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A geographic mosaic of trophic interactions and selection: trees, aphids and birds

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Abstract

Genetic variation in plants is known to influence arthropod assemblages and species interactions. However, these influences may be contingent upon local environmental conditions. Here, we examine how plant genotype-based trophic interactions and patterns of natural selection change across environments. Studying the cottonwood tree, *Populus angustifolia*, the galling aphid, *Pemphigus betae* and its avian predators, we used three common gardens across an environmental gradient to examine the effects of plant genotype on gall abundance, gall size, aphid fecundity and predation rate on galls. Three patterns emerged: (i) plant genotype explained variation in gall abundance and predation, (ii) G×E explained variation in aphid fecundity, and environment explained variation in gall abundance and gall size, (iii) natural selection on gall size changed from directional to stabilizing across environments.

Introduction

Genetic variation within a single plant species can strongly influence the associated community of interacting species, including vertebrates, arthropods and microbes (Maddox & Root, 1987; Whitham *et al.*, 2003, 2006; Johnson & Agrawal, 2005; Bailey *et al.*, 2006; Crutsinger *et al.*, 2006; Shuster *et al.*, 2006; Schweitzer *et al.*, 2008; Barbour *et al.*, 2009; Keith *et al.*, 2010). It is well known that individual plant genotypes vary greatly in their susceptibility to diverse herbivores (e.g. aphids – Moran, 1981; Service, 1984; moths – Whitham & Mopper, 1985; beavers – Bailey *et al.*, 2004; a diverse suite of arthropods – Maddox & Root, 1987), which can then lead to differential abundance of organisms at higher trophic levels and their interaction (Bailey *et al.*, 2006; Johnson, 2008; Mooney & Agrawal, 2008). For example, using replicated clones of the riparian tree, *Populus angustifolia* James, planted in a common garden, Bailey *et al.* (2006) showed that individual tree genotypes varied in the abundance of galling aphids and in the frequency of avian predation of those galls. In another study, Johnson (2008) showed that individual primrose (*Oenothera biennis*) plants varied in population densities of aphids and the ants that feed on their honeydew. Similarly, Mooney & Agrawal (2008) showed that milkweed (*Asclepias syriaca*) genotype affected ant–aphid interactions. These studies are important because they demonstrate the power of plant genetics as a bottom-up force shaping trophic interactions.

Although genetic variation in a wide range of plants has been shown to influence other species, foundation plant species are likely to have the most pronounced effects (Whitham *et al.*, 2006). Foundation species create locally stable conditions for many other species, which can define an entire ecological community (Dayton, 1972; Ellison *et al.*, 2005). For example, different genotypes of *P. angustifolia* (narrowleaf cottonwood) support a large, diverse community, including canopy arthropods (Shuster *et al.*, 2006), belowground microbial community (Schweitzer *et al.*, 2008), trophic interactions (Bailey *et al.*, 2006) and microbial processes important for nutrient cycling (Schweitzer *et al.*, 2008).

In addition to being influenced by genetic variation, species interactions and patterns of natural selection can be shaped by local environmental conditions, such as changes in local community composition (e.g. Strauss & Irwin, 2004; Thompson, 2005). For example, research

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with goldenrod (*Solidago altissima*), a galling fly and gall predators, showed that the pattern of selection on gall size changed as a function of time and geography (Abrahamson *et al.*, 1989; Weis *et al.*, 1992; Craig *et al.*, 2007). In these studies, parasitoids attacked smaller galls, whereas woodpeckers tended to forage on larger galls, resulting in intermediate-sized galls having the highest fitness. Because woodpecker's presence was geographically and temporally variable, so too was selection on gall size. Where woodpeckers were present, selection favoured intermediate-sized galls and where they were absent, larger galls were favoured. Here, we also examine the geographical variation of trophic interactions and selection on gall size. Like earlier studies (Abrahamson *et al.*, 1989; Weis *et al.*, 1992; Craig *et al.*, 2007), we show that selection on gall size varies across environments. However, unlike the previously mentioned studies of *Solidago*, we incorporate genetic information about the plant, *P. angustifolia* into our examination of species interactions, patterns of natural selection and how they change geographically. We examined three relationships: (i) we used individual common gardens of replicated *P. angustifolia* genotypes to quantify the effects of tree genotype on aphid fecundity, gall size, gall number and predation on galls by avian predators; (ii) we used three replicated common gardens across three environments to examine how the effect of tree genetics on the above-mentioned traits may be contingent upon the environment (i.e. in addition to genotypic effects, our full model included environment and genotype-by-environment interaction (G×E) in examining the influences on the above-mentioned traits); and (iii) we examined the pattern of natural selection acting on gall size across environments. Our results suggest that genetic and environmental variation is responsible for observed variation in trophic organization and the pattern of natural selection. Thus, over short geographical distances, changes in genetics and environment can result in very different trophic interactions and patterns of natural selection.

Methods

Study system – common gardens

To measure the effects of plant genotype on trophic interactions (i.e. the bottom-up effects), we used three common gardens of replicated *P. angustifolia* genotypes. Each genotype was replicated between three and seven times (92 total trees), and we used the same six replicated tree genotypes in each of three gardens. Cuttings were taken from trees growing wild along the Weber River, UT, between the elevations of 1300 m and 1400 m. Five of the genotypes were collected from a single stand at approximately 1400 m in elevation, and the sixth genotype was collected approximately 1300 m in elevation. This elevation range spans the lower two common gardens, and hence, our collection sites of wild genotypes were near two of the common gardens (see later). These saplings were planted in the common gardens between 1982 and 1990 and were fully grown and sexually mature at the time of this experiment in 2005. The three common gardens were planted at elevations of 1300, 1392 and 1587 m (hereafter referred to as the low-, mid- and high-elevation gardens, respectively) and spanned 55 km. Although our gardens were planted at different elevations, we did not replicate elevation in our experiment. Consequently, 'elevation' is used only to name the different common gardens and not to infer any causation of elevation.

Surveys of aphids and trophic interactions

For measures of gall abundance and predation rates, we randomly chose 100 shoots from at least two branches on each tree (9200 shoots in total) and counted the number of galls per 100 shoots (gall abundance). We used two metrics for predation rate. First, we counted the number of attacked galls per 100 shoots, and second, we divided the number of attacked galls by gall abundance. Galls opened by predators (mostly birds) are easily identified as they slice open the gall, leaving a distinctive wound as evidence of their removal of aphids (Bailey *et al.*, 2006). To measure gall size and aphid fitness, we collected 10–15 galls per tree, including attacked galls, and the mean gall size and aphid fecundity per tree was used in the following analyses (see later). Galls were placed into ziploc bags on ice within a cooler to prevent eclosion and were later stored in a freezer until they were measured. Surveys for gall abundance and gall collections were carried out over 9 days in late June, when galls were fully formed, but before aphid emergence. We used digital callipers to measure gall length and width to the nearest 0.01 cm. Length and width were then multiplied together to estimate gall area. After measuring, we dissected the galls and counted the number of aphids inside. The number of aphids per gall is a good measure of the fecundity of the colonizing stem mother, who initiates the gall and reproduces by parthenogenesis within (Whitham, 1989).

We used restricted maximum likelihood (REML) (Falconer & Mackay, 1996; Conner & Hartl, 2004) to examine the effects of tree genotype, environment (i.e. elevation) and plant genotype-by-environment (G×E) interaction on gall abundance, gall size, aphid fecundity and predation. In our full model, plant genotype and G×E were random effects, and environment was a fixed effect. In addition, we also analysed the two low-elevation gardens individually to examine whether the influence of plant genotype remained in the face of environmental variation. The significances of genotype and G×E were tested with a log-likelihood ratio test, and the significance of environment was tested using an *F*-test (Conner & Hartl, 2004). JMP 7.0.2 was used for all analyses.

Measuring and characterizing selection

We used linear regression (Lande & Arnold, 1983; Conner & Hartl, 2004) and the cubic spline method (Schluter, 1988) to quantify and characterize natural selection on gall size; we used regression to calculate ß and/or γ, and we used the cubic spline method to further estimate the shape of the fitness function. We first used the approach of Lande & Arnold (1983) and regressed relative fitness onto the standardized gall area. Relative fitness (w) was calculated by taking the mean aphid fecundity on each tree and dividing it by the mean aphid fecundity of the common garden. We standardized gall size (z) by taking the mean gall size on each tree, subtracting the mean gall size of the common garden and dividing by the common garden's standard deviation (Conner & Hartl, 2004). Each common garden was analysed separately. The resulting shape of this line suggested the type of selection, where a linear fit suggested directional selection and a negative curvilinear fit, with a mode or high point at some intermediate phenotype, suggested stabilizing selection (Brodie *et al.*, 1995; Conner & Hartl, 2004). We also used the cubic spline method, which minimized the generalized cross-validation (GCV) score, to estimate the shape of the fitness function (Schluter, 1988). We used QUICKSAND to run and graph the cubic spline (Walker, 1998).

Inferring avian predators as agent of selection on gall size

In the scatter plots used for measuring and characterizing selection (Fig. 3), it is important to note that each point in the scatter plot represents the average size and aphid fecundity from several galls collected from a single tree (see earlier). Some galls had been attacked by birds, which were sliced open and had their aphids removed (eaten) by birds, resulting in galls with zero aphids inside. These attacked galls with no aphids inside were included in calculating the average gall size and aphid fecundity used in the scatter plots to measure and characterize selection.

Results

Effect of tree genetics, environment and G×E on trophic interactions

Consistent with our hypothesis, we found geographical variation in gall traits and species interactions. There was a strong environmental effect on gall abundance across the three gardens. Galls were 40 times more abundant at the lower two gardens than at the high-elevation garden ($\chi^2_1 = 48.03$, $P < 0.0001$, Fig. 1a). The low number of galls at the high-elevation garden virtually eliminated the possibility of trophic interactions with avian predators at this site. Consequently, for our examination of the influence of genotype, environment, and G×E in shaping trophic interactions and our examination of selection on gall size, we limited the remainder of our statistical analysis to the low- and mid-elevation sites.

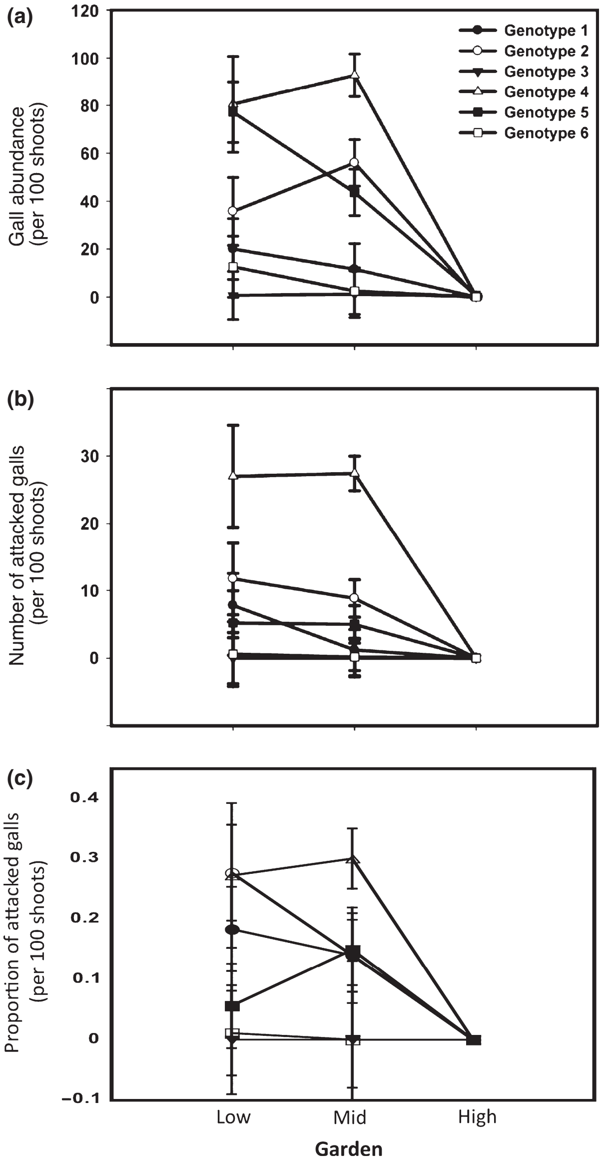

Fig. 1 Geographical variation in trophic-level interactions. Reaction norms showing plant genotype variation in gall abundance (a), total attacked galls (b) and the proportion of attacked galls in three different common gardens. Each point represents the genotype mean (± 1 SE).

Across the low- and mid-elevation gardens, we found evidence to support our hypothesis that tree genetics influenced gall traits and predation rates (Table 1). Examining the two low-elevation gardens individually, genotype explained a significant amount of variation in all traits, except predation at the low-elevation site

Table 1 Results from restricted estimated maximum likelihood (REML) model with genotype, environment and genotype-by-environment interactions for total galls, predation rates, aphid fecundity and gall size. These data are for the low- and mid-elevation gardens only. The high-elevation garden was omitted from our statistical model (see the Results section). Degrees of freedom for the χ^2 tests (for the effect of genotype and G×E) were 1. The degrees of freedom for the *F*-ratio tests (for the effect of environment) are listed below.

Phenotype	Full model Test statistic, *P*-value	Low elevation	Mid elevation
Total galls			
Genotype	χ^2 = 8.2; 0.0042	χ^2 = 19.4, 0.0010	χ^2 = 50.3, <0.0001
Environment	$F_{1,5.12}$ = 0.114; 0.75		
G×E	χ^2 = 0.82; 0.37		
Predation (total galls attacked)			
Genotype	χ^2 = 14.88; <0.0001	χ^2 = 2.26, 0.1438	χ^2 = 53.5, <0.0001
Environment	$F_{1,45.12}$ = 0.27; 0.61		
G×E	χ^2 = 0; 1		
Predation (proportion of galls attacked)			
Genotype	χ^2 = 5.48; 0.0192	χ^2 = 2.18, 0.1398	χ^2 = 5.76; 0.0164
Environment	$F_{1,42.75}$ = 0.007; 0.9359		
G×E	χ^2 = 0.02; 0.8875		
Aphid fecundity			
Genotype	χ^2 = 0.96; 0.33	χ^2 = 45.8, < 0.0001	χ^2 = 10.4, 0.0013
Environment	$F_{1,5.41}$ = 0.2; 0.66		
G×E	χ^2 = 6.86; 0.0088		
Gall size			
Genotype	χ^2 = 2.72; 0.0991	χ^2 = 14.4, 0.0036	χ^2 = 13.2, 0.0003
Environment	$F_{1,4.49}$ = 12.86; 0.0009		
G×E	χ^2 = 1.96; 0.1615		

(Table 1). When using the full model, which included G×E and environment as explanatory variables, genotype explained variation only in predation and gall abundance (Table 1).

We also found evidence to support the hypothesis that the environment and G×E significantly explained variation in some traits. Averaged across all tree genotypes, galls were approximately 40% larger at the mid elevation compared to the low elevation (Table 1, Fig. 2a). All tree genotypes tended to support larger galls at the mid-elevation site, and one tree genotype in particular supported galls that were twice as large at the mid-elevation site (Fig. 2a). Whereas gall size may have been influenced by environment, gall abundance, aphid fecundity and predation on galls did not seem to change across the two gardens (Table 1).

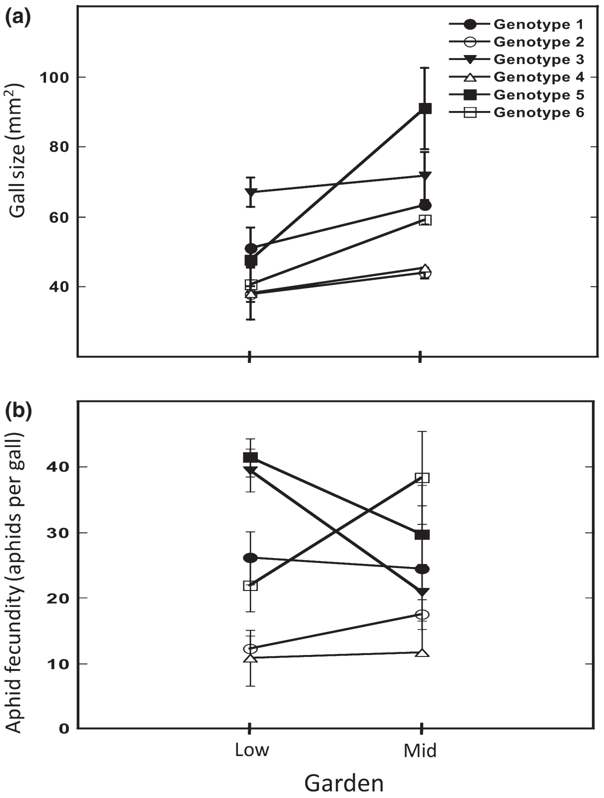

Fig. 2 Reaction norms showing plant genotype differences in gall size (a) and aphid fecundity (b) in two different common gardens. Each point represents the genotype mean (± 1 SE).

Genotype-by-environment interaction explained a significant amount of variation in aphid fecundity (Table 1, Fig. 2b). The two tree genotypes that supported the highest levels of aphid fecundity at the low-elevation garden supported only moderate levels of aphid fecundity at the mid-elevation garden. Conversely, two genotypes that supported moderate levels of aphid fecundity at the low-elevation garden supported the highest amount of aphid fecundity at the mid-elevation garden (Fig. 2b).

Selection on gall size

We found significant evidence for selection on gall size at both the low- and mid-elevation gardens; however, the type of selection shifted from directional to stabilizing across these two gardens. At the mid-elevation garden, we detected stabilizing selection on gall size (Fig. 3a). Regressing relative aphid fitness onto standardized gall size, we found that a negative curvilinear line was the best fit (Fig. 3a). Even when the two extreme points, which exceeded three standardized units of gall area, were removed, the best fit was still curvilinear. We also used cubic spline to explore the fitness function of gall size. Like quadratic regression, the cubic spline detected a mode in the fitness function, that is, an intermediate gall size supported the highest aphid fitness. The attacked

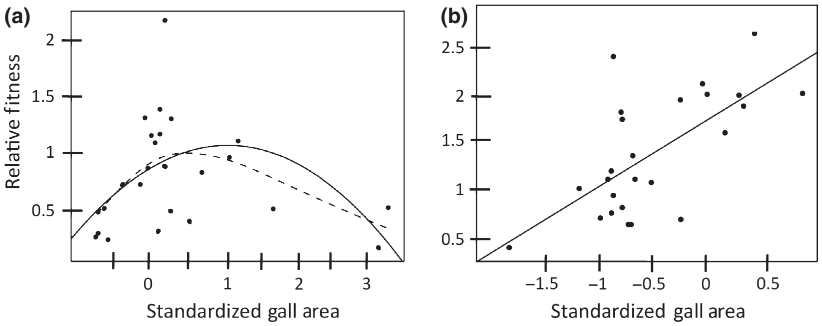

Fig. 3 Natural selection on gall size at the low and mid-elevation. At the mid-elevation site (a), there is a quadratic relationship between gall size and aphid fecundity ($\gamma = -0.42$, $P = 0.032$). In panel (a), the solid line is the regression line, and the dotted line is the result of the cubic spline. In both cases, the high point is at an intermediate phenotype, suggesting stabilizing selection. At the low-elevation site (b), gall size is linearly related to aphid fecundity indicating directional selection ($\beta = 0.61$, $P = 0.0003$). The line in (a) is the result of both linear regression and the cubic spline; the two lines were indistinguishable.

galls seem to be what is driving down average aphid fecundity in the larger galls at the mid-elevation site (Fig. 3a).

In contrast to the mid-elevation garden, galls at the low-elevation site seemed to experience directional selection for large gall size. Regressing relative aphid fitness on standardized gall size, the best fit was linear (Fig. 3b). Although predators were present and attacked galls at this site, they did not seem to significantly change mean aphid fecundity. Consequently, the largest galls at this site supported the greatest aphid fecundity.

Discussion

Summary of results

In this article, we showed that the genetics of a common tree, the environment and G×E can influence geographical variation in trophic interactions. We found that tree genetics explained a significant amount of variation in gall abundance, predation on galls, gall size and aphid fitness (measured as the number of aphids per gall). We also found that species interactions and patterns of natural selection changed across the three environments we examined. Especially noteworthy is the small scale over which these environmental differences occurred. Over a gradient of just 20 km and 100 m in elevation (the range between the low- and mid-elevation gardens), gall size varied by 40% and selection on gall size changed from directional to stabilizing. Over an additional 35 km and 200 m in elevation (including the high-elevation site), galls and hence their associated trophic interactions nearly disappeared. In examining the potential factors shaping these patterns, plant genotype, the environment and G×E were all important in influencing trophic interactions across the landscape. Whereas this article examined geographical variation, species interactions and patterns of natural selection may also change across time (Craig *et al.*, 2007).

Geographical variation in species interactions

Although other environmental parameters may cause communities to change across the landscape, spatial genetic variation in the host plant(s) may cause changes in the surrounding community. Barbour *et al.* (2009) found that *Eucalyptus globulus* trees collected from different provinces, then grown in a common environment, supported different arboreal arthropod and fungal communities. This study supports the mechanism that spatial genetic structure of host plants can influence the composition of other species. In other words, large-scale genetic structure of plants may be an important driver to the changes we see in community composition and species interactions as we move across the landscape.

A major hypothesis regarding geographical variation in patterns of natural selection is that there is geographical variation in the distribution of interacting species. For example, Weis *et al.* (1992) examined the selection pressure on gall traits across multiple locations and showed that as the presence of woodpeckers varied across the landscape, so too did the selection regime on gall traits. Our results indicate that there was no geographical variation in the presence of the tree, galls or avian predators across the low- and mid-elevation gardens. The two main avian predators of *P. betae* galls are the Black-headed Grosbeak (*Pheucticus melanocephalus*) and the Black-capped Chickadee (*Poecile atricapilla*) (Bailey *et al.*, 2006). Working in the same common gardens as this study, Bridgeland *et al.* (2010) did not find a difference in the bird communities between the low- and mid-elevation gardens. However, we did find significant differences in patterns of natural selection on gall size, switching from directional to stabilizing across the low- and mid-elevation gardens. Such changes in the patterns of natural selection may be driven by geographical variation in gall size as previous studies have found that a population's distribution of gall sizes correlated with the local pattern of selection (Weis & Kapelinski, 1994). In our study, we found that galls were approximately 40% larger at the mid-elevation garden. Further, the garden with the largest galls experienced stabilizing selection, and the garden with smaller galls experienced directional selection. For gall size to evolve as a response to selection, it must be a heritable trait of the aphid. In other systems, it is known that gall size is a heritable trait of the galler (e.g. Weis & Abrahamson, 1986); however in this system, it is unknown whether or not gall size is a heritable trait of *P. betae*.

Consistent with previous work (Whitham, 1989; Moran & Whitham, 1988; Moran, 1991), we found galls were nearly absent from the high-elevation site. The absence of galls, and hence their associated trophic interactions, may be because of genetic variation in *P. betae*. Using two of the same sites as this study (the mid- and high-elevation sites), previous research has shown that aphids at the high-elevation site differs in their genetic-based life history (Moran & Whitham, 1988; Moran, 1991). Specifically, they showed that high-elevation aphids have largely reduced their association with *P. angustifolia* and, instead, spend several successive generations on secondary hosts (*Rumex* and *Chenopodium*). Consequently, even though aphids are present at higher elevations, galls, and hence their associated trophic interactions are absent from these locales. Further, as a food and shelter resource for other organisms, the presence of *P. betae* galls has shown to influence diverse communities, including fungi, arthropods and vertebrates (Dickson & Whitham, 1996; Schweitzer *et al.*, 2005; Bailey *et al.*, 2006; Keith *et al.*, 2010). Consequently, the absence of galls at higher elevations has the potential to effect trophic interactions as well as a much larger community of organisms.

One fascinating aspect of geographically variable species interactions is that they may lead to evolutionary distinct lineages across the landscape and speciation of dependent community members. Several studies have found that populations of herbivores are adapted to particular trees (e.g. Mopper *et al.*, 1995, 2000; Evans *et al.*, 2008). In the same cottonwood study system and sites that we report here, Evans *et al.* (2008) found that two cryptic species of the gall-forming mite, *Aceria parapopuli*, have evolved in relative close proximity, one in the hybrid zone on F_1 type hybrids, and another in the narrowleaf zone on *P. angustifolia*. In general, because speciation may follow from locally adapted, differentiated populations of arthropods (e.g. Via, 2001; Drès & Mallet, 2002), the geographical mosaic of selection documented in the present study may result in the genetic differentiation of individual community members and even speciation as shown by Evans *et al.* (2008). Such differentiation may extend to multiple trophic levels. For example, multiple herbivores (Stireman *et al.*, 2005) and their parasitoids (Abrahamson *et al.*, 2003; Stireman *et al.*, 2006) are genetically differentiated on two closely related sympatric species of *Solidago*, indicating that host plants can affect species' evolution at multiple tropic levels.

Conclusions

Two frameworks, community genetics and geographical mosaic theory (Thompson, 2005), help explain community structure, species interactions and patterns of natural selection. First, community genetics explains how genetic variation within one species may affect the presence of other species and how they interact, such as the trophic interactions reported here. Studies in community genetics have shown that genetic variation in a single species can strongly influence the associated community of interacting species, including microbes (Schweitzer *et al.*, 2008), arthropods (e.g. Johnson & Agrawal, 2005; Keith *et al.*, 2010) and vertebrates (Bailey *et al.*, 2006). Often, however, community structure and its inherent species interactions change geographically, owing to changes in abiotic conditions, species' ranges and/or the population genetic structure of species. To incorporate these geographical factors in our understanding of species interactions, another framework is needed.

Geographical mosaic theory explains how species interactions and natural selection regimes can change across environmental gradients (Thompson, 2005). Although some research and theory argues that geographical mosaic theory pertains strictly to coevolutionary and/or reciprocal interactions (Gomulkiewicz *et al.*, 2007), this framework can also be used to explain geographical patterns in all kinds of species interactions and patterns of natural selection, coevolutionary or otherwise. For example, in his book on the geographical mosaic theory of coevolution, Thompson (2005) argues that one way that species interactions can change across environments is through differences in the genetic structures of populations. Although not in a coevolutionary context, Barbour *et al.* (2009) show that genetic-based racial differences in *E. globulus* drove differences in the community structure of herbivores.

Overall, community genetics and the geographical mosaic theory are complementary approaches to examining ecological and evolutionary processes. With increased emphasis and understanding of genetics, the community genetics framework may become a powerful approach to understanding how genes play a role in shaping species interactions and the evolutionary process. In addition, the geographical mosaic theory describes how species interactions may change across environmental gradients. Together, these two frameworks will provide approaches for quantifying and understanding of the mechanisms of the evolutionary process as well as the broad macroecological and evolutionary patterns in nature.

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