…tically, maximum beta species di-
…habitat patches are large, or fairly large, and the total amount of edge in the landscape is also large. These countertrends need to be considered in forest and wildlife management and landscape design in general. Fahrig (1997) discussed the effects of habitat loss and fragmentation on population extinction.

Island biogeographical theory can help in determining just how large the patches should be (the minimum critical size of ecosystems; Lovejoy et al. 1986). See Harris' (1984) book entitled *The Fragmented Forest*, which builds on the theory of island biogeography regarding the management and preservation of biotic diversity.

4 Island Biogeography

Statement

MacArthur and Wilson (1963, 1967) first published the theory of island biogeography. Simply stated, the **island biogeography theory** holds that the number of species on an island is determined by the equilibrium between the immigration of new species and the extinction of those species already present. As rates of immigration and extinction depend on the size of islands and their distance from the mainland, a

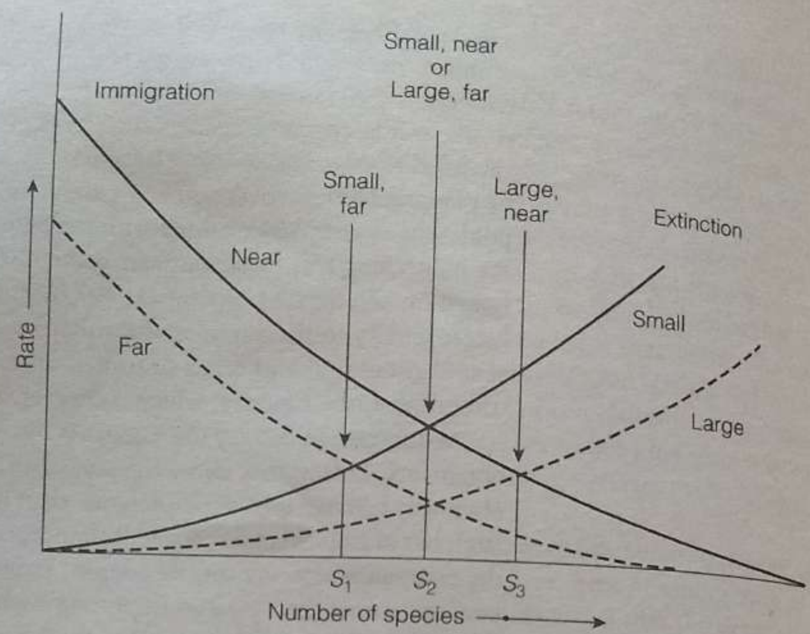


Figure 9-8. Theory of island biogeography. The number of species on an island is determined by the equilibrium between rate of immigration and rate of extinction. Four points of equilibrium are shown, representing different combinations of large and small islands either near or far from continental shores (after MacArthur and Wilson 1963, 1967).

general equilibrium can be diagrammed, as presented in Figure 9-8. Four equilibrium points are shown, representing a small, distant island predicted to have few species, S_1; a small, nearby or a larger, distant island, predicted to be intermediate in terms of species richness, S_2; and a large, nearby island that should support many species, S_3. This model demonstrates the interplay of isolation, natural selection, dispersal, extinction, and speciation that has attracted the attention of population ecologists and evolutionary biologists to island biogeography for more than a century. This model is of fundamental importance in landscape ecology and conservation biology.

Explanation

Islands have fascinated biologists, geographers, and ecologists since Charles Darwin visited the Galápagos Islands. It has also become apparent that landscape patches on the mainland likely function as islands within the landscape mosaic. For example, the Andes Mountains of Ecuador stirred the imagination of Alexander von Humboldt (1769–1859), who laid the foundations of **mountain geoecology** there. Some argue that these Andean landscapes—the cradle of Humboldt's work—should be considered the birthplace of ecology, especially holistic ecology (Sachs 1995; F. O. Sarmiento 1995, 1997). The peaks of such mountains, especially at approximately the same elevations, function as terrestrial islands regarding plant and animal community types. J. H. Brown (1971, 1978) investigated the insular biography of these "islands" in regard to small mammal and bird population diversity and abundances.

These patches, which vary in size—large and small—and distance—near and far—fit the theory of island biogeography as proposed by MacArthur and Wilson (1963). For example, a patch of forest may be located in a "sea" of agricultural cropland (see Fig. 9-1A), isolated from other patches in the landscape. The effect of patch size and isolation appears to have a pronounced influence on the nature and diversity of species within these landscape patches. Preston (1962) formalized the relationship between the area of the island and the number of species present as follows:

$$S = cA^z$$

where S is the number of species, A is the area of the island or patch, c is a constant measuring the number of species per unit area, and z is a constant measuring the slope of the line relating log S and log A (in other words, z is a measure of the change in species richness per unit area).

Thus, the theory of island biogeography states that the number of species of a given taxon (insects, birds, or mammals) present on an island or within a patch represents a dynamic equilibrium between the rate of immigration of new colonizing species of that taxon and the rate of extinction of previously established species (see Fig. 9-8).

Examples

Simberloff and Wilson (1969, 1970) removed all arthropods (by insecticide treatment) from small mangrove islands in the Florida Keys and observed recolonization. The patterns of recolonization of the islands by arthropod populations tended to verify the MacArthur-Wilson dynamic equilibrium model based on the theory of island biogeography. Since that time, similar studies have been conducted (for example, J. H. Brown and Kodric-Brown 1977; Gottfried 1979; Strong and Rey 1982; Williamson 1981), helping to explain the distribution of arthropod, bird, and small mammal species among habitat patches and on islands.

Others have suggested that the theory of island biogeography provides a basis for the design of reserves established to preserve natural diversity, to protect endangered species, or both. Accordingly, a large reserve is preferable to a group of smaller reserves with the same total area. Harris (1984), in his award-winning book *The Fragmented Forest,* also built on the theory of island biogeography by relating it to forest and wildlife management. The idea that corridors should be maintained between reserves or refuges whenever possible was suggested by E. O. Wilson and Willis (1975) based on the equilibrium theory of island biogeography.

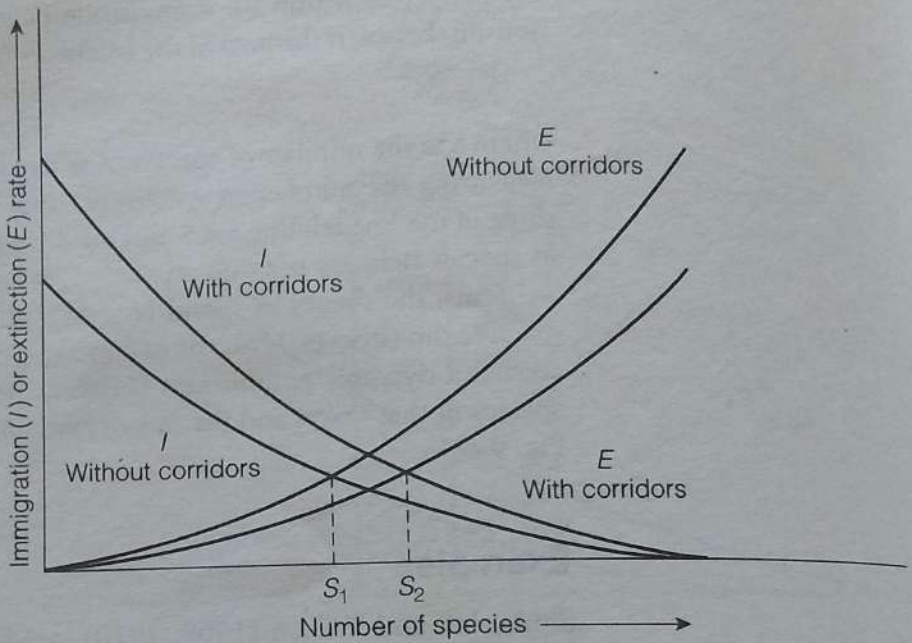
Ecological principles based on the theory of island biogeography help planners and resource managers to design nature preserves. When a preserve is to be carved from a homogeneous landscape matrix, the following landscape principles are frequently used regarding the design of the preserve, in order to maximize species richness and to minimize the role of disturbance and edge effects on ecological processes:

- One large patch is better than several smaller patches of the same total size;
- Corridors connecting isolated patches are preferable to a total lack of corridors; and
- Circular or square patches that maximize area-to-perimeter ratios are preferable to elongated, rectangular patches with much edge.

It should be kept in mind that nature preserves must be designed and managed in accordance with plant and animal life histories, special requirements (such as nesting sites, salt licks, and food resources), and the need to minimize the invasion of exotic species.

Simberloff and Cox (1987) provided a model encompassing rates of immigra-

Figure 9-9. Effect of corridors on rate of immigration, *I*, rate of extinction, *E*, and the resulting number of species in equilibrium based on the island biogeographic model. S_1 is the equilibrium number of species without corridors; S_2 is the equilibrium number of species with corridors. (From Figure 1 in Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1:63–71. Copyright 1987 Blackwell Publishing.)



tion and extinction between patches that were either isolated or connected by corridors (Fig. 9-9). Harris (1984), among others, suggested that corridors act by increasing the rate of immigration—thus, the extinction of a dwindling population would be slowed or even halted by an influx of immigrants (the **rescue effect**; J. H. Brown and Kodric-Brown 1977). Furthermore, the individuals of some species, especially large mammals, must range widely and maintain a large home range in order to meet food requirements, and if population sizes are too small, inbreeding depression will ensue and lead to extinction—a concern regarding the small, isolated population of the Florida panther (*Felis concolor coryi*). Figure 9-9 provides a model to test these concerns and hypotheses.

In summary, any patch of habitat isolated from similar habitat by a different, relatively inhospitable terrain or matrix that is navigated with difficulty by organisms of the habitat patch may be considered an *island*; these patches include mountaintops, small lakes, bogs, areas fragmented by human land use, woodlots, or forest patches clear-cut for experimental purposes. How these experimental patches affect the population dynamics of species of small mammals and butterflies has been documented by Bowne et al. (1999), Haddad and Baum (1999), Mabry and Barrett (2002), and Mabry et al. (2003).