

Chapter 4. Simulating dynamics in ecological communities

So far I have treated theoretical ideas in community ecology in a largely qualitative manner. While many of the greatest conceptual advances in biology have come via qualitative reasoning (Wilson 2013), mathematical models are essential to further progress for several reasons (Otto and Day 2011, Marquet et al. 2014). First, they provide critical tests of our intuition: if we are unable to produce a quantitative representation of a particular phenomenon, we must wonder whether there are holes in our qualitative logic. They also force us to be explicit about simplifying assumptions, which we might not even realize we are making. Models provide a means to explore the sensitivity of particular outcomes (e.g., stable coexistence) to various kinds of conditions (e.g., the pattern of temporal environmental fluctuations), and to generate quantitative predictions or forecasts for what one might expect to see in nature. Finally, they provide a vehicle for conceptual unification in that one can hope to show that many specific models are special cases of one or a few more general models.

My aims in this chapter are: (i) to illustrate expected community dynamics and patterns under different combinations of simple underlying processes; (ii) to provide students with the tools to explore scenarios on their own – a very effective means for learning about the process-pattern link – without requiring much in the way of mathematical ability; (iii) to support the argument that most models in community ecology are just different combinations of a few basic ingredients.

Getting started with modeling

Many modeling frameworks can be applied to predicting and understanding the dynamics and structure of ecological communities. A distinction is commonly made between analytical models and numerical or simulation models. (The analytical vs. numerical distinction often refers more to how one works with an equation or set of equations rather than how they are constructed to begin with, but I will refer to them as different kinds of models for simplicity.) Analytical models are those with a “closed-form” or “general” solution, meaning that once equations are written down, they can be “solved” to predict the outcome(s) of interest (e.g., population size of a given species) at any arbitrary time in the future based on initial conditions and the values of the model parameters. Models for exponential population growth, logistic growth, the Lotka-Volterra equations (see Chapter 2), and their hundreds of descendants fall into this category. A great advantage of such models is that their behavior can be understood quite precisely, with outcomes traceable to specific causes. They can also be applied with just a paper and pencil, and, perhaps most importantly, they are aesthetically very pleasing to a mathematician.

Beyond a certain degree of complexity, it becomes near-impossible to find (or make sense of) closed-form solutions to analytical models, in which case researchers use simulations. In a simulation model, the researcher first defines the initial state of the system (e.g., the population size of each interacting species) as well as a set of equations or rules that govern subsequent changes. A computer is then used to explore dynamics under different scenarios. In addition to allowing incorporation of greater complexity, simulation models also have the appeal of permitting a less abstract mental mapping of what happens in the model to what happens in nature. For example, in lines of simulation code I can “see”, in my mind’s

eye, a canopy tree dying, seeds being dispersed, and then competition among saplings to replace the fallen canopy tree (Pacala et al. 1993). For someone adept at mathematics, some intuitive scenarios like this can be converted into an analytical model, provided the scenario is not overly complex (Otto and Day 2011). But most ecologists are not sufficiently adept at mathematics to convert an ecological scenario into equations with closed-form solutions, or even to easily follow experts through the analysis of such models.

For the reasons just described, I believe that simulations of even simple ecological models (i.e., for which analytical versions are possible) can be of great pedagogical utility in allowing students to explore theoretical ecological dynamics on their own, which is far more conducive to learning than simply following a teacher walking through a model. After learning how to convert “pseudo-code” (i.e., verbal instructions for how a simulation should work) into functional computer code, a world of theoretical possibilities is opened up for exploration. Learning how to do this requires a non-trivial initial effort, but no more than mastering the dozens of bells and whistles on a new iPhone, and it requires very little mathematics. To be clear, this is not an argument that sophisticated mathematics is not of immense importance in ecology, but it is an acceptance of the fact that many students of ecology find the theoretical literature inaccessible, and probably always will. I hope that by exploring ecological simulations, students can gain easier access to the core theoretical ideas in community ecology. Perhaps some students will even be inspired acquire the skills needed to build analytical models of their own.

All of the simulations presented here were conducted using the R programming language (R Core Team 2012). In order to maximize accessibility, I assume no knowledge of R whatsoever, with detailed explanations provided for the simulation code. Code for the first model (neutral dynamics in one local community) is provided here in the book itself (see Box 1) so that readers can get a sense of how things work without needing to refer elsewhere. All other code (Online Boxes 1-8) can be accessed at <http://mvellend.recherche.usherbrooke.ca/TOEC.html>. In order to reproduce particular figure panels, readers will need to set parameters to particular values before running simulations.

Local community dynamics: ecological drift

I begin with as simple a scenario as I can imagine, using a model known as the Moran model, originally designed to understand changes in allele frequencies in populations (Moran 1958) see also (Hubbell 2001, Nowak 2006). For dynamics in a neutral, closed community with no speciation, here is the recipe, or pseudo-code:

- 1) Specify an initial community of J individuals divided among S species; each species i has N_i individuals.
- 2) Select an individual at random to die.
- 3) Select an individual at random to produce one offspring, which replaces the dead individual.
- 4) Repeat from step one.

The beauty of this model lies in its simplicity: a wide range of dynamics and patterns can be produced just by changing the rules at step 3 for selecting an individual to reproduce. Modifying step 2 could achieve

the same goal. On the surface, step 3 might seem a bit odd biologically (one offspring from one individual), but it is equivalent to assuming that all individuals produce many offspring, only one of which will become a new recruit to the community at a given point in time. Because we will be working with simulations, I will henceforth use the notation and font (`Courier New`) that appears in the R code to refer to variables and parameters in the code itself. Variables and parameters that don't appear explicitly in the R code and whose meaning is otherwise not obvious will remain in regular font.

The state of the community is specified by the vector of species abundances, $[N_1, N_2 \dots N_S]$, in which N_i is the abundance or population size of the i^{th} species. With an assumption of constant J , we can keep track of species frequencies ($\text{freq}.i = N_i/J$), as described in Chapter 3. With only two species, $\text{freq}.2 = 1 - \text{freq}.1$, so we only need to keep track of one of the species frequencies as a complete specification of what's happening in the community. That is, pattern in the community is fully accounted for by a single "response" variable. We can consider J repetitions of this cycle as one time step, which for simplicity we can think of as a "year" for organisms with an average life span of one year.

Let's start with the neutral model just described in a community with two species, 1 and 2. R code for this model is shown in Box 1, which is deliberately a bit longer than necessary in order to permit the addition of selection in as simple a way as possible. (To use R to explore analytical models like those discussed in chapter 1, see Stevens (2009).) Since all individuals have the same probability of being chosen to reproduce, the probability that the reproducing individual will be of species 1 is simply the frequency of this species in the community: $\text{Pr}.1 = \text{freq}.1 = N_1/J$. The resulting dynamics are due solely to drift. Species frequencies bounce up and down at random until one or the other species goes extinct (Fig. 4.1). Drift is slower in larger communities, and the probability that a given species eventually "wins" is equal to its initial frequency (Fig. 4.1; (Kimura 1962, Hubbell 2001)).

Box 1. Simulating neutral dynamics in a local, two-species community (with no speciation) using R.

In the image below, the numbers on the right correspond to the pseudo-code, and the numbers on the left serve as references for the explanations below. In order to function in R, these numbers must be removed. Fully annotated code that can be used in R is provided at

<http://mvellend.recherche.usherbrooke.ca/TOEC.html>.

<pre> 1. J <- 50 2. init.1 <- J / 2 3. COM <- vector(length = J) 4. COM[1:init.1] <- 1; COM[(init.1 + 1):J] <- 2 5. num.years <- 50 6. year <- 2 </pre>	<div style="font-size: 3em; line-height: 1;">}</div>	<p>(1) Specify initial community (& time instructions)</p>
<pre> 7. freq.1.vec <- vector(length = num.years) 8. freq.1.vec[1] <- init.1 / J </pre>	<div style="font-size: 3em; line-height: 1;">}</div>	<p>Set up vector for data collection</p>
<pre> 9. for(i in 1:(J * (num.years - 1))) { 10. freq.1 <- sum(COM == 1) / J 11. Pr.1 <- freq.1 12. COM[ceiling(J * runif(1))] <- sample(c(1, 2), 1, prob = c(Pr.1, 1 - Pr.1)) 13. if (i %% J == 0){ 14. freq.1.vec[year] <- sum(COM == 1) / J 15. year <- year + 1 16. } 17. } </pre>	<div style="font-size: 3em; line-height: 1;">}</div>	<p>(2,3,4) Run simulation</p>
<pre> 18. plot(1:num.years, freq.1.vec, type = "l", xlab = "Time", 19. ylab = "Frequency of species 1", ylim = c(0, 1)) </pre>	<div style="font-size: 3em; line-height: 1;">}</div>	<p>Create a graph of simulation</p>

1. Define the local community size, J . J is defined as an object, and $<-$ places the number 50 in this object.
2. Define the initial population size of species 1, $init.1$. By default, the initial population size of species 2 will be $J - init.1$.
3. Create an empty vector of length J to represent the community, and call it COM .
4. Set the initial population sizes of species 1 and 2 by making elements 1 through $init.1$ of COM equal to 1, and the rest equal to 2.
5. Set the number of years over which to run the simulation.
6. Define the first year to be simulated as year 2 (the initial specified community will be year 1). If we want to record output each year, as opposed to after each individual birth-death event, we need this to keep track of years in the loop.
7. Create an empty vector to hold the output. We only need to keep track of the frequency of species 1, so we call this vector $freq.1.vec$ (the frequency of species 2 is $1 -$ the frequency of species 1).
8. Record the initial frequency of species 1 in the first element of $freq.1.vec$.
9. Initiate the simulation. Since each year involves J birth-death events, we need to go through the loop (i.e., repeat the birth-death cycle) $J * num.years$ times in order to simulate the specified number of years. The variable i keeps track of how many times we've gone through the loop: the first time through the loop, $i = 1$; the second time, $i = 2$, and so on.
10. Calculate the current frequency of species 1, $freq.1.COM == 1$ creates a vector with a "TRUE" (read quantitatively as 1) for any element equal to 1, and a "FALSE" (quantitatively zero) otherwise (in this case when it is a 2). So, taking the sum of $COM == 1$ gives us the current population size of species 1, and dividing by J gives the frequency.
11. $Pr.1$ is the probability that an individual of species 1 is chosen to reproduce; since this model is neutral, it is equal to $freq.1$.
12. Select an individual to die and replace it with an individual of the species chosen to reproduce. $runif(1)$ draws one random number from a uniform distribution between 0 and 1, so $J * runif(1)$ generates a random number between 0 and J . But we need an integer to select an individual from the community, and the `ceiling` function rounds up our random number to provide a random integer between 1 and J . This is the individual that will die. On the right hand side, we determine the species

identity of the reproducing individual based on `Pr.1`. `c(1,2)` concatenates the numbers 1 and 2 together in a vector, and we sample 1 number from this vector based on the probabilities `Pr.1` for species 1 and `1 - Pr.1` for species 2. Thus, we chose a 1 or a 2 to replace the dead individual.

13-15. After each sequence of J deaths, record data. `i %% J` returns the remainder of `i` divided by J , and each time that J deaths have occurred this will be equal to zero, so this is an efficient way to tell R to “stop” the program, record the frequency of species 1 (line 14), and increment the year tracker by 1 (line 15).

16-17. Terminate the `if` loop and the `for` loop.

18-19. Plot the results. `1:num.years` is the data for the x-axis and `freq.1.vec` the data for the y-axis. `type="l"` specifies a line graph, `xlab` and `ylab` the axis labels, and `ylim` specifies limits on the y-axis values.

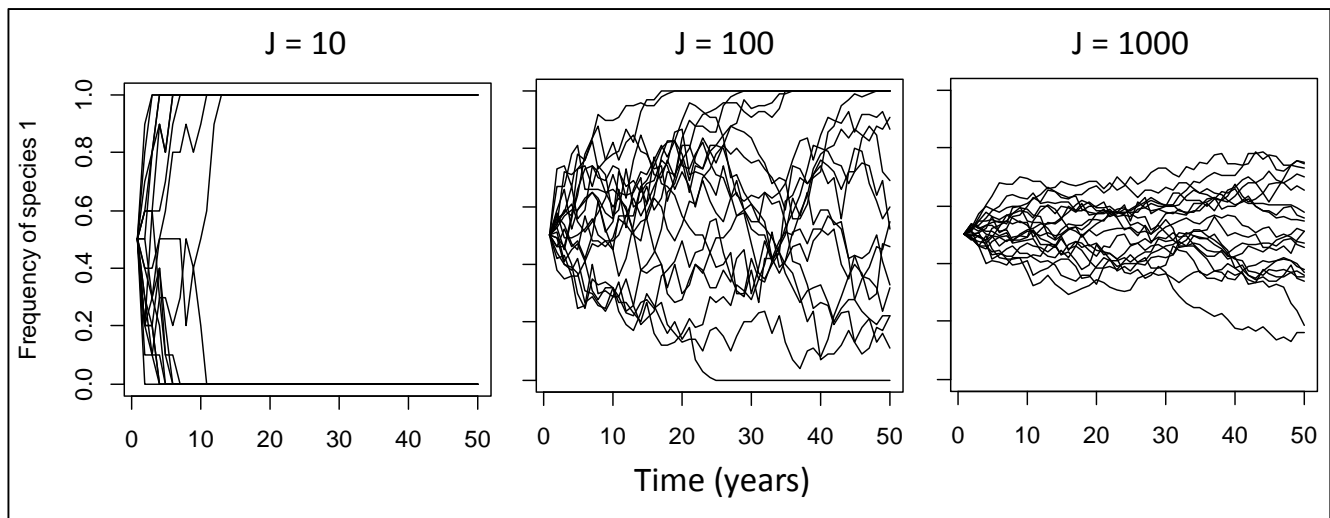


FIGURE 4.1. Dynamics of two-species communities under pure ecological drift. Each panel shows 20 independent simulations using a given community size (J) and a starting frequency of species 1 (`init.1`) of 0.5 (see code in Box 1 and Online Boxes 1-2).

Local community dynamics: selection

Selection occurs when fitness differs between species, that is, when a species' probability of being chosen to reproduce is different from its frequency: $Pr.1 \neq N_1/J$. Imagine a community with 10 individuals of species 1 and 30 of species 2, so $freq.1 = 10/40 = 0.25$ and $freq.2 = 30/40 = 0.75$. If the per capita reproductive outputs (i.e., fitnesses) of the two species over a given time step are 20 and 10, respectively, we expect species 1 to produce $10 \times 20 = 200$ offspring and species 2 to produce $30 \times 10 = 300$ offspring. If we are going to choose just one of these offspring at random to replace a dead individual, the probability that this offspring will be of species 1 is equal to the proportion of all offspring that were produced by species 1: $10 \times 20 / (10 \times 20 + 30 \times 10) = 200 / (200 + 300) = 0.4$. So, because it has higher fitness, species 1's probability of producing a successful recruit in the community ($Pr.1 = 0.4$) is greater than its frequency ($freq.1 = 0.25$). To generalize, if the fitnesses of species 1 and 2 are `fit.1` and `fit.2`, respectively, then $Pr.1 = fit.1 * freq.1 / (fit.1 * freq.1 + fit.2 * freq.2)$ (Ewens 2004). By

dividing the numerator and denominator of this equation by `fit.2`, we can see that it is only the ratio of the two fitness values that matters, not their absolute values:

```
Pr.1 = (fit.1/fit.2)*freq.1/((fit.1/fit.2)*freq.1 + freq.2).
```

We can call `fit.1/fit.2` the fitness ratio (`fit.ratio`). The R code for local models with selection (Online Box 2) includes only `fit.ratio` and not `fit.1` and `fit.2` as separate parameters.

In the following sections on local community dynamics with selection, we will explore situations in which the relative fitnesses of the two species (`fit.ratio`) depends on two parameters: (1) the fitness ratio averaged across all possible species frequencies (`fit.ratio.avg`), which quantifies the strength of constant selection, and (2) the direction and strength of the relationship between fitness and species frequencies (`freq.dep`), which quantifies frequency-dependent selection. The R code for these models is presented in Online Box 2. If `fit.ratio.avg = 1` and `freq.dep = 0`, the model is entirely neutral, and so equivalent to the code in Box 1. In exploring scenarios with selection, we will first assume that `freq.dep = 0`, with the strength of constant selection set by `fit.ratio.avg`. We will then explore various scenarios of frequency-dependent and temporally variable selection. By exploring simulations with different values of J , we also can stay ever cognizant of the fact that when a community has relatively few individuals (i.e., J is small), the outcomes expected based on fitness differences among species are not guaranteed. That is, stochastic drift can, in principle, overwhelm deterministic processes.

Competitive exclusion via constant selection

If species 1 has consistently greater fitness than species 2 (i.e., `fit.ratio > 1` always), species 1 will tend to competitively exclude species 2, and vice versa (Fig. 4.2). In order to simulate this, the only changes required to the R code in Box 1 are the assignment of the average fitness ratio, and alteration of the equation for `Pr.1` (i.e., step 3 in the pseudo-code). For example, keeping `freq.dep = 0`, we can set `fit.ratio.avg = 1.1`, giving species 1 a small fitness advantage (see Online Box 2).

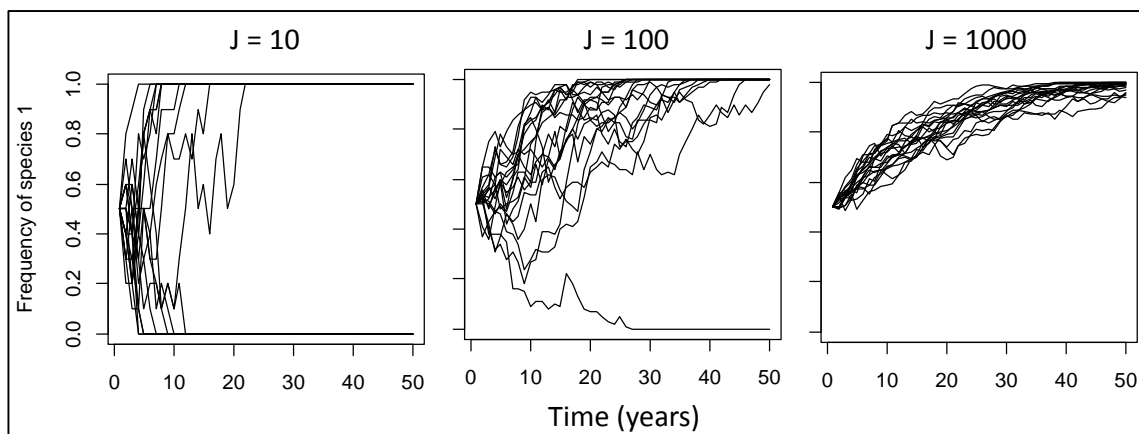


FIGURE 4.2. Dynamics of two-species communities under constant selection, favoring competitive exclusion of species 2 by species 1 (`fit.ratio.avg = 1.1`, `freq.dep = 0`). Each panel shows 20 independent simulations using a given community size (J) using the R code in Online Box 2.

Stable coexistence via negative frequency-dependent selection

If the fitness of species 1 is greater than the fitness of species 2 when species 1 is common, and vice versa, effectively each species has a relative advantage when rare and there should thus be a stable equilibrium point at which both species have non-zero abundance (Chesson 2000b). That is, the two species should coexist via negative frequency-dependent selection. For stable coexistence, it is not enough for species' fitnesses to be negatively related to their frequencies, but this tendency must be strong enough relative to any average fitness difference such that $\text{fit.ratio} > 1$ when species 1 is extremely rare, and vice versa ((Adler et al. 2007); Fig. 4.3). This scenario can be implemented using the R code in Online Box 2.

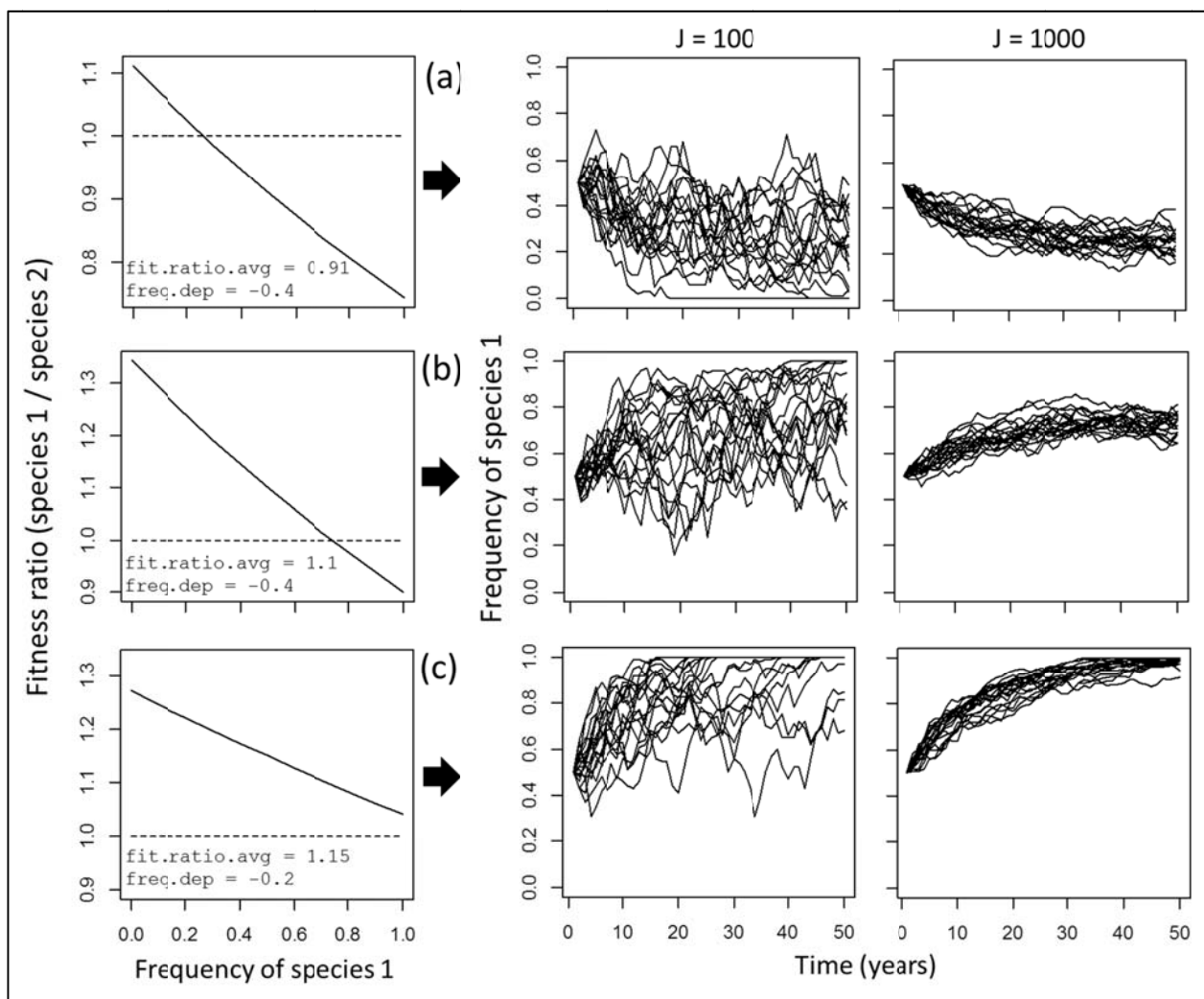


FIGURE 4.3. Dynamics of two-species communities under negative frequency-dependent selection. Each panel shows 20 independent simulations using a given different community size (J). In the first two rows, frequency-dependent selection is strong enough relative to average fitness differences to lead to a stable equilibrium (the intersection of the solid and dotted lines in the left panels) and thus species coexistence. In the third row, coexistence is not possible despite negative frequency-dependent selection because species 1 always has an advantage. See Online Box 2 for R code.

To simulate negative frequency-dependent selection, we need to specify the relationship between fitness and frequency. Most simply, the ratio of fitnesses of species 1 and 2 (`fit.ratio`) should be related negatively to the frequency of species 1 (Fig. 4.3, left panels). The details are not critical in order to understand the key outcomes of this scenario, but to ensure symmetry in the relative (dis)advantages experienced by the two species, we can specify the log ratio of `fit.ratio` as a linear function of species' frequencies (see Appendix 4.1 and Online Box 2). The parameter `freq.dep` specifies the slope of this relationship. The parameter `fit.ratio.avg` is the value of `fit.ratio` when species frequencies are both 0.5, effectively shifting the fitness-frequency relationship up or down (see Fig. 4.3). A negative value of `freq.dep` corresponds to what Chesson (2000b) calls a “niche difference” between species and `fit.ratio.avg` corresponds to his “fitness difference”.

Temporally fluctuating selection

In the simple simulations so far with large communities, community composition (i.e., species frequencies) converges smoothly toward a stable equilibrium. However, this general “rule” about stable coexistence emerging from negative frequency dependence applies to *long-term* expected advantages when species are rare, which may arise via mechanisms that involve temporal fluctuations. There are some important specific conditions that need to be met in particular models (Chesson 2000b, Fox 2013), but most simply, fitness (dis)advantages can fluctuate over time such that each species spends enough time at an advantage to overcome population declines experienced while at a disadvantage. An additional condition is the presence of some means by which a species can “hang on” (e.g., dormant propagules) when conditions are strongly unfavorable (Chesson 2000b) and/or some mechanism to prevent a dominant species from taking over completely when favored (Yi and Dean 2013). Fitness variation can be driven by extrinsic fluctuations (e.g., climate) or by environmental fluctuations driven intrinsically by the organisms themselves (e.g., via resource use, (Armstrong and McGehee 1980, Huisman and Weissing 1999, 2001)). Just for purposes of illustration (i.e., without getting into the nitty gritty mathematical requirements for indefinite coexistence), we can see that giving each of the two species a fitness

advantage in alternating 10-year periods (e.g., via climate fluctuations) can contribute to the possibility of each species tending to bounce back from being rare (Fig. 4.4, see Online Box 3 for R code). A comparable situation involving environmental differences across space will be explored in subsequent sections.

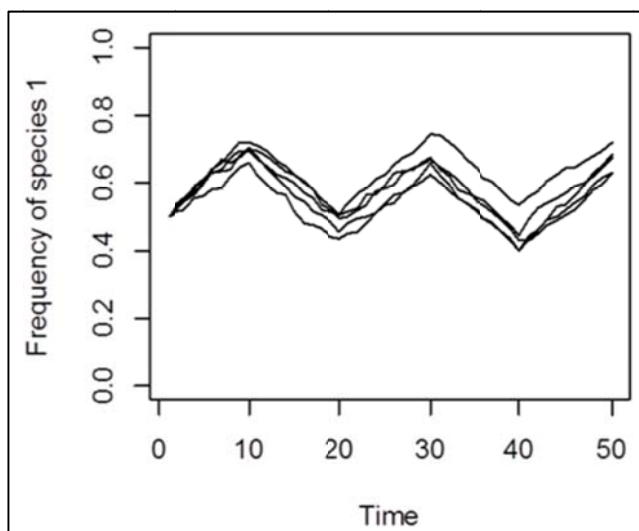


FIGURE 4.4. Dynamics of two-species communities under temporally fluctuating selection. Five independent simulations are shown with $\sigma = 4000$ and alternating fitness ratios of 1.1 and 0.91 (the reciprocal of 1.1) each 10 time steps (R code in Online Box 3). In these simulations, eventually one or the other species will “win”; long-term stable coexistence depends on additional criteria, such as the ability to buffer population losses.

The potential for cyclical dynamics

Many ecological models also have equilibria that are not represented by single points (e.g., a given species frequency) but rather by regular fluctuations or cycles that are expected to continue indefinitely. Most such models involve an explicit accounting of trophic interactions (e.g., predator-prey cycles), but the key feature is a tendency to repeatedly “overshoot” a sort-of equilibrium point, and this emerges even in some single species population models (May 1974) or in multi-species models with only competition (Gilpin 1975). There are exceedingly few empirical examples of limit cycles caused only by “horizontal” interactions among species, so the simulations here are presented largely for theoretical interest, capturing an important class of possible community dynamics (i.e., this topic does not feature prominently in the empirical chapters 6-8).

Using our simulation framework, we can illustrate “overshoot” dynamics by adding a delay in the response of species’ fitnesses to their frequencies. Specifically, if we use the species’ frequencies at the start of a “year” (i.e., a sequence of J deaths) to calculate a `fit.ratio` that will stay constant for the whole year, very strong frequency dependence can create indefinite fluctuations (Fig. 4.5). To implement this in the R code (see Online Box 4), instead of one time loop with $J \times \text{num.years}$ steps, we create two nested loops, the first with `num.years` steps and the second with J steps, and `fit.ratio` defined between the start of the first and the second loops. Cycles can also emerge in models with “intransitive competition” among three species (Gilpin 1975), which means that the three species effectively play a game of rock-paper-scissors, which is inherently frequency-dependent: rock beats scissors, paper beats rock, and scissors beats paper. As any one of the three species (e.g., rock) increases in abundance, a different species (e.g., paper) gains an advantage, and the three species take turns dominating the community (Gilpin 1975, Vellend and Litrico 2008).

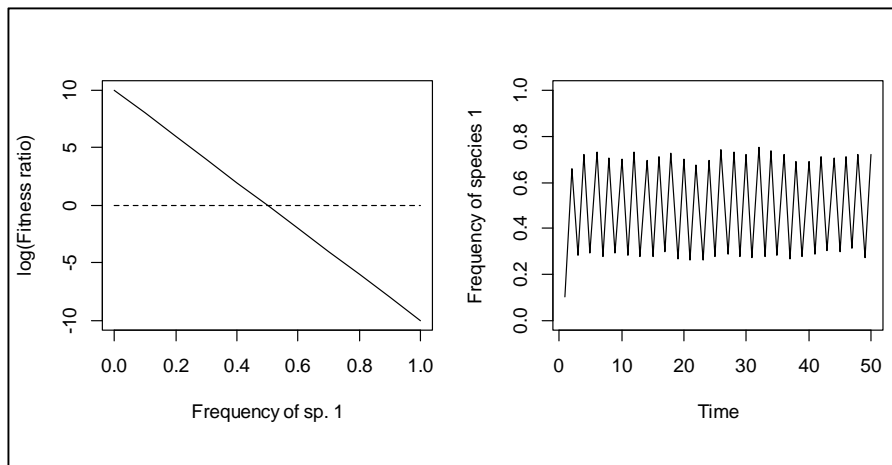


FIGURE 4.5. Dynamics of a two-species community under very strong frequency-dependent selection. In this simulation (Online Box 4) species fitnesses stay constant for a year at a time (i.e., they are not updated after every death). Fluctuations are only evident with `freq.dep < -10`. One simulation is shown here with $J = 500$, `freq.dep = -20` and initial frequency = 0.1 (see Online Box 4). Note that the y-axis in the left panel is shown with a log scale, so the reference line for equal fitness across species is at zero instead of one.

Priority effects and multiple stable equilibria via positive feedbacks

If species' fitnesses are positively related to their frequencies such that $\text{fit.ratio} < 1$ when species 1 is rare, and vice versa, then whichever species starts at a high frequency will tend to exclude the other (i.e., there are strong priority effects). All that is needed to simulate priority effects is to switch the sign of freq.dep (in Online Box 2) to be positive (Fig. 4.6). This model illustrates one of the simplest possible situations in which one can generate multiple stable equilibria, in this case dominance by one species or the other. Many more complex and often system-specific models also predict multiple stable equilibria, often with respect to multiple biotic and abiotic attributes of an ecosystem simultaneously, such as dominance vs. near absence of particular functional forms (e.g., aquatic macrophytes) and major shifts in environmental variables (e.g., water clarity) (Scheffer 2009). At the core of all such models are positive feedbacks of one sort or another (e.g., facilitation of some species by others), so the basic lesson here is more general than the extremely simply model might seem on the surface.

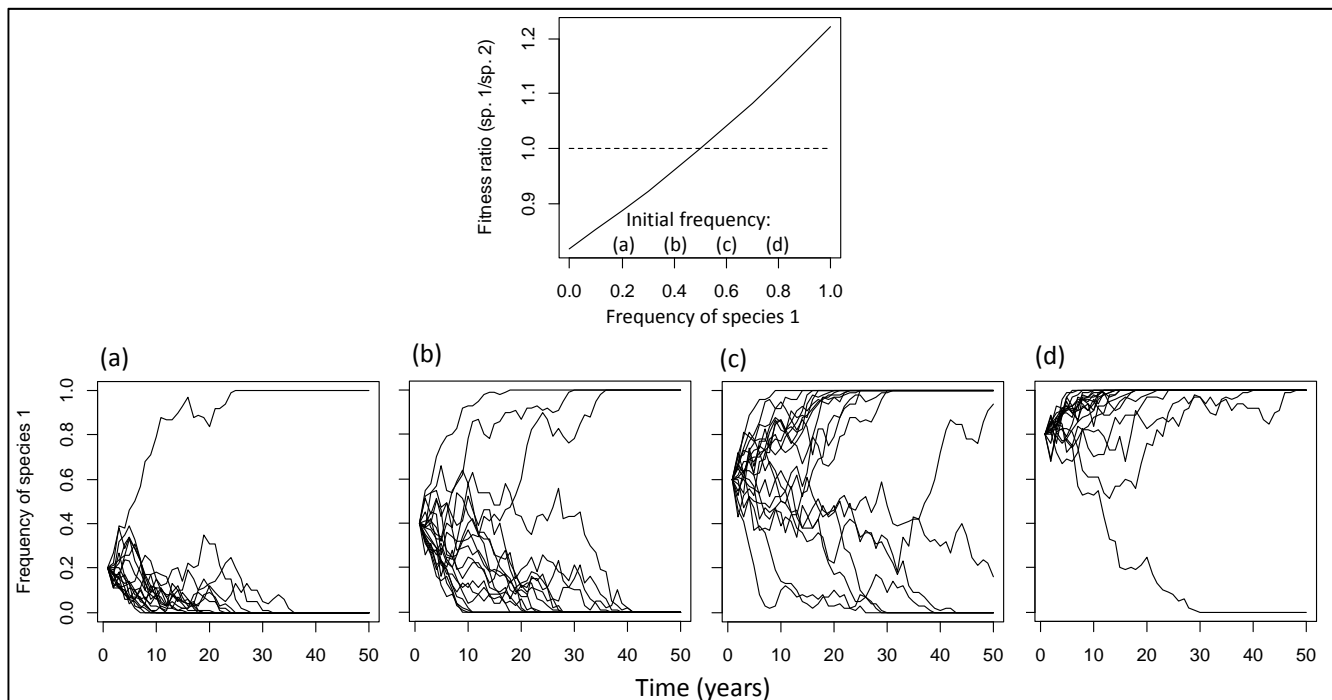


FIGURE 4.6. Dynamics of two-species communities under positive frequency-dependent selection. At initial frequencies of species 1 > 0.5 , species 1 has a fitness advantage, and vice versa ($\text{freq.dep} = 0.4$, $\text{fit.ratio.avg} = 1$). In all cases, $J = 100$. In panels (b) and (c), initial frequency is sufficiently close to 0.5, that frequencies can often drift to one side or the other of 0.5, thus favoring competitive exclusion of one species or the other. In panels (a) and (d), initial frequencies are further from 0.5, thus leading to more predictable competitive exclusion. Each panel shows 20 independent simulations using different initial frequencies: (a) 0.2, (b) 0.4, (c) 0.6 and (d) 0.8. Panels a-d were produced using the R code in Online Box 2.

Local communities linked by dispersal

At the end of this chapter, we will simulate dynamics in communities with larger numbers of species under the influence of dispersal and speciation. However, some of the key community-level consequences of dispersal, as well as the consequences of spatially variable selection, can be most easily

understood by continuing with simulations of the dynamics of two-species communities, now in two or more local communities, or habitat “patches”. Online Box 5 shows the R code needed to simulate the dynamics of two species in an arbitrary number of habitat patches (`num.patch`), each with J individuals. The entire set of patches is the metacommunity. Within patches, local selection (of any form) operates exactly as described above, but the patches are now potentially linked by dispersal. Specifically, with probability m (the dispersal parameter), the reproducing individual at step 3 of the Moran model (described at the start of the chapter) is chosen at random from the entire metacommunity rather than from the local patch where a mortality event occurred.

The interaction of drift and dispersal

In a purely neutral model with no dispersal, composition in each community drifts randomly, creating compositional variation (i.e., beta diversity) among patches (Fig. 4.7). With dispersal, the dynamics are no longer independent among patches. Composition (in this case just the frequency of species 1) in the entire metacommunity is still prone to drift, but given the large size of the metacommunity ($\text{num.patch} \times J = 10 \times J$ in Fig. 4.7), drift at this level is relatively slow. With very high dispersal, there is essentially no biological meaning to “local” communities, except that they represent a subset of one larger community that behaves as a single entity. At intermediate levels of dispersal, composition in each patch can fluctuate about the average composition of the metacommunity, which is itself prone to drift (Fig. 4.7).

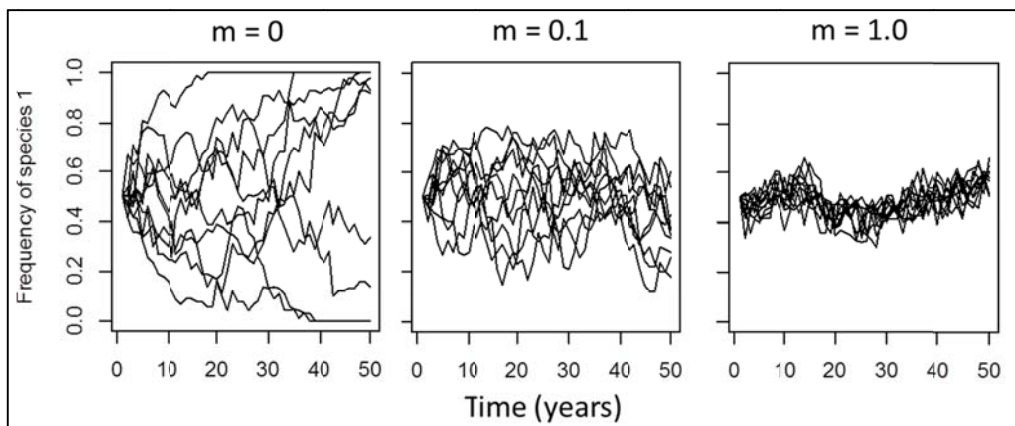


FIGURE 4.7. Dynamics of two-species in 10 local communities (habitat patches) in a purely neutral model with $J = 100$ in each local community, and different levels of dispersal (m). See Online Box 5 for R code.

The interaction of dispersal and selection

With two habitat patches, each selectively favouring one of the two species, both species can potentially coexist indefinitely in both patches if there is some dispersal. In other words, spatially variable selection can promote diversity both within and across patches. If selective (dis)advantages are symmetric across patches – i.e., species 1 has the same selective advantage in patch 1 as species 2 does in patch 2 – species coexistence across the metacommunity is expected regardless of the level of dispersal. With no dispersal, each species excludes the other in one of the patches (Fig. 4.8). With increasing levels of dispersal, the selectively disadvantaged species in a given patch occurs there at higher and higher abundance because of constant influx from the patch where it has an advantage (Fig. 4.8).

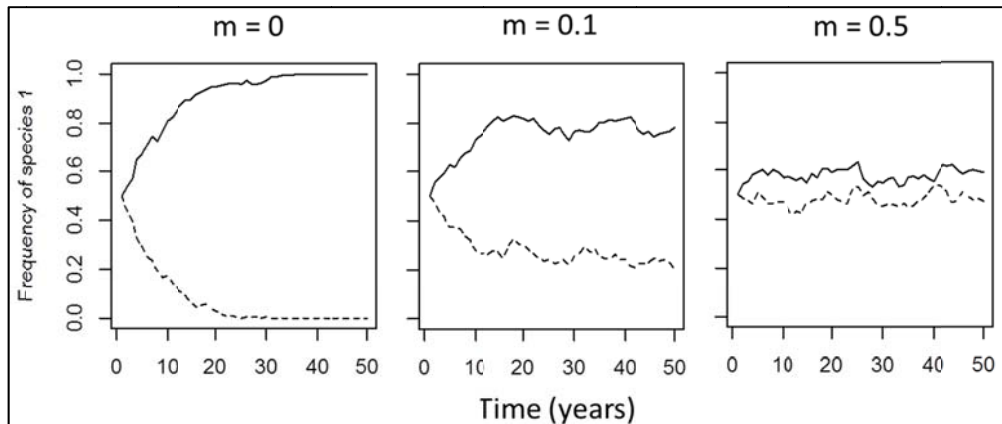


FIGURE 4.8. Community dynamics in two habitat patches, one selectively favoring species 1, the other species 2. The fitness ratio is 1.2 in one patch (solid line) and 1.2^{-1} in the other (dashed line). $\tau = 1000$ in each community. See Online Box 5 for R code.

When selection is asymmetric among habitat patches, such that species 1 has a greater selective advantage in patch 1 (e.g., fitness ratio = 1.5) than species 2 has in patch 2 (e.g., fitness ratio = 1.1^{-1}), high enough dispersal can lead to the extinction of species 2. In this scenario, in the absence of dispersal, each species excludes the other in the patch where it has a selective advantage. With increasing dispersal, individuals of species 2 recruiting to patch 1 find themselves at a severe selective disadvantage, while recruits of species 1 in patch 2 are at a less severe disadvantage. As such, beyond a certain level of dispersal, the composition of patch 2 is “pulled” toward that of patch 1, ultimately leading to the demise of species 2 across the whole metacommunity (Fig. 4.9).

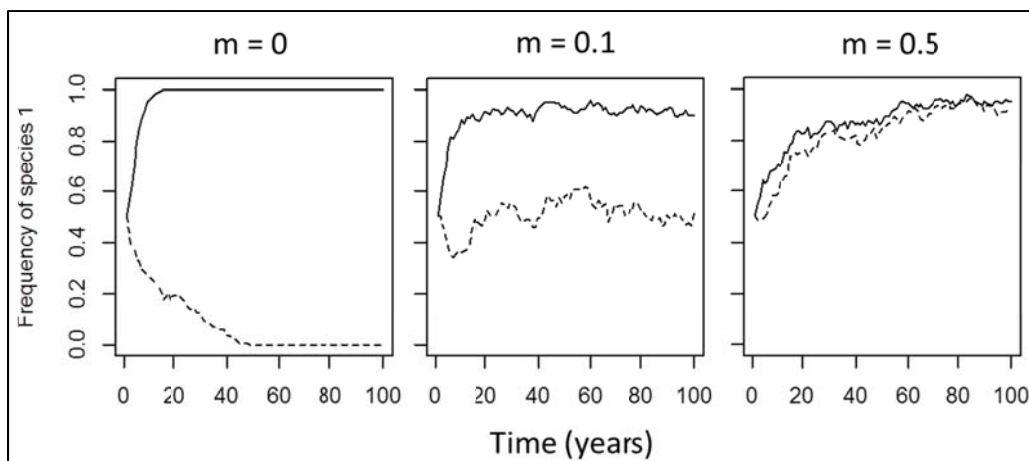


FIGURE 4.9. Community dynamics in two habitat patches, one selectively favoring species 1, the other species 2. In this case, fitness ratios are asymmetric: 1.5 in one patch (solid line) and 1.1^{-1} in the other (dashed line). $\tau = 1000$ in each community. See Online Box 5 for R code.

Selection at the dispersal stage: competition-colonization trade-offs

The code in Online Box 5 implicitly assumes that all species have the same dispersal ability. When new recruits are drawn from the metacommunity rather than the local community, the draw is random. However, just as different species might make different per capita contributions to the local offspring pool, thus having different probabilities of local success, species might also vary in their relative contributions to the pool of offspring that disperses among patches. This can be modeled by considering

dispersal ability effectively as a component of fitness, specifically with respect to defining the probability of a new recruit drawn from the whole metacommunity being of one species or the other.

A new fitness ratio (`fit.ratio.m`) can be defined (see Online Box 6), and then when dispersal is implemented in the `for` loop, we first calculate the frequency of species 1 in the entire metacommunity, and then use that in conjunction with `fit.ratio.m` to calculate `Pr.1`, exactly as done when recruitment happens locally. This introduces the possibility of counteracting fitness components: species 1 might have an advantage locally (`fit.ratio > 1` in both patches), while species 2 has a superior dispersal ability (`fit.ratio.m < 1`). Fitness components along these lines have often been referred to as “competition ability” and “colonization ability”, respectively. With a sufficiently strong tradeoff between these “abilities” and neither too little nor too much dispersal, species coexistence in the metacommunity is possible (Levins and Culver 1971, Tilman 1994). In mathematical terms, with identical local selection in multiple patches, the metacommunity is like one big patch in which some recruitment events (“local” ones) favour species 1 and others (“dispersal”) favour species 2. The results nonetheless illustrate the potential for life-history tradeoffs to promote the maintenance of diversity (Fig. 4.10).

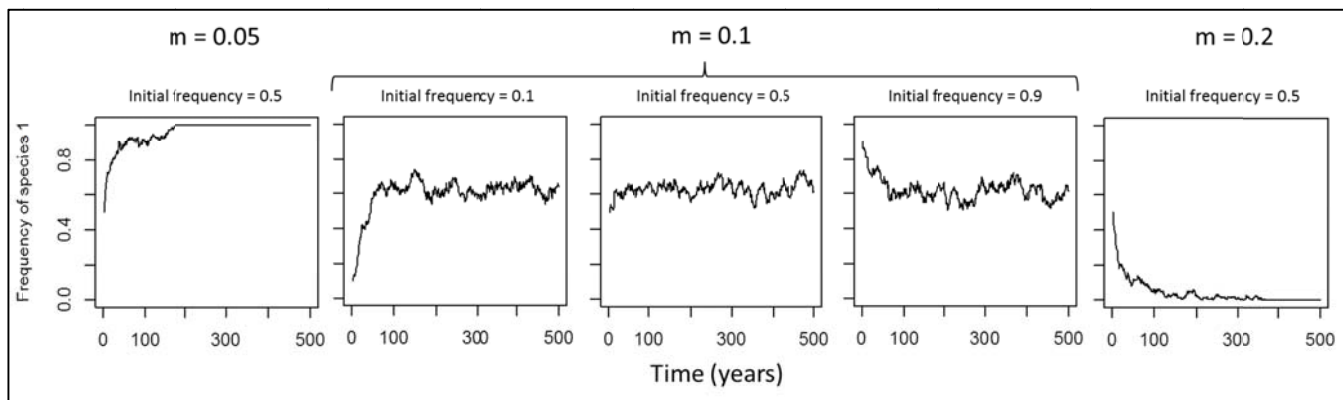


FIGURE 4.10. Dynamics in a metacommunity of two habitat patches ($J = 1000$ each), both of which selectively favor species 1 (`fit.ratio.avg = 1.2`). There is dispersal among patches (m), at which stage species 2 has a “fitness” advantage (`fit.ratio.m = 1/5`) (see Online Box 6). Because local parameters are identical in the two patches, only the metacommunity-level frequency is shown. Different initial frequencies are shown for $m = 0.1$ to demonstrate the tendency for convergence toward an equilibrium frequency ~ 0.6 . When dispersal is low ($m = 0.05$) species 1 “wins”; when dispersal is high ($m = 0.2$) species 2 wins.

Overview of models with dispersal

These fairly simple simulations illustrate many well-known theoretical results. First, spatially variable selection (i.e., via environmental heterogeneity) can be a potent force maintaining diversity (Levene 1953). Second, dispersal can often maintain sink populations of species, thereby elevating diversity at the local scale (MacArthur and Wilson 1967). Dispersal also causes community composition across habitat patches to converge (i.e., beta diversity will decline), regardless of local selection (Hubbell 2001, Chave et al. 2002). If there is some asymmetry in the selective advantages enjoyed by different species in different places, very high levels of dispersal can ultimately erode diversity across the metacommunity (Mouquet and Loreau 2003). Finally, if dispersal ability and local selective advantages are negatively

correlated across species (i.e., there is a trade-off), species coexistence can be maintained despite spatially homogenous local selection (Levins and Culver 1971, Tilman 1994).

Models with speciation

Two final points can be illustrated by incorporating speciation into simulations of community dynamics. First, a higher speciation rate increases species richness as well as the evenness of species abundances. Second, local-scale diversity is greater when immigrants are drawn from a regional species pool where the speciation rate has been higher. Here we will first simulate “regional” community dynamics as a balance between speciation and drift. Then, using different regional communities as sources of immigrants (i.e., “mainlands”), we will simulate a local balance between immigration (via dispersal) and drift, as in the classic island biogeography model (MacArthur and Wilson 1967). In neither case will there be any selection, so as to focus on the effects of speciation without additional complications.

A neutral model with speciation looks much like the “local” neutral model already encountered (see Box 1), except that with a small probability ν (often denoted by the Greek symbol ν) a new recruit to the community will be of a new species (see Online Box 7). We need to keep track of different species using different numbers, and the `COM` vector may have many different species in it. Using this code, we can see that an increasing speciation rate leads to a more diverse pool of species with more equitable abundances (Fig. 4.11).

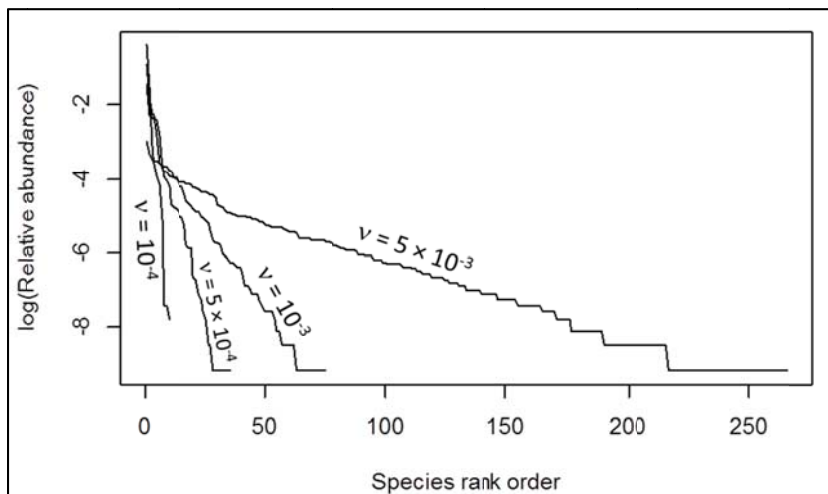


FIGURE 4.11. Relative abundance distributions in a neutral model of a single community under different speciation rates (ν). In all cases, $\tau = 10,000$. Results are shown at a single point in time after 10,000 years. See Online Box 7 for R code.

To explore the influence of speciation rate – via its influence on the regional species pool – on local diversity, we can simulate local community dynamics with immigration. With probability m , a local recruit is chosen from the regional pool, which is

defined by one of the relative abundance distributions in Fig. 4.11. A species’ relative abundance (i.e., frequency) in the regional pool defines its probability of being chosen to provide the new recruit when an immigration event occurs. This is basically an individual-based version of the island biogeography model (MacArthur and Wilson 1967). The R code for this is shown in Online Box 8.

With these simulations, we see the well-known results that species richness increases with both area (represented by local τ), and with the immigration rate, m (Fig. 4.12). We can also see that drawing immigrants from a regional pool with a higher speciation rate leads to greater local diversity (Fig. 4.12). This is the crux of the species-pool hypothesis for explaining trends in species diversity along

environmental gradients (Taylor et al. 1990): if we imagine that panels (a) and (b) in Fig. 4.12 represent two different habitat types (e.g., unproductive and productive), local diversity is greater in (b) due to a higher regional speciation rate rather than any difference in the nature of local selection in regulating diversity.

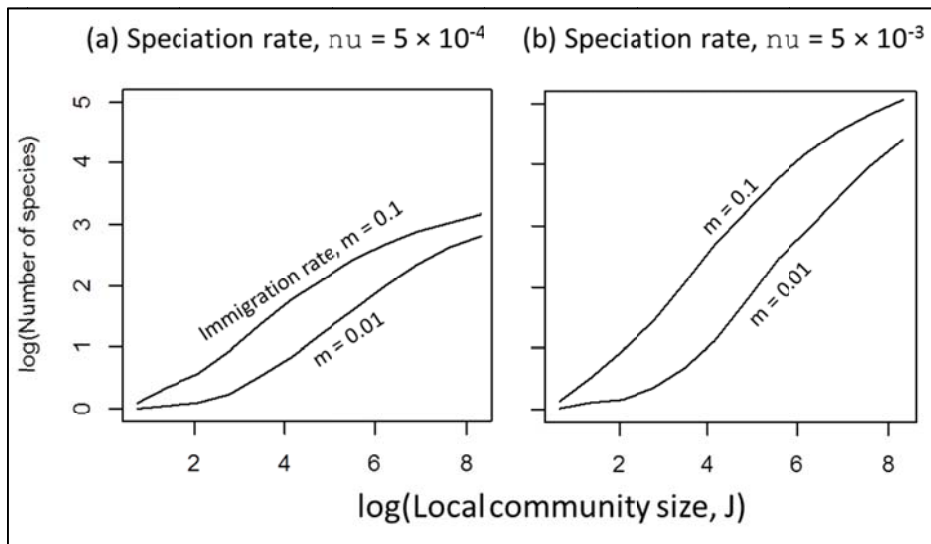


FIGURE 4.12. Relationships between species richness and community size (i.e., “area”) among independent local communities with immigration at different rates (m) and from species pools with different speciation rates (ν). See Online Box 8 for R code.

Overall summary

The different kinds of dynamics described in this chapter might be underlain by innumerable specific mechanisms, involving nutrients, disturbance, predators, pathogens, environmental fluctuations, physiological and life-history trade-offs, biogeographic context, and so on. However, these fairly simple scenarios illustrate the key features of a very large number of models describing the dynamics among species interacting on the same trophic level in a local community, or in a set of local communities linked by dispersal and ultimately influenced by speciation. Importantly, they can all be generated by altering a few lines of computer code.

Many researchers already comfortable working with mathematical models will no doubt find these simulations unnecessarily crude, given the availability of analytical models with which the same phenomena can be illustrated, and given certain simplifying assumptions (e.g., constant τ) that are not especially amenable to incorporation of certain phenomena of interest (e.g., predator-prey interactions). My target audience in this chapter is the other 95% of ecologists. By converting some simple rules for how things change over time into a language a computer can read, we can provide an accessible entry point to understanding the key features of a huge class of ecological models for interacting species. And the underlying high-level processes are strikingly few: drift (as influenced by community size), dispersal, speciation, a few forms of selection, and how these vary across space and time.

Appendix 4.1

Intuitively, the term “negative frequency-dependent selection” explains itself: the fitness advantage of a given species decreases as a function of that species’ frequency. But a monotonic negative function can take many shapes. The qualitative lessons don’t depend on the details (within reason), but computer code requires specific instructions. Because the important parameter is the ratio between species’ fitnesses (rather than the difference), a fitness advantage of 1.2 for species 1 (vs. 1.0 for species 2) does not represent a degree of selective advantage equivalent to the disadvantage represented by a fitness of 0.8. In both cases, the fitness difference is 0.2, but the ratios are not the same. In the first case, species 1 has an advantage of $1.2/1.0 = 1.2$, while in the second case species 2 has an advantage of $1.0/0.8 = 1.25$. A fitness ratio of $1.2^{-1} = 0.833$ provides the same advantage to species 2 that species 1 experiences when the fitness ratio is 1.2. To ensure symmetry of this nature in the relationship between fitness and frequency, we can define it using log ratios as follows:

```
log(fit.ratio) <- freq.dep*(freq.1 - 0.5) + log(fit.ratio.avg)
```

The “- 0.5” serves to define `fit.ratio.avg` as the value of `fit.ratio` when the two species frequencies are equal, as well as the average back-transformed logarithm of the fitness ratio averaged across all frequencies. Calculation of the raw `fit.ratio`, which is needed to calculate `Pr.1`, is as follows (see Online Box 2):

```
fit.ratio <- exp(freq.dep*(freq.1-0.5) + log(fit.ratio.avg))
```

The relationships in the left panels of Fig. 4.3 are slightly curvilinear because `freq.dep` defines a linear relationship with `log(fit.ratio)` rather than with `fit.ratio`. The left panel of Fig. 4.5 shows `log(fit.ratio)` on the y-axis and is thus perfectly linear.