

# ECOLOGY LAB FINAL PREPARATION

## Introduction to Ecology Lab Introduction to Ecology Lab

### 01 Ecology Statistics

#### Data Analysis

**Variable:** any defined characteristic that varies from one biological entity to another.

**Population:** the entire collection of measurements of a variable of interest.  
**Example:** if we are interested in the heights of pine trees in Everglades National Park (Plant height is our variable) then our population would consist of all the pine trees in Everglades National Park .

**Sample:** smaller groups or subsets of the population which are measured and used to estimate the distribution of the variable within the true population

**Parameter:** any calculated measure used to describe or characterize a *population*

**Statistic:** an estimate of any population parameter

Why use statistics?

It is not always possible to obtain measures and calculate parameters of variables for the entire population of interest.

Statistics allow us to estimate these values for the entire population based on multiple, random samples of the variable of interest.

The larger the number of samples, the closer the estimated measure is to the true population measure.

Statistics also allow us to efficiently compare populations to determine differences among them.

Statistics allow us to determine relationships between variables.

## Statistical analysis of data

Measures of central tendency

Measures of dispersion and variability

Measures of central tendency

Where is the center of the distribution?

mean ( $\bar{x}$  or  $\mu$ ): arithmetic mean.....

median: the value in the middle of the ordered data set

mode: the most commonly occurring value

Measures of dispersion and variability

How widely is the data distributed?

range: largest value minus smallest value

variance ( $s^2$  or  $\sigma^2$ )

standard deviation ( $s$  or  $\sigma$ )

## Measures of dispersion and variability

Normal distribution of data is when a data set in which most values are around the mean, with fewer observations towards the extremes of the range of values

The distribution is symmetrical about the mean

Proportions of a Normal Distribution

We use an equation to tell us how many standard deviations from the mean the X value is located:

We then use a special table to tell us what proportion of a normal distribution lies beyond this Z value

Z table

Probability distribution tables

There are multiple probability tables for different types of statistical tests.  
e.g. Z-Table, t-Table,  $\chi^2$ -Table

Each allows you to associate a “critical value” with a “P value”

This P value is used to determine the significance of statistical results

### Using Excel

Program used to organize data

Produce tables

Perform calculations

Make graphs

Perform statistical tests

Organizing data in tables

Allows you to arrange data in a format that is best for analysis

### Analyzing Data in Excel

#### **Statistical tests can be done to determine:**

**Whether or not there is a significant difference between two data sets  
(Student's t-test)**

**Whether or not there is a significant difference between more than two  
data sets (ANOVA)**

**Whether or not there is a significant relationship between two variables  
(Regression analysis)**

### Analyzing Data in Excel

The following steps must be followed:

Choose an appropriate statistical test

State  $H_0$  and  $H_A$

Run test to produce Test Statistic

Examine P-value

Decide to accept or reject  $H_0$

Normally, you would have to calculate the critical value and look up the P value on a table

All tests done in Excel provide the P value for you

This P value is used to determine the significance of statistical results

**This P value must be compared to an  $\alpha$  value**

**$\alpha$  value is usually 0.05 or less (e.g. 0.01)**

**Less than 5% chance that the null hypothesis is true**

The lower the  $\alpha$  value the more certain we are about rejecting the null Hypothesis

First thing you must do is select which statistical test you want to perform

### **t-Tests**

Your Null Hypothesis is always:

There is no significant difference between the two compared populations ( $\mu_1 = \mu_2$ )

Your Alternative Hypothesis is always:

There is a difference between the two compared populations ( $\mu_1 \neq \mu_2$ )

### **ANOVA**

Your Null Hypothesis is always:

There is no significant difference between the compared populations ( $\mu_1 = \mu_2 = \mu_3 = \mu_4 \dots$ )

Your Alternative Hypothesis is always:

There is a difference between the compared populations ( $\mu_1 \neq \mu_2 \neq \mu_3 \neq \mu_4 \dots$ )

Remember:

The ANOVA result will only tell you that...

None of the data sets are significantly different from each other

OR

At least two of the data sets among the data sets being compared are significantly different

If there is a significant difference between at least two data sets, it will not tell you which two.

## **Regression analysis**

**Your Null Hypothesis is always:**

**There is no significant linear relationship between the two variables**

**Your Alternative Hypothesis is always:**

**There is a significant linear relationship between the two variables**

**The regression line fits the data well**

**The points all lie fairly close to the line, so there is a defined linear relationship between the two variables**

**“x” can be used to predict “y”**

## **Ecological study**

**Aim: To determine whether or not there are changes in heights of Pine trees with distance from the edge of a forest trail in Everglades National Park.**

**Hypotheses:**

**HO: There is no significant relationship between distance from the edge of the trail and Pine tree height**

**HA: There is a significant relationship between distance from the edge of the trail and Pine tree height**

**Results:**

**Discussion/Conclusion:**

**The gap created by the trail may be adversely affecting Pine trees, such that they are shorter near the trail and become taller with distance from the trail.**

**Three questions:**

**T-test**

**Single factor ANOVA and Two-way ANOVA**

**Regression analysis**

# 02 Sampling techniques

*Ecological techniques*

## Field sampling

### I. Introduction to ecological systems

Ecologists frequently refer to their subject of study as a system that they investigate (O'Neill 2001). A group of potentially interbreeding individuals of the same organism (a population) is a system; an assemblage of different species in a given area (a community) is a system; and a large area of land containing many populations of organisms arranged in different local communities over areas with unique abiotic environments is also a system (an ecosystem). All ecological systems share two important traits, **structure** and **function**. The structure of a system is defined by its measurable traits at a single point in time and can include living (biotic) and non-living (abiotic) components. Ecological systems function as the component parts exchange energy through time.



**Figure 1:** Prescribed fire in a Miami-Dade County pine rockland community.

A significant challenge to ecologists is to measure components of structure and function. In the example below we can see how many different kinds of components need

to be measured in order to adequately describe and understand how the ecosystem functions.

*Following a fire, the structure of a fire-dependent plant community like pine rocklands (Figure 1) could be described by the biomass of vegetation, the number of species and their relative abundances, and the soil chemical properties (e.g., nutrient content and pH). These same variables could be measured annually for two decades. By measuring these variables repeatedly through time, we could gain insight into how this plant community functions. After a fire, initial plant biomass will be low, but then it will rise slowly for a few years and then will rise quickly. Eventually plant biomass will stabilize and remain stable until the next disturbance. The number of species will follow a similar pattern for the first few years following a fire. After reaching its peak, species number in the pine rockland will decline to fewer species that remain present until the next fire; however, seeds of the declining species generally remain in the soil waiting for the next fire to create the specific environment needed for germination and establishment. Meanwhile, soil nutrient content and pH are also changing with plant biomass and species number. By making such detailed measurements in a pine rockland community through time, we can understand the emergent functional properties of this ecological system.*

## **II. Field sampling and measurement of biomass**

As in the above example, ecologists collect data, often in a natural setting, to understand the structure and function of the systems that they study. Field sampling is one of the most important aspects of ecological investigation, and it is important that you gain an understanding of some common methods that ecologists use to describe ecological systems. In this lab you will learn and employ sampling techniques that are widely used in ecology. Not surprisingly, there can be large differences in the methods used to sample plants and animals or even different communities of plants or animals. However, there are several techniques that can be used in a wide variety of situations. The first step in choosing a sampling technique is to determine what question you are interested in. Do you want to learn about the distribution and abundance of a particular species? Are you interested in understanding patterns of community composition? It is important to keep in mind that you must pick the best sampling technique for a given ecological system, and that not every method will work in every situation. Several basic ecological sampling techniques are reviewed below.

### **Plot (quadrat) sampling**

Plot (or quadrat) sampling is commonly used to sample populations/communities of plants and animals with limited mobility in a variety of aquatic and terrestrial ecosystems. Plot sampling is used to intensively sample a subset of the system in question to obtain a representative sample. Plot data should be replicated a number of



times, in a random way, to ensure that the data represent an unbiased picture of the system. When true randomness cannot be obtained, haphazardly selecting plot locations is often used. Determining where to place a sample of plots is critical to a good study, and there are a variety of techniques available. Some of these include “over the shoulder tosses,” randomly generated positions, and stratified samples.

Once a plot has been selected, the total number of individuals of each species can be counted to determine densities and species composition. While this method is objective, it can be extremely time consuming, especially when some species are very abundant. Some species do not lend themselves well to the count method because it is hard to differentiate individuals (e.g., plants that exhibit vegetative reproduction, corals, etc.) or individuals are too numerous to easily count. A measure of the percentage of area within the plot covered by these species (percent cover) is often used. Accurately estimating percent cover can be very difficult, although advances in digital cameras and imaging software have alleviated some of the problems. Because of the difficulties involved with obtaining accurate values for percent cover, the Braun-Blanquet method is often used for these species. This method involves delineating a specific area (the plot or quadrat), identifying all species in that area, and then assigning a code to each species based on its percent cover. An example of Braun-Blanquet codes is:

- 0: species not present
- 1: species <5% of total
- 2: species 5-10% of total
- 3: species 10-25% of total
- 4: species 25-50% of total
- 5: species 50-90% of total
- 6: species >90% of total

Clearly, these are subjective classifications, so it is important that the same observer make code classifications whenever possible.

### **Transect sampling**

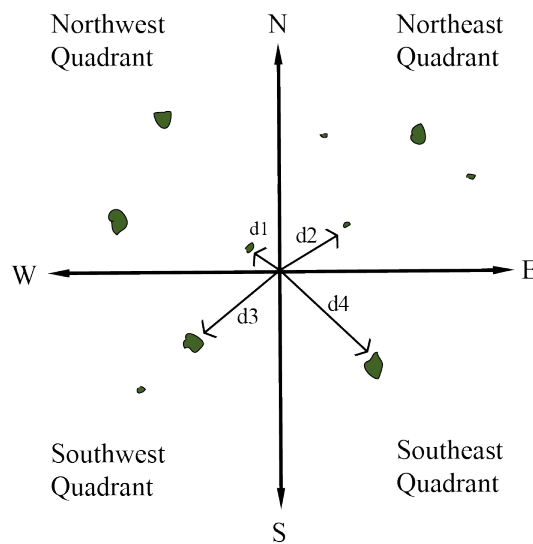
Transect sampling is one of the most widespread ecological techniques for sampling both plants and animals. To implement this technique, the investigator establishes a line (i.e., the transect line) between two points. There are three major types of transects: belt transects, line-intercept, and strip census (or line transect). In a belt transect all individuals within a specified distance from the transect line are counted. Based on the length and width of the transect, densities of species can be calculated. During line-intercept transects, only individuals that come in contact with the transect line are counted and the length of the transect line they occupy is often measured. This type of transect is mainly used by plant ecologists. Strip censuses are typically used for mobile organisms. The researcher walks along the transect, recording individuals encountered. The data collected represent an index rather than a density. Densities can be



estimated if the distance to each observed individual is measured. As with plot and point-quarter samples, it is important to have replicate transects within the same area.

### Point-quarter sampling

Point-quarter sampling is more complex than plot sampling but expands on the same concept in an attempt to reduce the amount of intensive labor involved in plot sampling. Rather than quantify the exact make-up of a specific plot, point-quarter sampling involves generating a random number of points in an area and then measuring the distance to the nearest species to that point in each of the four quadrants surrounding every point (Figure 2). Replicate samples (points) are also necessary for the point-quarter sampling method. This method is sensitive to deviations from a random distribution of individuals.



**Figure 2:** Point-to-plant distances for the point-quarter sampling.

The total density of all individuals (TD) in individuals / m<sup>2</sup> can be calculated with the following equation

$$TD = 1 / (\sum d_i / 4k)^2$$

Where  $\sum d_i$  is the sum of all point-to-plant distances and k is the number of points sampled.

### **III. Designing ecological experiments**

In future labs, we will discuss the hypothesis testing method. At this point, you should be aware that, in order to test a hypothesis, you must design appropriate experiments and sampling methods. Making inferences (i.e., deciding whether or not to reject a hypothesis) requires experiments designed with statistical tests in mind. Design your observations in order to explain variability in the system of study so that you understand its structural and functional properties. Excellent experiments usually require

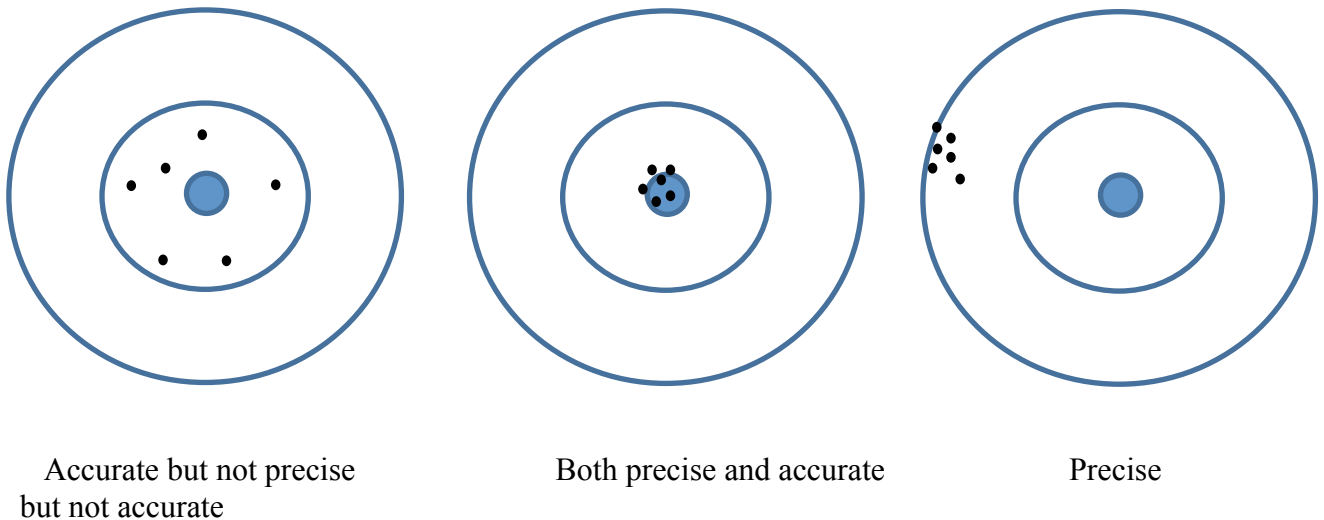
familiarity with basic biological principles in addition to the properties of specific systems. Keep in mind that there are many different experimental and sampling designs, and your selection of the appropriate design depends on the objective(s) of the experiment.

#### IV. Are your results representative of the population?

As we will see this week there are myriad sources of error that can intrude into estimation of population parameters. Often times these are intrinsic to the methodology that you are using. For example some methods consistently overestimate parameters while in other cases human error is the source of biased or erroneous estimates. One way to evaluate your results and/or evaluate your samples is to consider them in the context of precision and accuracy (Figure 3).

-Precision refers to the degree of repeatability of a single measurement. Imprecise measurements are made, for example, when someone does not consistently read a ruler correctly.

-Accuracy refers to the degree to which single measurements reflect the true value of the object being measured.



**Figure 3:** Examples of accuracy and precision

There is often a tradeoff that ecologists must make when investigating populations and ecosystems. Time, space, technology and often money represent significant barriers to gaining estimates that are both accurate and precise. As a result of these limitations, the investigator may sacrifice precision or accuracy when choosing a methodology. These compromises can be cause for consternation among scientists;

however, the ability to compromise when designing experiments or field studies is often a large part of ecological studies. Because different methodologies often produce accurate, yet biased results, comparing estimates collected by different methods (or observers) can be problematic.

#### **IV. Objectives**

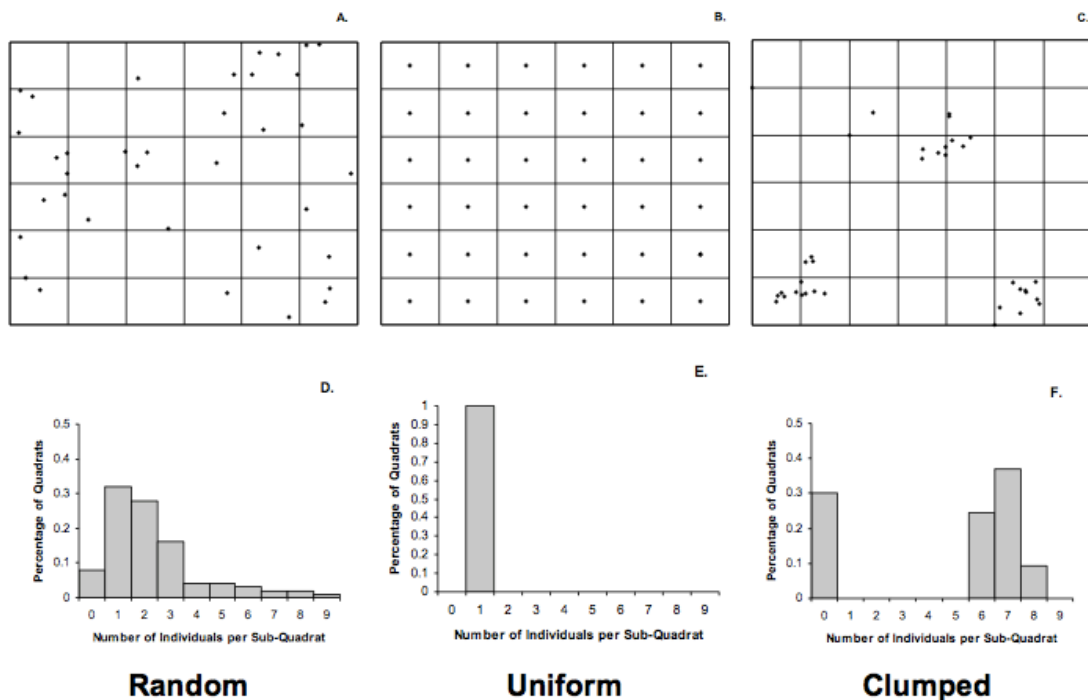
In this lab, we will use two field sampling methods to measure the density of organisms. The objective is to compare two field sampling methods: Plot (quadrat) and Transect, and test for sources of bias in the data that your class collects.

# 03 Dispersion patterns.docx

## Worksheet 3: Population dispersion/distribution patterns

### I. Introduction to population dispersion patterns

The **dispersion** of individuals in a population describes their spacing relative to each other. Different species and different populations of the same species can exhibit drastically different dispersion patterns. Generally, dispersion can follow one of three basic patterns: **random**, **uniform** (evenly spaced or hyper-dispersed), or **clumped** (aggregated or contagious; see Figure 2). Species traits such as territoriality, other social behaviors, dispersal ability, and allelochemistry will shape individual **dispersal** (i.e., movements within a population), **emigration**, and **immigration**, all of which affect population dispersion patterns. In addition to species traits, the distribution of resources or microhabitats links population dispersion patterns to the surrounding abiotic environment.



**Figure 2:** Common dispersion patterns are represented above. Figures A, B, and C represent the spacing of individuals within a population relative to each other. The entire square indicates the entire quadrat, and each small square indicates one sub-quadrat. Figures D, E, and F indicate the number of individuals within each sub-quadrat. Note that Figure D is derived from a randomly dispersed population, and that it indicates a Poisson distribution (example data and figure from S. Whitfield).

### II. Measuring population dispersion

Population dispersion is commonly quantified by population ecologists. With mobile organisms, this requires intensive sampling; therefore, we will measure

the dispersion - patterns of less mobile species. Analyses of population dispersion patterns usually follow a standard method in which observed patterns are compared to predicted, random dispersion patterns modeled on the **Poisson distribution**. Deviations from the predicted, random pattern suggest that the population under study exhibits either a uniform or clumped dispersion pattern. In today's lab exercise, we will utilize two different techniques to characterize the dispersion pattern of our focal species: (1) a quadrat-based method and (2) a point-to-plant method.

## Exercise 1. Using the quadrat method to estimate population dispersion

The **quadrat method** involves counting the frequency of occurrences of the species of interest in each of the 100 individual 10 X 10 cm sub-quadrats that compose the 1 m<sup>2</sup> quadrat. If the individuals within the population are randomly dispersed, there will be a random number of individuals in each quadrat, centered about the mean (see Figure 2A, D). If the individuals in the population are uniformly dispersed, there will be the same number of individuals in each sub-quadrat (see Figure 2B, E). If the individuals in the population are clumped in dispersion, there will be a few quadrats with many individuals, and many quadrats with no individuals (see Figure 2C, F). To analyze the data from the quadrat method we will use a **chi-square test** of hypothesis. The chi-square test compares a given distribution to the Poisson distribution. We will use an equation to generate a Poisson distribution with the characteristics that we would expect from a randomly dispersed plant species that has a mean number of plants per sub-quadrat equal to our sample population. This equation is called the 'Poisson expression' by Cox (2001), and it looks like this...

$$P(x) = \mu^x / (e^\mu * x!)$$

...where e = the base of the natural log = 2.7182818,  $\mu$  = mean, and x = the frequency category.

For example, we sample 40 sub-quadrats/cells. Nine cells have 0 individuals, 22 have 1 individual, 6 have 2, 2 have 3, 1 has 4 and none of the quadrats/cells have 5 individuals (Table I). Given these values, we can calculate the Poisson probability P (xi) for each category.

**Table I:** Example data -- there are 40 total sub-quadrats, 44 total individuals, and a mean of 1.1 individuals per sub-quadrat.

Number of Individuals per Sub-Quadrat (xi)	Number of Sub-Quadrats (fi)	<i>fi * xi</i>
0	9	9 * 0=0
1	22	1 * 22 = 22
2	6	2 * 6 = 12
3	2	3*2=6

4	1	4*1=4
5	0	5*0=0
Σ	40	44
	1.1	-

To calculate the mean value for data in this format use the following equation...

$$X = (\sum f_i x_i) / (\sum f_i)$$

...in which,  $f$  is the number of sub-quadrats and  $x$  is the number of individuals per sub- quadrat for each row in Table I. We can use the Poisson probabilities to generate expected probabilities with which we can calculate expected values for each row in Table I.

$$P(x_0) = \frac{(1.1)^0}{(2.718)^{1.1}(0!)} = \frac{1}{3.004} = 0.3329$$

$$P(x_1) = \frac{(1.1)^1}{(2.718)^{1.1}(1!)} = \frac{1.1}{3.004} = 0.3662$$

$$P(x_2) = \frac{(1.1)^2}{(2.718)^{1.1}(2!)} = \frac{1.21}{6.008} = 0.2014$$

$$P(x_3) = \frac{(1.1)^3}{(2.718)^{1.1}(3!)} = \frac{1.331}{18.023} = 0.0739$$

$$P(x_4) = \frac{(1.1)^4}{(2.718)^{1.1}(4!)} = \frac{1.4641}{72.091} = 0.0203$$

$$P(x_5) = \frac{(1.1)^5}{(2.718)^{1.1}(5!)} = \frac{1.6105}{360.456} = 0.0045$$

Note, that you can use excel to calculate  $P(x)$ . The formula is:

$$P(x) = (\mu^x) / ((EXP(\mu)) * (FACT(x)))$$

We can then use these expected probabilities to calculate expected values using the equation below (essentially, multiply each probability above by the total number of quadrats, in this case, 40.):

$$E(x_i) = P(x_i) \sum f_i$$

$$E(x_0) = P(x_0) \sum f_i = 0.3329 * 40 = 13.316$$

$$E(x_1) = P(x_1) \sum f_i = 0.3662 * 40 = 14.648$$

$$E(x_2) = P(x_2) \sum f_i = 0.2014 * 40 = 8.056$$

$$E(x_3) = P(x_3) \sum f_i = 0.0739 * 40 = 2.956$$

$$E(x_4) = P(x_4) \sum f_i = 0.0203 * 40 = 0.812$$

$$E(x_5) = P(x_5) \sum f_i = 0.0045 * 40 = 0.18$$

Use these expected values to compare with our observed values using a chi-square test. The test statistic for the chi-square test is  $\chi^2$ .

$$\chi^2 = \sum [(O - E)^2 / E]$$

In this example, the expected values for quadrats with three or more individuals are combined for the Chi-square analysis because those quadrats have small sample sizes (2 quadrats with 3 individuals, 1 quadrat with 4 individuals, and no quadrats with 5 individuals; see Table II).

After collecting the data, you should set up a table as a class that will allow you to conduct the analysis of dispersion. The  $\chi^2$  statistic for our example is 5.703 (Table II,b).

**Table II.** Example of a Poisson Table – In a., the  $X^2$  value was calculated using the raw data. However in b, categories for 3, and 4 individuals per quadrat were combined into one class in order to better meet assumptions of the Chi-square test. Note the difference in  $X^2$  values between the two tables.

a.

Number of individuals per quadrat ( $X_i$ )	Observed frequency (O)	P(x)	Expected frequency (E)	(O-E) <sup>2</sup> /E
0	9	0.3329	13.316	1.399
1	22	0.3662	14.648	3.690
2	6	0.2014	8.056	0.525
3	2	0.0739	2.956	0.309
4	1	0.0203	0.812	0.044
$\Sigma$	40	1	-	5.967

b.

Number of individuals per quadrat ( $X_i$ )	Observed frequency (O)	P(x)	Expected frequency (E)	(O-E) <sup>2</sup> /E
0	9	0.3329	13.316	1.399
1	22	0.3662	14.648	3.690
2	6	0.2014	8.056	0.525
3	3	0.0942	3.768	0.157*
4	-	-	-	-
$\Sigma$	40	1	-	5.771

Once you have calculated the Chi-square statistic, you will then need to calculate degrees of freedom (df) to obtain your p-value.



The degrees of freedom (df) is used to locate the  $X^2$  statistic on a Chi-square table:

$$df = k - 2$$

...where k is the number of categories remaining after you perform any necessary adjustments to the number of rows in the table. In the example above, after adjusting the table, we end up with 4 categories (instead of the original 5). Therefore the degrees of freedom =  $4 - 2 = 2$ .

### **Use the Chi-square statistic and the degrees of freedom to obtain the associated p-value.**

The  $\chi^2$  statistic for our example is 5.771. You can locate this value on the Chi-square table and then find the associated p-value, or use the following Excel formula to get a precise p-value:

$$=CHIDIST(\chi^2, df)$$

...where  $\chi^2$  is the test statistic you calculated and df are the degrees of freedom. Using the following equation in Excel: =CHIDIST(5.771,2), we get an associated p-value of 0.0558.

### **Exercise 2. Using distance based methods to estimate population dispersion**

The point-to-plant distance method utilizes a ratio to detect deviation from a random dispersion pattern. We use this method to sample dispersion for organisms that cannot easily be sampled using a 1 m<sup>2</sup> quadrat (like trees or species that occur much more spaced out). To collect the appropriate data, you will haphazardly select a point of origin (by throwing an object of some sort), and then measure the distance from that point to the nearest two individuals of the species of interest. Each team will measure 10 haphazardly selected points. These data will be used to calculate the sample coefficient of aggregation (A) ...

$$A = (\sum d_1^2/d_2^2) / n$$

where n = the number of sample points, and d = the distance from the selected location and tree 1 or 2. This coefficient of aggregation will always be between 0 and 1, and the expected value of A for a randomly dispersed population is 0.5. For this hypothesis, the z-equation is used...

$$z = \left| (0.5 - A) / (0.2887 / \sqrt{n}) \right|$$

...where n = the number of sample points, 0.2887 = the standard deviation of A values for a randomly dispersed population. **If z is less than 0.5, the dispersion is uniform and if z is greater than 0.5 the dispersion is aggregated.** Note that this is very similar to the equation for a t-test from the first lab. The z-equation is

simply a special version of the t-equation, except that the degrees of freedom are irrelevant because the number of sample points (n) must always be greater than 30. Also note that in this equation you are calculating the absolute value of your calculated z (i.e. change negative z values to positive).

To test if the aggregation index A is significantly different from 0.5 use your calculated z statistic to find an associated p-value. You can use excel to calculate the p-value from the z-table (z is your calculated z-value) using the following equation:

$$=1-\text{NORMSDIST}(z)$$

In our example  $z = (0.5 - 0.434) / (0.2887 / \sqrt{40}) = 1.446$

The associated p-value (obtained from Excel) =  $1-\text{NORMSDIST}(1.446) = 0.074$

### III. Objective

The field portion of today's lab will involve collecting data on the dispersion pattern of populations of a small, herbaceous plant and a large tree species chosen by your TA. The objective of Lab 3 is determine if the dispersion patterns of the populations you investigate are random, uniform, or clumped.

# 04 Competition

## Lab 4 - Resource Competition

### Intra and Interspecific Competition

Hutchinson's concept of a **niche** is a multi-dimensional hypervolume comprised of the physical and biological environmental conditions that describes a species' suitable habitat. In basic terms, a species' niche includes how an organism lives in its environment; how it reacts to competitors, resource abundance and alters the environment for others. For example, a plant in the forest may grow when a neighboring tree falls over and increases available sunlight. As this tree grows it will create shade, suppressing the growth of younger trees in the immediate vicinity. Temperature, salinity, nutrients, precipitation, predators, prey, and competitors are all examples of environmental parameters that can define a species' niche.

**Resource competition** occurs when individuals utilize the same resource pool to increase their growth, reproduction, or survival (Tilman, 1980). This means that there is **niche overlap** among individuals. **Resources** are any material that is consumed upon use and made unavailable to other organisms. Some common examples of resources are nutrients, sunlight, food, and open space. For example, two plants may be competing for a shared source of nitrogen or two barnacles may be competing for a bit of open substrate on a rock.

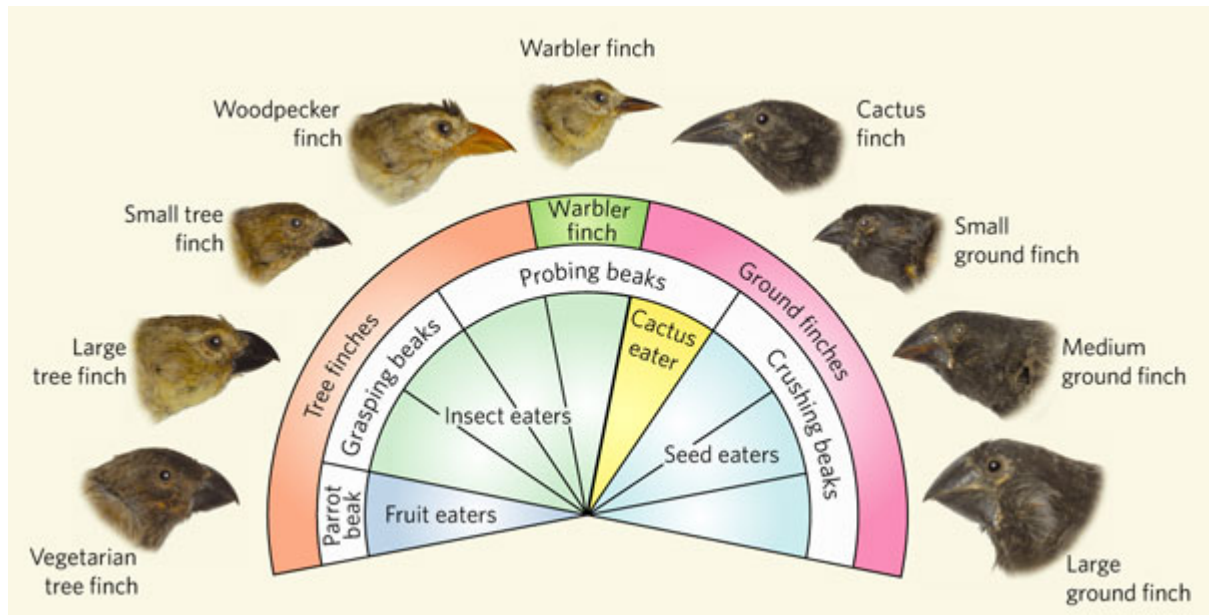
There are two main types of competition. **Intraspecific competition** is when individuals of the *same* species are competing for a shared resource. **Interspecific competition** is when individuals of *different* species compete for a resource. The strength of competition depends upon the amount of overlap in the niche of the species. Here, the **niche** is the Hutchinson concept of a niche, involving all aspects of a species use of the physical and biological environment. The intensity of competition is contingent upon the amount of niche overlap among individuals. Greater overlap means more shared resources, resulting in stronger competitive effects. One can see that **intraspecific** competition is usually stronger as the two individuals require a nearly identical suite of resources.

Competition can modify ecosystem structure and function. Strong territorial behavior, a sign of competition among individuals for limited resources, can result in a **uniform** distribution of individuals in space. Also, in the presence of interspecific territorial aggression, some species may not be able to forage efficiently inside the territory of a different species. Accordingly, in the presence of competitors, individuals often experiences lower growth rates, reproductive output, or survival. Radishes grown in high density aggregations often have smaller tubers than when grown in isolation. In the presence of territorial damselfish, many reef fishes experience higher mortality as there is less available shelter open for them to hide from predators.

The purpose of this lab is also to familiarize you with the concept of **density-dependent competition**. We will use basic activities to demonstrate both intra- and interspecific competition between resource specialists and resource generalists.

Noticing different beak size and shapes of birds in the Galapagos Islands was integral in Darwin's development of the theory of evolution. By noticing that some beaks were long, others short, some curved, some straight, Darwin was able to theorize that the shapes of these species beaks evolved as species competed with each other over a finite set of resources. In order to

persist, species needed to adapt to different foraging strategies. For example, some species developed long curved bills to be able to extract nectar from flowers while others developed strong thick bills that were useful for cracking open seeds. In this activity we will simulate foraging strategies while using different bird beaks to highlight the concepts of competition.



*Nature*, Vol. 442, p. 515, 2006

The lab will be split into four groups of six individuals. Before start decide with your TA how many treatments and replications each group will be doing. For data analysis, we are interested in comparing the effect of **inter-** and **intraspecific** competition. You can use the whiteboard to record the entire class data (next page has an example of a table you can use to record your treatments).

Boxes full of dry rotini pasta and wood chips will be seeded with two different resources (large white and small black beans). The individuals will compete for 5 minutes or until all beans have been recovered as explained below. The competition will be repeated 5 times for each pairing.

To quantify **intraspecific** competition, the box will be seeded with black beans and two individuals from the group will use tweezers to compete for the black beans.

The same process will take place using black beans and tongs. The same 2 individuals will compete each time.

Then **intraspecific** competition will be quantified using the same set up. However, this time the large white beans will be used. The same 2 individuals will compete each time (not the same 2 that competed previously).

To quantify interspecific competition the boxes will be seeded with both white and black beans. One individual from the group will have tongs and the other will have tweezers. The same 2 individuals will compete each time.

# 05 Life tables

*Population ecology*

## Lab 5: Population life tables

### I. Introduction to ecological populations, life tables, and population growth models

This week we begin a new unit on population ecology. A **population** is a set of individuals of the same species living in a given region or habitat. Populations are examples of ecological systems. As such, they exhibit both structural and functional properties. The total number of individuals in a population, the age distribution of those individuals, the sex ratio of adults, probabilities of survival (or mortality), and rates of fecundity are key traits of **population structure**. Ecologists employ a variety of methods to study the structure of populations.

Life history tables, or **life tables**, are a method of quantifying population structure that addresses all of the above population traits. Life tables provide age-specific information on survival and fecundity rates for a particular population. An ecologist can collect two very different types of life history data for individuals in a population which can lead to two kinds of life tables. **Horizontal** (dynamic or cohort) life tables require ecologists to follow all the individuals of a single cohort in a population from birth to death. Construction of horizontal life tables frequently depends on the recapture of marked individuals for mobile species or repeated, representative samples of sessile species. Since individuals must be followed from birth to death, the horizontal life table technique is not well suited for the study of long-lived individuals. **Vertical** (static or time-specific) life tables consist of data on individuals of all ages in a population from a single point in time. In vertical life table studies, it is important to work with a large, random sample of individuals to ensure that the data is representative of the entire population. For example, the age distribution of your sample of individuals should reflect the age distribution of the whole population. Non-destructive sampling methods are particularly useful for the construction of vertical life tables as they minimize the impact of large sampling efforts on population dynamics.

Both dynamic and static observations of population structure can be used 1) to quantify the age structure of a population; 2) to estimate an optimal age of sexual maturity; and 3) to predict population growth rates. Population growth projections are based on mathematical models such as the exponential growth model:

$$N_t = N_0 (e^{rt}).$$

In the exponential growth model, the number of individuals **at any time (t)** can be predicted using the **number of individuals at the starting time ( $N_0$ )**, the base of the natural logarithm ( $e = 2.7182818$ ), the **intrinsic rate of population growth (r)**, and the time (t) since  $N_0$ . The intrinsic rate of population growth (r) is a direct consequence of the age structure of a population. Environmental conditions, seasonal effects, and population

densities also shape population growth rates. In general, populations only exhibit exponential growth when resources are not limited. Therefore, ecologists developed **density-dependent growth models** to simulate the effects of environmental stress on population growth. Other population growth model alternatives include the **Leslie matrix** and **Lotka-Volterra model**.

## II. Anatomy of life tables.

A life history table contains information on age classes ( $x$ ), the total number of individuals in each age class ( $n(x)$ ), survival rates for each age class ( $l(x)$ ), fecundity rates for each age class ( $b(x)$ ), and the number of offspring produced per individual at each age class ( $l(x)*b(x)$  and  $l(x)*b(x)*x$ ). The following is an example of a horizontal life table:

*Example 1: Horizontal Life Table*

Age class (months) $x$	Number/age class $n(x)$	Survival rate $l(x)$	Fecundity $b(x)$	Offspring/ind $l(x)*b(x)$	Age-weighted fecundity $l(x)*b(x)*x$
0	134	1.00	0.00	0.00	0.00
1	117	0.873	0.00	0.00	0.00
2	82	0.612	6.28	3.84	7.69
3	64	0.478	9.60	4.59	13.76
4	52	0.388	12.10	4.70	18.78
5	43	0.321	13.60	4.36	21.82
6	23	0.172	17.40	2.99	17.92
7	13	0.097	14.50	1.41	9.85
8	3	0.022	15.00	0.34	2.69
9	2	0.015	0.00	0.00	0.00
10	1	0.007	8.30	0.06	0.62
11	0	0.000	5.00	0.00	0.00
<b>Sum</b>				22.28	93.12
			<b>R<sub>0</sub></b>	22.28 offspring	
			<b>G</b>	4.18 months	
			<b>r</b>	0.74 ind/month	
			<b>Optimal age for sexual maturity</b>	5 months	

You will be provided with fecundity rates ( $b(x)$ ) and pre-determined age classes ( $x$ ) for life tables in this lab. Calculation of the other parameters depends on the type of life table you are constructing. **The important differences between horizontal and vertical life tables relate to their respective sampling approaches (described above) and calculations of survivorship.**

*Horizontal (dynamic or cohort) life tables*

When using cohort information, calculate the survival rate for an age class ( $l(x)$ ) as the number of individuals in that age class ( $n(x)$ ) divided by the number of individuals alive in the first age class ( $n(0)$ ). In the above table, survival at age class 0 ( $l(0)$ ) is  $n(0)/n(0)$  or  $134/134 = 1.000$ . At age class 1,  $l(1) = n(1)/n(0)$  or  $117/134 = 0.873$ . Next, use the provided fecundity data to calculate the offspring produced per individual in each age class ( $l(x)*b(x)$ ) and the age-weighted number of offspring for each age class ( $l(x)*b(x)*x$ ). Once the horizontal life table is completed, you can calculate the net reproductive rate ( $R_0$ ), mean generation time ( $G$ ), and intrinsic growth rate ( $r$ ) of the population.

Net reproductive rate ( $R_0$ ) is the sum of the  $l(x)*b(x)$  column. It represents the expected number of offspring an individual will produce over its lifetime in the population. If  $R_0 > 1$ , then population size increases. If  $R_0 < 1$ , then population size decreases, and if  $R_0 = 1$ , then population size does not change. In the population described by the horizontal life table above, an individual is expected to produce 22.28 offspring over its lifetime. Mean generation time ( $G$ ) is the sum of the  $l(x)*b(x)*x$  column divided by the net reproductive rate ( $R_0$ ). The intrinsic growth rate ( $r$ ) is an estimate of population growth; it is equal to the natural log of the net reproductive ( $R_0$ ) divided by the mean generation time ( $G$ ):

$$r = \ln (R_0) / G.$$

The optimal age for sexual maturity in the population corresponds to the age class with the greatest age-weighted fecundity ( $l(x)*b(x)*x$ ).

### Vertical (static or time-specific) life table

When using time-specific information, you need to count all of the individuals you sampled.

First, record the number of individuals at each age class in your sample ( $s(x)$ ). See the following vertical life table example.

### *Example 2: Vertical Life Table for a Gambusia holbrooki population*

Age class (days) $x$	Sample/age class $s(x)$	Number/age class $n(x)$	Survival rate $l(x)$	Fecundity $b(x)$	Offspring/ind $l(x)*b(x)$	Age-weighted fecundity $l(x)*b(x)*x$
0	130	759	1.00	0.00	0.00	0.00
30	190	629	0.829	0.00	0.00	0.00
60	240	439	0.578	0.00	0.00	0.00
90	120	199	0.262	24.00	6.29	566.32
120	60	79	0.104	27.00	2.808	336.96
150	15	19	0.025	29.00	0.73	108.89
180	3	4	0.005	32.00	0.17	30.36
210	1	1	0.001	0.00	0.00	0.00
240	0	0	0.000	0.00	0.00	0.00
<b>Sum</b>	759				9.998	1042.53
				<b><math>R_0</math></b>	9.998 offspring	



<b>G</b>	104.27 days
<b>r</b>	0.0221 ind/day
<b>Optimal age for sexual maturity</b>	90 days

Next, you must determine how many individuals are alive in each age class ( $n(x)$ ) using data you collect at a single time in the field. The assumption stands that each individual you sampled was alive in the first age class ( $x = 0$ ). For example, if you sample 759 individuals, all of them had to have been alive at the first age class ( $x = 0$ ). So,  $n(0) = 759$  or the sum of the  $s(x)$  column (see the above vertical life table example). If 130 of the individuals in your total sample were between 0 and 29 days old (age class 0), then 629 individuals in your sample were alive at the second age class ( $x = 30$ ). Once you have calculated the number alive at each age class ( $n(x)$ ), you can determine the survival rate ( $l(x)$ ) for each age class. Survival rate for a specific age class ( $l(x)$ ) is the number alive in that age class ( $n(x)$ ) divided by the number alive in the first age class ( $n(0)$ ), or  $l(x) = n(x) / n(0)$ . In the above vertical life table example, the survival rate at age class 0 ( $l(0) = 759/759 = 1.000$ ),  $l(30) = 629/759 = 0.829$ , and so on.

All other calculations for vertical life tables are the same as described above for horizontal life tables.

### III. Objectives

The field portion of today's lab will involve collecting data on mosquitofish (*Gambusia*) populations from a pond on campus. *Gambusia holbrooki* is a small, live-bearing fish found throughout south Florida, including the Everglades. In this lab exercise, you will also analyze previously published data on the structure of clam (*Musculium*) populations. *Musculium partumeium* is a freshwater clam from Virginia.

The objectives are:

- 1) To generate life history tables for *Gambusia* and *Musculium*.
- 2) To compare and contrast the life history tables you generate for both organisms.

# 06 species diversity

## *Species diversity*

### I. Ecological communities

Ecological communities are assemblages of populations of interacting species. People conceptually recognize communities because they are perceptually obvious. Examples of ecological communities include forests, prairies, wetlands, estuaries, lakes, deep ocean hydrothermal vents, and coral reefs. The essential feature of communities is that they are assemblages of species that predictably co-occur. The community concept became a central focus for ecologists in the early 1900s because of the work of Clements. Clements spurred the development of a probabilistic theory of community development when he suggested that the predictability of community development (i.e., succession) was proof for the existence of a super-organism. This super-organism was proposed to be composed of the assembled organisms, much like organisms are composed of assemblages of tissues. Though the super-organism concept of Clements has widely lost favor among ecologists, it is true that ecological systems are more than the sum of their parts.

The structure of ecological communities is measured with a number of different metrics. One method of analyzing ecological communities is the construction of food webs, which address the functional relationships among the species of a community. Species diversity and species richness are also important measures of community structure. Species richness is a measure of the number of species per unit area. Species diversity is a non-dimensional, numerical index generated for a given community, which takes into account both richness and abundance of individual species. Because of the problems associated with mathematical measures of species richness that arise in certain situations, many ecologists elect to use measures of species diversity to describe ecological communities.

### II. Sampling effort curves and diversity indices

Ecologists face two main problems when quantifying differences in the abundances of species in communities. First, the total number of species found correlates with the sample size because you are more likely to find a rare species as you increase your sampling frequency. This means that diversity cannot be compared between communities that were sampled at different intensities. Second, the number of individuals representing a species may not be a good indication of the functional importance of that species to the community. To some degree, the functional roles that species play in a community vary in proportion to their overall abundance.

There are cases where this is not true, however. An excellent example of a species whose functional role is not proportional to its overall abundance in a community is a keystone predator. A keystone predator species may be represented by only a few individuals, but it plays a critical role in structuring the community in which it lives. The

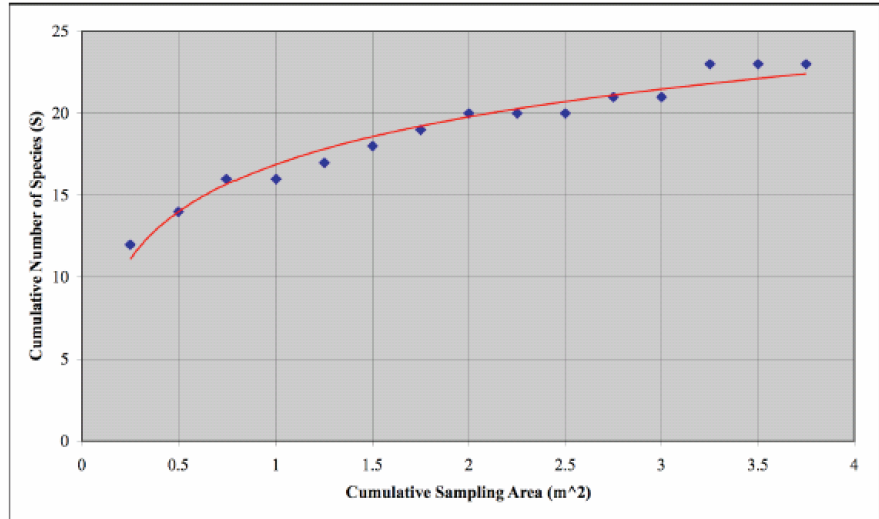
Florida panther in the Everglades is a good example of such a keystone predator. Thus, it is best to have some measure of the functional roles of species in a community in addition to simple measures of the numbers of individuals that represent each species.

One part of the discovery process in assessing communities is identifying when we have exerted a sufficient sampling effort to determine species richness and diversity with some level of confidence. Construction of a **species-area curve** (Figure 1) is one approach to determining adequate sampling effort.

Species-area curves plot the area examined with repeated samplings (x-axis) versus the total number of species found in those samplings (y-axis). Alternatively, a **sampling effort curve** (Figure 2) plots the cumulative number of individuals sampled (x-axis) against the total number of species represented by those individuals (y-axis). Both curve types address the same question (i.e., whether species richness is increasing or has leveled off in your sample) but may be appropriate for different situations. For example, Conservation International's Rapid Assessment Program (RAP; <https://learning.conservation.org/biosurvey/RAP/Pages/default.aspx>), created in 1990, is intended to quickly assess species diversity in areas of conservation concern to better inform sound conservation decisions. A RAP survey is performed during a 3-4 week period where several different scientists (botanists, ornithologists, entomologists, zoologists, etc.) are flown in to quickly move through the forest documenting the species and individuals found in the area. RAPs do not include accurate measures of area covered but do include numbers of individuals sampled. In such a scenario, a sampling effort curve would be more informative than a species-area curve.

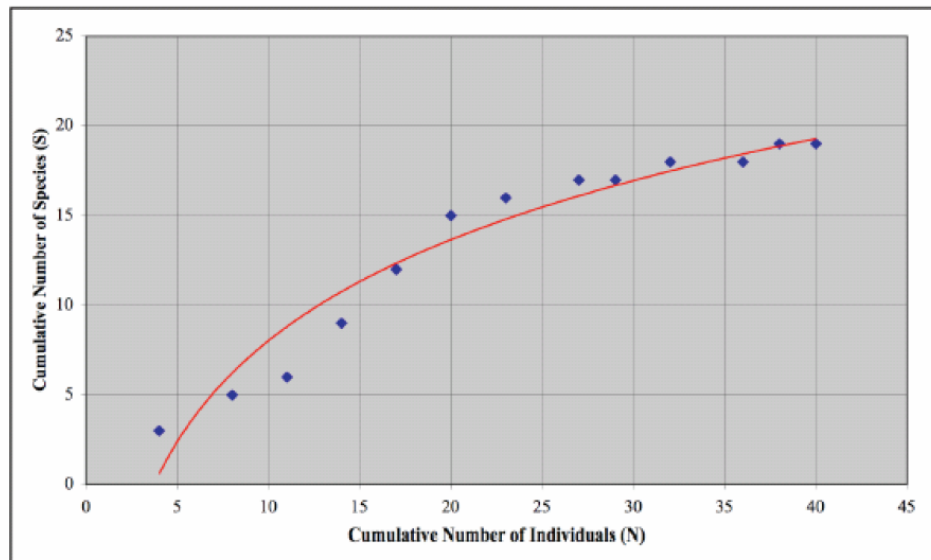
The result for both curve types is a line that increases steeply at first but eventually levels off at an asymptote. The point at which the species-area and sampling effort curves level off is the point where additional sampling is yielding no additional information about the number of species. In other words, the leveling off point or asymptote represents the optimal sample size in terms of area or individuals, depending on the type of curve. The total number of species in a community strongly determines how large the sample should be to reach this optimum, though the number of rare species also plays a critical role.

Area (m <sup>2</sup> )	Cumulative # of Species
0.25	12
0.5	14
0.75	16
1	16
1.25	17
1.5	18
1.75	19
2	20
2.25	20
2.5	20
2.75	21
3	21
3.25	23
3.5	23
3.75	23



**Figure 1:** Herbaceous Plant Species-Area Curve for the FIU Environmental Preserve (shown with data used to generate graph).

Plant #	Cumulative # of Species
4	3
8	5
11	6
14	9
17	12
20	15
23	16
27	17
29	17
32	18
36	18
38	19
40	19



**Figure 2:** Herbaceous Plant Sampling Effort Curve for the FIU Environmental Preserve (shown with data used to generate graph).

Once you have adequately sampled the species in a community, you can then calculate an index to quantify the species diversity and/or dominance in that community. The two most common indices for this are the **Simpson's index (D)** and the **Shannon-Wiener index (H)**.

The Simpson's index is a measure of *dominance* representing the likelihood that two randomly chosen individuals will be the same species. This species emphasizes common species, and is affected very little by rare individuals. D ranges from 1 to the number of species found. The higher D is the more even the population; the lower D is the more one species dominates the population.

The Shannon-Wiener index is a measure of species *diversity*. H ranges from 0 to 5 and typically falls between 1.5-3.5. The higher value of H the greater the diversity.

Both indices are calculated using information about the proportion ( $p_i$ ) of individuals in the total sample ( $N_{total}$ ) that are represented by a given species ( $i$ ), such that, for each species...

$$p_i = n_i / N_{total}$$

Simpson's index (D) is calculated as...

$$D = 1 / \sum p_i^2$$

The Shannon-Wiener index (H) is calculated as...

$$H = - \sum [p_i * \ln (p_i)]$$

All of these calculations can be made in Excel. Try the examples below before calculating values for your own data:

#### Site 1

Species	Abundance n	=B4/99 p	=C4^2 p^2	=ln(C4) ln p	=E4*C4 (ln p)*p
A	47	0.474747475	0.225385165	-0.74497	-0.35367
B	35	0.353535354	0.124987246	-1.03977	-0.3676
C	7	0.070707071	0.00499949	-2.64921	-0.18732
D	5	0.050505051	0.00255076	-2.98568	-0.15079
E	3	0.03030303	0.000918274	-3.49651	-0.10595
F	2	0.02020202	0.000408122	-3.90197	-0.07883
	99		0.359249		-1.24416
	N = SUM of n		SUM of p^2		SUM of ln(p)*p
Simpson's index (D) = 1/(SUM(p^2)) =			2.783584		
Shannon-Weiner (H) = -1*(SUM(ln(p)*p)) =					1.244162

#### Site 2

Species	Abundance n	=B4/99 p	=C4^2 p^2	=ln(C4) ln p	=E4*C4 (ln p)*p
A	48	0.457142857	0.208979592	-0.78276	-0.35783
B	23	0.219047619	0.047981859	-1.51847	-0.33262
C	11	0.104761905	0.010975057	-2.25607	-0.23635
D	13	0.123809524	0.015328798	-2.08901	-0.25864
E	8	0.076190476	0.005804989	-2.57452	-0.19615

F	2	0.019047619	0.000362812	-3.96081	-0.07544
	105		0.289433		-1.45704
	N = SUM of n		SUM of p <sup>2</sup>		SUM of ln(p)*p
Simpson's index (D) = 1/(Σ(p <sup>2</sup> )) =			3.45503		
Shannon-Weiner (H) = -1*(Σ(ln(p)*p)) =					1.457036

### III. Objectives

You will conduct a survey of the insect community on the FIU Preserve. Your TA will describe the methods on how to gather, identify, and count number of species and individuals in the Preserve. When complete, your TA will pool together the class data and you will create a species sampling effort curve showing the amount of individuals needed to effectively collect the most insect diversity within this habitat.

# 07 Species interactions

Lab 7-1

## Lab 7: Species interactions

### I. Ants as Examples of Consumer-Resource and Competitive Interactions

In nature we can find different types of species interactions. In today's lab, we will analyze one interaction that involves the consumption of resources. In some cases like in predation one participant is the **resource (prey)** and the other is the **consumer (predator)**. In the same way, some organisms called **herbivores** use plants for food.

Herbivory is a term used to describe a particular species interaction in which a plant is consumed (whole or in part) by some consumer organism. The consumer (Herbivore) may range greatly in size from organisms that are smaller than the plant on which they feed (e.g. insect larvae, moths), to large grazing animals (e.g. deer, elephants).

There are numerous types of herbivores, which have adopted methods for feeding on different parts of their host plant. As such, on any given plant, the leaves, buds, stems, bark, flowers, fruits, seeds, roots, or nectar may be consumed. Accordingly, herbivores have developed numerous feeding methods, which allow them to effectively exploit certain plant resources. Herbivore feeding may include techniques such as removing and chewing fruits, leaves and stems, stripping and consuming bark, boring into buds, seed and roots or drinking nectar and eating pollen from flowers.

Ants are an example of insects that interact with plants in several different ways. Some ant species (from two ant genera: *Atta* and *Acromyrmex*) cut leaves and use the material to cultivate fungus in their nests that ant larvae feed on. Other ant species drink nectar from a plant's extrafloral nectaries. Extrafloral nectaries are nectar producing glands not associated with the flower. These glands can be located on just about any part of the plant: leaves, petioles, bracts, stipules, fruit, etc. Over 2,000 plant species and more than 64 plant families have been found to have extrafloral nectaries. Often, herbivorous ants which feed on this nectar will help defend the plant from other herbivores acting as important biotic protective agents of plants. Most ants are omnivorous, and will take nectar, as well as oil and protein sources; some ants are exclusively carnivorous. Other species of ants may switch their preferences according to what's available at the time (e.g., when there is an abundance of insect prey, some species of ants will not take nectar).

Ants also experience intra and interspecific competition for resources. By protecting the plants that provide extrafloral nectaries, ants are competing with herbivores for the energetic resources of the plants. Some species of ants attack and take over neighboring ant colonies. In the United States, *Solenopsis invicta*, or red imported fire ants (RIFAs) compete successfully against other ants, and have been enlarging their range to almost every state of the American South, from Texas to Maryland, since being introduced from a container ship in Mobile Alabama in the 1930s. Fire ants feed on seeds, fruits, leaves, roots, bark, nectar, sap, fungi, and carrion, and they compete with other ant species and other organisms for these food resources.

Ants are ubiquitous, and south Florida has an enormous number of species (not surprising for a subtropical locale), including fire ants. The social organization of many ant species allows for the discovery of food by foraging workers who return to the nest to recruit their relatives to the food source. The more individual ants there are in a habitat, the greater the probability of one stumbling across a bait (i.e. nectar, specific plant species, etc.). Lab 7-2

### II. Species Habitat Use

The habitat of an organism is the place where it lives, but is more accurately defined as the



resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism. Habitat implies more than the defining vegetation or vegetation structure of an area. It is the sum of the specific resources that are needed by organisms. Habitat may be used for foraging, cover, nesting, resting, escape, denning, or other life history traits. Selection of habitat by animals is therefore an active behavioral process whereby the organism searches for features of the landscape that are directly or indirectly associated with the resources that an animal needs to reproduce, survive, and persist. Ant communities vary in species composition and diversity depending on habitat type and land use patterns.

### **III. Objectives**

We will compare the activity of ants in four different situations: hammock (shady) vs. pineland (open) vs. mowed grass vs. pavement. We'll use the discovery of baits as an indication of ant activity (and indirectly, ant abundance) at a given site. To try to sample all the ants, we will use two types of baits to simulate nectar (honey) and flesh/oils (tunafish). Each group will be responsible for two (1 honey, 1 tuna) 10 m transects in one of the four habitats (each group samples in a different habitat). The baits will be placed on numbered index card squares placed at 1 m intervals and monitored for 1 hour. It is important to record your initial time as the time the first bait hits the ground, and to try to put down all the baits in the first five minutes, so you can return to monitor the baits every 5 minutes. Walk along one path only, to minimize disturbance to the ants in the habitat. On the data sheets, record the time of each transect-run (trap-line!), the number of ant species and individuals at each bait (more than 12 = many), and the size & color of the ants present (morphospecies). When the hour is up, collect representative specimens of each ant species and put in a vial of alcohol. Label with a small slip of paper labeled as to site, bait, and ant description on a slip of paper written in pencil (ink will run in alcohol) inserted into the vial.

#### **Equipment:**

Timer, index card squares (2cm x 2cm, labeled 1-10, 2 sets per group); data sheets (6 per group); pencils, vials with ETOH, honey (1 vials/group), potted meat (1 vials/group); aspirators, forceps. Keeler, K.H. 1980. Distribution of species with extrafloral nectaries in temperate ecosystems.

# 08 Predator Prey interactions

8-1

## LAB 8: PREDATOR-PREY INTERACTIONS

**Predation** refers to the interaction between two organisms, in which one (the prey) is killed and consumed by another (the predator). These interactions may occur between two organisms belonging to different species, or between two individuals of the same species. Dynamic models of predator-prey interactions have been developed which show how the population sizes of both predator and prey species fluctuate over time. Past research has revealed that predation rates and patterns of population fluctuation vary considerably in frequency and intensity in response to a number of key factors. Primary among these factors are:

- Relative abundances of predators and prey
- Relative sizes of predators and prey
- Predator gender
- Prey physical/behavioral attributes (e.g., cryptic color, escape mechanisms)
- Energetic quality of prey
- Predator condition or gut fullness
- Predator experience
- Habitat heterogeneity

**Predator functional response:** There are many examples in nature which demonstrate that predators can control the numbers of their prey or a consumer can control the item they are consuming. For example, predatory lampreys almost eliminated the lake trout in the Great Lakes between 1950 and 1960. Wolves kept the elk numbers in check in the Yellowstone area before humans eliminated the predator. Cows and other grazing animals regularly eat all the grass in a paddock. The goal of this lab is to take a closer look at the nature of predator/prey interactions (but this lab could easily be applied to a consumer/resource model such as cattle grazing on grass). When predators are faced with increasing local density of their prey, they often respond by changing their consumption rate. This relationship of an individual predators' rate of food consumption to prey density was termed the **functional response** by C.S. Holling in 1959. Another way to think about predator functional response is that the rate of prey capture by the predator depends on the abundance of the prey. Generally, when there is more prey, the predator consumes more. In this lab, we will repeat the method Holling used to establish the basis for the analysis of the functional response. He developed the conceptual model using blindfolded human subjects (the "predator") and 4-cm sandpaper discs (the "prey").

### The Three Types of Functional Responses

Figure 1 illustrates the three general types of curves expected in various predator-prey situations.

**Type I** is a linear relationship, where the predator is able to keep up with increasing density of prey by eating them in direct proportion to their abundance in the environment. If they eat 10% of the prey at low density, they continue to eat 10% of them at high prey densities. However, even Type I predators should reach a saturation point because eventually an organism can consume no more (dashed line). This Type of functional response is the rarest type in nature.

*Ecological example* – a passive predator such as a spider. The number of flies caught in the net is proportional to fly density. Prey mortality due to predation is constant.

**Type II** describes a situation in which the number of prey consumed per predator initially rises quickly as the density of prey increases but then levels off with further increase in prey density.

*Ecological example* – Wolves feeding on elk in an open habitat can increase consumption of elk as elk populations increase. However, once elk become very abundant the wolf now spends very

little time catching elk and more time feeding on and processing the elk. 8-2

**Type III** resembles Type II in having an upper limit to prey consumption, but differs in that the response of predators to prey is depressed at low prey density.

*Ecological example* – Insect feeding birds often eat whatever bug is most abundant in nature. Let's say species A is an abundant bug year round but species B only hatches once a year. When species B hatches there are many more individuals of species B than species A. The bird that is initially feeding on species A may not notice species B at first or maybe the bird has never fed on species B before. As species B becomes more and more abundant, the bird begins to eat more of species B because it is more abundant and the bird is better at finding species B. However, over time the bird reaches a maximum capacity to eat and process species B.

Figure 1: Three types of functional response relating Prey Density to Number of Prey Eaten per unit Time per predator.

#### **What affects the Functional Response?**

Two factors dictate that the functional response should reach a plateau.

- First, the predators may become satiated (i.e., their stomach completely filled), at which point their rate of feeding is limited by the rate at which they can digest and assimilate food.
- Second, as the predator captures more prey, the time spent handling and eating the prey lowers the searching time. Eventually, the predator reaches the minimum time it takes to search, capture and consume. The predator cannot find prey and eat it any faster. The consumption rate cannot increase when the ability of the predator to catch and eat is at a maximum.

C.S. Holling described this relationship between search time, handling time, and consumption rate by a simple expression known as the “**disc equation.**” The equation was developed using blindfolded human subjects trying to find and pickup small discs of sandpaper on a flat surface. Any such task, including subduing and eating a prey item (whether a model of sandpaper disc “prey” or a real prey) requires the following measurable elements that we will incorporate into a mathematical equation following the logic of Holling:

$N$  = Number or density of prey item

$\alpha$  = A constant representing capture rate or searching efficiency of a predator. As  $\alpha$  increases, the predator becomes more efficient and effective at consuming the prey. 8-3

$T$  = Total time (a combination of handling time and searching time)

$T_h$  = Total time handling prey

$P_e$  = Number of prey items eaten during a certain amount of time

$$P_e = \frac{\alpha TN}{1 + \alpha T_h N}$$

Here we do not derive the equation but rather skip over the algebra and logic to explore what it means ecologically. By looking at this equation we can see that the number of prey eaten ( $P_e$ ) during a given time will increase as the ability of the predator to catch prey ( $\alpha$ ), total time foraging for prey ( $T$ ) and/or the number of prey items ( $N$ ) increases. Also, as the time spent handling prey ( $T_h$ ) approaches 0,  $P_e$  will increase.

This equation describes a Type II functional response, and is known as the Holling “disc equation.” Note that the equation describes the amount eaten during a specified period of time:  $T$ . The density of the prey ( $N$ ) is assumed to remain constant throughout that period. In experiments, this can be guaranteed by replacing any prey that is eaten. An additional point is that  $\alpha$  is assumed to remain constant regardless of prey density ( $N$ ). One final aspect of this equation must be explained before proceeding.  $T$  is actually dependent on two components  $T_s$  and  $T_h$ .  $T_s$  is the time spent searching for prey and  $T_h$  is time spent handling the prey. Once a predator catches a prey, it is handling the prey ( $T_h$ ) and cannot be searching for prey. Therefore the relationship can be expressed as:

$$T = T_s + T_h$$

# 09 Ecosystem metabolism

9-1

*Ecosystem ecology*

## Lab 9: Ecosystem metabolism

### I. Ecosystems and their metabolism

A.G. Tansley (1935) published the term **ecosystem** roughly 20 years after Clements described the superorganism concept. He wrote: But the more fundamental conception is, as it seems to me, the whole *system* (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome – the habitat factors in the widest sense. Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system... These *ecosystems*, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom (Tansley 1935).

**Figure 1:** Example ecosystem, the Florida Everglades

Tansley's definition stressed the conceptual unification of organisms (biotic components) and contextual physical factors (abiotic components) into a single system. Thus, we define an ecosystem as the biotic components of a given habitat (i.e., the communities) and the abiotic environment of that habitat. Ecosystem-level approaches in ecology emphasize the interaction between biotic and abiotic elements. Frequently ecosystem scientists study exchanges between ecosystem components. Such exchanges 9-2

produce emergent functional properties of the ecosystem itself. Examples of ecosystem emergent properties are **energy flow** and **nutrient cycling**.

Energy flow is a fundamental property of ecosystems that links organisms to their environment. Photosynthetic **autotrophs** capture energy from their environment (i.e., sunlight) to create organic molecules from inorganic carbon, water, and nutrients. Energy stored in photosynthate moves up a food chain or across a food web when heterotrophic organisms consume autotrophs or other **heterotrophs**. Energy transfer during these consumption events is not perfectly efficient. The second law of thermodynamics states that although an energy transformation or transfer does not change the total amount of energy within a closed system (e.g., the universe), the amount of energy available to do work after the transfer is always less than the original amount of energy (Purves et al. 1998). That is, **trophic efficiency** at any level in a food web is always less than 100%. Only 10 – 20% of the energy at one trophic level in a food web is actually transferred to the next trophic level.

## II. Measuring ecosystem metabolism

Ecosystem ecologists measure whole-system metabolism in a manner similar to the way an organismal biologist measures the metabolic rate of a single organism. Since **oxygen** and **carbon dioxide** can be stoichiometrically related to **photosynthesis** (i.e., autotrophic processes) and **respiration** (i.e., heterotrophic processes), following their transfer is a way to measure ecosystem metabolism. Consider oxygen flux in an ecosystem. If there is a net gain of oxygen in a system over time, then photosynthesis has exceeded respiration, meaning that the system is **autotrophic**. A net loss of oxygen over time indicates that ecosystem respiration exceeds photosynthesis, meaning that the system is **heterotrophic**. By definition, all terrestrial systems are heterotrophic at night since no sunlight is available for photosynthesis. If over an entire 24 hour period a system fixes more carbon than is consumed, the system is autotrophic because photosynthetic carbon gains exceed respiratory carbon losses.

To experimentally examine system metabolism, ecologists utilize enclosures to measure respiration (R) as oxygen change in the absence of light (e.g., in a dark enclosure or a clear enclosure at night) and **net primary production** (NPP) during the day in a clear enclosure. The latter is a measure of NPP and not **gross primary production** (GPP) because both photosynthesis and respiration occur during the day in a clear enclosure. If respiration in the absence of light can be assumed to be equal to respiration in the clear enclosure, then GPP can be calculated as the clear chamber oxygen change plus the dark chamber oxygen change ( $GPP = NPP + R$ ).

## III. Ecosystem metabolism is not limitless

Autotrophs (i.e., primary producers) introduce the majority of all energy input to the ecosystem food web. There are some important exceptions, though. Some ecosystems receive energy as organic matter that flows in from outside the system. A lake fed by rivers is an example of such an ecosystem that receives **allochthonous** energy inputs in addition to the **autochthonous** energy captured within the system by suspended phytoplankton and wetland plants in the lake's shallows fringe. Since energy flow in ecosystems strongly depends on primary production, we can investigate the factors that control primary production rates and, thereby, ecosystem metabolism. Both the biotic and abiotic components of an ecosystem control its metabolism. Biotic controls include genetic limits to organismal growth rates or competition among organisms in ecosystems. Abiotic ecosystem components that regulate whole-system metabolism are also termed **forcing functions**. Examples of forcing functions are **light** and **nutrient availability**. 9-3



#### IV. Control of light on system metabolism

Since the biochemical entry point for energy flow through food webs (i.e., photosynthesis) depends on sunlight, the control of light on primary productivity in an ecosystem is obvious. In terrestrial ecosystems, light availability is influenced by **shading**, which drives competition among plant species. While shading is also a factor in aquatic ecosystems, the main control on light availability across water depths is light **attenuation**. As water depth increases, available light declines exponentially from the amount available at the water surface. Clear water has a low attenuation coefficient, meaning that light penetrates to relatively greater depths. Turbid or colored water bodies tend to have higher attenuation coefficients.

#### V. Control of nutrients on system metabolism

The availability of inorganic nutrients also frequently controls ecosystem-level primary productivity. The German chemist Justus von Liebig (1803 – 1873) investigated the mineral nutrition of plants in agricultural systems. During his studies he realized that crop yield could be increased by fertilizer additions only if the soil present contained all the other necessary nutrients (Liebig 1840). Since then, his ideas have been generalized into **Liebig's Law of the Minimum**, which states that the elemental nutrient least available in a system relative to its requirement by primary producers is the limiting nutrient. Carbon (C), nitrogen (N), and phosphorous (P) are known as macronutrients since primary producers require relatively large amounts of these elements to grow. For example, inorganic N is required for plants to synthesize amino acids and proteins while inorganic P is essential for synthesis of nitrogenous bases, adenosine triphosphate (ATP) and related compounds, and nucleic acids. C, N, and P often limit ecosystem metabolism by limiting primary productivity.

The ratios of C, N, and P that primary producers require vary among species. For unicellular algae such as phytoplankton and the algae in periphyton, this ratio is very close to 106:16:1 on a molar basis. The 106:16:1 ratio is known as the **Redfield ratio**, named after the late Harvard physiologist Alfred C. Redfield (1890-1983). Using this ratio along with data on nutrient availability, we can determine which nutrient is limiting for primary production in any environment. For example, if we know that N and P availabilities in a habitat are 6000 and 300 mg/m<sup>3</sup>, respectively, then we can divide each value by its corresponding Redfield ratio number (e.g., 6000/16 = 375 for N and 300/1 = 300 for P). The result is that the lowest value is produced for P, which is then the limiting nutrient for primary production in our example. While ecologists and physiologists have typically considered the Redfield ratio to be an optimal ratio for primary production, recent research has shown that the Redfield ratio is actually an average that is subject to change depending on future levels of nutrient availability and competition in the environment (Klausmeier et al. 2004).

#### VI. Objectives

In today's lab, you will use the light-dark bottle enclosure method to look at ecosystem metabolism in aquatic habitats on campus. The ecosystem enclosures will be clear and black bottles that we will fill, seal, and incubate for a set period of time. NPP (net primary production = net oxygen gain), R (respiration = oxygen consumed), and GPP (gross primary production = oxygen consumed and oxygen produced) for the purposes of our experiment will be as follows:  
NPP = ([O<sub>2</sub> light bottle] final – [O<sub>2</sub> light bottle] initial)  
R = ([O<sub>2</sub> dark] initial – [O<sub>2</sub> dark] final) GPP = NPP + R  
The units for all three variables (NPP, R, and GPP) will be **mg O<sub>2</sub>/L/hour**.

If you enclose autotrophs, the final oxygen concentration in your light bottles should be greater than the initial concentration while the final oxygen concentration in your dark bottles should be less than the initial oxygen concentration. To measure oxygen concentrations, you will use

oxygen electrode 9-4

meters, which use a gold-tipped electrode to electrically estimate oxygen concentration based on the rate of oxygen diffusion across a permeable membrane that fits over the electrode.

The Everglades ecosystem is oligotrophic (i.e., nutrient poor) and P limited. Recent evidence of historical P limitation in the Everglades comes from the effects of P fertilizer applied to sugar cane fields north of the Everglades. Fertilizers arrive as P-enriched runoff to marsh plant communities in the Everglades where, as a result, cattail (*Typha domingensis* Pers.) expands as oligotrophic-adapted sawgrass (*Cladium jamaicense* Crantz) (Doren et al. 1997, King et al. 2004). To investigate limits on metabolism in aquatic habitats similar to those in the Everglades, we will work in ponds on campus. Specifically, we will use experimental additions of P and different light availabilities in a light-dark bottle experiment to determine whether or not P and light control metabolism in our pond system.

Today in lab you will complete the following objectives:

- 1) Compare ecosystem metabolism in the presence and absence of P additions
- 2) Compare ecosystem metabolism in the sun and in the shade.