

9

Island Biogeography: Evaluating Correlational Data and Testing Alternative Hypotheses

*James Robertson***Introduction and Background**

The earth's surface is spatially complex—even the most casual observer is readily aware of this. From the lush tropical zones of the equator to the desolate arctic zones of the poles, habitat diversity exists on both a global and local scale. Organisms live in almost every imaginable habitat on earth. However, no one species is able to persist in all of earth's habitats (aside from humans, perhaps). As you will remember from earlier chapters, the constraints of any environment mean that no single strategy is likely to be optimal in all environments. As natural selection acts and evolution occurs, diversity emerges. The interdisciplinary field of biogeography seeks to understand what influences the distribution of species. Biogeographers document the geographic distributions of species (both present and past), and try to understand the underlying processes that have led to these spatial patterns (Brown and Lomolino, 1998). As early as the eighteenth century, naturalists, precursors to today's biogeographers, attempted to record the geographic distributions of species, particularly species with discontinuous distributions. In some cases, discontinuous distributions can be explained by a dispersal event across an inhospitable habitat. However, when a number of species have the same discontinuous distribution, the most parsimonious explanation is the formation of a natural barrier separating geographic regions. Vicariance biogeography is the study of closely related taxa that are separated geographically as a result of the formation of natural barriers to dispersal. Many classic examples of vicariance biogeography make sense in light of plate tectonics. The earth's outermost layer is broken into large plates that float and shift on a molten underlying layer. In the late 1960s this theory (originally proposed by Antonio Snider-Pelligrini in 1858) became widely accepted and was used to explain global distributions of many plant and animal taxa. Before plate tectonics were understood, widely distributed species were assumed to have dispersed across vast distances to colonize hospitable regions.

Consider the distribution of ratites, large flightless birds (including emus and ostriches). They are found throughout the southern hemisphere. Their distribution was assumed to have been the result of multiple oceanic dispersal events. The theory of plate tectonics, however, provided a more parsimonious explanation: ratites occupied the Southern Hemisphere when South America, Africa, and Australia were still a single landmass. As plates shifted, these three landmasses drifted, and ratites became isolated on each continent. Eventually, as a result of isolation, possible founder effects, and local selective pressures, the ratites became today's African ostriches, South American rheas, and Australian emus

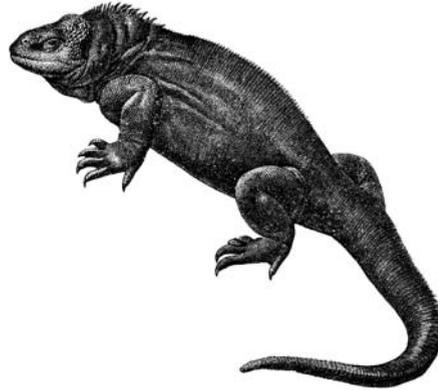


FIGURE 9.1. Land iguana, one of the Caribbean lizards.

and cassowaries. The theory of plate tectonics helps explain many such global species distributions (Brown and Lomolino, 1998).

Biogeographers are not only interested in understanding the origin and spread of species; they are also interested in understanding the factors responsible for geographic patterns in both the numbers and the types of species. For example, naturalists in the nineteenth century noted a general trend in the diversity of island species: as island size increases, the number of species present typically increases. This relationship can be expressed graphically with the species-area curve (Brown and Lomolino, 1998). Scholars originally focused on understanding the biogeography of (oceanic) islands, but today, species-area curves have been extended to include *functional* “islands”: e.g., a series of ponds separated by land, or a series of mountain peaks separated by low-lying deserts. These are functional islands because organisms living there may be unable to move among isolated habitable areas across intervening inhospitable areas.

MacArthur and Wilson (1969) explained the species-area correlation as a balance between extinction and immigration. They suggested that larger islands will have greater habitat diversity and thus allow more species to persist (i.e., avoid extinction). The island’s distance from the mainland also influences the immigration rate; more distant islands are more rarely colonized (figure 9.1 and table 9.1). The extension of the species-area curve to include functional islands is particularly interesting in today’s world of rapid human population growth and urban sprawl. As human populations increase globally, natural habitats have become increasingly fragmented. These fragmented patches, which in most cases continue to decrease in size, serve as island habitats for many species of plants and animals. Conservation biologists have used species-area curves to predict extinction rates due to habitat loss.

The allometric equation was invented to understand how size (or biomass, or some other reflection of size) affects processes, from metabolic rates to species diversity. In the 1920s a Swedish scientist, Arrhenius, adapted the allometric equation to describe the species-area curve: $S = cA^z$. In this equation, S is the number of species present and A is the area of the island. Both c and z are fitted constants, with z setting the shape and c the placement of the curve. This relationship can be expressed linearly by taking the logarithm of both sides of the equation. This is a linear conversion of the relationship of island size and species number: z is the slope of that line, and the constant, $\log(c)$, is the y -intercept. To evaluate this model, we need data on both the area and the number of species on islands of interest (see table 9.1).

TABLE 9.1.
Herpetological biodiversity in the West Indies.

Island name (West Indies)	Area (km ²)	Species no.	log (area (km ²))	log (species no.)
Redona	2.6	3	0.4138	0.4771
Saba	12.7	5	1.104	0.699
Montserrat	104	9	2.016	0.9542
Puerto Rico	8816	40	3.945	1.602
Jamaica	11669	39	4.067	1.591
Hispaniola	77793	84	4.891	1.924
Cuba	103723	76	5.016	1.881

Source: Darlington (1957).

$$\begin{aligned}
 S &= cA^z, \\
 \log(S) &= \log(cA^z), \\
 \log(S) &= \log(c) + \log(A^z), \\
 \log(S) &= \log(c) + z \log(A).
 \end{aligned}
 \tag{9.1}$$

The model requires that the c and z constants do not vary within a pooled data set. If they do, then the equation will be a poor predictor of the relationship between island size and species number. The question, then, is how to avoid pooling data with different c and z constants. We must be able to predict when the c and z constants will differ; to do this we must have a *biological* understanding of these constants. There has been a great deal of controversy concerning the biological implications of these two constants. The general view is that the value of c (which affects the placement) depends on the taxon and the biological region of the globe, and that z (which affects the shape of the curve) depends on the degree of island isolation.

This approach is valid only when you are comparing within a group with similar mobility and life history (usually taxonomically close groups), on environmentally similar islands, with similar degrees of isolation. For example, you do not want to pool species of ants and species of birds on the same graph, or to compare islands in the arctic tundra of Alaska with islands in the Caribbean, or to compare islands just off the Florida coast with the relatively isolated islands of Hawaii. Unfortunately, there is no standard method for determining what data are appropriate to pool—and as a result, pooling is often the result of an investigator's intuition. Problems of inappropriate data are common to many types of analysis, not just species-area curves. Always consider this potential problem when evaluating reported results (Brown and Lomolino, 1998).

Homework for this exercise takes approximately 45 minutes.

Objectives of This Exercise

In this exercise you will use the basic principles of island biogeography to examine data critically. You will calculate and compare coefficients of determination to decide how well the data fit island biogeography models.

Case Studies and Data

The relationship between island size and species number is very appealing to biogeographers. Fortuitously, when we began to think about island biogeography, extensive data already existed and could be used to test our hypotheses. As long ago as 1957, Philip J. Darlington, Jr. compiled data on the number of reptilian and amphibian species on islands in the West Indies in the Caribbean. What pattern do you expect when you graph the “raw” data? What if you plot the log of the area against the log of the species number, as in figure 9.2?

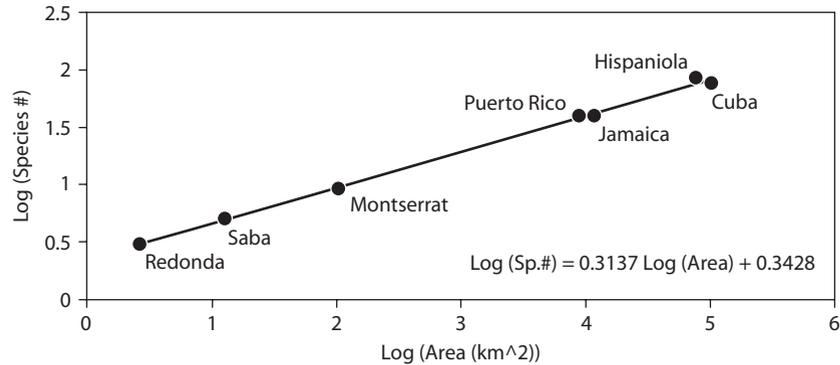


FIGURE 9.2. Species-area curve: Amphibians and reptiles of the West Indies.

If the allometric equation $S = cA^z$ correctly predicts the relationship between island size and species number, then we expect the log-log graph to be a neat straight line. We can see that the values do, in fact, lie along a straight line. The line on the graph is the least squares regression “line of best fit” (see chapter 14). In this case the data fit almost perfectly—for these data, the equation $S = cA^z$ closely predicts the relationship between island size and species number. Other data sets, however, may not fit so well, in large part depending on how effectively isolated the islands are, or how well island size predicts available ecological diversity.

We need a way to quantify how well the data fit a linear relationship. One standard method used to quantify how well the line describes the relationship is to calculate the proportion of the variation in the Y variable (here, the log of the number of species) that is explained by the X variable (here the log of island area). We call this R^2 , the coefficient of determination.

$$R^2 = \frac{[n(\sum x_i y_i) - (\sum x_i)(\sum y_i)]^2}{[n(\sum x_i^2) - (\sum x_i)^2][n(\sum y_i^2) - (\sum y_i)^2]} \quad (9.2)$$

See chapters 14 and 15 for more examples, details, and explanation of R^2 .

Questions to Work on Individually Outside of Class

1. Examine the species area curve for West Indies reptiles and amphibians (figure 9.2); you can readily see that the line has a positive slope and that the R^2 will be close to 1. We still, however, need to calculate the actual value. Fill out table 9.2 so that you will be able to

TABLE 9.2.

Worksheet for calculating coefficient of determination for West Indies amphibian and reptile species-area curve.

Island name (West Indies)	log (area (km ²)) (x)	[log (area (km ²))] ² (x) ²	log (species no.) (y)	[log (species no.)] ² (y) ²	log (A) log (species no.) (x)*x(y)
Redona	0.4138	.1712	0.4771	.2276	.1974
Saba	1.1040		0.6990		
Montserrat	2.0160		0.9542		
Puerto Rico	3.9450		1.602		
Jamaica	4.0670		1.591		
Hispaniola	4.8910		1.924		
Cuba	5.0160		1.881		
Sum	21.4500				

calculate R^2 for the next question. Several cells have been calculated for you; ignore them initially and use them to check your calculations.

2. Calculate the coefficient of determination (R^2). SHOW YOUR WORK!!!

3. Would you have predicted this result simply by looking at the graph? If points were added to the graph that did not fall on or near the line what would happen to R^2 ?

Now, we will add two more data sets, and make specific comparisons across them.

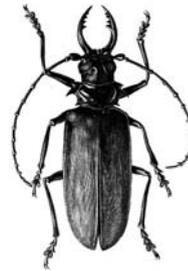


FIGURE 9.3. Long-horned beetle.

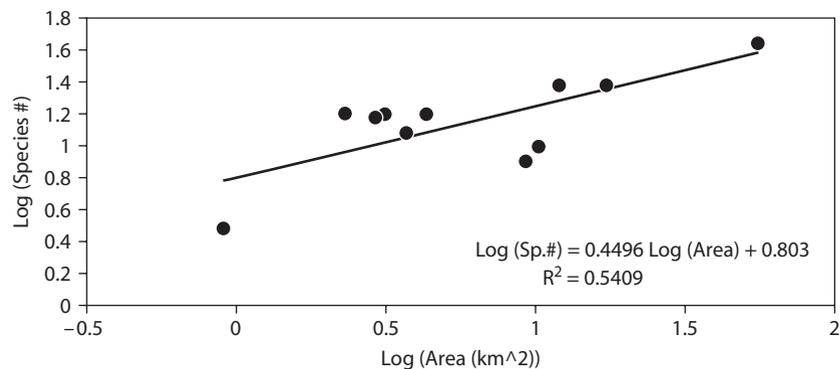


FIGURE 9.4. Species-area curve : Cerambycid beetle species of the Florida Keys (from Brown and Peck, 1996).

TABLE 9.3.
Long-horned beetle species numbers in the Florida Keys.

Island name (Florida keys)	Area (km ²)	Distance (km)	Species no.	log (distance)	log (species no.)
Key Largo	55.1	13	44	1.114	1.643
Matecumbe Key	4.3	32	16	1.505	1.204
Fat Deer Key	3.7	66	12	1.82	1.079
Key Vaca	2.9	72	15	1.857	1.176
No Name Key	3.1	76	16	1.881	1.204
Nig Pine Key	17.1	79	24	1.898	1.38
Big Torch Key	2.3	88	16	1.944	1.204
Cudjoe Key	9.2	95	8	1.978	0.903
Sugarloaf Key	10.2	100	10	2	1
Key West	11.9	121	24	2.083	1.38
Dry Tortugas	0.9	131	3	2.117	0.477

Source: Brown and Peck, 1996.

Cerambycid Beetles of the Florida Keys Browne and Peck (1996) sampled long-horned beetle species (Family: Cerambycidae; figure 9.3) in the Florida Keys to examine the relationship between island area and species number. They found 53 different species across 11 different islands, which varied both in size (from .9 to 55.1 km²) and in distance (from 13 to 131 km) from the Florida coast. Table 9.3 includes some of their data. Figure 9.4 is a log-log plot of island area and species number. Included in the graph is the equation for the best-fit line, along with R^2 .

Land Birds of the West Indies Terborgh's (1973) data on the relationship between island area and species number for bird species in the West Indies are found in figure 9.5.

Across 19 islands (varying in size from 83 to 114,521 km²) there are finches, warblers, thrushes, mimic thrushes, hummingbirds, pigeons, flycatchers, woodpeckers, owls, hawks, and falcons. Examine the log-log plot of island area and species number. Included in the graph is the equation for the best-fit line, along with R^2 .

Examine the map of the Caribbean Sea including islands of the West Indies and the Florida Keys (figure 9.6).

4. Complete table 9.4 so that you can compare the data on the different taxa.

TABLE 9.4.
Comparison of MacArthur and Wilson's model across taxa.

Taxon group	Location	log (c)	c	z	R^2
Amphibians/reptiles	West Indies				
Beetles	Florida Keys				
Birds	West Indies				

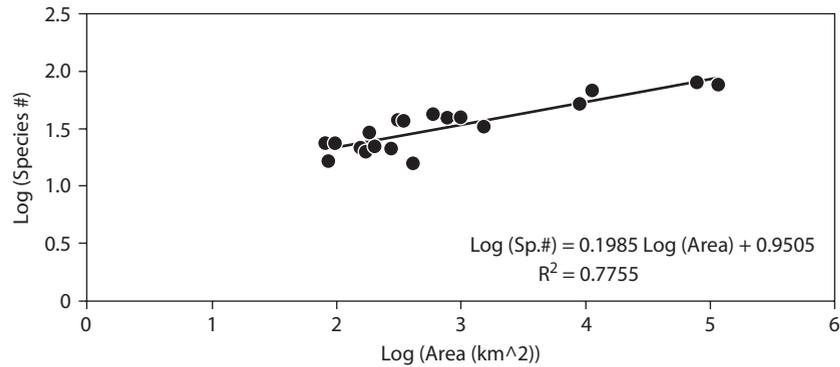


FIGURE 9.5. Species-Area Curve: Land Birds of the West Indies (from Terborgh, 1973).

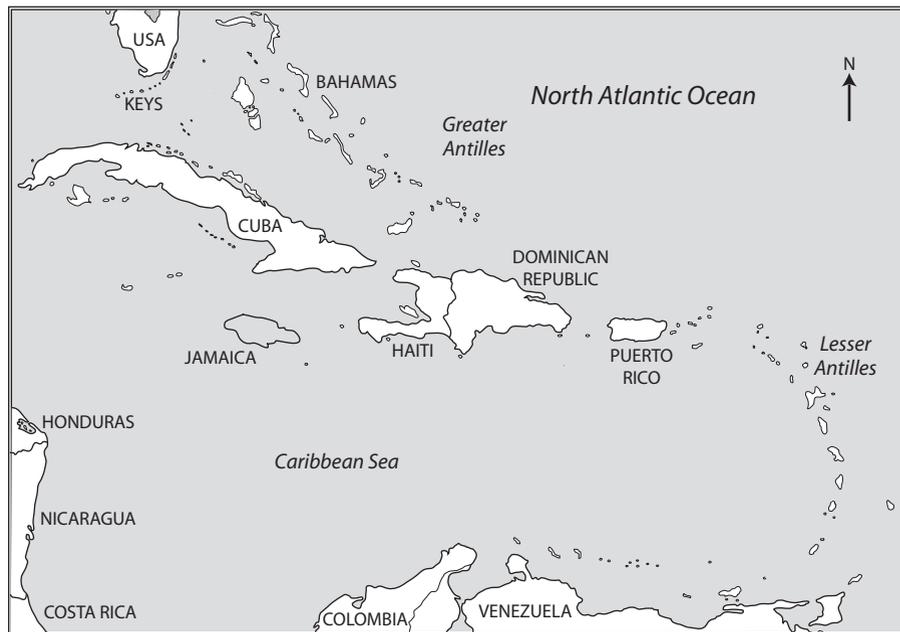


FIGURE 9.6. Map of the Caribbean.

Would pooling the three data sets (reptiles and amphibians, beetles, and birds) be appropriate? Why or why not? You should consider all aspects of the biological interpretation of these constants in your answer. You may also want to consult the Caribbean map.

5. How well does each of the three data sets support the relationship predicted by the equation $S = cA^z$? Assume that R^2 above 0.85 is excellent, between 0.70 and 0.85 is good, and below 0.70 is poor. Provide both a biological and a statistical explanation for these results.

Small-Group/In Class Exercise

Understanding Biogeography of Channel Island Birds

The allometric equation $S = cA^Z$, introduced by Arrhenius in the 1920s, predicted a specific and testable relationship between island size and species number. Biogeographers have examined this relationship, expressed graphically as the species-area curve, in a variety of taxonomic groups and in extremely diverse island habitats. Some of these data sets, such as Darlington's (1957) data on reptiles and amphibians of the West Indies, strongly support the predicted relationship between island area and species number. Many other data sets, however, have low coefficients of determination (R^2), suggesting that perhaps a more complex relationship between species number and island area exists (Brown and Lomolino, 1998; Spellerberg and Sawyer, 1999). Motivated in part by the inconsistencies in the species-area curve across examples, Robert H. MacArthur and Edward O. Wilson (1967) examined the relationships among island size, degree of isolation, and species number. Both men were very familiar with island systems. MacArthur had studied bird species on montane "islands" of the southwestern United States, islands of the West Indies, and islands off the coast of Maine and Panama. Wilson had studied ant species on islands of the East Indies, Polynesia and the Florida Keys. In their seminal work, *The Theory of Island Biogeography* (1967), MacArthur and Wilson incorporated many preexisting concepts in ecology, population biology, and biogeography into a single island biogeographic model (Brown and Lomolino, 1998; Spellerberg and Sawyer, 1999). Figure 9.7 depicts the relationship between species number and both the rate of colonization and the rate of extinction for a particular island. The intersection of the colonization rate and the extinction rate represents the species number at equilibrium as indicated on the x -axis. The point P located

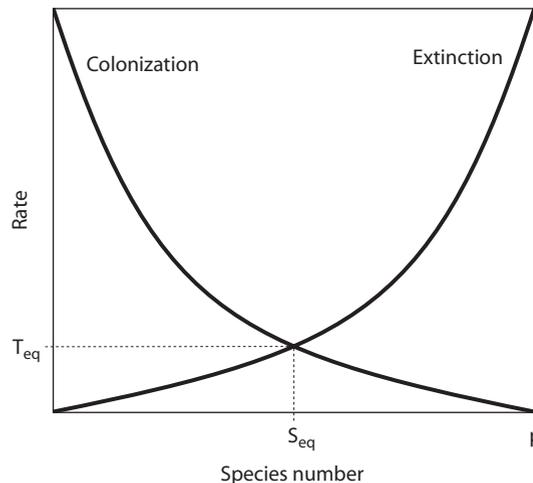


FIGURE 9.7. The relationship between species number and both the rate of colonization and the rate of extinction for a particular island. The intersection of the colonization rate and the extinction rate represents the species number at equilibrium as indicated on the x -axis. The point P located on the x -axis indicates the number of species in the source pool or on the mainland. The species turnover rate occurs at the y -intercept of the intersection point (adapted from MacArthur and Wilson, 1967).

on the x -axis indicates the number of species in the source pool (e.g., on the mainland). The species turnover rate occurs at the y -intercept of the intersection point (adapted from MacArthur and Wilson, 1967).

In MacArthur and Wilson's model, the equilibrium number of species on an island depends on the balance between rate of colonization and the rate of extinction. MacArthur and Wilson argued that the colonization rate should decrease as species number increases. Initially, any species reaching the island would be new to the island and therefore represent a colonization event. Eventually, the colonization rate should decrease until all the species found on the mainland are also found on the island. If a species goes locally extinct on the island, then that species may again eventually recolonize the island, contributing again to the colonization rate. The extinction rate, however, should increase as species number increases. Initially, extinction rates are zero because there are no species to go extinct. However, as the number of species on the island increases, the number of species that can potentially go extinct will also increase, thereby increasing the possible extinction rate. In theory the balance between these two rates produces a stable equilibrium species number, (the x -coordinate of the intersection point). Interestingly, although the number of species on the island should remain the same over time, the actual species represented on the island should change continuously. This is a consequence of the ongoing processes of extinction and recolonization that occur even at the equilibrium point. The rate at which species are replaced on the island when the number of species is at the equilibrium species number is the species turnover rate (the y -coordinate of the intersection point) (figure 9.8).

The concept of a species turnover rate was critical to the MacArthur and Wilson model. Biogeographers had previously assumed that so long as the island environment remained relatively constant, the particular species on the island would not change. MacArthur and Wilson, however, suggested that even if the island environment remained constant the particular species present on the island would continue to change (Brown and Lomolino, 1998; MacArthur and Wilson, 1967; Spellerberg and Sawyer, 1999). MacArthur and Wilson also considered how island area and degree of isolation would influence the rate of colonization and the rate of extinction. They suggested that colonization rates depended largely on the degree of island isolation from a mainland source, decreasing with isolation. They noted that increases in island size might increase colonization rates because of the increased likelihood of immigrants finding the larger island (referred to as the target effect). However, they argued that the influence of island size on colonization rates would be insignificant when considered along with the influence of isolation (MacArthur and Wilson, 1967).

Extinction rates, MacArthur and Wilson suggested, depend largely upon population size. As the population size decreases, we see increasing influence of stochastic processes that can lead to local extinction. For example, a few random deaths in a very small population will have a greater impact than the same number of deaths in a large population. Populations of small size are also more likely to be affected by inbreeding depression (an increased rate of homozygosity of deleterious recessive alleles due to mating between closely related individuals; see chapter 12 for detailed examples). In some cases this can also lead to local extinction (Lincoln et al., 1998). Population size should increase as island area increases, as a result of an increase in available resources. Therefore, extinction rates should decrease with increasing island size. The balance between colonization rate (dependent on the degree of island isolation) and extinction rate (dependent on island size) determines the number of species at equilibrium and the species turnover

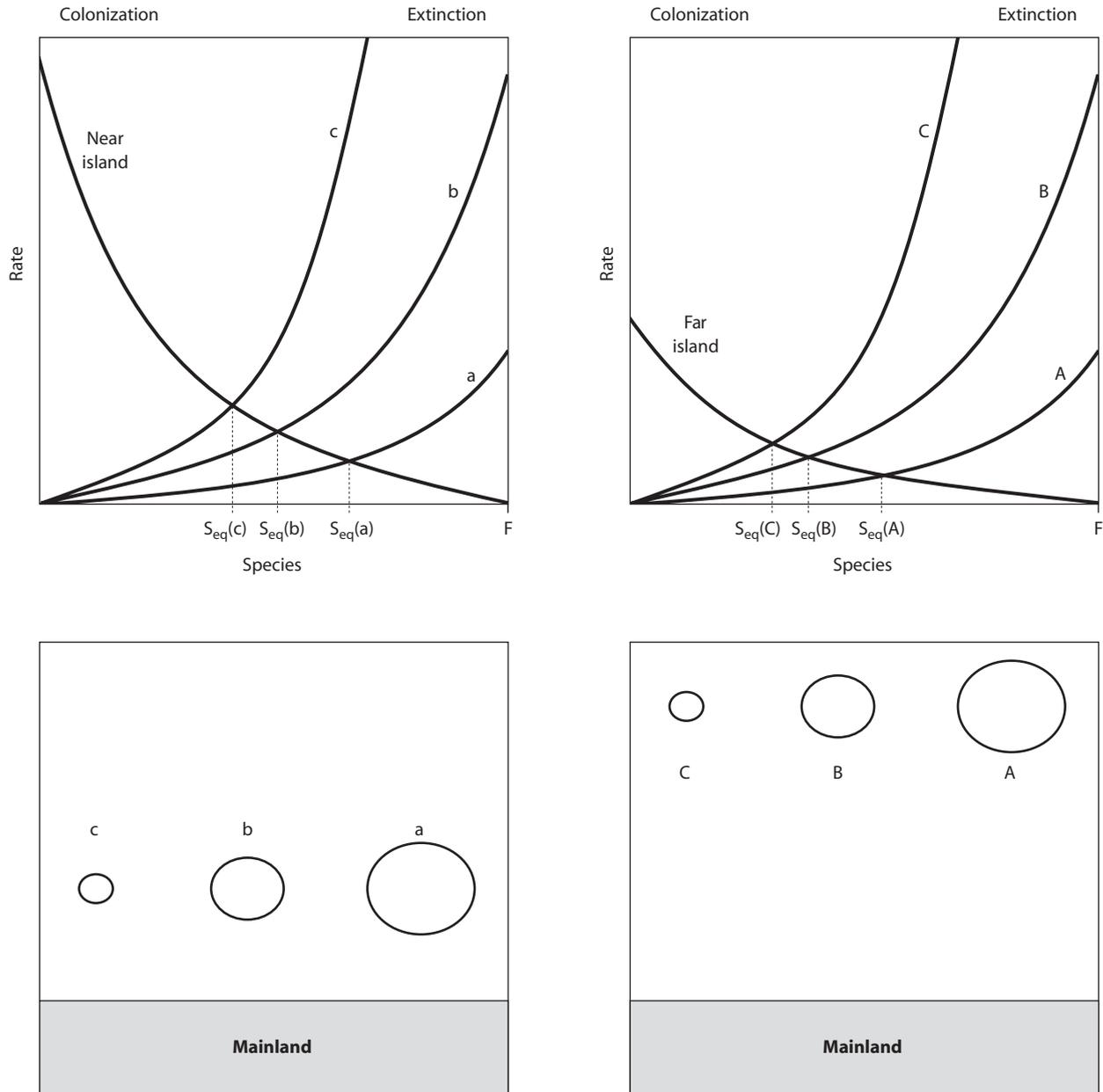


FIGURE 9.8. Both the rate of colonization and the rate of extinction vary for islands of different size and distance from the mainland or source population. The predicted equilibrium species number is indicated on the x-axis (adapted from MacArthur and Wilson, 1967).

rate (Brown and Lomolino, 1998; MacArthur and Wilson, 1967; Spellerberg and Sawyer, 1999).

MacArthur and Wilson did not consider the influence of island isolation on extinction rates, but extinction rates may be influenced by the degree of island isolation. For example, if an island is relatively close to a mainland source, or to other islands, then a constant flow of new immigrants can maintain even small populations and thereby reduce the frequency of local extinction (referred to as the rescue effect).

Case Study

Jared Diamond (1969) examined the basic principles of the island biogeography model in bird species (both land and freshwater) breeding on nine of the Channel Islands off southern California. Diamond chose this study system because bird species had been surveyed on these same islands in 1917, 51 years prior, providing a comparison for examining one of the fundamental concepts of MacArthur and Wilson's model: the species turnover rate (figure 9.9)

Part A: Written Study Proposal

You will now have a chance to apply what you have learned about species-area curves and various aspects of the MacArthur and Wilson island biogeography model. As a group, you will develop a written proposal to test the various predictions made in the island biogeography model with data on Channel Island bird species. Some of your analyses may simply involve comparisons between columns; however, other analyses may require log transformation and evaluation of correlation coefficients. You may find it necessary to test ideas not directly addressed in the models; however, if you do so, you must justify



FIGURE 9.9. Channel Islands.

TABLE 9.5.
Channel Island birds species tallies.

Island name	Area (km ²)	Distance (km)	Species no. (1968)	No. extinct	Human introduced	Colonization	Turnover (%)
Los Coronados	2.6	13	11	4	0	4	36
San Nicholas	57	98	11	6	2	4	50
San Clemente	145	79	28	9	1	4	25
Santa Catalina	194	32	30	6	1	9	24
Santa Barbara	2.6	61	10	7	0	3	62
San Miguel	36	42	11	4	0	8	46
Santa Rosa	218	44	14	1	1	11	32
Santa Cruz	249	32	36	6	1	6	17
Anacapa	2.9	21	15	5	0	4	31

your reasons for including these analyses. If the model predicts that two variables are not correlated, you may wish to test the relationship between those variables. You may test only data included in table 9.5. For example, you have no data on environmental variation between islands, and therefore you cannot test how this may influence species number.

Write a brief proposal to test predictions of the models with data from the Channel Islands. Your proposal should address each of the following:

- What aspect of MacArthur and Wilson's model are you testing?
- How would you analyze the data?
- What do you expect to see if the data support the model, and what do you expect to see if the data do not support the model?
- What assumptions must you make when analyzing the data?
- What other information do you wish we had collected on these islands?

After you have completed your written proposal, your instructor will give you, when possible, the graphical and statistical analyses that you requested. You will then be able to evaluate the data and present your conclusion to the class.

Part B: Oral Presentation of Analytical Results

Carefully examine the analyses provided by your instructor. As a group, you can now prepare an oral presentation discussing your prediction, the analysis, and your conclusions. You must specifically address whether the data support your analysis of the particular aspects of the model you chose to examine. You should clearly outline all of your assumptions and any limitations of the analysis you are presenting.

Finally, consider the following criticism of Diamond's work and outline further work that could clarify our understanding of Channel Island bird biogeography.

In his original paper Diamond (1968) pointed out that the extinction rates, as well as the turnover percentage, have probably been grossly underestimated. This is because multiple species may have colonized the islands and then gone extinct between the two survey times; they would not have been included in the data. Species present during either or both of the surveys may also have gone extinct and recolonized the islands any number of times between the two surveys. Based on this, Diamond concluded that the actual extinction rate and subsequent turnover percentage would most likely be higher than the values estimated in table 9.5.

Lynch and Johnson (1974) pointed out that many of the island extinctions could be attributed to human influences. For example, the disappearance of birds of prey like the Osprey, Bald Eagle, and Peregrine Falcon, which accounted for a large portion of the extinctions, was most likely due to pesticide poisoning and habitat modification. They also argued that much of the colonization was the result of the immigration of house sparrows and European starlings. Both of these species were introduced from Europe and are considered invasive (introduced species capable of significantly increasing their distribution from the point of introduction, and in the process out-competing native, endemic species with similar ecological requirements). In such cases the endemics may be driven to extinction (Brown and Lomolino, 1998, Lynch and Johnson, 1974).

Diamond continued to monitor bird species on Santa Catalina for several years after the study. He found year-to-year variation in the particular species breeding on the island. However, in most cases, only highly migratory birds varied in their presence or absence on the island. Even a distance of several kilometers would most likely have little meaning to these birds (Brown and Lomolino, 1998; Jones and Diamond, 1976).

Your group will have five minutes to explain your prediction, analysis, and interpretation of the results provided by the instructor. In addition, be sure to take a minute to explain further work you might want to perform to further test the equilibrium model and species area predictions for the Channel Islands.

References

- Brown, J. H., and M. V. Lomolino. 1998. *Biogeography*. Sunderland, Mass.: Sinauer Associates.
- Browne, J., and S. B. Peck. 1996. The long-horned beetles of south Florida (Cerambycidae: Coleoptera): Biogeography and relationships with the Bahama Islands and Cuba. *Journal of Zoology* 74: 2154–2169.
- Darlington, P. J., Jr., 1957. *Zoogeography: The Geographic Distribution of Animals*. New York: John Wiley & Sons.
- Diamond, J. M. 1968. Avifaunal equilibrium and species turnover rates on the Channel Islands of California. *Proceedings of the National Academy of Science* 64: 57–63.
- Jones, H. L., and J. M. Diamond. 1976. Short-time-base studies of turnover in breeding bird populations on the California Channel Islands. *Condor* 78: 536–549.
- Khazanie, R. 1990. *Elementary Statistics in a World of Applications*. New York: Harper Collins.
- Lincoln, R., G. Boxshall, and P. Clark. 1998. *A Dictionary of Ecology, Evolution and Systematics*. Cambridge: Cambridge University Press.
- Lynch, J. D., and N. V. Johnson. 1974. Turnover and equilibria in insular avifaunas, with special reference to the California Channel Islands. *Condor* 76: 370–384.