Intermediate Disturbance Hypothesis

Background

The composition of species in an area is not static; ecological succession follows a more or less predictable progression in the species that comprise a local community at different stages. However, because disturbance plays an important role in the composition and structure of ecological communities, one cannot always predict which species will be present when and where. For example, forest communities can be disrupted by fires, blow-downs, floods, and hurricanes. Alpine plant communities can be devastated by landslides or avalanches. Marine systems, such as coral reefs, can be decimated by storms, ravaged by predators, or trashed by inconsiderate tourists. On a smaller scale, many habitats can be disturbed both above and below ground by burrowing creatures such as gophers or moles. All of these ecological disturbances can change the composition of species in a habitat and can also change relative species abundances.

Both the intensity and the frequency of disturbance can influence how the composition of species in an area will change. In general, when disturbance is minimal or rare, then the species that are best at competing with other species for resources will eventually take over. Alternatively, when disturbance is extensive or frequent, then species that are good colonizers or can recover from disturbances rapidly will be at an advantage and will dominate. For example, a forest that has not been disturbed for a long time generally hosts late-successional species of trees and other plants that can grow under low light, but will not include many early-successional plants such as grasses or bushes. If the same area were burned periodically, the trees would rarely have time to become established. Instead, a grassland community comprising species capable of rapid colonization and growth following a fire would dominate.

Species diversity is a measure of how many species occur in an area, and how rare or common each species is. The "intermediate disturbance hypothesis" states that intermediate levels of disturbance will lead to the greatest species diversity. The rationale behind the intermediate disturbance hypothesis is that in low-disturbance environments, a small number of competitively dominant species will take over, and in high-disturbance environments, only species that tolerate disturbance will survive. With intermediate levels of disturbance, neither type of species will be excluded, allowing for higher species diversity. In this lab you will investigate whether the intermediate disturbance hypothesis holds true in a simple model system involving a forest community that is subject to fire.

To complete the lab you will need some way to quantify species diversity. One measure would be just the total number of species in the plot of land you're studying. However, if there are 9991 individuals of one species in the area, and 1 individual each of 9 other species, this is obviously not as diverse as if there are 1000 individuals of each species. Several statistics for measuring diversity have been devised that take into account both the numbers of species and the relative population sizes of each species. This lab uses one called Simpson's index of diversity. Simpson's index uses the population size of each species in the study area to generate a single number indicating diversity. This number will be low when diversity is low (it has a minimum of 1), and will be higher as diversity increases. If you are interested in how the index is calculated, the mathematical formula is below.

Simpson's diversity index:

$$D = \frac{1}{\sum_{i=1}^{S} p_i^{\,2}}$$

where S is the number of species, and pi is the population size of species i divided by the total population size of all species (the proportion of individuals that are of species i). Note that if you look in different sources, Simpson's index may be defined slightly differently. You should be able to find explanations of this index and others in most ecology texts.

Outline of This Lab

In this lab, you will use a computer simulation to investigate a fire-prone forest ecosystem in the eastern part of the United States. The simulated fires burn everything in their paths to the ground. Out of this scorched earth, first grasses and other annual plants spring forth. These colonizers are followed by blackberry bushes and other shrubs, which are in turn followed by white pines, sugar maples, oak trees, and then finally hickory trees, which are the climax species. Fires burn all these species, leaving empty patches where succession starts again. You can vary both the frequency at which fires start and the likelihood that the fire will spread once it starts. In the first part of this lab, you will generate data to test the intermediate disturbance hypothesis. In the second part, you will investigate your own "burning" question about either succession or disturbance.

The Simulation Model

The simulation in this lab is built around a transition matrix — a table with numbers systematically organized in rows and columns comprising the probabilities that an individual from one group will be replaced by one from various other groups in the next time step. For instance, each year there is a chance that a patch of grass will yield to a blackberry bush. There is also a chance that the patch will remain grass. These chances, expressed as probabilities, are determined by underlying ecological processes. Grass might sprout up faster in bare soil than bushes or trees, but over time the bushes and trees may be able grow over and replace the grass. The presence of certain species might also facilitate the growth of certain other species. A transition matrix is used, because it provides a convenient way to organize the probabilities of all possible transitions for each species. Every year, the simulation determines which plant species is present in each square of land, and then uses the "transition probabilities" stored in the matrix to randomly determine what will be in each of the squares the following year.

Exercise 1: The Intermediate Disturbance Hypothesis

[1] Read the introductory sections of the workbook.

[2] Start **SimBio Virtual Labs®** by double-clicking the program icon on your computer or by selecting it from the Start menu.

[3] When the program opens, select the Intermediate Disturbance Hypothesis lab from the **EcoBeaker®** suite.

When the lab opens, you will see several panels:

- The **FOREST** panel (on the left) shows a plot of the forest where you will conduct your experiments; at the beginning this area has been completely cleared of all species.
- The **SPECIES LEGEND** panel (top right) indicates the species in the simulation; the buttons link to the SimBio Virtual Labs Library, where you can find more information about each.
- The GRAPH panel (under the legend) displays the current population size for each plant species or group involved in forest succession. Under the graph, you will see the current value of Simpson's **DIVERSITY INDEX** for the forest.
- The **FIRE CONTROL & SETTINGS** panel (bottom right) allows you to change the frequency and size of fires, and to control other aspects of the simulation later in the lab.

[4] Click the **SPECIES LEGEND** panel to read about the natural history of the various plant species, and then answer the following questions.

[4.1] Which of the following tree species is described as having suffered population declines that have likely resulted from acid pollution? Circle your answer.

White Pine   Sugar Maple   Oak   Hickory

[4.2] Which of the following is/are described as potentially invasive or 'weedy'?

Blackberry Bushes   American Witch-Hazel   Stickywilly

[5] Running the simulation will begin the process of succession. Start running the simulation without any fires by pressing the **GO** button in the Control Panel. Watch the process of succession and note how the graph and Diversity Index change over time.

[6] When the forest has reached equilibrium (nothing is changing much over time), stop the simulation by clicking the **STOP** button in the Control Panel.

[6.1] Briefly describe the pattern of succession you saw over time. Did the Diversity Index change over time? How? Describe in the space below.

[6.2] What was the value of the diversity index when you stopped the simulation? Provide a brief explanation of what this value indicates. (If you are not sure how to interpret the value, review the introductory section of the workbook.)

The next step is to start some fires using the Fire Control panel. The top number in the panel controls the average number of fires that will start in a given year. If this number is less than one, then the value corresponds to the probability that a single fire will start each year. The bottom number determines the chance a fire will spread to adjacent flammable plants; this number ranges from 0 to 1. You will notice that initially the number of fires per year is zero, indicating that no fires start.

[7] Set the average number of fires per year to 0.2 to give a 20% chance of a fire starting each year. Then click the **SET** button.

[8] Reset the simulation so that you start from bare land again by clicking on the **RESET** button in the Control Panel.

[9] Run the simulation again by clicking the **GO** button. You will see small fires cropping up every now and then in different places around the forest, burning down everything in their path and leaving behind a patch of scorched earth.

[9.1] How do the fires influence the pattern of diversity? Describe in the space below.

In the next few exercises, you will use the table below to record the values for Average Number of Fires per Year and Chance of Fire Spreading in the first two columns. In the third column, you will record the value of the Diversity Index. Note that the Diversity Index value may change over time—you will have to decide on a consistent way to measure it. You might, for instance, stop and start the simulation several times (with the **STOP** and **GO** buttons) and record the mean value.

AVG. # FIRES PER YR.	CHANCE OF SPREAD	DIVERSITY VALUE

[10] To test the intermediate disturbance hypothesis, you need to run the simulation at different disturbance levels, recording the diversity for each. Do this first using the Chance of Fire Spreading parameter to manipulate fire size. In the first 5 rows of the table's second column, write down 5 levels (between 0 and 1) for chance of spread that you will try. Be sure to try some high values (e.g. 0.95) so that you have some very large fires. You will leave the Average Number of Fires per Year at 0.2 for each of these runs, so enter 0.2 in the first five rows of the first column.

[11] **RESET** and run the simulation at each level of Chance of Fire Spreading in your table and record the Diversity Index value at each level in the third column of the table.

[11.1] Using the axes below, plot Diversity vs. Chance of Fire Spreading from the values in your table. Be sure to label the axes of the graph.

[12] Next you will investigate how changing the Average Number of Fires per Year influences diversity. In rows 6-10 of the table's first column, write down 5 different levels for this parameter. Pick one value of Chance of Fire Spreading that you think will result in interesting patterns and record that number in rows 6-10 of the second column.

[13] **RESET** and run the simulation for each value of Average Number of Fires per Year in your table, and record the Diversity Index value at each level in the third column.

[13.1] Using the graph axes below, plot Diversity vs. Average Number of Fires per Year, labeling the axes.

[14] **(**Optional) If you have a graphing program, you can create a 3-D plot of diversity vs. both Average Number of Fires per Year and Chance of Fire Spreading. If you do this, you may want to conduct additional simulation runs to fill in that graph more fully.

[14.1] Looking at your graphs, what conclusions can you draw about the role of disturbance in this system? Does your data support the intermediate disturbance hypothesis? Explain.

[15] Click the **TEST YOUR UNDERSTANDING** button in the bottom right corner of the screen and answer the question in the window that pops up.

Exercise 2: On Your Own

The second part of this lab is open-ended, allowing you to experience the entire scientific process on your own. In your study you can change fire size and frequency, as you did above. You can also vary the flammability of species, making some more and some less likely to burn when exposed to fire, and you can vary the rate at which species replace each other in the successional series. Each of these new types of manipulations involves making changes to the simulation model, as described in the next several steps.

Changing the Chance a Species Will Burn if Exposed to Fire

In the real world, species vary in their flammability. For instance, grasses tend to burn very easily, while some trees have bark that protects them against burning.

[1] Choose **'ON YOUR OWN'** from the **SELECT AN EXERCISE** drop-down menu at the top of the screen.

[2] At the bottom right, click the **MODEL SETUP** button to open the Model Setup window.

[3] Select the **FLAMMABILITY** tab at the top of the Model Setup window.

[4] A list of the forest's plant species will appear, with a number next to each that represents its flammability. In this simulation model, 'flammability' is the probability that fire will destroy the individual plant. You will see that the flammability for each species is initially set to 1.0, meaning that all individuals are killed by fires that spread to their locations. To change the flammability of a species, click in the associated box and type the new probability of burning for that species (remembering that probabilities are always between 0 and 1).

[5] As an example, try making hickory trees 90% fire-proof by setting the flammability for this species to 0.1 (so hickory trees have a 10% chance of burning if exposed to fire). When you have changed the value, click the **SET** button.

[6] Set the parameter values for Average Number of Fires per Year and Chance of Fire Spreading in the Fire Control panel to 0.5 (for both) and run the simulation.

[6.1] Under these conditions, do the community dynamics change? Explain in the space below.

Changing the Rate or Pattern of Succession

Recall that succession occurs because some species can colonize bare ground after a fire faster than others, and also because some species grow better when other species are present. These factors are simulated in the model and generate the successional pattern you have been seeing in the lab. The succession in the lab occurs in one direction only—species that are higher in the successional series cannot be replaced by species lower in the series. Furthermore, the rates at which each species replaces the other are fixed. To change the succession process, you must change the transition matrix.

[7] Review the section of the introduction that describes how a transition matrix works.

[8] If the Model Setup window is not already open, click the **MODEL SETUP** button to open it. Select the **TRANSITIONS** tab at the top of this window.

[9] Select **GRASSES** from the drop-down list of species at the top.

[10] Each line in the 'Transitions' table shows the chance that a patch of ground containing Grasses this year will be replaced by some other species in the next year.

For example, the transition probability from Grasses to Annuals is 0.14, meaning that a patch hosting grasses this year has a 14% chance of hosting annuals next year. There is also a 4% chance that it will have Blackberry bushes next year, and an 82% chance that it will remain a patch of grass. Of course, these probabilities must all add up to 1.

[11] Suppose you wanted to add a small (1%) chance that a Grass patch would transition directly to a hickory tree in one year. Find the transition probability 'To Hickory Trees', and change this value to 0.01. You must then subtract 0.01 from one of the other probabilities so that they all sum to 1. Subtract 0.01 from the 'To Grasses' probability (which represents no change), making its value 0.81. Click the **SET** button in the lower right of the Model Setup window to establish these new values. **RESET** the simulation.

[12] Now when you run the simulation, occasionally a patch of grass will be replaced by a hickory tree.

[12.1] How does this change the dynamics of the community?

[13] Another way to change the pattern of succession is to alter settlement, which controls how new individuals become established after a fire. In the real world, this relates to such phenomena as seed dispersal, regrowth from root stock, and germination from the soil's seed bank. To change settlement in the simulation, select the **SETTLEMENT** tab at the top of the Model Setup window. The values on this tab define the probabilities that a newly colonizing plant will be an individual from one of the species listed. By default, new colonizers consist only of Grasses (66%) and Annuals (34%). Change these values and explore how your changes affect the resulting successional dynamics (resetting and rerunning the simulation for each parameter change). You can make notes below about your investigation.

Your Experiment

[14] Now that you have these new tools, your challenge is to come up with a question to ask of this system. The question can be about succession, diversity and its causes, the role of fire in ecological communities, or about any other ecological topic of interest to you that can be addressed with these tools. Next you will conduct the necessary experiment(s) and record your results. When you are done, you will describe your investigation and findings in a written report.

[14.1] Write down your question in the space below.

[14.2] Now rewrite your question in the form of a hypothesis.

[14.3] In the space below, outline some experiments you can do to test your hypothesis using the tools available in this lab. Indicate what data you will collect and how you will use the data (e.g., what comparisons will you make?) to test your hypothesis.

[15] Conduct your experiments using additional paper or your lab notebook to record your data. When you are done, write a short scientific paper summarizing your investigation.

Notes and Comments

Managers for parks and nature reserves regularly deal with issues such as those we explored in this lab. For years it was a common policy to put out fires as soon as they started and not to let any forest burn. More recently, managers have started considering fires and other disturbances as part of the natural processes that help to rejuvenate the land and perhaps lead to a greater diversity of life. This may or may not be due to what we saw in this lab—that having some disturbance (but not too much) creates space for colonizers that normally would be out-competed by other species. Certainly, there are other factors as well. For instance, the seeds of some species of trees will germinate only after a fire has come through. Regardless of what factor is most important, there is no doubt that disturbance is a major factor in structuring ecological communities.

Another result of disturbance you witnessed in this lab was the development of patchy distributions of species. When you look closely at a chunk of land that might look fairly uniform from afar, you may notice that some areas have different collections of species than others. In this simulation model, we saw patches of ground that were just burned had one set of species, and other patches that hadn't been burned in a while had another set of species. Patchy distributions like this can be formed through disturbance, such as in this example, through uneven distributions of some resource in the environment, or through interactions between individuals. For instance, many animals travel in herds, schools, or other groupings, giving rise to patchy distributions of these animals. Among the important causes of patchy distributions in the world today are people—who cut down forests, transform prairies into agricultural fields, and so on, leaving only fragments of the natural habitats. Because species living in habitats that have been fragmented may be at an elevated risk of extinction, conservation biologists are especially interested in they types of dynamics explored in this lab.

References

Ecologists have been studying succession of species after a disturbance for a long time. One of the pioneers in this area wrote the following seminal paper:

Clements, F. E. 1936. Nature and structure of the climax. J. Ecology 24: 252-84. You can find this paper reprinted in: Real, L. A. and J. H. Brown, eds. 1991. *Foundations of ecology : classic papers with commentaries*. University of Chicago Press, Chicago.

Humans create a lot of disturbances. Many prairies probably exist today because of burning by Native Americans. Here's a paper that explores succession after humans clear land in tropical forests and then abandon the land.

Finegan, B. 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *TREE 11: 119-124*

