REVIEW AND SYNTHESIS

Ecological consequences of genetic diversity

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Abstract

Understanding the ecological consequences of biodiversity is a fundamental challenge. Research on a key component of biodiversity, genetic diversity, has traditionally focused on its importance in evolutionary processes, but classical studies in evolutionary biology, agronomy and conservation biology indicate that genetic diversity might also have important ecological effects. Our review of the literature reveals significant effects of genetic diversity on ecological processes such as primary productivity, population recovery from disturbance, interspecific competition, community structure, and fluxes of energy and nutrients. Thus, genetic diversity can have important ecological consequences at the population, community and ecosystem levels, and in some cases the effects are comparable in magnitude to the effects of species diversity. However, it is not clear how widely these results apply in nature, as studies to date have been biased towards manipulations of plant clonal diversity, and little is known about the relative importance of genetic diversity vs. other factors that influence ecological processes of interest. Future studies should focus not only on documenting the presence of genetic diversity effects but also on identifying underlying mechanisms and predicting when such effects are likely to occur in nature.

INTRODUCTION

Genetic diversity, defined here as any measure that quantifies the magnitude of genetic variability within a population (Table 1), is a fundamental source of biodiversity. For more than 80 years, the study of genetic diversity has principally been the domain of evolutionary biologists (Wright 1920; Fisher 1930). The pioneering work of the modern evolutionary synthesis provided the theoretical and empirical foundation for the study of genetic diversity, including the derivation of new standard quantitative metrics of genetic diversity such as heritability and genetic variance (Fisher 1930; Haldane 1932; Wright 1968). Since the modern synthesis, interest in genetic diversity has focused on its origin and maintenance, its role in the evolution of sexual reproduction and how the level and types of genetic variance affect the rate of evolutionary change within populations (Futuyma 1986).

Genetic diversity provides the raw material for evolution by natural selection (Fisher 1930). The widespread evidence for evolution by natural selection in nature confirms the presence of genetic variation for traits that influence fitness

(e.g. Ford 1964; Endler 1986), and a straightforward corollary is that individual genotypes must vary in ecologically important ways. However, the simple presence of heritable trait variation does not mean that different levels of genetic diversity will have predictable ecological consequences. For example, by allowing for increases in fitness, genetic diversity can increase the population growth rate, but only if the population is not regulated by other factors and is experiencing directional selection (Fisher 1930, p. 35). More generally, as elaborated in this paper, individuals with different genetically determined trait values can interact in unpredictable ways. Thus, despite the obvious presence of genetic variation for ecologically important traits, we know relatively little about the range of potential ecological effects of genetic diversity for population dynamics, species interactions and ecosystem processes (Fig. 1).

Early interest in the ecological effects of genetic diversity occurred in several fields in addition to evolutionary biology. For instance, in agronomy, there have long been efforts to increase crop yield by planting genetically diverse varieties within a single field (Wolfe 1985; Smithson & Lenne 1996). Although not universal, there is evidence that increasing

Table 1 Definitions of genetic diversity commonly used in evolutionary and ecological studies

Type of trait	Metric of diversity	Definition
Discrete allelic states	Allelic diversity	An index of molecular genetic diversity (e.g. Shannon–Wiener diversity) that incorporates information about the average number and relative frequency of alleles per locus. Allelic diversity is typically measured using molecular markers of putatively neutral loci.
	Allelic richness	The average number of alleles per locus.
	Genotypic richness	The number of genotypes within a population. Genotypic richness can be measured as the number of haplotypes using molecular markers, or it can be manipulated in experiments by varying the number of clonal genotypes or sib-families.
	Heterozygosity	The average proportion of loci that carry two different alleles at a single locus within an individual. Observed heterozygosity (H_o) can be estimated with co-dominant molecular markers, but estimates are biased by the number of individuals sampled within a population. Expected heterozygosity (H_e) can be estimated with both dominant and co-dominant markers when assumptions are made about the mode of inheritance, as well as the size and structure of populations.
	Mutational diversity and effective population size (Θ)	A measure of nucleotide diversity that provides a combined measure of effective population size (N_e) and mutation rate. Θ is typically calculated using Watterson's (1975) estimator ($\theta = 4N_e\mu$), which is equal to the expected number of segregating sites between two genotypes. Estimates of θ assume an infinite number of nucleotide sites and no recombination.
	Nucleotide diversity (π)	The average number of nucleotide differences per site between two random individuals selected from a population.
	Percentage of polymorphic loci	The percentage of loci that are polymorphic.
Continuous traits	Coefficient of genetic variance (CV)	Genetic variance in a trait (V_G) corrected by the trait mean, calculated as ($V_G^{0.5}$/mean$_{trait}$) × 100%. Unlike genetic variance, CV is not biased by the magnitude of trait means and is arguably the best measure of genetic diversity for phenotypic traits when variance scales with the trait mean.
	Genetic variance (V_G)	The variance in a phenotypic trait among individuals due to genetic differences. Genetic variance is measured using parent–offspring regressions, controlled breeding designs that allow for sibling analyses or with detailed genealogical information. Total genetic variance can be further partitioned into additive and non-additive (dominant and epistatic) components of genetic variance. Genetic variance often scales positively with mean trait values.
	Heritability	The ratio of the genetic variance to the total phenotypic variance in the population. Heritability values are influenced by both genetic and environmental variance and therefore offer a poor estimate of genetic diversity.

varietal diversity can lead to greater yield, as well as decreased damage by herbivores and pathogens (Cantelo & Sanford 1984; Smithson & Lenne 1996). The significance of these effects is apparent in current agricultural practices: the planting of genetically diverse crops is now being applied on a large scale in some areas as an effective means to maximize

the yield by minimizing damage by pathogens (Zhu *et al.* 2000).

Conservation biology, and the related field of conservation genetics, have also raised awareness of the potential short-term ecological effects of genetic diversity, particularly in small or endangered populations (Lande 1988; Frankham
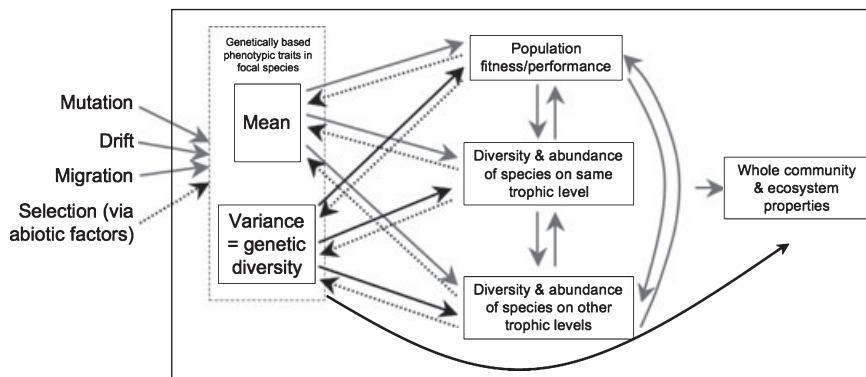
Figure 1 Processes underlying potential direct and indirect effects of genetic diversity on the ecological properties of populations, communities and ecosystems. Solid black lines indicate direct ecological consequences of genetic diversity *per se*; dotted black lines indicate effects of natural selection, which depend on genetic diversity; grey lines represent causal effects not directly related to genetic diversity *per se*.

et al. 2002). This work, initially sparked by observations of low genetic variation in high-profile species such as the cheetah, often focuses on relationships between population size, genetic diversity and fitness (e.g. Leimu *et al.* 2006). These studies illustrate that genetic bottlenecks and inbreeding can alter genetic diversity, with ecological consequences such as reducing a population's ability to persist in stressful or changing environments (Frankham *et al.* 2002).

Two lines of research within the field of ecology provide a foundation for the study of the ecological effects of genetic diversity. First, interest in the ecological consequences of biodiversity has focused on how the number of species and functional groups (e.g. trophic groups, guilds, etc.) within communities affects the stability and functioning of ecosystems (Elton 1958; May 1973; Hooper *et al.* 2005). Second, there is a growing focus on the ecological effects of not just the mean value of a particular explanatory variable, but the variance around the mean within experimental or observational units (e.g. Bolnick *et al.* 2003; Clark *et al.* 2004; Inouye 2005). For example, characterizing inter-individual variation (regardless of the origin of such variation) in the response of particular tree species to environmental variation, rather than only the species average, can greatly improve the predictive ability of models of forest dynamics (Clark *et al.* 2004). Although there is a long history of work on how the genetic differences between individuals (i.e. genotype identity) influence species interactions (Turkington & Harper 1979) and the interplay of genetic and ecological dynamics (Birch 1960; Ford 1964; Pimentel 1968), there has been little work until recently that is specifically focused on the ecological effects of population genetic diversity to parallel work on species diversity.

Finally, the field of community genetics has recently sought to bridge the fields of evolutionary biology, population genetics and community ecology (Antonovics 1992; Whitham *et al.* 2003). In so doing, community genetics

has highlighted that biodiversity is inherently a hierarchical concept that is not restricted to any one taxonomic or genetic level. In fact, phenotypic variation within species can be as large or larger than that observed among species (Bangert *et al.* 2005; Shuster *et al.* 2006). As long as there is variation in ecologically important traits (growth rate, competitive ability, immune function, virulence, etc.), the amount of diversity at any level can have important ecological effects.

The recent surge of interest in merging ecological and evolutionary investigations (Whitham *et al.* 2006; Fussmann *et al.* 2007; Johnson & Stinchcombe 2007) has led to a flurry of studies that focus on: (i) the proximate ecological consequences of standing genetic diversity in a population and (ii) whether population genetic diversity can affect the ecological interactions within communities via evolutionary change. Studies relevant to these issues come from a variety of fields, using a range of different methods and specific focal questions. As this field moves forward, there is a need to establish clear definitions and expectations for ecological effects of diversity and to synthesize existing evidence across studies. To that end, here we address three main questions: (i) how does one study the effects of genetic diversity in ecology? (ii) what are the mechanisms by which diversity, and genetic diversity in particular, affects ecological properties? and (iii) what is the evidence for ecological effects of genetic diversity? We conclude with predictions regarding when genetic diversity is likely to be most important for ecological processes and we discuss directions for future research in this field.

EFFECTS OF GENETIC DIVERSITY: DEFINITIONS, MEASUREMENT AND MANIPULATION

Studies that investigate the ecological consequences of genetic diversity are complicated by the variety of possible

definitions of 'genetic diversity' and related terms (Table 1). We focus on genetic diversity that is measured or manipulated at the population level, in contrast to studies that investigate differences among particular genotypes. Effects of individual genotypes on ecological processes and patterns (reviewed by Whitham *et al.* 2006) are a prerequisite for ecological consequences of genetic diversity, but they do not address genetic diversity *per se*. Here we outline the main ways in which genetic diversity can be measured or manipulated.

Quantifying genetic diversity

Genetic diversity is most often characterized using data that depict variation in either discrete allelic states or continuously distributed (i.e. quantitative) characters, which lead to different possible metrics of genetic diversity (Table 1). The variation in allelic states or phenotypic traits may either be neutral or non-neutral with respect to fitness consequences. For example, molecular markers, such as microsatellites, AFLPs, direct DNA sequences or protein polymorphisms (Avise 2004), typically represent discrete allelic states that are assumed to be neutral. While molecular markers are probably the most common way that genetic diversity has been assayed in natural populations, neutral variation in and of itself cannot, by definition, have any ecological consequences. While neutral traits are typically measured as discrete allelic states, not all traits measured as discrete allelic states are neutral (Ford 1964), as illustrated in some cases of flower colour (Schemske & Bierzychudek 2001), for example. In theory, quantitative traits may also be neutral, although in most cases researchers focus on quantitative traits with known or presumed functional significance.

With discrete allelic states, metrics of genetic diversity reflect either the number of alleles or haplotypes within a population (e.g. alleles per locus or summed allelic richness), and/or the evenness of allele or haplotype frequencies (Frankham *et al.* 2002). The latter can be measured by estimating the probability that two randomly chosen alleles or haplotypes in a population are expected to differ, given specific assumptions about the genetics and ecology of the population (expected heterozygosity, gene diversity, etc.). A variety of other metrics can also be used to depict genetic diversity for discrete traits (Table 1), and although they are often tailored to account for the type of inheritance of a particular genetic marker (Weir 1996), for the most part they all reflect either the number (richness) and/or relative frequencies (evenness) of alleles.

For quantitative traits, the measurement of genetic diversity begins by estimating the variance in a phenotypic trait among individuals that is due to genetically inherited differences. This involves either detailed knowledge about the pedigree of a natural population or a separate experiment that replicates multiple genetic families (i.e. sib analysis) collected from a single population (Falconer & Mackay 1996). The simplest measure of genetic diversity is total genetic variance in a trait (V_G), which is often further partitioned into its additive and non-additive components (Table 1). Detailed methods for calculating these different sources of genetic variance are outlined elsewhere (Falconer & Mackay 1996).

Within a single generation, genetic variance for a given trait may have important ecological consequences regardless of its genetic architecture, in which case V_G is a relevant metric. Across generations, the key component for understanding how genetic diversity can influence the rate of evolution is the additive genetic variance (V_A). V_A is used to estimate the narrow-sense heritability for a trait (Table 1), which reflects evolvability, but heritability does not quantify genetic diversity *per se* because it is confounded by environmental variation (Houle 1992). The coefficient of genetic variance is a more appropriate measure in this case (Houle 1992).

How to test for effects of genetic diversity

Using one or more of the metrics described above, observational studies can test for correlations between genetic diversity and some ecological response of interest. Such studies offer advantages with respect to realism and the ability to span relatively large spatial/temporal scales, but it can be difficult if not impossible to assign a direction of causation between two measured variables (e.g. genetic diversity and productivity), because causation may run in both directions (Vellend & Geber 2005). In addition, genetic diversity may be correlated with other variables (e.g. population size or density) in a natural setting that are also affecting the process of interest, making it difficult to interpret their relative importance. Because of these limitations of observational studies, we focus our review on experimental studies that directly manipulate genetic diversity, although we emphasize that observational studies can provide a valuable complement to experimental approaches.

Experimental manipulations of genetic diversity present their own significant challenges, which vary depending on the particular objectives of a given study. In some cases, a specific response variable such as the diversity of insect consumers on a plant species is of interest, in which case particular traits may be hypothesized to be important (e.g. Johnson & Agrawal 2005). Creating a continuous range of variation in genetic diversity for particular traits is possible, but is rare in practice due to the considerable challenge of being able to identify the genetically based trait values of a large number of individuals, which can then be combined to create synthetic populations that quantitatively vary in the

amount of genetic diversity for those traits (but see Underwood 2004; N. U., unpublished data). In addition, the initial level of quantitative trait variation or heterozygosity could itself change during multi-generational experiments as a result of sexual reproduction, recombination, selection, drift and gene flow. Thus, few researchers have directly manipulated any of the most commonly measured indices of genetic diversity such as heterozygosity or quantitative genetic variance (Table 1), but rather have taken more indirect approaches, as described below.

The most common experimental approach has been to focus on organisms that reproduce clonally, particularly plants, and to manipulate the number of clonal genotypes (i.e. genotypic richness) in each experimental replicate (Booth & Grime 2003; Hughes & Stachowicz 2004; Reusch *et al.* 2005; Crutsinger *et al.* 2006; Johnson *et al.* 2006). In this approach, each clonal genotype represents a unique genome: single genotype experimental populations contain no genetic diversity at all, whereas populations of two or more genotypes do contain genetic diversity. Approaches related to the clonal-genotype method involve manipulating the number of maternal families represented in each experimental replicate (Gamfeldt & Kallstrom 2007), or comparing clonal offspring of single maternal plants to sexual offspring of the same mother plants, in which case genetically uniform populations are compared with populations in which each individual is genetically different (Kelley *et al.* 1988). These experiments provide a simple means of examining the ecological consequences of genetic diversity, but it is important to recognize that genotypic richness is not a close proxy for other metrics of genetic diversity, as described below.

The relationship between the number of genotypes in a population- and genetically based variance in phenotypic traits is not straightforward (Fig. 2d). Except for single genotype populations, which by definition have the lowest genetic variance (zero), the relationship between the number of genotypes and variance is cone-shaped, with many possible levels of variance in populations with few genotypes, converging to the variance of the entire pool with large numbers of genotypes (Fig. 2d). For example, with a few genotypes selected at random from the source population, genetic variance can be very high if extreme values are represented, or very low if the few genotypes are quite similar, but on average the variance will be no different from treatments with many genotypes (Fig. 2d). The central tendency of this distribution is weakly positive, at least when all possible combinations of genotypes in a given pool are considered, but the overriding pattern is that the number of genotypes is not tightly related to genetically controlled variance in phenotypic traits. Thus, manipulations of the number of clonal genotypes can characterize the effects of going from zero to non-zero levels of quantitative trait variance, but not effects of different non-zero levels of trait
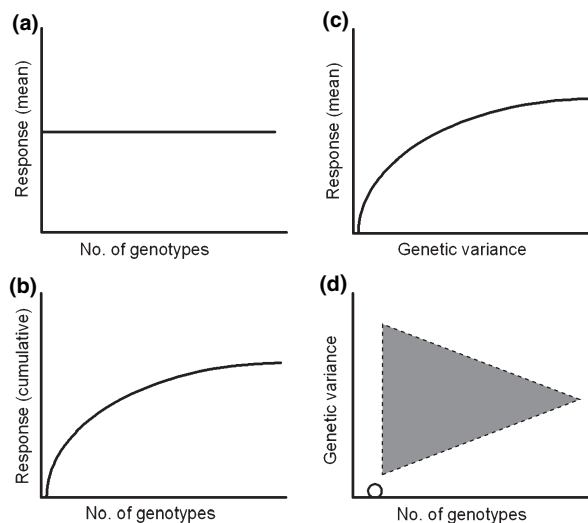

Figure 2 (a–b) Idealized expectations for the additive effect of genetic diversity if the ecological response of interest is a (a) mean or (b) cumulative response, assuming that experiments are performed on a sufficiently short time scale that the number and identity of genotypes in each population is unlikely to change, and that all genotypes are equally represented. Any observed deviation from these expectations represents a non-additive effect. (c) Jensen's inequality can result in an increasing mean response with increasing coefficient of genetic variance within a population, even when the same response shows no relationship to the number of genotypes in a population [cf. panels (a) and (c)]. (d) The relationship between the number of genotypes and the genetic variance within a population. The shaded cone illustrates that there are many possible levels of variance in populations with few genotypes, converging to the variance of the entire pool with large numbers of genotypes. The point near zero genetic variance in the lower left of the figure represents populations of a single genotype.

variance. Such manipulations do characterize the degree to which different numbers of distinct values along particular trait axes influence ecological properties of interest. We elaborate more fully on this topic in the Future directions section.

EFFECTS OF GENETIC DIVERSITY: MECHANISMS AND EXPECTATIONS

Genetic diversity has the potential to affect a wide range of population, community and ecosystem processes both directly and indirectly (Fig. 1). However, these effects are contingent upon genetic diversity being related to the magnitude of variation in phenotypic traits (McGill *et al.* 2006). Thus, the ecological effects of manipulations of putatively neutral molecular marker diversity will depend on the relationship between those neutral markers and phenotypic variation. Although diversity as measured by neutral markers is not expected to have any ecological

consequences in and of itself, in some cases it is correlated with levels of genetic diversity for ecologically relevant traits (Reed & Frankham 2001).

When genetic diversity corresponds with phenotypic diversity within populations, any observed net effect of genetic diversity can result from the simultaneous action of multiple mechanisms. Identifying fundamental commonalities and differences among types of mechanisms should help foster a more general understanding of when and where genetic diversity is likely to yield effects that differ from those predicted from the ecological effects of individual genotypes. As a starting point, we outline differences between additive and non-additive effects of genetic diversity (not to be confused with additive/non-additive genetic variance); these distinctions can facilitate how candidate mechanisms underlying ecological effects of genetic diversity may be distinguished experimentally. Then within this context, we describe mechanisms for effects of genetic diversity in more detail including, when relevant, how they relate to the mechanisms that drive the more often studied effects of species diversity.

Additive mechanisms and expectations

We define additive mechanisms as those for which the ecological response of individual genotypes measured in monoculture, and knowledge of the initial relative abundance of each genotype in a population, are jointly sufficient to predict the same ecological response for a genetically diverse population. For example, the abundance of herbivores on a mixture of plant genotypes could be an average of the abundance of herbivores on each genotype when grown in isolation, weighted by the relative representation of each plant genotype within a population. By this definition, one necessary (but not sufficient) condition for additive mechanisms is that genotypes will express the same phenotype in genetically uniform populations and mixtures.

One commonly discussed additive mechanism is the sampling effect: diverse mixtures have a higher probability of including a genotype that strongly affects the response of interest. Note that an effect of genetic diversity that appears to be caused by the sampling effect may also be due in part to particularly productive genotypes becoming numerically dominant over time, which is a form of the so-called selection effect (Huston 1997; Tilman *et al.* 1997). The selection effect is not additive because the response will not depend only on initial genotype frequencies. In order to distinguish a selection effect from other mechanisms, investigators would have to collect data on the relative abundance of each genotype, or the evolutionary response of specific heritable traits, in a population over time.

The expectations for additive effects can differ depending on whether ecological responses are measured as the mean

or cumulative sum across genotypes in a population (Fig. 2). For many ecological responses, the mean (e.g. average productivity) will be of primary interest. Probability theory shows that the expected mean of a sample of genotypes does not depend on the number of genotypes in the sample, assuming all genotypes are equally represented across diversity levels in an experiment (Fig. 2a). Thus, if genotypes exhibit phenotypic differences and all genotypes have equal and independent contributions, then the expected additive effect of genetic diversity has no change in the mean ecological response. Specifying this null expectation is important because deviations from this expectation reveal the operation of non-additive mechanisms, such as facilitation or rapid evolution.

Other ecological responses reflect either a function of the cumulative trait value across the population or a trait that shows categorical variation among genotypes. For these responses, the expected additive effect is an increasing function of the number of genotypes in a population (Fig. 2b). For example, assume that plant genotypes are associated with different numbers of arthropod species. If genotypes influence arthropods independently, total arthropod species richness in mixture can never be lower than the species richness for the plant genotype that has the largest number of associated arthropods. Thus, the expectation is that arthropod richness will have a positive, typically saturating, relationship with the number of plant genotypes. The additive expectation is similar if plant genotypes differ categorically in some trait that affects arthropod species composition, such as flower colour. Because the number of 'categories' will increase as the number of plant genotypes increases, the relationship between genotypic richness and response will also be positive.

Non-additive mechanisms

The majority of mechanisms for effects of diversity are ones we consider non-additive, in that the response in a diverse population is not predictable solely from measurements of the same ecological response in genetically uniform populations. Such mechanisms include niche partitioning, facilitation/inhibition, Jensen's inequality and evolutionary processes. Although non-additive mechanisms are not predictable from measurements of the same response for genotypes in isolation, they are not necessarily inherently unpredictable; in some cases, additional data on the phenotype of each genotype allows accurate predictions of the response to genetic diversity. However, if genotypes express different phenotypes in mixtures than in isolation, the result can be considered an emergent property of genetic diversity (Salt 1979) because it will not be predictable from measurements of genotypes in isolation. One way to describe scenarios in which a genotype expresses different

phenotypes in different contexts is by extending the concept of epistatis to include intergenomic or interspecific interactions (Wade 2007). In the section below on 'Identifying mechanisms', we elaborate on reasons for investigators to collect data on the phenotypic properties of genotypes in both monoculture and mixtures.

Two widely studied non-additive ecological mechanisms are niche partitioning and facilitation/inhibition (note that, in many cases, the term 'complementarity' is used to refer jointly to these two mechanisms; see e.g. Cardinale *et al.* 2007). Under niche partitioning, if species or genotypes differ in resource use in complementary ways, then diversity can positively influence processes such as total resource utilization or production (Tilman 1999). Niche partitioning can be viewed as a non-additive effect if each genotype performs differently *per unit density* (i.e. better, assuming intra-genotype competition is less severe) in genetically diverse populations than in monoculture. A variety of processes fall under the broad umbrella of facilitation or inhibition; these represent non-additive mechanisms because the outcome of genotype interactions cannot be predicted *a priori* due to changes in either the phenotypes of individual genotypes or the behaviour of other interacting species responding to diverse vs. uniform populations. An example of this mechanism is associational resistance or susceptibility to parasites, where the resistance of one plant species or genotype alters the resistance of neighbours to herbivores (Hambäck *et al.* 2000). Additional mechanisms for non-additive effects of species or genetic diversity include plasticity and frequency-dependent competition, predation or other biotic interactions that lead to a rare genotype advantage (Antonovics & Ellstrand 1984; Kelley *et al.* 1988; Tsutsui *et al.* 2003). Importantly, the plastic response of individuals to diverse vs. homogeneous environments through mate and kin recognition systems represents a mechanism specific to effects of genetic diversity (Tsutsui 2004).

Evolution is the best-studied non-additive mechanism that can contribute to ecological effects of genetic diversity, and it is a key reason why the ecological effects of genetic diversity may differ from those of species diversity. For example, evolution provides a means of creating new phenotypes within populations and restoring genetic diversity after it is lost; with the exception of immigration, comparable processes rarely exist for species diversity effects, at least on ecological time scales. There are several principal mechanisms that influence evolutionary change within populations (mutation, immigration/emigration, genetic drift and natural selection), and all of these mechanisms can alter the amount of genetic diversity within populations. However, the ecological effects of these mechanisms only depend on the level of standing genetic diversity when evolution is caused by natural selection, because increased additive genetic variance enhances the

potential for evolutionary change within populations (Fisher 1930; Falconer & Mackay 1996). Despite this apparent simplicity, quantitative expectations for evolutionary mechanisms will be difficult to derive, as the emergence of novel genotypes/phenotypes may invalidate expectations based only on the traits of genotypes present at the start of an experiment. Response to selection could alter a wide variety of relevant traits, including competitive ability, facilitation or niche partitioning, or resistance/defence levels, all of which may influence a range of ecological outcomes.

In the previous examples, we have focused on effects of the *number* of genotypes in a population, but at least one mechanism for effects of genetic diversity is instead specific to effects of genetic *variance* in phenotypic traits within a population. If genetic traits have a nonlinear effect on an ecological response, then changes in the degree of genetic variance (even with constant trait mean) can affect the mean of that response, because the mean of a function across trait values is not equal to the function evaluated at the mean trait value (Fig. 2c; Ruel & Ayres 1999; Inouye 2005). This general mathematical property of nonlinear functions is known as Jensen's inequality. For example, if a genetically based plant quality trait positively affects herbivore population growth via an accelerating function, then increasing genetic variance in plant quality will lead to higher herbivore population sizes, irrespective of changes in mean quality (cf. Fig. 2a,c,d; Underwood 2004, N. U., unpublished data). The importance of differences among populations in genetic variance will increase as the degree of nonlinearity in the effect of genetically based traits increases.

EFFECTS OF GENETIC DIVERSITY: EMPIRICAL EVIDENCE

There is experimental evidence in the literature for many of the ecological effects of genetic diversity hypothesized in Fig. 1. Below we highlight studies at the population, community and ecosystem levels of organization that provide some evidence for mechanisms in an attempt to emphasize both the generalities among studies and the gaps in our understanding. Additional representative studies are presented in Table 2. Several recent reviews have documented the accumulating evidence for rapid evolution (Altizer *et al.* 2003; Hairston *et al.* 2005) and its ecological consequences (Fussmann *et al.* 2007; Johnson & Stinchcombe 2007), so we focus largely on ecological mechanisms for effects of genetic diversity.

Population-level effects

The most commonly documented ecological effects of genetic diversity involve the productivity or fitness of the focal population, and they can occur via a variety of

Table 2 Representative examples illustrating the levels of ecological organization and response variables for which the consequences of genetic diversity in a focal species have been experimentally assessed

Level of organization	Response variable	Examples (focal species in which genetic diversity was assessed)
Population	Behaviour	**Tsutsui *et al.* 2003 (invertebrate)**; Boncoraglio & Saino 2007 (vertebrate)
	Fitness components	Ellstrand & Antonovics 1985 (plant); Gamfeldt *et al.* 2005 (invertebrate); **de Roode *et al.* 2005 (parasite);** Kelley *et al.* 1988 (plant); **Johnson *et al.* 2006 (plant);** Kron & Husband 2006 (plant)
	Productivity/biomass	**Bell 1991 (alga)**; Smithson & Lenne 1996 (plant*); Gruntman & Novoplansky 2004 (plant); **Crutsinger *et al.* 2006 (plant); Dudley & File 2007 (plant); Mattila & Seeley 2007 (invertebrate)**
	Response to disturbance	Schmitt and Antonovics 1986 (plant); Peacock *et al.* 2001 (plant); Boles *et al.* 2004 (bacteria); Hughes & Stachowicz 2004 (plant); Pearman & Garner 2005 (vertebrate); **Reusch *et al.* 2005 (plant)**
	Variability/predictability	Tarpy 2003 (invertebrate); **Jones *et al.* 2004 (invertebrate)**; Gamfeldt & Kallstrom 2007 (invertebrate)
Community-1 trophic level	Invasibility	Weltzin *et al.* 2003 (plant); Crutsinger *et al.* 2008 (plant)
	Species diversity	**Booth & Grime 2003 (plant); Lankau & Strauss 2007 (plant)**
Community-multitrophic	Disease dynamics	Schmid 1994 (plant); Mundt 2002 (plant*); Altizer *et al.* 2003 (host and parasite*); Ferguson *et al.* 2003 (parasite); Crawford *et al.* 2007 (plant) Rauch *et al.* 2007 (parasite)
	Consumer–resource dynamics	**Yoshida *et al.* 2003 (alga); Yoshida *et al.* 2007 (bacteria)**
	Consumer abundance	Power 1988 (plant); Bohannan & Lenski 2000 (bacteria*); Peacock *et al.* 2001 (plant); **Reusch *et al.* 2005 (plant)**
	Consumer species diversity	**Crutsinger *et al.* 2006 (plant); Johnson *et al.* 2006 (plant)**
Ecosystem	Decomposition	**Schweitzer *et al.* 2005 (plant); Madritch *et al.* 2006 (plant)**
	Nutrient cycling	**Hughes & Stachowicz 2004 (plant)**

Bold indicates studies that are discussed in more detail in the text.
*Indicates review article.

mechanisms. For example, Bell (1991) found that mixtures of algal (*Chlamydomonas reindhartii*) genotypes were more productive than monocultures. Because the average performance of mixtures was highly correlated with the performance of the component genotypes in monoculture, the enhanced productivity in mixture likely resulted from the sampling and selection effects, in which one genotype dominated the mixture and drove the observed patterns of performance (Bell 1991). Similar effects have long been recognized in agricultural systems, where increasing the number of genetic varieties of a particular crop species often increases crop yield (Smithson & Lenne 1996), although the sampling effect has generally been inferred rather than tested directly. Consistent with species diversity manipulations (Cardinale *et al.* 2007), negative selection effects have been documented in some systems such as seagrasses, with the most productive genotypes in monoculture actually less common in mixture (Reusch *et al.* 2005).

In the seagrass example above, niche partitioning or facilitation among genotypes outweighed the negative sampling effect, yielding an overall positive effect of

diversity (Reusch *et al.* 2005). Facilitation among genotypes also likely contributed to increasing primary productivity with increasing diversity of the dominant plant *Solidago altissima* (Crutsinger *et al.* 2006). Genotype interactions also contribute to population-level effects of genetic diversity in non-plant systems. For example, single-strain malaria infections exhibit higher parasite density than mixed-strain infections due to competition among strains (de Roode *et al.* 2005). In addition, complementarity in the form of genetic task specialization likely contributes to positive effects of diversity in honey-bee colonies: high-diversity colonies (sired by many males) maintain more uniform temperatures than low-diversity colonies in response to temperature stress, probably because workers vary genetically in the threshold temperature at which they begin their fanning behaviour (Jones *et al.* 2004). More diverse honey-bee colonies also exhibit increased productivity and colony longevity (Mattila & Seeley 2007), although the precise mechanism is not clear. Because there is strong evidence of this genetic task specialization across eusocial insects (Oldroyd & Fewell 2007), a positive effect of diversity

may be common in these species. However, the benefits of diversity do not likely increase indefinitely, as decreased relatedness among members may eventually disrupt colony dynamics.

Community-level effects: same trophic level

Although fewer studies are available, genetic diversity can have community-level effects within the same trophic level (Fig. 2; Table 2). For instance, multi-species communities of grassland plants with higher genetic diversity (per species) maintained higher species diversity over time than did communities with lower genetic diversity (Booth & Grime 2003). In this system, genotype interactions contribute to the effects of diversity (Fridley *et al.* 2007; Whitlock *et al.* 2007): competition depends on the genetic identity of the competitor, not just the species identity (i.e. some genotypes of 'subordinate' species can outcompete genotypes of 'superior' species). Similar intransitive competitive interactions also contribute to species coexistence in another plant community (Lankau & Strauss 2007). In this case, black mustard (*Brassica nigra*) genotypes producing a high concentration of the chemical sinigrin have a competitive edge over other species, but low-sinigrin genotypes outcompete high-sinigrin genotypes. To complete the cycle, low-sinigrin genotypes are inferior to at least three other species (Lankau & Strauss 2007). Thus, in the absence of genetic variation, either *B. nigra* would go extinct (if sinigrin production were low) or it would outcompete other species (if sinigrin production were high) (Lankau & Strauss 2007). These empirical results are consistent with modelling results indicating that increasing genetic diversity within species can have a positive effect on the coexistence of competing species (Vellend 2006). In contrast to these positive effects on coexistence, plant genetic diversity can also inhibit the colonization of novel plant species (including non-natives) by increasing the density of the focal species and thereby reducing available resources for colonizers (Crutsinger *et al.* 2008).

Mechanisms underlying the effects discussed so far apply equally to effects of species diversity as genetic diversity, but mechanisms specific to genetic diversity can also contribute to community-level impacts. The effects of variation in genetic diversity on kin recognition has been implicated in the successful invasion of the Argentine ant (*Linepithema humile*); the low allelic diversity of the invader decreased the precision of the recognition system, allowing this species to form large, competitively dominant super-colonies (Tsutsui *et al.* 2003). Genetic diversity also appears to influence behaviour in this species, with ants from low-diversity colonies showing greater aggression and lower mortality in encounters with ants from high-diversity colonies (Tsutsui 2004). Similar plasticity in response to the relatedness of neighbours has also been demonstrated in plants, with effects on below-ground biomass (Dudley & File 2007).

Community-level effects: across trophic levels

Several recent studies have addressed how plant genetic diversity influences higher trophic levels. The number of plant genotypes affected the arthropod community found on *Oenethera biennis*, translating into positive effects on total arthropod species richness but not total abundance (Johnson *et al.* 2006). Interestingly, the mechanisms underlying these effects differed depending on arthropod trophic level: increases in predator richness and abundance could be attributed to the sampling effect, but spatial and temporal niche complementarity among genotypes contributed to the increase in abundance of omnivorous species. In the seagrass study mentioned above, genotypic richness increased the abundance of seagrass-associated species by increasing plant abundance following disturbance (Reusch *et al.* 2005), while *Solidago* genotypic richness positively affected arthropod species richness by increasing both the total abundance and the diversity of plant resources available (Crutsinger *et al.* 2006). Several recent observational studies also suggest effects of plant genetic diversity on the abundance and/or diversity of invertebrate communities (Wimp *et al.* 2004; Bangert *et al.* 2006; Tovar-Sanchez & Oyama 2006).

Effects of genetic diversity on community dynamics across trophic levels can also occur due to rapid evolution (Pimentel 1968), as illustrated by modified predator–prey and host–pathogen dynamics with and without genetic variation in microcosms of rotifers (predators) and algae (prey) as well as bacteria (host) and phage (pathogen) (Yoshida *et al.* 2003, 2007). As predicted by Doebeli (1997), population fluctuations in these antagonistic interactions can be substantially dampened by adaptive evolution in one of the partners (Yoshida *et al.* 2007).

Ecosystem-level effects

Genetic diversity in dominant plant species can also influence fluxes of nutrients and energy – that is, ecosystem-level processes. In hybridizing cottonwoods (*Populus fremontii*, *Populus augustifolia*), for example, genotypic richness of the leaf litter can have dramatic impacts on the rate of decay and nutrient flux that are comparable with the effects of species diversity in other studies (Schweitzer *et al.* 2005). In this study, it is likely that genetic diversity influenced decomposition and nutrient flux via niche complementarity and non-additive impacts on the decomposer community (Schweitzer *et al.* 2005). Genetic identity and genotypic richness also affect decomposition and nutrient release in aspen (*Populus tremuloides*) forests (Madritch *et al.* 2006).

Similar ecosystem responses to phenotypic diversity in oak (*Quercus laevis*; Madritch & Hunter 2002) suggest these effects may be common, although genetic diversity and environmental variation could not be fully disentangled in this study.

Although primary production of plant communities is often used as an indicator of ecosystem processes, we discuss the productivity under population level effects because in these studies productivitiy is measured from only the focal species.

EFFECTS OF GENETIC DIVERSITY: FUTURE DIRECTIONS

Our review of empirical evidence reveals important ecological consequences of genetic diversity in a wide range of systems and via several different mechanisms, but it also highlights the need for more studies that manipulate genetic diversity. For example, there are clear taxonomic biases in the literature, where studies have focused most on the genetic diversity of vascular plants, with less representation of other organisms such as vertebrates. In addition to further documentation of ecological effects of genetic diversity, we feel that exciting avenues for future research include (i) examining whether the results of genotypic richness manipulations are representative of other diversity metrics, especially genetic variance for phenotypic traits; (ii) quantifying the relative importance of these effects compared with other mechanisms driving ecological patterns and processes; and (iii) explicitly testing the mechanisms driving effects of genetic diversity.

Genotypic richness and other measures of genetic diversity

As mentioned previously, most genetic diversity experiments have manipulated the number of genotypes or clones. These studies have generated important insights, with experimental designs analogous to experiments on the effects of species diversity (Hooper *et al.* 2005). However, it is not clear that the results of these studies reflect the potential ecological consequences of variable levels of quantitative trait variance, or of genetic diversity in sexual populations more generally. As described earlier, if genotypes are drawn randomly from a given genotype pool, mean genetic variance for quantitative traits (the mean across experimental replicates) increases from one- to two-genotype populations, but it may not increase further with additional genotypes (Fig. 2d). Beyond two, genotypic richness represents simply the number of unique trait values in the population (assuming no two genotypes have identical trait values). However, this leads to the interesting conclusion that when an ecological response of

interest changes as a function of genotypic richness (beyond two genotypes), as found in a number of studies (Hughes & Stachowicz 2004; Crutsinger *et al.* 2006; Johnson *et al.* 2006), the underlying mechanism(s) must involve the number of different trait values rather than variance in quantitative traits. Differences between monocultures and multi-genotype treatments may or may not be due to a difference in trait variance *per se*. Thus, these experiments do not permit conclusions on the ecological consequences of different levels of variance in quantitative traits, which is typically what gets measured in evolutionary ecology or ecological genetics. Overcoming the logistical difficulties of manipulating quantitative trait variance directly is an important challenge for future studies (Underwood 2004).

Two additional limitations of most experiments to date, and therefore challenges in future experiments, are also worth noting. First, manipulating the number of clones (and following only those clones) negates the possibility of the creation of novel genotypes through sex and recombination – an important potential consequence of genetic diversity that generally does not apply to other levels of biodiversity. In addition, experiments to date have typically minimized variation in the evenness of genotypes; this can be an important component of biodiversity, as demonstrated in some studies of effects of species diversity on ecosystem function (Hooper *et al.* 2005).

Relative importance

In addition to expanding the scope of genetic diversity experiments to include other genetic diversity metrics in multiple systems, we need to understand the magnitude of these effects and their importance relative to other factors (Fussmann *et al.* 2007; Johnson & Stinchcombe 2007). In some manipulations, plant genetic diversity can explain as much of the variation in the response of interest (e.g. arthropod species richness, decomposition) as species diversity in comparable experiments (Schweitzer *et al.* 2005; Crutsinger *et al.* 2006; Johnson *et al.* 2006). However, species diversity research indicates that the effects of diversity revealed in controlled, small-scale manipulations can be swamped by other factors in more natural settings or by larger-scale processes (Levine 2000; Stachowicz & Byrnes 2006). Evidence thus far from studies of genetic diversity in natural populations is mixed, suggesting that genetic diversity can sometimes, but not always, have effects of sufficient magnitude to influence population and community processes. For example, plant (cottonwood, *Populus* sp.) population genetic diversity was significantly correlated with arthropod species diversity, explaining nearly 60% of the variation among natural stands (Wimp *et al.* 2004). However, factors such as

genetic identity or environment can overwhelm effects of genetic diversity in other cases (Madritch *et al.* 2006). Thus, in addition to documenting the presence and strength of genetic diversity effects in experimental manipulations, we need to examine the relative importance of genetic diversity and other factors in natural populations. One approach to do so would be to experimentally manipulate multiple factors, including genetic diversity, across realistic ranges of values, or to compare small-scale experimental results to larger-scale patterns observed in the field.

Identifying mechanisms

Although ecological effects of genetic diversity depend upon a strong association between genotype and phenotype, few studies in this field have quantified the specific phenotypic traits underlying genetic diversity effects (but see Schweitzer *et al.* 2005; Wimp *et al.* 2004; Lankau & Strauss 2007). In contrast, evolutionary biology provides a rich history of studies examining genotype–phenotype links (Wright 1920; Ford 1964). More recently, detailed analyses of genetic polymorphisms (e.g. Schemske & Bierzychudek 2001) have enhanced our understanding of natural selection and its ecological relevance in natural communities. We suggest that future studies of the ecological effects of genetic diversity should draw on classic approaches in evolutionary biology to identify genotype–phenotype relationships, which should advance our mechanistic understanding of genetic diversity effects.

The range of possible mechanisms for ecological effects of genetic diversity is large, and relatively few studies have clearly distinguished among potential mechanisms; this is also true of research on ecological effects of species diversity (e.g. Cardinale *et al.* 2007). In addition, methods from the species diversity literature are seldom applicable to differentiating among mechanisms of genetic diversity. For example, the approach of Loreau & Hector (2001) would fail to distinguish an ecological 'selection effect' – which can also be caused by plastic responses – from potential effects of natural selection that causes trait evolution (Cardinale *et al.* 2007). Although documentation of net effects of genetic diversity can have important implications for applied research (Zhu *et al.* 2000), without information about the mechanisms that underlie these effects it will be difficult to reach general conclusions or make predictions about the consequences of changes in genetic diversity. More generally, understanding mechanisms for ecological effects of genetic diversity can improve our understanding of the interplay between evolutionary and ecological processes and help to reconcile seeming disparities among studies. As a way forward, we propose that a first step is to construct models for expectations under additive effects of diversity

(see 'Mechanisms and expectations' above). Deviations from these expectations can be used to identify when effects of diversity are due, at least in part, to non-additive mechanisms.

A focus on identifying mechanisms will usually require that researchers go beyond measuring a single response over different levels of genetic diversity. Quantifying ecological mechanisms will also require data on the traits of each genotype alone and in genetically diverse populations. For example, evaluating associational resistance would require determining whether the resistance of individual genotypes is influenced by the presence of neighbouring genotypes. Evaluating the components of an observed complementarity effect would require measurements of resource use profiles for different genotypes in monoculture and in genetic mixtures (Kahmen *et al.* 2006); a change in resource use would implicate facilitation as opposed to niche partitioning.

For some studies, especially those that last multiple generations, there is an additional potential for evolutionary mechanisms to be important. Despite a growing number of examples of rapid evolution (Hairston *et al.* 2005), few experiments have examined how changes in the relative abundance of genotypes over time contribute to the ecological effects of genetic diversity (Bohannan & Lenski 2000; Whitlock *et al.* 2007). In sexual populations, following the fates of individual genotypes for more than one generation is not possible because every individual within the population is a unique genotype. Even in cases where molecular markers are available, recombination can quickly dissolve linkage between neutral molecular markers and genes with ecological effect. If evolutionary mechanisms are likely to be important, ancillary experiments will be necessary to quantify heritable variation in the ecologically relevant traits, patterns of selection on these traits and genetic aspects of phenotypic plasticity.

In discussing mechanisms for the effects of genetic diversity, we have emphasized distinctions that hinge on whether genotypes express different phenotypes in mixtures and in isolation. An example of this is the additive sampling effect, where the productivity of plant genotypes is equal in monocultures and mixtures, vs. a non-additive facilitation effect where the productivity of plant genotypes might be greater in mixtures than in monocultures. Thus, characterizing the phenotypic expression of genotypes under different conditions will be important to distinguishing additive and non-additive effects.

WHEN SHOULD GENETIC DIVERSITY BE IMPORTANT?

Clearly, genetic diversity will not always be an important driver of ecological processes. We argue that genetic

diversity will have its largest ecological effects when four non-exclusive conditions are met. First, when a community or ecosystem is dominated by one or a few primary habitat-providing species (Whitham *et al.* 2006), genetic diversity can play a role similar to species diversity in other systems (Crutsinger *et al.* 2006). Interestingly, relatively few of the studies we examined focused on the genetic diversity of foundation species. However, the most wide-ranging effects (i.e. at the ecosystem level) all result from changes in diversity within habitat-forming plant species (Table 2), suggesting that greater focus should be placed on the genetic diversity of these dominant species. Second, when genetic diversity in one species affects the abundance or distribution of a keystone species (i.e. a species with an effect disproportionate to its biomass in the community), it can have large indirect ecological impacts (Whitham *et al.* 2003; Crawford *et al.* 2007). Third, an obvious yet nonetheless important prediction is that genetic diversity will only have prominent ecological effects for species that exhibit measurable genetic diversity within populations for relevant traits, and thus these effects cannot be assumed in the absence of genetic diversity data. For example, populations that are highly selfing, inbred or have experienced a recent selective sweep for genes controlling ecologically important traits will likely exhibit low genetic diversity. Finally, given the documented importance of genetic diversity (Hughes & Stachowicz 2004; Reusch *et al.* 2005) and species diversity (Hooper *et al.* 2005) for disturbance response and stability, we predict that genetic diversity will be most relevant in highly variable environments or those subject to rapid anthropogenic change.

Multiple unidirectional ecological relationships can occur simultaneously, leading to reciprocal effects and the potential for feedbacks (Fig. 1; Agrawal *et al.* 2007; Hughes *et al.* 2007). Like species diversity, genetic diversity can be both a cause and consequence of ecological processes (Vellend & Geber 2005). For example, genetic diversity enables prey populations to evolve, which can affect predator population dynamics and in turn drive further ecological and evolutionary changes within the prey population, leading to predictable predator–prey eco-evolutionary dynamics (Abrams & Matsuda 1997; Yoshida *et al.* 2003). In addition, genetic variation in one species can allow for coexistence with its competitors, while at the same time, competitor species diversity maintains this genetic variation (Lankau & Strauss 2007). There are undoubtedly numerous additional reciprocal effects between genetic diversity and ecological factors (Fussmann *et al.* 2007), as genetic diversity and evolutionary processes can influence a range of population, community and ecosystem responses (see above) that are known to produce changes in allele or genotype frequency (Fussmann *et al.* 2007).

CONCLUSION

It is clear that the level of genetic diversity within a population can affect the productivity, growth and stability of that focal population, as well as inter-specific interactions within communities, and ecosystem-level processes. The key now is to identify how widespread these patterns are and how important genetic diversity is relative to other ecological factors typically studied in ecology. To do this, we will need a better understanding of the mechanisms contributing to documented effects. In addition, we need to study the ecological effects of genetic diversity in a wider diversity of systems and using a broader array of observational and experimental approaches that incorporate genetic richness, variance and evenness. Finally, long-term studies that focus on the interplay between the ecological and evolutionary effects of genetic diversity will go a long way towards determining when and where genetic diversity will be important in ecological research. Ultimately, the ability to predict responses as we assemble (or disassemble) populations and communities with different levels of genetic diversity has important applications in conservation, restoration and agriculture, and can improve our understanding of the interplay between evolution and ecology.

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