REVIEWS AND SYNTHESES

Connections between species diversity and genetic diversity

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Abstract

Species diversity and genetic diversity remain the nearly exclusive domains of community ecology and population genetics, respectively, despite repeated recognition in the literature over the past 30 years of close parallels between these two levels of diversity. Species diversity within communities and genetic diversity within populations are hypothesized to co-vary in space or time because of locality characteristics that influence the two levels of diversity via parallel processes, or because of direct effects of one level of diversity on the other via several different mechanisms. Here, we draw on a wide range of studies in ecology and evolution to examine the theoretical underpinnings of these hypotheses, review relevant empirical literature, and outline an agenda for future research. The plausibility of species diversity–genetic diversity relationships is supported by a variety of theoretical and empirical studies, and several recent studies provide direct, though preliminary support. Focusing on potential connections between species diversity and genetic diversity complements other approaches to synthesis at the ecology–evolution interface, and should contribute to conceptual unification of biodiversity research at the levels of genes and species.

Keywords

Biodiversity, coexistence, community ecology, drift, genetic diversity, migration, neutral model, population genetics, selection, species diversity.

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INTRODUCTION

Individual organisms within a community may represent different species or different genetic variants within species. The birth, death and movement of individuals determine the dynamics of both populations and communities, and therefore both genetic diversity within populations and species diversity within the community. Species diversity and genetic diversity have traditionally received independent treatment by community ecologists and population geneticists, respectively, despite repeated recognition in the literature over the past 30 years of potential connections between these two most fundamental levels of biodiversity (Antonovics 1976, 1992, 2003; Harper 1977; Huston 1994; Hairston *et al.* 1996; Amarasekare 2000; Kassen 2002; Chave 2004). The recent emergence of 'community genetics' (Antonovics 1992) as 'the study of the interaction between genes within a species and populations of other species in a community' (Agrawal 2003) has revived intense interest in understanding the interplay between ecological and evolu-

tionary processes in determining community structure and dynamics. Elucidating the different ways in which species diversity and genetic diversity may be linked promises to help achieve this goal, and to provide a basis for conceptual unification in biodiversity research. Here we review the hitherto loosely associated set of ideas pointing to connections between species diversity and genetic diversity, drawing on basic theory in ecology and evolution to provide a conceptual framework and agenda for research on links between these two levels of biodiversity.

Species diversity and genetic diversity may be related in three main ways (Fig. 1); these cases are not mutually exclusive. If locality characteristics (or any common cause) influence the two levels of diversity in a parallel manner (Fig. 1, case I), a positive correlation between them may result. To the extent that genetic variation determines a population's demographic performance and viability, or that genetic variation in a dominant species determines the biotic environment experienced by the rest of the community, species diversity may be causally influenced by genetic
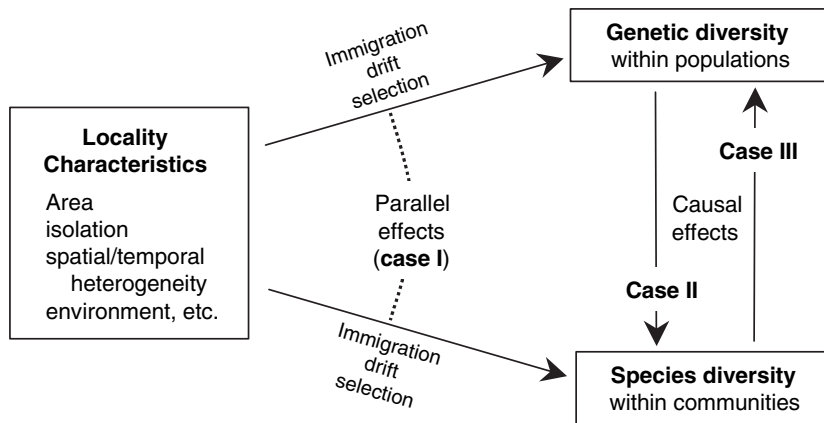
Figure 1 Potential connections between species diversity and genetic diversity.

diversity within component species (case II). Conversely, if the species diversity of a community influences the selection regime experienced by component populations, genetic diversity may be causally influenced by the diversity and relative abundances of coexisting species (case III). These simple depictions belie a tremendous degree of complexity in the details of how species diversity and genetic diversity may be related. In this paper, we outline the theoretical underpinnings of each of the three general hypotheses, highlighting relevant empirical studies, gaps in our knowledge and key observations or experiments needed to fill these gaps.

A vast literature falls under the general themes of species and genetic diversity. A narrowing of scope is therefore needed to restrict attention to the key points of contact between the two levels of diversity. First, we will consider only 'local' diversity measured in patches of habitat or experimental plots ('localities') within a single region. In the framework presented here, genetic diversity within particular species must be measured or manipulated in different localities; when considering diversity patterns at large spatial scales (e.g. latitudinal gradients), this is not possible even in theory because variation in species diversity is often accompanied by complete turnover in species composition (i.e. none of the species can be sampled in all localities). Second, at the community level, we only consider diversity within a single trophic level. Different genotypes of the same species may interact in much the same way as different species within a trophic level, but there is no population-level analogue for multitrophic interactions, except perhaps in the special case of cannibalism. Additional constraints that define our domain of application are presented in subsequent sections. Following Chase & Leibold (2003), we use the Tilman (1982) resource competition model in several sections for the purpose of graphical illustration of theoretical concepts. Our conceptual framework is not limited to communities in which resource competition

controls dynamics, but this model provides an intuitively straightforward basis for illustrating selected examples.

DEFINITIONS

Species diversity and genetic diversity can be defined, measured or manipulated in a number of different ways. Species diversity is most often measured as species richness, the number of species in a given locality. In studies that experimentally manipulate species diversity (reviewed by Loreau *et al.* 2001), it is also most often species richness that is varied among treatments. Several indices of species diversity incorporate information about the relative abundances of species in a locality, with higher diversity indicated by a more even distribution of abundance among species – higher 'evenness' (Magurran 2004). This paper is concerned largely with species richness.

When discrete alleles or genotypes can be distinguished in a population, as in studies employing molecular markers, measurements of genetic diversity are closely analogous to those of species diversity. Allelic or genotypic richness is the number of different alleles or genotypes, respectively, in a population. The probability that two randomly chosen alleles or genotypes are different is equivalent to the Hardy–Weinberg expected heterozygosity when estimated for loci in the nuclear genome of diploid organisms, and is also referred to as 'gene diversity' for other kinds of genetic markers (Nei 1987). Gene diversity is identical to the Simpson index of species diversity (Magurran 2004). With DNA sequence data, nucleotide diversity (π) is the equivalent of gene diversity for individual nucleotide positions rather than loci, and nucleotide polymorphism (θ) is the proportion of nucleotide positions that are variable, or segregating, in a sample of sequences. For quantitative traits, genetic diversity is measured as the genetic variance, or the component of the total phenotypic variance in a population attributable to genetic differences

among individuals (Falconer & Mackay 1996). The relative magnitude of quantitative genetic variance in large numbers of populations of the same species is reported far less frequently than genetic diversity at loci with discretely recognizable variants (e.g. molecular markers), and is also quite difficult to manipulate experimentally (we return to the latter issue later in this paper.) For this reason, our arguments in this paper pertain largely to genetic diversity measured using discrete alleles or genotypes, although it is important to note that the component of quantitative genetic variance that is inherited additively is directly related to heterozygosity at the underlying loci (Falconer & Mackay 1996).

Genetic diversity can be measured for traits that are neutral (often assumed for molecular markers) or traits that are under selection. This distinction has important implications for predicting either the effects of different processes on genetic diversity, or the effects of genetic diversity on population or community characteristics. These differences are highlighted in the Theoretical underpinnings section below.

For natural or experimental populations comprised of clonal, non-recombining genotypes, as in many populations of bacteria, zooplankton and clonal or apomictic plants (at least over short periods of time), the measurement and manipulation of genetic diversity is exactly analogous to that of species diversity. For simplicity, our theoretical illustrations using the resource competition model consider genetic diversity as the number of clonal genotypes in a given species. We consider cases in which the interest is in genetic diversity in one particular focal species, and also cases in which the interest is in genetic diversity in each of two or more competing species, although in most empirical studies genetic diversity is measured in only one species from the community. In all cases, we are interested in genetic diversity within populations of particular species.

THEORETICAL UNDERPINNINGS

Parallel processes – case I

Theories of species diversity and genetic diversity share many striking similarities, to the point that individual models are often described as applying equally well to both (e.g.

Amarasekare 2000; Chase & Leibold 2003). Empirical data have revealed a predominance of positive relationships between species diversity and genetic diversity (see section Empirical research past and future), and here we focus on potential processes acting in parallel at the two levels that may create such relationships in the absence of direct causal effects of one level of diversity on the other.

Genetic diversity is controlled by four processes, mutation, drift, migration and selection, each of which has an analogue at the level of species diversity (Table 1). Speciation creates new species much as mutation creates new alleles. However, because speciation and mutation occur on very different time scales and speciation is unlikely to explain variation in diversity among localities within a region (but see Losos & Schluter 2000), we restrict our attention to the remaining three processes, which may create variation in diversity among localities in very similar ways at the two levels.

Drift and migration

As a necessary consequence of populations and communities being comprised of finite numbers of individuals, both genes and species are prone to random fluctuations in abundance (i.e. drift), possibly to the point of local extinction. Immigration may provide new species or novel alleles at one or more loci that counteract the effects of drift. Drift and migration influence species and genetic diversity in fairly similar and straightforward ways (but see section Caveats). Neutral diversity is regulated almost entirely by the action of drift and migration (plus mutation and speciation; Kimura 1983; Hubbell 2001), but these processes can also have important effects on non-neutral diversity (e.g. Lenormand 2002; Mouquet *et al.* 2004; Vellend 2005). The effects of drift and migration are frequently manifested as positive correlations of diversity with the area or connectivity of localities (Rosenzweig 1995; Frankham *et al.* 2002), and these variable locality characteristics may, in turn, drive positive correlations between species diversity and genetic diversity (Vellend 2005).

Selection and environmental heterogeneity

The influence of selective processes on diversity is considerably more complex than that of neutral processes. Only non-neutral genetic diversity is relevant here, except to the extent that selection may alter overall population size,

Table 1 Processes that influence diversity, defined to emphasize the parallels at the levels of genetic diversity and species diversity

Mutation/speciation: the creation of new alleles/species
Drift: random changes in the relative frequencies of alleles/species
Migration: movement among populations/communities of alleles/species
Selection: processes that favour particular alleles/species over others

and therefore genetic diversity for neutral traits as well. At the most basic level, selection favours some individuals over others and these individuals may represent different species or different genetic variants within species. There are far too many selection-based theories of diversity in community ecology to deal with individually, so to determine which theories may be relevant to explaining correlated patterns of species and genetic diversity, it is useful here to highlight the subtle distinction between models of species coexistence, and models of diversity patterns in space or time. Studies of coexistence generally aim to discover processes that prevent one type dominating all others (Gause 1934). As such, models of coexistence are often applied to understanding community dynamics at a single locality, and may or may not help explain why one place has more diversity than another. In the context of this review, the only mechanisms of coexistence that need be considered are those in which the strength of the underlying process varies among localities. As will be explained below, for some mechanisms this is plausible, while for others it is not.

Spatial and temporal heterogeneity in the environment may create diversifying selection that is thought to be a powerful mechanism of maintaining both species diversity and genetic diversity and so may generate correlations between them. Different species or genotypes can coexist if species- or genotype-specific fitness varies in space or time such that each type is favoured over the others in enough places or at enough times to avoid local extinction in the long term (Chesson 2000; Barot & Gignoux 2004). The spatial or temporal environmental heterogeneity can be of two general types. Exogenous heterogeneity includes spatial or temporal variation in factors such as soil characteristics or climate. Such heterogeneity is ubiquitous in nature (Bell *et al.* 1993), and because localities may vary in the magnitude of internal heterogeneity, they may also differ in diversity (e.g. Tews *et al.* 2004). Endogenous heterogeneity arises from the activities of organisms themselves. For example, if some species or genotypes have high survival rates in the face of competition but low colonization rates of newly opened microsites, or *vice versa*, coexistence of many species is possible (Tilman 1994). However, given the same potential species pool in different localities, it is difficult to imagine how the strength of such a process could vary among localities in such a way as to drive patterns of species and genetic diversity in predictable and parallel ways, even though colonization–competition tradeoffs may operate both within (e.g. Solbrig & Simpson 1974) and among species (Tilman 1994). On the other hand, if spatial or temporal variability in the identity of neighbours (i.e. competitors) is considered a source of endogenous heterogeneity (Huston & DeAngelis 1994), the potential arises for direct effects of one level of diversity on the other. This potential is addressed in subsequent sections.

Simultaneous responses of species diversity and genetic diversity

The preceding discussion points to three variable locality characteristics as strong candidates for having parallel effects on, and creating correlated patterns in, species diversity and genetic diversity. Locality area influences both levels of diversity via drift; isolation via immigration; and exogenous heterogeneity via spatially or temporally varying selection. We do not consider variation among localities in average environmental quality (e.g. productivity and soil moisture) to be a likely driver of parallel variation in species and genetic diversity. Although average environmental conditions are often strong predictors of diversity, the underlying mechanisms are likely to vary among systems (e.g. Waide *et al.* 1999), and each species is likely to respond individualistically to the environment, so we cannot make any general predictions about parallel effects on species and genetic diversity. This represents an important limit to the domain of application of the present approach.

While the factors that influence species diversity and genetic diversity in isolation have received thorough theoretical treatment, relatively little is known about the simultaneous response of the two levels of diversity to variable locality characteristics. Figure 2 illustrates one scenario in which environmental heterogeneity may increase both species diversity and genetic diversity when species and genotypes compete for resources. A recent modelling study of both levels of diversity under a range of scenarios produced some results that adhere to expectations based on separate community and population models, while other results were more surprising (Vellend 2005). In this individual-based and spatially explicit simulation model of plant communities, locality area and immigration rate had universal positive effects on both species diversity and genetic diversity, regardless of whether or not variants were neutral with respect to selection (Vellend 2005). Area and isolation drove positive correlations between species diversity and genetic diversity and the correlations were stronger when genetic diversity was measured for common vs. rare species. In these models, spatial environmental heterogeneity always had a strong positive effect on species diversity by allowing coexistence of species with fitness optima at different positions along an environmental gradient. However, although genotypes differed within species in much the same way that species differed within the community, the effects of environmental heterogeneity on genetic diversity were highly variable and context dependent. If the total number of individuals in a locality is fixed (the zero-sum assumption, which is equivalent to 'soft' selection), adding species to the community by increasing heterogeneity necessarily reduces the average population sizes of the component species. As a result, the interacting effects of diversifying selection and population size – both of
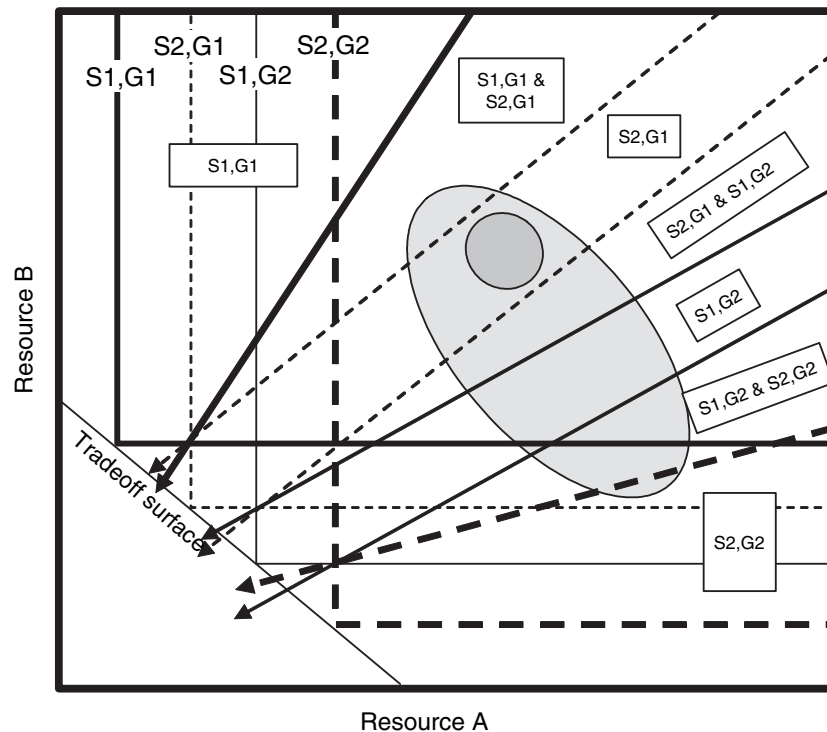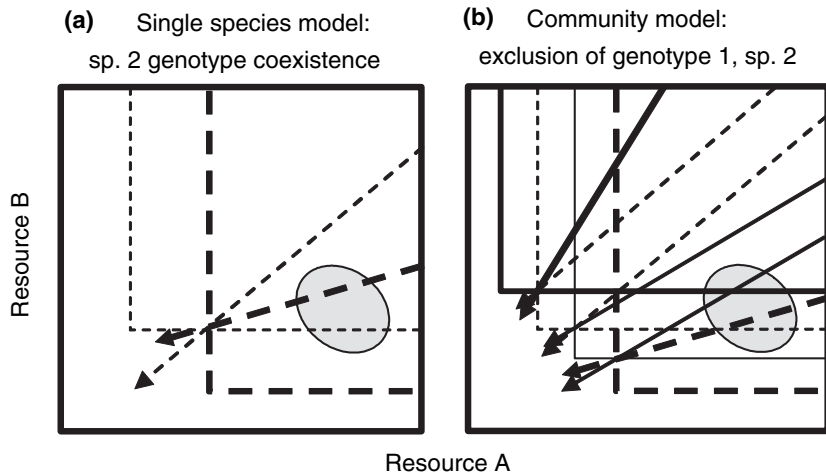
Figure 2 Environmental heterogeneity increases both species diversity and genetic diversity. In this graphical representation of the Tilman (1982) model of competition for two essential resources, vertical and horizontal lines indicate the zero-net-growth-isoclines (ZNGIs) for two genotypes (G1 and G2) in each of two species (S1 and S2). ZNGIs define the resource levels below which a genotype cannot maintain itself, and arrows represent the relative rates of consumption of the two resources (consumption vectors) of each genotype. Genotypes show tradeoffs in their response to (ZNGI) and effect on (consumption vector) the two resources; thus, the genotypes with ZNGIs toward the upper left of the tradeoff surface have a high requirement for resource B, a low requirement for resource A, and a greater effect on resource B than A (i.e. a steep consumption vector). The species/genotypes listed in boxes indicate those that will coexist at equilibrium given different possible resource supply points; the positions of consumption vectors are drawn to delineate these coexistence regions (their direction is constant throughout the bivariate space). Resource supply points define the supply of the two resources by the environment (see Chase & Leibold 2003 for details). At low environmental heterogeneity (range of resource supply points in dark shaded region), species 2, genotype 1 excludes all other types. At high heterogeneity (resource supply points in light shaded region) both genotypes of both species coexist. The scenario here of genotypes across different species showing significant overlap in their competitive characteristics is supported by empirical data, particularly for plants (Aarssen 1983; Aarssen & Turkington 1985).

which change with increasing heterogeneity – caused genetic diversity to vary with species diversity in several different ways depending on the fitness optimum and abundance of the species for which genetic diversity was measured; positive, negative and unimodal relationships were all observed. The key insight here was that single species models of genetic diversity, which predict positive relationships between diversity and heterogeneity, might fail when individual fitness depends strongly on community context. An illustration of this latter point using the graphical resource competition model is shown in Fig. 3. There is clearly a wealth of opportunities for further theoretical work addressing the simultaneous response of diversity within and among species to different locality characteristics.

Differences in underlying processes
Before moving on, it is important to recognize what is probably the most fundamental 'difference' between factors influencing the two levels of diversity. Recombination and interactions among alleles and loci within individuals can play an important role in regulating genetic diversity, but have no obvious analogue at the level of species diversity (Antonovics 1976, 1978; Hairston *et al.* 1996), except perhaps in the special case of horizontal gene transfer between bacterial taxa (Ochman *et al.* 2000). However, when genetic variance for particular traits is largely additive, models for diploid organisms are qualitatively very similar to models for haploids (Hartl & Clark 1997); haploid models of genetic diversity are, in turn, essentially identical to models of species diversity. Although the genetic architecture of

(a) Single species model:
sp. 2 genotype coexistence

(b) Community model:
exclusion of genotype 1, sp. 2

Figure 3 Maintenance of genetic diversity depends on community context. Using the framework from Fig. 2, both genotypes of species 2 coexist when competing alone, given the range of resource supply points in the shaded area. When both genotypes of both species are present, only genotype 2 of species 2 persists, along with genotype 2 of species 1.

particular traits in particular species is highly case specific, genetic diversity is often correlated with locality character-istics such as area, isolation, and habitat heterogeneity (Frankham *et al.* 2002) – the same variables that often correlate with species diversity (Huston 1994; Rosenzweig 1995). Our thesis is that the similarities between processes influencing species and genetic diversity outweigh their differences. Only empirical data can resolve the issue.
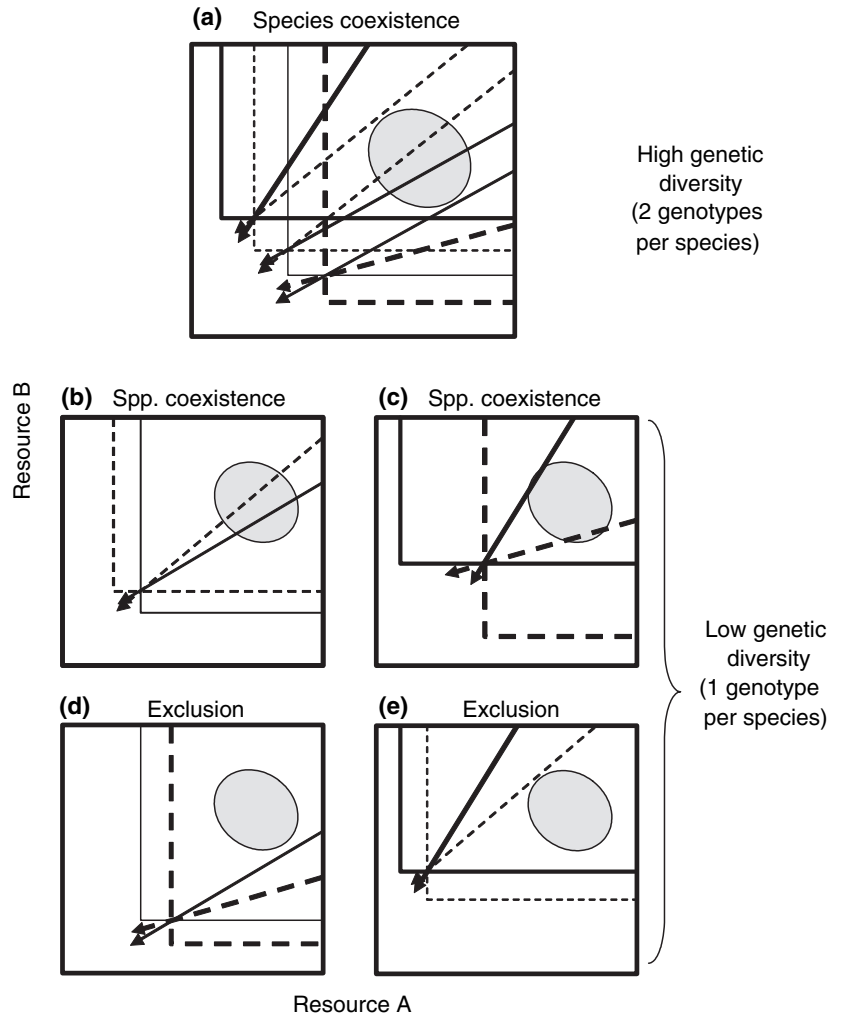
Effects of genetic diversity on species diversity – case II

The population-level consequences of genetic diversity are well-studied theoretically, having long attracted attention from evolutionary biologists interested in the consequences of sexual reproduction (e.g. Williams 1975), and more recently from conservation biologists concerned about the consequences of declines in population-genetic variation (Frankham *et al.* 2002). Here the relevant genetic diversity is for traits related directly or indirectly to individual fitness, and the interest is in the consequences of genetic diversity, not necessarily its causes. Genetic diversity can enhance population fitness and therefore decrease extinction risk under a variety of scenarios, a full accounting of which is beyond the scope of this review. The three primary mechanisms are: (i) if different genotypes have comple-mentary resource use (Antonovics 1978); (ii) if genetic diversity provides insurance in the face of spatial or temporal environmental variability (Williams 1975) and (iii) if genetic diversity provides a buffer against the negative effects of enemies (Burdon 1987). When relatively constant environ-mental conditions favour particular alleles or genotypes, genetic diversity may in fact reduce population fitness, but in these cases this 'genetic load' is expected to be purged relatively quickly (Crnokrak & Barrett 2002).

The population-level effects of genetic diversity in a single species may extend to the community level if the community consists of relatively few species, or if the focal species is numerically dominant (Whitham *et al.* 2003). Losing one species from a species-poor community (because of limited genetic diversity) represents a significant change. For community dominants, at least two scenarios can be postulated under which genetic diversity may affect species diversity. First, different species may be favoured in competition with different genotypes of the dominant, such that genetic diversity represents a form of spatially varying selection; this is the 'diversity begets diversity' hypothesis (Whittaker 1975) recast to cross organizational levels from genes to species. Second, genetic diversity in the dominant may enhance productivity or efficiency of resource use, such that other species will tend to be excluded from the community. This is a variation on the Elton (1958) hypothesis that diversity lowers community invasibility; the predicted effect of genetic diversity on species diversity is negative.

What happens to species diversity if all (or multiple) species in a community have low or high genetic diversity? If population dynamics of different species are more or less independent, species diversity may be reduced where genetic diversity is low simply because each species is more likely to go locally extinct. In competitive communities, the conse-quences of reduced genetic diversity across all species may also ultimately reduce species diversity because evolution requires the existence of genetic diversity, and co-evolution of competitors may promote their coexistence (MacArthur & Levins 1967; Pimentel 1968; Aarssen 1983; Taper & Case 1992). Simple competition models can be modified to include variation among genotypes within a species (Levin 1971; León 1974), and under some conditions these models imply that coexistence may be enhanced by the possibility of sorting among genotypes (e.g. Fig. 4). In the example of Fig. 4a, genetic diversity within species is ultimately lost via competitive exclusion of genotypes, so it is initial genetic

Figure 4 Genetic diversity promotes species diversity. For the range of resource supply points indicated by the shaded area, the two species coexist when all genotypes are present (a). For the four pair-wise combinations of one genotype per species (b–e), in two of four cases one species excludes the other.

diversity that ultimately promotes species coexistence. In a more complex model of forest dynamics, Clark *et al.* (2004) have recently shown that differences among individuals within species in their response to environmental conditions can make a large contribution to stochasticity in recruitment, which, in turn, can promote coexistence by ensuring that different species have advantages at different places and times. Genetic diversity seems a likely source of at least some of this interindividual variation.

Effects of species diversity on genetic diversity – case III

Populations evolve in a community context and species diversity in the community may represent an important component of the selection regime experienced by each species' population. Two main hypotheses propose causal effects of species diversity on genetic diversity. Again, these are variants of the hypotheses that diversity reduces invasibility (Elton 1958) and that diversity begets diversity

(Whittaker 1975), this time with the causal arrow pointing from the community to the population. First, if a diverse community of competitors constrains the ability of a focal species to utilize different parts of a heterogeneous environment, species diversity may act as a source of stabilizing selection. Only a subset of a species' genotypes may be able to coexist with a diverse community of competitors, whereas a wider range of genotypes may be able to coexist with only a few different competitors (Fig. 5). This idea is also related to Van Valen (1965) 'niche variation' hypothesis, which states that species' niche breadths should be greater in species-poor vs. species-rich communities; if greater niche breadth means greater genetic diversity, the prediction is a negative effect of species diversity on genetic diversity. The second hypothesis proposes that species diversity acts as a source of diversifying selection because different species favour different genotypes of the focal species in competition (Harper 1977); the prediction, then, is a positive effect of

(a) 3 species model:
1 genotype of sp. 2 persists

(b) 2 species model:
both genotypes of sp. 2 persist
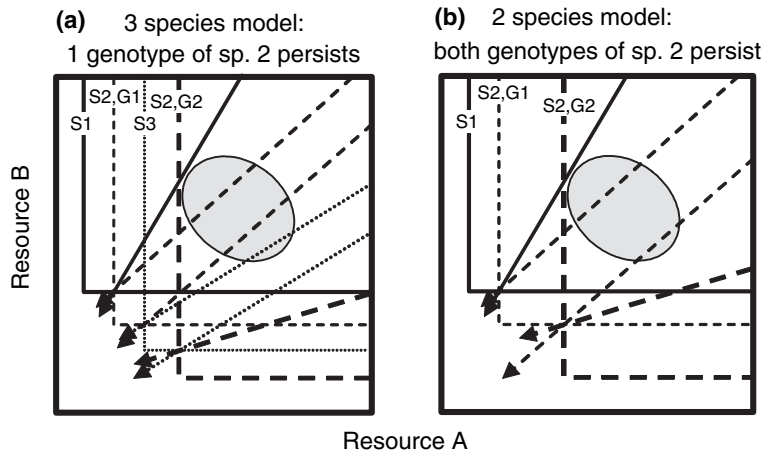
Figure 5 Species diversity reduces genetic diversity. In this scenario, two genotypes of species 2 compete with one genotype of either one or two other species. For the range of resource supply points indicated by the shaded area, only one genotype of species 2 coexists with species 1 and 3 (a), but both genotypes can coexist with only species 1 (b).

species diversity on genetic diversity. Both hypotheses assume non-neutral genetic variation.

If the total number of individuals in a community is fixed (the zero-sum rule), species diversity may also influence genetic diversity via its effects on population size (C. Wehenkel, F. Bergmann and H.-R. Gregorius, unpublished work; Vellend 2005). In zero-sum communities, adding species to a community necessarily decreases average population sizes of the component species. If these decreases are sufficiently severe, genetic diversity for both neutral and non-neutral traits may also decrease because of drift. The likelihood of this mechanism operating may depend on the process causing variation in species diversity in the first place. In one set of simulations in Vellend (2005), higher immigration rate caused species diversity to increase, but most new species remained sufficiently rare that changes in population size were minor and the positive effect of immigration rate dominated the genetic response. By contrast, in other simulations, increasing spatial environmental heterogeneity permitted species adapted to initially rare environmental conditions to increase in abundance to the point that population sizes and genetic diversity of the remaining species were drastically reduced (Vellend 2005).

EMPIRICAL RESEARCH PAST AND FUTURE

A number of studies have asked whether species diversity and genetic diversity co-vary in nature, in some cases using statistical approaches to assess possible underlying processes. Very few studies have focused explicitly on evaluating the potential for different processes to act as described in the preceding sections. However, many studies have addressed some of the conditions that point to the plausibility of the hypotheses outlined in Fig. 1. In the subsequent sections, we first summarize what is known

about empirical patterns of co-variation between species diversity and genetic diversity. We then draw on a broader literature to evaluate the likelihood of different processes connecting the two levels of diversity, and we point to important future directions.

Patterns

Are species diversity and genetic diversity related in non-random ways in nature? The answer appears to be yes. In the first data compilation focused explicitly on this question, Vellend (2003) analysed 14 data sets from the literature on islands and found that the median correlation coefficient between species richness and genetic diversity at molecular-marker loci was 0.63, significantly greater than zero. We have added three more recent data sets to this compilation (Table S1), and they confirm the result of a tendency for positive, and sometimes strong, species diversity–genetic diversity correlations on islands (Fig. 6a).

In mainland habitats, six relationships between species diversity and genetic diversity have been reported in the literature. Significantly positive relationships were reported by Morishima & Oka (1979) for weed species diversity × morphological variation in West African rice populations, and by Vellend (2004) for plant species diversity × molecular-marker diversity in populations of *Trillium grandiflorum* in eastern North American forest fragments. Significantly negative correlations were reported by Karlin *et al.* (1984) for allozyme heterozygosity in the salamander *Desmognathus fuscus* × the number of co-occurring congeners in eastern North America, and by Wehenkel *et al.* (C. Wehenkel, F. Bergmann and H.-R. Gregorius, unpublished work) for tree species diversity × allozyme heterozygosity in beech (*Fagus sylvatica*) populations in Germany. Wehenkel *et al.* also found a non-significant correlation for allozyme heterozygosity in spruce (*Picea abies*), and Odat *et al.*
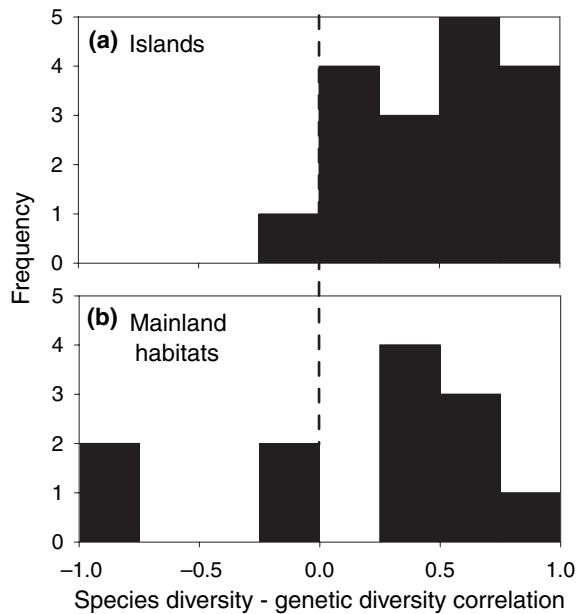
Figure 6 Empirical Pearson correlations between species diversity and genetic diversity in (a) 17 data sets for oceanic islands (from Vellend 2003 and Table S1) and (b) 12 data sets for mainland habitats (from Table S1).

(2004) found no significant relationship between amplified fragment length polymorphism (AFLP) variation in *Ranunculus acris* populations and plant species diversity in their grassland habitats in Germany.

By matching community and genetic studies from the literature (and in some cases requesting raw data from authors), we have calculated six additional species diversity–genetic diversity correlations for mainland habitats (Fig. 6b; Table S1). Although the number of data sets is fairly small, and the samples sizes sometimes quite low (data sets were included with as few as five sampling sites), the mainland correlations are mostly positive and they appear to show more variability than the island data sets (Fig. 6). Interestingly, the mean and median of the absolute values of the mainland correlations (0.50 and 0.49) differ highly significantly from that expected under a null hypothesis of no correlation. That is, species diversity and genetic diversity tend to be correlated, but the sign of correlation can be either positive or negative. For this analysis, we first randomly shuffled the species diversity and genetic diversity values in each of the 12 mainland data sets 1000 times; for each permutation we then calculated the mean and median absolute correlations between species diversity and genetic diversity across the 12 data sets. The observed mean and median absolute correlations were greater than all of those generated by the null model (i.e. $P < 0.001$ for both). Publication bias was not likely a factor in these analyses:

none of the island data sets were collected for the purpose of testing for a species diversity–genetic diversity relationship, and the six mainland data sets collected specifically for this purpose (see previous paragraph) showed absolute correlations (mean = 0.49, median = 0.44) that were not significantly different from the data sets collected for different purposes (mean = 0.51, median = 0.50, $P = 0.91$ for t-test on mean values).

These results establish that species diversity and genetic diversity do not, in general, vary independently in nature. While correlations alone do not establish underlying processes, for some of these data sets additional analyses have pointed to likely candidates; these are addressed in subsequent sections.

Parallel processes – case I

Parallel processes appear to create correlated patterns of species diversity and genetic diversity in some cases. In all but one of the data sets summarized in Fig. 6 (Morishima & Oka 1979), genetic diversity was measured using molecular markers. Under the assumption that these markers are neutral, the most parsimonious explanation for positive species diversity–genetic diversity relationships is the parallel action of neutral processes on the two levels of diversity. Indeed for the island data sets, positive correlations were driven largely by parallel effects island area on both levels of diversity (Vellend 2003), presumably via the effect of area on community and genetic drift, although a possible effect of environmental heterogeneity (often correlated with island area) on species diversity cannot be ruled out. Species diversity universally correlates with island area, so if genetic diversity also correlates with island area, a positive correlation results. Somewhat surprisingly, island isolation did not appear to be important in driving positive correlations. In forests growing on former agricultural fields ('secondary' forests) in New York State, historical bottlenecks at both the community and population levels have created a positive correlation between species diversity and genetic diversity when comparing plants across both primary and secondary forests (Vellend 2004). Morishima & Oka (1979) measured morphological variation in rice populations, and concluded that the positive correlation they observed with weed species diversity was driven by variation in the degree of environmental heterogeneity. These results indicate that species diversity and genetic diversity frequently vary in concert because of processes acting in parallel at the two levels, and that different processes are capable of creating positive correlations. To date, relatively few studies have collected data with the specific purpose of assessing the degree of similarity between processes underlying patterns at the two different levels, so it is not possible at present to generalize further.

For a wide range of systems a tremendous amount is known about the correlates of spatial variation in species diversity (Huston 1994; Rosenzweig 1995), even if the processes underlying such relationships are not always well understood. Systems where variation in species diversity is predicted largely by a single variable (e.g. isolation or environmental heterogeneity) provide excellent opportunities to look for parallel variation in genetic diversity predicted by the same variable. Theory predicts that positive correlations are more likely to be found when genetic diversity is measured in common vs. rare species (Vellend 2005); other species' traits such as dispersal or breeding system may also influence patterns of genetic diversity (Frankham *et al.* 2002), and therefore the nature of correlations with species diversity. Measuring genetic diversity in multiple species that vary in abundance or other life-history traits in the same set of localities will allow these ideas to be explored further. Measuring genetic diversity for quantitative traits rather than molecular-marker loci will permit more meaningful tests of parallel effects of environmental heterogeneity on the two levels of diversity. While observational research of this kind is necessarily exploratory, establishing the range of possible patterns in nature and testing their generality and context-dependence will provide a foundation for more mechanistic studies.

Mechanistically testing the ability of different processes to drive parallel patterns of species and genetic diversity will require an experimental approach; this angle of inquiry is virtually unexplored. Size, immigration rate and environmental heterogeneity are strong candidates for locality characteristics that may drive correlated patterns of the two levels of diversity. Varying these experimentally is straightforward. Systems, in which locality characteristics can be easily modified, such as laboratory or field-based plots with plant communities, or aquatic microcosms, would provide ideal arenas for testing these hypotheses. Environmental heterogeneity is of particular interest here because of its potentially complex effects on species and genetic diversity; for example, theory predicts that the influence of environmental heterogeneity on genetic diversity may be constrained by a community of competitors (e.g. Fig. 3). Measuring the response of genetic diversity to environmental heterogeneity both alone and in the presence of a community of competitors will provide a critical test of this hypothesis.

Effects of genetic diversity on species diversity – case II

A substantial empirical literature supports the contention that genetic diversity can enhance population performance (e.g. Antonovics *et al.* 1988; Kelley *et al.* 1988; Smithson & Lenné 1996; Booy *et al.* 2000), which is expected to be inversely related to extinction risk (e.g. Newman & Pilson

1997). In some cases, genetic diversity may in fact be required for population persistence, such as when mating can only occur among different genotypes (e.g. self-incompatible mating systems). Another well-known phenomenon involves the role of genetic diversity in reducing the detrimental effects of disease in agricultural plants where enemy attack occurs in a frequency-dependent fashion (Smithson & Lenné 1996). Thus, if genetic diversity is reduced in each species in a community, species diversity should also decline as individual species go extinct or change radically in abundance.

We know of only one study of the consequences of low genetic diversity in all the species in a community on species diversity. In their landmark study, Booth & Grime (2003) created experimental communities of grassland plants starting with 16 individuals of each of 11 perennial plant species. Each species was represented by 1, 4 or 16 different clonal genotypes (no sexual reproduction was allowed). After 5 years, Shannon–Weiner species diversity varied positively with the number of genotypes, although the trend was not statistically significant. However, variation in species composition among replicates was far greater in the low than the high diversity treatments. This result suggested an important sampling effect, in that the particular genotypes included in the low diversity treatments were an important determinant of community dynamics. Although 5 years is generally considered a fairly long duration for an ecological experiment, the species in this system are all long-lived perennials so dynamics are relatively slow; the data suggested a slow divergence in species diversity among the treatments, although it may take 10 or more years to be fully manifested. Experiments with shorter-lived plants, or aquatic microcosm experiments, might allow a fuller accounting of the dynamics, and more powerful tests of the ultimate effect of genetic diversity on species diversity.

As outlined earlier, genetic diversity in dominant species may have important community consequences (Whitham *et al.* 2003). Several situations have been described recently in which genetic variation in one species has important consequences for interacting species on other trophic levels (Neuhauser *et al.* 2003; Whitham *et al.* 2003). Effects of genetic variation on interactions within a trophic level have received less attention. Mixtures of genotypes of particular plant species often show increased productivity relative to monocultures (Smithson & Lenné 1996); increased productivity may, in turn, suppress the diversity of competing species. Just as high species diversity can reduce the invasibility of communities to new species (e.g. McGrady-Steed *et al.* 1997; Levine 2000), genetic diversity within species may have similar effects on species' invasion. In experimental populations of *Arabidopsis thaliana* with different numbers of genotypes, Weltzin *et al.* (2003) found no effect of genetic diversity on invasion success by *Arabidopsis*

suecica. However, phenotypic variability among *A. thaliana* genotypes was deliberately constrained (Weltzin *et al.* 2003) and it is precisely phenotypic variability that may make diverse populations different from depauperate ones. The hypothesis that genetic diversity in a dominant species may act as a source of diversifying selection is supported by empirical evidence that the performance of particular pairs of species in competition depends in some cases on which genotypes (not just which species) are competing (Aarssen & Turkington 1985; Ehlers & Thompson 2004). Palmer & Maurer (1997) found that species diversity of agricultural crops promoted species diversity of the associated weed communities, although we know of no similar studies in which genetic diversity was experimentally manipulated.

To test the causal effect of genetic diversity on species diversity, experiments similar to those of Weltzin *et al.* (2003) are needed in which phenotypic variability among genotypes is maximized, and invasion success of multiple species (i.e. species diversity) is evaluated. Despite the simplicity of such experiments, they may yield results with potentially profound implications for understanding the community consequences of variable levels of diversity in natural populations, agricultural populations, and in populations created as part of restoration efforts. As the effects of genetic diversity on population performance might be particularly important under stressful conditions (Nevo 2001), crossing genetic diversity treatments with environmental treatments (e.g. drought) should yield important insights.

Effects of species diversity on genetic diversity – case III

Hypotheses positing an effect of species diversity on genetic diversity are essentially the same as those positing an effect of genetic diversity in a dominant species on the diversity of coexisting species. One level of diversity either acts to constrain or enhance the other. Again, studies demonstrating that species diversity reduces invasion by other species suggest that species diversity may also constrain the diversity of genotypes of a given species. In contrast, a number of studies report 'increased' invader success in more diverse communities (reviewed in Levine & D'Antonio 1999). In addition, different genotypes within a species may vary in their response to competition with different species, suggesting the occurrence of local adaptation to the identity of neighbours (e.g. Turkington & Aarssen 1984; Turkington 1989; Vavrek 1998). These latter studies point to a potential positive effect of species diversity on genetic diversity via spatially varying selection. Neither of these two contrasting hypotheses has been explicitly tested despite intense interest in the consequences of species diversity on other community and ecosystem characteristics.

Karlin *et al.* (1984) provided a compelling argument that genetic variation in *Desmognathus fuscus* is constrained by the number of co-occurring congeners, which varied from one to four across 27 sampling sites in eastern North America. A range of potential predictor variables was controlled for, and genetic diversity and species diversity were very tightly correlated ($r = -0.90$, $P < 0.001$). Under the hypothesis of neutrality for allozyme variation, a likely explanation for this result is that competition reduces population size and therefore genetic diversity, although arguments based on selection cannot be completely ruled out. The other strong negative relationship in Fig. 6 was reported by Wehenkel *et al.* (C. Wehenkel, F. Bergmann and H.-R. Gregorius, unpublished work), who found a negative correlation between allozyme variation beech (*Fagus sylvatica*) and tree species diversity ($r = -0.94$, $P = 0.02$, $n = 5$), although the underlying cause was not clear. It is interesting to note that the sampling units in these two studies were non-discrete and relatively small 'sites' or forest 'stands', whereas for most of the other studies in Fig. 6 islands or habitat patches with discrete boundaries were sampled. It seems at least plausible that the relatively small and uniform scale of sampling in these two studies increased the probability of detecting direct negative effects of species diversity on genetic diversity via population size, whereas sampling across islands or habitat patches with highly variable sizes or degrees of isolation increased the probability of detecting parallel effects of habitat characteristics on the two levels of diversity. An important direction for future empirical studies will be explicitly addressing the influence of spatial scale.

Testing the potential influence of species diversity on genetic diversity is highly amenable to experimentation. Species diversity manipulations are commonplace in the contemporary literature (reviewed in Loreau *et al.* 2001), and the design of such experiments is essentially identical to that required here, but with a different response variable. To test for effects of species diversity on genetic diversity, genetically variable populations of a focal species need to be placed in natural or experimental communities of varying species diversity, and the dynamics of different genotypes followed. As in the case of genetic diversity, the effects of species diversity may be manifested most strongly under stressful conditions (e.g. Mulder *et al.* 2001), indicating a need for experiments to be conducted in multiple environments. We might predict, *a priori*, that species diversity is more likely to constrain genetic diversity in well-mixed communities (e.g. in aquatic systems) where each individual experiences a very similar local environment, and to enhance genetic diversity in communities of sessile organisms (e.g. plants or sessile marine invertebrates) where each individual may experience a very different local environment (see also Huston & DeAngelis 1994). This contrast corresponds to

'coarse-grained' vs. 'fine-grained' environments respectively (Levins 1968).

Methodological issues: how to measure and manipulate genetic diversity?

In principle, the types of experiments required to test the hypotheses outlined above are straightforward. Three variables, environmental conditions, species diversity and genetic diversity, need to be manipulated independently, and the population and community responses measured. In practice, implementing such experiments introduces some logistical challenges. Foremost among these is the question of how to manipulate and measure genetic diversity.

Genetic diversity has traditionally been manipulated in one of two ways. First, one can manipulate the relatedness of individuals that make up a population via controlled matings; closely related individuals harbor less genetic diversity than more distantly related individuals. For example, Antonovics *et al.* (1988) and Kelley *et al.* (1988) have compared the fitness of sexually produced progeny of single mother plants to asexually produced progeny in *Anthoxanthum odoratum*. This is an extreme case in which the 'low diversity' populations were genetically uniform. Creating populations that vary continuously in relatedness confounds the effects of inbreeding and the effects of genetic diversity *per se* (e.g. Newman & Pilson 1997). If experiments are allowed to proceed through multiple generations, using organisms that reproduce sexually also allows for recombination to alter population-level genetic diversity in unpredictable ways. As such, measurement of genetic variation for selected traits during or at the end of the experiment would require additional common-garden experiments. The advantage of this approach is that it likely mimics many scenarios in nature where genetic diversity has been eroded.

An alternative approach is to use clonal organisms and to create populations with different numbers of genotypes (e.g. Booth & Grime 2003; Hughes & Stachowicz 2004). As long as sexual reproduction is prevented (or biologically impossible) during the course of the experiment, observing the changes in the abundance of different genotypes is all that is needed to measure genetic diversity. This can be carried out visually if clones vary morphologically, or using molecular markers. This approach, which is inherent in Figs 2–5, makes the manipulation and measurement of genetic diversity exactly analogous to that of species diversity. If phenotypic characteristics of different genotypes are characterized *a priori,* genetic diversity can be measured not only based on the numbers and relative frequencies of genotypes, but based on variation in genetically determined traits without the need for additional experiments; this is analogous to 'functional diversity' in

community ecology (Díaz & Cabido 2001). The main drawback of this approach is that in most natural systems reproduction is not strictly clonal. However, we feel that the advantages in terms of experimental tractability make this approach preferable, at least during the initial stages of this research programme when the potential for basic processes to operate is being tested.

CAVEATS

In considering the potential for connections between species and genetic diversity, we have touched on a wide range of topics. Readers will no doubt identify highly relevant topics that we have addressed either inadequately or not at all. A few of these are worth special mention. First, our treatment of migration among localities as a process with fairly simple outcomes (i.e. increased local diversity) is oversimplified. In some cases, high levels of migration among localities may either inhibit (Lenormand 2002) or enhance (Cottenie & DeMeester 2004) the action of selective forces acting within localities, and the effect of immigration may depend on how the composition of the regional population or community compares with that of the locality in question (e.g. Mouquet *et al.* 2004). These complexities could be easily incorporated into the experiments reviewed or proposed in this paper.

Second, we have given short shrift to the extensive literature on the interplay between ecology and evolution in microbial microcosms. While experimental communities of microbes have provided powerful tests of ecological theory (Jessup *et al.* 2004; Kassen & Rainey 2004), the distinction between genotypes and species, and between different trophic levels, both of which are generally quite clear for most plants and animals, is often highly blurred for microbes. It was thus difficult to embrace this literature under the present framework, despite the fact that these studies have much to offer the more general field of community genetics.

Third, we made only a brief explicit mention of frequency-dependent selection as a mechanism for the maintenance of diversity. Environmental heterogeneity, which we have considered, represents a type of frequency dependence in that as particular genotypes or species become very abundant, they may be less likely to occupy suitable microsites, thereby decreasing that genotype's or species' average fitness (e.g. Vellend 2005). Frequency-dependent fitness is also implicit in the resource competition model in Figs 2–5, in that competition for particular resources is stronger within genotypes than among them. However, we have neglected the potentially important role of natural enemies (e.g. pathogens and predators), which are thought to maintain both species diversity and genetic diversity via frequency-dependent selection (e.g. Burdon

1987; Barot & Gignoux 2004). The question of whether the strength of enemy-mediated frequency-dependent selection varies in parallel at both levels is an important direction for future research.

Finally, it is important to recognize that species are ultimately created by partitioning gene pools, which decreases genetic diversity within species. There is mounting evidence that rates of molecular evolution are greater in areas with high energy input (e.g. the tropics) where species diversity is also highest (Davies *et al.* 2004; Gillooly *et al.* 2005). Thus, high species diversity may in some cases be driven by a high rate at which genetic diversity is created, although this would not be manifested as co-variation between the two levels of diversity across space because of the continual splitting of gene pools at speciation. Nonetheless, these data indicate that there are at least some species diversity–genetic diversity connections at larger spatial and temporal scales than considered in this review.

CONCLUSIONS

Many of the hypotheses described in this paper represent new research angles stemming from long-standing themes in ecology and evolution. What processes create spatial patterns in diversity? What are the consequences of diversity for populations, communities, and ecosystems? These questions have inspired a vast body of research, and are central to both the basic and applied branches of ecology and evolutionary biology. We hope to have demonstrated that basic ecological and evolutionary theory in combination with some well-documented empirical phenomena point to potentially important links between the two most fundamental levels of biodiversity: species diversity and genetic diversity (see also Antonovics 1976, 1992, 2003). The empirical studies reviewed here provide preliminary support for some of these hypotheses, but in most cases explicit tests are lacking. Exploring and testing for species diversity–genetic diversity connections represents an exciting new opportunity for furthering our understanding of how phenotypic variation within and among species interact to determine the structure and dynamics of communities, and for evaluating the potential for conceptual synthesis across subdisciplines in biodiversity research. Our proposed research directions complement the many other approaches to merging ecological and evolutionary perspectives, such as the incorporation of microevolution into models of consumer–resource interactions (e.g. Neuhauser *et al.* 2003), examination of the community consequences of plant hybridization (Whitham *et al.* 2003), and incorporation of phylogenetic considerations into analyses of species co-occurrence and community assembly (Webb *et al.* 2002). Together, these approaches promise to push us ever closer to the elusive goal of true synthesis between ecology and evolutionary biology.

SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article:

Table S1 Fifteen data sets compiled to calculate Pearson correlation coefficients (*r*) between species diversity (SD) and genetic diversity (GD). These data sets were added to those reported in Vellend (2003) to create Fig. 6. Data sets were only included if at least five populations/communities were sampled.

REFERENCES

Aarssen, L.W. (1983). Ecological combining ability and competitive combining ability in plants: towards a general evolutionary theory of coexistence in systems of competition. *Am. Nat.*, 122, 707–731.

Aarssen, L.W. & Turkington, R. (1985). Biotic specialization between neighbouring genotypes in *Lolium perenne* and *Trifolium repens* from a permanent pasture. *J. Ecol.*, 73, 605–614.

Agrawal, A.A. (2003). Community genetics: new insights into community ecology by integrating population genetics. *Ecology*, 84, 543–544.

Amarasekare, P. (2000). The geometry of coexistence. *Biol. J. Linn. Soc.*, 71, 1–31.

Antonovics, J. (1976). The input from population genetics: 'the new ecological genetics'. *Syst. Bot.*, 1, 233–245.

Antonovics, J. (1978). The population genetics of species mixtures. In: *Plant Relations in Pastures* (ed. Wilson, J.R.). CSIRO, Melbourne, Vic, Australia. pp. 223–252.

Antonovics, J. (1992). Toward community genetics. In: *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, Genetics* (eds Fritz, R.S. & Simms, E.L.). University of Chicago Press, Chicago, IL, pp. 426–449.

Antonovics, J. (2003). Toward community genomics? *Ecology*, 84, 598–601.

Antonovics, J., Ellstrand, N.C. & Brandon, R.N. (1988). Genetic variation and environmental variation: expectations and experiments. In: *Plant Evolutionary Biology* (eds Gottlieb, L.D. & Jain, S.K.). Chapman and Hall, New York, NY, pp. 275–303.

Barot, S. & Gignoux, J. (2004). Mechanisms promoting plant coexistence: can all the proposed mechanisms be reconciled? *Oikos*, 106, 185–192.

Bell, G., Lechowicz, M.J., Appenzeller, A., Chandler, M., DeBlois, E., Jackson, L. *et al.* (1993). The spatial structure of the physical environment. *Oecologia*, 96, 114–121.

Booth, R.E. & Grime, J.P. (2003). Effects of genetic impoverishment on plant community diversity. *J. Ecol.*, 91, 721–730.

Booy, G., Hendriks, R.J.J., Smulders, M.J.M., Van Groenendael, J.M. & Vosman, B. (2000). Genetic diversity and the survival of populations. *Plant Biol.*, 2, 379–395.

Burdon, J.J. (1987). *Diseases and Plant Population Biology*. Cambridge University Press, Cambridge, UK.

Chase, J.M. & Leibold, M.A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago, IL.

Chave, J. (2004). Neutral theory and community ecology. *Ecol. Lett.*, 7, 241–253.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

Clark, J.S., LaDeau, S. & Ibanez, I. (2004). Fecundity of trees and the colonization-competition hypothesis. *Ecol. Monogr.*, 74, 415–442.

Cottenie, K. & DeMeester, L. (2004). Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. *Ecology*, 85, 114–119.

Crnokrak, P. & Barrett, S.C.H. (2002). Purging the genetic load: a review of the experimental evidence. *Evolution*, 56, 2347–2358.

Davies, T.J., Barraclough, T.G., Salvoinen, V. & Chase, M.W. (2004). Environmental causes for plant biodiversity gradients. *Phil. Trans. R. Soc. Lond. B*, 359, 1645–1656.

Díaz, S. & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Tree*, 16, 646–655.

Ehlers, B.K. & Thompson, J. (2004). Do co-occurring plant species adapt to one another? The response of *Bromus erectus* to the presence of different *Thymus vulgaris* chemotypes. *Oecologia*, 141, 511–518.

Elton, C.S. (1958). *The Ecology of Invasion by Plants and Animals*. University of Chicago Press, Chicago, IL.

Falconer, D.F. & Mackay, T.F.C. (1996). *Introduction to Quantitative Genetics*. Prentice Hall, New York, NY.

Frankham, R., Ballou, J.D. & Briscoe, D.A. (2002). *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, UK.

Gause, G.F. (1934). *The Struggle for Existence*. Williams and Wilkins, Baltimore, MD.

Gillooly, J.F., Allen, A.P., West, G.B. & Brown, J.H. (2005). The rate of DNA evolution: effects of body size and temperature on the molecular clock. *Proc. Natl. Acad. Sci. USA*, 102, 140–145.

Hairston, N.G.J., Ellner, S. & Kearns, C.M. (1996). Overlapping generations: the storage effect and the maintenance of biotic diversity. In: *Population Dynamics in Ecological Space and Time* (eds Rhodes, O.E.J., Chesser, R.K. & Smith, M.H.). University of Chicago Press, Chicago, IL.

Harper, J.L. (1977). *The Population Biology of Plants*. Academic Press, New York, NY.

Hartl, D.L. & Clark, A.G. (1997). *Principles of Population Genetics*, 3rd edn. Sinauer Associates Inc., Sunderland, MA.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biogeography and Biodiversity*. Princeton University Press, Princeton, NJ.

Hughes, A.R. & Stachowicz, J.J. (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc. Natl. Acad. Sci. USA*, 101, 8998–9002.

Huston, M.A. (1994). *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge, UK.

Huston, M.A. & DeAngelis, D.L. (1994). Competition and coexistence: the effects of resource transport and supply rates. *Am. Nat.*, 144, 954–977.

Jessup, C.M., Kassen, R., Forde, S.E., Kerr, B., Buckling, A., Rainey, P.B. *et al.* (2004). Big questions, small worlds: microbial model systems in ecology. *Trends. Ecol. Evol.*, 19, 189–197.

Karlin, A.A., Guttman, S.I. & Rathbun, S.L. (1984). Spatial autocorrelation analysis of heterozygosity and geographic distribution in populations of *Desmognathus fuscus* (Amphibia: Plethodontidae). *Copeia*, 2, 343–356.

Kassen, R. (2002). The experimental evolution of specialists, generalists, and the maintenance of diversity. *J. Evol. Biol.*, 15, 173–190.

Kassen, R. & Rainey, P.B. (2004). The ecology and genetics of microbial diversity. *Ann. Rev. Microbiol.*, 58, 207–231.

Kelley, S.E., Antonovics, J. & Schmitt, J. (1988). A test of the short-term advantage of sexual reproduction. *Nature*, 331, 714–716.

Kimura, M. (1983). *The Neutral Theory of Molecular Evolution*. Cambridge University Press, Cambridge, UK.

Lenormand, T. (2002). Gene flow and the limits to natural selection. *Trends. Ecol. Evol.*, 17, 183–189.

León, J.A. (1974). Selection in contexts of interspecific competition. *Am. Nat.*, 108, 739–757.

Levin, B.R. (1971). The operation of selection in situations of interspecific competition. *Am. Nat*, 25, 249–264.

Levine, J.M. (2000). Species diversity and biological invasions: relating local processes to community pattern. *Science*, 288, 852–854.

Levine, J.M. & D'Antonio, C.M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, 87, 15–26.

Levins, R. (1968). *Evolution in Changing Environments*. Princeton University Press, Princeton, NJ.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A. *et al.* (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.

Losos, J.B. & Schluter, D. (2000). Analysis of an evolutionary species-area relationship. *Nature*, 408, 847–850.

MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, 101, 377–385.

Magurran, A.E. (2004). *Measuring Biological Diversity*. Blackwell Publishing, Oxford, UK.

McGrady-Steed, J., Harris, P.M. & Morin, P.J. (1997). Biodiversity regulates ecosystem predictability. *Nature*, 390, 162–165.

Morishima, H. & Oka, H.-I. (1979). Genetic diversity in rice populations of Nigeria: influence of community structure. *Agro-ecosystems*, 5, 263–269.

Mouquet, N., Leadley, P., Mériguet, J. & Loreau, M. (2004). Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. *Oikos*, 77, 77–90.

Mulder, C.P.H., Uliassi, D.D. & Doak, D.F. (2001). Physical stress and diversity-productivity relationships: the role of positive interactions. *Proc. Natl. Acad. Sci. USA*, 98, 6704–6708.

Nei, M. (1987). *Molecular Evolutionary Genetics*. Columbia University Press, New York, NY.

Neuhauser, C., Andow, D.A., Heimpel, G.E., May, G., Shaw, R.G. & Wagenius, S. (2003). Community genetics: expanding the synthesis of ecology and genetics. *Ecology*, 84, 545–558.

Nevo, E. (2001). Evolution of genome-phenome diversity under environmental stress. *Proc. Natl. Acad. Sci. USA*, 98, 6233–6340.

Newman, D. & Pilson, D. (1997). Increased probability of extinction due to decreased genetic effective population size: experimental populations of *Clarkia pulchella*. *Evolution*, 51, 354–362.

Ochman, H., Lawrence, J.G. & Groisman, E.A. (2000). Lateral gene transfer and the nature of bacterial innovation. *Nature*, 405, 299–304.

Odat, N., Jetschke, G. & Hellwig, F.H. (2004). Genetic diversity of *Ranunculus acris* L. (Ranunculaceae) populations in relation to species diversity and habitat type in grassland communities. *Mol. Ecol.*, 13, 1251–1257.

Palmer, M.W. & Maurer, T.A. (1997). Does diversity beget diversity? A case study of crops and weeds. *J. Veg. Sci.*, 8, 235–240.

Pimentel, D. (1968). Population regulation and genetic feedback. *Science*, 159, 1432–1437.

Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, New York, NY.

Smithson, J. & Lenné, J. (1996). Varietal mixtures: a viable strategy for sustainable productivity in subsistence agriculture. *Ann. Appl. Biol.*, 128, 127–158.

Solbrig, O.T. & Simpson, B.B. (1974). Components of regulation of a population of dandelions in Michigan. *J. Ecol.*, 62, 473–486.

Taper, M.L. & Case, T.J. (1992). Coevolution among competitors. *Evol. Biol.*, 8, 63–109.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. *et al.* (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.*, 31, 79–92.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.

Turkington, R. (1989). The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture V. the coevolution of competitors. *J. Ecol.*, 77, 717–733.

Turkington, R. & Aarssen, L.W. (1984). Local-scale differentiation as a result of competitive interactions. In: *Perspectives on Plant Population Ecology* (eds Dirzo, R. & Sarukhán, J.). Sinauer Associates Inc., Sunderland, MA, pp. 107–127.

Van Valen, L. (1965). Morphological variation and width of ecological niche. *Am. Nat.*, 99, 377–390.

Vavrek, M.C. (1998). Within-population genetic diversity of *Taraxacum officinale* (Asteraceae): differential genotype response and effect on interspecific competition. *Am. J. Bot.*, 85, 947–954.

Vellend, M. (2003). Island biogeography of genes and species. *Am. Nat.*, 162, 358–365.

Vellend, M. (2004). Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. *Ecology*, 85, 3043–3055.

Vellend, M. (2005). Species diversity and genetic diversity: parallel processes and correlated patterns. *Am. Nat.* (in press).

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I. *et al.* (1999). The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.*, 30, 257–300.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.*, 33, 475–505.

Weltzin, J.F., Muth, N.Z., Von Holle, B. & Cole, P.G. (2003). Genetic diversity and invasibility: a test using a model system with a novel experimental design. *Oikos*, 103, 505–518.

Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M. *et al.* (2003). Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology*, 84, 559–573.

Whittaker, R.H. (1975). *Communities and Ecosystems*. MacMillan Publishing Company, New York, NY.

Williams, G.C. (1975). *Sex and Evolution*. Princeton University Press, Princeton, NJ.