Using a multi-site, student-collected data to explore forest species composition and dynamics: a computer lab exercise.

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***Presented at REEFS: Resources for Ecology Education, Fair and Share at ESA Annual Meeting in Fort Lauderdale, FL August 2016.***

# Forest Species Composition:

# *Seeing the forest for the trees*

**Intended Learning Outcomes**

On completion of this laboratory exercise students will be able to

* Represent tree community data in graphic form
* Analyze species composition across multiple forests
* Articulate community composition dynamics

**Schedule**

1-hour: Developing Research Questions

3-hours: Data Analysis

**Introduction**

 In this lab, students will learn foundational concepts of forest community dynamics and apply quantitative skills to data analysis and interpretation activities. Students will use species data collected from four different forests in three states. The data were generated from a shared method protocol (Kuers et al. 2014) and database of the Permanent Forest Plot Project (PFPP) of the Ecological Research as Education Network (EREN; www.erenweb.org). Here, students will analyze and interpret data to articulate forest species composition dynamics. This lab is designed to train students in *real-world* skills and experiences of a collaborative ecologist.

**Background**

**I. A Few Key Concepts in Forest Ecology**

**Species Composition**

***Species composition*** is the identities and abundances of all the species in a community or area. A ***community*** is a group of organisms of different species living and influencing each other in one area. Interactions between members of a community can change its species composition over time (Connell and Slatyer 1977). Because species hold different ecological roles, knowing the identity of species is as important as knowing how many different species are in an area. We often depict species composition in graphical form, so that we can assess species composition in an area and compare species compositions among areas. In the example species composition figures below, you can see that each site has the same species, but in different abundances (Fig. 1). The top figure depicts an oak-hickory forest (i.e., oaks and hickories are the most abundant of all of the canopy trees). The bottom figure represents a beech-sugar maple forest. Knowing what the most abundant canopy trees are gives us information about what other species may be in the forest, soil quality and moisture, and successional stage.

 

**Figure 1. Example species composition figures.**

**Foundation species**

Species hold different roles in communities and some species contribute more to the ecosystem functioning of a community than other species do. Species that have strong influences on communities are called ***foundational species*** and can operate in different ways (Ellison et al. 2005). Here are some examples.

● ***Dominant species*** are very good competitors and can competitively exclude other species (Grime 1984). Because dominant species are good competitors, they tend to be very abundant. Being abundant means that they may influence the dynamics of a community more than if they were less abundant (Clements et al. 1929). Dominant species are often the most numerous species in a particular canopy layer.

● ***Structural species*** best fit the role of trees in the forest. These species create the structure of the ecosystem just as coral creates the coral reefs. Trees not only provide the structure of forests, but also play a dominant role in controlling nutrient flow, creating habitat, and affecting the physical environment (a forest floor has less sunlight and less wind than an open field) (Huston 1994).

**Forest Vertical Structure**

Forests are made up of *vertical layers* and are created by the trees and other plants that grow to different heights. Trees can have different ecological roles depending on which layer they are in. The tallest trees in the forest are dominant trees. These trees have crowns that emerge above the main canopy of the forest. Codominant trees have crowns that make up the main portion of the canopy. Together dominant and codominant trees make up the overstory of a forest and tend to have the largest trunk diameters. The midstory of a forest is made up of intermediate trees whose crowns enter into the main canopy, but do not reach the top of the main canopy. Overtopped trees are also part of the midstory and are taller than 1.37 m tall (the height at which we measure tree diameter: DBH), but shorter than the main canopy. The understory of a forest are all plants shorter than 1.37 m tall, and is usually the most diverse forest layer because it contains tree seedlings, shrubs, and herbaceous species. See the different terms used in each forest vertical layer in Figure 2.



 **Figure 2. Diagram of vertical forest structure and terms.**

We can use tree diameter as a surrogate for which vertical layer a tree is in. Overstory trees (dominant and codominant) tend to have the largest diameter, Intermediate trees have smaller diameters, and overtopped trees have the smallest diameters as is evident from the forest plots in Bennett Springs and Timberview (Figure 3).

Each species fills a different niche, which can help in assessing forest dynamics. Most trees are not reproductive until they reach codominant or dominant crown class (i.e., overstory). Tree species adapted to the midstory may never grow taller than the intermediate crown class. When assessing the midstory of a forest it is important to know which individuals are “just passing through” on their way to the canopy and which ones are fully mature. In the Species List at the end of the lab exercise, species that reproduce in the midstory and canopy are noted (Appendix 1).

A wide variety of factors control forest structure. Physical characteristics such as topography, soil type, and aspect can determine the type of forest structure. Aspect is the compass direction the slope is facing (i.e., north vs. south facing slope). What affect do you think aspect would have on forest structure and why? Disturbance regimes (such as frequent fire) can cause open midstories, whereas fire suppression can cause thick sapling and shrub layers to develop.

The complexity of the vertical structure and the number and abundance of species in a forest impacts the animal composition of a forest. For example, the acorns produced by oak trees can support numerous animal populations including weevils, blue jays, white-tailed deer, and black bear. Higher tree diversity may provide more complex habitat allowing more animal species to thrive.

 ***A note about terminology*** -- Before we move on, note that in the above sections, **dominant** was used in two different ways. ***A dominant species*** is one that is a good competitor and is often in high abundance. ***A dominant tree*** is a tree that is among the tallest in the forest.

 

**Figure 3. Mean DBH (± 1 StDev) of trees in each crown class (Dominant and codominant (DC), intermediate (I) and overtopped (O)) at two sites in Virginia.** **The DC trees (the tallest trees in the forest) had the largest DBH. DC trees also had high standard deviations because there were some very large diameter trees in this category (e.g. 107 cm).**

**Ecological Succession in Forests**

Community species composition is constantly changing in forested ecosystems and is largely driven by the changes in tree species composition. This process of continual change is called ***ecological succession***. The understanding of ecological succession is a key element in restoring communities and ecosystems after natural or anthropogenic disturbances.

The historical view of ecological succession was that it was orderly and predictable (Cowles 1889, Clements 1936, Connell and Slatyer 1977, Odum 1969). According to this view, a predetermined sequence of communities would replace one another leading toward a final, self-replacing community called the climax. Studies of succession following glacial retreats, massive deposition of volcanic ash, or creation of new sand dunes all revealed a progression of species composition over time that followed consistent trends. These are examples of ***primary succession***, in which the communities assemble without any significant influence of prior communities.

Far more common is ***secondary succession***, community change following a lesser disturbance such as forest fire, hurricane damage, or tree diseases, as well as reversion of an agricultural area to forest. In these cases the prior community can have an important effect on the course of succession. There are a huge number of factors that can influence the course of secondary succession, many environmental (Gleason 1926), and the sequence of species composition change is not so easily predicted (Turner et al. 1998). Of current interest is how global climate change will potentially shift the geographic range of tree species due to changing environmental conditions, such as temperature and rainfall. For example, Johnstone and Chapin (2003) found the northward expansion of lodgepole pine (*Pinus contorta*) to not be in equilibrium with the current climate.

Examining the species composition of trees in different size classes (e.g., using DBH) can indicate whether a forest is undergoing shade tolerance succession. In secondary succession, ***early successional species*** are those whose seedlings grow fast in high light conditions and dominate early after a disturbance. When they become adults, their shade prevents their own seedlings to thrive, making them ***shade intolerant species***. ***Shade tolerant species***,seedlings that survive in lower light environments, become more abundant as they replace the early successional species, making them ***intermediate successional species***. In time, the most abundant large trees in a forest are the ***late successional species*** whose seedlings can tolerate the lowest light conditions. Therefore the shade tolerant model of succession would predict early successional species (e.g., pines, yellow-poplar, aspen) to be replaced by intermediate successional species (e.g., oaks, red maple, black cherry) to be replaced by late successional species (e.g., sugar maple, American beech, eastern hemlock; Appendix 1).

**II. Ecological Research as Education Network (EREN)**

 Read about EREN on the web page: http://erenweb.org/project/rcn-project/

A. Start with the “About” tab and read

1. The Missions and Goals

2. Look around the rest of the web pages.

3. Find where the PFPP (Permanent Forest Plot Project) is described and read about it.

B. Take what you read and summarize what EREN and PFPP are about (in your words; don’t copy and paste). Answer in a well-developed paragraph and include in your answer what the acronym EREN stands for.

**III. Study Sites**

Carvins Cove Nature Reserve is a 4,500 ha of protected forest surrounding a 320 ha Reservoir in Roanoke County, VA ([http://www.roanokeoutside.com/carvinscov](http://www.roanokeoutside.com/carvinscove)e). There are four research plots at each of two research sites: Timberview and Bennett Springs. Timberview is an upland site on acidic soils (pH mean 4.5) whereas Bennett Springs is in a floodplain with seasonal standing water and higher pH (mean 6.5). Roanoke College students established the Timberview plots in 2011 and the Bennett Springs plots in 2012. The four plots at each site are about 20-60 m apart in the same forest type making them replicate plots for each site. Therefore, all the trees in an 800 m2 area was measured at each site (Timberview and Bennett Springs).

The Colby College Cross-Country Trails study site, in Waterville, Maine, consists of open field with tall grass and mostly wooded area with maple, birch, aspen and oak trees. The forest was logged and began regeneration in 1950. The study location falls within a humid temperate climate and receives an average of 910 cm of annual precipitation. The Colby College location has 5 separate study sites with six plots within each study site (3 with invasive species removed and 3 control) for a total of 30 plots - three control plots were used for this data exercise, for a total analysis area of 1200 m2. All plots are interior forest plots, lie under 100 m in elevation, and are in the Buxton Silt Loam soil order. Invasive species found within the plots include *Rhamnus cathartica, Rosa multiflora, Celastrus orbiculatus,* and *Lonicera morrowii*.

The Macalester College study site is located 27 km from St. Paul at the Katharine Ordway Natural History Study Area in Inver Grove Heights, MN. The 113 ha reserve is comprised of eastern broadleaf continental forest with an average of 634 cm of annual precipitation, and is situated along the Mississippi River. The Macalester College location has a total of 12 plots within this one study site - four plots were used for this data exercies, for a total analysis area of 1600 m2. All plots are interior forest plots, situated at approximately 230 m in elevation, and contain alfisol soils. Invasive species found within the plots include honeysuckle, buckthorn, and garlic mustard.



 **Figure 4. Map of the study site locations.** (Google Maps)

 **Developing Research Questions/ Hypotheses**

Using resources from class or group discussions, lectures, and readings, develop your research question or hypothesis below. To test your hypotheses, you will be provided datasets from four forests that include the species name, DBH and size class for each tree identified. Be sure to explain the ecology that led you to these questions or hypotheses. This information will be very helpful when you interpret your results.

**Data Analysis**

**I. Overview of Datasets**

The dataset file contains data on 801 different trees that were located in 15 different 400 m2 plots across the four study sites described above. The data columns from the PFPP datasets are: the institution where the data were collected, the site name, plot name, tree number, inventory status, stem type (single or multi-stemmed), species code (see Appendix A for full names and vertical layer), diameter in cm at breast height (DBH), and soundness. These data only include trees that were given the inventory status of *initial living*. Dead trees were excluded because dead trees will not contributing to the future species composition. The column of DBH class was added and the classes are as follows, small: 2.5-7.9 DBH, intermediate: 8-17.9 DBH, and large >18.0 DBH. Find a full description of data collection methods in the PFPP Protocol (Kuers et al. 2014). Each site is on a different worksheet in the Excel data file.

**II. Download Data**

1. Your instructor will tell you where to access the file **EREN Species Composition Data**.

2. Download it and save it under a different name that way if you end up downloading the data again, it will not overwrite the file you have been working on.

3. Open the file and notice that there are four worksheets; one for each site. Your instructor will tell you which or how many of the sites you will be working with.

4. Each worksheet has ten columns of data: institution where the data were collected; the site name where the plots were located; plot names for the 400m2 areas where the trees were measured; tree number - the number on the metal tag nailed to each tree; stem type - single stem or multi-stem; species code - see the species list in appendix 1; dbh - diameter of each tree in cm; soundness is a measure of how much rot is in a tree; DBH class as described above.

**III. Making a Species Composition Figure**

*You will use Pivot Tables to summarize the total number of trees by species and DBH class.*

1. Go to the worksheet for the first site for which you are making a species composition figure.

2. Select all of the data including the header row.

a. Make sure you have not selected any empty rows or columns

3. Go to the **Insert** tab along the top

4. Select **Pivot Tables** (it is all the way to the left under Insert)

5. Click **OK** (the pivot table will be entered into a new worksheet - be sure to label the new worksheet according to the site location you are working on)

6. Move

a. **DBH class** into the **Column Labels**,

b. **species code** into **Row Labels**

c. **species code** into **Ʃ Values**.

7. Make sure under **Ʃ Values** it says **Count of species code**.

*This pivot table has added up all the trees in each species by DBH class. Take the time to figure out what Excel is doing. That way you will learn how to use and apply pivot tables to other tasks. In this lab, we will not use Grand Totals because you cannot always tell what they are (sums, means, etc.)*

*The data in the pivot tables are hardwired back to the original data. You are now going to copy and paste the data using the following procedure to break that link so that you can manipulate the data.*

8. Select all the species names and the values for all the DBH classes.

a. Do not select any header or grand totals.

9. Copy

10. Highlight a cell in column A, a couple of rows down from your pivot table

11. Right click on that cell and choose **Paste Special…**

a. Select **Values**

b. Click **OK**

c. Write some notes in the margin here on what you did so you can remember for next time.

d. You may need to adjust the column widths so that you can see the data better.

*Next, you are going to move the data around and sort the data so that your species composition figure shows the LARGE DBH trees in the first and in descending abundance*.

12. In the cell above the first species, write the site name (e.g., Colby College) so you don’t forget.

13. In the row above the numbers you copied, type in the correct size class by looking at your original data (i.e., Intermediate, Large, Small)

14. Using the **Copy** and **Paste** functions, rearrange the columns so that they are in descending order (Large, Intermediate, Small)

15. Lastly, you will sort your data

a. To sort, select all your data and your header row.

b. Go **Data** in the menu bar at the top

c. Select **Sort** (be sure to check the box, my data has headers)

d. Sort by **LARGE** from **Largest to Smallest**

*Next you will make your figure.*

16. Select all of your data and your header row.

a. Go to **Insert** and select **Chart**

b. Choose the first **Column** figure

c. Work on formatting your figure so that it is similar to Figure 5.

17. Copy and paste it into a Word document (portrait), where you will add a great figure legend.

**IV. Additional Figures**

If you were assigned to make additional species composition figures return to step III 1.



**Figure 5. Species Composition**……. Write a really good figure legend remember to use the correct units on your y axis label.

**V. Interpreting Species Composition Figures**

1. Before you interpret the data in your species composition figure, practice on figure 5.

a. What type of forest is this?

i. Typically the most abundant, large trees determine the forest type. Of the trees in the large diameter size class, which three species are the most abundant? Use the species list in Appendix 1 to help.

b. Are these species likely to persist as the most dominant large trees in the future?

 i. To answer this question look to see how abundant the intermediate and small diameter trees of these species are compared to other species. Are there species with more intermediate and small diameter trees?

c. Is the species composition of this forest likely staying the same or changing? Does the pattern of change follow the predictions from the concepts of succession or failed oak regeneration or another concept you learned about?

d. Discuss your answers with other students and your instructor.

e. Now, use this approach to analyze the species composition in the figures you made to articulate the forest dynamics that may be operating.

**Literature Cited**

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Footnotes for Appendix 1.

\*Indicates no native species
^Canopy species mature and usually reproduce at codominant or dominant size. Midstory species mature and usually reproduce as an overtopped or intermediate size and rarely reach codominant size.
# Shade tolerance of seedlings. Low is indicative of an early successional species; intermediate is indicative of intermediate successional stage, and high is indicative of late successional species.

**Appendix 1: Species List**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Species Code | Scientific name | common name | mature size^ | Shade tolerance# |
| ABIBAL | Abies balsamea | balsam fir | Canopy |  |
| ACENEG | Acer negundo | boxelder | Canopy |  |
| ACERUB | Acer rubrum | red maple | Canopy | Intermediate |
| ACESAC | Acer saccharum | sugar maple | Canopy | High  |
| ALNINCR | Alnus incana subsp. rugosa | speckled alder | Canopy |  |
| AMEARB | Amelanchier arborea | downy serviceberry | Midstory |  |
| BETPAP | Betula papyrifera | paper birch | Canopy | Low  |
| BETPOP | Betula populifolia | gray birch | Canopy | Low  |
| CAROVA | Carya ovata | shagbark hickory | Canopy | Intermediate |
| CARSPP | Carya spp | hickory spp. | Canopy | Intermediate |
| CARTOM | Carya tomentosa | mockernut hickory | Canopy |  |
| CELOCC | Celtis occidentalis | hackberry | Canopy |  |
| CERCAN | Cercis canadensis | eastern redbud | Midstory |  |
| CORAMO | Cornus amomum | silky dogwood | Midstory |  |
| CORFLO | Cornus florida | flowering dogwood | Midstory |  |
| FAGGRA | Fagus grandifolia | American beech | Canopy | High |
| FRAAME | Fraxinus americana | white ash | Canopy | Intermediate |
| FRANIG | Fraxinus nigra | black ash | Canopy | Intermediate |
| FRAPEN | Fraxinus pennsylvanica | green ash | Canopy | Intermediate |
| HAMVIR | Hamamelis virginiana | witch-hazel | Midstory |  |
| LIRTUL | Liriodendron tulipifera | yellow-poplar | Canopy | Low |
| MAGACU | Magnolia acuminata | cucumber magnolia | Canopy |  |
| MALSPP | Malus spp | crabapple species | Midstory |  |
| NYSSYL | Nyssa sylvatica | black tupelo | Midstory |  |
| OSTVIR | Ostrya virginiana | eastern hophornbeam | Midstory |  |
| OXYARB | Oxydendrum arboreum | sourwood | Canopy |  |
| PINECH | Pinus echinata | shortleaf pine | Canopy | Low |
| PINSTR | Pinus strobus | eastern white pine | Canopy | Low |
| PINVIR | Pinus virginiana | Virginia pine | Canopy | Low |
| PLAOCC | Platanus occidentalis | sycamore | Canopy |  |
| POPGRA | Populus grandidentata | bigtooth aspen | Canopy | Low |
| POPTRE | Populus tremuloides | quaking aspen | Canopy | Low |
| PRUAVI | Prunus avium | sweet cherry | Canopy |  |
| PRUSER | Prunus serotina | black cherry | Canopy | Intermediate |
| PRUVIR | Prunus virginiana | chokecherry | Canopy |  |
| QUEALB | Quercus alba | white oak | Canopy | Intermediate |
| QUEELL | Quercus ellipsoidalis | northern pin oak | Canopy | Intermediate |
| QUEMAC | Quercus macrocarpa | bur oak | Canopy | Intermediate |
| QUEMON | Quercus montana | chestnut oak | Canopy | Intermediate |
| QUERUB | Quercus rubra | northern red oak | Canopy | Intermediate |
| QUEVEL | Quercus velutina | black oak | Canopy | Intermediate |
| RHACAT | Rhamnus cathartica | common buckthorn\* | Midstory |  |
| TSUCAN | Tsuga canadensis | eastern hemlock | Canopy | High |
| ULMAME | Ulmus americana | American elm | Canopy | Intermediate |
| UNKSPP | Unknown species | Unknown species | Canopy |  |
| VIBPRU | Viburnun prunifolium | blackhaw | Midstory |  |
| VITRIP | Vitis riparia | Riverbank grape | Canopy |  |
| VITSPP | Vitis spp | grape vine | Canopy |  |
| ZANAME | Zanthoxylum americanum | Prickly ash | Canopy |  |

# Forest Species Composition:

# *Seeing the forest for the trees*

Instructor Notes

**Theoretical Framework, Research Question and Hypothesis Development**

Before students can develop hypotheses or research questions, instructors need to determine which theoretical framework they will use for this exercise. Here we provide three alternative theoretical frameworks and corresponding research articles that instructors can select from to help students develop research questions or hypotheses. Instructors may want to assign readings before the data analysis is done in class. The data analysis and figure construction sections described below can be used for all three frameworks.

A. General Research Questions:

The most general approach to these data would be to have the student compare whether species composition appears to be changing among the sites.

*Possible Research Questions*

Is there evidence that species composition is changing at any one site? Is there evidence that species composition is changing across sites in the same way?

*Background Reading*

The instructor should review with students the key background concepts of species composition, how canopy trees are dominant and structural species in forest communities, and that canopy trees have larger diameters (concepts included in student instructions). The instructor could assign Elliston et al. 2005 to reinforce these concepts.

Elliston *et al*. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479-486.

This review article introduces/reinforces the concept that species affect other species/habitat can occur in functional categories: **foundation species**, **core species**, **dominant species, keystone predators, structural species, and ecosystem engineers.** The instructor could steer students to think about oaks as structural or dominant species. Students can then use these concepts to consider how shifting species composition and structure alters forest ecosystem function.

*Interpreting Results*

 Instructors can use the same interpretation outlined below in the failed oak regeneration (Framework B), focusing not on oak and red maple, but rather what the most abundant large trees are in each forest location. Are these abundant large tree species likely increasing or decreasing in abundance, and which tree species may be replacing them?

B. Failed Oak Regeneration

Prominent in the forestry literature are the concepts of “failed oak regeneration” and the increase in red maple abundance (Abrams 1998, Collins and Carson 2004). Oaks have higher economic value and arguably greater ecological value then maples. Therefore, many researchers have focused on examining this shift in species composition, possible causes, and management solutions (Iverson et al. 2005). Using species composition figures from each site separately, we can see if there is evidence that species composition may be changing.

*Possible Research Question*

 Is red maple replacing oak in the forest canopy of four different forests?

To address this question we can use the assumption that the abundance of any one canopy species is

1. stable if the abundance of that species is relatively the same across diameter classes

2. decreasing if there are a lot more large diameter trees than smaller diameter trees

3. increasing if there are a lot more smaller diameter trees than large diameter trees.

*Background Reading*

To introduce the concepts of failed oak regeneration and the increase in abundance of red maple in eastern forests, I assign the following papers. I divide the class into three groups. Each group reads one paper. In class, each group discusses their paper to make sure they understand the main points as it relates to oak and red maple abundance. Then the groups reform such that there are students who are experts on each paper in each group and they teach their paper to the other students.

Abrams, Mark 1998. The Red Maple Paradox: What explains the widespread expansion of red maple in eastern forests? BioScience 48:355-364.

The article describes the pattern of increasing red maple in eastern forests and suggests that phenology and physiology makes this species a *super-specialist* - it can thrive in many conditions. The evidence is circumstantial but does a good job at laying the groundwork for students. This review contains a lot of information and uses some forestry terms that students may not be familiar with.

Collins, R and W. Carson. 2004. The effects of environment and life state on *Quercus* abundance in the eastern deciduous forest, USA. Are sapling densities most responsive to environmental gradients? Forest Ecology and Management 201: 241-258.

The authors conduct a review and an observational study of which site conditions and demographic factors are correlated with the abundances of oaks across life stage. The upshot is that sapling-sized oaks abundances (tomorrow’s adults) are not correlated with today’s adult abundances. This study suggests that the relative abundance of oaks in oak forests will decline in the future because of a lack of juvenile oaks.

Iverson, L, T. Hutchinson, A. Prasad and M. Peters. 2005. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7 – year results. Forest Ecology and Management 255: 3025-3050.

This primary literature article reviews the case for failed oak regeneration then demonstrates through experiments that fire reduces the relative abundance of red maple and promotes the relative abundance of oaks. Thus, one explanation for the replacement of oaks with red maple in eastern forests is fire suppression.

*Interpreting the results:*

Timberview Plots: This is an oak forest. The three most abundant large diameter trees are black, white, and chestnut oak. There are very few intermediate and small diameter oaks suggesting that these oaks are not replacing themselves in the canopy. Red maple has higher abundances of intermediate and small diameters than large diameters suggesting that red maple is increasing in abundance here. So to address the research question: Yes it appears that red maples are replacing oaks

Macalester College Plots: This is also an oak forest with northern red oak as the most common large diameter species and the four most abundant large diameter species are all oak. Like Timberview, there are few intermediate and small diameter oaks suggesting that oaks are decreasing in the canopy. There are no red maple in this forest so red maple is not increasing. Instead American elm and black cherry have many more intermediate and small diameter trees compared to large diameter trees suggesting that these two species are increasing in abundance. So to address the research question: Yes it appears that oaks are being replaced, but they appear to be being replace by black cherry and American elm, not red maple. Therefore, an increase in red maples is not occurring everywhere in eastern forests.

 Colby College Plots: This is not an oak stand. Aspen is the dominant large tree in this forest far outnumbering other large diameter trees. Northern red oak has many more small diameter trees than large diameter trees so it appears to be increasing in abundance in this forest (along with white ash). Red maple may have just started to invade this forest, it has some small diameter trees. So to address the research question: Is red maple replacing oaks? No, this is not an oak forest, northern red oak appears to be increasing in abundance, and red maple may also be increasing but is a much less common species. Time will tell if red maple replaces oaks in the future but it is not right now. Northern red oak appears to be regenerating well, therefore northern red oak is not failing to regenerate everywhere.

 Bennett Springs Plots: This is also not an oak forest but rather a mixed mesophytic, earlier successional forest, with white ash, Virginia pine, and sycamore as the most abundant largest diameter trees. White ash appears to be replacing itself because all diameter classes are of similar abundances. The most abundant smaller diameter trees are redbud, dogwood, witch hazel, eastern hophornbeam, and blackhaw. All of these are midstory species that will not reach the canopy, therefore they will not replace any of the canopy trees. Northern red oak has low abundance at this site, but has more small diameter trees than large diameter trees suggesting that it may be increasing in abundance. Red maple is the fifth most abundant canopy tree and has higher abundance of intermediate and small diameter trees than large diameter trees suggesting that it is increasing in abundance. So to address the research question: this is not an oak forest, red maple is increasing, but may not be replacing the most abundant large diameter tree because it (white ash) seems to be replacing itself. Oak is a minor component this forest community and likely will remain that way.

C. Ecological Succession in Forests

These data can be used to explore ecological succession in forests tree species. The section on succession in the background will give students a great jumping off point. It is certainly true that many factors influence successional patterns and prominent among them are past land use history, disturbance history, and abundance of white-tailed deer. The effect of land use history on succession means that different forests even if they are close together may have a different successional dynamics. This can make succession seem site specific and idiosyncratic. Nonetheless, there are mechanisms that drive succession and even through the noise of land use history and other factors, we can still see a predictable replacement of tree species over time. In the eastern deciduous forests and in some tropical wet forests, the mechanisms that often drives forest succession is shade tolerance. Tree species differ in the degree to which their seedlings and saplings can tolerate shade. Therefore in early secondary succession forest are dominated by species whose seedlings can grow fast in high light. When the adults grow up and shade the understory, the seedling and sapling layer will become dominated by species whose seedlings can tolerate some shade. In late successional forests the most abundant tree species tend to be those whose seedlings can tolerate shade and wait for a small disturbance or a canopy gap opening to then grow to fill the gap and reach the canopy. Therefore if a forest were undergoing succession via shade tolerance, we would expect that if the most abundant large trees are either early or intermediate successional species that there would be few small trees of that species. And we would expect that the most abundant small trees would be later successional species. If some other mechanism is operating, than we might see intermediate trees species being replaced by other intermediate tree species, for example.

*Possible Research Question/Hypothesis*

* Are the four forests all exhibiting a shade tolerance model of succession?
* In all four forests, early successional species will be most abundant in the large diameter class and later successional species will be the most abundant species in the small diameter class because late successional species have seedlings that are more shade tolerant.

*Interpreting the results*

Timberview Plots: The three most abundant large diameter trees are black, white, and chestnut oak, which are generally intermediate in shade tolerance and successional stage. Red maple has higher abundances of intermediate and small diameters than large diameters suggesting that red maple is increasing in abundance here, which is also intermediate in shade tolerance. Therefore it does not seem like the shade tolerance model of succession is operating here.

Macalester College Plots: This is also an oak forest with northern red oak as the most common large diameter species and the four most abundant large diameter species are all oak. American elm and black cherry have many more intermediate and small diameter trees compared to large diameter trees suggesting that these two species are increasing in abundance. So here again we have an intermediate shade tolerance and successional stage species that seems to be being replaced by two other intermediate shade tolerant and successional stage species. Therefore, the species composition at this forest does not support the shade tolerance model of succession.

 Colby College Plots: Aspen is the dominant large tree in this forest far outnumbering other large diameter trees. Northern red oak has many more small diameter trees than large diameter trees so it appears to be increasing in abundance in this forest (along with white ash). Because aspen is an early successional species and northern red oak and white ash are intermediate successional species, then this forest does appear to be following the shade tolerance model of succession.

 Bennett Springs Plots: White ash, Virginia pine, and sycamore are the most abundant largest diameter trees. White ash appears to be replacing itself because all diameter classes are of similar abundances. The most abundant smaller diameter trees are redbud, dogwood, witch hazel, eastern hophornbeam, and blackhaw. All of these are midstory species that will not reach the canopy, therefore they will not replace any of the canopy trees. Red maple (another intermediate successional stage tree) may be increasing in abundance as well. Therefore, this forest does not appear to be following the shade tolerance model of succession.

 So, what does it mean that we only find evidence for a shade tolerance model of succession in one of three forests? Likely because some other factor is playing a stronger role in determining changes in forest dynamics. Students could speculate on what those might be based on papers they read or other lecture materials the instructor builds in.

In recent decades, ecologists have been moving from an equilibrium view of ecology (shade tolerance model) to a non-equilibrium view. During this transition there has been a range of views on ecology and how ecological information can best be used to support good environmental management (Moore *et al*. 2009). The type of questions that can be asked in the context of this laboratory exercise are thus timely and reflective of the current research in ecology.

**Data Analysis**

 Having each student create a species composition figure for each of the four sites may be tedious for the students. Consider whether you want each student to choose (or your assign) two sites to do. Or consider having four students work together where each student does one species composition figure that they all share.

 Instructors may want to give students a pep talk about quantitative analyses along the lines of : *Learning new quantitative skills can be hard and it can be frustrating. But such skills are very important in this day and age. Step by step instructions are a great way to learn new techniques, but they still can be challenging the first time through. Ask for help and keep a positive attitude. Commonly when researchers analyze data they end up having to go back and start again because of mistakes or technical problems. It is part of the process. Here are some suggestions for smooth data analysis: rename and save your data file when you first download it, save it often, read several steps ahead, then go back and do those steps, and when you figure out how to do something make a note to yourself in the margins of this document. Also know that these instructions are written for a current PC version of Excel. Your version may be different, but should have the same functionalities that are in these instructions. You may need to look for some functions in different places.*

 These instructions are written for the student who knows some basics about Excel (how to move between worksheets, how to copy and paste). They are also written so that students will have to figure some things out. Students with a lot of Excel experience will move quickly; those with less experience will likely need more help.

**Interpreting Results**

Figure 5 is showing both failed oak regeneration and shade tolerant succession. This is an oak stand with the most abundant large trees being: white, northern red and northern pin oak. There are relatively fewer intermediate or small oaks compare large oaks, although there are just as many intermediate white oaks as red maples. The most abundant small diameter species are red maple and sugar maple. Therefore it appears that red maples are replacing oaks (failed oak regeneration) and that sugar maple are replacing oaks (shade tolerant succession). These data a not clear cut which is typical in ecological data but we can see apparent patterns.

**Assignment**

This exercise lends itself well to having the students turn in the figures that they made using the format that you assigned and writing a two or three page interpretation, where they interpret their results in terms of the research questions/hypotheses that they developed in the beginning. They can bring in information from the articles that they read to help support their interpretation. In doing so hopefully they will articulate their understanding of the forest dynamic concepts that you focused the lab on.