Intermediate Disturbance Hypothesis

Approximate time to complete: 1 — 2 hours

Background

Most habitats are subject to disturbances. A disturbance can be anything which changes that habitat, usually fairly dramatically. Forests, for instance, are subject to fires and blow-downs. Plants living on sides of hills or mountains get hit by landslides. Similarly, marine systems such as coral reefs can be decimated by storms, ravaged by predators, or trashed by inconsiderate tourists.

Disturbances can change which species live in a habitat, and can also change how common each species is. In general, when there is very little disturbance in some habitat, then the species that are best at competing with other species over the long term will eventually take over. When there is a very high level of disturbance, then species that can recover from a disturbance quickly or colonizing species that can move into a disturbed area quickly will take over. Thus, as the size or frequency of disturbance in an area changes, you will see changes in the distribution of species in that area. For instance, in a forest that has been around for a long time without being burned, you find certain species of trees and other plants that can grow under low light, but you don't find many grasses or bushes. If the same area were burned periodically, then those trees would never get established. Instead, you would get a prairie with grasses and other plants that could quickly move back and grow up fast following a fire.

There is a theory called the *intermediate disturbance hypothesis* that tries to predict how species diversity will change with changing levels of disturbance. Species diversity is some measure of the how many species there are in an area, and how rare or common each species is. A rain forest has a very high species diversity, a temperate forest has not as high species diversity, and the Antarctic has very low species diversity. The intermediate disturbance hypothesis states that intermediate levels of disturbance will lead to the greatest species diversity. This is because, as described above, in a rarely disturbed environment, the most competitively dominant species will take over, and in a very highly disturbed environment, only species that deal with the disturbance well will survive. In the middle, both types of species will be around, thus giving higher species diversity. Or at least that's what this theory would lead you to believe. In this lab we'll check whether this hypothesis really works in a simple model.

Before starting on the lab, we need to decide how we're going to measure species diversity. One way would be to look at the total number of species represented in the plot of land we'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. We'll use one of these here to measure the diversity in the model as we change the level of disturbance.

The diversity index we will look at is called *Simpson's index of diversity*. This index takes as input the population size of each species in the study area, and spits out a single number indicating diversity. This number will be low when diversity is low (it has a minimum of 1), and will get higher as diversity gets higher.

<Optional> For those of you who are mathematically inclined and interested in how the index is calculated, here is the formula:

$$\text{Simpson's diversity index } D = \frac{1}{\sum_{i=1}^{S} p_i^{\,2}}$$

where S is the number of species, and p_i 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 differently. You should be able to find explanations of this index and others in any ecology text.

Outline of This Lab

In this lab, we will look at a forest ecosystem in the eastern part of the United States that is being ravaged by fires. Each time a fire comes through, everything in its path is burned to the ground. Out of this empty earth, first grass and other annual plants spring forth. These are followed by blackberry bushes and other shrubs, then by white pines, sugar maples, oak trees, and finally hickory trees, which are the *climax species.* If there were no fires around, eventually this whole forest would be composed entirely of hickory trees. However, whenever a fire burns an area of the forest, the whole process starts again from scratch.

What we will do is vary the numbers of fires, and how big each fire gets once it starts. This will give us different levels of disturbance of the landscape. For each level of disturbance, we will measure the diversity of species in the forest. From this data, we should be able to say whether the intermediate disturbance hypothesis seems to hold for this model.

<Optional> If you are interested in how the model works, here is a short description. This model is built around a *transition matrix* — a list of probabilities that specifies the chance of an individual from one group becoming an individual from another group in the next time step. In this case, the time steps are years. For instance, every year there is a chance that a patch of ground that had grass growing will now have a blackberry bush. Then the next year, there is a chance that the blackberry bush will be replaced by another shrub, a pine tree, or a maple tree. There is also a chance that the blackberry bush will remain there (no change in what's growing in that piece of land). Each of these chances is gathered together into something called a matrix, which is just a convenient way of organizing all these numbers. Every year, the program goes through each square of land, looks at what's there currently, and then randomly determines what will be there next year according to the probabilities that the plant now occupying the square will be replaced by some other plant.

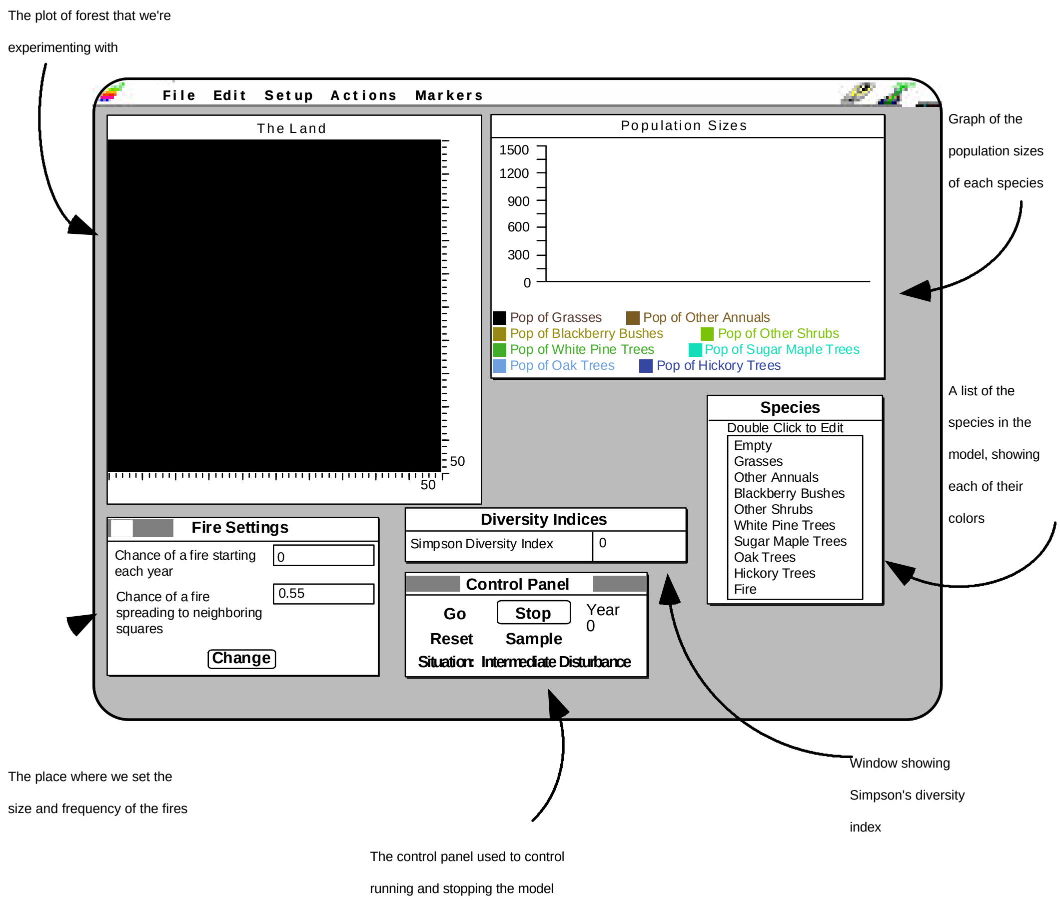
If you want to see how this works in practice, you should read about transition matrices in the manual, and then look at the species setup box for each of the species. To get to the species setup box of a species, find the name of the species in the Species window, and double-click on it. A dialog box will appear, and on the right of the dialog box will be the chance per year that a plant of this species will be replaced by a plant of each of the other species. Note that empty spaces also have a transition matrix. The transition matrix of Empty gives the chance for each of the other plant species to start growing in an empty square (this is colonization).

The Lab

1. Run EcoBeaker (click twice quickly on its icon).

2. Open the situation “Intermediate Disturbance Hyp” (use the ‘Open’ command in the File menu).

You should see several windows laid out on the screen as follows:



The upper-left window shows the plot of forest that we'll be experimenting with. Black indicates land that has just been burned and so is empty of all species. Each plant species has its own color, and these are shown in the Species window in the bottom right. As the model is running, you can see how many individuals of each species are in the forest by looking at the graph of population sizes. Below that is a window that shows the value of Simpson's diversity index, which I discussed in the Background section of this lab. The window at the middle bottom is the Control Panel, which we'll use to control running the simulation, and the final window in the bottom left, Fire Settings, is where we can change the size and frequency of fires.

As you can see in the window showing the forest, the model starts out just after a gigantic fire burned down everything, so that the whole plot of land is empty (black indicates scorched earth). We'll start out by running the model without any fires. What do you think will happen? After the model has run for a while, how diverse do you think the forest will be? (Think about what will happen without fires according to the outline above.) What will the diversity index read (remembering that 1 means a single species and higher numbers mean higher diversity)?

3. Write down your answers to the above questions.

4. Run the simulation (push the 'Go' button in the Control Panel).

5. When the forest has reached an equilibrium (nothing is really changing much), then stop the simulation (push the 'Stop' button in the Control Panel).

6. How good were your predictions?

The next step is to start some fires. Look for a window labeled "Fire Settings" in the lower-left corner of the screen. There you will see two numbers, one the chance that a fire will start in a given year, and the other a number that determines how far on average the fire will spread once it starts. Both these numbers run between 0 and 1. You will notice that currently the chance of a fire starting is set to 0, so there are no fires initially.

7. Set the chance of a fire starting to something between 0 and 1. Then push the 'Change' button to change the settings in the model.

8. Reset the model so that we start from an empty patch of land again (press the 'Reset' button).

9. Run the simulation again (push 'Go').

Now watch what happens in the simulation. You will see little fires cropping up every now and then in different places around the forest, burning down everything in their path. This creates a patchy landscape, with different areas at different stages of recovering from burns, and a few areas that haven't been burned in a while. Patchiness is a big concept in ecology right now, with lots of work being done on whether and when it is significant (see Notes and Comments below).

10. Watch the diversity index until it seems to be more or less stable, or at least hovering around a certain value. Then stop the model, write down the level of disturbance (the chance of a fire starting and the chance of a fire spreading) and the value of the diversity index.

OK, now you have all the tools to test the intermediate disturbance hypothesis. Try out a few different settings for the fires to get a feel for the range of patterns you can get (remembering to push the ‘Change’ button each time you change settings). Then plan out a series of values that you will try with each of those parameters, to increase from low levels of disturbance, to moderate levels of disturbance, to high levels of disturbance.

11. Write down your planned experiments, and what you predict the diversity index will be at each disturbance level (or better yet, draw a predicted graph of diversity versus disturbance level).

12. Perform the experiments you outlined above. At each level of disturbance, write down the values of the parameters and the values of the diversity index.

Note that you are going to have to decide when to measure diversity, since it will go up and down as the fires come and go. So you have to pick some consistent measure of diversity — perhaps averaging it for a few years, or picking a certain year and always measuring in that year, or some other method. You might also note if the diversity varies more at some levels of disturbance than at others.

13. When you have several measurements of diversity at different levels of disturbance, make a graph of diversity versus disturbance level. What level of disturbance gives the most diversity? What level gives the least? Does your data support the intermediate disturbance hypothesis?

More Things to Try

If you want to play further with this model, here are some suggestions. Try playing with the transition matrices, and see both how they affect diversity and how they change the effects of the fires. See my description of transition matrices in the Outline section of this lab or in the manual. For instance, you could speed up the rate of succession by increasing the chance that each species will be replaced by another species higher up in the successional ladder. You could also try adding death to the simulation, by including a small chance that a square that holds a given species this year will be empty next year (set the chance of transition to “Empty” to be something larger than 0). You could also changing the succession so its not just a one way street. In the original model, grass can be replaced by bushes, which can be replaced by trees, but not the other way around (unless a fire comes and clears things out). Forests may indeed work this way, but in other ecosystems this sequence wouldn’t be true. You could try adding in chances for the succession to go “backwards”. With all of these changes, take a look at the effects on diversity if there are no fires, and then run fires at a few different settings, as you did in the lab, to see whether the maximum diversity is achieved at the same setting as before.

Notes and Comments

Managers for park lands and preserves regularly deal with issues such as those we explored here. For years, there was a policy in many parks to try 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 effect may or may not be due to what we saw in this model, that having some disturbance (but not too much) lets in 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. However, regardless of whether the intermediate disturbance hypothesis holds, there is no doubt that disturbance is a major factor in structuring ecological communities.

Another effect you saw in this lab was a patchy distribution of species, or *patchiness* for short. Patchiness just means that when you look closely at a chunk of land that might look fairly uniform from afar, you will see that some parts have different collections of species than others. In this 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 either 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 like to go around in herds, schools, or other groupings, giving patchy distributions of these animals. Among the important creators of patchy distributions in the world today are people, who cut down forests, farm prairies, and so on, leaving only bits and pieces of the native ecosystems. Thus conservation biologists are also very interested in the effects of patchiness and how to deal with them.. If you're interested, there are other EcoBeaker labs that explore the effects of disturbance and the effects of patchiness.