Ecological and Genetic Models of Diversity

LESSONS ACROSS DISCIPLINES

Mark Vellend and John L. Orrock

ECOLOGY AND EVOLUTIONARY BIOLOGY HAVE BEEN LINKED to varying degrees throughout their histories as scientific disciplines (Collins 1986, Holt 2005). As recognized by Darwin and countless biologists since, evolutionary change can hardly be understood without knowledge of ecological context, and many of our most cherished ecological patterns, such as relationships between species diversity and area or latitude, ultimately require evolutionary explanations, at least in part (Dobzhansky 1964, Schluter 2000, Ricklefs 2004). The degree of integration between ecological and evolutionary studies has waxed and waned over the years, but in response to the rise of molecular biology during the 1960s, a group of leading researchers in ecology and evolution, including Robert MacArthur, Richard Levins, Richard Lewontin, and Edward Wilson, made a concerted effort to draw the two disciplines together under the unifying banner of population biology (Wilson 1994, Odenbaugh 2006). One of the defining contributions of this era was *The Theory of Island Biogeography* (MacArthur and Wilson 1967), which emerged from the integration and synthesis of seemingly disparate branches of organismal biology, in large part thanks to MacArthur and Wilson's "faith in the ultimate unity of population biology" (p. xi).

The arguments laid out by MacArthur and Wilson (1967) are broadly representative of the way in which ecology and evolution were being integrated at the time, and indeed to some degree the way in which ecology and evolution have been brought together over the past forty years. As in the 1960s (Birch 1960, Levins 1968, MacArthur and Wilson 1967), a major focus today remains on how ecological and evolutionary processes combine to produce the patterns of species distributions, traits, and diversity over space and time (Collins 1986, Ricklefs and Schluter 1993, Johnson and Stinchcombe 2007, Fussmann et al. 2007). The last decade in particular has produced a steady stream of studies demonstrating the necessity of considering both ecological and evolutionary processes to

understand phenomena ranging from the outcome of species interactions in small-scale experiments (Yoshida et al. 2003, Lankau and Strauss 2007) to broad-scale patterns of species diversity (Ricklefs 2004). This has spawned a number of recent viewpoints on how to reinvigorate the effort to more fully integrate ecology and evolution (Holt 2005, Vellend and Geber 2005, Johnson and Stinchcombe 2007, Fussmann et al. 2007). While we are enthusiastic proponents of these efforts, we also believe that there is a different and equally important way in which ecology and evolution might be integrated. Not only do ecological and evolutionary processes act in concert, but even if we consider ecological and evolutionary dynamics in isolation, some of the processes involved show remarkable parallels across disciplines (Vellend and Geber 2005). These parallels are strongest in the subdisciplines of ecology and evolution that are focused specifically on species diversity and genetic diversity—namely, community ecology and population genetics, respectively.

The processes that drive changes in the frequencies of alleles or genotypes in populations—mutation, drift, migration, and selection—are much the same as the processes that drive changes in the relative abundances (and therefore composition and diversity) of species in communities (Antonovics 1976, 2003, McPeek and Gomulkiewicz 2005). Compared to treatments of population genetics, ecological texts typically offer a much longer list of processes that drive changes in communities, including the usual suspects of competition, predation, dispersal, succession, and so on. However, as we will argue in more detail later, these processes can be readily grouped, as in population genetics, into four parallel categories: speciation, drift, migration, and selection (see also Vellend and Geber 2005). Examining parallel models in population genetics and community ecology more carefully may be quite useful in that portions of theory in these two disciplines could potentially be merged.

The similarities between processes underlying patterns of species diversity and genetic diversity have been repeatedly noted (Antonovics 1976, 2003, Hubbell 2001, Chase and Leibold 2003, McPeek and Gomulkiewicz 2005, Vellend and Geber 2005), but this recognition has not permeated the two disciplines, as evidenced by repeated, independent developments within ecology and genetics of separate models with essentially the same underlying processes. This is clearly illustrated in the central model of *The Theory of Island Biogeography*, in which the diversity of species on an island is modeled as a balance between a rate of input (colonization) and a rate of output (extinction). The underpinning of the model is illustrated with a cartoon showing islands of variable size and distance from a mainland, the two key island characteristics assumed to determine rates of extinction and colonization (figure 16.1A). The MacArthur-Wilson model is widely admired as a landmark, original

A. MacArthur & Wilson's
Theory of Island Biogeography
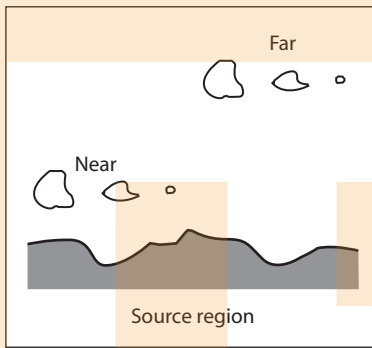
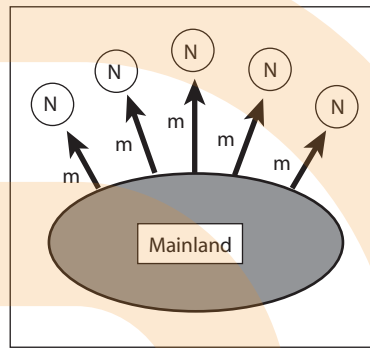**B.** Wright's mainland-island model of population genetics

Figure 16.1. Schematic diagrams illustrating the central model in *The Theory of Island Biogeography* (A) and Wright's (1940) mainland-island model of population genetics (B). The two diagrams are adapted from MacArthur and Wilson (1967) and Hedrick (2000), respectively.

contribution to biology, but more than a quarter of a century earlier, Sewall Wright (1940) developed a strikingly similar model, the mainland-island model of population genetics, which predicts patterns of genetic diversity in a set of "island" populations based on a rate of input (immigration from the mainland) and a rate of output (genetic drift). The figure often used to illustrate Wright's model (figure 16.1B) bears a close resemblance to the MacArthur and Wilson model (figure 16.1A), with the parameter N representing the size of each island population and therefore the importance of drift, and the parameter m representing the rate of immigration. It is easy to point out differences in the specifics of the two models, but qualitatively they are much the same if we simply exchange the two words "species" and "allele." So why, given the explicit integration of ecological and evolutionary thinking in the work of MacArthur, Wilson, and others at the time, was the earlier and extremely similar island model from genetics not drawn upon, or even acknowledged in the citations of MacArthur and Wilson (1967; there is no citation of any of Wright's papers, though he is mentioned once in a different context)? Are there other models in population genetics that could be drawn on to provide novel insights into pressing questions in community ecology? We return to these questions in subsequent sections.

We argue that a broader recognition of the conceptual parallels between community ecology and population genetics can contribute to significant advances in these disciplines in at least three ways. First, consideration of

processes acting in parallel on species diversity and genetic diversity can generate novel, testable predictions concerning patterns of biodiversity in nature. This topic has been treated in depth elsewhere (Vellend 2003, 2005, Vellend and Geber 2005), and is not discussed further here. Second, theoretical progress can be accelerated by drawing on existing models in one discipline whose counterparts have yet to be developed in the other. And third, the way we structure and organize the different facets of the two disciplines can benefit from consideration of the success or lack thereof of different organizational frameworks within community ecology and population genetics. Community ecology in particular has struggled to define its identity (Lawton 1999, Simberloff 2004), and might glean some useful lessons from the structure of population genetics as a discipline. Here we focus largely on ideas and concepts in population genetics that might be put to use in community ecology. We begin by briefly outlining the key parallels between processes in population genetics and community ecology. We proceed with a treatment of genetic analogues of two key models presented in *The Theory of Island Biogeography*, with an emphasis on novel lessons concerning (1) effects of size and migration on diversity, and (2) the conditions that influence successful establishment of new variants. We then draw on the organizational structure of population genetics to suggest how a similar structure might help provide a greater degree of coherence and order to what has been referred to as a bit of a "mess" in community ecology (Lawton 1999).

Parallels between Population Genetics and Community Ecology

Many aspects of the evolutionary process, such as epistasis, pleiotropy, inbreeding, and recombination, have either no parallels, or only very loose parallels at best, in community ecology. However, if we narrow our focus to the bare bones of population genetics—single-locus haploid models—the parallels with community ecology are striking.

Both population genetics and community ecology are essentially concerned with variation over space and time in the relative abundance and diversity of discrete biological variants: alleles or species, respectively. Four logically distinct processes can change the abundances and diversity of biological variants (Vellend and Geber 2005). First, due to the finite number of individuals in a population or community, the relative frequencies of alleles or species will to some degree change stochastically. This is genetic or ecological drift. When an individual organism moves between localities (i.e., migration), it may introduce novel alleles to a population or it may represent a new species in the recipient community. Selection occurs when particular alleles or species are deterministically favored

over others. These three processes—drift, migration, and selection—act in closely analogous ways in genetic and ecological models of diversity. Finally, mutation and speciation are the analogous processes that create globally novel alleles or species, respectively, but admittedly the parallel here is not as strong. Nonetheless, as detailed in subsequent sections, mutation is often treated in models simply as the appearance of a new allele, which is much the same way species invasion or immigration is often treated in ecological models.

Area and Isolation in Genetic and Ecological Models of Diversity

Chapter 3 in *The Theory of Island Biogeography* presents the now famous crossing colonization and extinction curves as functions of the number of species on an island. The model was inspired by empirical patterns demonstrating a positive effect of island area, and a negative effect of distance from a mainland, on species richness. While the model does indeed predict these patterns, these were not new predictions. One of the novel predictions offered by the MacArthur-Wilson model was that the slope of the species-area curve in log-log space should be steeper on archipelagoes far from the mainland than on those close to the mainland (or on sections of the mainland itself) (figure 16.2A). A data set on the species richness of ants in insular faunas of different parts of the world vs. nested sections of the large island of New Guinea was offered as support for this prediction, with a steeper species-area curve in the former than in the latter (figure 16.2B). Some data sets agree with this prediction, but meta-analyses have not found general evidence that the slopes of species-area relationships are steeper on more isolated islands (Schoener 1976, Connor and McCoy 1979, Williamson 1988). One possible explanation is that islands in distant archipelagos receive considerable interisland dispersal, and are thus not as effectively isolated as distance-to-mainland calculations imply (Schoener, this volume).

The prediction of steeper species-area relationships on far versus near islands is intuitively appealing in that it essentially states that isolation and small size should act multiplicatively rather than additively to reduce species diversity. However, from another perspective the crossing-curves model is difficult to intuit because the unit of analysis in the mathematics is the species, with no underlying population dynamics of these species, either explicitly or implicitly. Thus, despite the widespread appeal of the *The Theory of Island Biogeography*, Hubbell (2001) has argued that in fact "there is no theoretical foundation for species-area curves that derives from fundamental processes of population dynamics" (Hubbell 2001, but see Hanski, this volume). Hubbell (2001) also makes the important point
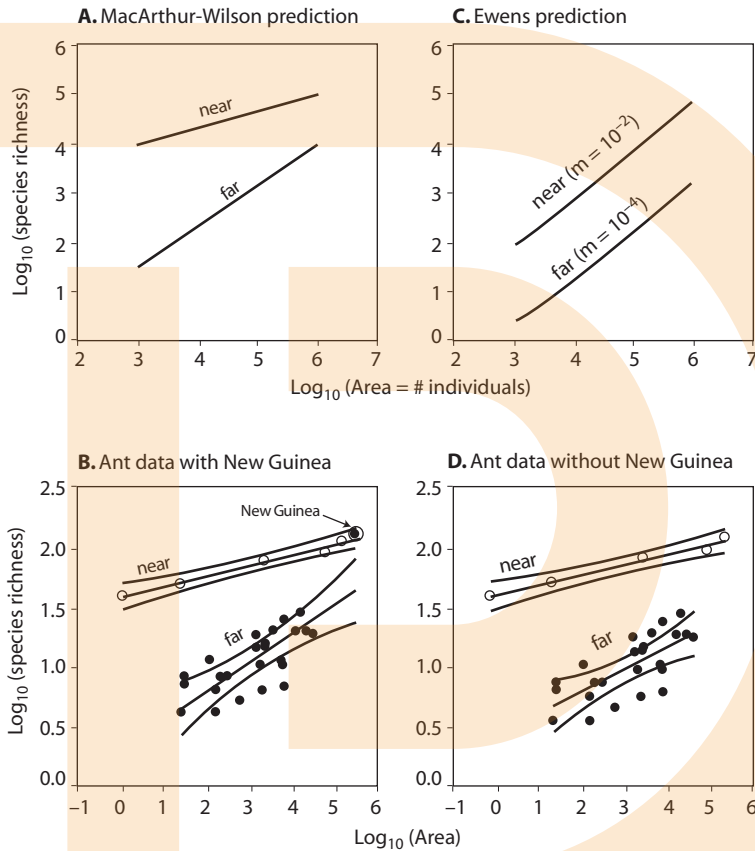
Figure 16.2. Predictions for the slopes of species area relationships with high and low rates of immigration (near and far islands, respectively). The theory of island biogeography predicts a steeper slope at a lower level of immigration (A) and the haploid version of Ewen's sampling formula predicts equal slopes in the two cases (C). Using data on ants in insular faunas (filled symbols) and on mainland portions of New Guinea (open symbols), the two data sets show significantly different slopes ($p<0.01$ for the interaction term with area in a general linear model) if the full island of New Guinea is included in both data sets (B), but the slopes are not significantly different ($p>0.06$) if New Guinea is excluded (D).

that despite the many verbal arguments in *The Theory of Island Biogeography* for why differences among species matter, in fact the crossing-curves model itself is essentially neutral, requiring no functional differences among species to produce its predictions (see also Hubbell, this volume).

The development of neutral theory in population genetics began in the first half of the twentieth century, and underwent a major period of

refinement and elaboration during the 1960s and 1970s when emerging
molecular data sparked the debate on whether widespread polymorphisms
were the product of neutral or non-neutral processes (Lewontin 1974,
Kimura 1983). As described already, the mainland-island model of Wright
(1940) is essentially the genetic analogue of the crossing-curves model of
MacArthur and Wilson, with one important difference being the inclusion
of implicit population dynamics in the genetic theory. Another difference
is that Wright's model makes explicit predictions for levels of heterozygos-
ity and population differentiation, but not the number of alleles (the ana-
logue of species) expected in populations of different sizes. At least for one
specific scenario, this problem was solved by Ewens (1972).

Assuming an isolated population of constant size and a given rate of
mutation (under the infinite alleles model), the expected number of al-
leles in a sample of individuals of a given size can be calculated using the
famed Ewens sampling formula (Ewens 1972). By taking the haploid ver-
sion of the model, inserting metacommunity size, J_M, in place of popula-
tion size, and inserting a speciation rate, v, in place of the mutation rate,
Hubbell (2001) applied this model to predict the number of species, $E(S)$,
expected in a sample of J individuals from the metacommunity:

$$E(S) = \theta/\theta + \theta/(\theta+1) + \cdots + \theta/(\theta+J-1).$$

Apart from the number of individuals in the sample, this equation has
only one composite parameter, $\theta = 2J_M v$. By considering portions of the
metacommunity of different sizes and degrees of migration among them,
Hubbell (2001) calculated expected species-area relationships at differ-
ent levels of migration. On the surface, this seems comparable to a pre-
diction for islands with different levels of immigration, but in fact it is
very different. The MacArthur-Wilson model concerns discrete islands of
different sizes and different rates of input via immigration from outside,
while Hubbell calculated species accumulation curves for larger and
larger areas of the same landmass. These two kinds of relationships are
quite different (Whittaker and Fernández-Palacios 2007), and this point
is made obvious by the fact that Hubbell finds lower, rather than higher,
species richness as the rate of migration is increased.

Surprisingly, despite some highly sophisticated elaborations of neutral
theory in ecology (e.g., Etienne and Alonso 2005, Etienne 2007), we still
lack quantitative predictions based on underlying population dynamics
for what *island* species-area relationships might look like with variable
levels of immigration. As a first approximation, one way to do this is to
assume that each island is its own isolated (meta)community; to think of
immigration from the mainland as akin to speciation (the introduction of
new variants); and then to apply the Ewens sampling formula to calculate

the expected number of species on islands of different size, J_M, and rates of immigration, m (which we insert in place of the mutation rate, v). In contrast to the MacArthur-Wilson prediction of different species-area slopes at different rates of immigration (figure 16.2A), the modified Ewens formula predicts precisely equivalent slopes above a threshold community size of $J \approx 10^3$ (figure 16.2C).

In light of this altered prediction, it is worth taking a second look at the ant data initially presented in support of the MacArthur-Wilson model. The different slopes shown in figure 16.3B are in fact highly dependent on one data point for the island of New Guinea. Since New Guinea anchors the right end of the "mainland" curve, and is also the largest island in the insular curve, then as long as species richness is generally lower in small insular faunas than on mainland portions of New Guinea (a separate issue), this data point will force the slopes to be different (figure 16.2B). Excluding New Guinea, the difference in slopes is quite modest, and indeed not statistically significant (figure 16.2D). Of course this is only one empirical case study of hundreds, but it helps highlight the point that the evaluation of island species-area curves at different degrees of isolation need not be viewed simply as a test of the MacArthur-Wilson model, but as a test among competing alternatives models (see also Schoener, this volume).

The more general point of this section is that a simple and elegant theory of diversity with underlying population dynamics was sitting on the genetic shelf for decades before Hubbell (2001) imported it into ecology, the result being arguably the most influential contribution to ecology in the last decade (Hubbell's book has been cited more than 1100 times in only eight years). Neutral theory still has many unexplored angles that may provide new insights into ecological patterns (island species-area curves being one example), and the genetic shelf has got lots of other models that ecologists might make great use of. A number of ecological studies have done this already (e.g., Norberg et al.2001, McPeek and Gomulkiewicz 2005, Orrock and Fletcher 2005, Fox 2006), but we feel there is still plenty of untapped potential. At the same time, many ecological models—including recent elaborations of neutral theory that go beyond traditional population-genetic models—might be imported into population genetics with the same potential benefits.

Genetic and Ecological Models of the Establishment of New Variants

Chapter 4 of *The Theory of Island Biogeography* is concerned with estimation of the "probability that a propagule of a given species will establish a successful colony" (MacArthur and Wilson 1967, p. 92). Assuming

density-dependent population growth and overlapping generations with birth and death rates of λ and μ, respectively, MacArthur and Wilson estimated the probability of establishment starting from single propagule (e.g., a single seed or pregnant female) to be approximately r/λ, where r is the intrinsic rate of population increase, and $r = \lambda - \mu$. Throughout this paper we refer to r as the expected rate of population growth, because even in the absence of competition the expectation for r will depend on the environment (and is therefore not really "intrinsic"). With the birth rate in the denominator, according to this model the ideal colonist achieves success largely via a particularly low death rate. This somewhat odd result appears to us to be a consequence of overlapping generations in the model, with the most likely fate of a new propagule (i.e., extinction) avoided only if the first individual does not die before reproducing. The more general result would seem to be that the probability of establishment is proportional to the rate of population growth when rare, r.

As with their colonization-extinction model of diversity, MacArthur and Wilson's species establishment model has some close analogues in population genetics. From a mathematical viewpoint, establishment of a new species in a community is similar to the establishment of a new allele in a population. When a new mutation arises in a population, ultimately it must disappear, rise in frequency to fixation, or be maintained in a stable polymorphism. Mutation fixation models, as the name implies, focus on estimating the probability of fixation, but as originally formulated using the mathematics of branching processes, they can at least loosely be interpreted as addressing "the course of events in a population where the new factor is present in such numbers as to be in no danger of extinction by mere bad luck" (Haldane 1927, p. 838). The specific "new factor" of interest to Haldane was a mutation, but his language makes clear that it could be any kind of new variant, such as an immigrant. Haldane assumed a population of infinite size and a positive selection coefficient s, and estimated the probability of fixation to be approximately $2s$ for small values of s. Recognizing that in a population or community of fixed size, the selection coefficient, s, is equivalent to the expected rate of population growth, r, we can see a clear parallel between the two models. The probability of establishment of an allele in a population or a species in a community is approximately proportional to the degree of deterministic advantage when rare, despite different assumptions concerning the underlying population dynamics in the different models. Haldane's model preceded the MacArthur-Wilson model by forty years, again begging the question of why it was not drawn upon or acknowledged in *The Theory of Island Biogeography* (Haldane is not cited but is acknowledged in a different context).

Over the past forty years the clear parallel between the establishment of species in communities and alleles in populations has been recognized (e.g., Haccou and Iwasa 1996, McPeek and Gomulkiewicz 2005, Orrock and Fletcher 2005), but not fully explored. Indeed many of the qualitative lessons that might be taken from fixation models would not represent particularly deep insights in ecology, such as the positive effect of r or initial population size on the probability of establishment (Kimura 1962). However, most community models do not include a parameter for the total community size, J, and when this enters into fixation models things can get ecologically quite interesting. A general model for the probability of fixation of both beneficial and deleterious mutations was presented by Kimura (1962), the haploid version of which we can apply to the probability of invasion, $Pr(inv)$, of new species in communities:

$$Pr(inv) = (1 - \exp(-2J_e r p))/(1 - \exp(-2J_e r)).$$

In this equation, r is the expected rate of population growth as before, p is the initial frequency of the invader (i.e., the initial population size divided by the census community size, N_{init}/J), and J_e is the effective community size. J_e represents the community-level equivalent of the effective population size, and can differ from J according to factors such as fluctuating community size, which reduces J_e relative to the arithmetic mean of J over time. This model is appealing in that it captures a key characteristic of the invading species (p), a key characteristic of the recipient community (J_e), and a parameter summarizing the interaction between the species' traits and the local abiotic and biotic conditions (r). Admittedly the model treats as a black box the details of many of the ecological interactions (e.g., competition and predation) that determine r, and also makes an assumption of constant (or at least extrinsically determined) community size, which may apply only under fairly restrictive conditions (Houlahan et al. 2007). Nonetheless, we feel it provides an appropriate point of departure for an initial consideration of the potential ecological consequences of finite community size.

Analysis of this model reveals some interesting and, in our opinion, non-intuitive lessons for community ecology and invasion biology. We focus here on selected results for species with positive r (i.e., those deterministically favored to invade). First, if initial population size is relatively small, failure to invade is the most likely outcome even for species with a large value of r (figure 16.3), as all invaders are susceptible to stochastic loss when rare (see also McPeek and Gomulkiewicz 2005). This model prediction is consistent with the many cases in which highly successful invasions were preceded by repeated failures (Sax and Brown 2000, Sakai et al. 2001). Second, for a given expected rate of increase, r, and
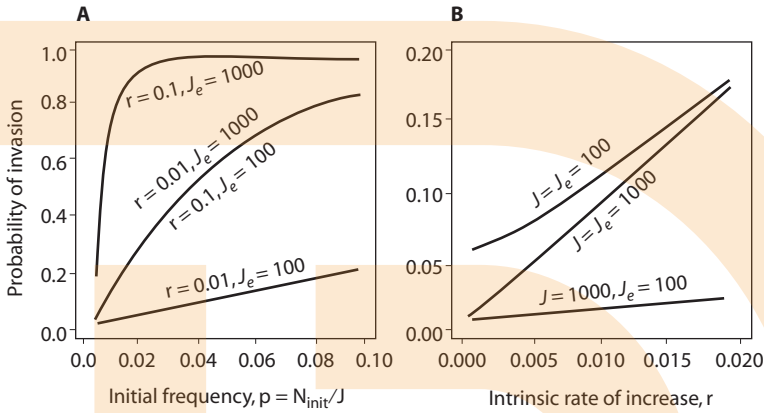
Figure 16.3. Invasion probabilities, *Pr(inv)*, from the haploid version of the Kimura (1962) model as a function of: (A) the initial frequency ($p = N_{init}/J$) of the introduced species with different expected rates of increase, r, in communities of different effective size, J_e; and (B) the expected rate of increase, r, for communities of different census size, J, and effective size, J_e, and an invader with initial population size, $N_{init} = 5$.

initial frequency, p, an introduced species is more likely to invade a large community than a small one (figure 16.3A). The reason for this is that for a given p, the initial population size is higher in large than small communities, and therefore much less likely to go extinct. We can imagine this comparison applying to lakes of different sizes in which boat traffic is the main vector of exotic species propagules: if boat traffic is approximately proportional to lake size, then exotic species invade large lakes with larger initial population sizes (N_{init}) but approximately equivalent relative frequencies ($p = N_{init}/J$) as in small lakes. In contrast, for a given initial population size, just the opposite is true—an invasive species is more like to invade a small community than a large one, at least for small values of r and J. Five exotic birds released on a small island with 100 birds in the same guild starts at an initial frequency of $p = 0.05$, whereas on a larger island with 1000 birds it starts at an initial frequency of $p = 0.005$, and is therefore more likely to go quickly extinct.

Finally, any factor that decreases J_e for a given J, will decrease the probability of invasion for species with positive r because the relative importance of drift increases relative to selection (figure 16.3; see also Orrock and Fletcher 2005). Fluctuating or declining community size due to periodic disturbance is one such factor that reduces J_e, although disturbance is also likely to have a strong influence on r that may outweigh its effects on J_e. On the surface this prediction would seem to contradict

intuition and empirical observations that habitat loss (declining community size) and repeated disturbance (fluctuating community size) seem to increase susceptibility to invasion (Elton 1958, Williamson 1996). However, this seeming contradiction may well help clarify the aspects of human-mediated disturbance that increase susceptibility to invasion. In all likelihood disturbance changes r for different species, specifically by increasing it for many introduced species. The effects of disturbance per se (i.e., the destruction of biomass [Grime 2001]) is unlikely to be an important factor in and of itself, and in fact may have the opposite effect if its influence were not swamped out by changes in r.

This analysis of the fairly simple Kimura model has revealed some lessons that are of clear relevance to community ecology, although admittedly the conditions under which the effect of J_e is important relative to the effects of initial population size or r may be quite limited. But really we have just scratched the surface. Mutation fixation models have been elaborated in a number of important ecological contexts, including spatially structured populations (Whitlock 2003), spatially heterogeneous environments (Whitlock and Gomulkiewicz 2005), and changing population sizes (Otto and Whitlock 1997). Each of these cases has clear analogues in community ecology, presenting some potentially fruitful avenues for theoretical elaborations.

In sum, we hope to have demonstrated in the last two sections that a close examination of analogous models in community ecology and population genetics, and subsequent importation of models where appropriate, can open up a range of new avenues for theoretical and empirical progress within these disciplines. Such opportunities abound.

A New Structure for Community Ecology

In this final section, we want to step back from thinking about specific genetic models that might be imported into ecology, and consider the broader structure of community ecology as a discipline and how it compares to population genetics. Community ecology is a particularly vibrant subfield of ecology, with ongoing, lively debates concerning issues such as the important determinants of species diversity and composition (Hubbell 2001, Chase and Leibold 2003), the relative importance of positive versus negative interspecific interactions (e.g., Bruno et al. 2003), and the causes and consequences of the architecture of complex interaction networks (e.g., Bascompte and Jordano 2007). But what exactly is community ecology, and how do these various topics fit together under a single framework?

We can start by defining community ecology most generally as the study of the diversity, abundance, and composition within groups of species that co-occur in arbitrarily delineated units of space and time. Thus, the central question of community ecology is: why do we find different numbers, kinds, and abundances of species in different places and at different times? Ecologists—community ecologists in particular—have been highly critical of their own discipline (Simberloff 1980, Peters 1991, Weiner 1995, Lawton 1999), to a degree that does not seem to be matched in population genetics and evolutionary biology. The frustration many ecologists have with the seeming lack of general (and nontrivial) ecological laws, and with the difficulty in making accurate predictions about future states of ecological systems given their great complexity, is often cited as a chronic symptom of "physics envy" (Cohen 1971). But since the subject matter of physics seems so distinct from that of ecology, the comparison between ecology and physics does not seem particularly illuminating (see also Simberloff 2004). Population genetics, and evolutionary biology more generally, seem like much more appropriate foils for community ecology, given that ecology, genetics, and evolution are in many ways sister disciplines (Chase and Leibold 2003). Should ecologists have "evolution envy"? Can the perceived "mess" in community ecology (Lawton 1999) be tidied up if we learn some lessons from the basic structure of population genetics as a whole?

Some general perceptions about the theoretical underpinnings of these disciplines seem clear. Many evolutionary biologists work within a common conceptual framework that traces back to key insights from Darwin and Mendel on mechanisms for adaptive evolution and inheritance, respectively, and the subsequent integration of these ideas into a broader framework by the architects of the modern synthesis (Kutschera and Niklas 2004). This is of course an oversimplification, as the modern synthesis is open to criticism for leaving aside important parts of evolutionary biology (Pigliucci 2007), but certainly if we narrow the scope to population genetics there is a strong and general perception that the discipline lies on a foundation of general theoretical principles. To be sure, community ecology has towering historical figures of its own and a rich tradition of theoretical developments (Kingsland 1995), but community ecologists do not in any obvious way work within a similarly coherent, unified framework based on general theoretical principles (Chase and Leibold 2003). Colyvan and Ginzburg (2003) stated the situation succinctly: "ecology lacks a grand, widely accepted, explanatory theory such as Darwinian evolution." This difference between population genetics and community ecology presents a conundrum, if, as we have argued, the processes underlying changes in allele frequencies and species abundances are much the same.

TABLE 16.1
Simplified Representation of the Points of Emphasis in General Treatments of the Disciplines of Community Ecology and Population Genetics

Community ecology	Population genetics
Patterns of diversity and abundance	Measurement of genetic diversity
Space and time	Mutation
Competition	Drift
Predation	Migration
Food webs	Selection
Niches	
General approach: Pattern first	General approach: Process first

Note: The rows of the table do not represent a one-to-one correspondence of analogous processes across the two disciplines (the lists are independent).

Some progress can be made in solving this conundrum by examining how practitioners organize the various parts of their respective disciplines, as reflected in the tables of contents of textbooks on community ecology (e.g., Putman 1994, Morin 1999) or population genetics (e.g., Hartl and Clark 1997, Hedrick 2000). Our interpretation of the organization of such texts, while admittedly and necessarily oversimplified, reveals distinct points of emphasis in the two fields. Treatments of community ecology typically emphasize community patterns, issues of space and time, competition, predation, food webs, and the concept of niches in one form or another (table 16.1). Treatments of population genetics emphasize how genetic variation is measured, and then the four main processes that cause genetic change: mutation, drift, migration and selection (table 16.1). The key difference, first pointed out to us by Joan Roughgarden (personal communication), is that in community ecology there is a tendency to approach things "pattern first," whereas in population genetics the approach is "process first.". Both pattern and process certainly feature prominently in both disciplines, but this difference in emphasis seems quite clear. Community ecologists ask: what broad and general patterns of species diversity, distribution, and abundance do we find in nature? They then seek theoretical explanations for the patterns. MacArthur (1972) was explicit in promoting the pattern-first approach: "To do science is to search for repeated patterns, not simply to accumulate facts." In contrast, population geneticists ask: what is the basic set of processes capable of producing changes in gene frequencies, and how do

they interact to drive evolution? With a firm understanding of potentially important processes, specific models can then be tailored to any particular situation in nature.

This simple difference between community ecology and population genetics—the pattern-first vs. process-first approach —likely traces to the origins of the two disciplines. Many ecological patterns, such as variation in species richness with latitude or area, were well known before ecology was even a named discipline (Brown and Lomolino 1998), so it would have been nearly impossible to approach theoretical analyses in community ecology without patterns in mind. Population genetics was initially developed as a theoretical discipline, with process-based models derived before empirical data on the frequency and diversity of alleles in real populations were even available to any great extent (Provine 1971). The pattern-process difference no doubt belies a more complex set of differences as well, but nonetheless, to us it highlights two important points. First, although population genetics appears to rest on a firmer theoretical foundation than community ecology, we are not actually any better at predicting broad scale patterns of genetic diversity than we are at predicting broad scale patterns in communities. If anything, the opposite is true. The difference is that in population genetics this is not considered a shortcoming given the coherent set of basic models that can be successfully tailored to meet the inherently contingent specifics of any particular case, whereas in ecology we are set up for disappointment when we hope for grand all-encompassing theories to make the contingencies disappear. Second, perhaps community ecology already has all of the building blocks to achieve the same level of theoretical generality as in population genetics, but simply lacks an organizational framework that emphasizes the generality of process over the contingency of pattern (see also Scheiner and Willig 2008).

Building on suggestions from Joan Roughgarden, here we propose an organizational structure for community ecology that is modeled after population genetics. We are not proposing that all of the important processes and phenomena in community ecology can be captured by population-genetic models, though the previous two sections demonstrate that there are particular situations for which this may be the case. Rather, regardless of how well the specifics translate across disciplines, we feel that the organizational framework of population genetics can be adapted for community ecology, with some important benefits. Specifically, our hope is to provide a framework that is simple in concept and terminology, but that also embraces all of what community ecologists actually do, thereby allowing clearer relationships to be defined between the many facets of the discipline. In our caricature of how community ecology is organized at present (table 16.1), patterns come first, and the rest of the items on
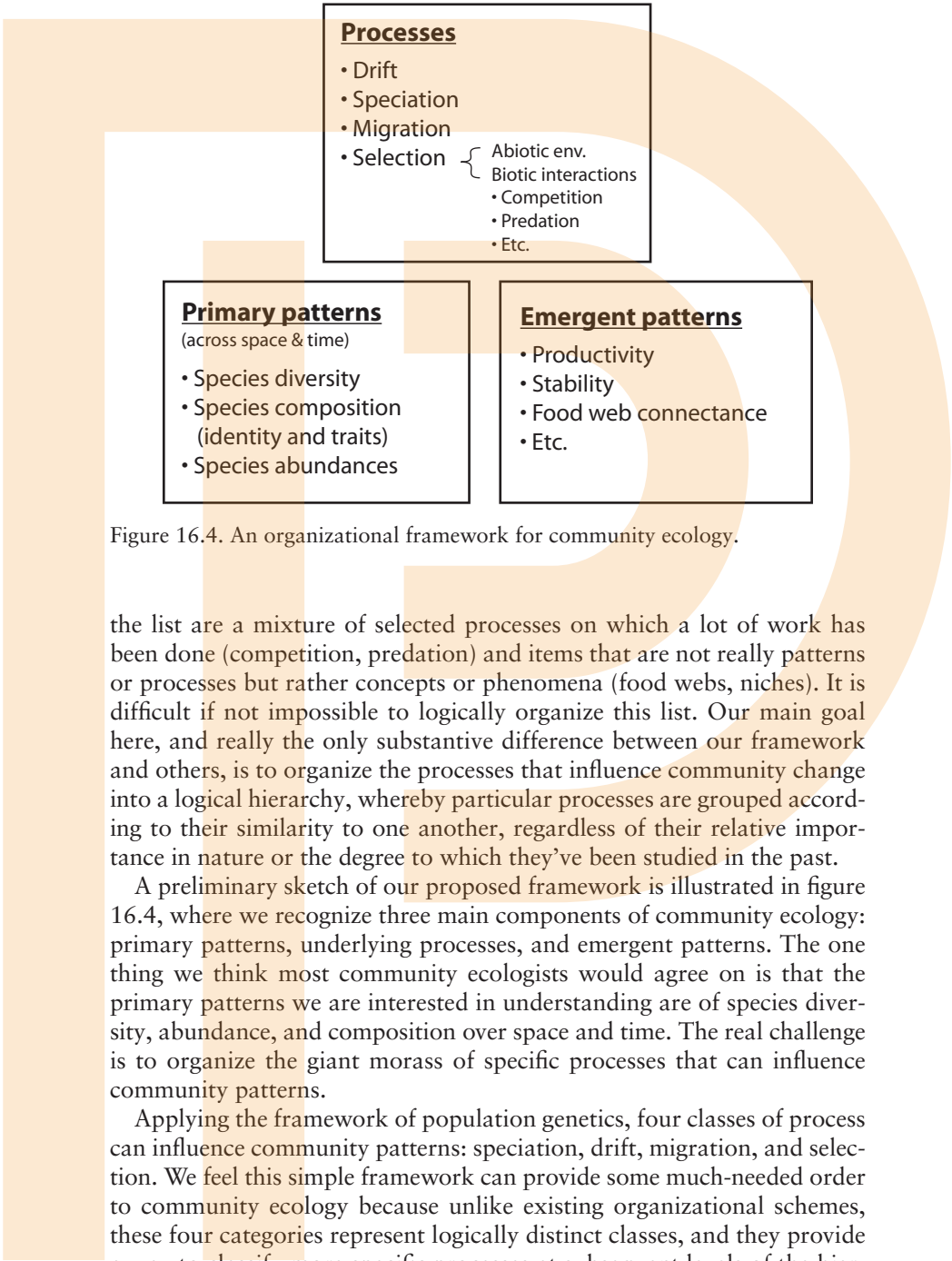
Processes
• Drift
• Speciation
• Migration
• Selection   Abiotic env.
                   Biotic interactions
                   • Competition
                   • Predation
                   • Etc.

Primary patterns
(across space & time)

• Species diversity
• Species composition
  (identity and traits)
• Species abundances

Emergent patterns
• Productivity
• Stability
• Food web connectance
• Etc.

Figure 16.4. An organizational framework for community ecology.

the list are a mixture of selected processes on which a lot of work has been done (competition, predation) and items that are not really patterns or processes but rather concepts or phenomena (food webs, niches). It is difficult if not impossible to logically organize this list. Our main goal here, and really the only substantive difference between our framework and others, is to organize the processes that influence community change into a logical hierarchy, whereby particular processes are grouped according to their similarity to one another, regardless of their relative importance in nature or the degree to which they've been studied in the past.

A preliminary sketch of our proposed framework is illustrated in figure 16.4, where we recognize three main components of community ecology: primary patterns, underlying processes, and emergent patterns. The one thing we think most community ecologists would agree on is that the primary patterns we are interested in understanding are of species diversity, abundance, and composition over space and time. The real challenge is to organize the giant morass of specific processes that can influence community patterns.

Applying the framework of population genetics, four classes of process can influence community patterns: speciation, drift, migration, and selection. We feel this simple framework can provide some much-needed order to community ecology because unlike existing organizational schemes, these four categories represent logically distinct classes, and they provide a way to classify more specific processes at subsequent levels of the hier-

archy. Speciation is the only process that can add new species to the global pool. As a necessary consequence of communities containing finite numbers of individuals, some changes in species abundances will occur due to random drift. The movement of individuals from place to place (i.e., migration) can impact communities in a variety of ways. Finally, any process involving deterministic differences among species in their rates of survival or reproduction can be grouped under the heading of selection.

Selection, of course, can arise in a myriad of ways, including differential effects of abiotic conditions or resources, competition, predation, mutualism, facilitation, disturbance, and so on. While the term selection has not traditionally been used this way in community ecology (but see Bell et al. 2006), it is now widely used in studies of the ecosystem consequences of species diversity (e.g., Loreau and Hector 2001), and it is the appropriate term for this general class of processes as it implies only differential success of individual organisms (Nowak 2006). Most models of interspecific interactions are essentially models of frequency- or density-dependent selection among types of individuals. In community ecology individuals are defined by their species identity rather than by allelic states as in genetics. Selection is also arguably where the vast majority of research in community ecology is focused, perhaps reflecting its overwhelming importance in determining community patterns. As such, it is important to emphasize that this framework is agnostic on the topic of which processes are more or less important. It only aims to provide organization and structure to the discipline. For example, competition is further down the hierarchy than drift not because it is any less important (it may or may not be), but because it shares a logical similarity with other kinds of biotic interactions in the same category, and is logically distinct from drift, migration, or speciation.

Finally, a wide variety of community properties can be measured that are neither primary patterns of diversity, abundance, and composition, nor processes. We refer to these as emergent properties of communities, and include common measurements of interest such as productivity summed over species, indices of the number, strength, and direction of species interactions, stability of any other primary or emergent pattern over time, and so on. Again, this framework in no way implies that these measurements are less important than the primary patterns, simply that considering them in a separate category can help provide some order to an otherwise disorderly discipline.

Unfortunately we haven't the space to flesh out this framework in any detail, but it is easy to see how general treatments of community ecology (e.g., in undergraduate courses) might present the subject matter in a more coherent and organized way. Incorporating the importance of spatial scale, we can envision how these processes interact across local, regional,
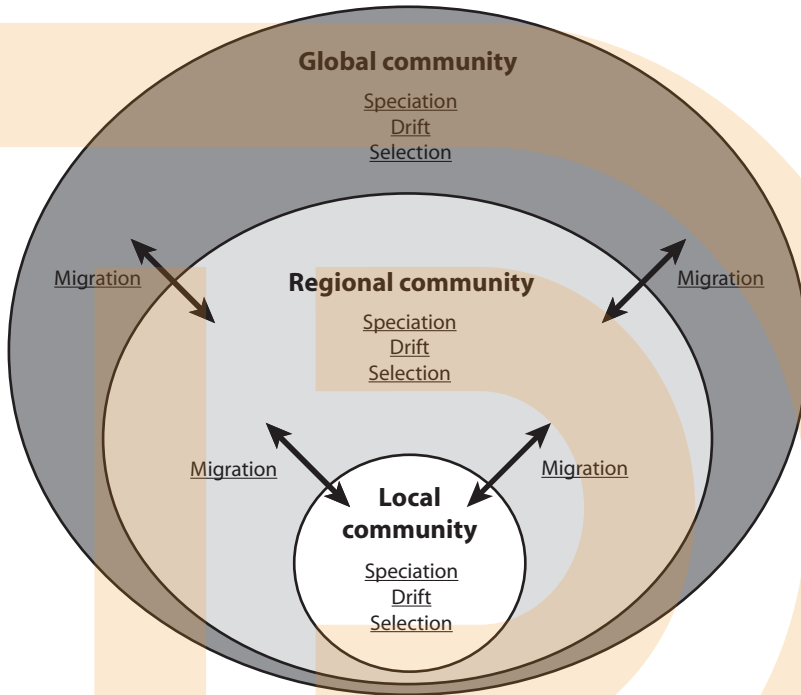
Figure 16.5. The interaction of processes acting across spatial scales in community ecology. We include all processes (underlined) at each scale to illustrate the full range of theoretical possibilities, even if some processes are unlikely to be important at particular scales (e.g., speciation at the local scale).

and global scales (figure 16.5), and it is fairly straightforward to place existing community models within this framework. For example, Hubbell's neutral model explores the balance between speciation and drift, while island biogeography explores the balance between immigration and drift. As mentioned earlier, models of local species interactions essentially address different kinds of frequency- or density-dependent selection among species, while the effects of abiotic gradients on community patterns treat the case of constant local selection. Stochastic versions of such models represent simultaneous selection and drift. Environmental heterogeneity among local habitat patches, which are connected by dispersal, represents selection-migration balance at the local scale, and spatially variable selection with migration at the regional scale. The list could go on (see also McPeek and Gomulkiewicz 2005). This framework also makes clear how community ecology links with other branches of ecology and biology more generally. Communities link to ecosystems via

their emergent properties and effects of energy and nutrient fluxes on selection. Evolution creates new species, modifies ecologically relevant traits of existing ones, and itself depends on community processes and patterns. Population ecology is in many ways a subset of community ecology in which all important community processes affecting an individual species are abstracted into the parameters of a population model such as r and K.

In sum, we hope this organizational framework can contribute to an ongoing discussion about how best to advance the science of community ecology. Advances in basic research are of course the cornerstone of such efforts, but reevaluation of the way we frame the discipline to begin with might go a long way as well.

Conclusions

We would like to end this contribution by returning to the question of why the contributions of Wright, Haldane, Kimura, and others were not drawn upon in the construction of analogous models in *The Theory of Island Biogeography*. At the conclusion of the presentation of the contents of this chapter in October 2007, E. O. Wilson himself provided the answer when he said, "it never occurred to us." Given that at the time of writing their book MacArthur and Wilson were as much evolutionary biologists as ecologists, this seems to be in need of explanation. We speculate that the different starting points of the two bodies of theory may be part of the explanation. As keen naturalists, MacArthur and Wilson approached the problem with a deep appreciation of the complexity of nature, and the importance of species differences and their myriad manifestations. As such, population-genetic models may have seemed far too simplistic to encapsulate the key elements of ecological communities, even if ultimately the two sets of models ended up in more or less exactly the same place. In the end, perhaps we are richer for having both, but hopefully the process of cross-fertilization between models and concepts in community ecology and population genetics can itself provide the inspiration for future advances in these fields.

Acknowledgments

458 • Vellend and Orrock

Literature Cited

Antonovics, J. 1976. The input from population genetics: "The new ecological genetics." *Systematic Botany* 1:233–45.

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

Bascompte, J., and P. Jordano. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 38:567–93.

Bell, G., M. J. Lechowicz, and M. J. Waterway. 2006. The comparative evidence relating to functional and neutral interpretations of biological communities. *Ecology* 87:1378–86.

Birch, L. C. 1960. The genetic factor in population ecology. *American Naturalist* 94:5–24.

Brown, J. H., and M. V. Lomolino. 1998. *Biogeography*, 2nd ed. Sunderland, MA: Sinauer Associates.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–25.

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

Cohen, J. E. 1971. Mathematics as metaphor. *Science* 172:674–75.

Collins, J. P. 1986. Evolutionary ecology and the use of natural selection in ecological theory. *Journal of the History of Biology* 19:257–88.

Colyvan, M., and L. R. Ginzburg. 2003. Laws of nature and laws of ecology. *Oikos* 101:649–53.

Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. *American Naturalist* 113:791–833.

Dobzhansky, T. 1964. Biology, molecular and organismic. *American Zoologist* 4:443–52.

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

Etienne, R. S. 2007. A neutral sampling formula for multiple samples and an "exact" test of neutrality. *Ecology Letters* 10:608–18.

Etienne, R. S., and D. Alonso. 2005. A dispersal-limited sampling theory for species and alleles. *Ecology Letters* 8:1147–56.

Ewens, W. J. 1972. The sampling theory of selectively neutral alleles. *Theoretical Population Biology* 3:87–112.

Fox, J. W. 2006. Using the Price Equation to partition the effects of biodiversity loss on ecosystem function. *Ecology* 87:2687–96.

Fussmann, G. F., M. Loreau, and P. A. Abrams. 2007. Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology* 21:465–77.

Grime, J. P. 2001. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd ed. Chichester, U.K.: John Wiley & Sons.

Haccou, P., and Y. Iwasa. 1996 . Invasion probability in fluctuating environments: A branching process model. *Theoretical Population Biology* 50:254–80.

Haldane, J.B.S. 1927. A mathematical theory of natural and artificial selection. V. Selection and mutation. *Proceedings of the Cambridge Philosophical Society* 23:838–44.

Hartl, D. L., and A. G. Clark. 1997. *Principles of Population Genetics*, 3rd ed. Sunderland, MA: Sinauer Associates.

Hedrick, P. W. 2000. *Genetics of Populations*. Sudbury, MA: Jones and Barlett Publishers.

Holt, R. D. 2005. On the integration of community ecology and evolutionary biology: historical perspectives and current prospects. In *Ecological Paradigms Lost: Routes of Theory Change,* ed. K. Cuddington and B. Beisner, 235–71. Amsterdam: Elsevier.

Houlahan, J. E., D. J. Currie, K. Cottenie, G. S. Cumming, S.K.M. Ernest, C. S. Findlay, S. D. Fuhlendorf, U. Gaedke, P. Legendre, J. J. Magnuson, B. H. McArdle, E. H. Muldavin, D. Noble, R. Russell, R. D. Stevens, T. J. Willis, I. P. Woiwod, and S. M. Wondzell. 2007. Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Sciences U.S.A.* 104:3273–77.

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

Kimura, M. 1962. On the probability of fixation of mutant genes in a population. *Genetics* 47:713–19.

———. 1983. *The Neutral Theory of Molecular Evolution*. Cambridge: Cambridge University Press.

Kingsland, S. 1995. *Modeling Nature: Episodes in the History of Population Ecology*, 2nd ed. Chicago: University of Chicago Press.

Kutschera, U., and K. J. Niklas. 2004. The modern theory of biological evolution: an expanded synthesis. *Naturwissenschaften* 91:255–76.

Johnson, M.T.J., and J. R. Stinchcombe. 2007. An emerging synthesis between community ecology and evolutionary biology. *Trends in Ecology and Evolution* 22:250–57.

Lankau, R. A., and S. Y. Strauss. 2007. Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science* 317:1561–63.

Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177–92.

Levins, R. 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton, NJ: Princeton University Press.

Lewontin, R. C. 1974. *The Genetic Basis of Evolutionary Change*. New York: Columbia University Press.

Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76.

MacArthur, R. H. 1972. *Geographical Ecology*. Princeton, NJ: Princeton University Press.

MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

McPeek, M. A., and R. Gomulkiewicz. 2005. Assembling and depleting species richness in metacommunities: Insights from ecology, population genetics and macroevolution. In *Metacommunities: Spatial Dynamics and Ecological Communities,* ed. M. A. Leibold, M. Holyoak, and R. D. Holt, 355–73. Chicago: University of Chicago Press.

Morin, P. J. 1999. *Community Ecology*. Oxford: Blackwell Science.

Norberg J., D. P. Swaney, J. Dushoff, J. Lin, R. Casagrandi, and S. A. Levin. 2001. Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. *Proceedings of the National Academy of Sciences U.S.A.* 98:11376–81.

Nowak, M. 2006. *Evolutionary Dynamics: Exploring the Equations of Life*. Cambridge, MA: Harvard University Press.

Odenbaugh, J. 2006. The strategy of "The strategy of model building in population biology." *Biology and Philosophy* 21:607–21.

Orrock, J. L., and R. J. Fletcher, Jr. 2005. Changes in community size affect the outcome of competition. *American Naturalist* 166:107–11.

Otto, S. P., and M. C. Whitlock. 1997. The probability of fixation in populations of changing size. *Genetics* 146:723–33.

Peters, R. H. 1991. *A Critique for Ecology*. Cambridge: Cambridge University Press..

Pigliucci, M. 2007. Do we need an extended evolutionary synthesis? *Evolution* 61:2743–49.

Provine, W. B. 1971. *The Origins of Theoretical Population Genetics*. Chicago: University of Chicago Press.

Putman, R. J. 1994. *Community Ecology*. New York: Chapman and Hall.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7:1–15.

Ricklefs, R. E., and D. Schluter. 1993. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. Chicago: University of Chicago Press.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–32.

Sax, D. F., and J. H. Brown. 2000. The paradox of invasion. *Global Ecology and Biogeography* 9:363–71.

Scheiner, S. M., and M. R. Willig. 2008. A general theory of ecology. *Theoretical Ecology* 1:21–28.

Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford: Oxford University Press.

Schoener, T. W. 1976. The species-area relation within archipelagos: Models and evidence from island land birds. In *Proceedings of the 16th International Ornithological Conference,* ed. H. J. Firth and J. H. Calaby, 629–42. Canberra: Australian Academy of Science.

Schrader-Frechette, K. S., and E. D. McCoy. 1993. *Method in Ecology*. Cambridge: Cambridge University Press.

Simberloff, D. 1980. A succession of paradigms in ecology: Essentialism to materialism to probabilism. *Synthese* 43:3–39.

———. 2004. Community ecology: Is it time to move on? *American Naturalist* 163:787–99.

Vellend, M. 2003. Island biogeography of genes and species. *American Naturalist* 162:358–65.

———. 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* 8:767–81.

Weiner, J. 1995. On the practice of ecology. *Journal of Ecology* 83:153–58.

Whitlock, M. C. 2003. Fixation probability and time in subdivided populations. *Genetics* 164:767–79.

Whitlock, M. C., and R. G. Gomulkiewicz. 2005. Probability of fixation in a heterogenous environment. *Genetics* 171:1407–17.

Whittaker, R., and J. M. Fernández-Palacios. 2007. *Island Biogeography: Ecology, Evolution, and Conservation.* Oxford: Oxford University Press.

Williamson, M. 1988. Relationship of species number to area, distance and other variables. In *Analytical Biogeography,* ed. A. A. Myers and P. S. Giller, 91–115. New York: Chapman and Hall.

———. 1996. *Biological Invasions*. London: Chapman and Hall.

Wilson, E. O. 1994. *Naturalist*. New York: Island Press.

Wright, S. 1940. Breeding structure of populations in relation to speciation. *American Naturalist* 74:232–48.

Yoshida T., L. E. Jones, S. P. Ellner, G. F. Fussman, and N. G. Hairston Jr. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* 424:303–30