

Species Diversity and Genetic Diversity: Parallel Processes and Correlated Patterns

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ABSTRACT: Species diversity and genetic diversity may be correlated as a result of processes acting in parallel at the two levels. However, no theories predict the conditions under which different relationships between species diversity and genetic diversity might arise and therefore when one level of diversity may be predicted using the other. I used simulation models to investigate the parallel influence of locality area, immigration rate, and environmental heterogeneity on species diversity and genetic diversity. The most common pattern was moderate to strong positive species-genetic diversity correlations (SGDCs). Such correlations may be driven by any one of the three locality characteristics examined, but important exceptions and patterns emerged. Genetic diversity and species diversity were more weakly correlated when genetic diversity was measured for rare versus common species. Environmental heterogeneity not only imposes spatially varying selection on populations and communities but also causes changes in species' population sizes and therefore genetic diversity; these interacting processes can create positive, negative, or unimodal relationships of genetic diversity with species diversity. When species are considered as part of multispecies communities, predictions from single-species models of genetic diversity apply in some instances (effects of area and immigration) but often not in others (effects of environmental heterogeneity).

Keywords: area, environmental heterogeneity, immigration, neutral theory, selection.

Theories of diversity in population genetics and community ecology bear many striking similarities (Watterson

1972; Antonovics 1976, 1992, 2003; Harper 1977; Van Valen 1982; Huston 1994; Hairston et al. 1996; Amarasakare 2000; Jain 2000; Bell 2001; Kassen 2002; Chave 2004). Although population genetics and community ecology share almost nothing in the way of history, they share a virtually identical interest in explaining the numbers and relative frequencies of biological variants found in nature. In population genetics, these variants are genotypes or alleles, while in community ecology they are usually species. The strength of these conceptual parallels is illustrated by considering the observation that a haploid genotype is functionally identical to a species, at least from a theoretical viewpoint (e.g., Antonovics 1976; Amarasakare 2000). Since most of the basic tenets of theoretical population genetics hold equally for haploids and diploids (Lewontin 1974; Bell 1997), many population-genetics models can be applied with equal validity to the species composition of a community and to the genetic composition of a population. Despite these striking parallels and the consequent potential for conceptual unification between community ecology and population genetics, species diversity and genetic diversity are rarely studied simultaneously. Here I use spatially explicit simulations of communities of sessile organisms to ask how species diversity and genetic diversity may be expected to co-vary among localities under a range of different scenarios. I know of no previous quantitative models that explicitly address the two levels of diversity simultaneously.

The parallel action of processes such as drift, immigration, and spatially varying selection on species diversity and genetic diversity (within single species) has led to the prediction that the two levels of diversity may be positively correlated across sampling localities (Antonovics 1992; Huston 1994; Vellend 2003; Etienne and Olf 2004). Small patches of habitat contain small populations and communities and are therefore expected to lose species and genotypes via drift. Immigration may counter the effects of drift at both the community and population levels. Selection favors certain individual organisms over others, and these individuals may represent different genotypes of the same species or different species. Data for 14 island

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archipelagos support the prediction of a positive species diversity–genetic diversity correlation, although the magnitude of correlations is highly variable (Vellend 2003). Other data show a negative correlation between the two levels of diversity (e.g., Karlin et al. 1984). Strong relationships between species diversity and genetic diversity hold the promise of potentially predicting one level of diversity on the basis of the other. However, there is no theoretical framework at present for predicting the conditions under which species diversity and genetic diversity should be strongly correlated or not. This article presents the first attempt to begin building such a framework.

Understanding how different habitat characteristics influence species diversity and genetic diversity in concert may be critical for predicting the overall response of biodiversity to habitat alterations. For example, habitat fragmentation is expected to reduce within-patch diversity at both levels as a result of decreases in population and community size and reduced immigration rate (Hubbell 2001; Frankham et al. 2002). However, if one level of diversity is more sensitive to such changes than the other, it may not be the case that species diversity and genetic diversity will vary in parallel over a given range of habitat patch size or isolation. In addition, the effects on genetic diversity within any one species may also depend on how other species in the community respond to fragmentation. While it may be tempting to assume that genetic models of single species will apply even when those species are embedded in multispecies communities, similar genetic and ecological models of diversity may be quantitatively incompatible, with neutral theories providing an illustrative example. Neutral models in genetics typically start by assuming constant population size, N (Kimura 1983), while neutral community models assume a constant total number of individuals across species, or community size, J (Hubbell 2001). If N and J are both constant, then species diversity cannot be changed by the action of any process. If we relax the assumption of constant N but retain the assumption of constant J , then any process that leads to the addition of species (e.g., immigration) will necessarily cause mean population sizes to decrease, with potentially negative consequences for genetic diversity. Thus, the potential for different processes to create correlations between species diversity and genetic diversity is not immediately obvious even if models describing diversity at the two levels are identical. Models addressing both levels of diversity simultaneously are essential.

Species diversity and genetic diversity are influenced by a complex set of processes across a range of spatial and temporal scales (Huston 1994; Rosenzweig 1995; Hedrick 2000; Frankham et al. 2002). The focus of this article is variation in diversity among localities within a region. A locality is defined here as a discrete patch of habitat in an

otherwise inhospitable matrix for the species pool under consideration, such as an island, a pond, or a forest patch in an agricultural landscape. Here I model the effects on diversity of three locality characteristics, each of which is predicted a priori to have a positive effect on both species diversity and genetic diversity: area, which affects diversity via drift; locality connectivity, which determines immigration rate; and spatial environmental heterogeneity, which creates spatially varying selection. Each locality characteristic may have a direct effect on species diversity or genetic diversity and possibly also an indirect effect via the other level of diversity. For example, if increasing species diversity via immigration reduces species' population sizes, the consequent negative effect on genetic diversity would be an indirect effect of immigration. The effects of each locality characteristic are explored in neutral and nonneutral communities.

Using the model results, I address three fundamental questions at the interface of ecology and genetics. First, when are the influences of locality characteristics on genetic and species diversity sufficiently similar to result in a correlation? Second, at the level of genetic diversity, are predictions of single-species models altered by community context? Third, what processes might be responsible for the tremendous variation observed in the magnitude of empirical correlations between species diversity and genetic diversity (Morishima and Oka 1979; Karlin et al. 1984; Gregorius et al. 2003; Vellend 2003, 2004; Odat et al. 2004)?

Methods

I used an individual-based simulation in which multiple emergent properties of the system can be assessed simultaneously (Huston 1994). I approached this modeling with a primary interest in plant populations and communities, although the model is applicable to any community of sessile organisms. Thus, I included a number of features that characterize virtually all plant communities (e.g., spatially limited dispersal, spatially autocorrelated environments), despite the fact that these features contribute appreciably to model complexity; some simplifying assumptions have been made to keep model complexity within limits. To minimize arbitrariness, parameters describing local dispersal, the spatial structure of the environment, and individual longevity were loosely based on information for temperate forest understory plants, the community with which I am most familiar (e.g., Vellend 2004).

Model Overview

The model is a spatially explicit simulation model (summarized in fig. 1). Each locality's dynamics are simulated independently but with immigrants coming from a com-

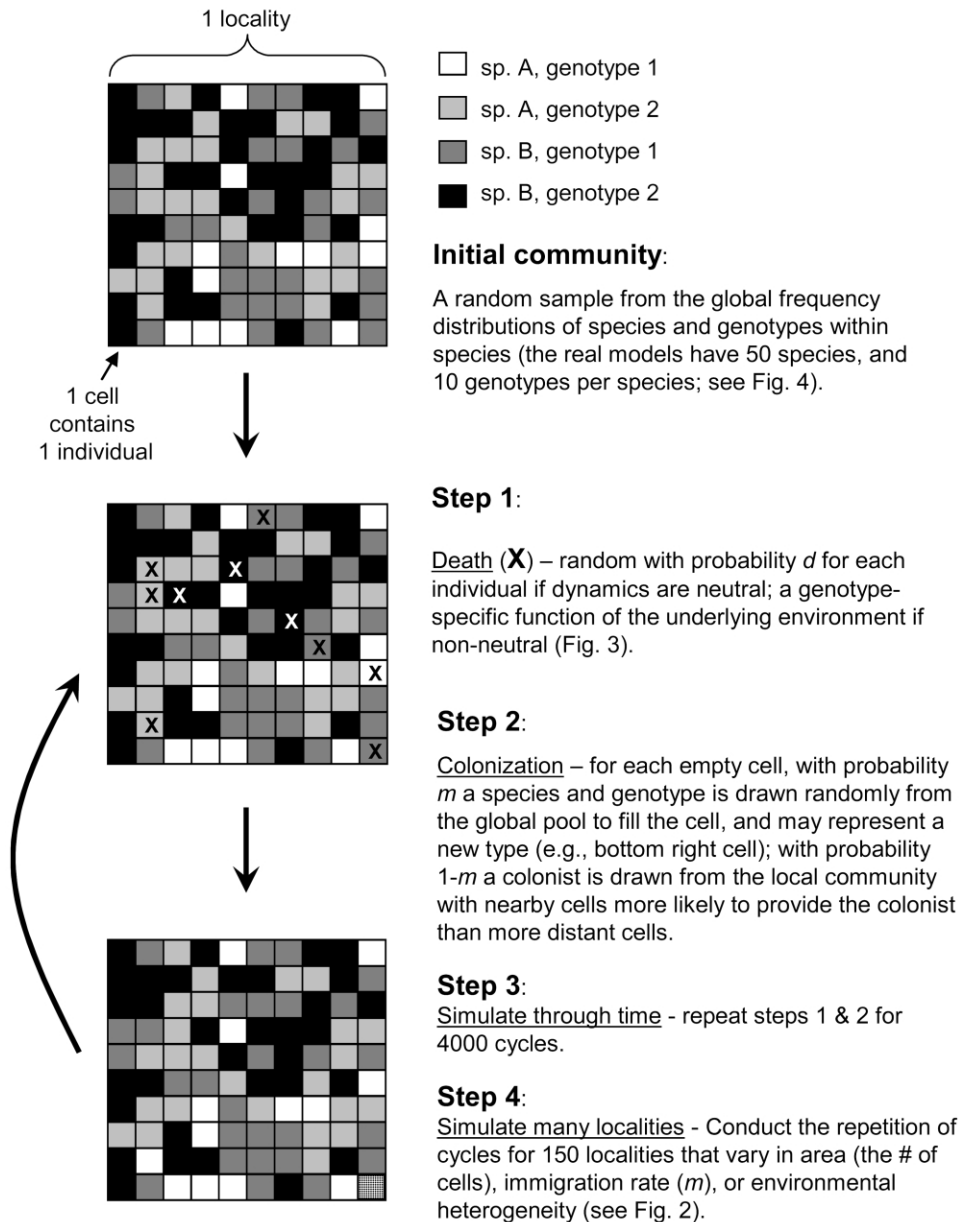


Figure 1: Schematic summary of the spatially explicit simulation model showing a hypothetical example with two species and two genotypes per species.

mon, unchanging global pool. A locality consists of a square matrix of cells, with one individual organism in each cell. When an individual dies, the resulting empty cell is colonized by a new individual during the same time step, so space is always completely filled. Life is thus a zero-sum game (Hubbell 2001). Each individual is defined by its species identity and its haploid genotype. Dynamics are determined entirely by the rules governing which individuals die during a given time step and which genotype

of which species colonizes each empty cell. There is no mutation or speciation.

For each parameter combination (see Fig. 2), simulations were conducted for 150 localities that varied in only one characteristic and whose dynamics were determined by an otherwise identical set of rules. Localities may vary in area (i.e., the number of cells), immigration rate (i.e., the probability that an empty cell is colonized by an individual from the global pool), or spatial environmental hetero-

Species: neutral Genotypes: neutral			NA
Species: non-neutral Genotypes: neutral			
Species: non-neutral Genotypes: non-neutral			
Value when constant:	10,000	0.01	10
Range when variable:	100-22,500	0.001-0.1	0.25-12.5
	Area	Immigration rate	Env. heterogeneity
	Characteristic that varies among localities		

Figure 2: Eight scenarios in which the dynamics of species diversity and genetic diversity were simulated. Under each scenario, all locality characteristics, except one, were identical across localities. Area is the number of cells per locality; immigration rate is the probability that empty cells are filled by an immigrant from the global pool; environmental heterogeneity is the standard deviation of environmental conditions among cells.

genity (see “Selection and Nonneutrality of Species and Genotypes”). Species and genotypes may be either neutral or not with respect to selection. Selection, when present, is mediated by species- and genotype-specific fitness functions along one environmental gradient, with each cell defined by a value along this gradient (fig. 3). Only viability selection was modeled; that is, the probability of death was the only component of fitness sensitive to environmental conditions in nonneutral communities.

All simulations began with a new seed for the random number generator and were run for 4,000 time steps, after which species diversity and genetic diversity no longer changed directionally. In trial simulations using each parameter combination, the correlation between time and different diversity measures was calculated in 1,000 time step windows. The number of time steps required for these correlations to reach 0 was determined and rounded up to the nearest thousand to determine the total number of time steps to run the simulations.

Dispersal

Dispersal within localities is spatially restricted. More specifically, when an empty cell is filled by a colonist from within the locality (i.e., not from the global pool), the colonist’s identity is determined by selecting a cell in a

random direction and at a random distance (from a negative exponential distribution) from the outer edge of the empty cell. The colonist takes the same species and genotype identity as the individual in the chosen cell, thus representing an offspring of this individual. The degree to which dispersal is spatially restricted is determined by the mean dispersal distance, $1/a$, in the negative exponential distribution, $P(\text{distance}) = ae^{-a \times \text{distance}}$. In all simulations reported here, $1/a = 2$. Since the distribution starts from the edge of the cell (i.e., $2^{1/2}/2 = 0.7$ spatial units from the center of the cell), then if each cell represents an area of about 50×50 cm, $1/a = 2$ represents a mean dispersal distance from the center of a cell of about 1.7 m, close to the mean dispersal distance for many forest understory plants (Cain et al. 1998).

The Global Migrant Pool

With probability m , an empty cell is filled by a random draw from the global migrant pool. Each species has a constant relative frequency (i.e., probability of being chosen) in the global pool, and species’ global relative frequencies follow a zero-sum multinomial distribution, which is that expected in large communities experiencing random drift (Hubbell 2001). I used the mean relative abundances from 100 replications of the numerical recipe

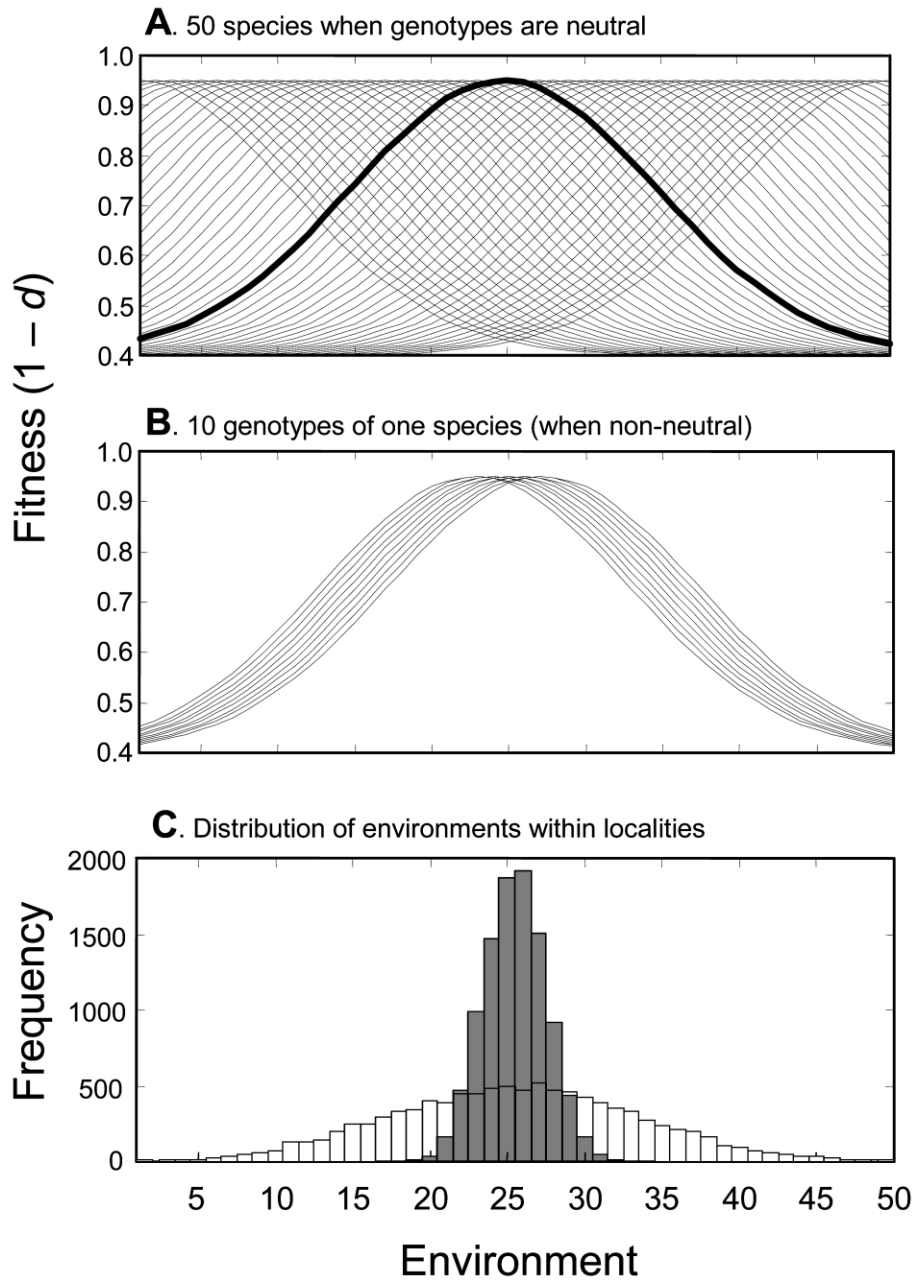


Figure 3: Fitness functions of species (A) and genotypes (B) along the environmental gradient and the distribution of environments within localities (C) with low heterogeneity (gray bars; standard deviation = 2) and high heterogeneity (open bars; standard deviation = 8). Fitness is defined as 1 minus the probability of individual death. Genotype fitness functions are shown only for the one species shown in bold in A.

of Hubbell (2001, p. 291) to generate a relative abundance distribution with $\theta = 5$ and $Jm = 22,500$, the size of the largest community studied here. This generated a maximum of 54 species, and I used the average relative frequencies of the 50 most common to define the species pool used in all simulations (see fig. 4A). (Note that re-

gardless of the underlying processes, empirical relative abundance distributions are often well described by zero-sum multinomials and that this is the same distribution expected for allele frequencies in large populations under genetic drift, assuming the infinite-alleles model of mutation [Ewens 1979].) Once the species identity is deter-

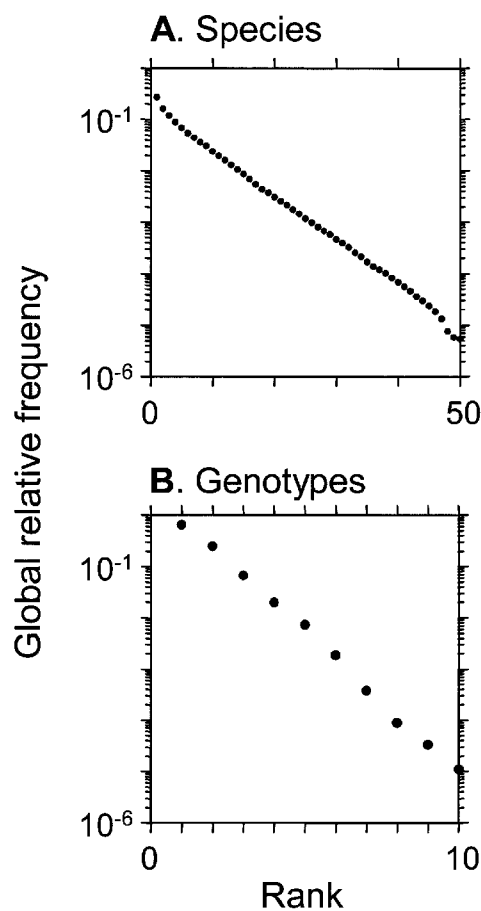


Figure 4: Global relative frequencies of the 50 species (A) and 10 genotypes per species (B).

mined, the genotype is chosen as a random draw from a zero-sum multinomial distribution of genotype frequencies for 10 genotypes per species; this distribution was generated as above, but with $\theta = 0.4$ and $Jm = 1,800$ (see fig. 4B). Using a global pool of immigrants in this way has been criticized because it avoids the question of how diversity is maintained in the global pool (Chesson 2000). However, at widely different spatial and temporal scales, diversity can be controlled by very different processes (Whittaker et al. 2001) in such a way that the metacommunity (i.e., the global pool) is essentially constant with respect to local population and community dynamics. This is an assumption of the models presented here.

The Neutral Case

In the simplest scenario, both species and genotypes are neutral, so no environmental information or species- and genotype-specific fitness functions need to be specified.

Localities may vary in area or immigration rate (fig. 2). At each time step, individual death occurs at random with probability $d = 0.1$, corresponding to a mean individual longevity of 10 years, which is typical of many forest understory plants (Bierzychudek 1982). After all deaths have occurred, empty cells are filled as described above.

Selection and Nonneutrality of Species and Genotypes

Environment-specific fitness differentials may occur among both species and genotypes or only among species; I do not consider the scenario in which species are neutral but genotypes are not (fig. 2). When nothing is neutral, each genotype of each species has a Gaussian unimodal fitness function identical in shape to all others but with optimal fitness at different points along the environmental gradient (see fig. 3A, 3B). Fitness is expressed as $1 - d$, where d is the probability of death. Optimal fitness occurs at $1 - d = 0.95$ and minimum fitness at 0.4 (fig. 3A, 3B). The environment at which optimum fitness occurs for each of the 50 species was set at the integers 1–50 (fig. 3A), and when the 10 genotypes were nonneutral, their fitness optima were separated by 0.5 environmental units (fig. 3B). Thus, genotype fitness peaks were separated by half the distance on the environmental gradient separating the species' fitness peaks. Global relative frequencies (fig. 4) were assigned randomly to species and genotypes with respect to the position of their fitness optimum for the first simulation, and the same assignment was then used in all simulations involving selection to maximize the comparability of results.

The action of selection requires that a value of an environmental variable be specified for each cell, and in all simulations, the environment was spatially autocorrelated. Spatial autocorrelation is a universal feature of the physical environment (Bell et al. 1993). I simulated two-dimensional spatially autocorrelated environments using a geostatistical model with an exponential covariance function, range = 8, nugget = 0.25, and sill = 1.25 in S+SpatialStats (Kaluzny et al. 1998). Assuming that each cell is 0.5×0.5 m, these parameters approximate those observed for soil characteristics in temperate forests (Palmer 1990; Lechowicz and Bell 1991). The mean value of environment was always at the center of the gradient (25.5; fig. 3C), and variation among localities in environmental heterogeneity was created by multiplying or dividing the deviation from the overall mean value of environment of each cell in a locality (fig. 3C).

Measuring Species Diversity and Genetic Diversity

Two measures of species diversity were calculated for each locality at the end of all simulations. Species richness (SR)

is the number of species present, and evenness (E) is the probability that two randomly chosen individuals are of different species, calculated using a version of Simpson's (1949) diversity index as $1 - \sum f_i^2$, where f_i is the relative frequency of species i such that $\sum f_i = 1$. Two exactly analogous measures of genetic diversity were measured for each species with ≥ 10 individuals in ≥ 30 (20%) of the 150 localities. Genotypic richness (GR) is the number of genotypes present, and expected heterozygosity (H) is the probability that two randomly chosen individuals within species are of different genotypes, calculated as for E but with f_i as the relative frequency of a particular genotype rather than species (Nei 1987).

The Relationship between Species Diversity and Genetic Diversity

For all simulations except those in which environmental heterogeneity was varied, the relationship between measures of species diversity and genetic diversity could be characterized by simple Pearson correlation coefficients; relationships were either positive, negative, or absent but never strongly unimodal or curvilinear. For simulations in which environmental heterogeneity was varied (fig. 2), measures of genetic diversity for some species showed unimodal relationships when plotted against species diversity. For each species in these simulations, a quadratic regression of genetic diversity (GD) on species diversity (SD) was performed ($GD = a_1 + a_2SD + a_3SD^2$). The strength of the linear and unimodal relationships between GD and SD were characterized by the partial r^2 for SD and SD^2 , respectively, in these analyses.

Robustness

The simulation models presented here could have been set up in any number of different ways. In addition to the scenarios just described, I conducted simulations under some additional parameter combinations to evaluate the robustness of the resulting patterns. Details are provided in appendix A in the online edition of the *American Naturalist*, and relevant results from these simulations are addressed in "Results" and "Discussion."

Results

Results are presented in three sections, one for each of the variable locality characteristics: area, immigration rate, and environmental heterogeneity (fig. 2). In a given scenario, the strength of correlations between SD and GD across localities may vary, depending on the characteristics of the species for which GD is measured. When both species and genotypes are neutral, species vary only according to their

relative global frequency. With nonneutrality, species vary according to both their global frequency and the position of their fitness optimum along the environmental gradient, for which the most relevant measurement is the distance from the center of the gradient (fig. 3). In each section, I first characterize variation among species in the strength of relationship between SD and GD according to these variable species attributes. Selected species or localities are then examined in more detail to illustrate the main results emerging from each section. For all simulations, species richness (SR) was equally or more strongly correlated with the variable locality characteristic than was evenness (E). As a result, relationships of GD with E were weaker than those with SR but not fundamentally different (but see app. A for one exception), so for simplicity here I report only the relationships of GD with SR. Results for E are presented in appendix B in the online edition of the *American Naturalist*.

Varying Locality Area

When localities varied in area, species richness (SR) was very tightly correlated with area; genotypic richness (GR) and heterozygosity (H) were universally positively correlated with SR, and there was a clear tendency for stronger correlations in more common species (fig. 5). These results did not depend on whether species or genotypes were neutral, and the strength of correlations did not depend on the position of species' fitness optima on the environmental gradient. Stronger correlations were found for GR than for H , with correlations ranging up to 0.8 and 0.7, respectively.

Differences between globally common and rare species in the magnitude of correlation between SR and GR or H were largely a result of differences in the strength of relationship between population size and area (fig. 6). (Since SR is so tightly correlated with area, only SR is plotted on the X-axis of fig. 6.) Population size of common species was strongly and linearly related to locality area (fig. 6A). Rare species were likely to be absent from the smallest localities, with population sizes predictably low at small area but highly variable at large area (fig. 6B). Effectively, rare species cover a narrower range of locality areas than common species. Genetic diversity is therefore more weakly correlated with area and, in turn, with species diversity in rare species than in common species.

Varying Immigration Rate

Species richness was a strong and approximately linear function of immigration rate (fig. 7A). Genetic diversity (both GR and H) tended to be positively correlated with SR, and the magnitude of correlation between GR and SR

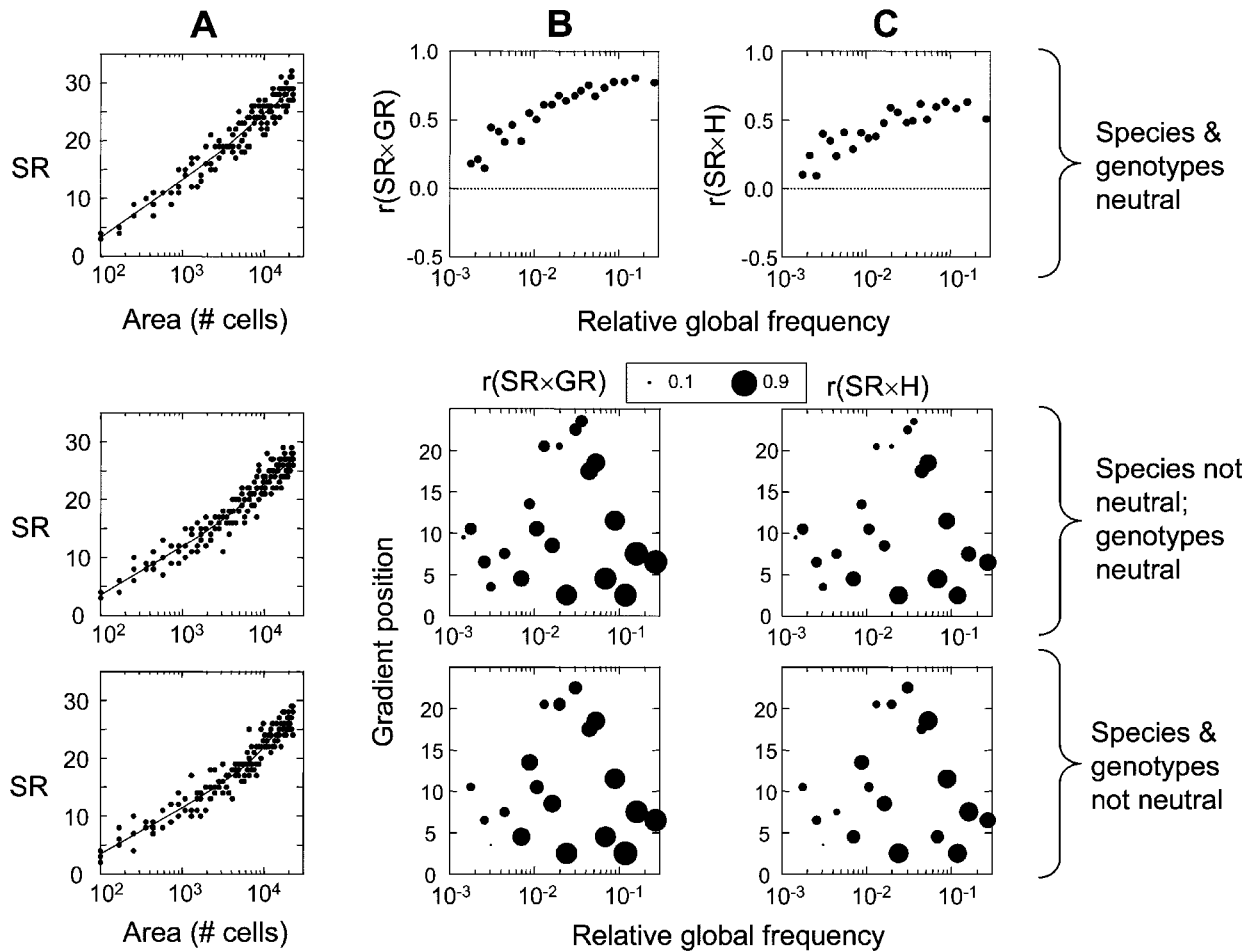


Figure 5: Relationships among locality area, species richness (SR), genotypic richness (GR), and expected heterozygosity (H) across 150 localities. *A*, Relationships between locality area and SR fitted with LOWESS (SYSTAT, ver. 10, SPSS) curves. *B*, Correlations between SR and GR in relation to species' characteristics: relative frequency in the global pool and position of fitness optimum on environmental gradient. *C*, Correlations between SR and expected H in relation to species' characteristics. Each data point in *B* and *C* represents genetic diversity measured for a different species, and in the bottom two panels the size of the circle is proportional to the magnitude of correlation. For example, in the bottom panel of *B*, the correlation was 0.74 for $SR \times GR$ when GR was measured for the species with a global relative frequency of 0.024 and a gradient position of 2.5. "Gradient position" indicates the distance of a species' fitness optimum from the middle of the environmental gradient (25.5).

increased with increasing species global frequency. However, the highest correlations between H and SR were found for species with intermediate global frequencies (fig. 7C). As for the cases in which area was varied, the results did not depend on species or genotype neutrality, and the strength of correlations did not depend on species' gradient positions. Again, correlations tended to be stronger for GR than for H .

The reason for low correlations between GR and SR for rare species was much the same as for the case in which locality area was varied. The relatively low correlations between H and SR had different explanations for rare and common species, which are illustrated most clearly for the

neutral case (fig. 8). For all species, the expected population size in a given locality is the community size (10,000) multiplied by the species' global frequency. However, the variation in realized population size is greater at low than at high immigration rates (fig. 8). For each species, expected H in the global pool is ~ 0.5 , and for common species H varies between 0.4 and 0.6 at high immigration rates (fig. 8C). At low immigration rates, stochastic variation causes H to be much less tightly regulated, varying from <0.2 to almost 0.7; the result is an overall weak but positive correlation between H and SR (fig. 8C). If immigration is very low, rare species are likely to be absent, but even when they are present in relatively

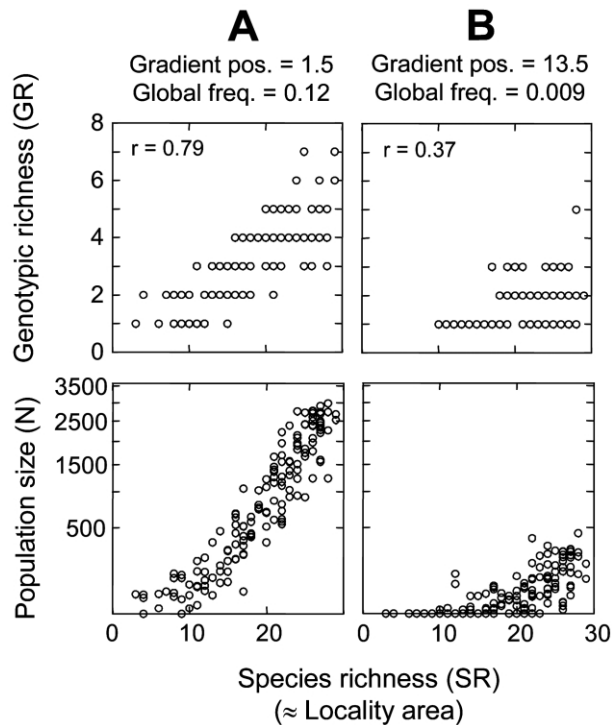


Figure 6: Relationships of species richness with population size and genotypic richness in a common (A) and a relatively rare (B) species when localities vary in area and species are nonneutral but genotypes are neutral. Species richness is to be interpreted here as a surrogate for locality area, because of their very tight correlation (see fig. 5).

large numbers, H is likely to be close to 0 (fig. 8A). At higher immigration rates, it is still the case that a relatively small proportion of immigration events will be of rare species; thus, H may take a wide range of values when community-level immigration is high, resulting in a relatively low correlation between H and SR. For species of intermediate global frequency, H is virtually never high at low immigration rates and almost never low at high immigration rates; the correlation between H and SR is, therefore, relatively strong (fig. 8B).

An exception to the generality that SR and E show similar relationships with locality characteristics (in this case immigration rate) is presented in appendix A. Briefly, with immigration rate varying up to 1.0, E may ultimately decline, thereby showing a unimodal relationship on immigration rate; results for relationships of GR and H with SR were unchanged (see app. A for details).

Varying Environmental Heterogeneity

Species richness was tightly correlated with environmental heterogeneity (fig. 9A). The strength of the linear com-

ponent of the relationship between GR and SR increased with increasing global relative frequency and was relatively weak or even negative for species near the middle of the gradient (fig. 9B, 9C). Similar patterns were observed for the correlation between H and SR, except that the strength of linear relationship was relatively weak for the most common species and weaker overall for H than for GR. For a few species with fitness optima near, but not quite at, the middle of the environmental gradient, relationships of both GR and H on SR showed significant unimodality.

Species' population sizes were strongly related to environmental heterogeneity, with the form of the relationship depending largely on the position of species' fitness optima (fig. 10). At low environmental heterogeneity, the environment in almost all cells takes a value near the middle of the gradient; at higher environmental heterogeneity, increasingly large proportions of cells take values nearer the ends of the gradient (see fig. 3C). Thus, the population sizes of species with fitness optima very close to the middle of the gradient decrease strongly with increasing environmental heterogeneity, potentially causing a negative relationship between SR and genetic diversity, at least for relatively rare species (fig. 10A). More common species with fitness optima near the middle of the gradient show an initial increase in genetic diversity with environmental heterogeneity (and therefore SR) due to spatially varying selection, followed by a decrease due to decreasing population sizes (fig. 10B). Species with fitness optima farther from the middle of the gradient sometimes show unimodal relationships of population size (and therefore genetic diversity) with environmental heterogeneity and SR (fig. 10C). When species' fitness optima are near the ends of the gradient, population size (and therefore genetic diversity) always increases with increasing environmental heterogeneity and SR because of increasing proportions of potentially suitable cells (fig. 10D).

Discussion

The idea that similar processes may drive patterns of biodiversity both within and among species has been raised for some time (see the introduction to this article), but very little research has addressed the issue of how we might expect species diversity (SD) and genetic diversity (GD) to co-vary among localities that vary in different characteristics. In simulated communities under a variety of scenarios, the most common pattern found here was for species diversity and genetic diversity to show moderate to strong positive correlations. Such correlations may be driven by locality area, immigration rate, or environmental heterogeneity. However, some important exceptions and patterns among species emerged, each providing testable hypotheses for future empirical studies. First, GD and SD

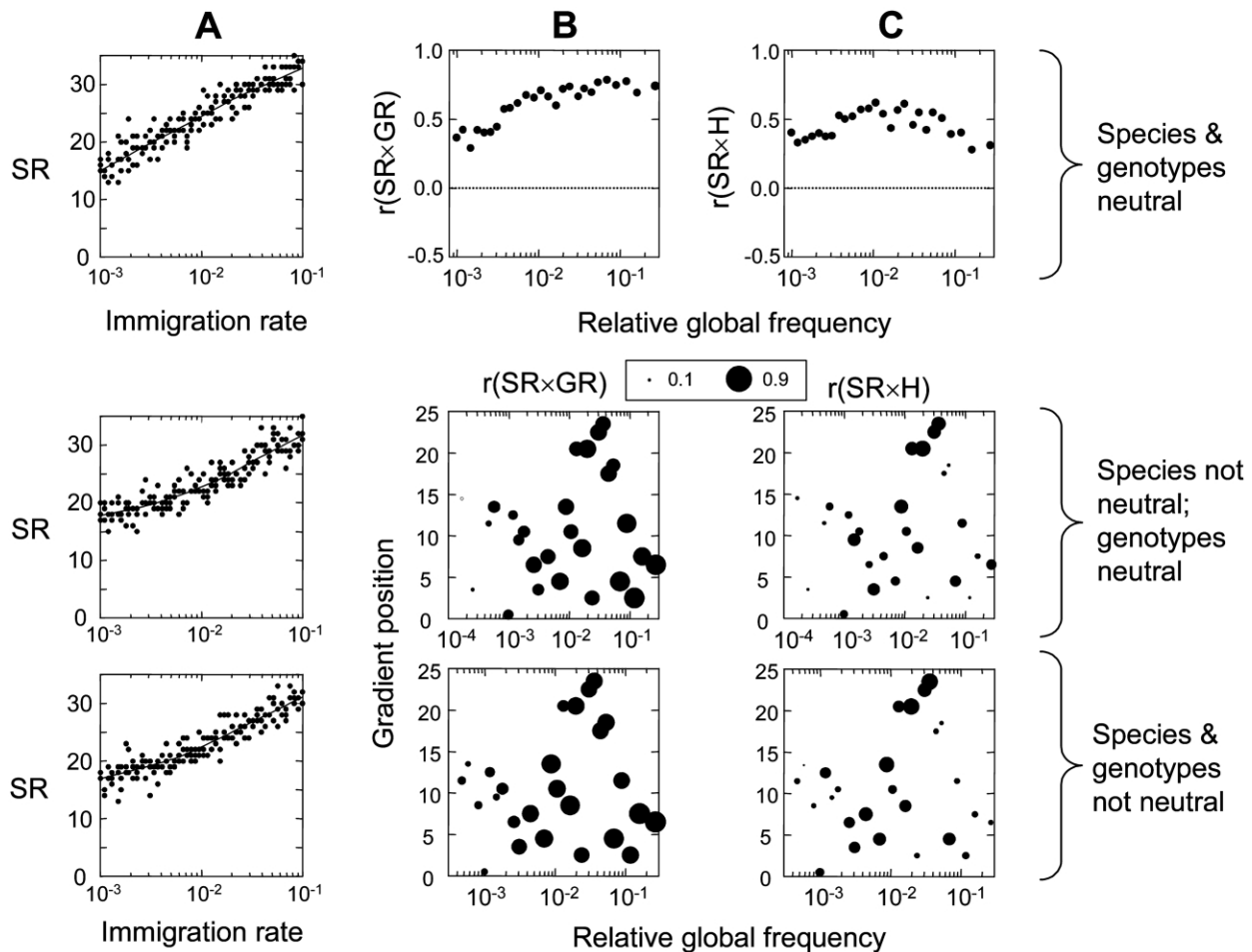


Figure 7: Relationships among immigration rate, species richness (SR), genotypic richness (GR), and expected heterozygosity (H) across 150 localities. *A*, Relationships between immigration rate and SR fitted with LOWESS (SYSTAT, ver. 10, SPSS) curves. *B*, Correlations between SR and GR in relation to species' characteristics: relative frequency in the global pool and position of fitness optimum on environmental gradient. *C*, Correlations between SR and expected H in relation to species' characteristics. Each data point in *B* and *C* represents genetic diversity measured for a different species, and in the bottom two panels the size of the circle is proportional to the magnitude of correlation. For example, in the bottom panel of *B* the correlation was 0.53 for $SR \times GR$ when GR was measured for the species with a global relative frequency of 0.024 and a gradient position of 2.5. "Gradient position" indicates the distance of a species' fitness optimum from the middle of the environmental gradient (25.5).

were less likely to be strongly correlated when GD was measured for rare species than for common species. Second, spatial environmental heterogeneity may drive correlations between SD and GD, but only seldom as a result of parallel effects of spatially varying selection. Interacting effects of environmental heterogeneity and consequent changes in population sizes on GD create several qualitatively different relationships between SD and GD, depending on the relative frequency and fitness functions of the species for which GD is measured. In the following discussion, I first address the effects of different locality characteristics on SD and GD in light of existing theoretical models and empirical patterns, highlighting similarities or

differences when the two levels of diversity are considered simultaneously. I then draw some general conclusions and implications from this study.

Area and Immigration Rate

Neutral theories in population genetics and community ecology are basically one and the same (Chave 2004; Etienne and Olff 2004), and for local populations or communities connected to a global pool via immigration, theory predicts increasing diversity with increases in the product of community or population size and the immigration rate (Wright 1940; Hubbell 2001). Abundant empirical

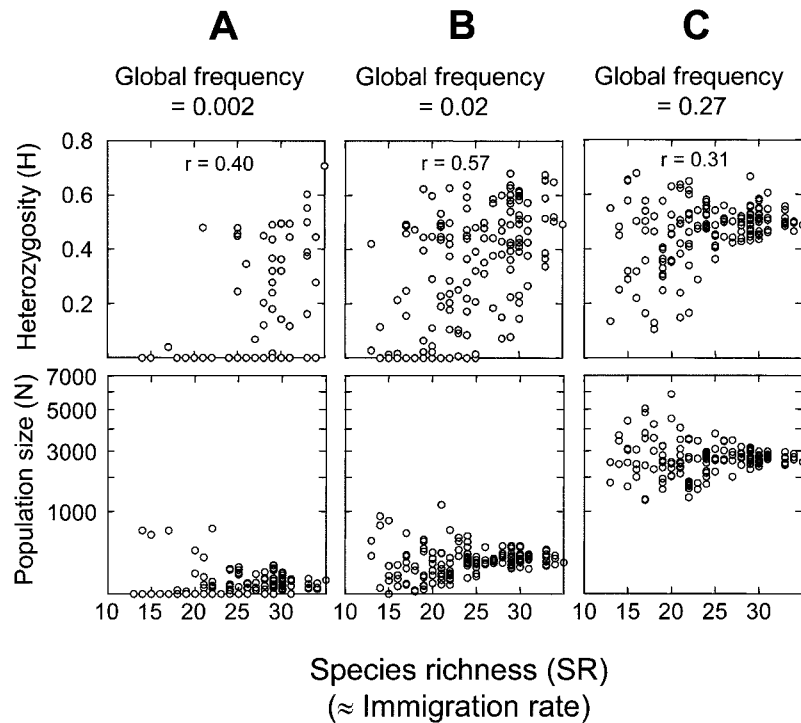


Figure 8: Relationships of species richness with population size and expected heterozygosity for species of low (A), intermediate (B), and high (C) global frequency when localities vary in immigration rate and both species and genotypes are neutral. Species richness is to be interpreted here as a surrogate for immigration rate, because of their very tight correlation (see fig. 7).

studies report increasing SD and GD with increasing area or population size and with increasing immigration rates (Rosenzweig 1995; Frankham et al. 2002; Foster and Tilman 2003; Vellend 2003, 2004; Mouquet et al. 2004). In this study, both SD and GD were strongly related to area and immigration rate, thereby creating positive correlations between the two levels of diversity (figs. 5, 7). Area and immigration have the same qualitative effects on GD in the multispecies models reported here as in single-species models. In the case of varying immigration rates, adding species to a community necessarily reduces average population sizes of the component species, but many of the species in high-SD communities are quite rare, so the direct effect of immigration on GD overwhelms the indirect effect of changes in population size. Since even the most species-rich and genotype-rich localities typically contained <80% of the species and genotypes in the global pool, it seems likely that mutation and speciation, if added to the model, would have effects similar to those of immigration.

With a finite number of species or genotypes in the global pool, richness may ultimately level off above some threshold area or immigration rate (e.g., Loreau and Mouquet 1999), although in the simulations presented here

this threshold was not reached. Species evenness (E) and expected heterozygosity (H), on the other hand, depend largely on the relative frequencies of the more common species or genotypes, and H was found here to be more or less invariant above $m \approx 0.01$ (with $J = 10,000$) for the most common species in the most species-rich localities (fig. 8; see also app. A). This created relatively weak correlations between SR and H for the most common species when immigration varied among localities (fig. 7). Weak correlations were also generally found when GD was measured for relatively rare species (figs. 5, 7). Small populations in rare species are strongly influenced by stochastic variation in individual death, local colonization, and immigration; GD for these species is, therefore, likely to be more weakly related to variation in area or immigration rate, and therefore SD, than GD for common species.

Interestingly, the effects of area and immigration rate on diversity patterns did not generally depend on whether species and genotypes were neutral with respect to selection (figs. 5, 7). One exception occurred for E , which was ultimately reduced at very high immigration rates ($m > 0.2$, probably unrealistically high) in nonneutral communities (see app. A) but not in neutral communities. When localities varied in area, only the two smallest lo-

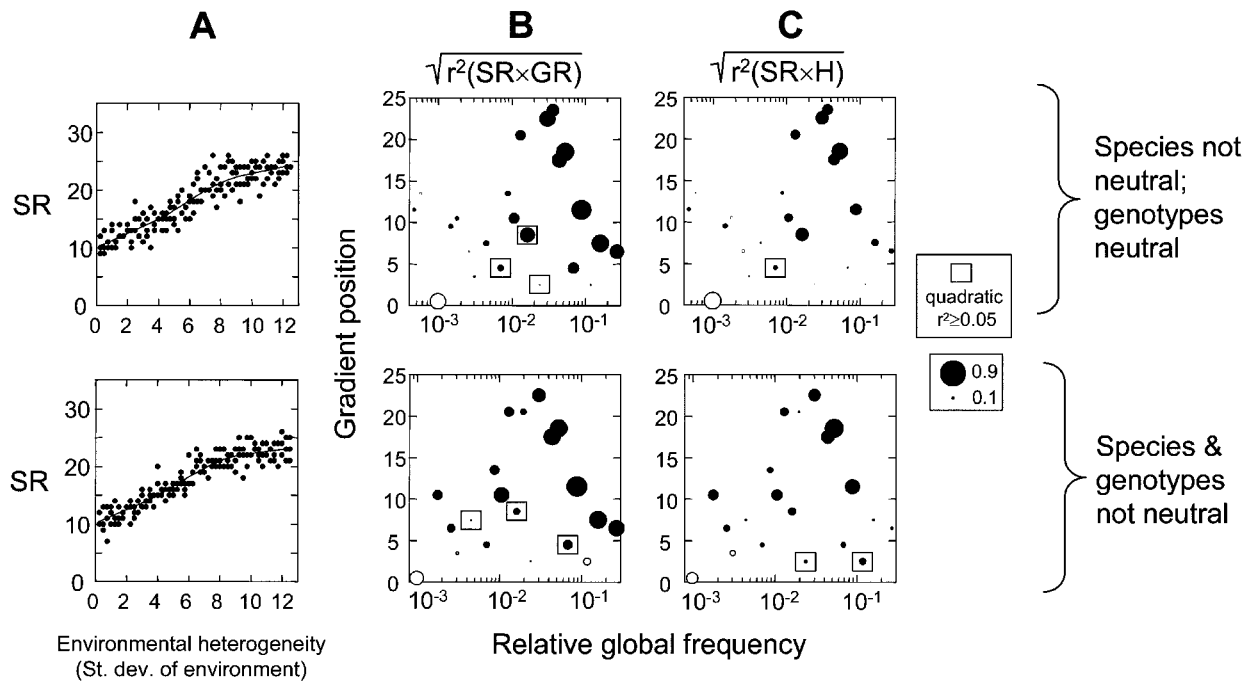


Figure 9: Relationships among environmental heterogeneity, species richness (*SR*), genotypic richness (*GR*), and expected heterozygosity (*H*) across 150 localities. *A*, Relationships between environmental heterogeneity and species richness fitted with LOWESS (SYSTAT, ver. 10, SPSS) curves. *B*, Square root of partial r^2 for linear effect of *SR* on *GR* in relation to species' characteristics: relative frequency in the global pool and position of fitness optimum on environmental gradient. *C*, Square root of partial r^2 for linear effect of *SR* on *H* in relation to species' characteristics. Each data point in *B* and *C* represents genetic diversity measured for a different species, and the size of the circle is proportional to the magnitude of correlation. Open symbols indicate negative linear effects, and squares indicate quadratic effects with partial $r^2 \geq 0.05$. For example, in the bottom panel of *B*, the square root of $r^2(\text{SR} \times \text{GR})$ was 0.063 (with no significant quadratic effect) when *GR* was measured for the species with a global relative frequency of 0.024 and a gradient position of 2.5. "Gradient position" indicates the distance of a species' fitness optimum from the middle of the environmental gradient (25.5).

calities had slightly reduced realized environmental heterogeneity compared to the rest (data not shown), so area did not act as a surrogate for environmental heterogeneity in these models, as it is thought to in many natural systems (Brown and Lomolino 1998). Consistent with these results, Chave et al. (2002) found very similar species area curves and relative abundance distributions in neutral models and in models with colonization-competition trade-offs among species or species-specific density dependence. (Chave et al. did not model environment-specific fitness.) Immigration rate has also been found to have a strong influence on local *SD* in competitive, nonneutral communities (Loreau and Mouquet 1999). Although environmental heterogeneity has a strong deterministic influence on species presence and abundance (e.g., fig. 10), immigration continually introduces new genotypes and species regardless of their local fitness. This process is akin to the disruption of local adaptation via immigration (Kirkpatrick and Barton 1997), which increases diversity but decreases the mean fitness of individuals. Thus, even in systems where

the environment and niche differences among species and genotypes are the main determinants of individual fitness, immigration and locality size can exert strong control over patterns of diversity that are well described by neutral models.

For oceanic islands, area is the dominant driver of correlations between *SD* and *GD*, while island isolation has far weaker predictive power (Vellend 2003). This would appear to conflict with the result here that area and immigration rate have similar abilities to drive positive species-genetic diversity correlations (SGDCs). One explanation is that area tends to vary among islands within archipelagoes more than isolation (Vellend 2003). It is also possible that frequently used indices of isolation or connectivity (e.g., distance to the nearest other island) are poor proxies for immigration rate, given that the typical distance between islands is likely to be well within the inherently unpredictable tails of dispersal kernels for most species. Island area is likely an excellent proxy for the number of individuals in the community.

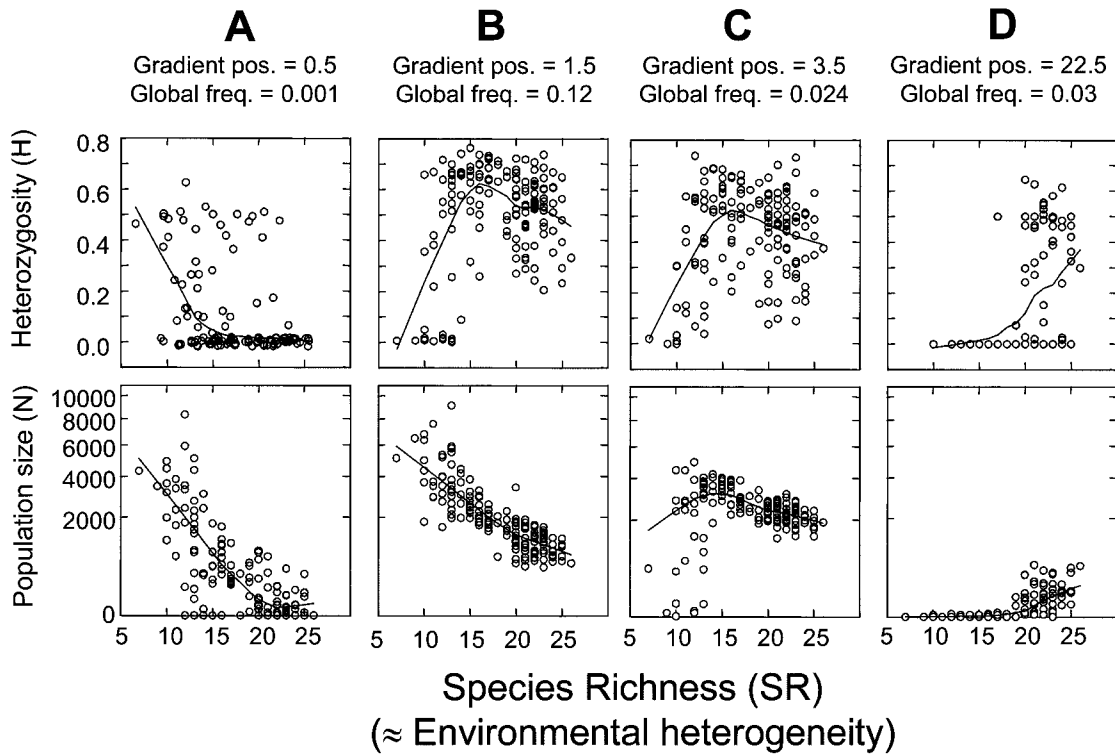


Figure 10: Relationships of species richness with population size and expected heterozygosity for species with fitness optima at different positions along the environmental gradient and different global frequencies. All relationships are fitted with LOWESS (SYSTAT, ver. 10, SPSS) curves. Localities vary in environmental heterogeneity, and both species and genotypes are nonneutral. Species richness is to be interpreted here as a surrogate for environmental heterogeneity, because of their very tight correlation (see fig. 9). In the top portion of A, data points have given a slight random jitter to reveal overlapping data points, mostly at $H = 0$.

Environmental Heterogeneity

Both theory and data support the notion that particular genotypes and species vary in their relative fitness across environments in such a way that more heterogeneous localities can harbor a greater diversity of both genes and species (Levene 1953; Levins 1968; Hedrick et al. 1976; Hedrick 1986; Burnett et al. 1998; Chesson 2000; Kassen 2002; Tews et al. 2004). But as environmental heterogeneity increases, its effects on diversity may be attenuated if mean locality-wide fitness of some or many of the genotypes or species declines as increasingly extreme microsites are added to the locality. Species richness was a strong positive function of environmental heterogeneity in the communities simulated here (fig. 9A), where the range of environmental variation in the most heterogeneous locality was deliberately constrained so as not to exceed too greatly the environmental position of the fitness optimum of the most extreme species. Note that with neutral genotypes, the relationship of SD with environmental heterogeneity represents the expectation for a single-species haploid model of GD. In the absence of other species, GD should increase

with environmental heterogeneity and perhaps plateau beyond some threshold. However, for species with fitness optima near the middle of the gradient—that is, those species for which we might expect heterogeneity to have the greatest influence on diversity—there was no strong tendency for GD to increase with heterogeneity. This counterintuitive result can be explained by considering the community context, as explained below.

As mentioned above, if community size is constant across localities, increasing SD necessarily leads to reduced average population sizes of the component species. For species with fitness optima very near the gradient center, population size decreased monotonically with increasing environmental heterogeneity (fig. 10A, 10B). For rare species, the decrease in population size completely overwhelmed any effect of environmental heterogeneity per se, resulting in a negative correlation between GD and SD (fig. 10A). For common species, small increases from very low to moderate levels of environmental heterogeneity allowed maintenance of higher levels of GD such that over a relatively narrow range, variation among localities in

environmental heterogeneity may drive positive SGDCs. However, further increases in environmental heterogeneity caused a decrease in GD as the relative fitness averaged over whole localities declined (fig. 10B). That is, the presence of other species with fitness optima at more extreme positions on the gradient dramatically altered the prediction we would make based on a single-species model. Genetic variation, and by extension microevolution, in heterogeneous environments cannot be understood without reference to the community context, in accordance with the community genetics perspective (Ackerly 2003; Neuhauser et al. 2003).

For species with fitness optima near the ends of the environmental gradient, GD tended to increase with environmental heterogeneity, not as a result of spatially varying selection but rather as a result of increasing population size as more microsites become suitable (fig. 10D). The importance of population size effects overriding effects of spatially varying selection is emphasized by the fact that very similar patterns of GD were found for neutral and nonneutral genotypes in heterogeneous environments (fig. 9).

A potential caveat of these results is that the range of environments covered by a given species' genotype-specific fitness optima was narrow relative to the width of the environmental gradient (fig. 3A, 3B). However, even when the separation between genotype fitness optima and the standard deviation of the fitness functions were both increased twofold, very similar qualitative patterns arose (see app. A). Plant communities will always occupy environmental conditions that extend well beyond the niche breadth of any one species, and the results presented here suggest caution in extrapolating from results of controlled experiments on the role of environmental heterogeneity in maintaining GD (Kassen 2002) to natural systems where the community context may be critically important. Field studies routinely demonstrate local adaptation (Linhart and Grant 1996), but the next step of asking whether GD increases with the environmental heterogeneity of sampling localities is rarely taken. This step has been taken frequently at the level of SD (e.g., Burnett et al. 1998; Tews et al. 2004), where interspecific niche differences are so pervasive as to be beyond debate, even for proponents of neutral community theory (Hubbell 2001). As a hypothetical genetic example, a plant species with local adaptations to discrete soil types is certain to harbor greater GD for relevant traits in habitat patches containing both soil types than in patches with only one soil type. However, whether this extends to continuous variation in the magnitude of environmental heterogeneity is an open question likely to be influenced by the community context.

Limitations

Several limitations and omissions from the models presented here deserve comment. First, a potentially powerful force maintaining diversity is negative frequency-dependent selection, whereby rare types are favored relative to common types (Chesson 2000). The models of environmental heterogeneity presented here represent a type of frequency dependence, in that as particular species increase in local abundance, they will become more and more likely to occupy microsites where their relative fitness is quite low, thereby reducing mean population fitness. However, negative frequency-dependent fitness can also arise via pressure from herbivores, pathogens, or a greater intensity of intraspecific versus interspecific competition (Janzen 1970; Connell 1971; Tilman 1982). If realistic scenarios can be postulated in which the intensity of these mechanisms varies among localities and acts in a similar way both within and among species, they may drive positive SGDCs. However, such situations seem highly unlikely to occur in nature (see also Hyatt et al. 2003), pointing to a potentially important limit to the domain within which SD and GD may be driven by processes acting in parallel at the two levels.

Perhaps the most fundamental difference between the underlying bases of GD and SD is the presence of recombination and interactions among alleles and genes within individuals in regulating genetic variation (Antonovics 1976; Hairston et al. 1996). From one perspective (Bell 1997; Amarasekare 2000), these phenomena are just special cases whose consideration can obscure the fundamental importance of basic demographic processes: birth, death, and movement of different biological types. The details of how genetic traits are expressed in phenotypes is, of course, of fundamental importance to the evolutionary process (Lewontin 1974), but it is also resistant to generalization with respect to their influence on how genetic variation may co-vary with characteristics of localities. The only caveat to offer is that the models presented here represent relatively simple scenarios whose predictions may change with more complicated assumptions about genetic architecture. Even for traits underlain by single genes, the selection regime may be quite different, such that SGDCs will likely vary depending not only on the species used for genetic analysis but also on the traits used to assay GD.

Finally, I have omitted the potentially important effects on diversity of environmental conditions (e.g., soil moisture, elevation) whose mean values may vary among localities. While environmental gradients are frequently strong drivers of variation in SD (Huston 1994), patterns of GD within species along environmental gradients should be highly species specific, making the formulation of general predictions regarding covariation with SD very difficult.

Conclusions and Implications

A number of hypotheses concerning the relationship between SD and GD have been articulated. An adaptation of the “niche variation” hypotheses states that niche breadth (and therefore GD) should be greatest in localities where SD is relatively low (Van Valen 1965; Johnson 1973); the prediction is a negative correlation between SD and GD. The major limitation of this hypothesis is that it does not address why SD ought to vary among localities in the first place. The one scenario in which a negative relationship arose here was when localities varied in environmental heterogeneity and GD was measured in a rare species whose fitness optimum was near the center of an environmental gradient. However, the decrease in GD with SD was driven by population size rather than by changes in niche breadth. From empirical patterns of diversity (Vellend 2003, 2004) and the theoretical results presented here, it appears that negative SGDCs are both rare in nature and theoretically unlikely. In most situations, the variables that drive variation in SD also drive variation in GD, so that an effect of one level of diversity on the other may be difficult to detect. This does not preclude the potential importance of such effects, particularly in systems under human management, where one or the other level of diversity may be independently controlled (Fridley 2001). Experimental communities provide a promising avenue for research into these issues, as exemplified by the recent work of Booth and Grime (2003), who demonstrated a positive effect of GD on SD in synthetic plant communities.

Clear theoretical parallels between the effects of area, immigration, and environmental heterogeneity on SD and GD have led to the hypothesis of positive SGDCs (see the introduction to this article), potentially driven by any one of these variables. However, environmental heterogeneity is accompanied by indirect effects on GD via the community context and population size (fig. 10). If variation in SD is driven largely by environmental heterogeneity, positive SGDCs may obtain when GD is measured for species whose populations increase in size along the same gradient. That is, the same underlying variable may drive covariation between the two levels of diversity via different processes. The question of how environmental heterogeneity influences SD and GD simultaneously presents a promising avenue for future experimental studies.

Etienne and Olff (2004) have suggested that positive SGDCs represent an affirmative test of neutral theory, but the results here point to alternate, nonneutral pathways to positive SGDCs. Nonetheless, the effects of area and immigration (i.e., neutral processes) on both levels of diversity appear to act largely independently of whether species or genotypes were neutral. Furthermore, area and immigration rate were particularly powerful drivers of

positive SGDCs, suggesting that empirical observations of positive SGDCs (Vellend 2003) are quite likely to result from the action of neutral processes influencing both levels of diversity in similar ways. Thus, the most likely scenario under which it may be possible to predict one level of diversity on the basis of the other is when neutral processes are the main drivers of variation in diversity among localities and localities vary sufficiently in area or connectivity. SD was often less likely to show positive correlations with GD in rare species than with GD in common species, pointing to the importance of empirical studies of genetic variation in multiple species across the same set of sites. Although there have been many such studies, the number of localities sampled is often too small to meaningfully evaluate interspecific differences in how GD maps onto locality characteristics and SD.

Species diversity and genetic diversity are clearly interrelated, and the tradition of treating them as independent phenomena in community ecology and population genetics, respectively, is now outdated. Great strides have been made in unifying perspectives at the levels of genes and species (Amarasekare 2000; Bell 2001; Vellend 2003, 2004; Etienne and Olff 2004), and continued synthesis and integration across disciplinary boundaries promises to advance our understanding of the causes and consequences of biodiversity.

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