

Forest Structure and Dynamics

Understanding how ecological communities change through time has been a formative challenge in the development of ecology. Early debates focused on succession toward a “climax” state and levels of interdependence among species in a community. More contemporary discussion considers communities as dynamic and non-equilibrial systems, with emphasis on the role of disturbance in shaping communities (see, for example, Acevedo et al. 1996). Debates about forest management underscore the importance of understanding community dynamics, because the nature of forest change determines whether management goals are achievable or even appropriate.

One reason behind debates about community dynamics, particularly in forests, is that change occurs slowly enough that it is difficult to observe directly. Field study often has relied upon spatial comparisons between sites to represent changes in individual sites through time. Representing temporal changes with spatial variation can be misleading, however. If spatial and temporal scales are not matched appropriately, spatial sampling may misrepresent the range or proportion of community states.

This exercise will avoid dangers of spatial analogies. Instead, we will apply temporal information contained in at least two generations of trees found in most forests: mature individuals and their offspring. We will evaluate the transitional nature of the current forest by estimating how much tree species composition might change when current seedlings and saplings become mature trees. We can view further into the future of the forest by analyzing species transition probabilities and the resultant distribution of species abundances. We will use a method originally developed by Henry Horn (1975), and subsequently adapted to study many additional aspects of forest dynamics (e.g., Metcalf et al. 2009; Strigul et al. 2012).

Horn’s model assumes that a forest is a collection of cells, each occupied by a mature tree and a number of young trees. When the mature tree dies, it will be replaced by one of the young trees. The probability that a given species will replace the current mature tree is proportional to the number of young trees of that species present. Consider the following example. Suppose that, of 100 saplings found under a number of mature Douglas fir trees, 40 were western red-cedar, 60 were western hemlock, and zero were Douglas fir. The probability that any given Douglas fir will be replaced by a western red-cedar is $40/100 = 0.40$, by a western hemlock is $60/100 = 0.60$, and by another Douglas fir is zero. Now suppose that such probabilities for all three species are as listed in the following table. Since the table lists probabilities, the sum of values in each row must equal one. The table is a matrix of probabilities of transition from one state (tree species at a given location) to another state.

		<u>Canopy Species</u>		
		Douglas fir	western red-cedar	western hemlock
Sapling Species	Douglas fir	0.10	0.10	0
	western red-cedar	0.40	0.50	0.40
	western hemlock	0.60	0.40	0.60

If you also know the proportion (or number) of each species among mature trees in the current forest, you can predict proportions in the next generation. The predicted number of mature Douglas fir trees in the next generation would be 0.10 times the number of currently mature Douglas firs plus 0.10 times the number of mature western red-cedars plus zero times the number of mature western hemlocks. This procedure can be repeated to predict proportions of each species in successive generations.

Horn’s model is one of the first in a class of models that apply the mathematics of “Markov chains” to describe forest dynamics. Most of the more recent models make extensive use of computer simulations of forests over extensive spatial and temporal scales, although some have used analytical

methods (e.g., Metcalf et al. 2009). We use the simpler version proposed by Horn in order to focus on study of forests in the field. The model makes several predictions that are consistent with our understanding of forest dynamics. First, it predicts the kind of tree occupying a given location will change over time. Second it leads to the same steady state proportions of species starting from a wide variety of initial conditions. Third, it includes the possibility that some early successional trees will persist in the community for long time periods.

Horn's Markov model makes several assumptions about forest dynamics. First, it assumes that transition probabilities are constant in space and time. This restricts appropriate use of the model to forests with similar soils and climates. The model would perform poorly during substantial climatic change. Second, it assumes that the probability of reaching adult size is proportional to sapling frequency. This assumption is equivalent to replacing a currently mature tree by randomly selecting one of the saplings growing beneath it. This assumption would be appropriate if trees were competing for light, but it would be violated if allelopathy influences sapling growth. Third, the model ignores disturbances larger than death of individual trees. This assumption may be violated in our study forest, but it will allow us to evaluate indirectly the role of disturbance.

The Markov model is flexible enough to represent three general views of successional change, reviewed by Gotelli (2008). The three views differ in relationships between the current state of a patch and the state(s) that follow. In the classical **facilitation** model, species in early successional stages alter soil and other environmental conditions that support establishment and growth of species in subsequent stages. This effect corresponds to large transition probabilities in the lower left portion of the matrix. In the **inhibition** model, individuals in the current stage prevent or retard establishment of other species. Inhibition is represented by large values for diagonal elements of the matrix and small values off-diagonal. In the **tolerance** model, species in one successional stage have a neutral effect on species in subsequent stages.

Application to Sehome Arboretum

We will apply this model to describe and forecast changing tree composition in Sehome Arboretum. Constraints on sample size restrict this project to four tree "species:" Douglas fir (*Pseudotsuga menziesii*), bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), and a combination of western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja occidentalis*). The latter two species are combined into one "state" because they share a similar shade tolerance and abundances too low to sample individually. Figure 1 provides a transition diagram for this simplified view of the forest.

Many applications of Markov models of succession focus on steady-state distribution of community states (e.g., Culver 1981). In systems distant from steady state distributions, one must specify the time interval(s) between state transitions to compare model predictions with field data. In this project, we will use two kinds of information to determine transition intervals. First, the forest in Sehome Arboretum began to re-establish about 110 years ago, following complete removal of trees and woody debris in the prior forest. Second, mature trees fall at varying intervals due to several mechanisms. We can estimate the distribution of those intervals by determining the number of large logs relative to standing mature trees.

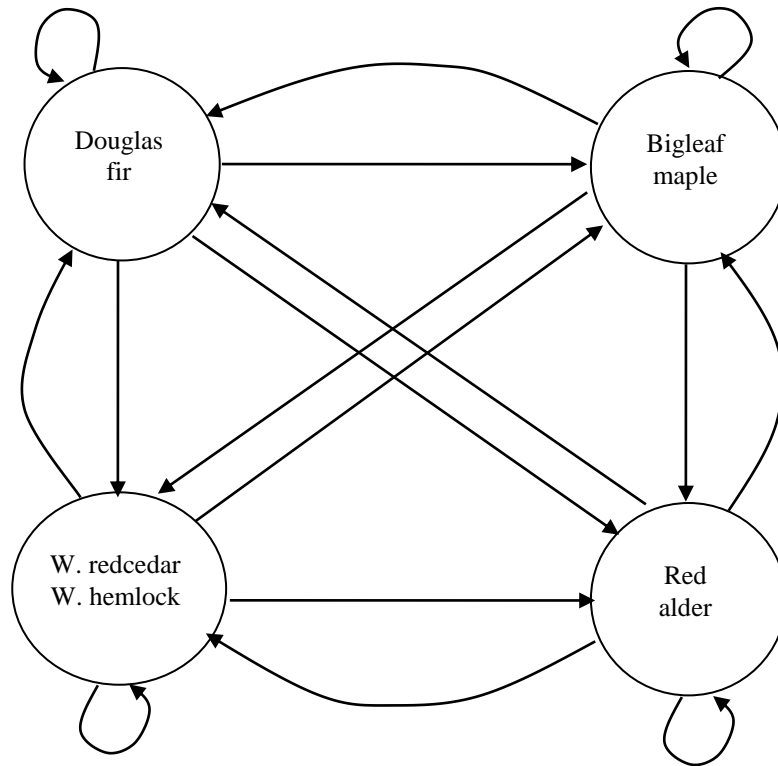


Figure 1 Loop diagram for Sehome Arboretum trees. Some transition probabilities may have values of zero. If all transition probabilities are non-zero, this diagram represents the tolerance model of succession. See Gotelli (2008) for loop diagrams for facilitation and inhibition models.

We will collect data and apply the model to two different kinds of areas within the Arboretum. In the first, most model assumptions are met at least partially, and the model should provide a reasonable approximation for changes in local forest composition. The second area contains one or more disease clusters of laminated root rot (*Phellinus weirii*), a soil-based pathogen that is affecting forest species composition at a coarser scale than Horn’s model assumes. Hardwood species are immune to *Phellinus weirii*, Douglas fir are highly vulnerable, western hemlock is often infected but rarely killed, and western redcedar is seldom infected and rarely killed (Hadfield et al. 1986). Effects of *Phellinus weirii* on forest composition and dynamics are discussed in Norse (1990).

Field Methods

We will collect three kinds of field data. First, we need a count of the total number of mature trees of each species in the study area. Second, we need a count of the number of (large) logs of each tree species in the study area. Define “mature” tree and “large” log as having diameter (dbh) at least 30cm. Third, we need the number of seedlings, saplings, and understory trees of each species present under a random sample of each species of mature (canopy) tree.. This third data set must be extensive and accurate. For this project, ignore shrubs and tree species other than the five listed above. You may find some saplings under the canopy of more than one mature tree; include these saplings with the sample for the nearest mature tree. Forms for recording these data are provided below.

Data Analysis

First, determine the mean patch occupancy time of a mature tree. We will assume that, following complete removal of the prior forest some 110 years ago, young Douglas firs dominated the study areas in rapidly growing stands. Then individual canopy trees began to fall occasionally several decades ago, leading to gap-phase replacement dynamics and more diverse tree species composition. This is the process we will analyze in this project. The average canopy residence time of a mature tree is determined by taking the inverse of the overall annual rate of treefall:

$$\text{rate}_{\text{treefall}} = \frac{\# \text{logs} / \# \text{trees}}{0.5 * T}, \text{ where } T = \text{time interval over which mature trees have been falling.} \quad (1)$$

For this project, assume trees reached mature size, and hence mature trees began falling, 50 years ago. Hence, the inverse of (1) becomes:

$$\Delta t = \frac{25 \text{ yr}}{\# \text{logs} / \# \text{trees}} \quad (2)$$

For example, if you find 10 large logs in a stand with 90 mature trees, then 10 of 100 trees fell within the last 50 years. Using (2), this leads to a projected mean residence time of 250 years/tree.

In study area 1, you recorded 29 logs and 15 trees, for a total of 44 trees 50 years ago. In study area 2a, you recorded 12 logs and 13 trees, for a total of 25 trees 50 years ago. In study area 2b, you recorded zero logs and 28 trees, for a total of 28 trees 50 years ago.

The number of each species in the next generation is predicted by multiplying adult frequencies by transition probabilities. By doing this repeatedly, you can predict species composition in the “climax” community as simulations in Gotelli (2008) show. Equivalent results are obtained as components of the dominant eigenvector for the transition matrix. (Alternatively, you can apply Markov theory to calculate the steady state vectors.) The following example shows predictions for three generations using the transition matrix on the preceding page. We will review how to perform these calculations, how to determine eigenvectors, and working with matrices in general in class.

	Generation 0	Transition Matrix	Generation 1	Generation 2	Generation 3
Df	100	0.00 0.40 0.60	20	28	28
wrc	100	0.10 0.50 0.40	120	116	106
wh	100	0.10 0.30 0.60	160	156	157

You should repeat this calculation for at least five generations, or until your predictions for adult numbers change little from one generation to the next as shown in Gotelli (2008). Alternatively, you can obtain identical information from elements of the dominant eigenvector as shown in class.

Complete the analytical process for both study areas, to provide results where individual tree growth and mortality determines forest composition and dynamics and where mortality by a fungal pathogen drives changes at a coarser scale.

Current abundances of canopy trees, from data collected on 25 January 2017:

Canopy species	Douglas fir	Bigleaf maple	Red alder	cedar/hemlock
Site 1 (root rot)	4	7	2	2
Site 2b (no root rot)	4	4	2	3
Site 2b (no root rot)	28	0	0	0

Transition probabilities estimated from data collected on 25 January 2017:

Study Area 1: root rot disease cluster, East of CF building

sapling species	Canopy species			
	Douglas fir	Bigleaf maple	Red alder	cedar/hemlock
Douglas fir	0	0.02	0	0
Bigleaf maple	0.12	0.07	0.09	0.13
Red alder	0.73	0.81	0.73	0.63
cedar/hemlock	0.15	0.09	0.18	0.25

Study Area 2a: East of Fairhaven College

sapling species	Canopy species			
	Douglas fir	Bigleaf maple	Red alder	cedar/hemlock
Douglas fir	0.50	0.22	0	0
Bigleaf maple	0.50	0	0	0
Red alder	0	0.56	1	0
cedar/hemlock	0	0.22	0	1

Study Area 2b: East of Fairhaven College

sapling species	Canopy species			
	Douglas fir	Bigleaf maple	Red alder	cedar/hemlock
Douglas fir	0.03			
Bigleaf maple	0.72			
Red alder	0.06			
cedar/hemlock	0.19			

Questions and Interpretation

- 1 How do your analyses suggest that the study areas will change in the future?
- 2 What is the predicted steady state, or “climax” composition of the forest stands you studied?
- 3 Are either of the stands you studied at steady state currently? Suggest why or why not. If they are not at steady state, how much time would pass before they reach it?
- 4 Analysis described above assumes disturbance larger than the scale of individual trees is not important. Based on your results, particularly comparisons between the two study areas, evaluate the validity of this assumption.

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Table 1: Tree and log abundances. All trees and logs should measure at least 30cm in diameter.

Study Area 1

Species	# Standing trees	# Logs
Douglas fir		
Bigleaf maple		
Red alder		
Western redcedar		
Western hemlock		

Study Area 2

Species	# Standing trees	# Logs
Douglas fir		
Bigleaf maple		
Red alder		
Western redcedar		
Western hemlock		

