Island Biogeography Laboratory

1 Learning Goals

At the end of this laboratory, the students should be able to:

- Describe the species–area curve and the equilibrium model of island biogeography;
- Use the equilibrium model of island biogeography to predict both (a) the equilibrium number of species on an island and (b) the equilibrium species turnover rate;
- Test the predictions of the model using a physical simulation (e.g., the Island Biogeography Game);
- Construct appropriate figures and tables to explain the species–area relationships; and
- Explain the link between the equilibrium model of island biogeography and the species–area relationship.

2 Introduction

Ecologists have repeatedly observed a striking relationship between the number of species on an island (species richness) and the island size or area. In general, larger islands support more species following a non-linear relationship like that shown in Figure 2. This pattern is called the *species–area relationship*.

This relationship is important not only on oceanic islands but on islands all around us. Ponds are islands in a sea of land; mountain tops are island refuges for boreal plants and animals left behind by retreating glaciers. A tree or small copse in a savanna can be considered an island for birds and insects. Urban parks can be studied as islands. Generally, any series of discontinuous patches of habitat can be modeled this way.

The species–area relationship is empirically described as $S = cA^z$, where S is the number of species on the island, A is the area of the island, c is a constant measuring the number of species per unit area, and z is the slope relating S to A. In practice, c and z are parameters determined empirically and z usually ranges between 0.15 and 0.35 when there are not strong interactions among species. Figure 2 illustrates what this curve looks like when $c = 9$ and $z = 0.2$.

As this pattern is so common, ecologists wonder what ecological processes might generate the pattern. McGuinness (1984) reviews four alternative hypotheses that have been suggested including:

- Random Placement Hypothesis. This is actually a null hypothesis that species should be randomly distributed.
- Habitat Diversity Hypothesis. This hypothesis assumes that as island area increases, new habitats tend to appear that might fulfill different organismal niche requirements.
- Disturbance Hypothesis. Populations on small islands are more susceptible to extinction.
- Equilibrium Theory. This idea was introduced by R. MacArthur and E. O. Wilson in their 1967 book titled *The Theory of Island Biogeography*. It combines the Habitat Diversity and Disturbance Hypotheses together and is the focus of this laboratory.

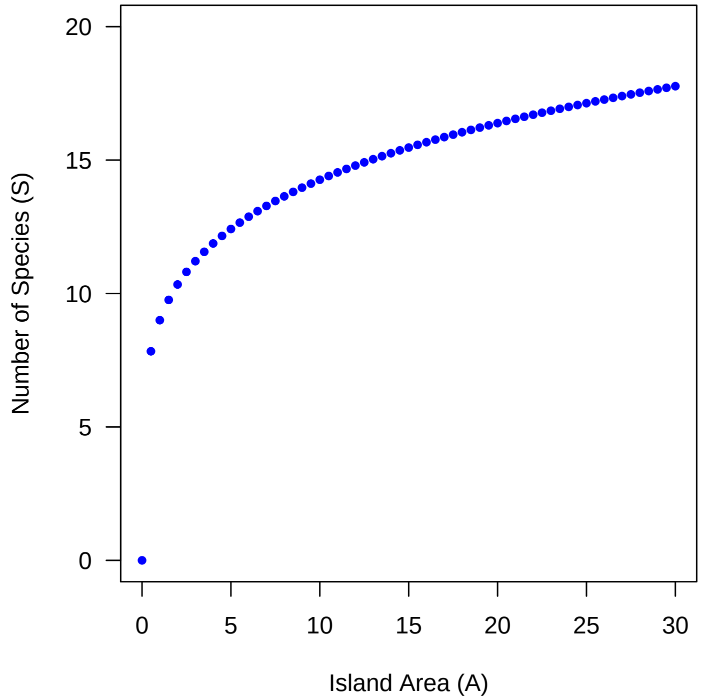

Figure 1: Hypothetical example of a species area curve, $S = cA^z$. In this example, $c = 9$ and $z = 0.2$.

3 Equilibrium Model of Biogeography

MacArthur and Wilson were proponents of the *equilibrium model of biogeography* as a hypothesis to explain the species area curve. The basic premise of the model is that the rate of change in the number of species on an island depends critically on the balance between (1) the *immigration* of new species onto the island and (2) the *extinction* of species from the island. We can then express the net rate of change in species number as follows:

$$\text{net rate of species change} = \text{Immigration} - \text{Extinction} \quad (1)$$

How might immigration and extinction work on an island? We will make two sets of biological hypotheses or assumptions regarding these processes.

immigration Individuals of each species have a constant and identical probability of arriving at the island. Further, the rate of immigration (I) of a new species only occurs upon the arrival of a new species (i.e., species can only colonize once). This implies that I will decline with the number of species (S) present on the island.

extinction The probability of extinction of any species is constant. This implies that the total rate of extinction (E) for an island will increase with the number of species (S).

Figure 2 graphically represents these hypotheses. In the absence of additional information, we have assumed that I and E are constant linear relationships defined as follows:

$$I = I_x - \left(\frac{I_x}{P}\right) S \quad (2)$$

$$E = \frac{E_x}{P} S \quad (3)$$

where I_x is the *maximum immigration rate* that occurs when the island contains no species, P is the pool of species available on the main land, and E_x is the *maximum extinction rate*, which occurs when all possible species are present on the island.

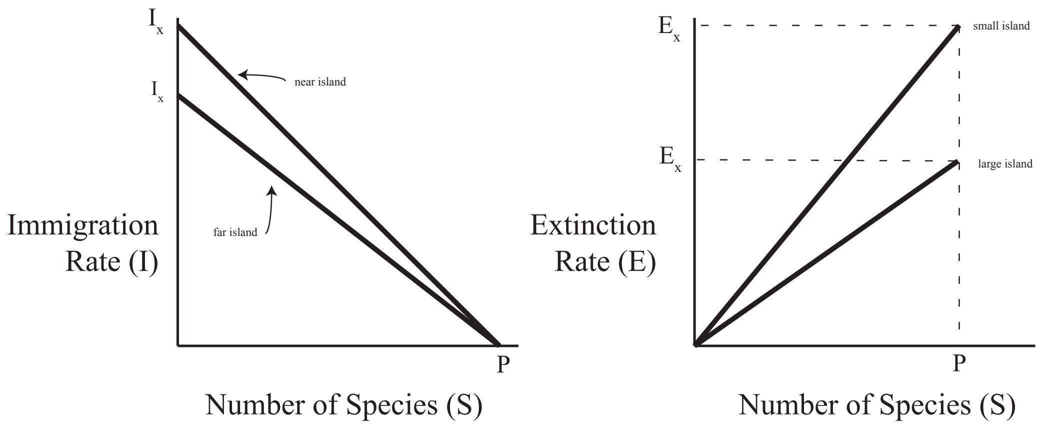

Figure 2: Immigration rate (I) and extinction rate (E) both vary with the number of species on the island.

We now consider a discrete-time model of Mac Arthur and Wilson's (1970) *Equilibrium Model for Island Biogeography*. This predicts how the number of species will change through time. We represent this as:

$$S(t+1) = S(t) + I(t) - E(t), \tag{4}$$

which states that the number of species on the island in one time step $S(t+1)$ is based on the total number of current species on the island $S(t)$ plus the new immigrants $I(t)$ minus the number of species who went extinct $E(t)$ during the time period. We can substitute equations (2) and (3) into equation (4) as

$$S(t+1) = S(t) + I_x - \left(\frac{I_x}{P}\right) S(t) - \frac{E_x}{P} S(t). \tag{5}$$

We can use this model to estimate the number of species expected to be on an island. Notice that in this model, we have not yet said anything about how *area* will effect the number of species; however, we could easily assume that maximal extinction rate would be larger on a small island. Why might this be a reasonable assumption?

3.1 Equilibrium Analysis

We can now use the model in equation (5) to find the number of species expected on the island at *equilibrium*, when the net rate of change in the number of species is zero. We will start by subtracting $S(t)$ from both sides of equation (5) such that

$$S(t+1) - S(t) = I_x - \left(\frac{I_x}{P}\right) S(t) - \frac{E_x}{P} S(t). \tag{6}$$

Next we recognize that $S(t+1) - S(t)$ is the net rate of species change, and set it equal to zero for our equilibrium analysis. We then solve the resultant equation for $S(t)$, which we rename as $\hat{S}$ because it represents the number of species expected at equilibrium.

$$0 = I_x - \left(\frac{I_x}{P}\right)\hat{S} - \frac{E_x}{P}\hat{S} \quad (7)$$

$$I_x = \left(\frac{I_x}{P}\right)\hat{S} + \frac{E_x}{P}\hat{S} \quad (8)$$

$$I_x = \left(\frac{I_x}{P}\right)\hat{S} + \frac{E_x}{P}\hat{S} \quad (9)$$

$$I_x = \left(\left(\frac{I_x}{P}\right) + \frac{E_x}{P}\right)\hat{S} \quad (10)$$

$$\frac{I_x}{\left(\left(\frac{I_x}{P}\right) + \frac{E_x}{P}\right)} = \hat{S} \quad (11)$$

$$\frac{I_x P}{I_x + E_x} = \hat{S} \quad (12)$$

What we do not know at this point is how long it will take for the number of species to reach an equilibrium value. How could we determine this? What is the expected turnover rate of species on the island?

3.2 Model Assumptions

Gotelli (2008, p. 166) notes that this model makes a number of critical assumptions, mostly at the population level. The assumptions he identifies are:

1. An island potentially can be colonized by a set of P source pool species that have similar colonization and extinction rates;
2. The probability of colonization is inversely proportional to isolation or distance from the source pool;
3. The population size of a given species is proportional to the area of the island;
4. The probability of a population going extinct is inversely proportional to its size; and
5. Colonization and extinction of local populations is independent of species composition on the island.

4 Island Biogeography Game

We will physically simulate the colonization of islands by species traveling from a mainland by playing the "Island Biogeography Game".

4.1 Materials

- deck of 52 cards
- game board
- 6-sided die

4.2 Procedure

We will simulate both immigration and extinction of species.

4.2.1 Immigration

Immigration success for a species is randomly determined by turning over cards. To determine how many columns you will move away from the continent, turn over a card from the deck. If the card is red, move out from the continent according to the face value of the card (ace=1, jack=11, queen=12, king = 13. If the card is black, move 13 units plus the face value of the card.

To determine the north-south position of immigration, turn over a second card. Go south (down from the top) according to the face value of the card regardless of color (ace=1, jack=11, queen=12, king=13). If your species game piece does not land on a square with an island, your colonist died. If the species was not successful or is already present on the island, ignore the attempt and repeat the procedure with the next species. In the first part of this exercise, the primary factor affecting colonization was island size. If the colonist did land on the island, do the following to take into account the decreasing probability of colonization with increasing distance from the mainland. Note the zone (I-VI) in which the colonist landed. Roll the die and check Table 1 to determine colonization success.

Table 1: Colonization success.

Zone	Die must be
I	1–6
II	2–6
III	3–6
IV	4–6
V	5–6
VI	6

If the colonization was unsuccessful, your species was unable to colonize the island because the distance from the continent was too great. If the die landed within the required range, the colonization was successful.

Repeat the immigration procedure until you have made 20 successful colonizations. Note: The colonizations will necessarily mean a single species may colonize several different islands and several different species may colonize the same island. However, no species may colonize an island more than once. Thus, if a species lands on an island where it is already present, it does not add a new species to that island and you must disregard the attempt at colonization.

4.2.2 Extinction

After completing the colonization phase, determine whether the species will actually survive on the island it has reached. Extinction rates depend on island size, with higher rates of extinction on smaller islands.

Islands on the board game range from small to medium to large (one of each size occurs in each zone). For each species that has colonized an island, determine if it becomes extinct by rolling the die and following the schedule shown in Table 2.

Table 2: Extinction Probabilities

Island Size	Die Numbers for Extinction	
small	4-6	$3/6 = 0.5$
medium	5-6	$2/6 = 0.333$
large	6	$1/6 = 0.1667$

Repeat this procedure for each species on each island. When you have completed the entire process, record the number of species on each island according to island size and distance zone.

5 Applying the Model to the Physical Simulation

The next step is to apply these theoretical considerations to the island biogeography game. Given the model, we can now predict the equilibrium number of species on each island on the game board. To do this, however, we must determine the values of I_x and E_x. Stop for a moment and consider what these might be.

5.1 Immigration or Colonization

Here, we assumed that the probability of successfully colonizing an island is only determined by (1) the distance of the island from the mainland and (2) the number of species on the island. Given these assumptions, I_m will only be affected by distance. Thus, the likelihood of successful colonization shown in Table 1 equate to the I_m values.

Notice that each island size in each zone will have a different I_x due to island *distance* from the main land.

5.2 Extinction

What is the maximum extinction rate E_x in our physical simulation? This is simply the probability of extinction that is defined in Table 2 multiplied by the total number of species on the mainland (P). We can write this as follows.

$$E = Ex * P \tag{13}$$

Notice that we have assumed that the maximal extinction rate depends on the size or *area* of the island.

5.3 Equilibrium Model Prediction

We can now plug in our values for Ix and Ex into our equilibrium solution in equation (12) to determine the expected number of species on each island. These calculations are built into a "spread sheet model" of this using Microsoft Excel that is available from the class website. If we assume that the number of species on the main land is ten ($P = 10$), then the equilibrium expectation is as shown in Table 3.

Table 3: Equilibrium number of species expected on the islands in the BIOL366 Island Biogeography game.

Island Size	zone 1	zone 2	zone 3	zone 4	zone 5	zone 6
Small	1.67	1.43	1.18	0.91	0.63	0.32
Medium	2.31	3.55	1.67	1.30	0.91	0.48
Large	3.75	6.30	2.86	2.31	1.67	0.91

If we have done the calculations correctly, then the values in Table 3 are our predicted outcomes of the simulation for the class.

6 Laboratory Assignment

Working with your group, play the Island Biogeography Game to address the following questions. Please summarize your results in one short laboratory report and submit this to your instructor for assessment.

1. Use the equilibrium model of island biogeography and the simulation values provided to predict the equilibrium number of species on each island for your simulation.

2. Combine your data with the rest of the class and enter the totals into a table like the one shown in Table 4.

3. Using the class results, construct three graphs:

   - species number vs. island size (use the total for each of the three island sizes from the class data)

- species number vs. distance of the island from the continent (use the total number of species on all islands within a given zone from class data)
- a combined graph showing dual effects of distance and island size on species number. (Think about how the combined data might be presented or look in a scientific journal for an idea; don't simply ask your instructor.)

4. Explain why your results support (or not) the equilibrium theory for island biogeography.
5. Explain why it is better to use class data instead of the individual group data for determining the species–area relationships. What does this suggest about sampling approaches for studying real islands.

Table 4: Example data table

Island Size	Zone I	Zone II	Zone III	Zone IV	Zone V	Zone VI
small						
medium						
large						

7 Recommended Reading

Gotelli, N. J. (2008) A primer of ecology. (4th edition). Sinauer Associates, Inc., Sunderland, MA.