

THE CONSEQUENCES OF GENETIC DIVERSITY IN COMPETITIVE COMMUNITIES

MARK VELLEND¹

National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300,
Santa Barbara, California 93101-3351 USA and
Departments of Botany and Zoology, and Biodiversity Research Centre, University of British Columbia,
Vancouver, British Columbia V6T 1Z4 Canada

Abstract. Several lines of evidence suggest that the species diversity and composition of communities should depend on genetic diversity within component species, but there has been very little effort to directly assess this possibility. Here I use models of competition among genotypes and species to demonstrate a strong positive effect of the number of genotypes per species on species diversity across a range of conditions. Genetic diversity allows species to respond to selection imposed by competition, resulting in both functional convergence and divergence among species depending on their initial niche positions. This ability to respond to selection promotes species coexistence and contributes to a reduction in variation in species composition among communities. These models suggest that whenever individual fitness depends on the degree of functional similarity between a focal individual and its competitors, genetic diversity should promote species coexistence; this prediction is consistent with the few relevant empirical data collected to date. The results point to the importance of considering the genetic origin and diversity of material used in ecological experiments and in restoration efforts, in addition to highlighting potentially important community consequences of the loss of genetic diversity in natural populations.

Key words: competition; genetic diversity; selection; spatial ecology; species diversity.

INTRODUCTION

Much of community ecology is predicated on the notion that the fitness of individual organisms depends on their own identity in relation to the identities and abundances of other community members. Overwhelming emphasis has been placed on species as the fundamental unit of observation, with the implicit assumption that all individuals of a given species share identical properties. However, genetic differences among individuals within species may have important consequences for community-level phenomena such as consumer–resource dynamics (Neuhauser et al. 2003) and competitive interactions (Pimentel 1968, Levin 1971, Aarssen 1989). Therefore, individual fitness may depend not only on the species identity of other community members, but on their genotypic identity as well (Aarssen 1983). In communities of competitors, if evolution via natural selection within species promotes species coexistence (MacArthur and Levins 1967, Pimentel 1968), the loss of genetic diversity should impede this process, thereby leading to a loss of species diversity (Vellend and Geber 2005). However, while recent research has demonstrated that species and genetic diversity are influenced by a common set of processes (Vellend 2003, 2004, 2005),

little research has addressed the potential direct effect of genetic diversity on species diversity. Here I use simple competition models with a realistically large number of species to explore the dynamics of communities in which each species is represented by a variable number of genotypes. Thinking of clonal genotypes as “quasi-species” (due the lack of recombination among clones), this paper explicitly addresses what Antonovics (2003: 600) identified as a crucial unanswered question in community genetics: “If we generated a community consisting of randomly sampled asexual individuals that are genetically uniform within each species, would this community be as stable as one consisting of quasi-species?”

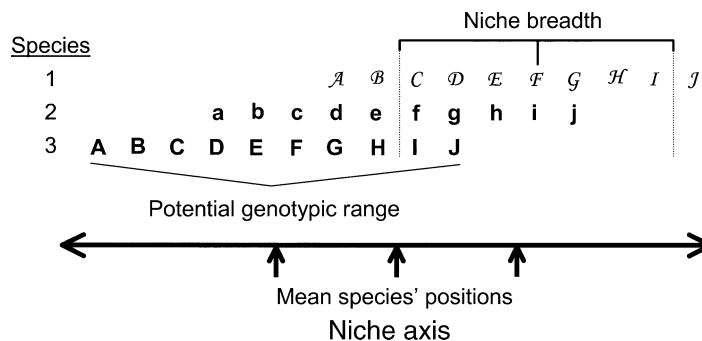
A range of empirical and theoretical results points to the potential for important community-level consequences of genetic diversity within species. For example, pairwise competition experiments have revealed genetic variation for competitive ability so that the outcome of competition between species depends on which genotypes are represented (Aarssen 1989, Turkington 1996). These empirical results provide the basis of Aarssen’s (1983) “competitive combining ability” hypothesis in which species-level coexistence depends, in part, on the ability of each species to respond to localized and spatially variable selection imposed by the identity of immediate neighbors. This hypothesis leads to the prediction that genetic diversity should promote species diversity, though this prediction has not been directly tested.

A vast literature addresses the potential for coevolution among competitors (Taper and Case 1992). An underlying assumption in models of competitor coevo-

Manuscript received 31 January 2005; revised 12 July 2005; accepted 21 July 2005; final version received 8 September 2005.
Corresponding Editor: E. Brodie III.

¹ Present address: Department of Botany, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia V6T 1Z4 Canada.
E-mail: mvellend@interchange.ubc.ca

FIG. 1. Schematic summary of the modeling framework showing three species with evenly spaced mean niche positions, and 10 genotypes per species, also showing evenly spaced niche positions. Genotypes compete with other genotypes (regardless of species) whose niche positions occur within their niche breadth. Fifty species were used in all simulations. In this hypothetical example, genotype F of species 1 (1F) competes strongly with genotypes 1C–I, 2F–J, and 3I–J, and weakly with all other genotypes. Competition is symmetrical, in that each of these genotypes has the same effect on 1F as 1F has on them.



lution is that there is genetic variation for characters that influence competition, and the focus in this field is to understand how characters evolve when species compete for resources. For example, species' traits are expected to converge or diverge depending on their initial degree of similarity (MacArthur and Levins 1967); empirical studies support both predictions (Taper and Case 1992). Either way, the implication is that genetic variation allows species to evolve so as to promote coexistence relative to the situation in which evolution is not possible (i.e., no genetic variation). However, while the complete absence of genetic variation must prevent any response to selection via competition, it is not immediately obvious whether coexistence should be influenced by different non-zero levels of genetic diversity. In this paper I model the consequences of randomly selecting different numbers of genotypes from a potential genotype pool within each of many competing species.

In the only empirical study I am aware of that explicitly manipulated genetic diversity within competing species, Booth and Grime (2003) created replicate herbaceous plant communities of 11 species in which each species was represented by 1, 4, or 16 clonal genotypes. After five years, species diversity varied positively, though not significantly, with genetic diversity, and community composition was far more variable in the low vs. high genetic-diversity treatments. The models presented here provide a theoretical framework for such experimental studies, and may have important implications for predicting the effects of genetic-diversity reductions in the field, such as when genetic diversity is reduced across a suite of species via habitat fragmentation (Frankham et al. 2002), or when genetic diversity is explicitly controlled in restoration efforts (e.g., Hughes and Stachowicz 2004). My study concerns genetic variation for traits of ecological significance, rather than neutral molecular variation. I begin with the classic Lotka-Volterra model of competition, and proceed with a simulation model of neighborhood competition for space in a homogeneous environment. Extensions to models with abiotic environmental heterogeneity are addressed via a modified simulation model (see Appendix).

METHODS

My approach was to run numerical "experiments" similar to the empirical experiment reported in Booth

and Grime (2003), in which the number of genotypes representing each species in the community is varied, and the species diversity and composition of the resulting communities examined as response variables. Competition was modeled in relation to a single niche axis, such as the size of food items for animals or rooting depth for plants (Fig. 1). Each species has up to 10 clonally reproducing genotypes, and each genotype has a fixed position along the niche axis. All genotypes of all species are identical except for their niche position. The mean values of each species' 10 genotypes are evenly spaced along the niche axis. Niche breadth is defined as a range on either side of a genotype's mean niche position within which competition is stronger than it is with types outside this range (see Fig. 1).

Genetic diversity has two components. The "potential genotypic range" is the range along the niche axis between the two extreme genotypes of a given species; all species have the same potential genotypic range, and genotypes within species are spaced evenly along the niche axis. "Genotypic richness" is the number of genotypes representing each species, which may vary from 1 to 10. In a given community, each species has the same genotypic richness, and genotypes (when <10) are chosen randomly within species. In sum, community dynamics depend on only three parameters, niche breadth, potential genotypic range, and genotypic richness, all of which are the same across species within a community. In all analyses presented here, communities were started with 50 species whose mean positions were set at the integer values 1–50 on the niche axis.

Lotka-Volterra competition model

The classic Lotka-Volterra model of competition provides a fundamental building block for theory in community ecology, and continues to provide important insights in contemporary studies. The population density, N , of genotype i , species m , is given by

$$\frac{dN_{im}}{dt} = r_{im}N_{im} \left[\frac{K_{im} - \sum_{n=1}^S \sum_{j=1}^{GR} \alpha_{im,jn} N_{jn}}{K_{im}} \right].$$

In this model, r_{im} is the intrinsic rate of increase and K_{im} the carrying capacity specific to genotype i of spe-

cies m . The $\alpha_{im,jn}$ values are the competition coefficients defining the per capita effect of genotype j , species n on genotype i , species m , with $\alpha_{im,im} = 1$. S is the number of species in the community, and GR is the genotypic richness per species. For large numbers of species, analytical solutions for the equilibrium population sizes of each type are not possible. Thus, for the parameter combinations described below, I obtained equilibrium population sizes for each genotype of each species numerically using the discrete-time version of the model. Species richness (i.e., the number of species present) was calculated at equilibrium.

In all communities, I set $r = 0.5$ and $K = 10\,000$ for all genotypes of all species. If a given pair of genotypes (regardless of species) are within each other's niche (see Fig. 1), $\alpha_{im,jn} = 1$; otherwise $\alpha_{im,jn} = 0.1$. In discrete time, the model thus simplifies to

$$N_{im}(t+1) = N_{im}(t) + rN_{im}(t) \left[\frac{K - \sum_{n=1}^S \sum_{j=1}^{GR} \alpha_{im,jn} N_{jn}(t)}{K} \right].$$

The population density of each genotype was started at $K/(S \times GR)$ such that the total number of individuals in the community always started at K . During simulations, if N_{im} was reduced below 1, N_{im} was set to zero (i.e., a genotype was considered extinct if its population density was < 1).

A simulation model of competition for space

The Lotka-Volterra model is unsatisfying to most plant ecologists because it assumes even mixing of individuals, whereas plants generally compete only with their immediate neighbors. To model competition for space among sessile organisms I used a spatially explicit simulation in which individual fitness (survival probability) is determined by the species and genotype identities of immediate neighbors. Individuals occupy cells in a 100×100 square lattice ("locality"), and cells that become empty via death are filled by colonists within the same time step; life is thus a zero-sum game. Each cell contains only one individual. Following the framework of Fig. 1, genotypes compete strongly if they occur within each other's niche, and weakly otherwise. Specifically, the probability of individual death at a given time step equals the proportion of the eight nearest neighbors whose niche position falls within the focal individual's niche breadth. If none of an individual's nearest neighbors is within its niche, the probability of death is 0.1. Individuals on the edge of a locality have five nearest neighbors; in the corners they have three.

Following death, empty cells are filled by random draws from within the locality; individuals may both die and provide colonists within a given time step (i.e., effectively seed dispersal precedes mortality). With no immigration from outside a locality, species richness can only decrease from its initial value of 50, and the

only stable equilibrium occurs when one genotype of one species occupies every cell. The question is thus whether genetic diversity within species slows the rate of decay of species diversity. Therefore, the response variable measured as "species diversity" in each simulation was the time taken to reach a 10% reduction in species richness (i.e., 45 species remaining). This cutoff was selected as a compromise between keeping simulation times manageable, and allowing a meaningful reduction in species diversity.

Parameter space

For both models, a given "run" of simulations consisted of 20 localities simulated at each of five levels of genotypic richness (GR): 1, 2, 4, 7, or 10 genotypes. For the Lotka-Volterra model, only one run of the 10-genotype model was needed because the outcome is entirely deterministic, so a Lotka-Volterra run consisted of a total of 81 rather than 100 localities. With $GR < 10$, the random selection of genotypes within species was independent across localities. Two parameters were varied among runs: potential genotypic range (PGR) was varied from 0.9 to 27, corresponding to spacings of 0.1–3 niche axis units between adjacent genotypes, and niche breadth (NB) was varied from 1 to 20. With $PGR = 0.9$, there is no overlap among species in the niche positions of their genotypes; with $PGR = 27$, the spacing between genotypes within species is three times greater than the spacing between species' means (see Fig. 1). When $NB > 2 \times (49 + PGR)$ (see Fig. 1), all individuals have identical properties (i.e., the model is neutral). Results are reported for all 20 combinations at four levels of PGR and five of NB. This parameter space corresponds to a wide range of variation in effective niche overlap among species and genotypes, which varies greatly among real communities. For plant communities, combinations of high niche breadth and high potential genotypic range are probably most realistic (Aarssen 1983), whereas lower values of both parameters may be realistic in at least some animal communities (Schoener 1974).

Response variables calculated were species richness (Lotka-Volterra), time to 10% species loss (spatial simulation), and variance in community composition among simulations within runs. For each parameter combination, variation in community composition was quantified by first calculating the mean variance in species' abundance across the 20 communities. This was divided by the mean species abundance across communities to control for variation among parameter combinations in community size (i.e., summed abundance across species). This correction was only necessary for the Lotka-Volterra model because community size was constant in the spatial simulations, though the same correction was applied to both to make the scales comparable.

RESULTS AND DISCUSSION

Species diversity

In most of the parameter space, both the Lotka-Volterra and spatial simulation models predict that species

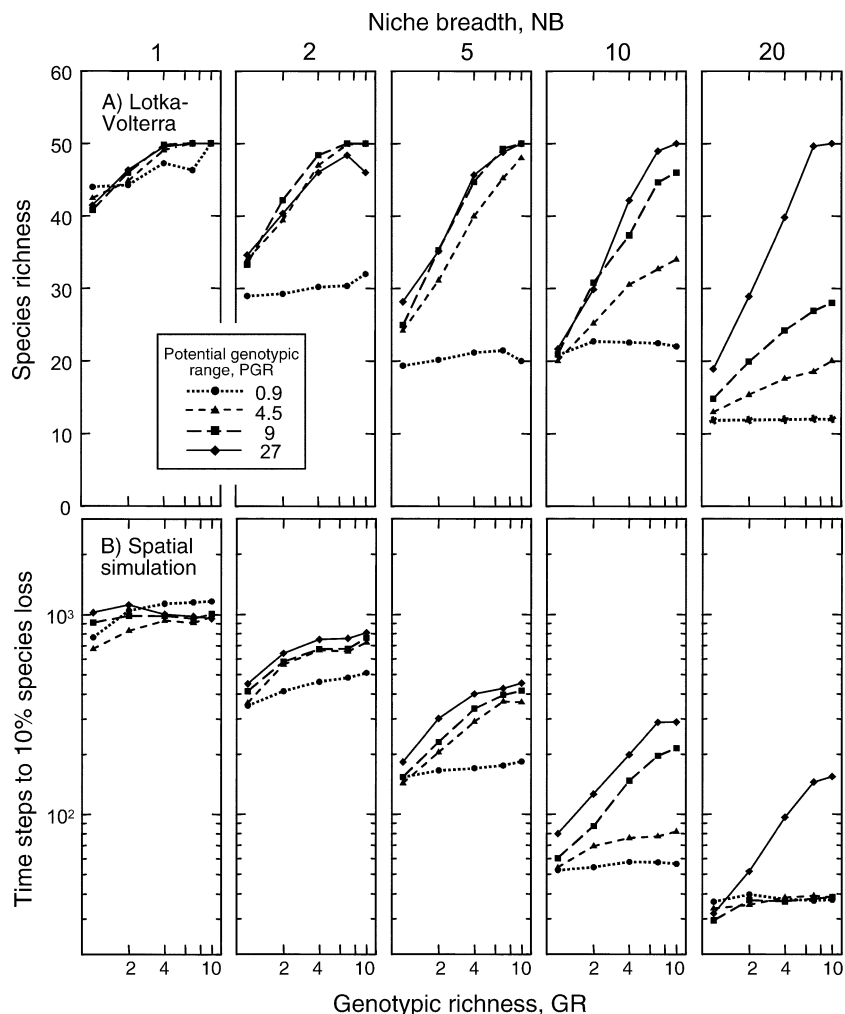


FIG. 2. Effects of genotypic richness (log scale), niche breadth, and potential genotypic range on species diversity (see *Methods* for descriptions: (A) species richness at equilibrium in the Lotka-Volterra model; (B) the time taken for 10% of species to be lost from communities in the spatial simulations. Error bars are omitted for clarity (in all cases they were very small relative to the variation among parameter combinations).

diversity increases with genotypic richness (GR) (Fig. 2). The two models are also in agreement that species diversity generally decreases within increasing niche breadth (NB) and increases with increasing potential genotypic range (PGR). In the Lotka-Volterra model, species diversity is uniformly high when $PGR = 27$ and $GR \geq 7$, while in the spatial simulation species diversity declines with increasing niche breadth at all values of PGR and GR (Fig. 2).

More detailed examination of the outcomes of the two models at selected parameter combinations reveals the mechanisms underlying the effects of NB, GR, and PGR on species diversity (Fig. 3). The main effect of increasing NB is to decrease the number of positions along the niche axis where genotypes can persist—“viable niches” (Fig. 3). At the beginning of each simulation all genotypes of all species have the same number of potential competitors except those genotypes

occupying positions at the ends of the niche axis where there are fewer competitors (see Fig. 1). These genotypes, therefore, tend to have high fitness and thereby “anchor” the community by outcompeting similar genotypes slightly further from the end of the niche axis, and, in turn, determining the positions of the other viable niches (Fig. 3). Niche breadth sets the spacing of the viable niches, though in the spatial simulations the exact positions of viable niches varies stochastically among runs. Genotypes at a given viable niche position are strong but equivalent competitors and do not compete strongly with genotypes at other viable niche positions. With fewer viable niches when niche breadths are large, some species may have no genotypes at all within one of the viable niches. Therefore, species diversity declines as niche breadth increases. It is important to note that evenly spaced viable niches arise in many models of competition (Taper and Case

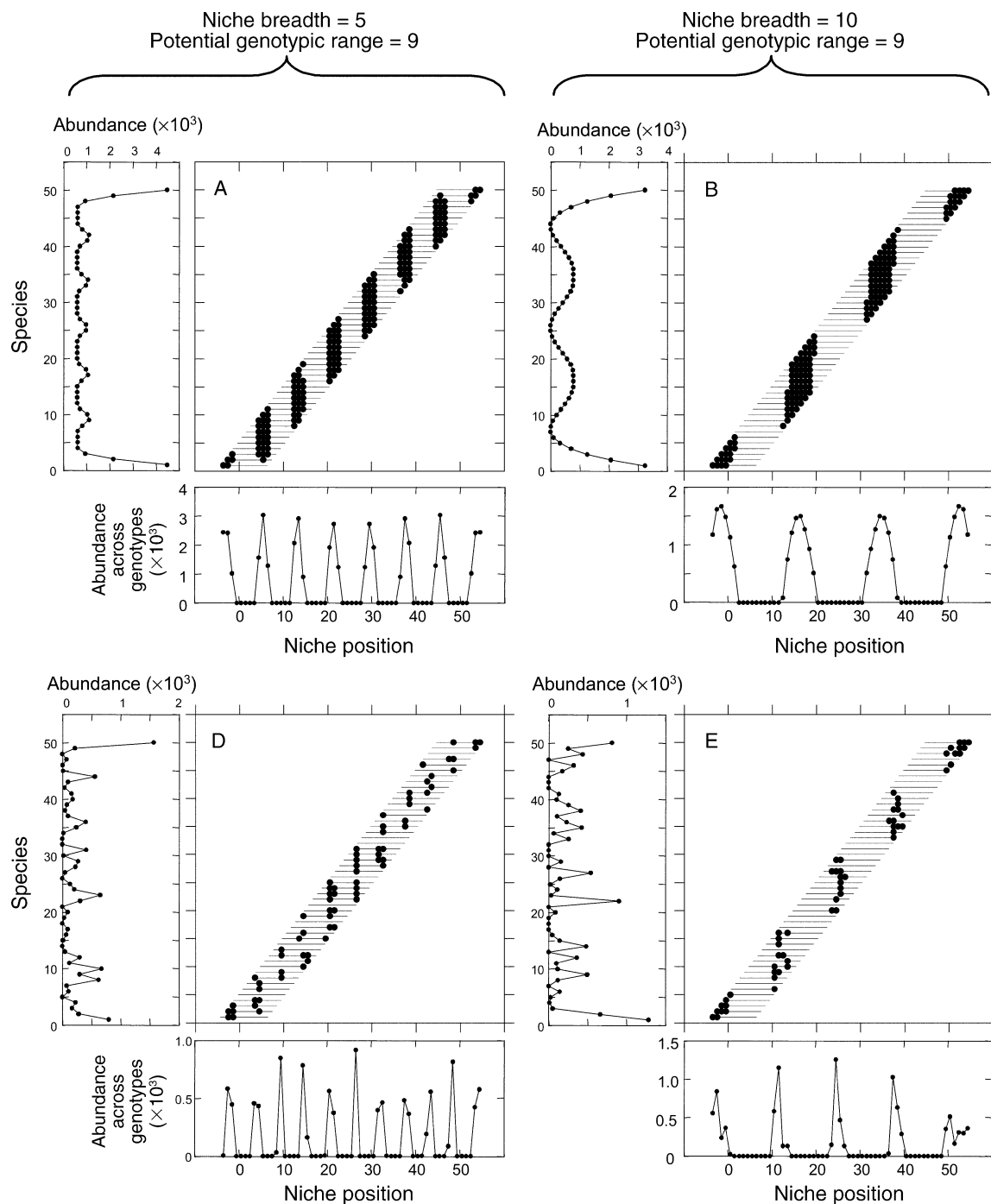


FIG. 3. Model results for three parameter combinations in the Lotka-Volterra model (A–C) and the spatial simulations (D–F, showing the outcome of a single simulation), in all cases with the maximum 10 genotypes per species. In the main part of each panel, horizontal lines indicate the positions of all potential genotypes in the community, and small solid circles indicate those with within-species frequency > 0.1 . In the bottom and left parts of each panel, abundance is summed across all genotypes at a particular niche position (bottom) or across all genotypes within a species (left). See *Methods* for descriptions.

1992, Leibold 1998, Tilman 2004), though certainly not all models (Abrams 1990), and as such are not an unusual artifact of the model structure here.

Given a particular set of viable niches, PGR and GR jointly determine the probability that any given species

will have one or more genotypes within one of the viable niches. For example, with $NB = 10$ and $PGR = 9$ all but a very few species have at least one genotype within a viable niche (Fig. 3B and E) whereas with $PGR = 4.5$ many more species are excluded because they lack any

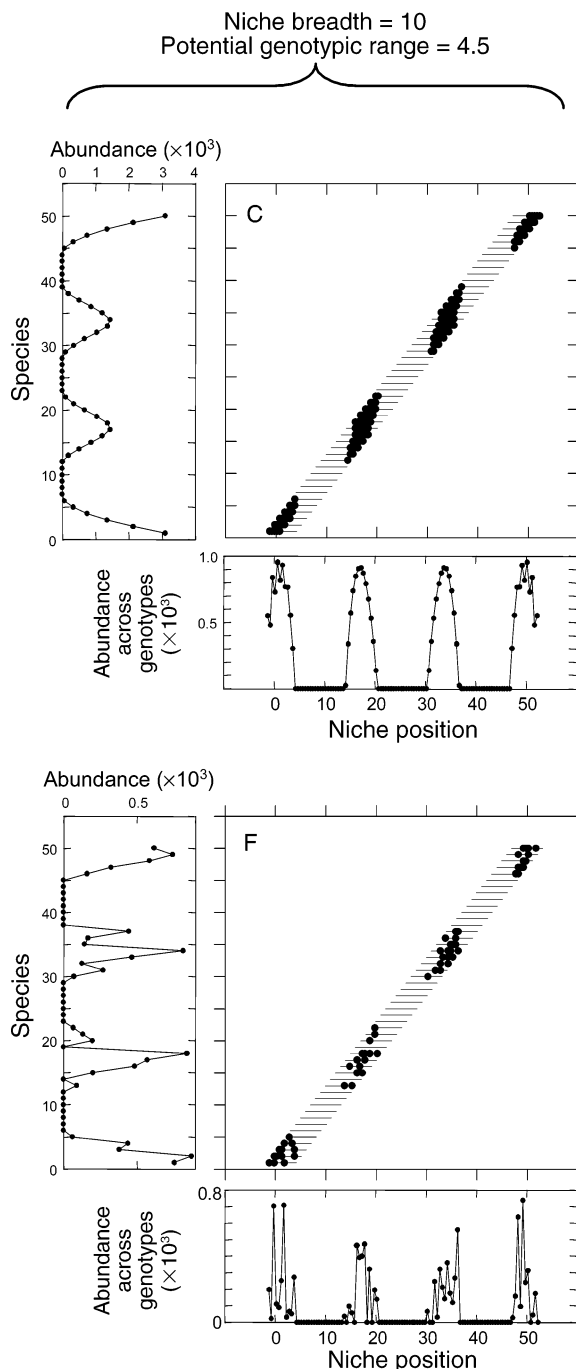


FIG. 3. Continued.

genotypes that fall within one of the viable niches (Fig. 3C and F). With fewer than 10 genotypes per species even more species fail to have any genotypes within a viable niche. In biological terms, GR and PGR determine the probability that each species possesses genetic variants that are able to persist in the face of multi-species competition. Thus, genetic diversity allows species to respond to complex selection pressures in diverse com-

munities in such a way that promotes their coexistence. This result is not a simple extension of single-species models in which genetic diversity enhances fitness because when space is the ultimate limiting resource some species benefit greatly when genetic diversity is low due to the demise of many other species. When genetic diversity is low, predicting the dynamics of any one species requires knowledge of the community context, which includes the genetic diversity and composition of competing species.

Community composition

Across the entire parameter space in the Lotka-Volterra model and most of the parameter space in the spatial simulations, variance in community composition decreased with increasing genotypic richness (Fig. 4). This was, in large part, a consequence of selecting genotypes randomly from a set pool. With GR = 10, the initial composition of each replicate community is identical; with GR < 10, each replicate community consists initially of a different combination of genotypes, and the number of such combinations increased as GR decreases. In effect, increasing genotypic richness decreases the variance across simulations in initial mean species' niche positions and in the range of functional types present within each species, thereby decreasing variation in the species-level outcome of competition.

Variation in community composition with respect to PGR and NB provided a complex set of results, the key points of which I interpret as follows. First, note that NB determines not only the number of viable niches, but also their width (Fig. 3A and B). When NB is small, each genotype interacts with few other genotypes and there are many viable niches so that most genotypes (and species) are maintained in the community (Fig. 2) and variance in composition among model runs is low (Fig. 4). When NB is large, many genotypes occupying positions between the few viable niches are predictably absent (Fig. 3C and E); if PGR is low when NB is large, the remaining genotypes will tend to belong to a predictable set of species (Fig. 3D and F). Thus, with large NB, the effect of PGR on compositional variance tends to be positive, at least in the Lotka-Volterra model (Fig. 4A). In the spatial simulations, drift among genotypes and species within the few viable niches at high NB creates large variance in abundance among simulations; when NB is lower the maximum population size of any one species within most viable niches is lower, thereby reducing potential variance among simulations. As a result, variance in species composition increases across the full range of NB rather than showing a unimodal pattern as observed for results of the Lotka-Volterra model. The key result from the point of view of empirical tests is that increasing GR is predicted to reduce variance in species composition within most of the parameter space.

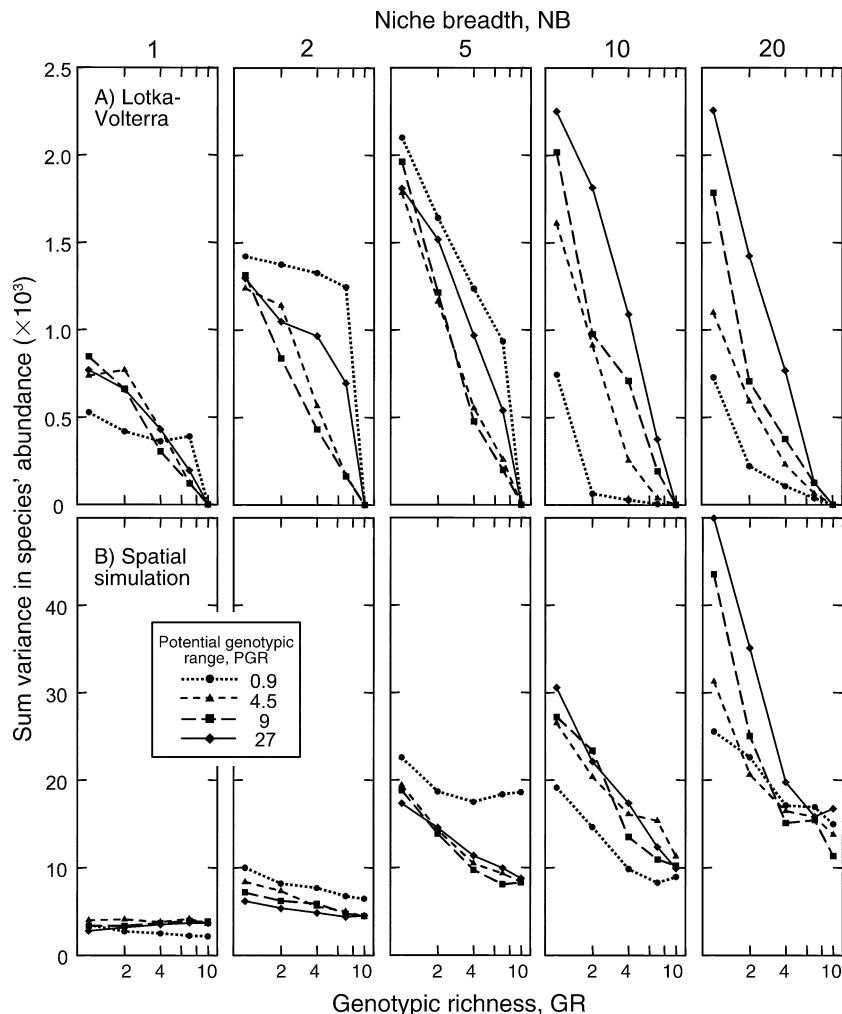


FIG. 4. Effects of genotypic richness (log scale), niche breadth, and potential genotypic range on variation among simulations in species composition, expressed as the summed variance in species' abundances across simulations divided by the mean species' abundance for (A) the Lotka-Volterra model and (B) spatial simulations.

Implications

The results described thus far suggest that when fitness depends on the degree of similarity between a focal genotype and its competitors, species diversity and composition may depend on genetic diversity within component species. Given that individual species' success often depends on the degree to which it can exploit the environment in ways that are distinct from its competitors (Taper and Case 1992, Silvertown 2004, Tilman 2004), this result may be fairly general, though less is known about niche relationships among genotypes within species. Though only a single niche axis was modeled, the key feature of the model appears to be that genetic diversity allows broader coverage of niche space; including additional niche axes should produce similar results. From a theoretical viewpoint, functional differences between species and genotypes are critical in at least two additional contexts. First, if individual fitness depends not on the identity of com-

petitors, but rather on the local abiotic environment in a space-limited system, again species diversity increases and variance in community composition decreases with increasing genotypic richness (Appendix). Second, in models with colonization-competition trade-offs, the establishment of new species depends on it being a sufficiently better colonizer than resident species (Tilman 1994). As such, genetic diversity should increase the probability that each invading species has appropriate characteristics to persist in competition with residents. Since these models encapsulate many of the ways competition is thought to operate in ecological communities, genetic diversity may be an important determinant of the outcome of competition in a range of systems.

The models presented here display the simultaneous action of multiple processes that are generally considered as competing explanations for community patterns, or as alternative outcomes of coevolution. In both mod-

els, community structure shows a strong signature of niche-based, or selective, processes (Fig. 3). The spatial simulations also reveal the simultaneous influence of drift among both species and genotypes. Even with maximum genetic diversity (i.e., all replicate communities start with identical functional composition), the exact positions of viable niches vary stochastically. In addition, the abundances of particular species are difficult to predict because within a given viable niche different genotypes are essentially equivalent. In agreement with other recent studies (e.g., Tilman 2004, Vellend 2004, 2005), these results point to the simultaneous importance of neutral and non-neutral processes in driving patterns of diversity and abundance.

Models of competitor coevolution predict either divergence or convergence of particular phenotypic traits depending on the initial spacing of species along a niche axis (MacArthur and Levins 1967, Taper and Case 1992). In the models presented here, species with mean positions near the same viable niche converged in the sense that genotypes with similar niche positions were favored. Species with mean niche positions near the midpoint between two viable niches diverged. Thus, both convergence and divergence of phenotypic characters (in this case mean niche position) may occur among species in a single community (see also Leibold 1998).

With respect to empirical studies, niche-based competition provides one plausible explanation for the results of Booth and Grime (2003), who found decreased variation in community composition and increased species diversity in communities with high compared to low genotypic richness. The results for species diversity were not statistically significant after five years (Booth and Grime 2003), which is not surprising given that diversity is expected to decay rather slowly in sessile perennial organisms (see Fig. 2B). More such experiments are needed to test the generality of these results, and ultimately to test for effects of characteristics such as average species' niche breadth and potential genotypic range. The results here also stress the potential importance of considering genetic diversity in interpreting the outcome of competition experiments, as well as in restoration efforts (e.g., Hughes and Stachowicz 2004). Finally, declines in genetic diversity in natural systems may have consequences not only for particular species but for community-level diversity and composition as well.

ACKNOWLEDGMENTS

NCEAS is funded by NSF (Grant number DEB-0072909), the University of California, and the Santa Barbara campus. Monica Geber, Jonathan Levine, Janneke HilleRisLambers,

John Drake, Lonnie Aarssen, Karl Cottenie, and two reviewers provided valuable discussions and comments.

LITERATURE CITED

- Aarssen, L. W. 1983. Ecological combining ability and competitive combining ability in plants: towards a general evolutionary theory of coexistence in systems of competition. *American Naturalist* **122**:707–731.
- Aarssen, L. W. 1989. Competitive ability and species coexistence: a 'plant's-eye' view. *Oikos* **56**:386–401.
- Abrams, P. A. 1990. Ecological vs. evolutionary consequences of competition. *Oikos* **57**:147–151.
- Antonovics, J. 2003. Toward community genomics? *Ecology* **84**:598–601.
- Booth, R. E., and J. P. Grime. 2003. Effects of genetic impoverishment on plant community diversity. *Journal of Ecology* **91**:721–730.
- Frankham, R., J. D. Ballou, and D. A. Briscoe. 2002. Introduction to conservation genetics. Cambridge University Press, Cambridge, UK.
- Hughes, A. R., and J. J. Stachowicz. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences (USA)* **101**:8998–9002.
- Leibold, M. A. 1998. Similarity and local co-existence of species in regional biotas. *Evolutionary Ecology* **12**:95–110.
- Levin, B. R. 1971. The operation of selection in situations of interspecific competition. *American Naturalist* **25**:249–264.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* **101**:377–385.
- Neuhausser, C., D. A. Andow, G. E. Heimpel, G. May, R. G. Shaw, and S. Wagenius. 2003. Community genetics: expanding the synthesis of ecology and genetics. *Ecology* **84**:545–558.
- Pimentel, D. 1968. Population regulation and genetic feedback. *Science* **159**:1432–1437.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* **185**:27–39.
- Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology and Evolution* **19**:605–611.
- Taper, M. L., and T. J. Case. 1992. Coevolution among competitors. *Evolutionary Biology* **8**:63–109.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2–16.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences (USA)* **101**:10854–10861.
- Turkington, R. 1996. Intergenotypic interactions in plant mixtures. *Euphytica* **92**:105–119.
- Vellend, M. 2003. Island biogeography of genes and species. *American Naturalist* **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. *American Naturalist* **166**:199–215.
- Vellend, M., and M. A. Geber. 2005. Connections between species diversity and genetic diversity. *Ecology Letters* **8**:767–781.

APPENDIX

A simulation model with environmental heterogeneity (*Ecological Archives* E087-015-A1).