

11

ISLAND BIOGEOGRAPHY

Objectives

- Explore the relationships of immigration and extinction rates and species richness to island area and distance from the mainland.
- Observe the accumulation of species on an island, and the approach of immigration and extinction rates and species richness values to equilibrium.
- Find equilibrium values of immigration and extinction rates and species richness, both graphically and algebraically.
- Understand species-area curves and the underlying mathematical relationships implied.
- Explore the interaction effects of area and distance.

INTRODUCTION

People have long known that larger islands, and islands closer to a mainland, support a greater number of species than smaller or more distant islands. Most ecology textbooks give examples of such species-area and species-distance relationships, not only for islands in the strict sense, but also for habitat islands such as mountaintops and lakes. Few books explicitly state the mathematical relationship between number of species and area or distance, but most show them as straight lines on log-log plots. This should indicate to you that the underlying relationships are power functions. (See Exercise 1, “Mathematical Functions and Graphs,” for definitions and examples of power functions and other kinds of functions.) On linear axes, both relationships are curves, hence the term “species-area curve” and what could be called the “species-distance curve.”

Having observed and quantified these relationships, ecologists proposed several hypotheses to explain them. One of the best-known hypotheses is the **equilibrium theory of island biogeography** developed by Robert MacArthur and Edward O. Wilson.

The MacArthur-Wilson Model of Island Biogeography

MacArthur and Wilson (1967) modeled **species richness** (the number of species present) on an island as the result of two processes: **immigration** and **extinction**. In their model, species immigrate to an island randomly from a mainland pool. The rate at which new species arrive at the island is determined by three factors:

- The distance of the island from the mainland
- The number of species remaining in the mainland pool that have not already established themselves on the island
- The probability that a given species will disperse from the mainland to the island

The rate at which species on the island go extinct is also determined by three different factors:

- The area of the island
- The number of species present on the island
- The probability that a given species on the island will go extinct

In the simplest version of the model, all species have equal probability of reaching the island and of going extinct once there. The model ignores interactions such as competition, predation, or mutualism between species on the island.

We will develop a spreadsheet model incorporating these ideas. Let us begin with immigration. It seems reasonable to suppose that the farther an island lies from the mainland, the lower the rate of immigration—in other words, immigration is inversely related to distance. Since immigrants are drawn from a finite pool, as more species establish themselves on the island, fewer species will remain in the pool that have not already established themselves on the island. Based on these considerations, we can write a simple equation for the rate of immigration to an island. Let

I = immigration rate (Note: This is overall immigration rate of species to the island, which is different from the probability that any one species will make that journey)

P = total number of species in the mainland pool

S = species richness of the island

D = distance of the island from the mainland

c = colonization probability, or the probability that a given species will make it to the island; here it is assumed to be equal for all species

f = a scaling factor for distance

Note that $(P - S)$ is the number of species in the mainland pool that have not already reached the island. Now we can write an equation for immigration:

$$I = \frac{c(P - S)}{fD} \quad \text{Equation 1}$$

We must determine a values for c and f from actual data. Based on the work of MacArthur and Wilson, we can begin with reasonable values of $c = 0.10$ and $f = 0.01$. Note that Equation 1 is a power function, in which the variable D is raised to a constant power, -1 .

Turning our attention to extinction, we can write a simple equation for that as well. Let

E = extinction rate

S = species richness of the island

A = area of the island

q = extinction probability for a given species (assumed to be equal for all species)

m = a power scaling factor for area

Now we can write an equation for extinction:

$$E = \frac{qS}{A^m} \quad \text{Equation 2}$$

Values of q and m must be determined from actual data, and based on work by MacArthur and Wilson, we can begin with a reasonable values of $q = 0.20$ and $m = 0.25$.

Note that Equation 2 is also a power function, in which the variable A is raised to a constant power, m .

If you consider Equation 1, you can see that as species accumulate on an island (i.e., as S increases), the immigration rate, I , will decrease. Inspection of Equation 2 shows that as S increases, the extinction rate, E , will increase. At some value of S , immigration and extinction will become equal (i.e., $I = E$), and species richness will come to an equilibrium. This is an equilibrium because every new species immigrating to the island is balanced by one already-established species going extinct, and vice versa.

This is an important point of the model: *Equilibrium species richness is determined by a balance between immigration and extinction.* Note that this is a statement about the model, not about species richness on real islands, which is certainly affected by other factors in addition to immigration and extinction. However, like other simple models, this one has proven fruitful in stimulating thinking and research.

A second important point of the model is that the equilibrium in species richness is a **dynamic equilibrium**. At equilibrium, immigration and extinction rates are equal, but neither is zero. The rate of immigration or extinction at equilibrium species richness is called the **turnover rate**.

According to the model, then, the particular species inhabiting an island continue to change, or turn over, indefinitely—even after species richness has reached equilibrium. That is, species continue to go extinct and are replaced by an equal number of immigrating species. A biologist revisiting the same island at different times would, according to the model, find different sets of species present, but (at least roughly) the same total number of species.

This prediction of continuing turnover is an important feature of MacArthur and Wilson's model. This model is often used in conservation biology to predict the number of species that would be expected to persist or go extinct in nature reserves (which are often habitat islands). However, it is not useful in planning for protecting specific species, because of this prediction of continuing turnover.

PROCEDURES

This exercise is presented in four parts. In each part you will develop a spreadsheet model and make graphs. Between parts, we return to a little mathematical exposition to lay the groundwork for modeling.

First you will build a spreadsheet version of the MacArthur-Wilson model of island biogeography. Using Equations 1 and 2, you will graphically estimate the species richness of an island. In the second part, you explore how the island's area and distance from the mainland affect its species richness. In the third part, you will examine the time-course of species accumulation on an island. In the fourth part, we derive equilibrium solutions for species richness and turnover rate.

As always, save your work frequently to disk.

INSTRUCTIONS

A. The MacArthur-Wilson island biogeography model.

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 1.

ANNOTATION

Enter the text items and values shown for "Parameters" and "Scaling factors." These are all literals, so just select the appropriate cells and type them in.

	A	B	C	D	E	F	G
1	Island Biogeography						
2	Assumes all species have equal dispersal ability and risk of extinction.						
3	Assumes no interaction between species on an island.						
4							
5	Parameters			Scaling factors			
6	Species pool on mainland (<i>P</i>)		1000			For distance (<i>f</i>)	0.01
7	Area of island (<i>A</i>)		200			For area (<i>m</i>)	0.25
8	Distance from mainland (<i>D</i>)		300				
9	Colonization probability (<i>c</i>)		0.10				
10	Extinction probability (<i>q</i>)		0.20				
11						Equilibrium values	
12	Immigration, extinction, and species richness					Species richness	
13	Fraction of pool	Species richness	Immigration	Extinction		Immigration rate	
14	0.0					Extinction rate	
15	0.1						
16	0.2						

Figure 1

2. Set up a series: 0.0, 0.1, 0.2, . . . , 0.9, 1.0 in cells A14–A24.

3. In cell B14 enter a formula to calculate the actual number of species present on an island.

4. In cell C14 enter a formula to calculate the rate of immigration to an island already colonized by the number of species in cell B14.

5. In cell D14 enter a formula to calculate the rate of extinction on an island already colonized by the number of species in cell B14.

6. Copy the formulae in cells B14–D14 down their columns to row 24.

7. Graph immigration and extinction rates against species richness.

8. Try changing the parameter values in cells C6–C10, one at a time, and observe how equilibrium species richness changes.

In cell A14 enter the value 0.

In cell A15 enter the formula =A14+0.1.

Copy the formula from cell A15 into cells A16–A24.

This series represents different fractions of the mainland pool present on the island, from 0% to 10% and so on to 100%.

In cell B14 enter the formula =A14*\$C\$6. This formula is based on the fraction of the mainland pool in cell A14 and the total number of species in the mainland pool.

In cell C14 enter the formula =\$C\$9*(C6-B14)/(G6*C8). This corresponds to Equation 1:

$$I = \frac{c(P - S)}{fD}$$

In cell D14 enter the formula =\$C\$10*B14/\$C\$7^G\$7. This corresponds to Equation 2:

$$E = \frac{qS}{A^m}$$

Select cells B14–D14. Copy.

Select cells B15–D24. Paste.

Save your work!

Select cells B14–D24 and make an XY graph. Edit your graph for readability. It should resemble the graph in Figure 2.

You should see that smaller or more distant islands have fewer species than larger or closer ones. We will examine these relationships more rigorously in the next part of the exercise.

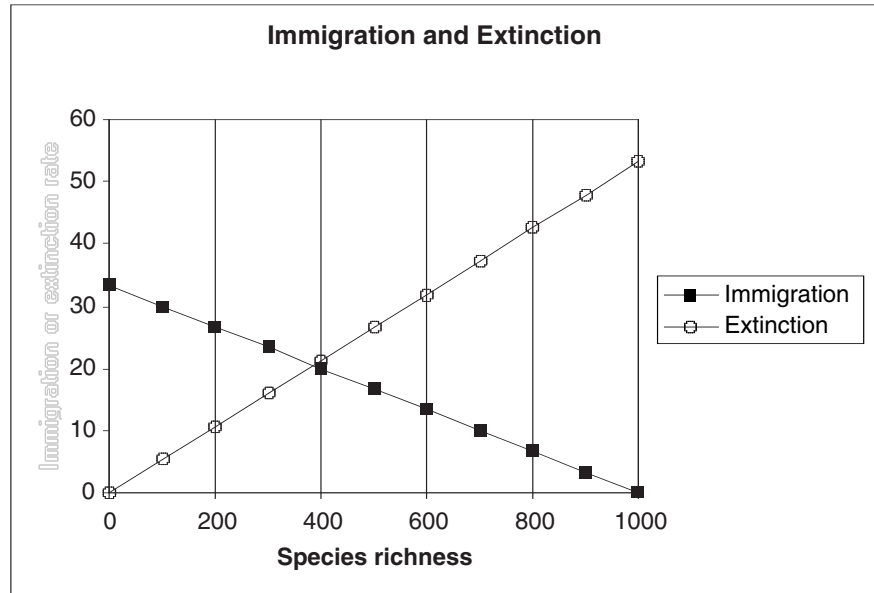


Figure 2

Effects of Island Area and Distance from the Mainland

In Step 8 of the preceding section of the exercise, you experimented with different parameter values to see the effects on species richness. In this section, we will examine the effects of an island’s area and its distance from the mainland somewhat more rigorously.

To quantify these effects, let us compare three islands of the same area, but at three distances from the mainland: 0.5, 1.0, and 2.0 times some distance that you specify (in cell C8 of your spreadsheet). Looking at Equation 1, which models the immigration rate, you can see that it includes distance but not area. Accordingly, we will compute immigration rates on these three islands, and estimate the effects on species richness.

We will also compare three islands at the same distance from the mainland, but having three different areas: 0.1, 1.0, and 10.0 times the area that you specified in cell C7 of your spreadsheet. Looking at Equation 2, which models extinction rate, you can see that it includes area but not distance. Accordingly, we will compute extinction rates on these three islands and estimate the effects on species richness.

INSTRUCTIONS

B. The effects of distance and area on the MacArthur-Wilson model.

1. Add the column headings shown in Figure 3 to cells I12–P13 of the spreadsheet you set up in Part A (see Figure 1).

ANNOTATION

These are all literals, so just select the appropriate cells and type them in.

	I	J	K	L	M	N	O	P
12	Fraction	Species	Effect of distance on immigration			Effect of area on extinction		
13	of pool	richness	Imm near	Imm medium	Imm far	Ext small	Ext medium	Ext large
14	0.0							
15	0.1							

Figure 3

2. Set up a series: 0.0, 0.1, 0.2, ... , 0.9, 1.0 in cells I14–I24.

3. In column J, calculate the actual numbers of species present on islands, based on the fraction of the mainland pool in cell I14 and the total number of species in the mainland pool.

4. In column L, calculate immigration rates to islands at the distance specified in cell C8, using the species richnesses calculated in column J.

5. In column K, calculate immigration rates to islands at half the distance specified in cell C8, using the species richnesses calculated in column J.

6. In column M, calculate immigration rates to islands at 2.0 times the distance specified in cell C8, using the species richnesses calculated in column J.

7. In column O, calculate extinction rates for islands of the area specified in cell C7, using the species richnesses calculated in column J.

8. In column N, calculate extinction rates for islands of 0.1 times the area specified in cell C7, with the species richnesses calculated in column J.

9. In column P, calculate extinction rates for islands of 10.0 times the area specified in cell C7, with the species richnesses calculated in column J.

Copy cells A14–A24 into cells I14–I24.

This series represents different fractions of the mainland pool present on the island, from 0% to 10% and so on to 100%.

In cell J14, enter the formula = I14*\$C\$6. Copy this formula into cells J15–J24.

In cell L14, enter the formula =(C\$6-\$J14)*\$C\$9/(C\$8*\$G\$6). This corresponds to Equation 1:

$$I = \frac{c(P - S)}{fD}$$

Note the use of an absolute column address for cell \$J14.

Copy this formula into cells L14–L24.

Copy the formula from cell L14 into cell K14, and edit it to multiply distance (cell C8) by 0.5.

The new formula should read =(C\$6-\$J14)*\$C\$9/(C\$8*0.5*\$G\$6).

Copy the formula from cell K14 into cells K15–K24.

Copy the formula from cell K14 into cell M14, and edit it to multiply distance (cell C8) by 2.0.

The new formula should read =(C\$6-\$J14)*\$C\$9/(C\$8*2.0*\$G\$6).

Copy the formula from cell M14 into cells M15–M24.

In cell O14, enter the formula =\$J14*\$C\$10/\$C\$7^\$G\$7. This corresponds to Equation 2:

$$E = \frac{qS}{A^m}$$

Again, note the use of an absolute column address for cell \$J14.

Copy the formula from cell O14 into cells O15–O24.

Copy the formula from cell O14 into cell N14, and edit it to multiply area by 0.1.

The new formula should read =\$J14*\$C\$10/(\$C\$7*0.1)^\$G\$7.

Copy the formula from cell N14 into cells N15–N24.

Copy the formula from cell N14 into cell P14, and edit it to multiply area by 10.0.

The new formula should read =\$J14*\$C\$10/(\$C\$7*10.0)^\$G\$7.

Copy the formula from cell P14 into cells P15–P24.

Save your work!

10. Graph immigration rates for near, medium-distance, and far islands along with the extinction rate for a medium-sized island against species richness.

Select cells J13–M24.

Hold down the control key or **⌘** while selecting cells O13–O24.

Make an XY graph. Edit your graph for readability. It should resemble the one in Figure 4.

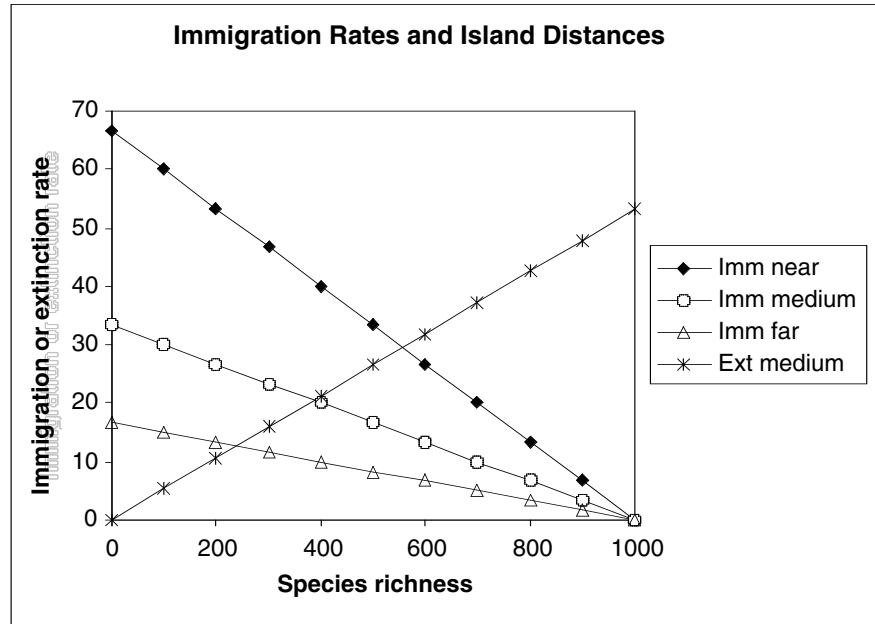


Figure 4

11. Graph extinction rates for small, medium-sized, and large islands, and the immigration rate for a medium-distance island, against species richness.

Select cells J13–J24.

Hold down the control key or **⌘** and select cells L13–L24.

Hold down the control key or **⌘** and select cells N13–P24.

Make an XY graph. Edit your graph for readability. It should resemble the one in Figure 5.

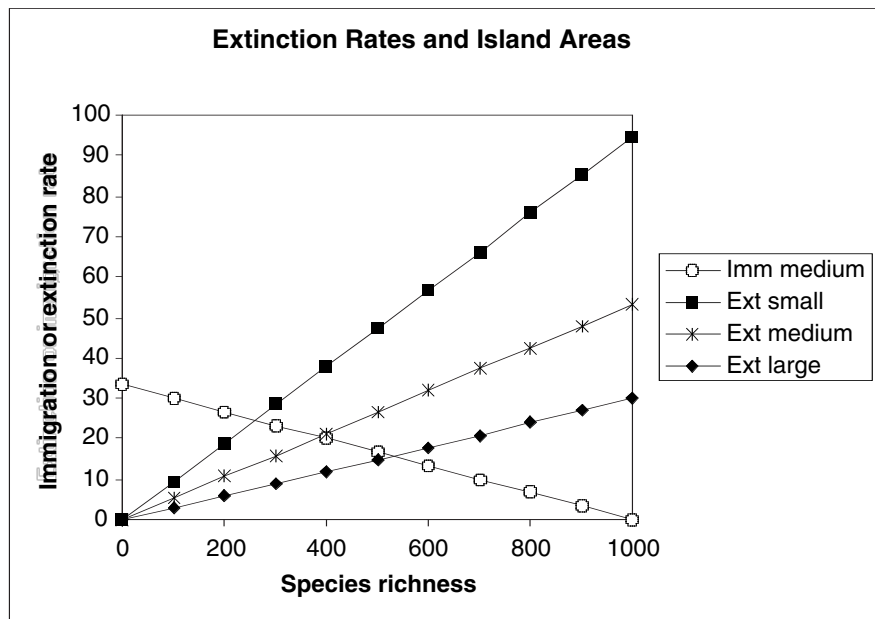


Figure 5

*12. As an OPTIONAL exercise, graph three immigration rates and three extinction rates on a single graph.

Select cells J13–P24, and make an XY graph. This will allow you to compare species richness and turnover rates on islands of three different sizes, at three different distances from the mainland. However, your graph might be rather cluttered and hard to read.

The Time-Course of Species Accumulation on an Island

The graphical analyses above answer a variety of questions about species richness on islands at equilibrium. However, they tell us nothing about how species richness changes over time as it approaches equilibrium. To find out about that, we must model the time-course of species accumulation.

We can follow the accumulation of species over time using a discrete-time model. The number of species present on an island at time $t + 1$ will be the number present at time t plus the number of new species that immigrated in the interval from time t to $t + 1$, minus the number of species that went extinct in the interval from t to $t + 1$. In symbols,

$$S_{t+1} = S_t + I_t - E_t$$

Substituting the right-hand side of Equation 1 for I_t and the right-hand side of Equation 2 for E_t , we derive

$$S_{t+1} = S_t + \frac{c(P - S_t)}{D} - \frac{qS_t}{A^m} \tag{Equation 3}$$

INSTRUCTIONS **ANNOTATION**

C. Model the time-course of species accumulation.

1. Add the column headings shown in Figure 6 to cells A26 and A27 though D27 of the spreadsheet you created in Part A (see Figure 1).

These are all literals, so just select the appropriate cells and type them in.

	A	B	C	D
26	Time-course of species accumulation			
27	Time	Species richness	Immigration	Extinction
28	0			
29	1			
30	2			

Figure 6

2. Set up a linear time series from 0 to 50 in cells A28–A78.

In cell A28 enter the value 0.
 In cell A29 enter the formula =A28+1.
 Copy the formula from cell A29 into cells A30–A78.

3. Begin with an uninhabited island.

Enter the value 0 in cell B28.

4. Enter a formula to calculate the number of species immigrating to the island in the interval from time 0 to time 1.

5. Enter a formula to calculate the number of species going extinct on the island from time 0 to time 1.

6. Enter a formula to calculate the number of species present on the island at time 1.

7. Copy the formulae in cells C28 and D28 into cells C29 and D29.

8. Copy the formulae in cells B29–D29 into cells B30–D78.

9. Graph species richness, immigration rate, and extinction rate against time.

Copy the formula from cell C14 into cell C28. This corresponds to Equation 1.

Copy the formula from cell D14 into cell D28. This corresponds to Equation 2.

In cell B29 enter the formula **=B28+C28-D28**.

This corresponds to Equation 3:

$$S_{t+1} = S_t + \frac{c(P - S_t)}{D} - \frac{qS_t}{A^m}$$

The formula calculates the number of species on the island as the number already there plus the number immigrating to the island, minus the number going extinct, in the preceding time interval.

Save your work!

Select cells A27–D78 and make an XY graph.

After you have made your graph, double-click on any data point in the species richness curve. In the Format Data Series dialog box, click on the Axis tab, and choose Secondary axis. Plot species richness on the secondary y-axis.

To label the second y-axis, open Chart|Chart Options|Titles.

Edit your graph for readability. Your graph should resemble the one in Figure 7.

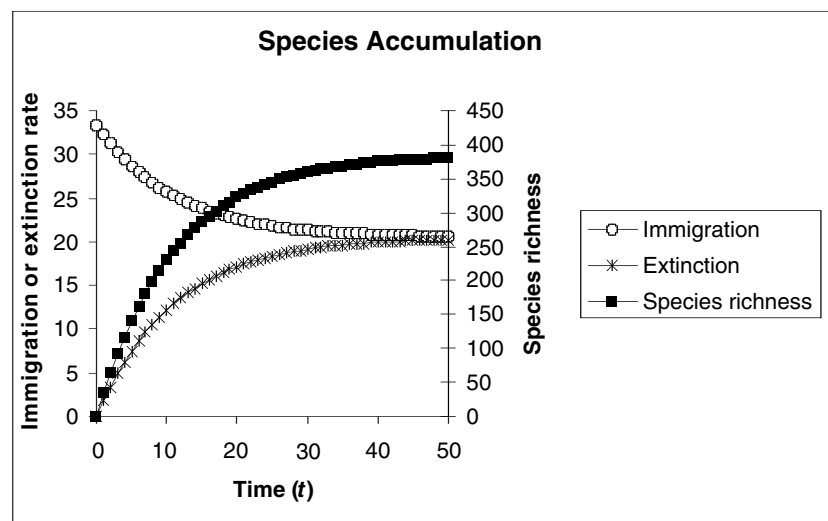


Figure 7

Equilibrium Solutions

So far, you have estimated equilibrium species richness using graphs. In the next section, we will calculate these quantities algebraically. We have two reasons for doing so.

First, calculations give us more precise results than estimating from a graph. Second, these calculations will allow us to close the loop, metaphorically, with the original motivation for MacArthur and Wilson's model. As we said at the beginning of this exercise, among the original observations from which this model sprang were the relationships of species richness to island area and distance from the mainland—the species-area curve. But nothing we have done so far explicitly shows a species-area curve. By finding equilibrium solutions, we can develop these curves, and briefly indicate how they have been used to test the model and to guide conservation decisions.

As we explained in the first section of this exercise, the MacArthur-Wilson model tells us that species accumulate by immigration and are removed by extinction, and that species richness reaches equilibrium when these two processes balance. Algebraically, we can find the equilibrium species richness of an island by solving for S_{eq} when $I = E$. So, let's do a little algebra.

$$\text{Let } I = E$$

Substituting from Equations 1 and 2 above, we can derive the equation for S_{eq} :

$$\begin{aligned} \frac{c(P - S_{eq})}{fD} &= \frac{qS_{eq}}{A^m} \\ A^m c(P - S_{eq}) &= fDqS_{eq} \\ A^m cP - A^m cS_{eq} &= fDqS_{eq} \\ A^m cP &= fDqS_{eq} + A^m cS_{eq} \\ A^m cP &= S_{eq}(fDq + A^m c) \\ \frac{A^m cP}{fDq + A^m c} &= S_{eq} \end{aligned} \quad \text{Equation 4}$$

Equation 4 isn't very pretty, but you can use it in your spreadsheet model to see how equilibrium species richness relates to island area, to colonization and extinction probabilities, and to the richness of the mainland species pool. In particular, we will see how the model predicts species-area curves for islands at different distances from the mainland.

INSTRUCTIONS

D. Calculate species equilibrium.

1. Enter a spreadsheet formula for equilibrium species richness into cell G11.
2. Enter the spreadsheet equivalents of Equations 1 and 2 into cells G12 and G13.

ANNOTATION

In cell G11 enter the formula `=C7^G7*C9*C6/(G6*C8*C10+C7^G7*C9)`. This corresponds to Equation 4:

$$\frac{A^m cP}{fDq + A^m c} = S_{eq}$$

In cell G12 enter the formula `=C9*(C6-G11)/(G6*C8)`.

In cell G13 enter the formula `=C10*G11/C7^G7`.

These are the rates of immigration and extinction, respectively, on an island already colonized by the number of species in cell B14 (Equations 1 and 2). Use the values in these cells to verify your graphical estimates in the previous parts of this exercise.

3. Enter the row and column labels shown in Figure 8 into cells R11–X13.

We will use this part of the spreadsheet to calculate species area curves for islands at different distances from the mainland.

	R	S	T	U	V	W	X
11	Species-Area Relationships at Different Distances						
12		Equilibrium species richness			Turnover rates		
13	Area	Near	Medium	Far	Near	Medium	Far
14	10						
15	50						
16	100						

Figure 8

4. To represent a wide range of island areas, set up a series 10, 50, 100, 500, 1000 ... , 500,000, 1,000,000 in cells R14–R24.

Enter the values 10 and 50 into cells R14 and R15, respectively. In cell R16, enter the formula `=R14*10`. Copy this formula into cells R17–R24.

5. In column T, calculate the equilibrium species richnesses of islands at the distance specified in cell C8, with the areas given in column R.

In cell T14 enter the formula `=R14^G7*C9*C6/(G6*C8*C10+R14^G7*C9)`, which again corresponds to Equation 4. Copy this formula into cells T15–T24. Note that the address `R14` has an absolute column reference but a relative row reference.

6. In column S, calculate the equilibrium species richnesses of islands at 0.1 times the distance specified in cell C8, with the areas given in column R.

Copy the formula from cell T14 into cell S14. Edit the formula to multiply distance by 0.1. The edited formula should read `=R14^G7*C9*C6/(G6*0.1*C8*C10+R14^G7*C9)`.

Copy the edited formula from cell S14 into cells S15–S24.

7. In column U, calculate the equilibrium species richnesses of islands at 10 times the distance specified in cell C8, with the areas given in column R.

Copy the formula from cell S14 into cell U14. Edit the formula to multiply distance by 10. The edited formula should read `=R14^G7*C9*C6/(G6*10*C8*C10+R14^G7*C9)`.

Copy the edited formula from cell U14 into cells U15–U24.

8. Graph equilibrium species richness against island area for islands at near, medium, and far distances from the mainland.

Select cells R13 through U24, and create an XY graph. Edit your graph for readability; It should resemble Figure 9. The three species-area curves will rise very quickly, almost following the vertical axis on the left, and then abruptly level out.

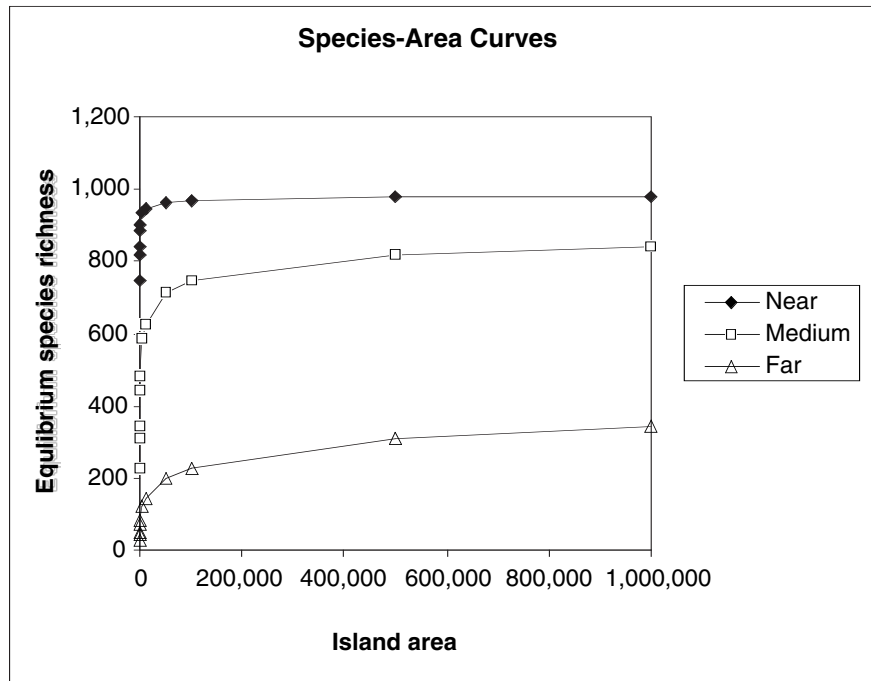


Figure 9

9. Change both vertical and horizontal axes to logarithmic scales.

As in Figure 10, the species-area curves should become almost straight lines on the log-log plot.

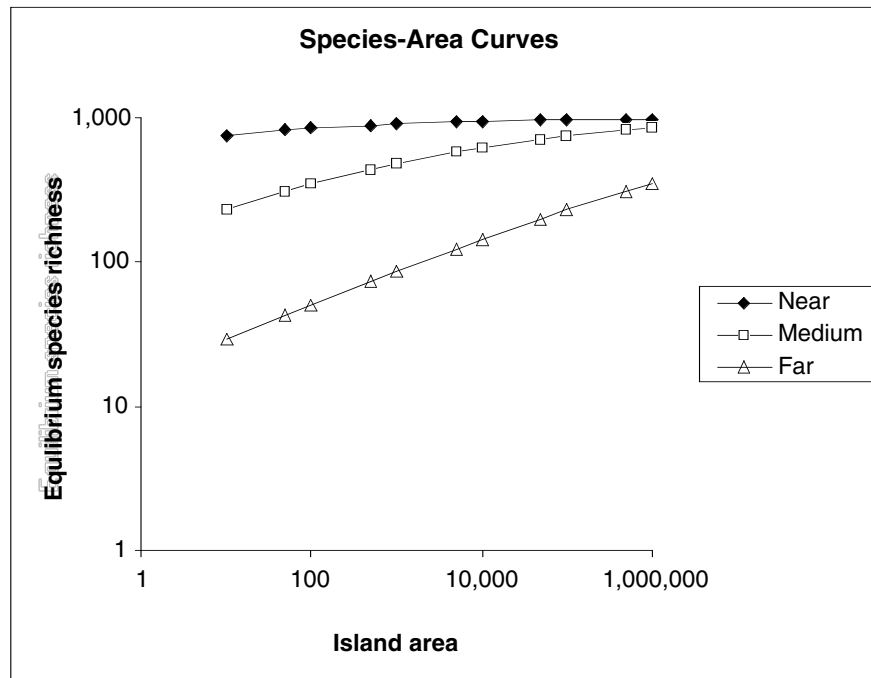


Figure 10

QUESTIONS

1. How can you estimate the equilibrium species richness of an island from Figure 2?
2. Is the equilibrium of species richness stable or unstable?
3. Is the equilibrium of species richness static or dynamic?
4. How does greater distance from the mainland affect species richness on an island?
5. How does greater distance from the mainland affect the turnover rate on an island?
6. How does larger area affect species richness on an island?
7. How does larger area affect the turnover rate on an island?
8. (OPTIONAL) How do area and distance from the mainland interact to determine species richness and turnover rate on an island?
9. How do species accumulate on an island over time? That is, does species richness increase linearly, exponentially, logarithmically, or otherwise?
10. What does Figure 7 tell us about the changing state of species equilibrium?
11. How is species richness related to island area?
12. How do the species-area curves differ for islands at different distances from the mainland?

LITERATURE CITED

MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.