more likely to be important in developing reproductive isolation than are founder effects.

SEE ALSO THE FOLLOWING ARTICLES

Inbreeding / Population Genetics, Island Models in

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FRAGMENTATION

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Fragmentation is a process that occurs when originally extensive and continuous habitats are broken into smaller areas and separated by other habitat or land use types that disrupt the continuity of the original habitat. At the landscape level, this process generates patches of a certain habitat type that somewhat resemble islands embedded within a matrix of distinct habitats. Fragmentation of natural habitats can influence the entire suite of ecological processes, from individual behavior through population dynamics to ecosystem fluxes. Although particular attributes of the environment determine the existence of natural fragments, most recent habitat fragmentation at the landscape level is human-caused.

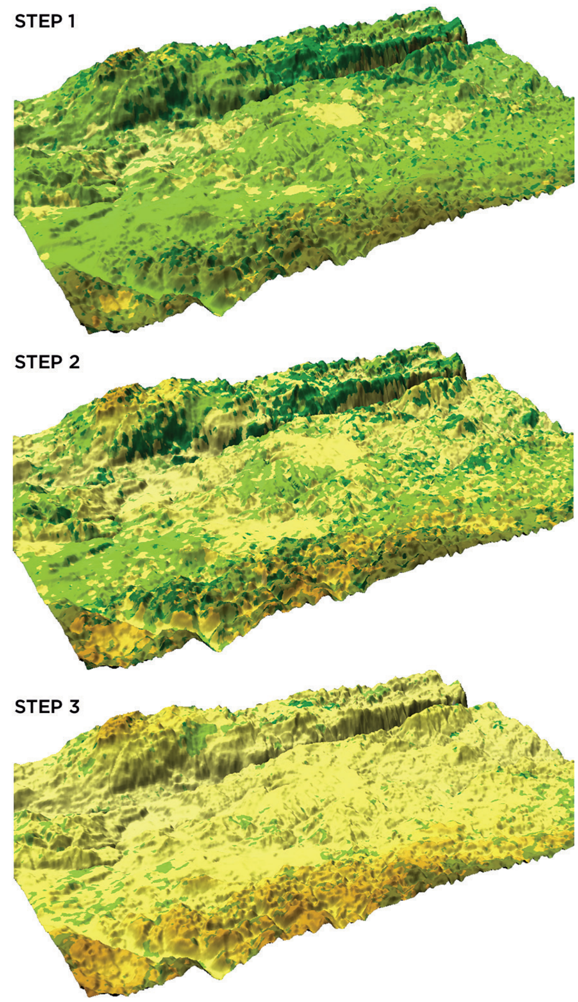

FIGURE 1 Illustration of how forest fragmentation proceeds in a real case study in the Highlands of Chiapas, southern Mexico, during the period 1975–2000. The fragmentation process typically begins with gap formation in the vegetative matrix (in green, Step 1). For a while, the matrix remains as natural vegetation despite the continuing progress of fragmentation (Step 2). As the gaps get larger and more numerous, they become the matrix, and the connectivity of the original vegetation is disrupted (Step 3).

THE FRAGMENTATION PROCESS

In terrestrial ecosystems, fragmentation typically begins with gap formation or perforation of the vegetative matrix as humans colonize a landscape or begin extracting resources there (Fig. 1, Step 1). For a while, the matrix remains as natural vegetation, and species composition and abundance patterns may be little affected (Fig. 1, Step 2). But as the gaps get larger and more numerous, they eventually become the matrix, and the connectivity of the original vegetation is disrupted (Fig. 1, Step 3).

The process of habitat fragmentation has two intrinsic components: (1) reduction of the area of the original habitat; and (2) change of the spatial configuration of what remains (henceforth referred to as "fragments," "patches," or "remnants"). The latter can be described through the pattern of fragmentation (e.g., size, shape, number, and distribution of habitat patches). Two landscapes can have the same amount of habitat but two completely different patterns of fragmentation. A considerable body of literature exists on how to describe the extent and pattern of habitat fragmentation. However, a situational definition should include some measure of the pattern of fragmentation to place it in context.

Fragmentation is also related to the process of insularization (formation of islands that are isolated from each other and, occasionally, from the mainland). This has brought about the application of island biogeography theory to the study of habitat fragmentation. However, important differences exist between these two processes, in both a temporal and spatial context; thus, caution must be taken when relying on these analogies to investigate the biological consequences of fragmentation.

BIOLOGICAL CONSEQUENCES OF FRAGMENTATION

Any land-use change can potentially result in habitat fragmentation. The most immediate effect is the elimination of species that occurred solely in the portions of the landscape that are destroyed. The habitat that remains is then broken into remnants that are isolated to varying degrees. The time since isolation, the distance between adjacent remnants, and the degree of connectivity between the remnants are all important determinants of the biotic response to fragmentation at any scale.

Fragmentation can affect plant and animal populations at several levels. At the landscape level, fragmentation causes once-continuous populations to break up into smaller subpopulations occupying the remaining habitat patches. Scientists believe that these subpopulations may act as metapopulations (collections of small populations occupying a number of habitat patches). Individuals occasionally move among patches, and populations can go extinct in individual patches as a result of chance events. However, the vacant patches may eventually be colonized and occupied again in the future. If colonization rates of vacant patches are higher than extinction rates, the metapopulation will persist. As fragmentation of the landscape proceeds, patches that are far from other patches will not exchange individuals with the other patches, and the small population remaining in the patch will eventually go extinct. As patches become more and more isolated from each other, the colonization rates will decline to the point that extinction rates exceed colonization rates, and the whole metapopulation will go extinct. Fragmentation thresholds may indeed reflect the point (quantity of habitat loss) where extinction overrides colonization, and species richness collapses at the community-landscape level.

At the fragment level, several factors affect a fragment's value as plant and wildlife habitat. In general, larger fragments are likely to support more species. This principle is supported by theoretical species–area relationships drawn from the field of island biogeography. Individual fragments are also affected by their surroundings. At the forest edge, wind and sunlight result in drier conditions than are found in the interior of the forest patch. Forest edges are also more accessible to predators and parasites that may occur in adjacent fields or developed areas. For example, house cats, which kill small birds, are often more common in forest edges adjacent to residential developments. Cowbirds, which are nest parasites, are also more common in forests adjacent to the open fields where they feed. Cowbirds lay their eggs in the nests of other birds. The host birds will care for the cowbird eggs. When the eggs hatch, the larger cowbird nestlings will outcompete the host nestlings for food and may even push the host nestlings out of the nest. Some plant and animal species ("interior species") are not able to tolerate the drier conditions or the predators and parasites that occur at the habitat edge. These species occur only in the core habitat of remnant patches.

Although most models predict negative effects of habitat fragmentation on biodiversity, empirical evidence to date suggests that the effects of fragmentation can sometimes be positive. For instance, some species do show positive edge effects. For a given amount of habitat, more fragmented landscapes contain more edge; therefore, positive edge effects could be responsible for positive effects of fragmentation on abundance or distribution of some species. Habitat fragmentation can also increase habitat complementation for species that require different kinds of habitats in different stages of their life cycles (e.g., some insects and amphibians), which has a positive effect on biodiversity. In addition, fragmentation, and subsequent habitat isolation, can be a trigger for diversification for many taxa. In the Hawaiian Islands, for example, genetic differences have been documented between habitat patches in forests naturally fragmented by lava (commonly known as kīpuka). This may allow sufficient isolation to initiate diversification.

THE THEORY OF ISLAND BIOGEOGRAPHY

The current concept of habitat fragmentation emerged from the theory of island biogeography. The two predictor variables in this theory are island size and island isolation, or distance of the island from the mainland. The theory of island biogeography essentially states that, as the size of an island increases, so does the number of species it contains. Some of the most plausible explanations to describe this phenomenon are that (1) as area increases, so does the diversity of physical habitats and resources, which in turn supports a larger number of species; (2) as area increases, the size of populations increases, thus reducing the probability of extinction; and (3) for a group of islands, or archipelago, populations within the islands are assumed to work as a metapopulation system. These subpopulations experience an equilibrium between extinction and colonization of species from other islands. Larger islands are less subjected to extinction because they can hold larger populations of their species, which in turn result in a positive imbalance between these two processes. An additional explanation is that only larger islands are likely to contain enough habitat to support species such as large mammals. Consequently, such species can become extinct as the area is reduced.

ISSUES OF SCALE AND THE SPATIAL CONCEPT OF FRAGMENTATION

The parallelism between habitat fragments and islands can be, however, deceptive. When the theory of island biogeography was conceptually extended from island archipelagoes to terrestrial systems of habitat patches, the concept of isolation changed; isolation was then seen as the result of habitat loss, which is enough to explain by itself an important loss of biodiversity.

In temporal terms, there are also important differences. Because island formation is generally a natural geological process, islands may need hundreds and thousands of years to experience the insularization and area effects upon their biota, whereas habitat fragments have generally been created in a much shorter timeframe and have not always had enough time to experience such effects. The temporal scale of investigation may therefore have a strong influence on the results of a study, with short-term crowding effects eventually giving way to long-term extinction debts.

Different organisms and ecological systems also experience the degree of fragmentation of a particular environment in variable, and even contradictory, ways. Species within the same landscape can respond to fragmentation in four distinct ways. First, a species can thrive in the matrix of human land uses; a number of weedy species worldwide fit this description. Second, a species can maintain viable populations within individual habitat fragments, but not in the matrix; this is an option only for species with small home ranges or otherwise modest requirements, such as many plants and invertebrates. Third, a species can be highly mobile and disperse through the matrix; this is the case for many birds. Fourth, a species may require a larger amount of habitat but may be not capable of thriving in or dispersing through the matrix, being thus bound for eventual extinction.

Additionally, the spatial concept of fragmentation often implies that habitat remnants are isolated by areas that function as hostile environments to the organisms within the remnants. There are many instances, however, where this concept of habitat distribution is not applicable. In Central America and other tropical regions of the world, for example, traditional slash-and-burn agriculture has led to a matrix partly dominated by secondary vegetation. The variegated nature of such landscapes must be utilized differently by different taxa. At one extreme, there are native species that grow successfully over the whole range of modifications; for these species, potential habitat forms a continuum across the landscape. The other extreme results from intolerance to most forms of interference; these species exist in a truly fragmented landscape, restricted to remnants in better conditions. The majority of species appear to fall somewhere between these two tolerances. For them, the landscape is a constantly shifting mosaic of habitats of varying suitability.

SEE ALSO THE FOLLOWING ARTICLES

Deforestation / Island Biogeography, Theory of / Metapopulations / Species–Area Relationship

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FRASER ISLAND

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Fraser Island, the world's largest sand island, is located off the eastern coast of Australia in the state of Queensland and is both a national park and, since 1992, a World