

Application of Model of Plant Population Structure and Phenotypic Divergence

Man-Kyu Huh*

Department of Molecular Biology, Dong-eui University, Busan 614-714, Korea

(Manuscript received 11 January, 2010; revised 22 December, 2010; accepted 5 January, 2011)

Abstract

In application and discussion of population structure and phenotypic divergence in plant community, the classic Lotka-Volterra models of competition and spatial model are conceived as a mechanism that is composed by multiple interacting processes. Both the Lotka-Volterra and spatial simulation formulae predict that species diversity increases with genotypic richness (GR). The two formulae are also in agreement that species diversity generally decreases within increasing niche breadth (NB) and increases with increasing potential genotypic range (PGR). 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. This was, in large part, a consequence of selecting genotypes randomly from a set pool.

Key Words : Population structure, Phenotypic divergence, Lotka-Volterra model, Spatial model

1. Introduction

Community ecology is predicted 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. Genetic differences among individuals within species may have important consequences for community level phenomena such as consumer-resource dynamics (Neuhauser, 2003) and competitive interactions (Vellend, 2005). Therefore, individual fitness may depend not only on the species identity of other community members, but on their genotypic identity as well.

Natural populations inhabiting the same environment often independently evolve the same

phenotype (McGuigan et al., 2005). Is this replicated evolution a result of genetic constraints imposed by patterns of genetic variation? The important concerns genetic variation for the characteristics of environmental significance, rather than neutral molecular variation.

When a species encounters novel environmental conditions, as can occur, for example, during range expansion, climate change, habitat degradation, or host plant shifts, some phenotypic characters may develop differently than in the ancestral environment. It has long been recognized that environmental perturbations of development have the potential to facilitate adaptive evolution and enable populations to reach new adaptive peaks (Mousseau et al., 2000; Price et al., 2003; West-Eberhard, 2003). As with genetic mutations, however, most environmental perturbations of development are likely to reduce fitness, at least initially. Natural selection would usually be expected to favor genetic changes that

*Corresponding author : Man-Kyu Huh, Department of Molecular Biology, Dong-eui University, Busan 614-714, Korea
Phone: +82-51-890-1529
E-mail: mkhuh@deu.ac.kr

restore the ancestral phenotype or compensate for the environmental change in other ways (Conover and Schultz, 1995). Compensatory evolutionary responses to environmental change have not gone unnoticed by evolutionary biologists, but the phenomenon deserves broader attention than it has received.

"Genetic accommodation" is a general term for gene frequency changes caused by selection in response to environmentally (or genetically) induced changes in the phenotype (West-Eberhard, 2003). When environmentally induced changes in the phenotype increase fitness, they may become genetically assimilated (Waddington, 1961). Genetic assimilation is a form of genetic accommodation in which environmentally induced phenotypes gradually become canalized and develop in the absence of the triggering environmental stimulus (Pigliucci and Murrena, 2003; West-Eberhard, 2003).

Geographic gradients in species richness have long been of interest to biogeographers, ecologists, and evolutionary biologists and have been hypothesized to reflect underlying geographical gradients in a great variety of ecological and evolutionary factors (MacArthur, 1965; Currie et al., 1999; Whittaker et al., 2001). However, species richness gradients can also arise through simple geometric constraints on species range boundaries in the absence of any environmental or historical gradients. In either one or two dimensions, random placement of species geographic ranges on a bounded map produces a peak of species richness near the center, the "mid-domain effect" (Colwell and Hurtt, 1994; Colwell and Lees, 2000).

This study was begun with the classic Lotka-Volterra model of competition and proceed with a simulation model of neighborhood competition for the space in a homogeneous environment. Extensions to models with abiotic environmental heterogeneity are addressed via a modified simulation model.

2. Materials and methods

2.1. Two models of competition community

The wetlands have chosen to analyze a system to study habitat selection in spatiotemporally fluctuating environments (Fig. 1). These areas will be assumed that the fitness of individuals in each habitat is a linear function of population density in that habitat and has a stochastic element that may or may not be correlated with the other habitat. At the start of each year, the adults will select habitat according to the expected fitness rewards in each habitat.

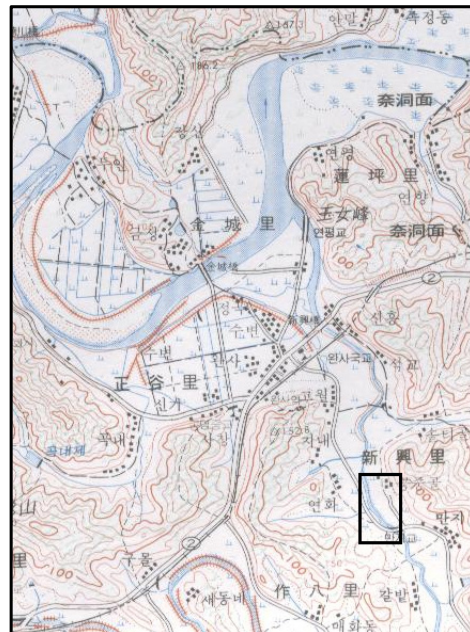


Fig. 1. Location of the population in this study.

A species has up to 10 genotypes, and each genotype has a fixed position along the niche axis according to the method of Vellend (2006) (Fig. 2). 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 their side of a genotype's mean niche position within which competition is stronger than it is with types outside this range.

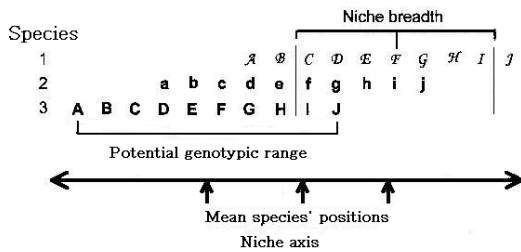


Fig. 2. Schematic summary of the modeling framework showing three species with evenly spaced mean niche positions, and ten genotypes per species, also showing evenly spaced niche positions. Genotypes compete with other genotypes (regardless of species) whose niche positions occur within their niche breadth (Vellend, 2006).

Genetic diversity has two components. The "potential genotypic range" is the 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. "genotype 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 genotype (when < 10) are chosen randomly within species.

The classic Lotka-Volterra model of competition community ecology, and continues to provide importance insights in contemporary studies (Vellend, 2006). The population density N_i 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 all communities, it sets $r = 0.5$ and $K = 10,000$ for all genotypes of all species. If a given pair of genotypes are within each other's niches, $\alpha_{im,jm} = 1$; otherwise $\alpha_{im,jm} = 0.1$. In discrete time, the model thus simplifies to

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

To model competition for space among sessile organisms, there were 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 10 x 10 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. Specially, the probability of individual death at a given time step equals the proportion of the eight nearest neighbors whose niche position falls within the local individual's niche breadth. If none of an individual's nearest neighbors is within its niche, the proportion of death is 0.1. Individuals on the edge locality have five nearest neighbors; in the corners they have three.

For both models, a given "run" of simulations consisted of 10 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 from 0.9 to 27, corresponding spacings of 0.1-3 niche axis units between adjacent

genotypes, and niche breadth (NB) was varied from 1 to 20. When $NB > 2 \times (49 + PGR)$, all individuals have identical properties and thus the model is neutral.

2.2. Genotype analysis

Three species, *Taraxacum mongolicum* H. Mazz., *Trifolium repens* L., and *Festuca ovina* L. were collected from a waste field at Sacheon-si in Korea (Fig. 1). One leaf per plant was sampled during 2000 to 2005.

Leaves were homogenized by mechanical grinding to release enzymes from cell and organellar membranes with Tris-HCl grinding buffer-PVP solution as described in Soltis et al. (1983). Electrophoresis was performed with a 12.0% starch gel. Twelve enzyme systems were assayed: acid phosphatase (ACP), fluorescent esterase (FE), peroxidase (PER), shikimate dehydrogenase (SKD), leucine aminopeptidase (LAP), and menadione reductase (MNR), were resolved on System 9 of Soltis et al.; glucose phosphate isomerase (GPI), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), malic enzyme (ME), 6-phosphogluconate dehydrogenase (PGD), and phosphoglucomutase (PGM) were resolved on System 10 of Soltis et al. (1983). Gels were run in a refrigerated chamber at 4°C. For enzymes resolving in more than one zone of activity, the most anodal isozyme is arbitrarily designated '1' and subsequent isozymes were sequentially assigned higher numbers. Likewise, alleles were designated alphabetically with the most anodally migrating allozyme designated 'a'.

2.3. Analysis of data

Various standard genetic parameters were estimated using a computer program (POPGENE, Ver. 1.31) percentage of polymorphic loci (P), mean number of alleles per locus (A), effective number of alleles per locus (A_E), the number of alleles per polymorphic locus (A_P), and gene diversity (H_{EP}).

Observed heterozygosity (H_{OP}) was compared with Hardy-Weinberg expected value using In addition, chi-square statistics were used to detect significant differences in allele frequencies among populations for each locus. Correlation between geographical and genetic distance was tested using Mantel's test as advocated by Smouse et al. (1986).

3. Results and Discussion

Significant differences were found in allele frequencies between localities for 3 loci (*Fe-1*, *Per-2*, and *Mdh-1*). In *T. mongolicum*, *Fe-1* is monomorphic while others are polymorphic. In *T. repens* and *F. ovina*, *Per-2* locus is also the same trend. The number of alleles (A) was 1.32 for *T. repens*, varying from 1.20 for *F. ovina* and 1.56 for *T. mongolicum* (Table 1). *T. mongolicum* had the highest expected diversity (0.125), while *F. ovina* the lowest (0.069). In addition, the correlation between genetic distance and geographic distance was low ($r = 0.51$, $p < 0.05$), and indicated that geographically close populations tended to be genetically similar and about 74% of the variation in genetic distance was caused by unknown factors other than distance.

Table 1. Genetic variation within the population studied. Percentage of polymorphic loci (P), mean number of alleles per locus (A), mean number of alleles per polymorphic locus (A_P), effective number of alleles per locus (A_E), observed heterozygosity (H_{OP}), and Hardy-Weinberg-expected heterozygosity or genetic diversity (H_{EP})

Species	P	A	A_P	A_E	H_{OP}	H_{EP}
<i>Taraxacum mongolicum</i>	40.0	1.56	2.40	1.20	0.101	0.125
<i>Trifolium repens</i>	32.0	1.32	2.00	1.12	0.062	0.083
<i>Festuca ovina</i>	20.0	1.20	2.00	1.11	0.053	0.069

Classical models of density-dependent habitat selection are deterministic and habitat quality is assume to be time invariant (Jonzen et al., 2004). In deriving a stochastic equivalent of the ideal free

distribution. The wetlands have been chosen to study a theoretical organism that has either full knowledge about the fitness consequences of choosing one habitat or the other and at each time step either selects the best habitat (deterministic habitat selection) or, in face of uncertainty, selects a habitat with a probability equal to the relative fitness in that habitat (stochastic habitat selection). Finding the correct optimal evolutionary strategy in a density-dependent and stochastic environment is indeed difficult, and the current trend is to use invasibility arguments to identify the evolutionarily unbeatable strategy (Benton and Grant, 2000).

In the present study, both the Lotka-Volterra and spatial simulation formulae predict that species diversity increases with genotypic richness (GR) (Fig. 3). The two formulae 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 formulae, species diversity is uniformly high when $PGR = 27$ and $GR > 6$, while in the spatial simulation species diversity declines with increasing niche breadth at all values of PRG and GR.

More detailed examination of the outcomes at selected parameter combinations reveals the mechanisms underlying the effects of NB, GR, and PGR on species diversity (Fig. 4). The main effect of

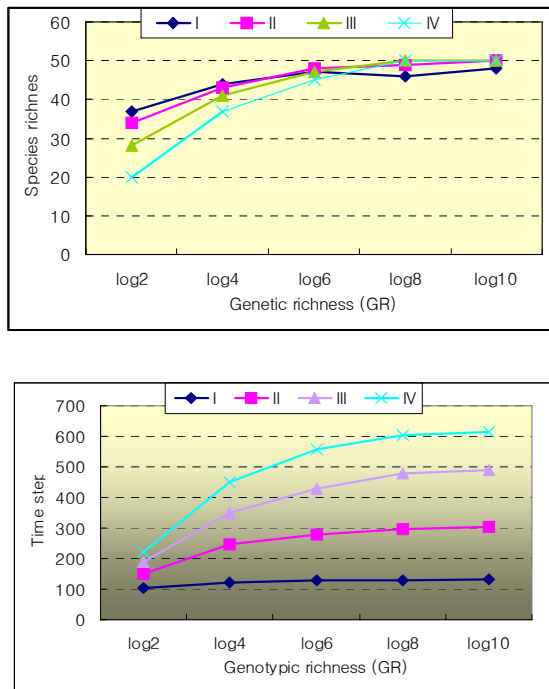


Fig. 3. The effects of genotypic richness (log scale), niche breadth, and potential genotypic range on species diversity at the species level (upper) and the time set level (below).

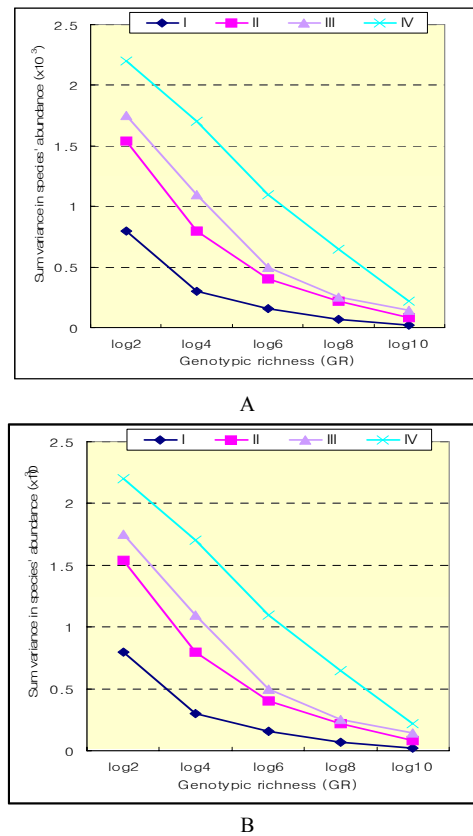


Fig. 4. The effects of genotypic richness (log scale), niche breadth, and potential genotypic range on variation among species composition, expressed as the summed variance in species' abundances across simulations divided by the mean species' abundance for (A) the Lotka-Volterra model parameter and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

increasing NB is to decrease the number of positions along the niche axis where genotypes can persist—"viable niches". At the beginning of each parameter 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. 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 niche. Niche breadth sets the spacing of the viable niches, though in the spatial simulations the exact positions of viable niche 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, 1992; Tilman, 2004), though certainly not all models, and as such are not an unusual artifact of the model structure here.

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 communities 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.

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 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.

Using a sufficiently fine-scale spatial grid, no species has a continuous range, but at large scales, ranges do appear increasingly continuous, in the sense of filling all cells of a grid between range boundaries. At the spatial scale, recorded occurrences of a species are more likely to be close together than far apart. Such positive spatial autocorrelation of incidence, or range coherence, is "an inherent quality of biogeographical data" (Rahbek and Graves, 2000).

4. Conclusions

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, 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. The two models and a experimental viewpoint are in agreement that species diversity generally decreases within increasing niche breadth and increases with increasing potential genotypic range. The information provided by this methodology can be used to corroborate that the way in which the models operate is congruent with general understanding of the system being modeled and that it reflects the way in which the real ecosystem operates to produce its behavior.

References

- Benton, T. G., Grant, A., 2000, Evolutionary fitness in ecology: comparing measures of fitness in stochastic, density-dependent environments, *Evol. Ecol. Res.*, 2, 769-789.
- Colwell, R. K., Hurtt, G. C., 1994, Nonbiological gradients in species richness and a spurious Rapoport effect, *Am. Nat.*, 144, 570-595.
- Colwell, R. K., Lees, D. C., 2000, The mid-domain effect: geometric constraints on the geography of species richness, *Trends in Ecol. & Evol.*, 15, 70-76.
- Conover, D. O., Schultz, E. T., 1995, Phenotypic similarity and the evolutionary significance of countergradient variation, *Trends in Ecol. & Evol.*, 10, 248-252.
- Currie, D. J., Francis, A. P., Kerr, J. T., 1999, Some general propositions about the study of spatial patterns of species richness, *Ecoscience*, 6, 392-399.
- Jonzen, N., Wilcox, C., Possingham, H. P., 2004, Habitat selection and population regulation in temporally fluctuating environments, *Am. Nat.*, 164, 103-114.
- MacArthur, R. H., 1965, Patterns of species diversity, *Biol. Rev.*, 40, 510-533.
- McGuigan, K., Chenoweth, S. F., Blows, M. W., 2005, Phenotypic divergence along lines of genetic variance, *Am. Nat.*, 165, 32-43.
- Mouseau, T. A., Sinervo, B., Endler, J. A., 2000, Adaptive genetic variation in the wild, Oxford University Press, Oxford.
- Neuhauser, C., Andow, D. A., Heipel, G. E., May, G., Shaw, R. G., Wagenius, S., 2003, Community genetics: expanding the synthesis of ecology and genetics, *Ecol.*, 84, 545-558.
- Pigliucci, M., Murrena, C. J., 2003, Perspective: genetic assimilation and a possible evolutionary paradox: can macroevolution sometimes be so fast as to pass us by?, *Evolution*, 57, 1455-1464.
- Price, T. D., Qvarnstrom, A., Irwin, D. E., 2003, The role of phenotypic plasticity in driving genetic evolution, *Proc. Royal Soc. London B*, 270, 1433-1440.
- Rahbek, C., Graves, G. R., 2000, Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale, *Proc. Royal Soc. London*, 267, 2259-2265.
- Smouse, P. E., Long, J. C., Sokal, R. R., 1986, Multiple regression and correlation extensions of the Mantel test of matrix correspondence, *Syst. Zool.*, 35, 627-632.
- Soltis, D. E., Hafler, C. H., Darrow, D. C., Gastony, G. J., 1983, Starch gel electrophoresis of ferns: A compilation of grinding buffers, gel and electrode buffers, and staining schedules, *Am. Fern J.*, 73, 9-27.
- Taper, M. L., Case, T. J., 1992, Coevolution among competitors, *Evol. Biol.*, 8, 63-109.
- Tilman, D., 2004, Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly, *Proc. Acad. Sci. USA.*, 101, 105-119.
- Vellend, M., 2005, Species diversity and genetic diversity: parallel process and correlated patterns, *Am. Nat.*, 166, 199-215.
- Vellend, M., 2006, The consequences of genetic diversity in competitive communities, *Ecol.*, 87, 304-311.
- Waddington, C. H., 1961, Genetic assimilation, *Advanced in Genetics*, 10, 257-290.
- West-Eberhard, M. J., 2003, Developmental plasticity and evolution, Oxford University Press, Oxford, 816.
- Whittaker, R. J., Willis, K. J., Field, R., 2001, Scale and species richness: toward a general hierarchical theory of species diversity, *J. Biogeography*, 28, 453-470.