Ecology

The Experimental Analysis of Distribution and Abundance

FOURTH EDITION

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To Joe Connell and Bob Paine
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Some organisms do not occupy all of their potential range, and if transplanted outside their normal range, they survive, reproduce, and spread. The absence of an organism from a particular area may thus be due to the species’ having failed to reach the area being studied. This simple possibility should be examined before more involved possibilities.

The transport, or dispersal, of organisms is a vast subject that has been of primary interest not only to ecologists but also to biogeographers, who wish to understand the historical changes in distributions of animals and plants. There are some very difficult problems associated with the study of dispersal. First, the detailed distribution is known for so few species that most dispersals are probably not noticed. Dispersal of individuals between different parts of the species’ range may occur often. Second, an organism may disperse to a new area but not colonize it because of biotic or physical factors.

If colonization is successful, dispersal will result in gene flow and thus affect the genetic structure of a population. If the dispersing individuals are not a random sample of the population, dispersal will result in a founder effect, and the new population may be genetically quite distinct from the source population. Not all dispersing individuals survive to breed, so gene flow may be quite restricted in many species (Ehrlich and Raven 1969). Dispersal is thus simultaneously an ecological process affecting distributions and a genetic process affecting geographic differentiation.

The most spectacular examples of transport affecting distribution are species that are introduced by humans and explode to occupy a new area. Other examples are exploited species recolonizing their original range. Let us look into a couple of these situations.

**GYPSY MOTH (Lymantria dispar)**

In 1850 a French astronomer employed at Harvard University near Boston brought some eggs of the European gypsy moth (*Lymantria dispar*) to his house in Massachusetts. A few of the caterpillars escaped in 1869 and they began one of the most devastating caterpillar plagues of the New England states. Gypsy moths defoliate a great variety of deciduous and coniferous trees, from apple to alder, basswood, oaks, poplars, willows and birches. Because of severe defoliation of deciduous trees, Massachusetts in 1889 initiated a control program and by 1900 the severity of the outbreaks was reduced so the program was terminated by the state. After 1900 gypsy moths began to spread in a wave across New England (Figure 4.1). The spread
discusses these problems in detail for fish populations. All indirect measures of survival involve some assumptions and should be used only after careful evaluation.

**Immigration and Emigration**

Dispersal—immigration and emigration—is seldom measured in a population study. In most cases, it is assumed that the two components are equal, or else work is done in an island type of habitat, where dispersal is presumably of reduced importance. Both assumptions are highly questionable. The capacity to disperse is an essential part of the life cycle of most organisms. Dispersal helps to prevent inbreeding and is the ecological process that produces gene flow between local populations. Dispersal can set limits on geographic distributions (as we saw in Chapter 4) and affects community composition (as we shall see in Chapter 25). Some populations sustain a net emigration and export individuals; others are sustained only by a net immigration. One example is small songbirds in woodlots of eastern United States. Small woodlots are not productive for birds, and these populations can only be sustained by immigration (Wilcove and Robinson 1990). Dispersal may be a critical parameter in population changes.

Dispersal can be measured if individuals can be marked in a population. The use of radio-telemetry has revolutionized the study of animal movements, particularly for larger organisms (Kenward 1987). The major technical problem in studying dispersal is the scale of the movements involved. Many animals move distances greater than the size of study areas, and information on long distance dispersal can be lost. One of the major unsolved problems of conservation biology is how to facilitate immigration and emigration from populations in isolated parks or refuges in a fragmented landscape (Chapter 19).

**LIMITATIONS OF THE POPULATION APPROACH**

Two fundamental limitations restrict the methods used for studying populations. First, how can we determine what constitutes a population for any given species?
Ecological communities do not all contain the same number of species, and one of the currently active areas of research in community ecology is the study of species richness or biodiversity. A. W. Wallace (1878) recognized that animal life was on the whole more abundant and varied in the tropics than in other parts of the globe, and the same applies to plants. Other patterns of variation have long been known on islands; small or remote islands have fewer species than large islands or those nearer continents (MacArthur and Wilson 1967). The regularity of these patterns for many taxonomic groups suggests that they have been produced in conformity with a set of basic principles rather than as accidents of history. How can we explain these trends in species diversity?

**MEASUREMENT OF BIODIVERSITY**

The simplest measure of biodiversity is to count the number of species. In such a count we should include only resident species, not accidental or temporary immigrants. It may not always be easy to decide which species are accidentals: Is a bottomland tree species growing on a ridge top an accidental species or a resident one? The number of species is the first and oldest concept of species diversity and is called *species richness*.

A second concept of species diversity is that of *heterogeneity*. One problem with counting the number of species as a measure of diversity is that it treats rare species and common species as equals. A community with two species might be divided in two extreme ways:

<table>
<thead>
<tr>
<th>Community 1</th>
<th>Community 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species A</td>
<td>99</td>
</tr>
<tr>
<td>Species B</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>50</td>
</tr>
</tbody>
</table>

The first community is very nearly a monoculture, and the second community would seem intuitively to be more diverse than the first. We can combine the concepts of number of species and relative abundance into a single concept of heterogeneity. Heterogeneity is higher in a community when there are more species and when the species are equally abundant.

A difficult problem arises in trying to determine the number of species in a biological community: *Species counts depend on sample size*. Adequate sampling can usually get around this difficulty, particularly with vertebrate species, but not always with insects and other arthropods, in which species counts cannot be complete.
Two different strategies have been adopted to deal with these problems. First, a variety of statistical distributions can be fitted to data on the relative abundances of species. One very characteristic feature of communities is that they contain comparatively few species that are common and comparatively large numbers of species that are rare. Since it is relatively easy to sample any given area and count the number of species on the area and the number of individuals in each of these species, a great deal of information of this type has accumulated (Williams 1964). The first attempt to analyze these data was made by Fisher, Corbet, and Williams (1943).

In many faunal samples, the number of species represented by a single specimen is very large, species represented by two specimens are less numerous, and so on until only a few species are represented by many specimens. Fisher, Corbet, and Williams (1943) plotted the data and found that they fitted a "hollow curve" (Figure 23.1), and that the data could be described mathematically by the logarithmic series. The most significant ecological observation is that the largest number of species in a community fall into the "very rare" category.

The logarithmic series arises in communities with relatively few species in which a single environmental factor is of dominant importance (May 1975). It describes an extreme type of "niche preemption" in which the most successful species preempts a fraction $k$ of the total resources, the next species a fraction $k$ of the remaining resources, and so on. This type of niche-preemption hypothesis predicts a logarithmic series distribution or "hollow-curve" as a description of species abundances in natural communities.

The logarithmic series implies that the greatest number of species has minimal abundance, that the number of species represented by a single specimen is always maximal. This is not the case in all communities. Figure 23.2 shows the relative abundance of breeding birds in Quaker Run Valley, New York. The greatest number of bird species is represented by ten breeding pairs, and the relative abundance

![Figure 23.1](image-url)

*Figure 23.1* Relative abundance of Lepidoptera (butterflies and moths) captured in a light trap in Rothamsted, England, in 1935. Not all of the abundant species are shown. There were 37 species represented in the catch by only a single specimen (rare species); one very common species was represented by 1799 individuals in the catch. A total of 6814 individuals were caught, representing 197 species. Six common species comprised 50 percent of the total catch. (Modified from Williams 1964.)