examine the ecological and evolutionary significance of how multiple arthropod species respond and assemble onto plant genotypes of *O. biennis*. Specifically, we asked the following questions: 1) can plant genotype affect the abundance of multiple individual arthropod species, and do species respond independently to genetic variation in *O. biennis*? 2) Does plant genotype shape the community composition of arthropods found on *O. biennis* over the entire

lifetime of plants, which is best studied using multivariate ordination methods (Dungey et al. 2000, Shuster et al. 2006). 3) Are the community-level effects of genotype-by-environment interactions identified in Johnson and Agrawal (2005) consistent over multiple years?

Methods

Study site and system

This experiment was conducted at Univ. of Toronto's field station, the Koffler Scientific Reserve at Jokers Hill (http://www.zoo.utoronto.ca/jokershill/jh.html). Jokers Hill is located on the western edge of the Oak Ridges Moraine, ca 40 km north of Toronto, Ontario, Canada.

The plant common evening primrose (*Oenothera biennis L.*, Onagraceae) is native to eastern North America and is common in open habitats. Although populations of several thousand plants do occur, it is rarely a dominant species of plant communities. *Oenothera biennis* primarily self-pollinates and possesses a permanent heterozygote genetic system (Cleland 1972), which typically results in the production of genetically identical seeds. Thus, reproduction is functionally clonal in this species, making it possible to replicate single plant genotypes across multiple environments.

The arthropod community on *O. biennis* is comprised of specialist and generalist herbivores, omnivores and predators (Dickerson and Weiss 1920, Kinsman 1982, Johnson et al. 2006, Johnson 2007a). Over the course of eight surveys in 2002 and 2003, we counted ca 47 000 individual arthropods from 123 species, made up of 46 herbivorous, 18 omnivorous and 59 predaceous arthropod species. A morphospecies definition was used to identify species in the field; identification of specimens by expert taxonomists confirmed the accuracy of our morphospecies. In a few cases, closely related taxa were treated as a single morphospecies. The omnivorous diet of arthropods was based on direct observation and a published database (Eubanks et al. 2003).

Experimental design

We previously described the experimental design of this study (Johnson and Agrawal 2005), so we only provide a brief description here. Seeds from 14 clonal maternal families (genotypes) were collected in 2001 and 2002. All genotypes were germinated simultaneously on filter paper in March 2002, and were soon after transferred to pots and grown in a greenhouse at Univ. of Toronto until spring. In May, 926 *O. biennis* plants from the 14 genotypes were moved to Jokers Hill and transplanted directly into the soil of five naturally occurring habitats. The five habitats represented a natural productivity gradient in which *O. biennis* locally occurs, and in order of increasing productivity, habitats were named Xeric, Mowed, Sandy, Mesic and Disturbed (Johnson 2007b). To account for environmental variation within habitats, each habitat was divided into four equal-sized contiguous spatial blocks, hereafter called "microhabitats". The importance of microhabitat variation for arthropod community structure was a focus in Johnson and Agrawal (2005), and is only included here to increase the power of statistical analyses.

Plants were evenly replicated and randomized within each microhabitat and habitat (ca 46 plants per microhabitat, 185 plants per habitat), and individual plants were arranged into a rectangular grid pattern with 1 m spacing between rows and columns. Of the 926 plants studied, 337 were annual and died in 2002, while the remaining 589 biennial plants flowered and/or died in summer 2003 (Johnson 2007b).

The arthropod assemblage on individual plants was characterized over the entire lifetime of all plants (two years). We sampled all arthropods on a plant by visually inspecting the upper and lower surfaces of the leaves, stem and inflorescence. Surveys were conducted every two to three weeks, four times a year, for a total of eight surveys over two years. Each survey was conducted in the same week each year to insure that our sampling was equivalent across years. Two additional censuses were conducted in 2002 (one early and one late sampling date) and reported in Johnson and Agrawal (2005), but were excluded from the current analyses so that the datasets from 2002 and 2003 were parallel. Because of difficulties in accurately counting certain taxa, we did not sample parasitoids, several endophytic herbivores or pollinators. In each year, the total number of individuals (larvae and adults) of each arthropod species on every plant was calculated as the maximum abundance across sampling dates. Maximum and total abundance across dates were highly correlated, but maximum abundance eliminates double-counting individuals between surveys. We did not sample the Disturbed habitat in 2003 because all plants flowered and died in 2002.

We define resistance as the inverse of abundance for an arthropod species (Roche and Fritz 1997, Leimu and Koricheva 2006), where more individuals on a plant correspond to lower resistance. Abundance was used instead of other measures of resistance (e.g. herbivore damage) because it allowed us to include arthropod species whose damage was inconspicuous (sap feeders), and also because we could not reliably distinguish between the damage caused by different chewing herbivore species.

In each year, we characterized the arthropod community on individual plants by quantifying the abundance, covariation, and multivariate composition of the

common arthropods on individual plants. We also measured Simpson's diversity index, total species richness and total arthropod abundance of all species (common and rare) on every plant. Common species were those that occurred on at least one-third of plants and made-up >1% of the total abundance of arthropods in a specific habitat during a given year. There were a total of eighteen common species, eleven in 2002 and sixteen in 2003 (Table 1, 2). Some of these species were common in multiple habitats, while others were only common in a single habitat. On average, the common species comprised 75% of all individual arthropods counted on plants in both years.

Detailed statistical methods for the analysis of all community patterns are provided below. To assess the covariation in abundance among common arthropod species, we correlated the mean abundance of species across plant genotypes within a habitat. We characterized arthropod community composition on each plant using ordination methods. The inverse of Simpson's diversity was calculated as $D = 1/\Sigma p_i^2$, where p_i is the proportional abundance of the ith species on a plant. Total species richness was simply the number of arthropod species found on a plant each year, and total arthropod abundance was the total number of individuals of all species combined.

Statistical analyses

Abundance of common arthropod species

We performed univariate analyses on the abundance of all common species. Because not all species were common in every habitat, analyses were performed in each habitat separately (for those species that met the criteria for commonness [see above]) using restricted maximum likelihood (REML) in Proc Mixed of SAS (SAS Inst.). The model for these analyses was: arthropod abundance = $\text{mean}_{\text{overall}}$ + genotype + microhabitat + genotype × microhabitat + error. All effects in

Table 1. Plant genotype and microhabitat effects on the abundance of common arthropods in 2002. Because species were not evenly distributed across all habitats, a species' abundance was only analyzed in the habitats where it was common (Methods). Effects significant at $p < 0.05$ are in bold.

	Microhabitat		Genotype		Microhabitat × genotype	
	χ^2	p	χ^2	p	χ^2	p
Philaenus spumarius						
Xeric	3.22	**0.04**	0	–	0.07	0.4
Mowed	3.23	**0.04**	0	–	0	–
Mesic	0.2	0.33	0.06	0.4	0	–
Disturbed	3.76	**0.03**	1.86	0.09	0.38	0.27
Euschistus servus						
Disturbed	1.09	0.15	0	–	0	–
Lygus lineolaris						
Disturbed	35	**<0.001**	45	**<0.001**	1.4	0.12
Plagionathus brunnescens						
Disturbed	3.3	**0.03**	2.8	**0.047**	0	–
Colapsis brunnea						
Mowed	6.36	**0.006**	1.3	0.13	0.16	0.34
Graphops pubescens						
Mowed	3.23	**0.04**	0	–	0.23	0.32
Tyloderma foveolatum (adults)						
Xeric	0	–	0	–	0	–
Sandy	2.14	0.07	0	–	0.16	0.34
T. foveolatum (eggs)						
Xeric	6.6	**0.005**	2.8	**0.047**	0.2	0.33
Mowed	16.2	**<0.001**	2	0.08	3.1	**0.04**
Sandy	6.1	**0.007**	11.1	**<0.001**	0.1	0.38
Mesic	6.6	**0.005**	22.9	**<0.001**	0	–
T. nigrum						
Xeric	1.25	0.13	0.19	0.33	1.69	0.1
Mompha stellela						
Disturbed	13.8	**<0.001**	7.6	**0.003**	1.4	0.12
Schinia florida						
Disturbed	2.7	**0.05**	23.4	**<0.001**	2.5	0.06
Opiliones spp.						
Disturbed	0	–	0	–	0	–

Table 2. Plant genotype and microhabitat effects on the abundance of common arthropods in 2003. Because species were not evenly distributed across all habitats, a species' abundance was only analyzed in the habitats where it was common (Methods). Effects significant at $p < 0.05$ are in bold.

	Microhabitat		Genotype		Microhabitat × genotype	
	χ^2	p	χ^2	p	χ^2	p
Philaenus spumarius						
Xeric	0.2	0.33	0.5	0.24	1	0.16
Mowed	18	**<0.001**	2.3	0.06	0	–
Sandy	0.1	0.38	0	–	0	–
Mesic	0	–	4.8	**0.01**	0.3	0.29
Cedusa incisa						
Mesic	4	**0.02**	5.1	**0.01**	0.1	0.38
Alydus eurinus						
Sandy	10.98	**<0.001**	0	–	0	–
Euschistus servus						
Sandy	0	–	4.08	**0.02**	0.32	0.29
Mesic	0	–	9.26	**0.001**	0	
Lygus lineolaris						
Mesic	0.36	0.27	4.11	**0.02**	0.58	0.22
Neurocolpus nubilis						
Sandy	0	–	11.4	**<0.001**	0.5	0.24
Mesic	0.04	0.42	5.83	**0.008**	0	–
Phyegyas abbreviatus						
Mesic	0.26	0.31	17.87	**<0.001**	0	–
Plagiognatus brunneus						
Mesic	1.19	0.14	4.38	**0.02**	0	–
Acanthoscelidius acephajus						
Sandy	0	**–**	1.55	0.11	0.01	0.46
Colapsis brunnea						
Mowed	11.18	**<0.001**	3.17	**0.04**	0	–
Graphops pubescens						
Mowed	2.34	0.06	1.71	0.1	0.85	0.18
Sandy	4.56	**0.02**	0.42	0.26	0	
Tyloderma foveolatum (adults)						
Sandy	0	–	0	–	0	–
T. foveolatum (eggs)						
Xeric	2.4	0.06	3.7	**0.03**	0.8	0.19
Mowed	3.3	**0.03**	10.9	**<0.001**	0	–
Sandy	0	–	5.1	**0.01**	0	–
Mesic	0	–	22.5	**<0.001**	0	–
Mompha stellella						
Xeric	2.44	0.06	3.02	**0.04**	2.01	0.08
Mowed	7.6	**0.003**	30.2	**<0.001**	0	–
Sandy	2.9	**0.04**	31.5	**<0.001**	0	–
Mesic	0	–	1.55	**<0.001**	0	–
Schinia florida						
Sandy	0.38	0.27	3.49	**0.03**	1.36	0.12
Mesic	0	–	16.7	**<0.001**	3.8	**0.03**
Sparganothis reticulatana						
Xeric	3.19	**0.04**	0.53	0.23	0	–
Mowed	1.23	0.13	1.4	0.12	0.38	0.27
Sandy	0	–	0.02	0.44	0	–
Mesic	3.2	**0.04**	4.1	**0.02**	0	–
Arachnid sp.						
Sandy	0	–	0	–	0	–

the model were random and their significance was assessed using χ^2-values from log-likelihood ratio tests (Littell et al. 1996). For these analyses, and the analyses of covariation (below), the number of eggs laid by *Tyloderma foveolatum* (a specialist weevil) was used instead of the number of adults, because the number of eggs varied more continuously and reflected the weevil's preference for plants.

Covariation in the response of common arthropod species to plant genotype

To examine whether the common arthropod species responded independently to plant genetic variation, we estimated genetic correlations for the mean abundance of arthropod species among plant genotypes as the Pearson product moment correlation coefficient. To do this, we calculated the mean abundance of all common arthropod species on each of the fourteen plant genotypes, and then calculated pairwise correlations among all species that were common in a given habitat and year. In total, we estimated 32 and 131 pairwise correlations in 2002 and 2003, respectively. The main patterns that emerged are summarized in the Results section; tables of individual pairwise correlations are reported in Johnson (2007a). Because 5% of correlations are expected to be significant by chance alone, we used the Binominal expansion test to assess whether the number of significant correlations deviated from the number expected by chance (Zar 1996).

In habitats where ten or more species showed evidence of covariation in abundance, we used hierarchical cluster analysis to assess whether ''clusters'' of species covaried in their response to genotypic variation (Legendre and Legendre 1998). Cluster analysis creates a tree or dendrogram that summarizes how arthropod species covary in abundance among plant genotypes, whereby the tips of the tree represent different arthropod species. The strength of this method is that it identifies the groups of species that naturally associated with one another across plant genotypes without bias with respect to the arthropods' traits. To perform cluster analysis, we first standardized the genotype mean abundances of each arthropod species to a mean of zero and a standard deviation of one, and then calculated the genetic Pearson correlation matrix in species abundances within each habitat. The linkage and distance between clusters were determined using Ward's linkage method, which minimizes the variance of genetic correlations among species within a cluster and maximizes the variance between clusters (Legendre and Legendre 1998).

We then asked: are arthropod species' responses to plant genetic variation related to the taxonomic or functional attributes of the species? To answer this question, we assessed whether genetic correlations between arthropod species were related to one of five categories: 1) taxonomy (Order-level), 2) host range (generalist-G, diet includes multiple plant families; specialist-S, diet restricted to Onagraceae; oligophagous-O, diet includes only two plant families), 3) feeding guild (predator-Pr, piercing-sucking-PS, exophytic chewing herbivore-Ch, endophyte-En), 4) trophic group (herbivore-H, omnivore-O, predator-P), or 5) location on the plant (entire plant-all, inflorescence-infl, cauline leaves-lf, stem-st, rosette leaves-ro). We used the statistically derived clusters as a sixth category, which provided a baseline with which to compare the strength of associations between species within each of the five functional groups.

For each of the five taxonomic/functional groups, we assessed whether the mean correlation coefficient among species within each group was greater than the mean correlation among species between groups (e.g. correlations among species within a trophic group vs correlations among species between trophic groups). This was also done for the statistically derived species' clusters, which should show the maximum correlation within groups and the lowest correlation between groups. The significance of the correlation coefficients within vs between groups was assessed using ANOVA.

Community composition of common arthropod species

We used correspondence analysis (CA) to understand whether plant genotype and environment affected the composition of the common arthropod species. CA is a robust multivariate ordination technique commonly used to study community patterns (Legendre and Legendre 1998). This method summarizes variation in the occurrence (presence/absence) and abundance of multiple arthropod species into a smaller number of variables (CA axes). These CA axes can be used to visually depict differences in arthropod community composition among individual plants, whereby each plant is represented by a coordinate in multidimensional space. Plants that are close to one another in space have similar arthropod communities, while the communities on plants far apart in space are less similar.

Correspondence analysis uses χ^2-distance to summarize community data. We used the abundance of each arthropod species and log-transformed these data to reduce the influence of extreme values. Ordination was performed on the χ^2-distance matrix using eigenanalysis in CANOCO ver. 4.53 (Biometris, Wageningen Univ.; ter Braak and Smilauer 2002). We used the broken-stick and the Kaiser-Guttmann methods to identify the optimal number of axes (Legendre and Legendre 1998), which identified two axes in 2002 and three axes in 2003.

An advantage of correspondence analysis is that it simultaneously creates a second ordination of the

association between arthropod species. This ordination can be used to assess the covariance in abundance among species, which is influenced by both variation among habitats and plant genotypes (not just plant genetic variation as above), as well as how arthropod species are associated with particular habitats and plant genotypes. Each arthropod species is represented by a vector in the same ordination space used to depict variation in arthropod communities among plants. When two arthropod species share the same vector, they positively covary in abundance; two arthropod species negatively covary in abundance when their vectors are of opposite sign. Likewise, when the direction of a species' vector corresponds to the location of a particular habitat or plant genotype in ordination space, that arthropod species is most commonly found on the corresponding plants.

We performed indirect gradient analysis (sensu Minchin 1987) to interpret how plant genotype and the environment contributed to the variation in ordinations and thus community composition. Specifically, we used REML to analyze the scores of plants along each CA axis using the model: CA axis = $\text{mean}_{\text{overall}}$ + habitat + microhabitat(habitat) + genotype + genotype × habitat + genotype × microhabitat(habitat) + error. This same model was used to analyze Simpson's diversity, species richness and total abundance. The effect of habitat was treated as a fixed effect, while all other effects were random. The significance of habitat was assessed with least-squares estimation and the F-statistic, and the degrees of freedom were adjusted according to the Kenward-Roger method (Kenward and Roger 1997). The significance of random effects were calculated with log-likelihood ratio tests, which have a χ^2 distribution (Littell et al. 1996).

Spatial consistency in genetic effects

A significant genotype-by-environment (G × E) interaction in this study indicates that plant genotype affects arthropod communities, but the effects of particular genotypes vary between habitats. Changes in the magnitude of genetic variation expressed in different habitats, or changes in the rank-order of genotypes between habitats, can result in a G × E. We quantified the relative contributions of these non-exclusive mechanisms using Cockerham's equation (Cockerham 1963), as implemented and explained in Johnson (2007b).

Temporal consistency in genetic effects

To assess temporal consistency in genetic effects on diversity and total abundance, we analyzed each year separately and then performed genetic correlations by correlating the genotype means for a community variable within a particular habitat between 2002 and 2003. If plant genotypes had temporally consistent effects on the community, then we expected to observe positive correlations between years. A single analysis that incorporated both years of the study was not possible because many plants were annual and therefore died at the end of the first year of the experiment.

Results

Abundance of individual arthropod species

Genetic variation in *Oenothera biennis* affected the abundance of multiple arthropod species in both years of the study. Arthropod abundance significantly varied among plant genotypes for 5 of 11 (45%) common species in at least one habitat during 2002 (Table 1), and 12 of 16 (75%) common species in 2003 (Fig. 1, Table 2). The majority (82%) of species common in 2002 were also common in 2003, and we detected an effect of plant genotype in both years for over half (56%) of these species (Fig. 1a–b), while one-third of taxa were only affected by plant genotype in the second year (Fig. 1c). Most species were common in only one habitat, while some species were common in most habitats in one or both years (e.g. *Philaenus spumarius*, *Tyloderma foveolatum, Mompha stellella, Sparganothis reticulatana*). We always detected an effect of plant genotype for some of these taxa (*T. foveolatum* eggs, *M. stellella*, *Schinia florida*), and for others the effect of genotype depended on the habitat and year (Table 1, 2).

Covariation in abundance of arthropod species across plant genotypes

We examined whether the abundance of the common arthropods was genetically correlated among plant genotypes. In 2002, genetic correlations varied from −0.34 to 0.61 and the mean correlation coefficient was positive but low (mean $r_g = 0.10$, SE = 0.05, n = 32 correlations). We detected two significant positive correlations, but this frequency of significant correlations was indistinguishable from the number expected by chance (Binomial expansion test: $p = 0.27$). In 2003, the magnitude of genetic correlation coefficients varied from −0.5 to 0.86 (Fig. 2) and the mean correlation between arthropods was again positive (mean $r_g = 0.35$, SE = 0.03, n = 131). Over one-quarter of the pairwise correlations were significant in 2003, and all were positive (36 of 131 pairwise correlations at $p < 0.05$). This frequency of significant correlations was unlikely to have occurred by chance (Binomial expansion test: $p < 0.001$).

The assemblage of common arthropods was sufficiently diverse in two habitats (Sandy and Mesic) of one year (2003) to test whether species formed distinct

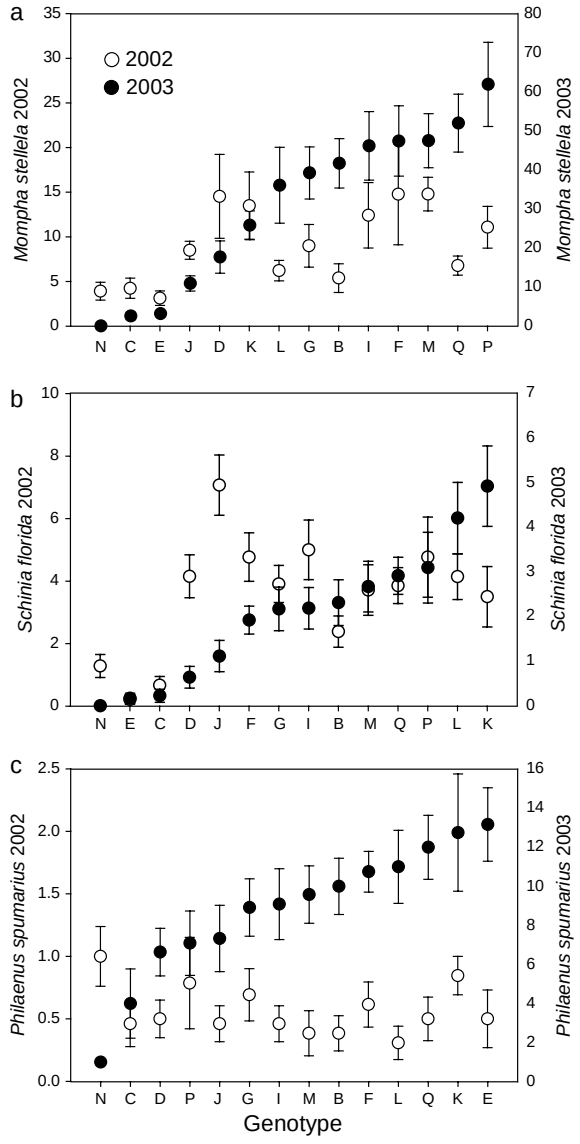

Fig. 1. Examples of the variation among *O. biennis* genotypes in the abundance of common arthropods observed during 2002 and 2003. Plant genotype significantly affected the abundance of the host-specific (a) *Mompha stellela* and (b) *Schinia florida* during 2002 (Disturbed habitat shown) and 2003 (Mesic habitat shown). (c) Plant genotype only influenced the number of *Philaenus spumarius* per plant in 2003 (Mesic habitat shown). The mean number of individuals per plant during 2002 is shown on the left axis, and the number of individuals per plant during 2003 is shown on the right axis. Note, plant genotypes are arranged according to increasing abundance of the respective insect species during 2003.

groups that covaried in abundance, and whether membership to these groups related to the taxonomic or functional affinity among arthropod species (Methods). Using cluster analysis, we detected four distinct covarying clusters of species in the Sandy habitat, and three clusters in the Mesic habitat (Fig. 3). As expected, the genetic correlation among species within the statistically derived clusters was significantly higher than the correlation among species between clusters in both Sandy and Mesic (Fig. 3). In the Sandy habitat, covariation among species was significantly related to the trophic group in which the arthropods belonged, but was unrelated to arthropod taxonomy, host range, guild, or the location on the plant (Fig. 3). In the Mesic habitat, no taxonomic or functional classification of the species explained covariation among species (Fig. 3).

Community composition

We used multivariate methods to determine whether plant genotypic variation scaled-up to affect the composition of common arthropod species on plants. Correspondence analysis (CA) explained 45% (two CA axes retained) and 52% (three CA axes retained) of the variation in community composition in 2002 and 2003, respectively. Ordinations revealed substantial variation in community composition within and between habitats during both years (Fig. 4).

In 2002, variation in the ordination was caused by differences in arthropod community composition between habitats and among plant genotypes (Table 3, Fig. 4). Plant genotype and habitat also interacted to explain variation along CA axis 1, and genotype and microhabitat influenced variation along CA axis 2 (Table 3). These interactions indicate that genotypic variation in *O. biennis* had important consequences for arthropod community composition in 2002, but the effects of plant genotype on the arthropod community depended on environmental variation within and between habitats. The genotype-by-habitat interaction was not simply due to changes in the magnitude of genetic variance between habitats, as 78% of the interaction variance was explained by changes in the rank-order of genotypes between habitats (Cockerham's equation, Methods). In other words, genotypes that supported a similar arthropod community composition in one habitat often had dissimilar communities in another habitat.

In 2003, habitat, microhabitat, and plant genotype all independently contributed to variation in community composition explained by CA axis 1 (Table 3). Genotype and habitat interacted to affect variation along CA axis 2, where 60% of the interaction variance was due to rank-order changes in plant genotype. The main effects of genotype, habitat, and microhabitat were important in explaining variation in community composition explained along axis 3 (Table 3).

The species ordinations combined with the univariate analyses of species abundances show that particular

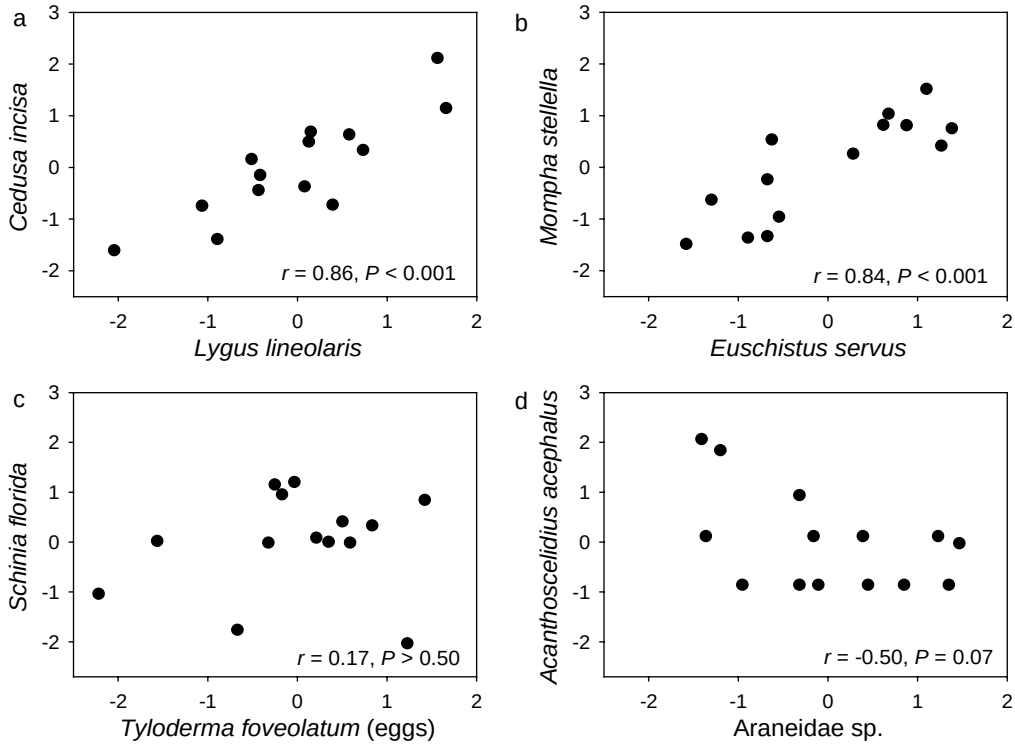

Fig. 2. Examples of genetic correlations of mean abundance of common arthropod species across plant genotypes in 2003. The four panels illustrate the range of correlations observed and include correlations between: (a) *Cedusa incisa* (Cicadellidae: Hemiptera) and *Lygus lineolaris* (Miridae: Hemiptera) in the Mesic habitat, (b) *Mompha stellella* (Momphida: Lepidoptera) and *Euschistus servus* (Pentatomidae: Hemiptera) in the Mesic habitat, (c) *Schinia florida* (Noctuidae: Lepidoptera) and *Tyloderma foveolatum* (Curculionidae: Coleoptera) in the Sandy habitat, and (d) *Acanthoscelidius acephalus* and an Arachnid sp. in the Sandy habitat. Each point represents mean arthropod abundance on one of fourteen plant genotypes. The abundance of arthropods is standardized to a mean of zero and a standard deviation of one, and the Pearson product moment correlation coefficient and its p-value are reported.

species were associated with particular habitats and genotypes (Fig. 4). For example, in 2002 two specialist flower-feeding herbivores (*S. florida* and *M. stellella*), as well as two generalist omnivorous mirid bugs (*Lygus lineolaris* and *Plagiognatus brunneus*), were strongly associated with the disturbed habitat (Fig. 4), but different genotypes within this habitat (Table 1). In contrast, two chrysomelid beetles that feed on the roots and leaves of *O. biennis* as larvae, one a specialist (*Graphops pubescens*) and the other a generalist (*Colaspis brunnea*), were strongly associated with the Mowed habitat (Fig. 4) but their abundance did not vary among plant genotypes (Table 1). Similar associations of arthropods between habitats and genotypes occurred in 2003 (Fig. 4, Table 2).

Diversity and total abundance of arthropods

Because plant genotype affected the abundance and composition of the common arthropods on *O. biennis*, we predicted that genotypic variation would shape the diversity and abundance of the entire arthropod fauna, including rare species not included above. In 2002 and 2003, plant genotype and habitat interacted to affect Simpson's diversity index (D), total richness, and total abundance of arthropods on *O. biennis* (Table 4, Fig. 5). These interactions were caused by changes in the magnitude of genetic variance between habitats (27–52% of the G × H variance) and changes in the rank-order of genotypes between habitats (48–73% of the variance).

The effects of particular plant genotypes on the arthropod community were inconsistent between years (Table 5). Genetic correlations between 2002 and 2003 for Simpson's diversity, species richness, and total abundance were negative in eight of the twelve pairwise comparisons (mean $r_g = -0.24$, SE = 0.09) and significantly so for two of these estimates; these significant correlations could have occurred by chance (Binomial expansion test, $p = 0.10$).

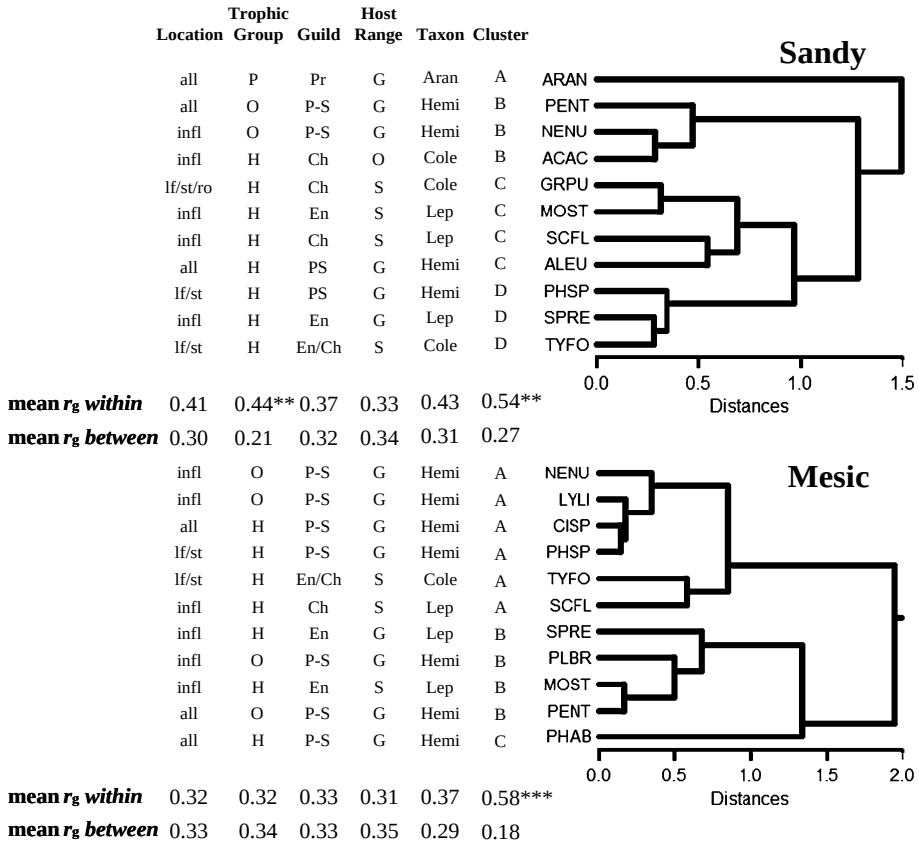

Fig. 3. Dendrograms from cluster analyses that depict the covariation in abundance among the common arthropods in the Sandy and Mesic habitats during 2003. Cluster analyses were performed using Ward's linkage method based on an association matrix from genetic correlations among plant genotypes for arthropod abundance. For each arthropod species, we map on the cluster (where the distance between species was <0.95), taxonomy (Order-level), host range (generalist-G, specialist-S, oligophagous-O), guild (predator-Pr, piercing-sucking-PS, chewing herbivore-Ch, endophyte-En), trophic group (predator-P, omnivore-O, herbivore-H), and location on the plant (entire plant-all, inflorescence-infl, cauline leaves-lf, stem-st, rosette leaves-ro). We contrasted the strength of genetic correlations within each of the six taxonomic/functional groups and clusters versus the strength of correlations between groups and clusters. Significant differences in mean correlation coefficients within versus between groups and clusters is denoted by * $p<0.05$, ** $p<0.01$, ***$p<0.001$. The four letter species identifiers are comprised of the first two letters of the genus, followed by the first two letters of the species epithet.

Discussion

Our results demonstrate that genetic variation in plants can have broad implications for both the ecology and evolution of plant-arthropod interactions. Three results are most pertinent to our interpretation and subsequent discussion. First, genetic variation in *O. biennis* affected the abundance of multiple arthropod species in both years of the study. Second, arthropod species did not respond independently to genetic variation in *O. biennis*, as species covaried in abundance across plant genotypes in 2003. Although species formed distinct clusters of covarying taxa, these clusters were not consistently related to the functional associations between species (i.e. taxonomy, host specificity, trophic position, feeding guild, location on the plant). And third, genetic variation in *O. biennis* affected the community composition of the common species and the overall diversity and abundance of arthropod communities, but the community-level effects of particular plant genotypes varied among habitats and years.

The response of arthropod populations to plant genotype

Arthropod species with similar traits or functional associations are predicted to respond in similar ways to genetic variation in plant traits (Fritz 1992). In our study, there was little covariation between species in 2002, whereas there was an abundance of positive correlations between species in 2003 (Fig. 3). This high

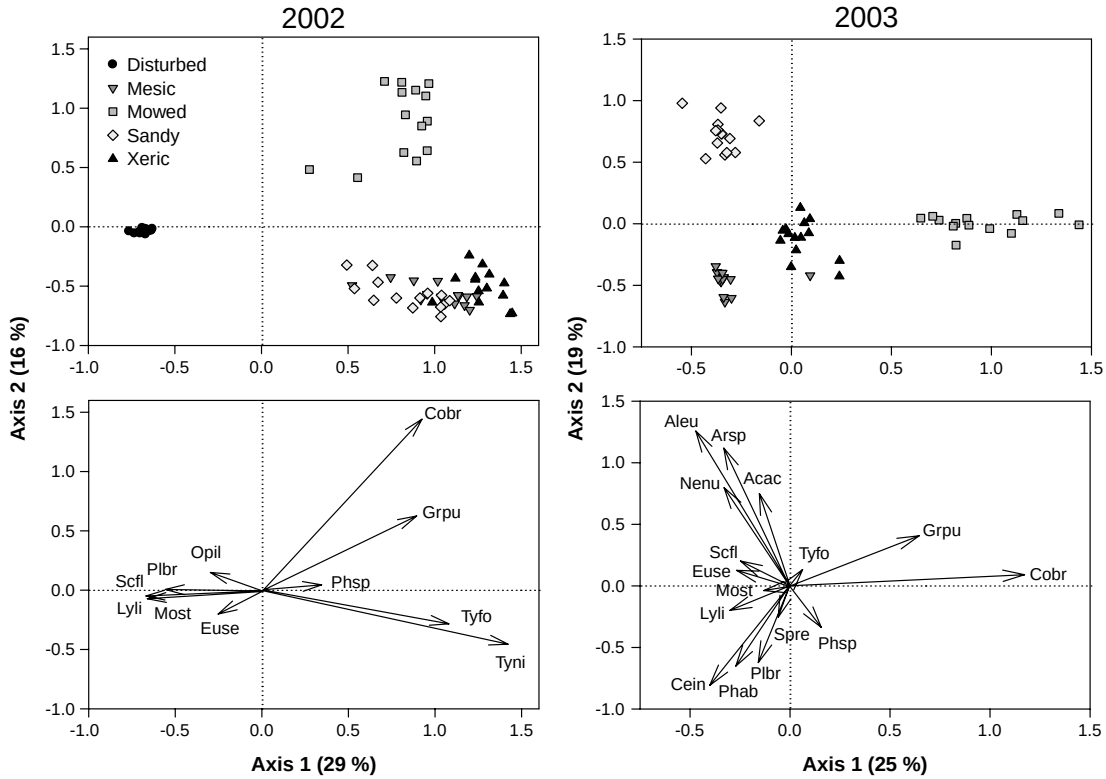

Fig. 4. Ordinations from correspondence analyses depicting arthropod community composition on plant genotypes and covariance among common arthropods species in 2002 and 2003. The top two panels depict variation among plant genotypes in the compositional abundance of arthropods, where each point represents the mean ordination score for a specific plant genotype in a habitat; standard error bars are excluded for illustrative purposes. Genotypes (individual points) that are close to one another had similar communities, while points that are far apart had less similar communities. These ordinations show that community composition varied substantially between habitats and genotypes (Table 1). The bottom panel shows the association between arthropod species and particular axes. Species that share a common vector positively covary in abundance, while species with opposite vectors negatively covary in abundance. In a similar way, the direction of vectors shows the association of arthropod species with particular plants and habitats. The four letter species identifiers are comprised of the first two letters of the genus, followed by the first two letters of the species epithet (Table 1, 2). All plants in the Disturbed habitat flowered and died in 2002, so this habitat was not included in 2003.

frequency of positive correlations among arthropod species is consistent with previous studies (Maddox and Root 1990, Roche and Fritz 1997, Leimu and Koricheva 2006). A principal result of Leimu and Koricheva's (2006) meta-analysis was that the covariance among natural enemies depends on the enemies' host specificity. Across studies, generalist enemies tended to respond to genetic variation in plants in the same way, as did specialists (Leimu and Koricheva 2006). Only three studies, however, have addressed this problem within a community of herbivores on an individual plant species, and none of these studies found a relationship between the covariance among arthropod species and host specificity (Maddox and Root 1990, Roche and Fritz 1997, this study). Several factors may explain this discrepancy between the meta-analysis and the individual studies. First, Leimu and Koricheva (2006) showed that genetic correlations are strongest among enemies when resistance is measured as damage to the plant, as opposed to enemy abundance, which was measured in the three studies. Second, the three experiments focused on arthropods, whereas the meta-analysis included mammalian herbivores and pathogens, in addition to arthropods. All the mammals and pathogens included in the meta-analysis were generalists, and they exhibited higher positive correlations than any group of arthropods. Finally, the strength of genetic correlations among generalist enemies, and especially among specialist enemies, were weak and would not have been found to be statistically significant in the individual studies. Thus, in the case of arthropods, it appears that host specificity will be a weak predictor of how multiple arthropods respond to genetic variation in plant traits.

Table 3. The effects of plant genotype and the environment on arthropod community composition during 2002 and 2003. To determine how habitat (H), microhabitat (M), genotype (G), and genotype-by-environment interactions affected the composition of the most common arthropod species, we reduced the complexity of the data using correspondence analysis. We used the scores of each replicate plant along the first two to three CA axes as the dependent variable in restricted maximum likelihood analyses (Methods). We provide the variance components (VC) of the untransformed data for all random effects. Significant effects (F-test for fixed effects and χ^2-test for random effects) are in bold ($p < 0.05$).

	2002					
	Axis 1 (29%)			Axis 2 (16%)		
Source	VC	χ^2/F	P	VC	χ^2/F	p
H	–	506.7	**<0.001**	–	205.5	**<0.001**
M(H)	0.2×10^{-3}	0.2	0.33	0	0	–
G	0.8×10^{-3}	2.7	**0.05**	0.1×10^{-3}	0	–
G × H	1.7×10^{-3}	6.7	**0.005**	0	–	–
G × M(H)	0	–	–	2.9×10^{-3}	3.3	**0.03**
Error	34.9×10^{-3}			44.4×10^{-3}		

	2003								
	Axis 1 (25%)			Axis 2 (19%)			Axis 3 (8%)		
Source	VC	χ^2/F	P	VC	χ^2/F	p	VC	χ^2/F	p
H		72.9	**<0.001**		208.7	**<0.001**		63.0	**<0.001**
M(H)	3.1×10^{-3}	56.8	**<0.001**	0.1×10^{-3}	0.5	0.24	0.8×10^{-3}	4.1	**0.02**
G	0.6×10^{-3}	6.4	**0.006**	0	–	–	1.0×10^{-3}	5.5	**0.01**
G × H	0.1×10^{-3}	0	–	0.7×10^{-3}	8.6	**0.002**	0.2×10^{-3}	0.1	0.38
G × M(H)	0	–	–	0	–	–	0	–	–
Error	10.7×10^{-3}			7.4×10^{-3}			21.7×10^{-3}		

Consequences for evolution

The fact that species' abundances were genetically correlated across plant genotypes suggests that arthropods have the potential to impose diffuse selection on *O. biennis* (Janzen 1980, Iwao and Rausher 1997). When resistance to two or more herbivores genetically covaries across plant genotypes, selection imposed by multiple arthropod species on plant traits, and the subsequent evolutionary response, cannot simply be predicted by the additive selective effects of the individual herbivore species (Inouye and Stinchcombe 2001, Stinchcombe and Rausher 2001, Strauss et al. 2005). On its own, the lack of genetic correlations between species in the first year of our study is consistent with independent pairwise interactions between *O. biennis* and each of the arthropod species. However, the positive correlations observed in year two are expected to select for generalized resistance traits effective against multiple enemies. Caution must be adopted in this interpretation, however, as it assumes that measuring resistance in terms of arthropod abundance (or damage) accurately reflects the fitness effects of individual arthropod species, and that the individual arthropods within the covarying groups are imposing selection on genetically variable plant traits (Strauss et al. 2005). To further elucidate the evolutionary consequences of these complex interactions, a long-term experiment is required that measures the strength of selection by arthropods on plant populations, and the predicted evolutionary response, over multiple generations of the plant. We are now conducting such an experiment.

The importance of plant genetic variation for arthropod community composition

A major goal of recent community genetics research has been to determine how widely genetic variation in plants affects the composition of diverse arthropod communities (Whitham et al. 2006). Community composition is typically studied using multivariate ordination, which summarizes variation in the abundance (no. of individuals) and occurrence (presence/absence) of multiple species. In our study, we found genetic variation to be important in affecting the composition of the arthropod community over two years (Table 3). Like other community variables (Simpson's diversity, species richness, abundance), the effect of plant genotype on the community varied among habitats. This genotype × habitat interaction was, in part, caused by species turn-over among habitats (Fig. 4), as well as changes in the expression of phenological and morphological plant traits (Johnson 2007a). A growing number of studies have found that genetic variation in hybrid plant systems influences the composition of arthropod communities (Dungey et al. 2000, Hochwender and Fritz 2004, Wimp et al. 2005,

Table 4. Effects of habitat (H), microhabitat (M), genotype (G), and genotype X environment interactions (G × H, G × M[H]) on the community-wide diversity and abundance in 2002 and 2003. We report the variance components (VC) for random effects, the χ^2 – statistic from log-likelihood ratio tests on random effects, and F-statistic for fixed effects, and their respective p-values.

	2002			2003		
	VC	χ^2/F	p	VC	χ^2/F	p
Simpson's diversity index						
H	–	5.3	**0.005**		16.89	**<0.001**
M(H)	1.16×10^{-2}	20.4	**<0.001**	0.09	2.5	0.06
G	1.04×10^{-2}	10	**0.001**	0.14	1.8	0.09
G × H	7.26×10^{-3}	4.4	**0.02**	0.37	8.5	**0.002**
G × M(H)	0	0	–	0.25	2.2	0.07
Error	1.79×10^{-1}	-	–	3.02	–	–
Total richness						
H	–	84.7	**<0.001**	–	46.7	**<0.001**
M(H)	0.23	16.6	**<0.001**	0.5	4.9	**0.01**
G	0.1	2.5	0.06	1.58	7.4	**0.003**
G × H	0.23	6.8	**0.005**	1.45	9.2	**0.001**
G × M(H)	0.07	0.3	0.29	0.58	0.5	0.24
Error	3.81	–	–	12.64	–	–
Total abundance						
H	–	67	**<0.001**	–	34.7	**<0.001**
M(H)	4.97×10^{-2}	54.6	**<0.001**	0.23	8.4	**0.002**
G	0	0	–	0.96	14.5	**<0.001**
G × H	4.92×10^{-2}	30.5	**<0.001**	0.52	10.3	**0.001**
G × M(H)	0	0	0.5	0.19	0.7	0.2
Error	3.51×10^{-1}	-	–	4.19	–	–

Tovar-Sánchez and Oyama 2006). Our results are among the first to show that genetic variation within a single species can have similar effects on the composition of large arthropod communities (see Supplemental material in Crutsinger et al. 2006, Shuster et al. 2006). The frequency of this result among hybrid and non-hybrid systems suggests that intraspecific genetic variation in plants may have consistently large effects on not only the abundance of individual arthropod species, but also the occurrence and interactions among multiple species within communities.

Spatial and temporal consistency of genetic effects

Plant genetic variation affected arthropod communities in nearly all habitats in both years of the study, however, the influence of particular genotypes was inconsistent across habitats, as plant genotype and habitat interacted to affect all aspects of the community (Table 3, 4). This interaction was partially caused by changes in the magnitude of variation among plant genotypes (i.e. genetic variance) between habitats (Fig. 5). The genotype × habitat interaction was also caused by pervasive changes in the rank-order of genotypes between habitats, where a genotype that harbored an above average diversity or abundance of arthropods in one habitat frequently harbored below average values in another habitat (Fig. 5). Thus, the prevalence of genotype × environment interactions reported from the first year of this study (Johnson and Agrawal 2005), persisted into the second year of the study and therefore over the lifetime of the plants.

The effects of particular genotypes on arthropod community structure changed across years, as there was some evidence of negative genetic correlations in arthropod diversity between 2002 and 2003 (Table 5). This result is in contrast to the consistency by which genetic variation has been observed to affect communities in other systems (Maddox and Root 1987, Fritz and Price 1988, Bangert et al. 2005, but see Roche and Fritz 1997). The temporal inconsistencies in our results are perhaps explained by a dramatic change in the phenotype of most plants between 2002 and 2003. Although *O. biennis* is typically described as a biennial (i.e. plants flower and die after two years of growth), plants exhibited genetic variation for an annual vs biennial flowering strategy (Johnson 2007b). Some genotypes were typically annual (flowered and died in 2002), while other genotypes were often biennial (flowered and died in 2003) (Johnson 2007b). As a result, annual plants tended to harbour a greater diversity of arthropods in the first year of the experiment compared to biennials (Johnson and Agrawal 2005), which remained as leafy rosettes in 2002 and flowered in 2003.

Nevertheless, there were still substantial community-level effects of plant genotype in the second year of the

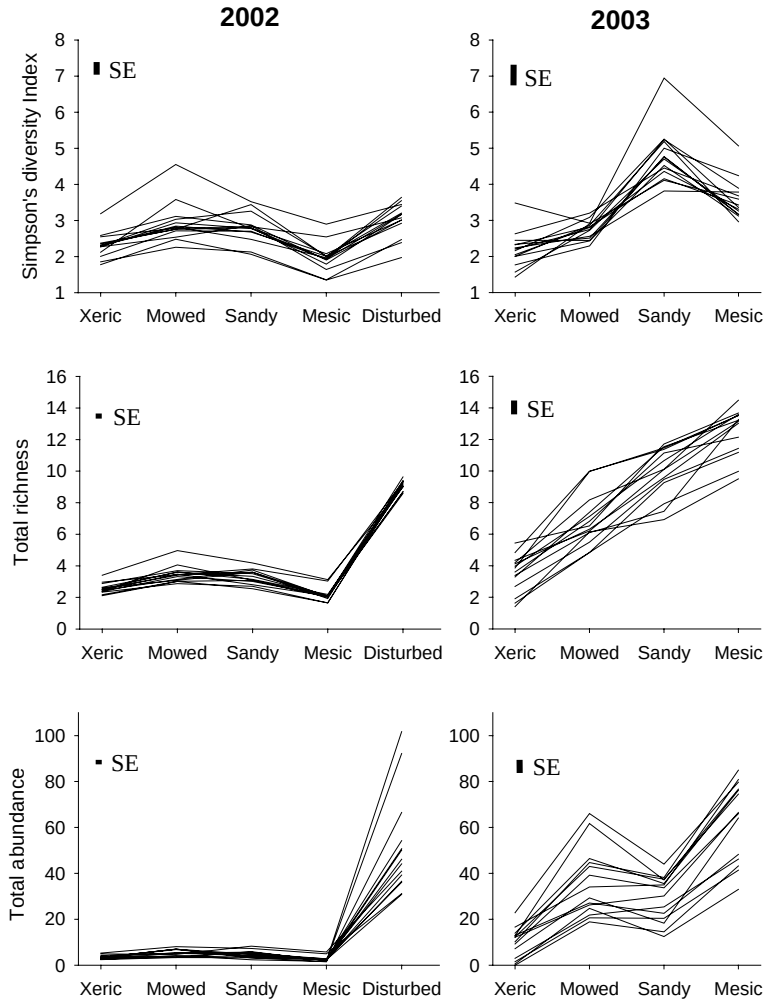

Fig. 5. The effects of plant genotype × habitat interactions on arthropod Simpson's diversity, total richness, and total abundance on *Oenothera biennis* during 2002 and 2003. Each line represents the breeding values for one of fourteen *O. biennis* genotypes, where lines connect individual genotypes between habitats. The average raw standard error of the mean is represented in the top left of each panel. Habitats are arranged in order of increasing productivity. All plants in the Disturbed habitat flowered and died in 2002 and therefore this habitat was not included in 2003.

study, when all plants flowered and/or died (Table 1, 4). We previously showed that such variation in the community is likely caused by genetic variation in flowering phenology, morphology, as well as specific resistance traits (Johnson and Agrawal 2005). Thus, we conclude that the influence of genetic variation in

Table 5. Genetic correlations between years for each community variable within each habitat. We report the Pearson correlation coefficients and respective p-value within each habitat separately. Uncorrected p-values <0.05 are in bold; no correlations are significant after correcting for multiple tests. No correlations were possible between years for the Disturbed habitat, where all plants flowered and died in 2002.

	Simpson's diversity		Species richness		Total abundance	
	r_g	p	r_g	p	r_g	p
Xeric	**−0.56**	**0.04**	−0.40	0.15	−0.33	0.25
Mowed	0.08	0.80	0.03	0.93	0.30	0.30
Sandy	**−0.56**	**0.04**	−0.48	0.08	−0.21	0.47
Mesic	−0.47	0.09	−0.28	0.34	0.00	1.00

O. biennis on the community changes at different ontogenetic life stages of the plant (Barrett and Agrawal 2004), and we speculate that temporal consistency in genetic effects is likely to be most common in long-lived perennials (e.g. shrubs and trees) in which a plant's phenotype may remain relatively constant from one year to the next.

Conclusions

Our results show that intraspecific genetic variation in plants has important implications for the evolutionary ecology of plant-arthropod interactions and the structure of a diverse arthropod community. Our findings contribute to a growing consensus that multiple arthropod species often respond in the same way to genetic variation in plants, but we found that the correlations between species correspond only weakly to functional associations between species. Our study also shows that when genetic variation in plants affects that abundance and covariation among multiple arthropod species, we expect to see plant genetic effects at higher levels of community organization, including the composition and diversity within communities. Although it is increasingly clear that intraspecific genetic variation cannot be ignored as an ecological factor, such community genetic effects can be complex as they vary in both space and time.

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