Figure 1.2: Numbers of insect species on a small mangrove island following defaunation. (From Simberloff and Wilson 1970, Fig. 1. © 1970 Ecological Society of America. Reprinted with permission of the publisher.)

    4. Provide "insight" to managers or planners (or others) by performing "what-if" simulations ("gaming").

1.3 Example: Island Biogeography

A biological example will help clarify some of these concepts. Biogeography is a discipline that combines elements of ecology and geography; its primary objective is to describe and explain the spatial distribution of plants and animals on the Earth's surface. The spatial scale for this field is broad: landmasses on the order of continents and large islands. Mapping the geographical distributions of species is a major component of biogeography, but it also examines patterns of numbers of species over geographical space. Island biogeography is a subdiscipline which restricts itself to islands.

1.3.1 Physical Setting

Ecologically, an island can be a true, oceanic island, or it can be a habitat island such as a patch of forest in a fragmented landscape. Biogeographers are interested in the final number of species that will occur on the island as well as the dynamics of the build-up of species on new islands or the extinction of species as island conditions change. An impressive field experiment performed by D. Simberloff and E. O. Wilson (Simberloff and Wilson 1970) tracked the number of insects on small mangrove islands following complete defaunation. The dynamics of numbers of species is shown in Fig. 1.2; the number of species after two years was nearly identical to the pre-defaunation level.

    The physical framework is shown in Fig. 1.3. Organisms from the mainland species disperse randomly. If an individual of a species not currently on the island intersects the island, that constitutes a colonization of a **new** species. If all of the individuals of a species on the island die, then the species has gone extinct. Consequently, the number of species on an island is the result of two processes: colonization and extinction.
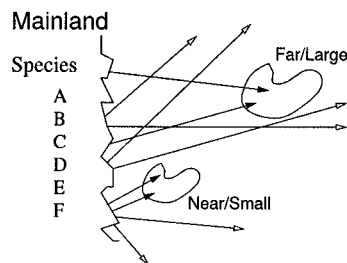
Figure 1.3: Physical picture of island biogeography theory. Organisms colonize randomly (arrows). Islands can vary by their distance to the mainland (near or far) and their size (large or small).

1.3.2 Theory

There are many approaches to the problem of describing the numbers of species on islands. For example, we could take Fig. 1.3 literally by mathematically creating a two-dimensional picture of a particular mainland and set of islands. We could then mathematically describe the movement of individuals of all species as they attempt to colonize the islands with random flight paths. This approach could incorporate extensive ecological and behavioral realism. Alternatively, we could simplify the figure by ignoring individual organisms, writing equations for the populations of each species on each island. MacArthur and Wilson (1967), however, took an even simpler approach. They simplified the problem by abstracting away populations of species and considered the system (S in Fig. 1.1) to be the number of species on an island, without regard to the numbers of organisms in the species. Thus, they describe a dynamic theory of biogeography in which the numbers of species is a balance of two processes: immigration and extinction. The rates of both processes depend on the number of species currently on the island. The **net rate** of change of species is the sum of these two "forces." When immigration is greater than extinction, the number of species increases; the number decreases if the opposite is true.

We make two very simple biological hypotheses concerning these processes:

- Individuals of each species have a constant probability of arriving at the island and this probability is identical for all individuals and all species. The rate of immigration (I) of new species only occurs upon the arrival of an individual of a species not currently on the island.

- The probability of extinction of any single species is constant. Consequently, as the number of species on the island increases, the probability that any one species goes extinct increases. Thus, the total rate of extinction (E) increases with R (number of species on the island).

Figure 1.4 graphically illustrates these hypotheses. In this figure, R is the number of species on the island, P is the number of species on the mainland (in the "pool"). We use the equations for a straight line to represent the rate of colonization and extinction. Immigration of new species decreases because as species accumulate there are fewer species that can be new. In the limit, if an island has as many species as the mainland, the rate of colonization must be 0. Extinction increases because on islands with many
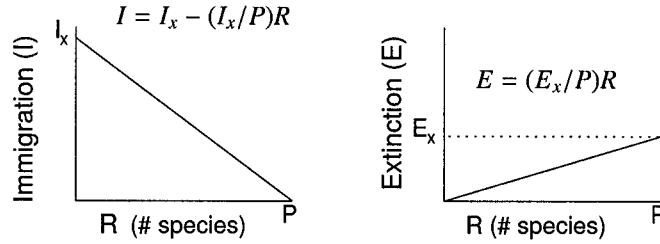
Figure 1.4: Quantitative relationships between number of species on an island (R) and rates of immigration (I) and extinction (E). P is the number of species in the mainland pool of species.

species, the total number of species going extinct will increase if there is a constant probability that any one species goes extinct.

These hypotheses (which might be based on data and prior knowledge) have simple mathematical expressions. The simplest model is a straight line in both cases.

$$I = I_x - (I_x/P)R$$

$$E = (E_x/P)R.$$

where I_x is the maximum colonization rate, and E_x is the maximum extinction rate.

We assemble these hypotheses into a single equation that describes the number of species on the island. For simplicity, we will consider time to be discrete, but later we will use continuous time.

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

$$= R_t + I_x - (I_x/P)R_t - (E_x/P)R_t. \tag{1.1}$$

Equation 1.1 mathematically represents our hypothesis that species dynamics are based on the relative strength of two processes: I_t (causing numbers to increase) and E_t (causing numbers to decrease). These types of data are difficult to collect in natural, field situations, but are possible in laboratory settings. Figure 1.5 is one such data set obtained from a classroom physical simulation of the colonization process (Haefner et al. 2002). In that exercise, organisms are the labeled lids of petrie plates. Using a mainland pool containing 20 different "species," students throw the lids at islands on the ground in front of them and measure the immigration and extinction rates during the "colonization" process. The linear regression lines for immigration and extinction rates are shown in Fig. 1.5a. Substituting these into Eq. 1.1 yields:

$$R_{t+1} = R_t + (8.963 - 0.395R_t) - (-0.011 + (0.0656)R_t). \tag{1.2}$$

The use of the regression equations, which are strongly influenced by the considerable statistical variation of the data, has some interesting implications for this model that are to be explored in the exercises.

Several interesting results can be obtained from Eq. 1.2. First, we can *iterate* the equation by assuming an initial value of R_t (e.g., $R_0 = 0$). Then, use the equation to
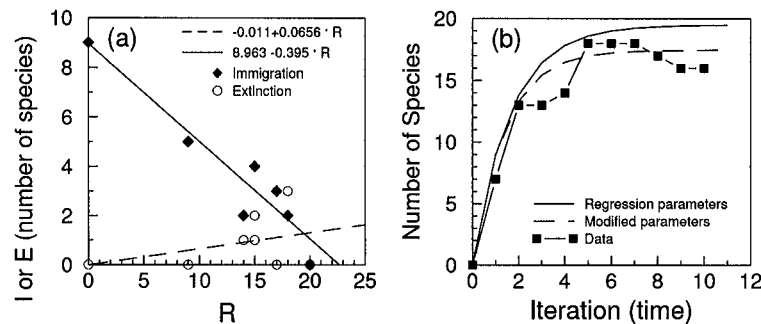
Figure 1.5: Data and results from a simulated biogeographical experiment. (a) Immigration rate (I, numbers/time, solid diamonds) and its best fit regression line (solid line). Also shown are Extinction rate (E, numbers/time, open circles) and its regression line (dashed line). (b) Observed and predicted number of species by iterating Eq. 1.2 using two estimates of parameters.

obtain R_1; insert this value on the right-hand-side of Eq. 1.2 and again use the equation to obtain R_2. Repeat this process indefinitely. For this simple equation, a calculator or spreadsheet is adequate. Once iterated, we can compare predictions with observations to test the adequacy of the model. Alternative models can be compared to the same data. For two sets of parameter values (i.e., the numerical constants in Eq. 1.2), Fig. 1.5b shows the performance of the model to observed data. See Exercise 7 to think about the reasons for different parameters.

MBS-CD contains `SimIslandBiogeog_FD` code implementing this model.

The second calculation we can make with Eq. 1.1 is to compute the equilibrium number of species on the island. This process is an important part of model analysis that we will discuss in later chapters, but for now the equilibrium number of species is that number at which the number of species is not changing. It is the number of species (R) at which $R_{t+1} = R_t$. We can compute this number by subtracting R_t from both sides of Eq. 1.1 and solving for the R_t that remains on the right-hand-side, which we refer to as $\hat{R}$:

$$0 = I_x - (I_x/P)\hat{R} - (E_x/P)\hat{R}.$$

This example illustrates the basic concepts to be developed in this book. First and foremost, the example shows the relation between the underlying biological hypotheses about mechanisms (Fig. 1.5a) and the immediately observable dynamics (Fig. 1.5b). When the purpose of the model is *understanding* (as it is in this example), then the central modeling problem is to develop quantitative hypotheses (representing the system S in Fig. 1.1) that explain the dynamics (response R in Fig. 1.1). An actual, alternative *control* use of the model is to address the question: What island-like conservation preserve design produces more species: a Single Large one, or Several Small, inter-connected ones? This problem is known as *SLOSS* (Simberloff 1988). Using the model for *prediction* we might want to predict how long it will take an island to recover if a disturbance at $t = 10$ (Fig. 1.5) reduces R by 50%. Second, the

example illustrates the mechanics of translating verbal hypotheses into mathematics and quantitative predictions using specific numerical values of parameters. And third, it demonstrates that models can be wrong when compared to data and that we must choose between alternatives (e.g., different parameters in Fig. 1.5b).

1.4 Classifications of Models

1.4.1 Forms of Models

Not all scientific models are precise, numerical, or quantitative. There are four forms:

1. *Conceptual* or *Verbal* – descriptions in a natural language.
2. *Diagrammatic* – graphical representations of the objects and relations (e.g., ecological "box-and-arrow" diagrams of energy flow, physiological diagrams of metabolic pathways such as the Krebs cycle).
3. *Physical* – a real, physical mock-up of a real system or object (either larger or smaller: a "tinker-toy" model of DNA or a scale model of an airplane for a wind tunnel).
4. *Formal* – mathematical (usually using algebraic or differential equations).

Our primary interest here will be in (2) and (4).

1.4.2 Mathematical Classification

The mathematical equation used to describe island species dynamics (Eq. 1.1) is known as a recursive finite-difference equation. It is only one form that a model could take. To show the scope of the range of mathematical models that are potentially applicable to biological systems, we construct a simple classification of mathematical models. The basis of the classification is whether the mathematics incorporates (or not) a particular mathematical structure. In some cases, it is a matter of opinion whether the mathematics displays the character or not.

1. **Does the mathematics have an explicit representation of mechanistic processes?**

   YES: *Process-oriented* or *mechanistic* models (e.g., hydrology models using Newtonian physics and chemistry, or population dynamics models with details of reproductive physiology).

   NO: *Descriptive* or *phenomenological* models (e.g., the island biogeography model, Boyle's law relating temperature, pressure, and volume, or a density-independent population dynamics model with reproduction represented as a single parameter).

2. **Does the mathematics have an explicit representation of future system states or conditions?**

   YES: *Dynamic* models (e.g., island biogeography model).

   NO: *Static* models (e.g., linear regression equation relating variables x and y).

3. **Does the mathematics represent time continuously?**

   YES: *Continuous* models, time may take on any values (e.g., 3.3 sec).

   NO: *Discrete* models, time is an integer only.