Chapter 1 2

Island Biogeography: Students Colonize Islands to Test Hypotheses

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Contents

Introduction: Instructor Guide

This document has two distinct parts. Part one is a lengthy set of instructions for the instructor. Since much of this exercise involves mathematical development and manipulations, and since this is a challenge to typical biology students and some biology instructors, we provide many details. Part two (Section: *Student Guide to Simulating Island Biogeography*) contains the much briefer instructions for the students.

Quick Introduction to the Exercise

This is a laboratory exercise on island biogeography theory designed for an upper-division field ecology course. It combines mathematical modeling through the equations for the MacArthur-Wilson theory of island biogeography with a student physical simulation of the island colonization and extinction process. While the mathematical part can be de-emphasized or eliminated, we feel that it is most important part of this exercise.

The pedagogical philosophy of the exercise is that students learn mathematical concepts in biology when the concepts are grounded in hands-on laboratory activities that generate data which they must evaluate from the context of the mathematics. The approach of this lab exercise is meant to eliminate the “plug-and-chug” method of presenting quantitative concepts to biologists. To avoid the plug-and-chug method, we employ a combination of small group activities, directed enquiry methods, and homework. The activities used will vary with instructor, but we describe some classroom activities that we have found useful.

The learning objectives and goals for the exercise are enumerated in the student hand-out. The major one that we stress is that mathematical models (equations that describe biological processes) play a central role in the scientific method: the equations provide the formal and logical machinery by which hypotheses are translated into testable predictions.

We use two 3-hour lab sessions to complete the exercise. Here is the outline of activities:

1. WEEK 1
   (a) (10-15 minutes) **Pre-test:** An example is included in Section *Homework and Tests*. There are 4 math questions and a questionnaire. The math questions test for (1) graphing, (2) simple linear algebraic manipulations, (3) estimating constants from data for a nonlinear curve, and (4) creating a model of a dynamic process from a verbal description.
   (b) (15 minutes) **Brief introduction to island biogeography:** Students in our lab class have had a general ecology course. We present data for 2 island biogeographical patterns: (1) the species-area curve (e.g., Begon et al. 1990) and (2) the dynamics of island colonization (e.g., Simberloff and Wilson 1969).
   (c) (25 minutes) **Concept Map of Island Biogeography:** After the patterns, we ask the question: Is there a single underlying process that explains both patterns? We then explain that we need a mathematical model and use concept maps to begin the process of defining math models. This is a small-group exercise.
   (d) (20 minutes) **Mathematical Model:** The instructor helps the students as a class develop the basic MacArthur-Wilson equations for rate of change of species numbers. This extensively uses directed enquiry (Cangelosi 1996).
   (e) (45 minutes) **Student Simulation of Island Colonization:** Using the tops and bottoms of plastic petri dishes thrown at string "islands." In groups of 3 or 4, students throw petri dish tops and bottoms at the target and observe the dynamics of species numbers and extinction and immigration rates to the island. In Week 1, we use one island size of 1 m^2 and two distances: 2 m and 4 m. This is a small group exercise performed outdoors.
   (f) (20 minutes) **Data Sharing:** Students copy data of all groups and are given a homework assignment due at Week 2.
2. WEEK 2
   (a) (30 minutes) **Class discussion** of student analysis of data from previous week. Students from groups present their results.
   (b) (10 minutes) **Brief review** of the math models already developed.
   (c) (20 minutes) **Mathematical equation** for species-area relationship.
   (d) (45 minutes) **Students simulate colonization** as in Week 1, but this time varying island size.
   (e) (30 minutes) **Class discussion** of math problems that can be solved with the models.
   (f) **Homework** for the next week.
3. LATER (Approximately 2 weeks later)
   After the second homework has been returned and students have had a chance to discuss it, the **post-test** is administered.

Building a Quantitative Model

The mathematics needed for this exercise is the ability to write the equation for a straight line, the ability to solve algebraically for the intersection of two straight lines, and (optionally) linear regression. We assume any instructor reading this is comfortable with the basic MacArthur-Wilson model (MacArthur and Wilson 1967). If not, Gotelli (1995) contains an approachable introduction.

Concept Maps: Qualitative Models

A concept map is just a diagram composed of circles and arrows. The circles denote processes; the arrows are influences. The initial circle of the map is the process or pattern to be explained (e.g., number of species on an island). When teaching, we illustrate the construction of a concept map with an example on the board. A good example is a concept map for the question "What processes explain the size of a tomato plant?"

We solicit input from the class at large beginning with the initial circle labeled "Plant Size." Students supply circles and arrows with the instructor acting as a scribe. Students readily think of "light," "soil nutrients," "competition," and so on. For example, there will be an arrow from a circle labeled "light" to another circle labeled "growth rate" which is connected to "Plant Size." A key concept that is rarely suggested by the class, but is important to the concepts developed for island biogeography, is *negative feedback*. An example is an arrow back from "Plant Size" to "growth rate."

After this illustration, the class breaks into small groups, are supplied with a hand-out (reproduced in the Appendix) with the initial circle labeled "Number of Species." They are given about 15 minutes to produce their own concept map of the causes of numbers of species on an island. The instructor consults with students as they do this exercise. Two groups are selected to present their concept map to the class and a discussion ensues. The maps produced include many of the words provided as a memory aid to the students; the students want to be inclusive. The instructor emphasizes: the complexity of the maps and the similarity among groups. In the end, the instructor brings the class to focus on factors that affect immigration and extinction. The next step is to develop a mathematical equation that will produce the two patterns.

Equations

Dynamic Equations

The dynamic equations of species numbers are developed with input from the class. We rely heavily on the analogy with a leaky bucket: water is flowing out at some rate and flows in at some rate; the rates may change as the amount of water in the bucket changes. The class is continually solicited for ideas on how to model the processes. We use the directed enquiry method in which the instructor poses a series of questions and problems that are answered through class discussion and small group activities.

We begin by getting the class to simplify as much as possible. Most come quickly to the idea that competition controls extinction rates. We ask for a hypothesized graphical relationship between extinction and competition (What is on the y axis? What is on the x axis? Does it increase or decrease? Is it straight or curved? Which is simpler?) We ask how to quantify this vague idea of competition. Many students will volunteer amount of food, number of individuals. Stressing that simplification is critical, the class is brought to the idea that *species numbers* is a reasonable surrogate for degree of competition. They are then asked to graph the effect species number on extinction rate as an x-y graph. The instructor draws the axes and asks for input on the axes labels and the qualitative relationship (linear with positive slope). This is repeated for the effects of species number on the rate of immigration of **new** species to the island. With increasing species numbers, immigration decreases linearly from a maximum rate to 0 when the number of species on the island is equal to the number on the mainland (and therefore no new species can possibly arrive). Figure 1 shows the relationships. Before writing the equations in the form shown, we ask the class for the equation. Everyone knows $y = mx + b$ for extinction. The negative slope takes more thought for some and we get them to suggest $y = q - rx$. We do not introduce the notation of Fig. 1 until later.

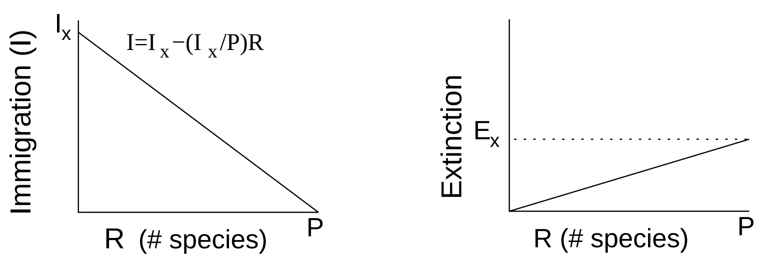

FIGURE 1: The basic hypotheses of the effect of species number on immigration and extinction rates. R is number of species on the island. P is the number of species in the pool (e.g., on the mainland). I_x and E_x are constants: maximum immigration and extinction rates, respectively.

Here is the equation for species dynamics:

$$\frac{dR}{dt} = \text{NR} = \underbrace{I_x - \frac{I_x}{P}R}_{\text{Immigration}} - \underbrace{\frac{E_x}{P}R}_{\text{Extinction}} \tag{1}$$

where R is numbers of species, NR is the “Net Rate of change of numbers of species” (NR is actually dR/dt, but we try not to scare away too many, even though many have had calculus), I_x is the maximum immigration rate (when $R = 0$), P is the number of species on the mainland, E_x is the maximum extinction rate (when $R = P$).

Most students do not recognize the derivative form of the equation, so we convert it into a difference equation so that we can generate the dynamics of species numbers. We usually do not attempt this until Week 2. Here is how to do it:

$$\text{NR} = \frac{dR}{dt} \approx \frac{\Delta R}{\Delta t} \quad = \quad I_x - \frac{I_x}{P}R - \frac{E_x}{P}R \tag{2}$$

$$\Delta R = R_{t+1} - R_t \quad = \quad I_x - \frac{I_x}{P}R - \frac{E_x}{P}R \tag{3}$$

$$R_{t+1} \quad = \quad R_t + I_x - \frac{I_x}{P}R_t - \frac{E_x}{P}R_t \tag{4}$$

We let Δt be 1, a single throwing bout. This last equation is known as a finite difference or recursion equation. If we know R_0 (R at time 0), then we can calculate R_1, substitute R_1 in the right side to compute R_2, and so on.

$$R_1 \quad = \quad R_0 + I_x - \frac{I_x}{P}R_0 - \frac{E_x}{P}R_0 \tag{5}$$

$$R_2 \quad = \quad R_1 + I_x - \frac{I_x}{P}R_1 - \frac{E_x}{P}R_1 \tag{6}$$

$$R_3 \quad = \quad R_2 + I_x - \frac{I_x}{P}R_2 - \frac{E_x}{P}R_2 \tag{7}$$

Using these formulae and the values for I_x, E_x, and P estimated from the data, we can iterate over time to predict the change of species numbers over time.

Species-Area Curve

The species-area curve is presented in Week 2. When we teach this material, we spend much less time on developing the relationship compared to the model of species dynamics. It can be done from the MacArthur-Wilson equations (MacArthur and Wilson 1967), but it requires more math and more patience than most students have.

Here is the equation for the species-area curve:

$$R = cA^z \tag{8}$$

where R is the number of species, A is the area of the island, and c and z are empirical constants.

We then ask: “If we have data for this relationship [draw example on board], how do we estimate the constants?” This is done with a log transform of both sides of the equations and since many students will have forgotten this, we go through it in great detail, reciting the verbal log rules as we solicit the operations from the students in the class. Taking 3–5 minutes to let the students try it before at their desks would be effective. We then emphasize that the result is a straight line and use this to get the constants.

Here is the log-transform:

$$\log R = \log c + z \log A \tag{9}$$

It is necessary to emphasize that the intercept is not c, but the log of c. This is an opportunity to discuss logarithms and anti-logarithms. All of this is covered in middle- and high-school math classes, and in undergraduate algebra classes, but most have forgotten it.

Logistics of Student Simulation of Colonization Rates

After the linear relationships between species number and extinction and immigration rate is hypothesized, we introduce the students to the experimental system (string and petrie plates) with which they are going to act out the colonization and extinction process. The students are assigned to groups (3 is optimal) and we then go outside.

Materials

Each group of 3 or 4 students will need the following:

1. A countdown timer or stopwatch to time the throwing ("colonization") bouts
2. Loops of string to simulate square islands
3. 4 stakes (e.g., large nails) for the corners of the island (masking tape for carpet if indoors)
4. One container of labeled plastic petri dishes (20 "species", 10 individuals per species). Their color markings or numbers distinguish species. This is the mainland or "source population" box.
5. 1 clipboard with 3 or 4 data sheets (1 data sheet for each simulation)
6. A meter stick or tape
7. A grassy (or carpeted) area at least 5 m away from other groups

Student Logistics

1. We have successfully done the exercise outside on a grass lawn and inside on a low-nap carpet. Each group should have either 4 or, preferrably, 3 students.

2. For each group, you will need an area about 6m by 8m, to prevent interaction among groups.

3. Each mainland species pool should have 20 species and 10 individuals per species. More individuals would probably be better, but there are cost and convenience issues. Individuals are standard plastic petri dishes, where each half is used as an individual. Each individual is marked with its species identification. We denote species using 2 methods: 10 species are numbered on white tape 1 through 10 for 10 species. The other 10 species are given colored tape codes: single lengths of tape about 2 inches long and two pieces of tape in a cross pattern (e.g., a length of blue tape and a length of black tape). This doesn't seem to confuse the students, but better labels would be all 20 species as upper-case letters of the alphabet on white tape. We store the mainland pool in plastic garbage bags.

4. Islands are loops of string stretched tautly into squares and affixed to the substrate at the corners. When outside, we use large nails as anchors; masking tape works well on carpet. Students are given the string for the islands already cut to length and knotted to remove one more confusing activity during the exercise.

5. The student hand-out indicates that the students should simulate 2 distances (2m and 4m) and 2 island sizes (1 m^2 and 0.25 m^2). In a 3 hour lab period, with all the group activities

and directed enquiry interaction, in Week 1 there is time only for 1 island size (1 m^2) and 2 distances (2 m and 4 m).

In Week 2, we test the species-area curve and distance on small islands. One group of students do small islands (0.25 m^2) at 2 and 4 m. Other groups do 2 replicates of 1 island 4 m from the mainland with sizes 0.09, 0.49, 0.81, and 2.0 m^2. These plus 0.25 and 1.0 m^2 gives 6 areas for estimating the constants of the species-area curve.

6. Here is the order of events during the simulation:

   (a) **Setup:** The students collect their materials and set up the first experiment: (1) Identify a spot for the thrower (i.e., the mainland); (2) using a meter stick, measure the distance being simulated from the mainland to either the edge or center of the island; (3) select the appropriate loop of string for the island area; (4) determine which student will be the *thrower*, *scorer*, and *timer/recorder*; (5) deposit all of the colonizing individuals within easy reach of the thrower at the mainland; (6) (Important!) Randomize the individuals in the mainland by mixing the pile well.

   (b) **Simulation:** (1) The timer signals to the thrower to begin, (2) the thrower grabs an individual from the mainland and sails it towards the island (those Frisbee skills are finally useful); (3) the thrower repeats this as rapidly as possible for 15 seconds; (4) after a 15 sec throwing bout, the scorer and recorder examine the island: they first identify and remove all extinct **individuals** and those that overlap the string by less than one-half their diameter; (5) the scorer reports to the recorder which species are present and the recorder marks those species on the appropriate line of the data sheet; (6) while this is occurring, the thrower returns the non-colonizing individuals to the mainland pile and re-mixes the pile, (7) the next throwing bout proceeds while the recorder calculates and records the number of immigrations and extinctions, and the resultant number of species on the island for the previous bout. See the hand-out at the end that gives a worked example.

   (c) **Scoring:** (1) an individual is killed when another individual lands on top of it; (2) an individual fails to colonize if less than 1/2 of its diameter is outside the square; (3) a species does not go extinct until the last individual of its species is killed.

   (d) **Recording:** (1) students record only presence or absence of a species by putting an “X” in the appropriate position in the data sheet; numbers of individuals are not used; (2) immigration rate: count the number of “X”s that were not present in the earlier throwing bout (line above current line of data sheet); record this number in the “I” column of the **line above the current data sheet line**; (3) extinction rate: count the number of data sheet cells (species) that do not have an “X” in the current line but did have one in the line above; record this number in the “E” column of the **line above the current data sheet line**; (4) number of species: from the line above the current data sheet line add “R” plus “I” minus “E” and record it in the “R” column of the **current data sheet line**.

The data sheets follow at the end of this document in the Appendix.

Logistics of Student Simulation of Species-Area Curve

The layout and organization of students is the same as above. Convenient areas to add to the 0.25 m^2 and 1.0 m^2 areas already done above are: 0.09, 0.49, 0.81, and 2.0 m^2. Assign one group to each area. Since the purpose of this exercise is only to get estimates of the equation parameters c and z, we do not need to estimate extinction and immigration rates. Each group should colonize as above, but after each bout, records only the number of species on the island. When the numbers are approximately contant over three consecutive bouts, the group can stop the simulation.

Sharing Data and Data Analysis

After the simulation, students return to the classroom and write their values of R, I_x and E_x on the board. All students copy the numbers on the summary data sheets provided in the Appendix.

After Week 1 (see homework below): Students should plot the data and estimate the constants in the model. With these, they can solve for the equilibrium number of species.

After Week 2 (see homework): The students can iterate the recursion equation to get species change. They should also analyze their area data by plotting R versus A, by taking the log of both sides of the species-area equation and plotting $\log R$ *versus* $\log A$.

There is an interesting discrepancy between real island extinction and that simulated here. In the petri plate world, individuals are killed only by new immigrants. In the real world, death due to competition produces starvation or physiological stress, most commonly by resident individuals. The result of this discrepancy is that in the petri plate world, extinctions are correlated with immigrations and any variable that changes immigration will also change extinction. In particular, distance affects immigration rates, so in our simulations it will also affect extinction rates. The usual (simple) presentation of island biogeography theory assumes distance affects only immigration and island size affects only extinction rates. In petri plate world, it is possible (and has been observed in our classes) that far islands will have more species than near islands because as distance decreases extinction rate is increased more than immigration rate is increased. This is worth working out on the board for the students.

Practice Problems

To prepare the students for the homework that is distributed at the end of Week 2, we spend about 30 minutes doing practice problems after completing the species-area simulation. In the classroom, we hand-out the problems without the solutions. We ask the students to help solve the problems as a group. Below are some examples that we use. Some of the problems benefit by breaking the students into small groups to give them some time to solve the problems. After all the problems have been discussed, we hand-out the solutions and the homework for the following week.

Example Practice Problem Set

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1. If $R = cA^z$, what are the "best" values of c and z given the following data?

Area	1	5	10	20	30	48
R	2	10	20	20	38	29

2. (a) Assume island size only affects extinction rates. What is the effect of size on equilibrium number of species (R)? Use a graphical argument.
   (b) Assume distance only affects immigration rates. What is the effect of distance on equilibrium R? Use a graphical argument.

3. What are the equations for Immigration and Extinction, given that (a) the island can not have more species than the mainland, and (b) extinction is maximum when the island has the same number of species as the mainland?

4. What is the formula for the equilibrium numbers of species on an island?

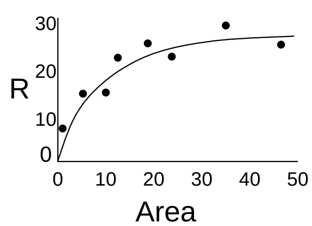
5. If I_x (maximum immigration rate) $= 8$, $P = 20$, and $E_x = 1.0$, complete the following table.

t = Time (bout)	0	1	2	3	4
R_t					

6. An island is at equilibrium at $\hat{R}$, and $P = 50$, $E_x = 5$, and the observed extinction rate at equilibrium is 4 species/year.
   (a) What is $\hat{R}$?
   (b) What is maximum immigration rate?
   (c) If the maximum immigration rate is increased by 2 times, what is the new $\hat{R}$?

Solutions

1.

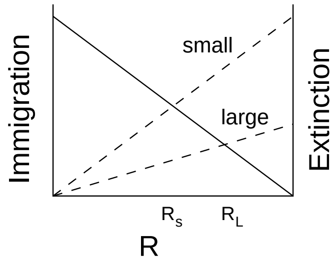


$$
\begin{aligned}
R &= cA^z \\
\log(R) &= \log(cA^z) \\
&= \log(c) + \log(A^z) \\
&= \log(c) + z\log(A)
\end{aligned}
$$

$\Longrightarrow$ straight line: $y = mx + b$
$x = \log(A)$, $m = z$, $b = \log(c)$

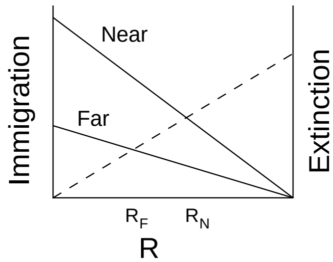
So, to find c and z: Take logs of area data and number of species data; do a regression.

2. (a)



$\downarrow$ size $\implies$ $\uparrow$ competition
$\implies \uparrow E$
$\implies \downarrow \hat{R}$

(b)



$\downarrow$ distance $\implies \uparrow I$
$\implies \uparrow \hat{R}$

3. Change in R from t to $t+1$ (e.g., from bout 1 to bout 2):

$$\Delta R = \text{NR} = \underbrace{I_x - \frac{I_x}{P}R}_{\text{Immigration}} - \underbrace{\frac{E_x}{P}R}_{\text{Extinction}}$$

4. 'Equilibrium' means no change in R, i.e. $\Delta R = 0$. So, let $\hat{R}$ be the number of species at equilibrium:

$$\Delta R = 0 = \underbrace{I_x - \frac{I_x}{P}R}_{\text{Immigration}} - \underbrace{\frac{E_x}{P}R}_{\text{Extinction}}$$

or

$$I_x - \frac{I_x}{P}\hat{R} = \frac{E_x}{P}\hat{R}$$

or

$$\hat{R} = \frac{I_x P}{I_x + E_x}$$

5. The change in R from t to $t+1$ is $\Delta R = R_{t+1} - R_t$

or

$$\begin{aligned} R_{t+1} - R_t &= I_x - \frac{I_x}{P}R - \frac{E_x}{P}R \\ R_{t+1} &= R_t + I_x - \frac{I_x}{P}R - \frac{E_x}{P}R \end{aligned}$$

In particular, if $R_0 = 0$, $I_x = 8$, $E_x = 1.0$, and $P = 20$, then

$$\begin{aligned} R_1 &= 0 + 8 - \frac{8}{20}0 - \frac{1}{20}0 = 8 \\ R_2 &= 8 + 8 - \frac{8}{20}8 - \frac{1}{20}8 = 12.4 \\ R_3 &= 12.4 + 8 - \frac{8}{20}12.4 - \frac{1}{20}12.4 = 16.06 \end{aligned}$$

and so on.

6. To solve problems like these, list the values you know and the things you want to know and think of an equation that relates them. Also it helps to draw a graph of the equations and label the graph with all the information you have.
   (a) Extinction rate at equilibrium = $\frac{E_x}{P}\hat{R}$ and we know $E_x = 5$, $P = 50$, and extinction rate = 4.0. So,
   $$\frac{5}{50}\hat{R} = 4$$
   $$\text{or } \hat{R} = 40$$
   (b) We know $\hat{R}$ and P, so we can use the equation for
   $$I = I_x - \frac{I_x}{P}\hat{R}$$
   or
   $$4 = I_x\left(1 - \frac{40}{50}\right)$$
   or
   $$I_x = 20$$
   (c) In problem 4, we derived a general equation for $\hat{R}$:
   $$\hat{R} = \frac{I_x P}{I_x + E_x}$$
   so
   $$\hat{R} = \frac{40 \cdot 50}{40 + 5} = 44.44$$

Homework and Assessment Tests

Week 1 Homework

1. (10 points) Use the class data to estimate the coefficients (constants) for extinction and immigration rates based on the mathematical theory developed in class. (You may use a spreadsheet if you wish, but it is not required.)
2. (5 points) Using the equations and constants estimated in problem 1, use algebra to solve for the equilibrium number of species on the islands.

Week 2 Homework

1. For many oceanic islands the constant z in the species area curve is between 0.20 and 0.40. Are the data collected in class consistent with this pattern? Why or why not?

2. Regressions of immigration rates and extinction rates against species numbers gave these equations.

$$\begin{aligned} I &= 7.8 - 0.55R \\ E &= 0.12R \end{aligned}$$

What is the equilibrium number of species?

3. How many species will on the island described in problem 2 for **each** of the first 5 colonization bouts?

4. In the table below are values of amphibians and reptiles on West Indian islands. (Values are logarithms of square kilometers and species numbers.)

$\log_{10}$ Area	0.415	1.30	2.06	4.02	4.11	5.11	5.32
$\log_{10}$ Number of Species	0.602	0.845	0.954	1.61	1.59	1.95	1.93

   (a) What are the constants of the species-area curve?
   (b) Plot the number of species versus area using an arithmetic scale (not a logarithmic scale).

5. In many cases, isolated patches of habitat within a continent act like islands for the organisms that require that habitat. Forest fragmentation and the reduction of habitat due to human activities (e.g., urban sprawl, logging, etc) is causing the decline of many populations, ultimately resulting in their local extinction in the affected areas. You are a manager of a forest preserve that is scheduled to have its area reduced by 0.5 due to a new housing development. Based on the following, how many species do you expect will exist in the preserve after the development?

   Assume: (a) the number of species on the preserve is constant, but there are annual extinctions and arrivals of new species, (b) the number of species in the area surrounding the threatened preserve that could colonize is 50, (c) the maximum immigration rate to the preserve is 8 species per year, (d) before development, the preserve lost 2 species per year, and (e) if the area is reduced by 0.5, the extinction rate doubles.

Solutions to Week 2 Homework

1. Take the logarithms of area: 0.09, 0.25, 0.49, 0.81, 1.0, and 2.0 and of the corresponding species numbers. Regress $\log(R)$ *vs* $\log(A)$ statistically or by "eye." The regression coefficients will give you the parameters: z is the slope, and c is 10 raised to the power of the intercept (if you used log base 10).

2. At equilibrium:

$$\begin{aligned} I = E &\implies 7.8 - 0.55\hat{R} = 0.12\hat{R} \\ &\implies \hat{R} = 7.8/0.67 = 11.64 \\ &\implies \hat{R} = 11 \qquad \text{since species are integers)} \end{aligned}$$

3. I = immigration rate, E = extinction rate

$$R_{t+1} = R_t + I - E$$

$$= R_t + 7.8 - 0.55R_t - 0.12R_t = R_t + 7.8 -).67R_t$$

or

$$\begin{aligned}
R_0 &= 0 \\
R_1 &= 0.0 + 7.8 - (0.67)(0.0) = 7.8 \\
R_2 &= 7.8 + 7.8 - (0.67)(7.8) = 10.374 \\
R_3 &= 10.374 + 7.8 - (0.67)(10.374) = 11.22 \\
R_4 &= 11.22 + 7.8 - (0.67)(11.22) = 11.503 \\
R_5 &= 11.503 + 7.8 - (0.67)(11.503) = 11.596
\end{aligned}$$

4. After taking logarithms and doing linear regression: $z = 0.28248$ and $c = 10^{0.4532} = 2.839$.
5. E_x = maximum extinction rate, I_x = maximum immigration rate.

GIVEN: $P = 50$ and $I = 8$

$$\implies I = 8 - 8/50R = 8 - 0.16R$$

GIVEN: $E = 2$ at equilibrium

$$\begin{aligned}
&\implies 8 - 0.16\hat{R} = 2 \\
&\implies \hat{R} = 37.66 \\
&\implies \text{E at } \hat{R} = 2 = (E_x/P)\hat{R} = (E_x/50)(37.66) \\
&\implies E_x = 2.655
\end{aligned}$$

GIVEN: Decrease area by 1/2

$$\begin{aligned}
&\implies E_x = 2.0E_{x,\text{old}} \\
&\implies \text{at new equilibrium: } I = E \implies 8 - 0.16\hat{R} = (2)(0.0531)\hat{R} \\
&\implies \hat{R} = 30.05 \approx 30
\end{aligned}$$

Example Pre-test

Pre-tests and post-tests are very good things to do. It not only gives the instructor essential feedback, but we have found that class averages do generally improve by about 15–20% in these skills. This can be useful ammunition when students complain to your superiors that the course is too difficult. In addition to testing for quantitative skills using the following math questions, we also request information about the student's previous math and biology courses including grades earned (omitted here). It is very revealing to correlate grades in calculus and performance on the pre-tests.

Assessment 1: Do NOT write your name.

1. Here are two equations:

$$\begin{aligned}
y_1 &= 3.0x \\
y_2 &= 10.0 - x
\end{aligned}$$

(a) Using the axes below, label the axes with numbers and graph the two lines.

(b) Use algebra (not the graph) and find the value of x where y_1 equals y_2. Show your work.

2. Below are data on the kilocalories required by birds of different sizes to fly 1 km.

   You want to statistically fit these data to the following equation:

$$y = ax^b$$

   (a) Describe in words how you would obtain the best estimates of a and b. Show any algebra manipulations you would do.

   (b) Without using a calculator, circle one of the following that you think is true:
   $b > 1$ $b = 1$ $0 < b < 1$ $b = 0$ $b < 0$.

3. Suppose we have a disease with these properties: Every year, the disease increases by N new cases, and every year a fixed proportion (c) of the diseased cases (D) are cured. Answer the following:

   (a) Write an equation for the rate of change of the disease:

$$\Delta D =$$

   (b) Over time, which of the following is true: (a) the disease will increase forever without bound, (b) the disease will go to extinction, or (c) the disease will level off at constant numbers. Use graphs to explain why you chose the answer you did.

Example Post-test

Assessment 2: Do NOT write your name.

1. Here are two equations:

$$y_1 = 1.0$$
$$y_2 = 2.0 - 0.4x$$

   (a) Using the axes below, label the axes with numbers and graph the two lines.

   (b) Use algebra (not the graph) and find the value of x where y_1 intersects y_2. Show your work.

2. Below are data relating heart rate (R) and body mass (M) for several species of vertebrates.

   You want to statistically fit these data to the following equation:

$$R = aM^b$$

(a) Describe in words how you would obtain the best estimates for a and b. Show any algebra manipulations you would do.

(b) Without using a calculator, circle one of the following that you think is true: $b > 1$ $b = 1$ $0 < b < 1$ $b = 0$ $b < 0$.

3. In the steamy jungles of South America, there lives a bird of great beauty: the exotic Resplendent Whoopee. Each year a constant (D) number of birds die. The number of new Whoopees born in a given year decreases from a maximum (M) linearly as the number of adult Whoopees (W) increases.

   Answer the following:

   (a) Write an equation for the rate of change of the Whoopee numbers:

   $$\Delta W =$$

   (b) Over time, which of the following is true: (a) the Whoopee will increase forever without bound, (b) the Whoopee will go to extinction, or (c) the Whoopee will level off at constant numbers. Use graphs to explain why you chose the answer you did.

Typical Results from Students

Figure 2 show typical results from the simulated colonization experiments. As can be seen, there is ample opportunity for discussing the nature of statistical variation both within and between student groups.

Improvements

The extinction rates are really too low. This can be increased with a rule like: “Individuals are killed if a new colonist falls within 3 cm.” But this would be difficult to implement without direct touching of the disks.

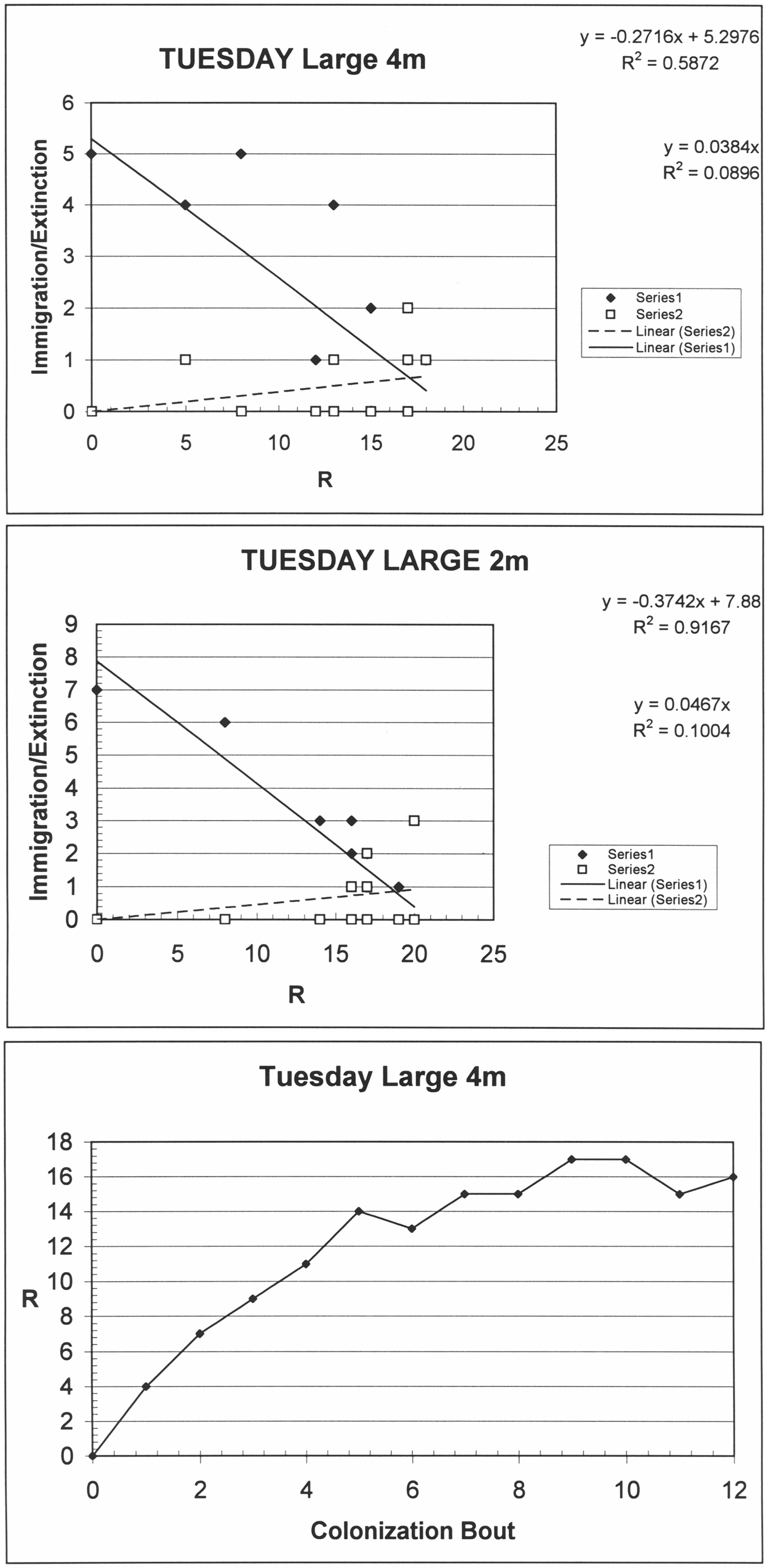


FIGURE 2: Student data for 1 m^2 islands 2 meters and 4 meters from the mainland.

Student Guide to Simulating Island Biogeography

Laboratory Goals

Understand the use of mathematics in the scientific method as it applies to formulating and testing the theory of island biogeography.

Laboratory Objectives

1. Identify key variables determining the number of species on an "island."
2. Qualitatively explain how key variables determine the number of species on an "island."
3. Demonstrate mathematically how key variables determine the number of species on an "island" and the equilibrium species richness.
4. Design a quantitative experiment that synthesizes the key variables that determine the number of species on an "island."
5. Statistically compare experimental data with theoretical predictions.

Materials

Each group of 3 or 4 students will need the following:

1. A countdown timer or stopwatch to time the "colonization" bouts
2. Loops of string to simulate square islands
3. 4 stakes for the corners of the island (masking tape for carpet if indoors)
4. One container of labeled plastic petri dishes (20 "species", 10 individuals per species). Their color markings or numbers distinguish species. This is the mainland or "source" population.
5. 1 clipboard with 3 or 4 data sheets (1 data sheet for each simulation)
6. A meter stick or tape to measure island distances and sizes
7. A grassy (or carpeted) area at least 5 m away from other groups

Experimental Protocol

Creating Your Islands

1. Determine what your group's square island dimensions and distance from the source population will be. It will be one of the following:

	Close (2m)	Far (4m)
Small (0.25 m^2)	X	X
Large (1.0 m^2)	X	X

2. With the meter stick, string, and stakes or tape, locate your island anywhere safe on the playing field. For example, you do not want your flight path intersecting with another group's flight path.
3. Establish your source population (i.e., the container with all the petri dishes). To do this, measure your group's island distance from the center of your island in any safe direction. Plant a flag or stake at this location. This is where you will be dispersing your species. Sit or kneel with the container containing your source population (the one with all the petri dishes) at this spot.

Division of Labor

Each group consists of 3 or 4 students. The following jobs need to be distributed among group members.

1. **Thrower:** This person should be your most precise and unbiased thrower (i.e., consistently accurate). Practice to determine this. The thrower tosses as many plastic discs from the source population box, while sitting or kneeling, as he or she can in 15 seconds. The thrower may not throw the next disc until the previously thrown disc has hit the ground. You may find it convenient to put the "immigrating" species in a pile in front of you.
2. **Timer/Scorer:** The time keeps track of the three replicates of 20, 15-second colonization events. The timer shouts start and stop to disc thrower at the beginning and end of a colonization event.
   The scorer examines the island and calls out to Recorder the identity of the resident species (R) after each 15-second colonization event. The scorer also returns unsuccessful colonists (discs outside the island) to the mainland area after each 15 second round. Be sure to mix the source population discs after each round to maintain an approximately random distribution.
3. **Recorder:** This person records on the data sheets the species present after a throwing bout as determined by the scorer. Furthermore, he or she keeps track of immigration (I) and extinction (E) events. All information is tallied on the data sheets provided (one sheet per replicate experiment of 20, 15 second bouts).

Figure 3 depicts the relationships of the three team members.

Scoring Definitions and Rules

After a colonization bout, the number of immigrants and extinctions are tallied. See the hand-out that illustrates how to score immigrations and extinctions.

1. **Immigrant (I):** An immigration event is the arrival on the island of an individual (disk) which was not present in the prior colonization bout. At least one-half of the disc must be inside the boundary to count as a successful individual.
2. **Extinctions (E) and Individual Deaths:** An individual dies and is removed from the island if another individual lands on top of it. A species goes extinct when the last individual in its

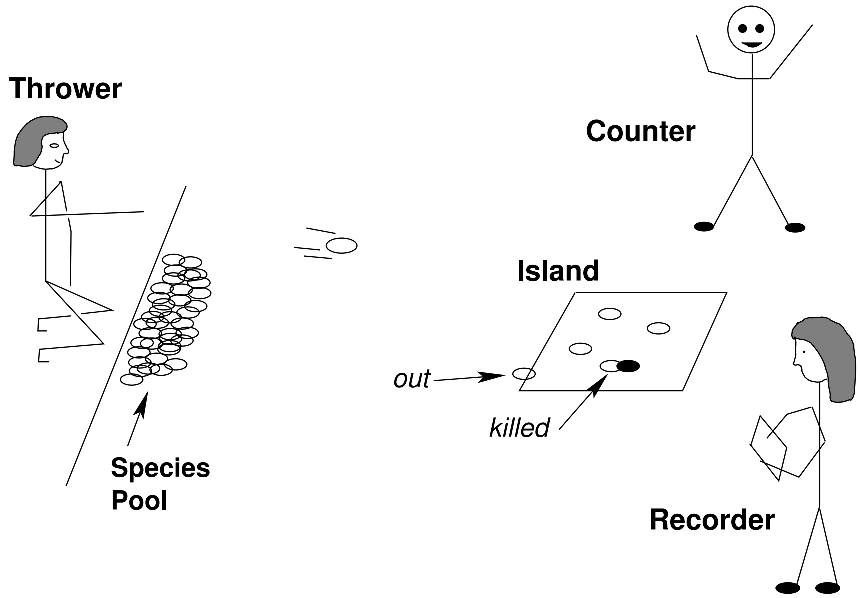


FIGURE 3: Schematic of experimental island colonization system

species is removed from the island. If this happens, there will be no “X” in its column on the data sheet and it will be recorded as an extinction event. Remove the dead individual by sliding it from under the new species and return it to the mainland. If a newly immigrating individual lands on one of two or more individuals on the island, both are killed and removed from the island. All discs coming to rest outside the island boundaries or more than halfway outside the island boundaries following a 15 sec colonization attempt are considered “dead” and recycled.

3. **Number of Resident Species:** The number of resident species (R) is the number of each species remaining on the island after a 15 second colonization event after taking into consideration any extinctions or new immigrations that took place.

Note: *Consult with your instructor if you have any questions about scoring. It is important that all groups are consistent.*

Important Tips

Your data will be best if you remember to do the following.

1. Take care with throwing. Throw as accurately but as quickly as you can in each 15 second bout.
2. After **each** bout, return all of the disks that are **outside** the island back to the Thrower. **Do not remove the disks from within the island.**
3. Randomize your source pool of species. Before each throwing bout, mix up the species pool of disks.

Tallying Data

After determining the number of immigrants and extinctions that occurred during the 15 sec bout, the scorekeeper records (with check marks) the number of resident species present after each colonization event (see worked example below). Species are listed across the top, and time (colonizing bout) along the side. **Remember:** Only presence or absence of species is important; we do not need to record numbers of individuals.

TABLE 2: Sample calculation of R, I,and E

	Species				Variables		
Bout	A	B	C	D	R	I	E
0	—	—	—	—	0	1	0
1		X			1	2	0
2	X	X	X		3	1	1
3	X	X		X	3	—	—

From bout = 0 to bout = 1, your island had 1 immigrant (species B) and, of course, no extinctions. So, a 1 is recorded in the I column at bout = 0, and the immigrating species B is checked (X) in the bout = 1 row. Therefore, the number of residents after the first colonization bout is 1 ($1 = 0 + 1 - 0$).

From bout = 1 to bout = 2, your island had 2 immigrants (species A and C) and no extinctions. So, a 2 is recorded in the I column at bout = 1 and a 0 in the E column at bout = 1. The species immigrating are checked in the bout = 2 row by placing an 'X' in columns A and C. Therefore, the number of residents after the second bout is 3 ($3 = 1 + 2 - 0$).

From bout = 2 to bout = 3, your island had 1 immigrant (species D) and 1 extinction (species C). So, a 1 is recorded in the I and E columns at bout = 2, and the species are checked in the bout = 3 row. Therefore, the number of residents after 3 bouts is 3 ($3 = 3 + 1 - 1$).

This process is continued until 20 15-second colonization bouts have been completed.

Pool the Data

When all the groups have completed 20 bouts (or told to stop by the instructor), write your data on I, E and R on the board. You will receive a summary data sheet for recording all of the class data.

Species-Area Curve

To estimate the parameters of the species-area curve, we need more than two areas. Some of the groups, as assigned by the instructor, will also simulate colonization at four other areas. The activities are exactly as before, **except** you do not need to record numerically immigrations and extinctions. Here, we are interested only in the equilibrium number of species. So, after each colonizing bout, kill the individuals that overlap, return the outside plates to the thrower, and record the number of species on the island. Repeat until the numbers of species is approximately constant over three bouts. Record the final number of species and pool your results with the other groups.

Acknowledgements

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Appendices: Data Sheets

The following data sheets are included.

1. Template for the Concept Map exercise.
2. Datasheet for student simulation of colonization: original version.
3. Datasheet for student simulation of colonization: New version using alphabet letters for species names
4. Example calculation of R, I, and E
5. Datasheet for class pooled colonization data
6. Datasheet for class pooled Species-Area curve data

CONCEPT MAP FOR BIOGEOGRAPHY: **POSSIBLE** ECOLOGICAL CONCEPTS
(Use ONLY the concepts you think are REALLY important.)

POP GROWTH RATE	PREDATION	MUTUALISM
K SELECTION	ABIOTIC ENV.	DISPERSAL
PHYSIOLOGICAL TOLERANCE	FITNESS	ALLOMETRY
PARAPATRY	ISLAND SIZE	SYNERGISM
COMPETITION	EVOLUTION	NUTRIENT CYCLING
SUCCESSION	NICHE	SPECIES DIVERSITY
DENSITY DEPENDENCE	CONSUMPTION	ENERGY FLOW
COOPERATION	PRIMARY PRODUCTIVITY	PLATE TECTONICS
MAINLAND DISTANCE	AGGRESSION	RESOURCE LEVELS
COOPERATION	CARRYING CAPACITY	GENETIC DIVERSITY
EFFICIENCY	POP. CYCLES	DEMOGRAPHY

Number of species on an island

t	Species: 1	2	3	4	5	6	7	8	9	10	Blue /	White /	Yellow /	Green /	Mask /	Pink /	Black /	Blue-Black X	Pink X	Mask X	R	I	E
0																							
1																							
2																							
3																							
4																							
5																							
6																							
7																							
8																							
9																							
10																							
11																							
12																							
13																							
14																							
15																							
16																							
17																							
18																							
19																							
20																							
21																							

R = # of resident species
I = # of new species immigrating
E= # of species going extinct

$$R_{t+1} = R_t + I_t - E_t$$

	Species																						
t	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	R	I	E
0																							
1																							
2																							
3																							
4																							
5																							
6																							
7																							
8																							
9																							
10																							
11																							
12																							
13																							
14																							
15																							
16																							
17																							
18																							
19																							
20																							
21																							

R = # of resident species
I = # of new species immigrating
E= # of species going extinct

$$R_{t+1} = R_t + I_t - E_t$$

Example Calculation of Species Numbers (R), Immigration Rate (I), and Extinction Rate (E)

An "X" indicates the species was present after the throwing bout (t). An immigration occurs when an an "X" appears; an extinction occurs when an "X" disappears.

t	Species 1	Species 2	Species 3	Species 4	Species 5	R	I	E
0						0	1	0
1	X					1	2	0
2	X	X	X			3	1	1
3		X	X	X		3	2	0
4	X	X	X	X	X	5		

R = # of resident species
I = # of new species immigrating
E= # of species going extinct

$$R_{t+1} = R_t + I_t - E_t$$

Example: After bout 3, Species 1 went extinct, Species 2 and 3 remained on the island, and Species 4 immigrated. In column "I" on the line above (t=2) record 1 immigration and in column "E" record 1 extinction. The number of species after bout 3 is: $R_3=R_2+I_2-E_2$ OR: 3 = 3 +1 −1

Island Area:			
Distance:			
Bout #	R	I	E
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
12			
13			
14			
15			
16			
17			
18			
19			
20			

Island Area:			
Distance:			
Bout #	R	I	E
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
12			
13			
14			
15			
16			
17			
18			
19			
20			

Island Area:			
Distance:			
Bout #	R	I	E
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
12			
13			
14			
15			
16			
17			
18			
19			
20			

Island Area:			
Distance:			
Bout #	R	I	E
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
12			
13			
14			
15			
16			
17			
18			
19			
20			

Island Area:			
Distance:			
Bout #	R	I	E
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
12			
13			
14			
15			
16			
17			
18			
19			
20			

Island Area:			
Distance:			
Bout #	R	I	E
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
12			
13			
14			
15			
16			
17			
18			
19			
20			

ISLAND AREA (square meters)	**NUMBER OF SPECIES**