



Sizing up community genetics: it's a matter of scale

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The burgeoning field of community genetics posits that genetic variation within species affects the structure and dynamics of associated communities and ecosystems. While many experiments support this hypothesis, we argue that the most commonly employed experimental design suffers from a fundamental flaw that might result in overestimating the importance of genetic variation. Specifically, most studies collect genotypes from a wide area but perform experiments in small common gardens. Since environmental and genetic variation typically increase with spatial scale, this mismatch in scale is predicted to artificially inflate estimates of the ecological importance of genetic effects. Furthermore, most existing studies have used study systems with particular ecological characteristics, which might further inflate the inferred importance of genetic variation. To critically examine this potential problem, we reanalyze previous studies in community genetics and show how current methods lead to biased conclusions. More specifically, while a growing body of literature shows that intraspecific genetic variation can have an effect, it does not accurately estimate its effect size. As a remedy to this bias, we propose an experimental design that can accurately quantify the importance of genetic and environmental variation in affecting communities and ecosystems.

The recent emergence of community genetics emphasizes that genetic variation in one species may have far-reaching community and ecosystem-level effects (Antonovics 1992, Whitham et al. 2003, 2008, Johnson and Stinchcombe 2007, Keith et al. 2010). Indeed, the last two decades have seen a flurry of studies that examine how genetic variation in one species affects surrounding community and ecosystem processes (Antonovics 1992, Whitham et al. 2006). These studies reveal effects of intraspecific genetic diversity on an astonishing array of responses, including primary productivity (Hughes and Stachowicz 2004, Crutsinger et al. 2006, Harmon et al. 2009, Bassar et al. 2010), community structure (Crutsinger et al. 2006, Johnson et al. 2006, Harmon et al. 2009), species coexistence (Lankau and Strauss 2007), food web structure (Bukovinszky et al. 2008), nutrient fluxes (Bassar et al. 2010), and community and ecosystem stability (Hughes and Stachowicz 2004, Reusch et al. 2005, Keith et al. 2010, Schindler et al. 2010). Such studies have thereby opened a new frontier in biology that examines the interplay between ecological and evolutionary patterns and processes (Whitham et al. 2006, Johnson and Stinchcombe 2007, Rowntree et al. 2011).

While the promising first results have allowed the field of community genetics to take off with great speed (reviewed by Whitham et al. 2006, Bailey et al. 2009), the question of whether a community genetics perspective is really necessary or even informative for studies and systems more broadly is an issue under current debate (Morin 2003, Ricklefs 2003, Hersch-Green et al. 2011, Schoener 2011).

On one hand, recent reports suggest that genetic variation may have consistently large effects on communities and ecosystems (Whitham et al. 2006, Bailey et al. 2009). For example, in a study on cottonwood trees, Schweitzer et al. (2004) found that 55–63% of the variation in the net mineralization rate of nitrogen in poplar leaf litter was explained by condensed tannin concentration, which itself is highly heritable in this study system. Moreover, genotypic variation among cottonwood trees explained 50–63% of the variation in the associated herbivore community (Shuster et al. 2006). Likewise, Crutsinger et al. (2006) detected a strong impact of the genetic diversity of goldenrod on both primary production and arthropod species richness (explaining 36% and 26% of the variation, respectively).

On the other hand, Hersch-Green and colleagues (2011) argue that current data are still insufficient to determine the ultimate need for a community genetics perspective – simply because we know too little about how the relative importance of intraspecific genetic variation compares to that of other ecological factors (e.g. environmental variation; see also Johnson and Stinchcombe 2007, Hughes et al. 2008). To achieve progress, future studies need to quantify the relative contribution of genotype to that of other ecological factors in shaping community structure and ecosystem processes. In doing so, each source of variation should be compared using multifactor experiments where factors are manipulated to exhibit the range of variation observed in nature.

In this critical review, we highlight methodological flaws common to most studies published in community genetics,

including some of our own work. Although these problems apply to all types of study systems, we focus here on plant–insect interactions to illustrate our argument as most studies have focused on these organisms. First, we examine the fundamental relationship between spatial scale and measures of variance in ecological studies. Second, we pinpoint the spatial scales at which genotypes and environments have been sampled in studies of community genetics, and point to a mismatch in the scale from which genotypes (of any organism) are collected and the scale of the experimental design. Third, we use quantitative analyses to explore how discrepancies in the scale of sampling genotype and the environment may affect resultant estimates of the balance between the two. We also point to additional features of published studies that may affect the perceived importance of genotype and the environment: the disproportionate use of hybrid and clonal plant species and the dependence of the results on the insect guild studied. As a result of extant biases and our analyses of the existing literature, we argue that the large genotypic effects reported from current experimental work likely artificially inflate the ecological and ecosystem-level importance of genetic variation. As a remedy, we propose a basic design that can be employed in future studies.

Foundations of ecological and community genetics

Community genetics builds on the foundations of ecological genetics by merging three disciplines – genetics, evolutionary biology and community ecology (Antonovics 1976, 1992, Whitham et al. 2006, Johnson and Stinchcombe 2007, Wade 2007). Understanding the ecological and ecosystem-level consequences of genetic variation and evolution relies on a solid understanding of the processes and patterns underlying each of these disciplines, and how they intersect with one another.

The unification of genetics and evolution was championed after decades of theoretical and empirical research that resulted in the modern synthesis of evolutionary biology (Huxley 1945, Provine 1971, Mayr and Provine 1980). This synthesis recognizes populations as the fundamental evolutionary unit and points to five principle mechanisms responsible for the evolution of populations: mutation, natural selection, genetic drift, dispersal (gene flow) and non-random mating (Wright 1968). It was Darwin (1859) who recognized the importance of genetic variation as the raw material for all evolutionary change. Since the publication of ‘The origin of species’, literally hundreds of studies have quantified the amount of genetic variation underlying phenotypic traits within plant (Geber and Griffen 2003) and animal populations (Mousseau and Roff 1987), and more recently the molecular basis for this variation (Mackay et al. 2009). These studies show that most populations contain substantial heritable genetic variation for multiple functional traits (Mousseau and Roff 1987, Geber and Griffen 2003). At the same time, we have come to recognize that the origin, maintenance and amount of genetic variation within populations is shaped by the interaction of mutation, selection (e.g. mutation–selection balance, frequency-dependent selection, genotype-by-environment interactions; Christiansen 1975, Allen and Clarke 1984, Gillespie and Turelli 1989, Hedrick

2000, Zhang and Hill 2005), as well as by the past and current size of populations.

The community and ecosystem-level effects of genetic variation are mediated by intraspecific variation of phenotypic traits. The experiments of early ecological geneticists (Wright 1920, Turesson 1922, Clausen et al. 1940) showed that intraspecific variation in these traits is influenced by an individual’s genotype (G), the environment in which it lives (E ; representing both the abiotic and biotic environment), and the interaction between genotype and the environment ($G \times E$). The consequence of this for community genetics research is that to study the extended consequences of genetic variation (i.e. community genetics), one must study and control for all three of these sources of variation. The relative roles of genotype and the environment will ultimately depend on the particular traits, the characteristics of the population examined, and especially the spatial scale at which populations and environments are studied. While the importance of spatial scale has been considered at length, especially in studies examining the role of genotype \times environment-interactions in maintaining genetic variation (Stratton 1994, Juenger and Bergelson 2002), these issues have received much less attention in community genetics research (Johnson and Agrawal 2005, Whitham et al. 2006, Bangert et al. 2008).

The relevance of spatial scale and of system-specific attributes

Both intraspecific genetic variation (V_G) and environmental variation (V_E) are expected to increase with spatial scale (Fig. 1, Bell 1992). As a consequence, conspecific individuals collected across a wide area are expected to show more genetic variation than a collection of conspecific individuals from a single local population. Likewise, locations from a small area probably show greater similarity in their environmental conditions than locations sampled across a large area (Fig. 1, note that the ‘environment’ may represent both biotic and abiotic variation).

Given these fundamental patterns, a meaningful comparison between the relative effects of V_G and V_E on phenotypic variation, as well as their extended effects on communities and ecosystems, can only be built on samples collected at comparable spatial scales (Fig. 1). By contrast, when genotypes are collected from a vast geographic area, whilst the experiment is conducted in a single common garden/environment, we will likely overestimate the importance of genetic variation compared to biotic and abiotic environmental effects.

If V_G and V_E vary with spatial scale as depicted in Fig. 1, then the overwhelming majority of recent studies in community genetics are built on biased representations of V_G and V_E . Picking an example from our own basket, Johnson and Agrawal (2005) collected genotypes from populations separated by as much as 57 km, which they subsequently planted into 15×13 m common gardens separated by a maximum of 2.9 km. Hence, while they reported a similar amount of variation explained by host plant genotype and the environment within a single common garden, the comparison was partially biased by the mismatch in selected spatial scales: genotypic variation could be exaggerated by collecting genotypes from a wide geographical area, whereas

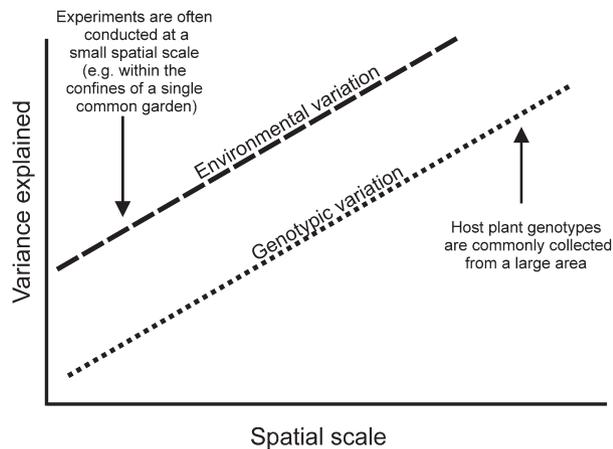


Figure 1. Why spatial scale matters when establishing the relative importance of host plant genotype in structuring associated insect communities. In general, both genotypic variance and environmental variance increase with spatial scale (Bell 1992) – though not necessarily at the same rate or linearly. In the current example, the rate of increase is similar for genotype and environment (parallel lines), and the variation explained by host plant genotype (V_G) is smaller than that of the environment (V_E) at all spatial scales. Importantly, the ratio between V_G and V_E becomes distorted when host plant genotypes are collected from a wide area (as shown by the right arrow) and planted within a small area (left arrow). Hence, while in the current example the environmental variation is in reality larger than the genetic variation, an artificial mismatch of spatial scales in the experimental design can lead to a higher fraction of the variation being attributed to host plant genotype.

environmental variation within the common garden was kept to a minimum.

Mismatch in the scale of sampling is not the only potential pitfall encountered when designing an adequate study. To compare the relative roles of V_G and V_E in affecting phenotypic variation, the samples taken should adequately represent the population of genotypes and the population of environments. Only by sampling these reference populations randomly across the spatial scale selected will we gain unbiased estimates of the variation present (Underwood 1997). While intuitively straight-forward, this logic has frequently been violated. For example, several studies have selected the most divergent genotypes or environments for study (Fritz and Price 1988, Johnson and Agrawal 2005, Kotowska et al. 2010) – but the level of variation uncovered may then be more representative of the biases underlying the experimental design, as opposed to an unbiased characterization of the environmental and genetic variance inherent to a particular system.

To assess whether a community genetics approach is needed in biology, ideally studies should be done on taxa that represent wide phylogenetic and life-history diversity, and within taxa genotypes and environments should be selected in a random fashion. By contrast, if study systems are chosen on the basis of highest probability of finding positive proof for the effect postulated, then we will learn little about the distribution and strength of said effect in nature. Hence, to achieve a general understanding of the prevalence of phenomena in nature, we need to reduce bias and thereby test target taxa with different attributes, and then relate the incidence or strength of the phenomenon to these

characteristics. Here, past studies on community genetics seem disproportionately focused on taxa with specific ecological features. For example, Karban (1992) noted that, in the context of plant-insect interactions, many studies focused on clonally reproducing plants; this observation is still true today. Likewise, many experiments have been centred on hybrids (Fritz et al. 1994, Dungey et al. 2000, Whitham et al. 2003, Tovar-Sánchez and Oyama 2006) and functionally asexual plant species (Vellend et al. 2010, Johnson 2011), likely due to the high amount of genetic variation often associated with these systems (Fritz et al. 1999, Whitham et al. 1999, Johnson 2011). This focus on such plant species may increase the perceived impact of host plant genotype on the associated community. Among herbivore communities, a disproportionate focus on particular insect species and/or guilds may also increase the impact of host plant genotype: some insect species (e.g. gall-inducing arthropods; Stiling 1994) spend their entire development exposed to host plant tissues, a life style which may accentuate their response to host plant genotype (Mopper 1996, Stiling and Rossi 1998).

A meta-analysis of biases in the current literature

Data extraction

To examine whether the most common experimental designs might have biased our interpretations of the ecological importance of genotypic effects, we conducted a meta-analysis of community genetics studies. To this end, we first searched the Web of Science in December 2010 for relevant studies using the terms ‘community genetics’, ‘common garden’, ‘intraspecific genetic variation’ and ‘plant genotype’ in all possible combinations. We then identified papers that experimentally assessed the impact of host plant genetic variation on the abundance of a single herbivore species or the entire herbivore community. When a study was selected, we further checked the list of references within this paper for additional studies. Finally, we searched for papers citing two key papers on this topic: Whitham et al. (2003) and Johnson and Agrawal (2005). This search resulted in a total of fifteen papers that could be included in the analyses.

From the studies compiled, we extracted estimates of the variance associated with genotype and environment for the abundance of individual species and of community descriptors, including species richness, species diversity, and community composition. As observational studies may confound genetic, environmental, and spatial factors (and their interactions), we excluded them from analyses. Likewise, studies presenting no statistics on the amount of variation explained by the environment (either replicate common gardens, or blocks within a common garden) were necessarily excluded. For this reason we were unfortunately unable to include much of the data from the important work in the cottonwood–arthropod system (reviewed by Whitham et al. 2006).

To quantify the relative amount of variation explained by host plant genotype and the environment, the most appropriate response variables are V_G (variance explained by host genotype), V_E (variance explained by the environment), and V_G/V_E (relative variation explained by genotype and the environment). However, as many studies did not report full

ANOVA tables needed to calculate actual variance estimates, we used the ratio R_G^2/R_E^2 as an alternative measure of 'relative variation explained'. Moreover, this solution offered the possibility to include those studies that only reported F- or p-values and associated degrees of freedom, as these statistics suffice for the calculation of R_G^2/R_E^2 . We also recorded the sample size of a study because sample size may reflect the statistical accuracy of variance estimates (i.e. precision). We assessed this possibility by conducting a separate set of analyses weighting each study by its number of observations.

To characterize the spatial scale from which host plant genotypes had been collected, and the spatial scale of the common garden experiment, we first compared multiple measures to quantify the spatial scale among genotype collection and common garden sites. Where available (e.g. where the publication included a map), we first extracted multiple distance metrics (i.e. mean distance, median distance, and maximum distance; measured in meters). We then used Pearson correlations to examine the correlation structure among individual metrics. As distance metrics were highly correlated (e.g. $r > 0.98$ for maximum versus median and mean distance among sites for both plant genotypes and environments; $n = 9$ and 10 , respectively), we chose the maximum distance between host plant genotypes (and environments) for the final analyses, as this metric was most frequently reported in the literature. If no exact distances were reported, we estimated the maximum distance based on the description in an article's text or by direct correspondence with the authors. Spatial mismatch was quantified as $\Delta_{\text{scale}} = \log_{10}(\text{maximum distance in meters between host plant genotypes used in the study}) - \log_{10}(\text{maximum distance in meters between blocks or common gardens in the experiment})$.

For all studies included in the final data set, we recorded several additional variables which have been suggested to affect the importance of host plant genotype, and which were reported frequently enough to allow meaningful comparisons. More specifically, we recorded whether the host plant genotypes used in the experiment were hybrids and whether the host plants naturally formed clonal patches. We also recorded the feeding mode of each herbivore species (exophagous [feeding on external parts of tissue] or endophagous [feeding on internal parts of tissue]).

For two specific case studies where we had access to the complete original data (Johnson and Agrawal 2007, Tack et al. 2010), we conducted additional detailed analyses aimed at quantifying how the scales at which host plants were collected and the experiment conducted influence our perception of V_G (variance explained by host genotype) and V_T (the total variance observed in the material). For both studies, we re-analyzed the data at matching versus non-matching spatial scales. In both cases, the non-matching scale was a single common garden, in which case host plant genotypes were collected from the wide surrounding area (a landscape of several km^2) but placed in a single common garden (less than 20 meters across). For the case of matching spatial scales, we analyzed the data across multiple common gardens replicated within the very same landscape from which the host plant genotypes were collected. For the re-analyses, we used mixed effects models (SAS 9.2). For the small scale, we constructed separate models for each site, including the

variables 'block' and 'genotype'. At the large scale, we constructed a single model including the variables 'location', 'genotype', the interaction 'genotype \times location', and 'block' (as nested within 'location'). To assess whether a systematic bias is associated with a mismatch of scales, we then compared the relative proportion of variation explained by genotype (V_G/V_T) when studied at matched and mis-matched scales.

Results

Spatial scales varied widely, ranging from a single field (Maddox and Root 1987) to an entire state or prefecture (Quiring and Butterworth 1994, Ito and Ozaki 2005). Likewise, spatial mismatch differed several orders of magnitude across studies. For example, Maddox and Root (1987) collected host plant genotypes from a single old field, and consequently planted them within a single common garden. In contrast, Ito and Ozaki (2005) collected host plant genotypes across the island of Hokkaido (ca 84 000 km^2), but then studied them within a single common garden.

Across fifteen studies, the relative amount of variation in species-specific abundances explained by host plant genotype was positively correlated with the spatial mismatch between provenances and the environment (Fig. 2; unweighted regression: $R^2 = 0.29$, $F_{1,108} = 44.31$ and $p < 0.001$; regression weighted by sample size: $R^2 = 0.47$, $F_{1,108} = 94.27$ and $p < 0.001$). In other words, the amount of variation in ecological and ecosystem-level characteristics explained by variation among plant genotypes was largest when genotypes were collected over a large spatial scale but then studied at a small spatial scale (e.g. within a single common garden). Studies of community descriptors (i.e. species richness, total abundance and community composition) were surprisingly few and therefore could not be included in formal meta-analysis.

In our re-analysis of the two case studies (Johnson and Agrawal 2007, Tack et al. 2010), the proportion of total variance explained by genotype (V_G/V_T) differed substantially between the comparison among matching versus non-matching spatial scales: when environmental variation is artificially confined to that encountered within a single common garden, the variance explained by host plant genotype is clearly overestimated (Fig. 3). In other words, when genotypes are collected from a large area and planted within a small area (e.g. the confines of a single common garden), we overestimate the role of genotypic variation in structuring the insect community in nature, since we compare the overall genetic variation present within a large area with the limited environmental variation occurring in the common garden experiment (Fig. 1).

We further detected a significant effect of feeding mode: endophagous insects responded more strongly to host plant genotype than did free-feeding insects ($F_{1,98} = 9.32$; $p = 0.0029$), possibly due to their more intimate association with their host plant (Stiling 1994, Mopper 1996, 2005). Support from this notion also comes from the direct comparison by Wimp et al. (2007), who showed that endophagous insects were driving strong host plant genotypic effects in the cottonwood–arthropod system. Moreover, more variation was explained by host plant genotype in study systems focusing

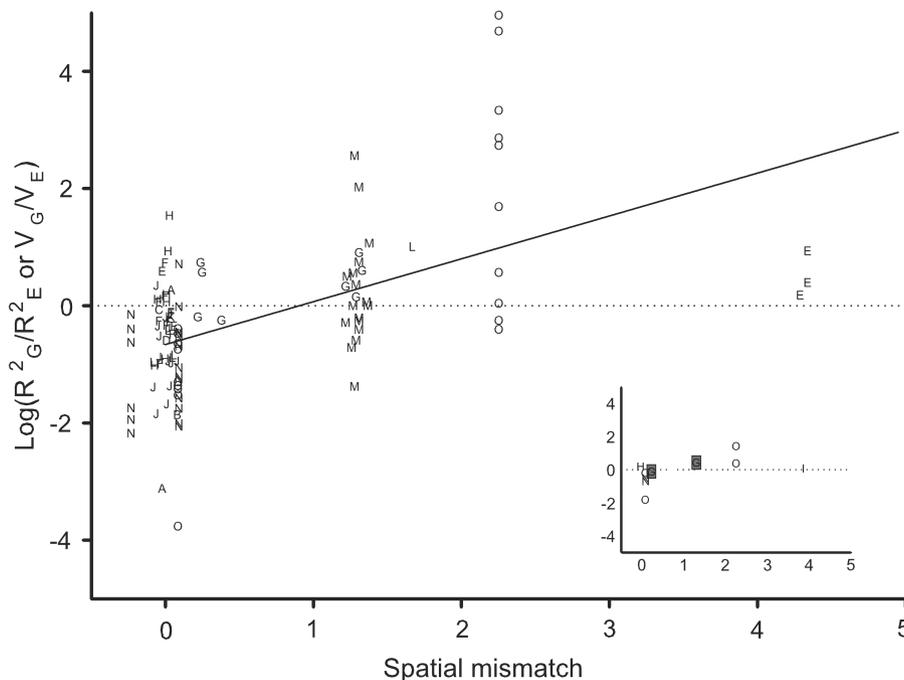


Figure 2. The relative variation explained by host plant genotype versus environment (log-transformed ratio R_G^2/R_E^2 or V_G/V_E) as a function of the spatial mismatch ($\Delta_{\text{scale}} = \log_{10}(\text{maximum distance in meters between host plant genotypes used in the study}) - \log_{10}(\text{maximum distance in meters between blocks or common gardens in the experiment})$). Letters refer to studies included in the reference list: A = Stiling 1994, B = Quiring and Butterworth 1994, C = Rossi and Stiling 1998, D = Stiling and Bowdish 2000, E = Ylioja et al. 2000, F = Maddox and Root 1987, G = Fritz and Price 1988, H = Graham et al. 2001, I = Ito and Ozaki 2005, J = Stiling and Rossi 1995, K = Stiling and Rossi 1996, L = Kittelson 2004, M = Fritz et al. 1998, N = Tack et al. 2010, and O = Johnson and Agrawal 2005; specific data points as described in Fig. 3). The inset shows data points representing species richness, species diversity and community composition (the latter with grey background). The dotted horizontal line illustrates a scenario where host plant genotype and environment explain a similar amount of variation. The solid regression line was fitted using the data points on species abundance. Data points are slightly jittered to decrease overlap.

on interspecific plant hybrids than on single host plant species ($F_{1,98} = 14.29$, $p = 0.003$). This result can likely be linked to the large amount of genetic variation in hybrids (Fritz et al. 1999, Whitham et al. 1999). However, we note that variation within parental species may explain more variation in the associated arthropod community than variation among cross types (as shown for the cottonwood–arthropod system; Shuster et al. 2006). No differences were found between clone-forming and obligate sexually reproducing plant species ($F_{1,98} = 1.12$, $p = 0.29$). Taken together, these results suggest that the specifics of the study system will likely affect the patterns found in terms of V_G , V_E and V_G/V_E . Nonetheless, the studies to date are few, and more detailed analyses will therefore have to await new data to come.

Perspectives

Overall, our quantitative review of the literature suggests that there is indeed a frequent mismatch in the spatial scale at which genetic and environmental effects are examined within community genetics studies, and that this mismatch inflates estimates of the fraction of variance explained by host plant genotype. Moreover, a disproportionate focus on endophagous insects (Fritz and Price 1988, Fritz 1990, Fritz et al. 1998, Rossi and Stiling 1998, Ylioja et al. 2000, Graham et al. 2001, Kittelson 2004, Tack et al. 2010) and on hybrid plant taxa (Boecklen and Spellenberg 1990,

Fritz et al. 1998, Dungey et al. 2000, Graham et al. 2001, Whitham et al. 2003, Hochwender and Fritz 2004, Ito and Ozaki 2005, Wimp et al. 2005, Tovar-Sánchez and Oyama 2006) in the published literature has likely exaggerated our perception of realized genotypic effects.

In evaluating our findings, we stress that the data for our analysis emanate from multiple study systems. Within systems, the exact relationship between V_G , V_T and spatial scale will ultimately depend on the exact relationships described by Fig. 1 – and such relationship may differ among systems. For example, in a series of papers, Bangert and colleagues (Bangert et al. 2005, 2006a, b, 2008) have used observational data to demonstrate that host plant genotype explains 36% and 7.5% of the variation in the arthropod community within a single cottonwood hybrid zone (a few km to >100 km) and at a regional scale (~720 000 km²), respectively. Hence, in their specific study system, host plant genotype seems to play a substantial role at a small spatial scale, and a decreasing yet still non-negligible role with increasing spatial scale. In contrast, Tack et al. (2010) showed that host plant genotypic variation in the pedunculate oak *Quercus robur* played a minor role in structuring the insect community both at a small landscape scale (~5 km²) and at the regional scale (~10 000 km²). Before generalizing too broadly regarding the exact scaling of V_G/V_T with increasing spatial scale, we will need studies across a greater number of study systems with greater phylogenetic and life-history variation.

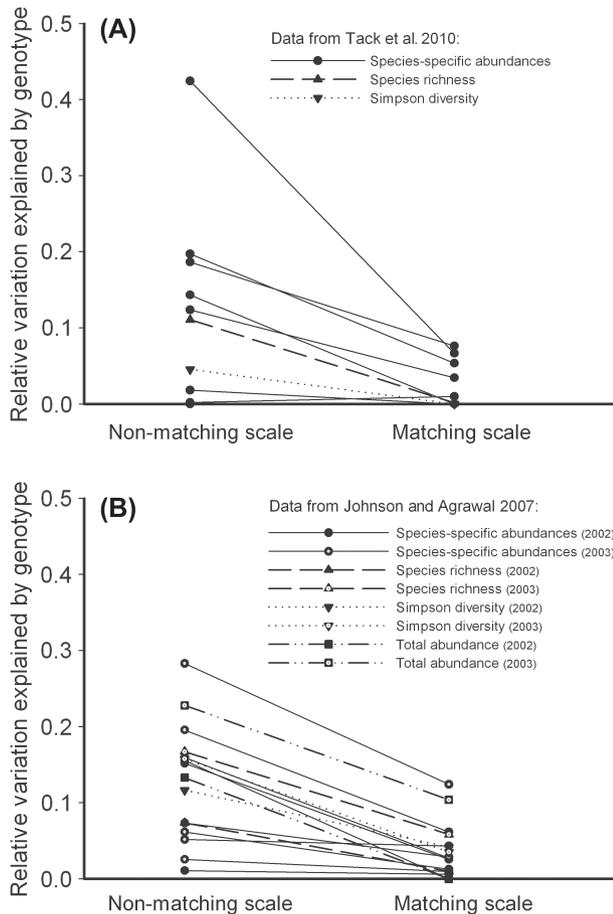


Figure 3. Variation in insect abundance and species diversity explained by host plant genotype at two spatial scales for two independent data sets. Importantly, the common garden at the small spatial scale contains host plant genotypes from a much larger area than encompassed by the experimental garden – and hence, we overestimate the variance explained by host plant genotype. Data shown are re-analyses of data published in (A) Tack et al. 2010 and (B) Johnson and Agrawal 2005, 2007 (the two non-local genotypes were excluded from the analysis). At the small scale, data points are average values across sites.

A new experimental protocol

As evidenced by our quantitative analyses, the current view that genotypic variation plays a major role in shaping community and ecosystem patterns in nature is based on biased estimates that do not necessarily reflect natural patterns. In particular, the common practice of collecting plant genotypes from larger spatial scales than that generating environmental variation has led to an inflation of the relative importance of host plant genotype in structuring the associated herbivore community. Hence, while accumulated evidence does show the important notion that plant genotype can have an effect, it does not accurately reflect how large this effect really is (Falconer and Mackay 1996, Roff 1997). Answering the latter question will require new types of experimental designs, aimed at comparing genotypic effects to that of other ecological factors as sampled randomly at realistic and relevant levels. Specifically, we advocate experiments where the environmental and genotypic variation are carefully matched and thereby represent the same spatial scale.

As one particular design for achieving comparable representations of V_G and V_E , multiple common gardens can be constructed within the very same landscape from which host plant genotypes were collected (examples of studies adopting this approach: Maddox and Root 1987, Stiling 1994). Importantly, when examining patterns at different spatial scales, the scale of host plant genotype collection and the scale of the environment should be changed in parallel (see Tack et al. 2010 for an example). Within a landscape, both host plant genotypes and environments should be sampled as randomly as is practical. When both host plant genotype and the locations of the common gardens are randomly chosen, the variation explained by genotype and the environment can be estimated directly using mixed model techniques (Littell et al. 2006, Hadfield 2009) or variance partitioning applicable to community matrices (Oksanen et al. 2010).

Once such designs and estimation techniques have been widely implemented, we believe that the field of community genetics will establish its generality, or lack thereof, whatever the case may be. From the seminal demonstration that genotypic effects can be strong, we will then be able to tell whether strong effects are really the rule, and what the average role of G and E are in nature. Importantly, the $G \times E$ interaction, as elucidated by the proposed design, will show whether the impact of host plant genotype will be consistent through space ('the genetic similarity rule'; Bangert et al. 2008), or interact with the environment (Johnson and Agrawal 2005). Only with this hurdle taken, community genetics may earn its legitimate place in future ecology textbooks. We hope that this paper will stimulate such critical assessment.

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