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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Aphid and ladybird beetle abundance depend on the interaction of spatial effects and genotypic diversity

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Abstract Intraspecific variation and genotypic diversity of host-plants can affect the structure of associated arthropod communities and the dynamics of populations. Similarly, neighboring plants can also affect interactions between host-plants and their associated arthropods. However, most studies on the effects of host-plant genotypes have largely ignored the potential effects of neighboring host-plants on arthropod communities. In this study, we used a common garden experiment to ask how spatial effects of neighboring patches, along with genotype identity and genotypic diversity in tall goldenrod (*Solidago altissima*), affect the abundances of a common goldenrod herbivore (*Uroleucon nigrotuberculatum*) and their dominant predator (*Harmonia axyridis*, a ladybird beetle). Aphid abundance varied 80-fold among genotypes, while ladybird beetle abundance was not affected by genotype identity. Additionally, there were strong effects of neighboring plots: aphid abundance in a focal plot was positively correlated to aphid abundance in nearby plots, suggesting strong spatial patterning in the abundance of aphids. Neither aphid nor ladybird beetle abundance was affected by genotypic diversity. However, focal plot genotypic diversity mediated the strength of the neighborhood effect (i.e., strong effects for genotype polyculture focal plots and weak effects for genotype monoculture focal plots). Our results show that aphids were directly influenced by host-plant genotype identity while ladybird beetles responded mainly to prey abundance, and suggest that genotypic diversity can influence the effects of spatial processes on the plant-herbivore interactions.

Keywords Community genetics · Intra-specific variation · Neighbors · Solidago altissima · Spatial variation

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Introduction

What determines the diversity and abundance of herbivores on their host-plants? Understanding the relative strengths of factors and interactions determining population change and community structure is a classic ecological question (e.g., Menge 1976; Hunter and Price 1992). One recent idea is that intra-specific variation among genotypes (i.e., genotype identity) and genotypic diversity (i.e., the number of genotypes) are related to the abundance and diversity of insects on plants (e.g., Whitham et al. 2003, 2006; Hochwender and Fritz 2004; Johnson and Agrawal 2005; Wimp et al. 2005; Bailey et al. 2006; Crutsinger et al. 2006, 2008). In fact, the effects of intra-specific variation among genotypes on community dynamics can be as strong as other, perhaps better-studied, ecological factors (e.g.,

trophic interactions, predator removals, nutrient additions, and elevated [CO_2]) (Bailey et al. 2009). Similarly, the magnitude of genotypic diversity effects on communities and ecosystems are sometimes comparable to the effect size of species diversity effects (e.g., Crutsinger et al. 2006). However, recent work has suggested that, for some species, plant genotype identity effects may play a subordinate role to spatial location when genotypes are planted in different gardens across large geographical areas (Tack et al. 2010).

The effects of host-plant genotypic diversity on community responses such as arthropod richness or abundance can be either "additive" or "non-additive." An additive response suggests that the arthropod community in a genotype mixture can be predicted based on the arthropod community in genotype monocultures, while a non-additive response suggests that genotypes interact in mixtures to support arthropod communities which differ from additive expectations. Non-additive responses can signal either over- or under-yielding, respectively, depending on whether the trait measured in mixtures is greater than or less than additive expectations. A non-additive response can occur for different reasons. For example, if different plant genotypes (or species) temporally or spatially partition the way in which they acquire nutrients, then non-additivity can occur due to "complementarity" effects (e.g., Tilman et al. 2001). Additionally, if certain genotypes (or species) become more dominant in the mixture over time, then non-additivity can occur due to "selection" effects (e.g., Whitlock et al. 2007).

Regardless of whether the effects of genotypic composition and genotypic diversity are additive or non-additive, many of the effects of genotype identity and genotypic diversity on associated communities may depend on environmental context (i.e., genotype by environment interactions; Johnson and Agrawal 2005; Tetard-Jones et al. 2007; Wimp et al. 2007; Bangert et al. 2008; Crutsinger et al. 2008; Bossdorf et al. 2009; Munzbergova et al. 2009). For example, arthropod abundance in a given patch may be similar to arthropod abundance in neighboring patches (irrespective of host-plant genotype) due to interactions among arthropod populations occurring at scales larger than the focal plot (Crutsinger et al. 2009a; Tack et al. 2010). Consequently, the distribution of arthropods in a patchy, genotypically heterogeneous environment will likely be shaped by both plant genotype identity and spatial interactions among arthropod populations on different patches of plants. While a few studies have begun to explore the interaction of spatial effects and genotype identity on biodiversity (Bangert et al. 2008; Crutsinger et al. 2009a), to our knowledge, no study has examined whether genotypic diversity interacts with neighborhood effects among nearby plots to determine arthropod abundance.

Here, we use a common garden experiment to ask three questions about the effects of variation among genotypes, levels of genotypic diversity, and neighborhood interactions in tall goldenrod (*Solidago altissima*) on its most common herbivore, the aphid (*Uroleucon nigrotuberculatum*), and on the key predator of this aphid, a ladybird beetle (*Harmonia axyridis*): (1) how important is genotype identity relative to spatial effects, and (2) are spatial effects on arthropod abundance affected by genotypic diversity? Because ladybird beetle abundance was not affected by any combination of the above factors, we also asked: (3) does ladybird beetle abundance respond to aphid abundance in a focal plot, average aphid abundance in neighboring plots, or both?

Materials and methods

Experimental design

Tall goldenrod (*S. altissima* L.) is a dominant perennial herbaceous species which is broadly distributed across North America, and reproduces both sexually and asexually (Barkley et al. 2006; Crutsinger et al. 2006). Natural patches of *S. altissima* vary in genotypic diversity (from 1 to 13 genotypes within a 0.75-m^2 patch; Maddox et al. 1989), creating the opportunity for genotypic diversity to influence plant–insect interactions. Different *S. altissima* genotypes display variation for a range of processes, including those influencing resistance to herbivorous arthropods and extended effects on higher trophic levels (e.g., Weis and Abrahamson 1986; Abrahamson and Weis 1997; Crutsinger et al. 2006; Craig et al. 2007), community composition (e.g., Maddox and Cappuccino 1986; Maddox and Root 1987; Crutsinger et al. 2006, 2008; Crawford et al. 2007), and ecosystem-level processes such as plant productivity (Crutsinger et al. 2006, 2008) and leaf litter decomposition (Crutsinger et al. 2009b).

We used a common garden experiment established at the National Environmental Research Park at Oak Ridge National Laboratory in Oak Ridge, Tennessee, to address the direct effects of genotypic diversity, genotype identity, and neighborhood effects from adjacent plots on species interactions. Genotypic diversity of *S. altissima* was manipulated at the plot level using a subset of 21 locally collected genotypes. The genotypes were identified as unique by amplified fragment length polymorphism (AFLP). In 2005, 63 1-m^2 plots, each containing 12 individual plants, were established in a grid pattern. Plots contained individuals of 1, 3, 6, or 12 randomly selected genotypes (i.e., clonally replicated, genetically identical lines; see Crutsinger et al. (2006) supplementary material for details). Monoculture plots ($n = 42$) included 2

replicate plots of each of the 21 genotypes. Genotypically diverse plots ($n = 21$) included 7 replicates of each of the 3, 6, and 12 genotype polycultures. The genotypic composition of polyculture plots was determined by a random assignment of genotypes to plots, with the stipulation that no two polyculture plots could have exactly the same constituent genotypes. Heavy plastic lined the edges of each plot to a depth of 30 cm to prevent ramets from spreading to neighboring treatments, but ramets were allowed to spread within each plot over time.

In July 2006, we divided each 1-m^2 plot into 0.25-m^2 sections and visually surveyed one randomly selected section of each plot to estimate the number of aphids and ladybird beetles. Approximately 15 min was spent each plot to estimate of the abundance of aphids (*U. nigrotuberculatum*, Dactynotus) and ladybird beetles (Coccinellidae). The extreme majority of aphids (>99%) were of the species *U. nigrotuberculatum*, and both winged and unwinged aphids were counted. The most common ladybird beetle species at our site (*H. axyridis*) accounted for >90% of the abundance of ladybird beetles. *H. axyridis* can track aphids in space and time, and displays peak oviposition just before the peak of aphid abundance (Osawa 2000). Neither ladybird beetle larvae nor parasitoids were considered for this study. Surveys were conducted over the span of 3 days in mid-July during peak aphid infestation for the season. Although the experiment included 63 plots of *S. altissima*, four plots were excluded from our analyses because those plots had one or zero neighboring plots containing *S. altissima*.

Statistical analyses

General statistical methods

We used three different models (described in the three subsequent paragraphs) to assess the statistical significance of our arthropod abundance results. For tests in which aphid abundance was the response variable, we used generalized linear models (Proc GENMOD, SAS 9.2) with a normal distribution and the identity link function. We analyzed the data on the abundance of ladybird beetles using generalized linear models (Proc GENMOD, SAS 9.2) with a Poisson distribution and the log link function. All χ^2 values were determined using likelihood ratio tests and type III analyses (Proc GENMOD, SAS 9.2). Although all tests treat plant genotypic diversity as a categorical variable (i.e., monoculture or polyculture plots), we also examined plant genotypic diversity as a continuous variable (i.e., 1, 3, 6, or 12 genotypes per plot) and found no major qualitative differences in our results. Additionally, we incorporated in our models the average level of genotypic diversity in a plot's neighbors to determine if this factor influenced arthropod populations, but again found no major differences in our

results. To determine the percent variation accounted for by each experimental factor, we used general linear models using the equation: (treatment sum of squares)/(total sum of squares) × 100% (Johnson 2008).

How important is genotype identity relative to spatial effects?

Our first model tested the relative importance of genotype identity and spatial effects (i.e., neighbor interactions). Unfortunately, an analysis of the complete dataset cannot include genotype identity as a factor, because the genotype of every individual in mixture plots is not known. Therefore, we only examined the relative importance of genotype and spatial effects in monoculture plots. The factors in this model were genotype identity and the average abundance of aphids in neighboring plots. We compared the amount of variation in aphid abundance explained by each factor when both were included in the model. Due to sample size limitations, we were unable to include the interaction of genotype identity and the average abundance of aphids in neighboring plots in our model.

Are spatial effects on arthropod abundance affected by host-plant genotypic diversity?

Our second model included all experimental plots and tested whether plant genotypic diversity (at the plot level) and interactions between neighboring patches of plants affected focal plot arthropod abundance. In this model, factors were plant genotypic diversity, the average number of arthropods on neighboring plots (aphid or ladybird beetle, depending on the response variable), and the interaction of these two factors. See below for a more thorough description of how the average number of arthropods on neighboring plots was determined. As for the first model, we compared the amount of variation in aphid abundance explained by each factor when both were included in the model.

Does ladybird beetle abundance respond to aphid abundance in a focal plot, average aphid abundance in neighboring plots, or both?

Average ladybird beetle abundance was not affected by genotype identity, genotypic diversity, or the average ladybird beetle on neighboring plots. In our third model, we examined how ladybird beetle abundance responded to aphid abundance, both within a focal plot and in neighboring plots. In this model, factors were plant genotypic diversity, focal plot aphid abundance, the average number of aphids in neighboring plots, and all possible interactions of these three factors.

Description of neighborhood effect calculations

Each of the above models includes a term for "average arthropod abundance in neighboring plots". To determine this value, we summed aphid and ladybird beetle abundance for a plot's nearest neighbors and then divided by the number of nearest neighbor plots (sensu Haddad et al. 2000). We defined nearest neighbor plots as those that shared an entire boundary with the focal plot (i.e., for the square plots, a maximum of four nearest neighbors were possible), and we excluded plots that had fewer than two nearest neighbors ($n = 4$ plots) for all neighborhood level analyses. Since each plot is a neighbor to many other plots, non-independence may be a problem which we need to control for when we calculate neighbor effects. To ensure that our method of calculating neighbor effects was not responsible for the observed relationship between focal and neighboring plot arthropod abundance, we used a null model to generate a set of values to which we could compare our observed results.

To create the null model for aphid abundance and neighbor effects, we created a matrix which reflected the spatial relationships between plots, and then shuffled (re-sampling without replacement) the observed aphid abundance values among all plots. Shuffling created a new set of neighbors for each experimental plot. We repeated our analysis of focal plot aphid abundance with respect to average aphid abundance in neighbor plots, and recorded the new regression statistics. Using the Monte Carlo simulation feature in PopTools 2.7, we repeated this process 1,000 times and compared the average regression statistics

for the shuffled plots to the regression statistics from the observed data. If the method of calculating neighbor effects does not influence the results, then we would expect the mean slope of the relationship between shuffled focal plot aphid abundance and shuffled the average number of aphids in neighboring plots to be statistically indistinguishable from zero. The mean slope from 1,000 runs of the null model was -0.02 (95% CI, -0.23 to 0.20). For comparison, the observed slope was 0.78 (95% CI, 0.64–0.93), indicating that the method of calculating neighbor effects was not responsible for the observed neighbor effects.

Results

How important is genotype identity relative to spatial effects?

In monoculture plots, both genotype identity and neighborhood effects influenced aphid abundance (LR $\chi^2_{20,39} = 72.12$, $p < 0.001$; Fig. 1), but neither influenced ladybird beetle abundance. Aphid abundance was 80 times higher on the most susceptible genotype (1,821 aphids plot^{-1}) relative to the least susceptible genotype (24 aphids plot^{-1}). The abundance of aphids in monoculture focal plot was positively correlated with the average number of aphids in neighboring plots (LR $\chi^2_{1,39} = 20.81$, $p < 0.001$). In monoculture plots, genotype accounted for 68% of the variation in aphid abundance, and neighbor aphid abundance accounted for only 6% of the variation.

Fig. 1 Aphid abundance (± 1 SE) as a function of genotype identity for 21 ($n = 2$) genotypes of *S. altissima* in a common garden experiment. Aphid abundance was measured for one quarter of each plot, and multiplied by four to obtain the plot level estimate presented in this figure. Estimates of percent variation explained (*Var %*) were obtained from general linear models using the formula (treatment sum of squares)/(total sum of squares) $\times$ 100%
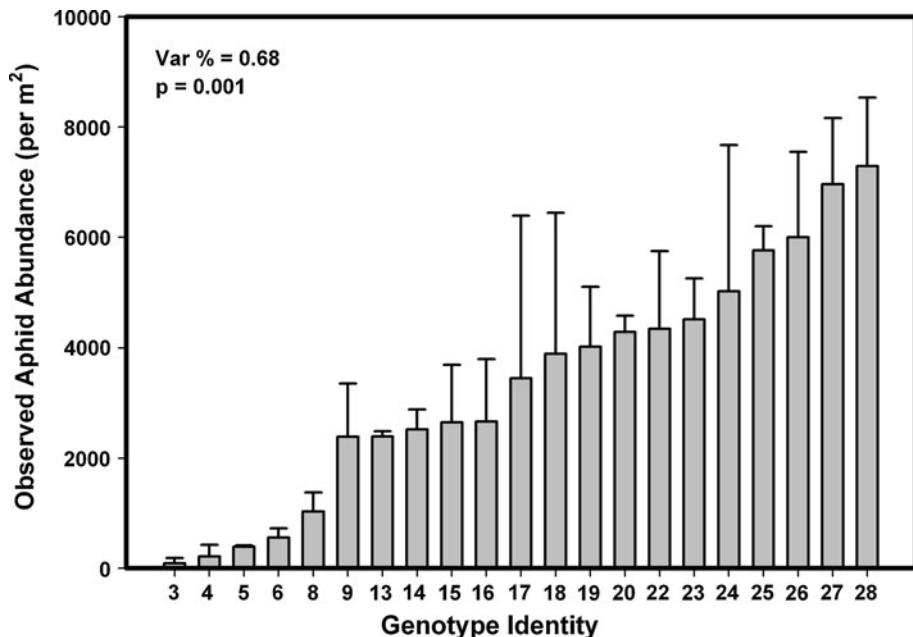
Table 1 Results of a generalized linear model which examines the effects of average aphid abundance in neighboring plots and focal plot genotypic diversity on focal plot arthropod abundance

	df	LR χ^2	p	Var %
Aphid abundance				
Neighbor aphid abundance	1	22.71	<0.001	34.9
Focal plot genotypic diversity	1	2.66	0.103	1.3
Neighbor aphid abundance × focal plot genotypic diversity	1	5.04	0.025	5.4
Ladybird beetle abundance				
Neighbor beetle abundance	1	0.07	0.795	
Focal plot genotypic diversity	1	0.28	0.597	
Neighbor beetle abundance × focal plot genotypic diversity	1	0.04	0.837	

Estimates of percent variation explained (Var %) were obtained from general linear models using the formula (treatment sum of squares)/(total sum of squares) × 100%. No estimates of Var % are given for ladybird beetle abundance because no factors were significant predictors

Are spatial effects on arthropod abundance affected by host-plant genotypic diversity?

Neither the abundance of aphids nor ladybird beetles differed between genotype monoculture and mixture plots (Table 1). Similar to the results from monoculture plots, the average number of aphids in a focal plot was positively correlated with aphid abundance in neighboring plots, and the abundance of ladybird beetles in a focal plot was not related to ladybird beetle abundance in neighboring plots (Table 1). Focal plot aphid abundance was affected by the interaction of genotypic diversity of the focal plot and the average number of aphids in neighboring plots (Fig. 2, Table 1). A comparable interaction was not found for ladybird beetle abundance. Genotypic diversity explained 1% of the variation in focal plot aphid abundance, while

Fig. 2 Aphid abundance on *S. altissima* as a function of host-plant genotypic diversity and average aphid abundance in neighboring plots. Aphid abundance was measured for one quarter of each plot, and multiplied by four to obtain the plot level estimate presented in this figure. *Filled circles* and *solid regression line* represent polyculture (i.e., multiple genotypes) focal plots; *open circles* and *dotted regression line* represent monoculture focal plots

the average abundance of aphids in neighboring plots explained 35% of the variation in focal plot aphid abundance. The slope (±1 SE) of the relationship between aphid abundance in neighboring plots and aphid abundance in focal plots was significantly higher ($t_{55} = 2.19$, $p = 0.033$) for genotype polyculture (1.336 ± 0.270) than for genotype monoculture focal plots (0.512 ± 0.157), indicating that changes in the average abundance of a focal plot's neighbors would have a greater effect on polyculture focal plots than monoculture focal plots. These results do not show a non-additive effect in the traditional sense (i.e., a difference in a response variable between monocultures and mixtures), but instead show that genotypic diversity can impact how spatial effects determine patterns of arthropod abundance across interacting patches.

Does ladybird beetle abundance respond to aphid abundance in a focal plot, aphid abundance in neighboring plots, or both?

Ladybird beetle abundance was influenced by a three-way interaction term including focal plot plant genotypic diversity, focal plot aphid abundance, and the average number of aphids in neighboring plots (Table 2). The three-way interaction term suggests that ladybird beetles respond to aphid abundance at spatial scales larger than 1 m × 1 m plots, and that the way ladybird beetles respond to aphid populations at two spatial scales (i.e., focal plot and neighboring plots) depends on whether the focal plot is a monoculture or polyculture plot.
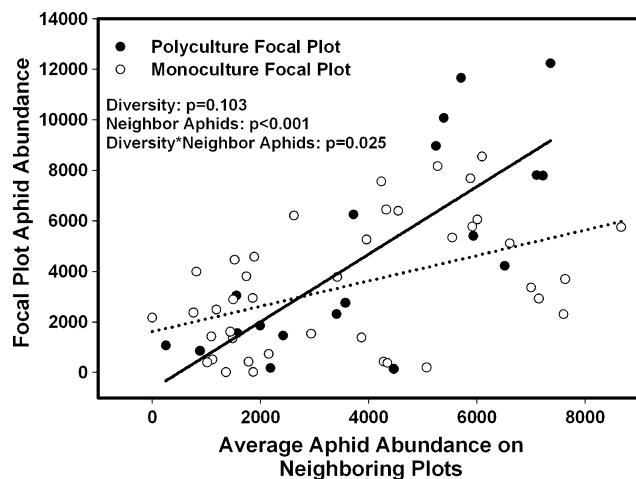
Discussion

Genotype identity

We found that genotype identity in *S. altissima* directly affected and explained 68% of the variation in aphid

Table 2 Results from a generalized linear model which examined the effects of focal plot aphid abundance, and neighborhood average aphid abundance, and focal plot genotypic diversity on focal plot ladybird beetle abundance

Ladybird beetle abundance	df	LR χ^2	p	Var %
Focal plot aphid abundance	1	9.36	0.002	16.2
Neighbor average aphid abundance	1	4.96	0.026	0.0
Focal plot genotypic diversity	1	4.35	0.037	8.4
Focal plot aphid abundance × neighbor average aphid abundance	1	7.14	0.008	4.9
Focal plot aphid abundance × focal plot genotypic diversity	1	6.99	0.008	5.4
Neighbor average aphid abundance × focal plot genotypic diversity	1	3.90	0.048	1.4
Focal plot aphid abundance × neighbor average aphid abundance × focal plot genotypic diversity	1	6.28	0.012	10.7

Estimates of percent variation explained (% Var) were obtained from general linear models using the formula (treatment sum of squares)/(total sum of squares) × 100%

abundance (Fig. 1). These results align with the results of previous studies suggesting that variation among host-plant genotypes within species can influence plant–insect interactions (e.g., Maddox and Root 1987; Fritz and Price 1988; Abrahamson and Weis 1997; Crawford et al. 2007). Additionally, a number of studies have found that plant genotype identity affects predators as well as herbivores (Bailey et al. 2006; Crutsinger et al. 2006, 2008; Johnson 2008; Mooney and Agrawal 2008). However, in our study, genotype identity did not affect ladybird beetle abundance, the most common predator of the aphids in our system. This may be because *H. axyridis* also preys on many other arthropods in addition to aphids (see Koch 2003 for review) such that *H. axyridis* populations may also be tracking other arthropods whose abundances were not measured in this study and might not co-vary with aphids. Another potential mechanism for the lack of a genotype identity effect on ladybird beetles is the idea herbivores and their predators respond to plant traits at different spatial and temporal scales (Crutsinger et al. 2009a), and ladybird beetles may not respond to genotype identity at the scale of 1 m × 1 m plots. For example, we found that ladybird beetle abundance was best predicted by aphid abundance at the plot level, aphid abundance at the neighborhood level (a slightly larger scale including multiple plots), and whether the focal plot is a monoculture or polyculture (Table 2).

Genotypic diversity

Genotypes grown in polyculture plots often have population- and community-level effects that are non-additive; that is, the patterns differ from expectations based on simply adding up the responses associated with individual genotypes. In several recent studies across multiple plant species, genotype polycultures displayed non-additive effects (Schweitzer et al. 2005; Crutsinger et al. 2006, 2008; Johnson et al. 2006; Crawford et al. 2007). According to Johnson et al. (2006), several mechanisms

could explain the lack of additive effects of genotypes in mixtures, including: (1) competition and facilitation between neighboring plants, (2) associational resistance (e.g., Tahvanainen and Root 1972) or susceptibility (e.g., Karban 1997), (3) source-sink dynamics of arthropods between plants in a patch, and (4) differences in the way arthropod species perceive genotype monocultures compared with genotype polycultures (e.g., Rodriguez-Saona and Thaler 2005; Crawford et al. 2007). For example, Crawford et al. (2007) showed a non-additive response of attack by the bunch galler *Rhopalomyia solidaginis* to host-plant genotypic diversity in *S. altissima*. Since bunch galling rates also varied across host-plant genotypes, this result suggests that *R. solidaginis* may perceive genotypes in diverse patches differently than those same genotypes in monoculture with respect to inducing bunch galls (Crawford et al. 2007). In this study, we did not find a traditional non-additive effect as described in the studies cited above (i.e., aphid abundance did not differ between monoculture and polyculture plots, which led us to reject the hypothesis that genotypic diversity directly affects aphid abundance). Instead, we found that focal plot genotypic diversity determined the strength of spatial effects between plots by influencing how populations of arthropods on neighboring patches interact.

Neighborhood effects

When the average abundance of aphids in neighboring plots was low, focal plot aphid abundance was higher in monocultures than in polycultures. However, when the average abundance of aphids in neighboring plots was high, focal plot aphid abundance was higher in polycultures than in monocultures (Fig. 2). Although we did not explicitly test for the mechanism of this effect, it is possible that the strong influence of plant genotype identity on aphid populations in monoculture focal plots (Fig. 1) makes these populations less responsive to interactions with populations on neighboring plots. Additionally, focal plot genotypic

diversity affected ladybird beetle abundance through a three-way interaction with focal plot aphid abundance and the average abundance of aphids in neighboring plots. This contrasts with earlier work that showed that genotype identity influenced trophic interactions through simple density dependence (Bailey et al. 2006) and suggests that ladybird beetle foraging behavior might depend on prey abundance within and among patches and patch-level genotypic diversity.

Spatial effects such as associational resistance, which refers to a decrease in herbivory on a particular plant when it grows in close proximity to heterospecific neighbors (Tahvanainen and Root 1972; Andow 1991) and associational susceptibility, which refers to an increase in herbivory when a particular plant grows in close proximity to heterospecific neighbors (Atsatt and O'Dowd 1976; Karban 1997), have been documented in ecological studies for decades. Species richness in arthropod communities can also be affected by neighbors. For example, Haddad et al. (2000) showed that arthropod species richness was correlated among neighboring experimental plots. In our study of aphid–*S. altissima* interactions reported on here, we documented a different type of spatial effect, one in which genotypic diversity affects how populations of aphids in neighboring patches of plants are spatially distributed. Specifically, aphid populations in polyculture plots responded more to average aphid abundance on neighboring plots than did aphid populations in monoculture focal plots. Overall, our results indicate that aphids and their predators respond to intra-specific variation with host-plant genotypes at different scales, and that genotypic diversity can influence the way arthropods on neighboring patches of plants interact.

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