From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization

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Using two genetic approaches and seven different plant systems, we present findings from a meta-analysis examining the strength of the effects of plant genetic introgression and genotypic diversity across individual, community and ecosystem levels with the goal of synthesizing the patterns to date. We found that (i) the strength of plant genetic effects can be quite high; however, the overall strength of genetic effects on most response variables declined as the levels of organization increased. (ii) Plant genetic effects varied such that introgression had a greater impact on individual phenotypes than extended effects on arthropods or microbes/fungi. By contrast, the greatest effects of genotypic diversity were on arthropods. (iii) Plant genetic effects were greater on above-ground versus below-ground processes, but there was no difference between terrestrial and aquatic environments. (iv) The strength of the effects of intraspecific genotypic diversity tended to be weaker than interspecific genetic introgression. (v) Although genetic effects generally decline across levels of organization, in some cases they do not, suggesting that specific organisms and/or processes may respond more than others to underlying genetic variation. Because patterns in the overall impacts of introgression and genotypic diversity were generally consistent across diverse study systems and consistent with theoretical expectations, these results provide generality for understanding the extended consequences of plant genetic variation across levels of organization, with evolutionary implications.

Keywords: community and ecosystem genetics; meta-analysis; intraspecific variation; introgression; genotypic diversity; genes to ecosystems

1. INTRODUCTION

Recent reviews in the field of community and ecosystem genetics have provided strong evidence that plant genetic factors can have distinct community and ecosystem phenotypes, that these phenotypes can be heritable and that the community phenotype can feed back to affect the fitness of the individual plant genotypes (Fritz 1999; Whitham et al. 1999, 2003, 2006, 2008; Bradley & Pregitzer 2007; Johnson & Stinchcombe 2007; Hughes et al. 2008). Reviews to date have covered a range of conceptual topics including (i) the role of plant hybridization in maintaining associated biodiversity (Fritz 1999; Whitham 1999), (ii) genes to ecosystems links (Whitham et al. 2003, 2006), (iii) the importance of functional genomics to community genetics (Whitham et al. 2008), (iv) the role of genetically based feedbacks in community genetics (Whitham et al. 2003, 2006; Schweitzer et al. 2008b), and (v) the effects of genotypic diversity on community- and ecosystem-level properties (Whitham et al. 2006; Bradley & Pregitzer 2007; Johnson & Stinchcombe 2007; Hughes et al. 2008). Such a diverse array of topics clearly link genetic variation in plants to community and ecosystem processes, and provide compelling evidence for the importance of bridging community and ecosystem
ecology with evolutionary biology. However, these
reviews are largely qualitative, providing conceptual
frameworks for understanding how genetic variation in
one species may affect community traits and ecosystem
services with little comparative synthesis of the broader
patterns in the strength of plant genetic effects within or
across systems.

Owing to the qualitative nature of the recent reviews
described above, it remains unclear whether plant
genetic variation affects all individual- and community-
and ecosystem-level phenotypes equally or whether
particular traits, community dynamics or ecosystem
processes, are more likely to be under genetic control. If
there is significant variation in the effects of plant
genetic variation across levels of organization, as we
expect, then a finding of significant effects of plant
genetic variation on community- and ecosystem-level
phenotypes reveals the specific traits and processes
upon which genetic variation may act most strongly
relative to the background average effect size.

Moreover, understanding the average effect size of
plant genetic variation across levels of organization
(i.e. individual-, community- and ecosystem-level
phenotypes; sensu Whitham et al. 2006) provides a
framework of comparison for future genes-to-ecosystems
research. These results may provide novel insights into
when and where we should expect genetic variation to
have its strongest effects, potentially reveal new
research questions and testable hypotheses that are
relevant to investigate and advance the broad field of
ecological genetics, and provide a comparison for other
ecological effect sizes.

Here, we apply meta-analysis to evaluate the
strength of plant genetic effects on individuals,
populations, communities and ecosystems across
multiple environmental gradients. Specifically, we
focus on the role of (i) introgression in a Populus
hybridizing system and (ii) genotypic diversity across
multiple plant systems. While these same relationships
are beginning to be examined in animal systems (Post
et al. 2008; Palkovacs & Post in press; Palkovacs et al.
in press), we focus on the effects of plant systems and
the linkage between plant genetics and community and
ecosystem phenotypes. In terms of introgression,
Populus represents a model system to examine how
hybridization affects community dynamics and ecosys-
tem processes across diverse environments. Populus spp.
are recognized as a ‘foundation’ riparian forest tree
(Allison et al. 2005) that can have significant impacts on
biodiversity and ecosystem functions, and it commonly
hybridizes wherever two or more species co-occur
(Eckenwalder 1984). Along the Weber River, Utah,
the ranges of Populus fremontii S. Wats and Populus
angustifolia James overlap in a 13 km zone, where the two
species naturally hybridize with introgression occurring
unidirectionally towards P. angustifolia (Keim et al. 1989;
Martinsen et al. 2001). Owing to unidirectional
introgression, hybridization represents a partial genetic
continuum between P. fremontii and P. angustifolia,
which results in a large amount of genetic variation
(Keim et al. 1989; Martinsen et al. 2001) with associated
variation in community and ecosystem phenotypes that
affect individual communities, community structure, biodiversity
and ecosystem processes (Whitham et al. 2006).

The abundance of ecological data on Populus has great
potential for synthesizing the effects of introgression
across levels of organization and environments (Bangert
et al. 2008).

The second common approach for examining the
strength of plant genetic effects on their associated
communities and ecosystems in diverse systems is to
examine the role of genotypic variation. Recent
studies have focused on the effects of plant genotypic
diversity on associated communities and ecosystem
processes (described in §§2 and 3). By manipulating
single and multiple genotype plots, studies of the
effects of genotypic diversity provide insights into how
increasing plant genetic variation and their associated
phenotypes may influence species interactions and
ecosystem processes.

Using these two approaches, we conducted a meta-
analysis to examine the role of plant genetic factors on
communities and ecosystems across environments to
examine two specific questions. First, does the effect of
genetic introgression vary across levels of organization?
Community and ecosystem phenotypes clearly rep-
resent complex traits where the genes of one species are
the environment of another species (i.e. interspecific
indirect genetic effects; Thompson 2005; Shuster et al.
2006; Whitham et al. 2006; Wade 2007). Because
the biotic environmental variation associated with
community and ecosystem phenotypes increases,
one would predict that the strength of the effects of
introgression on community and ecosystem pheno-
types is likely to decline across levels of organization,
with the greatest effects occurring at the individual level
and the weakest effects occurring at the ecosystem
level (box 1). Second, focusing on genotypic diversity,
we hypothesize that similar effects will be found,
although with different genetic mechanisms. Speci-
fically, we predict that the individual, community and
ecosystem consequences of genotypic diversity may be
weaker than those of introgression, as they result from
the combined interactions of individuals within a
population rather than the individual effects of
introgression. Taking this two-tiered approach allows
us to empirically examine the strength of genetic effects
and understand the broad consequences of plant
genetic factors across species and environmental
gradients. Relative to the background average effect
size in ecology of $r = 0.18–0.19$ established in a meta-
analysis of 42 meta-analyses based upon positive and
negative statistical results (Møller & Jennions 2002),
our results suggest that plant genetic factors may
explain up to twice as much variation in effect size
regardless of the level of organization.

2. MATERIAL AND METHODS
Meta-analysis is a statistical method that allows for the
combined analysis of independent studies that address a
similar scientific question. This combined analysis is done by
estimating a mean effect size for all tests (i.e. significant
and non-significant) used in the meta-analysis and then identi-
fying the factors that may influence the magnitude of the effect
(Gurevitch & Hedges 2001). We conducted two independent
meta-analyses to examine the strength of genetic effects on
community and ecosystem processes across environments,
one examining introgression and the other examining
Box 1

One would expect the effect size of genetic variation in one individual to decline across levels of organization. For example, consider a single gene $V_j$ that determines the phenotype $V_j$ of an individual. The phenotype of this individual affects the phenotype of its community $V_i$, which in turn affects the phenotype of the ecosystem $V_o$ to which this community belongs (figure A). For example, a single gene $V_j$ determines foliar condensed tannin concentration $V_j$ of an individual. Foliar condensed tannin concentration affects soil microbial community composition and activity $V_i$, which in turn affects soil nutrient cycling $V_o$. In this simple model, the gene is the independent variable and the ecosystem is the dependent variable. The phenotype and the community are intermediate variables. Assume that the relationship between any two variables is linear (if this were not true, consider small deviations from the mean, which makes a first-order approximation good enough). Let $X_i = (V_i - \bar{V}_i)/\sigma_i$ be the standardized variable $V_i$ (where $\bar{V}_i$ is the mean value of variable $i$ and $\sigma_i$ is its standard deviation). The coefficient in each path joining variables $V_i$ and $V_j$, $\beta_{ij}$, is the regression coefficient of variable $X_i$ on $X_j$, i.e. $X_i = \beta_{ij}X_j + \epsilon_{ij}$, where $\epsilon_{ij}$ is the error term. Coefficient $\beta_{ij}$ measures the effect of a change in variable $V_j$ on variable $V_i$, if all other variables remain constant. From path analysis (Wright 1934), the effect of a variable on another variable separated by $n$ paths is the product of the coefficients corresponding to those paths, e.g. the effect of gene $V_j$ on the ecosystem is $X_o = \beta_{o1}X_1\beta_{12}X_2 + \beta_{o3}$, where $\beta_{o3} = \beta_{o1}\beta_{12}\beta_{23}$, $\beta_{o3} + \epsilon_{o3}$ is the error term (note how the error term grows as we add paths). We are interested in determining under which conditions the effect of a variable $V_j$ on the variables in its immediate superior level of organization $V_j$ (where $j > i$) is greater than the effect of the same variable on variables in levels of organization above the immediate one $V_k$ (where $k > j$), i.e. $|\beta_{jk}| > |\beta_{kj}|$ for all $k > j$. Such condition implies that the effect of a particular variable decreases as we consider higher levels of organization. In the model presented, condition $|\beta_{jk}| > |\beta_{kj}|$ translates into three inequalities: $|\beta_{23}| > |\beta_{12}|$, $|\beta_{12}| > |\beta_{03}|$, and $|\beta_{03}| > |\beta_{01}|$. That is, the effect of a gene on a plant phenotype must be greater than the effect of that gene on an ecosystem phenotype (as acting through that trait), the effects of a gene on a plant phenotype must be greater than the effect of that gene on an ecosystem phenotype (as acting through that trait), and the effect of a gene on its community phenotype must be greater than the effect of that gene on its ecosystem phenotype. Using path analysis, we can replace coefficients $\beta_{03}$ and $\beta_{13}$ for the product of the coefficients joining variables $V_o - V_3$ and $V_1 - V_3$, respectively, obtaining $|\beta_{23}| > |\beta_{12}|||\beta_{03}| > |\beta_{01}|||\beta_{12}| > |\beta_{03}|||\beta_{01}|||\beta_{23}| > |\beta_{01}|||\beta_{23}| > |\beta_{01}|||\beta_{23}| > |\beta_{01}|$. These inequalities yield two simple conditions, namely the effect of the phenotype on the community and of the community on the environment have to be less than 1, i.e. $|\beta_{01}|, |\beta_{12}| < 1$. In general, if the effects of one variable on another variable are small, these conditions will be satisfied. If these effects are big, however, or the interaction between variables is not linear, the above conditions will not be satisfied. In a genes-to-ecosystems context, such nonlinear effects may be a consequence of (i) indirect genetic effects among interacting species and (ii) feedback loops among levels of organization. Indirect genetic effects occur when the genes of one individual influence the fitness and phenotype of an associated individual of the same species (intraspecific indirect genetic effects) or different species (interspecific indirect genetic effects; see Shuster et al. 2006), and are fundamental to the coevolutionary process.
Box 1. (Continued)

In figure B, we present a more complex interaction in which a gene in individual 1, \( V_{(3,1)} \), affects two traits in different individuals, \( V_{(2,1)} \) and \( V_{(2,2)} \), which in turn affects the phenotype of the community the first individual belongs to, \( V_{(1,1)} \). Let \( X_{(i,m)} \) be the standardized variable \( V_{(i,m)} \). The coefficient in each path joining variables \( V_i \) and \( V_j \), \( \beta_{ji} \), is the regression coefficient of variable \( X_{(i,m)} \) on \( X_{(i,m)} \), i.e. \( X_{(i,m)} = \beta_{ji} X_{(i,m)} + \epsilon_{(j,i,m)} \), where \( \epsilon_{(j,i,m)} \) is the error term. From path analysis, the effect of gene \( V_{(3,1)} \) on its ecosystem is \( X_{(0,1)} = \beta_{(0,1)} + \beta_{(0,1)}(\beta_{(1,1)})^{V_{(3,1)}} + \beta_{(1,1)}(\beta_{(2,1)})^{V_{(3,1)}} + \epsilon_{(0,1)} \), where \( \epsilon_{(0,1)} = \beta_{(0,1)}(\beta_{(1,1)})^{V_{(3,1)}} + \beta_{(1,1)}(\beta_{(2,1)})^{V_{(3,1)}} + \epsilon_{(0,1)} \), is the error term. If we carry out a similar analysis, we can conclude that the effect size will decline across levels of organization only under more restrictive conditions. Hence, as we add indirect genetic effects and interactions among levels of organization there is a greater chance that genetic effect size will not decline across levels of organization.

\[ \begin{align*}
& \text{B} \\
& \text{gene} \quad \beta_{(0,3)} \quad \beta_{(1,3)} \\
& \text{individual} \quad \beta_{(2,3)} \quad \beta_{(3,2)} \\
& \text{community} \quad \beta_{(1,2)} \quad \beta_{(2,1)} \\
& \text{ecosystem} \quad \beta_{(0,1)} \quad \beta_{(1,0)} \\
& V_{(1,1)} \quad V_{(2,1)} \quad V_{(2,2)} \\
& V_{(3,1)} \quad V_{(3,2)} \\
& V_{(0,1)} \quad V_{(0,2)} \\
& \epsilon_{(1,3)} \quad \epsilon_{(2,3)} \quad \epsilon_{(2,2)} \quad \epsilon_{(1,2)} \quad \epsilon_{(3,1)} \quad \epsilon_{(0,1)}
\end{align*} \]

*P. fremontii* molecular markers and associated phenotypes in a common garden experimental setting (see the electronic supplementary material for a complete list of studies and tests).

The second meta-analysis was focused on the strength of the effects of plant genotypic diversity in natural systems. In contrast to genetic introgression that focuses on the interspecific flow of genes between species, genotypic diversity is characterized as the intraspecific diversity of plant genotypes within a given location or population of a single species. We were specifically interested in those studies that experimentally manipulated the diversity of plant genotypes (e.g. 1, 2, 4, 8 and 16 genotype experimental units). Our search was conducted using the Web of Science search engine. We used the combination of the keywords, ‘plant genotypic diversity’, ‘biodiversity’ (for community phenotypes) and ‘ecosystem’. The search engine returned with 17 results (and several other studies were found within the literature cited of these papers). These were reduced to those studies conducted in natural systems and which experimentally manipulated the number of genotypes and focused on a range of community- and ecosystem-level phenotypes. When these studies included individual-level phenotypes, those were included as well, although studies focused solely on individual-level phenotypes were excluded from the analysis. For the second meta-analysis, we used 11 studies published since 2002, 1 unpublished dataset and 90 individual tests (see the electronic supplementary material). These studies covered seven different ecosystem types from aquatic seagrass (*Zostera marina*), herbaceous systems such as *Oenothera biennis* and *Solidago altissima*, to woody plants such as *Quercus laevis* and *Populus* spp. These plant systems are distributed broadly, primarily across North America. Data from these studies were characterized identically to the previous meta-analysis and the same methods of analysis were used (see the electronic supplementary material for a complete list of studies and tests). Because introgression and genotypic diversity are very different experimental approaches to the same types of questions, we believe that this is a robust approach to understanding the general consequences of plant genetic factors.

Meta-analysis was conducted using *MetaWin* v. 2.1 (Rosenberg et al. 2000). All studies used in these analyses examined the correlation between genetic introgression or genotypic diversity and individual-, community- and ecosystem-level phenotypes. Individual-level phenotypes that were surveyed included phytochemistry, architectural and physiological traits. Community-level phenotypes were characterized by species richness, total abundance and community composition. Ecosystem-level phenotypes were characterized by energy flow or energy transformation and included leaf litter decomposition studies, which are focused on productivity and carbon accumulation, as well as on soil nutrient dynamics. We used the Pearson product-moment correlation coefficient \( r \) to measure effect size. When correlation coefficients were not reported in a study, we calculated them from the \( F \) or \( X^2 \) values presented in figures and tables or calculated the square root of the coefficient of determination \( r^2 \); see Rosenberg et al. 2000 for formulae). When these statistics could not be obtained, the study was excluded from the meta-analysis. Because we were interested in the percentage of variation explained by plant genetic factors, we disregarded the sign of the relationship between genetic introgression and genotypic diversity and the response variables and focused on the absolute value of the correlation coefficient. The correlation coefficient from each individual test was \( Z \)-transformed and weighted by their sample size. We used a mixed-effects model to combine the
3. RESULTS

(a) Introggression

(i) Levels of organization and organism type

Consistent with our prediction, we found a significant decline in the strength of the effects of genetic introgression across individual- (e.g. chemical, morphological or resistance traits), community- (species richness, total abundance, composition or diversity) or ecosystem- (energy transformations or nutrient cycling) level phenotypes \( (Q_s = 6.47, p = 0.042; \text{figure 1a})\). The mean effect sizes of genetic introgression across levels of organization were moderate ranging from \( Z(r) = 0.45 \) for individual-, \( Z(r) = 0.29 \) for community- and \( Z(r) = 0.20 \) for ecosystem-level phenotypes (back-calculated \( r = 0.42, 0.28 \) and 0.20, respectively). These results are consistent with the hypothesis that when environmental variation increases, the role of plant genetic factors declines.

Importantly, while the overall strength of the effects of introgression was moderate across levels of organization, there were still some relatively strong interactions at the community and ecosystem levels. For example, effect sizes ranged from \( Z(r) = 0 \) to 1.47 among individual phenotypes, 0.05 to 1.22 among community phenotypes and 0 to 0.77 among ecosystem phenotypes. Such strong effects on particular groups suggest that specific organisms or processes may be more responsive than others to the effects of introgression.

Consistent with the prediction that there is variation in the effects of introgression among organism types, we found that the mean effects of introgression were larger on individual phenotypes of the plants, relative to the extended phenotypic effects on associated arthropods, microbes and fungi \( (Q_s = 54.39, p = 0.001; \text{figure 2a})\). The effect size was moderate overall and varied from \( Z(r) = 0.1 \) for microbes and fungi to 0.62 for plant traits, with arthropods being intermediate \( (Z(r) = 0.55 \text{ for plants and 0.36 for arthropods})\). Effect sizes ranged from \( Z(r) = 0.02 \) to 1.47 for plants, 0 to 1.22 for arthropods and 0 to 0.92 for microbes and fungi. These results indicate that there are broad effects of introgression across many types of organisms, but the effects tend to decline when the organisms are external to the plant itself.

(ii) Environment type

Consistent with our data and expectations, we found that the effects of introgression were greater in above-ground than below-ground environments \( (Q_s = 35.54, p = 0.001; \text{figure 3a})\). The mean effect size was moderate for above-ground environments \( Z(r) = 0.53 \) and weak for below-ground \( Z(r) = 0.15 \) (back-calculated \( r = 0.5 \) and 0.14, respectively), roughly a threefold difference. The effect sizes ranged from 0 to 1.37 for both above- and below-ground environments. However, as our sample sizes are skewed, where the measured microbes and fungi were associated with below-ground environments and canopy arthropods were associated with above-ground environments, it is difficult to accurately determine whether the effect sizes of introgression can be attributed to the specific organism upon which they are acting or to the environmental condition, but is likely some combination of the two. Because soil microbes generally mediate below-ground soil processes, it seems reasonable that the effects of introgression on below-ground environments are indirect.

In contrast to our prediction, the effects of introgression were not significantly different in aquatic versus terrestrial environments \( (Q_s = 0.92, p = 0.93; \text{figure 3b})\).

Figure 1. Comparison of the effect size of (a) introgression and (b) genotypic diversity across levels of organization (i.e. on individual-, community- and ecosystem-level phenotypes). (a, b) When tests are characterized as individual-, community- or ecosystem-level phenotypes, there is a significant difference in the effect size of introgression. Bars represent mean effect size ± 95% CI. Dashed line represents average effect size across all levels of organization.
Estimates of mean effect size were moderate for both environments. Effect sizes ranged from $Z(r) = 0.39$ in aquatic environments to 0.40 in terrestrial systems. The effect sizes ranged from 0 to 1.37 for terrestrial environments and 0 to 1.47 for aquatic environments.

(b) Genotypic diversity

(i) Levels of organization and organism type

Consistent with the results from the introgression meta-analysis, we found a significant difference in the effects of genotypic diversity when the data were...
characterized as individual-, community- or ecosystem-level phenotypes ($Q_s = 14.4$, $p = 0.003$; figure 1b). In general, the strongest effects of genotypic diversity were observed at the individual ($Z(r) = 0.29$) and community (0.23) levels. These effects declined at the ecosystem level (0.13), where the strength of the effects of genotypic diversity was roughly half that at the individual or community level (back-calculated $r = 0.3$, 0.25 and 0.13, respectively). We emphasize that while the overall mean strength of the effects of genotypic diversity was moderate across levels of organization, there were still some strong effects at the community and ecosystem levels. For example, effect sizes ranged from $Z(r) = 0$ to 0.42 among individual phenotypes, 0 to 0.47 among community phenotypes and 0 to 0.49 among ecosystem phenotypes. Such effects on particular groups suggest that specific organisms or processes may be more responsive than others to genotypic diversity.

Results bearing on the strength of the effects of genotypic diversity on particular organisms were inconsistent with patterns that were found in the genetic introgression meta-analysis. There were significant differences in the strength of the effect of genotypic diversity on individual phenotypes of the plants, relative to the extended phenotypic effects on arthropods or microbes ($Q_s = 9.37$, $p = 0.027$; figure 2b); however, the strongest mean effects of genotypic diversity were on the associated arthropods ($Z(r) = 0.15$, 0.23 and 0.14, respectively). In general, the effects of genotypic diversity were twice as strong on arthropods as they were on the plants themselves or soil microbial communities (back-calculated $r = 0.27$, 0.13 and 0.14, respectively). This may be an artefact of a small sample size in the category of individual-level plant phenotypes. Effect sizes ranged from $Z(r) = 0.03$ to 0.42 for plants, 0 to 0.47 for arthropods and 0 to 0.49 for microbes and fungi.

(ii) Environment type

Consistent with the effects of introgression in Populus spp., there was a significant difference in the effects of genotypic diversity on above-ground versus below-ground traits ($Q_s = 14.9$, $p = 0.002$; figure 3c). The effects of genotypic diversity were two times stronger above ground than below ground ($Z(r) = 0.24$ and 0.13, respectively), which is consistent with the moderate effects of genotypic diversity on soil microbes (back-calculated $r = 0.27$ and 0.13, respectively). However, interpretation is still confounded because the microbes and fungi quantified were associated with below ground environments.

Consistent with the introgression patterns, there was no difference in the mean effect sizes as they relate to genotypic diversity in terrestrial or aquatic environments ($Q_s = 0.42$, $p = 0.58$; figure 3d). Overall, the effects of genotypic diversity were equivalent ($Z(r) = 0.18$ and 0.22, respectively). These data indicate that genetically based links between terrestrial and aquatic systems may be important.

Consistent with the hypothesis that when environmental variation increases, the role of plant genetic variation declines, and there were significant differences in the strength of the effects of both genetic introgression and genotypic diversity ($Q_s = 24.5$, $p = 0.001$). The effect size of introgression was twice that of genotypic diversity ($Z(r) = 0.39$ and 0.20, respectively; back-calculated $r = 0.38$ and 0.20). Effect sizes ranged from $Z(r) = 0$ to 1.47 for the introgression study and 0 to 0.49 for the genotypic diversity study. This range of variation suggests that, irrespective of the approach, there can be strong effects of plant genetic factors on specific organisms or processes. As the study of genetic introgression is concerned with the specific genetic structure of individuals within populations and genotypic diversity is concerned with the genetic structure of populations, weaker genetic effects would be expected using a genotypic diversity approach due to increased environmental heterogeneity and subsequent selection gradients altering the genetic structure of the population.

4. DISCUSSION

The results to date suggest broad generality for the consequences of plant genetic variation on shaping the phenotypes of individuals, their associated communities and even ecosystem processes. Although plant genetic variation does not always have strong effects on all species in all environments, it can strongly affect particular phenotypes and processes across all of the systems examined. That said, the overall mean effect size of plant genetic factors based upon these meta-analyses can be considered moderate relative to Cohen’s benchmarks (Rosenberg et al. 2000; Møller & Jennions 2002). Because this meta-analysis was based upon both positive and negative statistical tests, the fact that the effects of plant genetic variation on community- and ecosystem-level phenotypes can be three times as high as the average ecological effect size from Møller & Jennions (2002) justifies a community genetics approach, and further analyses to determine under what circumstances these large effects occur. Our model (box 1) suggests that large effects at higher levels of organization arise from non-additive, nonlinear dynamics and interactions among levels of organization. While a few studies are emerging, demonstrating the importance of non-additivity and epistatic interactions among individuals to biodiversity and ecosystem function (Schweitzer et al. 2005; Crutsinger et al. 2006; Johnson et al. 2006; Hughes et al. 2008), the prevalence of and mechanisms for these effects are not well understood. Moreover, the consideration of multilevel selection in genes-to-ecosystems research (i.e. interaction among levels of organization) has not been well incorporated into the field and may provide novel theoretical inroads into the mechanisms of extended consequences of plant genetic factors (Shuster et al. 2006; Wade 2007).

(a) Declining effect size across individual, community and ecosystem levels

Although many aspects of communities and ecosystems are inherently variable (Lawton 1999), our results suggest that when plants provide the fundamental resources to organisms, there appears to be broad generality in the effects of plant genetic variation at the community and ecosystem levels. While interest continues to grow in the effects of genetic factors that extend beyond the individual, it is generally assumed that the
role of plant genetics declines at levels higher than the population (Whitham et al. 2003, 2006). Consistent with this hypothesis, using two different approaches to understanding the effects of plant genetic factors, we found a significant difference in effect size across levels of organization. Although the effects of introgression and genotypic diversity were strongest at the individual level and declined at the community and ecosystem levels, in some systems, plant genetics strongly affects trophic interactions, carbon accumulation and the nitrogen cycle (Schweitzer et al. 2004; Whitham et al. 2008).

Two hypotheses that may be related to these patterns are that the effects of plant genetic factors vary by the type of organism they affect or depending upon the environment in which they act. We predicted that genetic effects would be expressed most strongly in the individual possessing those genes and decline with increasing species interactions. As ecosystem processes, by definition, are focused on energy and nutrient dynamics in a specific environment that are dependent upon species interactions, one might expect that the effects of plant genetics would vary among organism types. Consistent with this prediction, our results indicate that the strength of plant genetic effects is greatest on individual phenotypes and becomes weaker on arthropods and still weaker on microbes and fungi. However, specific examples indicate that the effects of plant genetics on microbial communities can be large. For example, Schweitzer et al. (2008a) found that plant genotype predictably structured soil microbial community composition in P. angustifolia, and affected microbial biomass nitrogen pools. Such results have important implications for our understanding of feedbacks in natural systems (Palkovacs & Post 2008; Palkovacs et al. in press). Genetic variation for the process of nitrogen mineralization indicates that plants effectively determine their nutrient environment and affect their own fitness via interactions with soil microbes (Schweitzer et al. 2008a).

Our meta-analysis also indicated significantly reduced effects of plant genetic factors in below-ground versus above-ground environments. Because we cannot separate the effects of environment versus organism type (i.e. all microbes except one were sampled in below-ground environments and all arthropods were sampled above ground), it is difficult to say whether these reduced effects of plant genetic variation below ground are due to biotic or abiotic variation.

(b) Consistency of patterns across individual, community and ecosystem levels

We found the patterns, in the effects of introgression and genotypic diversity across seven different plant systems, broadly distributed across biomes of North America, across levels of organization to be consistent across studies. Because these patterns were generally in accord with theoretical models, our results suggest broad generality for the consequences of plant genetic variation across different levels of organization. Recent hypotheses in genes-to-ecosystems research have suggested that as environmental variability increases, the strength of plant genetic effects declines (Johnson & Agrawal 2005; Bangert et al. 2006a,b). In general, as more variation is explained by environment, less will be explained by genetics. While this hypothesis has largely been focused on the role of spatial or abiotic environmental parameters, at the community and ecosystem levels, the role of biotic environmental variation has a critical role in the coevolutionary process.

Phenotypic traits can be characterized at a number of levels that depend on traits at lower levels (Conner & Hartl 2004). An organism’s lifespan is influenced by behavioural, morphological and physiological traits, all governed by various gene loci. Typically, traits that are higher in this hierarchy are more complex and affected by more loci (Conner & Hartl 2004). Thus, the expression of complex traits often varies depending upon environmental factors (e.g. expression of phenotypic plasticity). Recent theory in the fields of community genetics (Shuster et al. 2006) and coevolution (Yoshida et al. 2003; Fussmann et al. 2005; Hairston et al. 2005; Thompson 2005; Jones et al. in press) has provided independent but convergent evidence that community and ecosystem phenotypes represent complex traits related to the fitness consequences of interspecific indirect genetic interactions among all interacting species (Thompson 2005; Shuster et al. 2006; Whitham et al. 2006). Because community and ecosystem phenotypes represent complex traits, one would predict that they probably vary phenotypically depending upon abiotic and biotic environmental factors and may even show genetic variance for phenotypic plasticity. Similarly, the effects of genetics on community and ecosystem phenotypes probably decline with increasing biotic and abiotic environmental variations (Garant et al. 2008; Pelletier et al. 2008; Ezard et al. in press; Portier et al. in press).

The theoretical framework for quantifying the heritability of arthropod communities of individual tree genotypes, mathematically defined in Shuster et al. (2006), argues that when the environmental effects of associated species are large the effects of plant genetic variation in structuring communities will be small. Because environmental variation can have a substantial role in the coevolutionary process and in feedbacks, it is critical that we understand the strength of the effects of plant genetic variation across environmental gradients.

(c) Terrestrial and aquatic

Our results suggest that the effects of terrestrial plant genetic effects on both terrestrial and aquatic communities are similar. Given the recent genes-to-ecosystems research in aquatic systems that demonstrates remarkable effects of coevolution among fishes on associated communities and nutrient cycling (Palkovacs et al. in press), these results suggest that links between forest and aquatic habitats could be stronger than previously appreciated (LeRoy et al. 2006, 2007). This review highlights an important research area warranting more attention.

(d) Odds and ends

Specific to the meta-analysis, only a few studies examined the effects of introgression or genotypic diversity on vertebrates (but see Bailey et al. 2004; Hughes & Stachowicz 2004). Owing to this disparity, these data were left out of the analysis of 'organism type', but were used for all other tests. More work needs to be conducted on the effects of introgression and genotypic
consistency of our findings is largely due to the fact that plant genetic factors may explain up to two times as much variation across the individual, community and ecosystem levels (Johnson et al. 2006a). Determining how genotypic diversity may feed back to affect patterns of foraging may provide some novel insights into the long-term temporal dynamics of plant tolerance and resistance to herbivory. While there is substantial work on leaf litter decomposition and carbon storage, there appears to be no research on the effects of plant genotypic diversity on soil processes including the nitrogen or phosphorus cycle.

(e) Conclusions

Our results indicate that the effects of plant genetic factors are moderate overall. Relative to the background average effect size in ecology of Pearson’s r = 0.19 (Møller & Jennions 2002), our study suggests that plant genetic factors may explain up to two times as much variation across the individual, community and ecosystem levels (r = 0.2–0.39). In addition, the effects of plant genetic factors can be strong, suggesting that specific organisms and processes respond more to plant genetic factors than others. Having shown that community and ecosystem phenotypes can be broadly detected, and that they are often heritable (e.g. Bailey et al. 2006; Shuster et al. 2006; Schweitzer et al. 2008a; Whitham et al. 2008), it becomes important to determine under what conditions these phenotypes might feed back to affect the fitness of the individual plant genotype (Whitham et al. 2006; Schweitzer et al. 2008a). If they do feed back to affect the fitness of the individual plant, then it becomes especially important to (i) study ecology and evolution within a community and ecosystem context, (ii) understand the specific targets of selection (Johnson et al. in press), and (iii) quantify the geographical variation in the strength and direction of the feed back to determine whether such selection results in a geographical mosaic of community structure and ecosystem processes. Our meta-analysis suggests that a community and ecosystem genetics approach is broadly applicable in diverse systems. We suspect that the consistency of our findings is largely due to the fact that all species have evolved in a community context of many interacting species and their abiotic environments.

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REFERENCES


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