

LETTER

Plant genetics shapes inquiline community structure across spatial scales

Gregory M. Crutsinger,^{1*} Marc W. Cadotte² and Nathan J. Sanders¹

¹Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

²National Center for Ecological Analysis and Synthesis, 735 State Street Suite 300, Santa Barbara, CA 93101, USA

*Correspondence: E-mail: gcrutsin@utk.edu

Abstract

Recent research in community genetics has examined the effects of intraspecific genetic variation on species diversity in local communities. However, communities can be structured by a combination of both local and regional processes and to date, few community genetics studies have examined whether the effects of intraspecific genetic variation are consistent across levels of diversity. In this study, we ask whether host-plant genetic variation structures communities of arthropod inquilines within distinct habitat patches – rosette leaf galls on tall goldenrod (*Solidago altissima*). We found that genetic variation determined inquiline diversity at both local and regional spatial scales, but that trophic-level responses varied independently of one another. This result suggests that herbivores and predators likely respond to heritable plant traits at different spatial scales. Together, our results show that incorporating spatial scale is essential for predicting the effects of genetically variable traits on different trophic levels and levels of diversity within the communities that depend on host plants.

Keywords

Alpha diversity, beta diversity, community genetics, gamma diversity, metacommunity, plant-insect, *Rhopalomyia solidaginis*, *Solidago altissima*, spatial structure.

Ecology Letters (2009) 12: 285–292

INTRODUCTION

The field of community genetics links intraspecific genetic variation at the population level to the trophic interactions and the diversity of associated communities (Whitham *et al.* 2003, 2006; Johnson & Stinchcombe 2007). Studies in community genetics often link genetic variation in traits, namely within local patches of a plant species, to variation in the distribution, richness and abundance of associated community members (Whitham *et al.* 2003, 2006). For example, recent work has examined how intraspecific genetic variation within host plant traits affects associated invertebrates (Wimp *et al.* 2005; Crutsinger *et al.* 2006, 2008a; Johnson & Agrawal 2005; Johnson *et al.* 2006; Bangert *et al.* 2008), vertebrates (Bailey *et al.* 2004), other plant species (Crutsinger *et al.* 2008b; Lankau & Strauss 2007), and microbes (Schweitzer *et al.* 2007). To date, community genetics studies have largely focused on genetic effects at the local scale. However, the diversity of species in communities arises from the combination of local species interactions and regional dispersal (Leibold *et al.* 2004; Cadotte & Fukami 2005; Holyoak *et al.* 2005; Chase & Bengtsson in press). Empirical tests of how intraspecific

genetic variation can influence both local and regional species diversity, and how local and regional diversity are related to one another, are lacking. This is despite the numerous potential connections between communities associated with host plants and other studies focusing on plant-based mesocosms in which patch heterogeneity is considered a key driver of associated species diversity (moss patches Gonzalez *et al.* 1998; bromeliads (Srivastava *et al.* 2008), pitcher plants (Kneitel & Miller 2003), or tree holes (Srivastava & Lawton 1998)).

In this study, we focus on arthropods associated with tall goldenrod (*Solidago altissima*), which is a rhizomatous perennial that dominates old fields and roadsides throughout eastern North America (Semple & Cook 2006). Local populations of *S. altissima* vary greatly in size from just a few to thousands of ramets, and genotypic diversity within natural patches can range from 1 to more than 12 genotypes m⁻² (Maddox *et al.* 1989). Clones exhibit considerable interclonal genetic variation in many plant traits, such as growth rate, leaf nutrient content, and plant defenses (Abrahamson & Weiss 1997; Crutsinger *et al.* 2006), all of which have the potential to affect a diverse community of associated arthropod species (Maddox & Root 1987; Crutsinger *et al.*

2006, 2008a). Here, we ask how host-plant genetic variation in *S. altissima* affects a diverse community of arthropods that occur within distinct habitat patches – rosette leaf galls created by the rosette-galling midge, *Rhopalomyia solidaginis* (Diptera: Cecidomyiidae). The rosette-galling midge specializes on the genus *Solidago* and initiates galls through oviposition in the apical meristem of *S. altissima*, preventing further elongation of the stem. This creates a conspicuous rosette (or ‘bunch’) of leaves typically at the tip of the plant and on lateral buds (Fig. 1; Raman & Abrahamson 1995; Wise *et al.* 2006). The rosette-galling midge is one of the most common galling species on *S. altissima* at our study site, attacking, on average, ~15% (range = 3–35%) of all *S. altissima* ramets (Crutsinger *et al.* 2008c). Rosettes are then secondarily colonized by ~75 different species of arthropods, including leaf beetles, leafhoppers, lepidopteran larvae, mites, weevils and spiders (Crawford *et al.* 2007).

We consider each rosette gall to represent a distinct local community for several reasons. First, arthropods that occur in galls overlap in composition by only ~25% with arthropods that occur on the ungalled portions of *S. altissima* and use these galls for both food and habitat (Crawford *et al.* 2007). Second, the presence of both eggs and offspring of herbivore and predator species in galls indicates that many inquiline species can maintain multiple generations in a single gall. Finally,

many species, particularly herbivores, in the goldenrod system tend to be sedentary (Root 1996), and so there is likely only modest dispersal once they have colonized an individual gall. Hereafter, we refer to those arthropods that secondarily use rosette galls as ‘inquilines’ and use the terms ‘gall’, ‘local patch’ and ‘local community’ interchangeably.

In this study, we partition the diversity of gall inquilines into local (within-gall) and regional (among-gall) diversity and examine the response of both local and regional inquiline diversity to heritable trait variation within *S. altissima* plants. We argue that these local communities are embedded with a metacommunity because these local communities are connected by dispersal among patches. Admittedly, we use a loose definition of a metacommunity (Leibold *et al.* 2004; Chase & Bengtsson *in press*), but our approach is not without precedent (e.g. moss patches Gonzalez *et al.* 1998; bromeliads (Srivastava *et al.* 2008), pitcher plants (Kneitel & Miller 2003). Specifically, we ask three inter-related questions: (1) Does host-plant genetic variation influence local and regional diversity of inquilines that occur within galls? (2) Within the inquiline community, do different trophic levels vary in the magnitude and spatial scale of their responses to host-plant genetic variation? (3) What potential host-plant traits might explain genetic variation in local and regional inquiline diversity?

METHODS

This study was conducted at Freels Bend, which is part of the Oak Ridge National Laboratory National Environmental Research Park near Oak Ridge, Tennessee (35°58′N, 84°17′W). The site consists of numerous old fields that are mowed annually to prevent succession. In 2005, we began a common garden experiment consisting of 1-m² plots initially planted with 12 ramets of 21 *S. altissima* genotypes in monoculture (two replicate plots each). Ramets were collected from local *S. altissima* patches growing in fields surrounding the study site, and we identified each ramet as a unique genotype by means of amplified fragment length polymorphisms (AFLPs). All 21 genotypes were found to be approximately equally related, indicating that there were no genotypes that were more or less similar to one another (Crutsinger *et al.* 2006). We propagated clones of each genotype from rhizome cuttings in a greenhouse for several weeks prior to planting in the field. The garden was established in a 15 m × 20 m area surrounded by several old fields in which *S. altissima* makes up to 47% of the aboveground biomass and 43% of total plant cover (Lara Souza unpublished data). Genotypes were arranged randomly within the common garden. Throughout the study, genotypes were allowed to spread clonally within experimental plots. Genotypes varied from ~80–190 ramets at the time of this study. For further details on the study site,



Figure 1 Rosette leaf gall initiated by *Rhopalomyia solidaginis* on a *Solidago altissima* ramet. Galls provide a microhabitat for a diverse community of arthropod species associated with the compacted leaves.

common garden establishment, or AFLP analyses see Crutsinger *et al.* (2006).

In July of 2006, we estimated gall load (no. of galls/no. of stems) in each plot and randomly collected five galls from each plot (21 genotypes \times 2 plots \times 5 galls = 210 galls total) and placed them in individual plastic bags. These galls were taken back to the laboratory on ice and dissected under a dissecting microscope. We counted the number of *R. solidaginis* larval chambers and identified all of the inquilines to trophic level and morphospecies (hereafter species) based on feeding morphology, observations in the field and previous studies (Crawford *et al.* 2007; Crutsinger *et al.* 2006, 2008a). We did not survey parasitism of the midge larvae. Galls were oven-dried at 65 °C for 3 days and weighed to obtain gall mass. Gall mass is tightly correlated with the amount of leaf area ($n = 25$, $r = 0.93$, $P < 0.0001$) available as habitat within a gall (Crutsinger *et al.* 2008c).

To test whether inquiline diversity was related to variation in gall quality produced by different *S. altissima* genotypes, we performed a bioassay using *Spodoptera exigua* (beet army worm) caterpillars. *S. exigua* is a generalist herbivore commonly used in plant quality bioassays (Barrett & Agrawal 2004). We allowed neonate *S. exigua* caterpillars to feed on galled leaves from each of the 21 genotypes. Individual leaves were collected from eight galls per genotype (four randomly chosen galls per replicate plot). A single *S. exigua* caterpillar was then placed on a single leaf in a 90-mm Petri dish lined with moistened filter paper. After 6 days, we weighed each *S. exigua* caterpillar and used final caterpillar mass (g) as a measure of *S. exigua* performance. The prediction is that biomass gained by individual caterpillars is indicative of gall quality as a food resource for herbivores. We recognize that different insect herbivores can perceive plant 'quality' differently, but using *S. exigua* caterpillars provides a good indication of how generalists might respond to the different *S. altissima* genotypes.

To test whether inquiline diversity was related to the diversity of arthropods associated with the external parts of host-plants (i.e. external species pool), we sampled arthropods from all plots within the common garden using a combination of sampling techniques, including vacuum sampling, visual surveys and hand collection. Arthropods were sampled immediately after galls were harvested. External herbivore richness varied by more than 50% and predator richness by 3.5-fold among genotypes (See Crutsinger *et al.* 2008d for detailed results).

Statistical analyses

We used separate one-way ANOVAs to test whether the number of *R. solidaginis* chambers, gall loads (no. of galls/no. of stems), gall size and gall quality varied among *S. altissima* genotypes. We also used separate one-way ANOVAs to test

whether herbivore and predator α , β and γ diversity varied among *S. altissima* genotypes. Local (α) diversity was estimated as the average inquiline richness within individual galls in a common garden plot (Fig. 2). Regional (γ) diversity was measured as the plot-level richness summed across all galls in a plot (Fig. 2). Turnover in diversity across the local patches, or β diversity, was measured as the difference between γ and α diversity (Lande 1996) (Fig. 2). We also used separate one-way ANOVAs to test whether external arthropod herbivore or predator richness (hereafter referred to as Ψ_H or Ψ_P) varied among *S. altissima* genotypes. In all analyses, plot is the unit of replication, and response variables were log-transformed as needed prior to analysis to improve normality. For clarity, we show the untransformed values in all of the figures. We used Pearson correlation coefficients to examine the relationship between gall loads, no. of chambers and gall size, along with the relationships between herbivore and predator α , β , and γ and gall size or Ψ (Table 1).

Finally, to examine whether potential genetically based plant traits might account for variation in α - β - and γ -diversity of inquilines, we first used principal components

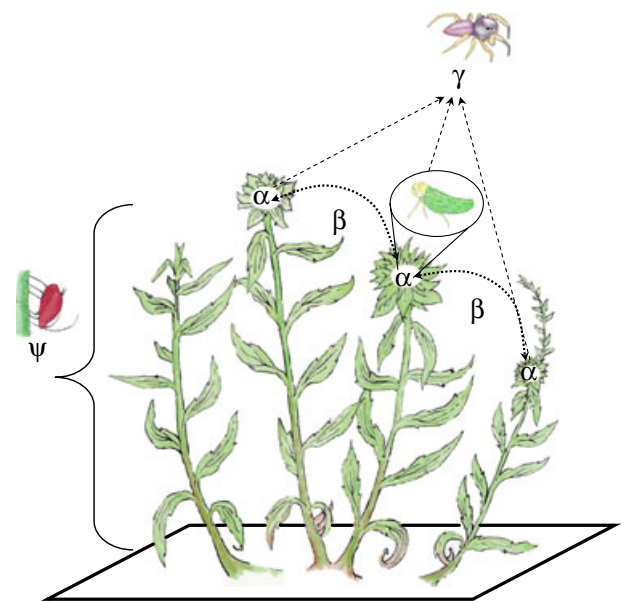


Figure 2 Schematic showing spatial partitioning of inquiline diversity from the local scale (α diversity) within individual rosette galls, to the regional scale (γ diversity) among rosette galls, as well as the turnover of species between the two scales (β diversity). Gall quality and size were significant predictors of inquiline herbivore diversity. Species associated with the ungalled portions of *Solidago altissima* plants (depicted as Ψ and red aphid) also varied among genotypes, but did not affect inquiline diversity. *S. altissima* genetic variation had stronger effects on inquiline herbivores at the local scale (pattern depicted by a leaf hopper), while predators tended to respond more at larger spatial scales (pattern depicted as a jumping spider).

Table 1 Pearson correlation coefficients between inquiline herbivore and predator α , β and γ , as well as herbivore and predator ψ (arthropods occurring outside of galls), gall loads, gall quality, gall size and the number of *Rhopalomyia solidaginis* larval chambers

	Herb α	Herb β	Herb γ	Pred α	Pred β	Pred γ	Herb ψ	Pred ψ	Gall quality	Gall load	Gall size	Chambers
Herb α	1											
Herb β	0.84	1										
Herb γ	0.92	0.99	1									
Pred α	0.04	0.15	0.12	1								
Pred β	-0.02	0.07	0.04	0.84	1							
Pred γ	0	0.09	0.07	0.91	0.99	1						
Herb ψ	0.3	0.27	0.28	0.11	0.03	0.05	1					
Pred ψ	0.14	0	0.05	0.07	0	0.02	0.52	1				
Gall quality	0.44	0.39	0.42	-0.05	-0.07	-0.07	0.25	-0.11	1			
Gall load	0.04	0.14	0.11	0.08	0.14	0.13	0.22	-0.07	-0.07	1		
Gall size	0.33	0.33	0.34	0.22	0.23	0.24	0.06	0	0.04	0.38	1	
Chambers	-0.24	-0.13	-0.17	-0.25	-0.17	-0.2	-0.05	-0.2	-0.07	0.44	0.25	1

Significant correlations ($P < 0.05$) are present in bold.

analysis (PCA) with a minimum eigenvalue of 1 to examine the correlation among host-plant traits (gall load, gall size, gall quality and ψ). We found that the first three axes of the PCA accounted for 74% of the trait variation among genotypes. Next, we used the least correlated traits from the PCA axes in separate forward stepwise multiple regressions (with $P = 0.10$ used as the threshold for variables to be included or excluded in the stepwise regression) to examine which traits best explained α - β - and γ -diversity of herbivores or predators. For inquiline herbivores, we included gall load, gall size, gall quality, ψ_H and predator α -diversity. For inquiline predators, we included gall load, gall size, ψ_P and herbivore α -diversity.

RESULTS AND DISCUSSION

We found that host-plant genetic variation determined midge host preferences, both in terms of larval chamber initiation and the distribution of galls among *S. altissima* genotypes in the common garden. The number of larval chambers initiated per gall varied by over threefold (range: 3–10 chambers) ($F_{20,21} = 2.66$, $P = 0.015$) and gall loads (no. of galls per ramet) varied by more than fourfold (range: 0.13–0.56) ($F_{20,21} = 3.54$, $P = 0.002$) among *S. altissima* genotypes. Gall size also varied by threefold among genotypes (range: 1.65–5.22 g) ($F_{20,21} = 4.03$, $P = 0.001$). Gall size was positively correlated with gall density (Table 1), indicating that larger galls were associated with more susceptible genotypes. Lastly, gall quality as a potential food resource for herbivores (measured as caterpillar performance) varied by over fourfold among genotypes ($F_{20,87} = 2.253$, $P = 0.005$).

These results support previous work in this system indicating that genetic variation within *S. altissima* affects the distribution of galling insects (Maddox & Root 1987;

Abrahamson & Weiss 1997; Crawford *et al.* 2007). Host-plant genetic variation determines both the distribution of galls and affects the size and quality of leaf galls available for subsequent inquiline species colonization. Therefore, much of the habitat heterogeneity in these local patches has an underlying heritable genetic basis. Put another way, host-plant genetics has the potential to alter local and regional inquiline diversity by affecting patch distribution, size and quality. Many other insect herbivores, such as leaf rollers, leaf tiers and leaf miners, alter plant architecture and can potentially provide local habitat patches for inquiline colonization (Marquis & Lill 2006). Other studies have also found a genetic basis underlying plant susceptibility to attack by herbivores that alter plant architecture (Martinsen *et al.* 2000; Hochwender & Fritz 2004; Bangert *et al.* 2008). Our results, and those from other studies (Marquis & Lill 2006), highlight that habitat-modifying herbivores are a useful system in which to investigate how intraspecific plant variation affects the distribution of local habitat patches, as well as the diversity of colonizing species.

Next, we found that genetic variation within *S. altissima* accounted for 63–76% of the variation in inquiline diversity across trophic levels and spatial scales. Herbivore α diversity varied by 7.6-fold, herbivore β diversity varied by 6.7-fold (marginally significant, $P = 0.09$), and herbivore γ diversity varied by 7-fold among *S. altissima* genotypes (Fig. 3, Table 2). One expectation is that effects of genetically based plant traits would become more diluted across trophic levels. However, we found that genetic variation accounted for even more variation in predator diversity than for herbivore diversity (Table 2). Predator α diversity varied by 5.5-fold, β diversity varied by 8.7-fold and γ diversity by ninefold among *S. altissima* genotypes (Fig. 3, Table 2). Herbivore and predator diversity were not correlated at any spatial scale (Table 1). These results reveal that intraspecific

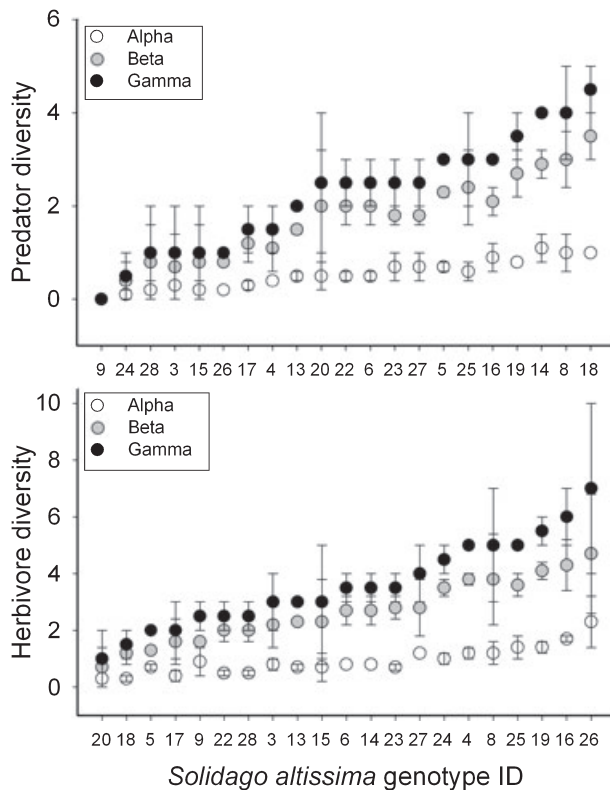


Figure 3 The relationship between arthropod inquilines diversity within leaf rosette galls and genotype identity of *Solidago altissima* plants grown in a common garden. Predators are shown in the top panel and herbivores in the bottom panel. Different coloured circles represent diversity at different spatial scales. α diversity (open circles) is the average species richness within individual galls in common garden plots. γ diversity (black circles) is the average richness summed across galls in plots. β diversity (gray circles) is the different between α and γ . Circles represent the mean (\pm SEM) for each of 21 different genotypes.

Table 2 Separate one-way ANOVA results examining the effect of *Solidago altissima* genotype on inquiline herbivore and predator richness at three scales of observation: α , β and γ (see Fig. 2), as well as herbivore and predator richness on ungalled portions of the plants (referred to as ψ)

	R^2	d.f.	MS	F	P -value
Herbivore α	0.70	20, 21	0.484	2.555	0.019
Herbivore β	0.63	20, 21	2.456	1.798	0.095
Herbivore γ	0.66	20, 21	4.880	2.113	0.048
Herbivore ψ	0.67	20, 21	11.078	2.164	0.043
Predator α	0.69	20, 21	0.198	2.370	0.028
Predator β	0.74	20, 21	1.732	3.094	0.006
Predator γ	0.76	20, 21	3.030	3.350	0.004
Predator ψ	0.81	20, 21	15.328	4.566	0.0005

genetic variation within a host-plant species determines the diversity of associated communities across trophic levels and spatial scales, but that patterns in one trophic level vary independently from the other. Our results differ from Bailey *et al.* (2006) who observed direct correlations between individual *Populus* genotypes, galling herbivore density and avian predation on herbivores.

Of course, the inquilines in this system, or any system, do not respond to host-plant genes; rather they respond to the numerous genetically based traits that vary among *S. altissima* genotypes. Heritable variation in the host-plant quality has been well established in goldenrods (Maddox & Root 1987; Abrahamson & Weiss 1997). For example, our previous work has shown variation in primary productivity, leaf nutrient content, *Spodoptera* caterpillar performance on ungalled leaves, and flower production (Crutsinger *et al.* 2006, 2008a). Trait variation in *S. altissima* plant quality can affect species sorting of inquiline herbivores, both in terms of colonization rates, as well as post-colonization survival. For instance, Craig *et al.* (2000) found that ovipositing females of the stem-galling fly, *Eurosta solidaginis*, preferred *S. altissima* genotypes with more rapid growth rates. *E. solidaginis* offspring survival also varied among genotypes but independently of female oviposition preferences. When we examined the relationships between several plant traits and inquiline herbivore diversity, we found that variation in gall quality and gall size accounted for ~ 25 – 30% of herbivore diversity from local to regional scales (Table 3). Larger galls provide greater habitat area for inquilines to colonize, and our previous work has shown that inquiline diversity is positively related to gall size in old fields neighbouring our common garden (Crawford *et al.* 2007). Herbivores in this system tend to be sedentary after colonization (Root 1996), so herbivores likely respond to genetic variation at the local scale (i.e. individual galls within a common garden plots, as depicted in Fig. 2). Because gall quality and size accounted for only a portion of the variation in herbivore diversity among plant genotypes, we cannot rule out the importance of other traits or that the response of individual herbivore species is idiosyncratic.

Unlike the results for herbivores, none of the plant traits we measured in this study accounted for significant amounts of variation in predator diversity (Table 3). This result is congruent with the fact that herbivore and predator diversity varied independently among plant genotypes. Generally, species at higher trophic levels are larger (Cohen *et al.* 1993), live longer (Brown *et al.* 2004), and tend towards a larger movement scale (Hui & McGeoch 2006). In this system, inquiline predators were predominately jumping spiders (Salticidae) that could readily move among galls in search of prey. Inquiline predators probably respond to gall characteristics at larger spatial scales than do herbivores (i.e. among galls within a common garden plot, as depicted in

	Variable	Parameter	Partial r^2	Model r^2	F -value	P -value
Herbivore α	Gall quality	1.191	0.195	0.296	10.218	0.003
	Gall size	0.146	0.101		5.584	0.023
Herbivore β	Gall quality	2.511	0.153	0.253	7.515	0.01
	Gall size	0.345	0.099		5.174	0.029
Herbivore γ	Gall quality	3.702	0.177	0.284	9.08	0.006
	Gall size	0.491	0.107		5.82	0.021
Predator α	Gall size	0.065	0.047	0.047	1.992	0.166
Predator β	Gall size	0.197	0.055	0.055	2.309	0.137
Predator γ	Gall size	0.262	0.056	0.056	2.377	0.131

Table 3 Results of stepwise multiple regressions examining the effects of *Solidago altissima* traits on inquiline herbivore and predator alpha (α), beta (β) and gamma (γ) diversity

Fig. 2). Our results contradict a recent study showing that area dependence of species increases with trophic level because of trophic dependencies between predators and their prey (Srivastava *et al.* 2008). Instead, we found that inquiline herbivores were related to gall size but predators were not, even though predators are generally more sensitive to area than are prey species (Holt & Hoopes 2005; Ryal & Fahrig 2006). Numerous other heritable traits in goldenrod that we did not measure in this study might account for variation in predator diversity. For example, traits such as how compact individual rosette galls grew or leaf trichome density could affect dispersal rates of inquiline predators. Documenting dispersal patterns of inquilines was beyond the scope of this study and deserves further attention. An important consideration to *S. altissima* genetic effects on predators is that *S. altissima* clones in natural fields are typically much larger than the square-meter plots in the common garden. So, even though inquiline predators may operate at scales larger than herbivores, the dispersal distances of predators could still be limited entirely within individual *S. altissima* clones.

We considered the effect of the external arthropod species pool (referred to as ψ) because arthropod inquilines in this system partially overlap with the arthropods that occur on the ungallo portion of a host-plant ramet (Crawford *et al.* 2007) and because a growing body of literature has demonstrated that the structure of local communities is often simply a function of the larger, more regional species pool (Ricklefs 1987; Gering & Crist 2002). There is substantial evidence that genetic variation within *S. altissima* determines richness and abundance of ψ (Table 2) (Maddox & Root 1987; Crutsinger *et al.* 2006, 2008a), which may partially explain the response of the inquiline community if ψ and gall inquiline diversity covary. However, ψ was not related to either inquiline herbivore or predator diversity in any of our regression models. Moreover, herbivore ψ diversity and predator ψ diversity were correlated, while diversity of herbivore and predator inquilines were not. The results indicate that gall communities respond to host-plant genetic variation independent of the arthropods occurring on ungallo portions of the plant.

CONCLUSIONS

Our results offer intriguing insights for community genetics. For instance, a major goal of community genetics is to predict community-level responses to genetic variation in natural populations. Shuster *et al.* (2006) demonstrated the existence of plant genetic basis for arthropod community organization and described how host-plant genetics can indirectly affect the fitness of associated species. In our system, inquiline herbivores and predators exhibit independent responses to genetic variation in different host-plant traits, such as gall size and quality. If different species within the community respond to different genetically based traits and at different scales, then incorporating the spatially explicit framework provided by metacommunity theory could greatly advance community genetics predictions. In addition, though our study was conducted over an ecological time scale (i.e. a single growing season), our results have evolutionary implications (Johnson & Stinchcombe 2007; Whitham *et al.* 2006). Selection can act on key host-plant traits, such as the size of galls produced by *S. altissima* plants or their susceptibility to galling (Abrahamson & Weiss 1997; Craig *et al.* 2007; Wise & Abrahamson 2008). In turn, selection on these traits could alter local and regional dynamics and selection on dependent community members (Thompson 2005; Urban & Skelly 2006; Whitham *et al.* 2006). Since inquiline herbivores and predators respond independently to host-plant genetic variation, then the consequences of evolution within the *S. altissima* population could vary between trophic levels.

Though gall inquilines fall under a loose definition of a metacommunity (Leibold *et al.* 2004; Chase & Bengtsson in press), our work also has implications for the development of metacommunity theory. In metacommunity studies, spatial dynamics and ecological patterns have been examined primarily for competitively structured communities (e.g., see Mouquet *et al.* 2005) or for single predator-prey interactions (e.g., Amarasekare 2006). However, incorporation of trophic dynamics into understanding spatial patterns of species diversity has not yet been thoroughly explored (but see Holt 2002; Fukami 2004; Steiner & Leibold 2004; Amarasekare

2006). Predators generally have lower abundances than their prey (Spencer 2000) due to inefficient energy transfer among trophic levels. This lower abundance also results in both greater susceptibility to local extinctions due to small population sizes and fewer dispersers colonizing open patches (Shulman & Chase 2007). Thus at larger scales, predator species are likely to be included due to increased sampling (Holt *et al.* 1999; Hoyle 2004), whereas prey species saturate at much smaller scales. In our study genetically-based habitat heterogeneity appeared to be more strongly related to predator β and γ diversity compared to herbivores, supporting larger scale saturation for higher trophic levels. Finally, species sorting effects of habitat heterogeneity may be strongest at different spatial scales for differing trophic levels, affecting our ability to make universal claims about how patch heterogeneity affects diversity. Future work linking genetically based host-plant traits and trophic dynamics in metacommunities could help uncover the mechanisms by which diversity varies, and evolves, within and among local communities.

ACKNOWLEDGEMENTS

We thank R. Shulman, M. Urban, T. Fukami, and three anonymous referees for helpful comments on the manuscript. M Habenicht provided field and laboratory assistance. GMC was financially supported by National Science Foundation Graduate Research Fellowship, an Environmental Protection Agency Science To Achieve Results Fellowship, and the Department of Ecology and Evolutionary Biology at the University of Tennessee.

REFERENCES

- Abrahamson, W.G. & Weiss, A.E. (1997). *Evolutionary Ecology Across Three Trophic Levels*. Princeton University Press, Princeton.
- Amarasekare, P. (2006). Productivity, dispersal and the coexistence of intraguild predators and prey. *J. Theor. Biol.*, 243, 121–133.
- Bailey, J.K., Schweitzer, J.A., Rehill, B.J., Lindroth, R.L., Martinsen, G.D. & Whitham, T.G. (2004). Beavers as molecular geneticists: A genetic basis to the foraging of an ecosystem engineer. *Ecology*, 85, 603–608.
- Bailey, J.K., Wooley, S.C., Lindroth, R.L. & Whitham, T.G. (2006). Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecol. Lett.*, 9, 78–85.
- Bangert, R.K., Lonsdorf, E.V., Wimp, G.M., Shuster, S.M., Fischer, D., Schweitzer, J.A. *et al.* (2008). Genetic structure of a foundation species: scaling community phenotypes from the individual to the region. *Heredity*, 100, 121–131.
- Barrett, R.D.H. & Agrawal, A.A. (2004). Interactive effects of genotype, environment and ontogeny on resistance of cucumber (*Cucumis sativus*) to the generalist herbivore, *Spodoptera exigua*. *J. Chem. Ecol.*, 30, 37–51.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.
- Cadotte, M.W. & Fukami, T. (2005). Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. *Ecol. Lett.*, 8, 548–557.
- Chase, J. & Bengtsson, J. (in press). Increasing spatio-temporal scales: metacommunity ecology. In: *Community Ecology* (eds Verhoef, H.A. & Morin, P.J.). Oxford University Press, Oxford, in press.
- Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldana, J. (1993). Body sizes of animal predators and animal prey in food webs. *J. Anim. Ecol.*, 62, 67–78.
- Craig, T.P., Itami, J.K., Schantz, C., Abrahamson, W.G., Horner, J.D. & Craig, J.V. (2000). The influence of host plant variation and intraspecific competition on oviposition preference in the host races of *Eurosta solidaginis*. *Ecol. Entomol.*, 25, 7–18.
- Craig, T.P., Itami, J.K. & Horner, J.D. (2007). Geographic variation in the evolution and coevolution of a tritrophic interaction. *Evolution*, 61, 1137–1152.
- Crawford, K.M., Crutsinger, G.M. & Sanders, N.J. (2007). Host-plant genotypic diversity mediates the distribution of an ecosystem engineer. *Ecology*, 88, 2114–2120.
- Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C. & Sanders, N.J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, 313, 966–968.
- Crutsinger, G.M., Collins, M.D., Fordyce, J.A. & Sanders, N.J. (2008a). Temporal dynamics in non-additive responses of arthropods to host-plant genotypic diversity. *Oikos*, 117, 255–264.
- Crutsinger, G.M., Souza, L. & Sanders, N.J. (2008b). Intraspecific diversity and dominant genotypes resist plant invasions. *Ecol. Lett.*, 11, 16–23.
- Crutsinger, G.M., Habenicht, M.N., Classen, A.T., Schweitzer, J.A. & Sanders, N.J. (2008c). Galling by *Rhopalomyia solidaginis* alters *Solidago altissima* architecture and litter nutrient dynamics in an old-field ecosystem. *Plant Soil*, 303, 95–103.
- Crutsinger, G.M., Reynolds, N., Classen, A.T. & Sanders, N.J. (2008d). Disparate effects of genotypic diversity on foliage versus litter-based arthropods. *Oecologia*, 158, 65–75.
- Fukami, T. (2004). Community assembly along a species pool gradient: implications for multiple-scale patterns of species diversity. *Popul. Ecol.*, 46, 137–147.
- Gering, J.C. & Crist, T.O. (2002). The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. *Ecol. Lett.*, 5, 433–444.
- Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M. & Evans-Freke, I. (1998). Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science*, 281, 2045–2047.
- Hochwender, C.G. & Fritz, R.S. (2004). Plant genetic differences influence herbivore community structure: evidence from a hybrid willow system. *Oecologia*, 138, 547–557.
- Holt, R.D. (2002). Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecol. Res.*, 17, 261–273.
- Holt, R.D. & Hoopes, M.F. (2005). Food web dynamics in a metacommunity context: modules and beyond. In: *Metacommunities: Spatial Dynamics and Ecological Communities* (eds Holyoak, M., Leibold, M. & Holt, R.). University of Chicago Press, London, pp. 68–93.
- Holt, R.D., Lawton, J.H., Polis, G.A. & Martinez, N.D. (1999). Trophic rank and the species-area relationship. *Ecology*, 80, 1495–1504.

- Holyoak, M., Leibold, M.A. & Holt, R.D. (2005). *Metacommunities: Spatial Dynamics and Ecological Communities*. University of Chicago Press, Chicago, IL.
- Hoyle, M. (2004). Causes of the species-area relationship by trophic level in a field-based microecosystem. *Proc. R. Soc. Lond. B Biol. Sci.*, 271, 1159–1164.
- Hui, C. & McGeoch, M.A. (2006). Evolution of body size, range size, and food composition in a predator-prey metapopulation. *Ecol. Complexity*, 3, 148–159.
- Johnson, M.T.J. & Agrawal, A.A. (2005). Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology*, 86, 874–885.
- Johnson, M.T.J. & Stinchcombe, J.R. (2007). An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.*, 22, 250–257.
- Johnson, M.T.J., Lajeunesse, M.J. & Agrawal, A.A. (2006). Additive & interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol. Lett.*, 9, 24–34.
- Kneitel, J.M. & Miller, T.E. (2003). Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *Am. Nat.*, 162, 165–171.
- Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, 76, 5–13.
- Lankau, R.A. & Strauss, S.Y. (2007). Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science*, 317, 1561–1563.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F. *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.*, 7, 601–613.
- Maddox, G.D. & Root, R.B. (1987). Resistance to 16 diverse species of herbivorous insects within a population of doldenrod, *Solidago altissima* – genetic variation and heritability. *Oecologia*, 72, 8–14.
- Maddox, G.D., Cook, R.E., Wimberger, P.H. & Gardescu, S. (1989). Clone structure in four *Solidago altissima* (Asteraceae) populations: rhizome connections within genotypes. *Am. J. Bot.*, 76, 318–326.
- Marquis, R.J. & Lill, J.T. (2007). Effects of herbivores as physical ecosystem engineers on plant-based trophic interaction webs. In: Ohgushi, T., Craig, T. & Price, P.W. (eds.), *Ecological Communities: Plant Mediation in Indirect Interaction Webs*, Cambridge University Press, pp. 246–274.
- Martinsen, G.D., Floate, K.D., Waltz, A.M., Wimp, G.M. & Whitham, T.G. (2000). Positive interactions between leafrollers and other arthropods enhance biodiversity on hybrid cottonwoods. *Oecologia*, 123, 82–89.
- Mouquet, N., Hoopes, M.F. & Amarasekare, P. (2005). The world is patchy and heterogeneous!: Trade-off and source-sink dynamics in competitive metacommunities. In: *Metacommunities: Spatial dynamics and Ecological Communities* (eds Holyoak, M., Leibold, M.A. & Holt, R.D.). University of Chicago Press, Chicago, IL, pp. 237–262.
- Raman, A. & Abrahamson, W.G. (1995). Morphometric relationships and energy allocation in the apical rosette galls of *Solidago altissima* (Asteraceae) induced by *Rhopalomyia solidaginis* (Diptera, Cecidomyiidae). *Environ. Entomol.*, 24, 635–639.
- Ricklefs, R.E. (1987). Community diversity: relative roles of local and regional processes. *Science*, 235, 167–171.
- Root, R.B. (1996). Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. *Ecology*, 77, 1074–1087.
- Ryal, K.L. & Fahrig, L. (2006). Response of predators to loss and fragmentation of prey habitat: a review of theory. *Ecology*, 87, 1086–1093.
- Semple, J.C. & Cook, R.E. (2006). *Solidago*. In: *Flora North America* Editorial Committee, eds. *Flora of North America*. Volume 20. Asteraceae, Part 2. Astereae and Senecioneae. Oxford University Press, Oxford, 107–166.
- Schweitzer, J.A., Bailey, J.K., Bangert, R.K., Hart, S.C. & Whitham, T.G. (2007). The role of plant genetic variation in determining above- and belowground microbial communities. In M.J. Bailey, A.K. Lilley, T.M. Timms-Wilson & P.T.N. Spencer-Phillips. *Microbial Ecology of aerial plant surfaces*. CABI Publishing, pp. 107–119.
- Shulman, R.S. & Chase, J.M. (2007). Increasing isolation reduces predator : prey species richness ratios in aquatic food webs. *Oikos*, 116, 1581–1587.
- Shuster, S.M., Lonsdorf, E.V., Wimp, G.M., Bailey, J.K. & Whitham, T.G. (2006). Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution*, 60, 991–1003.
- Spencer, M. (2000). Are predators rare? *Oikos*, 89, 115–122.
- Srivastava, D.S. & Lawton, J.H. (1998). Why more productive sites have more species: an experimental test of theory using tree-hole communities. *Am. Nat.*, 152, 510–529.
- Srivastava, D.S., Trzcinski, M.K., Richardson, B.A. & Gilbert, B. (2008). Why are predators more sensitive to habitat size than their prey? Insights from bromeliad-insect food webs. *Am. Nat.*, 172, 761–771.
- Steiner, C.F. & Leibold, M.A. (2004). Cyclic assembly trajectories and scale-dependent productivity-diversity relationships. *Ecology*, 85, 107–113.
- Thompson, J.N. (2005). *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago.
- Urban, M.C. & Skelly, D.K. (2006). Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology*, 87, 1616–1626.
- Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M. *et al.* (2003). Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology*, 84, 559–573.
- Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., Leroy, C.J. *et al.* (2006). A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Gen.*, 7, 510–523.
- Wimp, G.M., Martinsen, G.D., Floate, K.D., Bangert, R.K. & Whitham, T.G. (2005). Plant genetic determinants of arthropod community structure and diversity. *Evolution*, 59, 61–69.
- Wise, M.J. & Abrahamson, W.G. (2008). Ducking as a means of resistance to herbivory in tall goldenrod, *Solidago altissima*. *Ecology*, 89, 3275–3281.
- Wise, M.J., Abrahamson, W.G. & Landis, K. (2006). Edaphic environment, gall midges, and goldenrod clonal expansion in a mid-successional old-field. *Acta. Oecologia. Int. J. Ecol.*, 30, 365–373.

Editor, Marcel Holyoak

Manuscript received 11 December 2008

First decision made 18 January 2009

Manuscript accepted 26 January 2009