# A Theoretical Overview of the Processes Determining Species Richness in Forest Fragments

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Ecosystem or habitat fragmentation refers to "any sort of process which results in reducing an original area's size, creating a new, smaller, or several split ones" (Lovejoy, Bierregaard, et al. 1986). The literature concerning the subject is growing fast and deep, promoting formerly overlooked issues to the status of main areas of research. Besides increasing in number, studies of habitat fragmentation have also gained complexity, as exemplified by the use of nontrivial analytical methods related to percolation theory and critical phenomena (e.g., Andrén 1994; Bascompte and Solé 1996, 1998). With this growth in the literature, the overall scenario related to habitat fragmentation may be easily misunderstood, especially by people new to the field.

In this chapter we present a brief synthesis of the predicted effects of ecosystem fragmentation on species richness to provide an overview of the ecological mechanisms thought to be involved. We do not intend to present an extensive review of the theme, nor any new theoretical insights. Readers interested in a more specific approach should refer to other chapters of this book (see, for example, Chapters 8, 10, 13, 19, and 21). Those interested in broader approaches, such as landscape mosaics, as well as a broader geographical perspective, will find good reviews in Forman (1995) and Laurance and Bierregaard (1997a).

## Habitat Fragmentation

Ecosystem fragmentation can result from both natural and "non-natural" (human-induced) causes, such as rising ocean levels isolating tracts of vegetation or anthropogenic deforestation converting continuous habitats into scattered patches in a "sea" of disturbed habitat. Because of the structural similarity between such patches and true islands, as they themselves argued, MacArthur and Wilson's (1967) "theory of island biogeography," developed to explain patterns of species numbers on oceanic islands, should provide a valid first approximation to the biological dynamics in habitat patches left in man-made habitat mosaics. According to the model and its refinement by Brown and Kodric-Brown (1977), the number of species inhabiting an island or habitat fragment will be a dynamic equilibrium between opposing rates of extinction and immigration such that islands hold a relatively constant number of species.

Because the model treats all species equally, the identity of the species found on
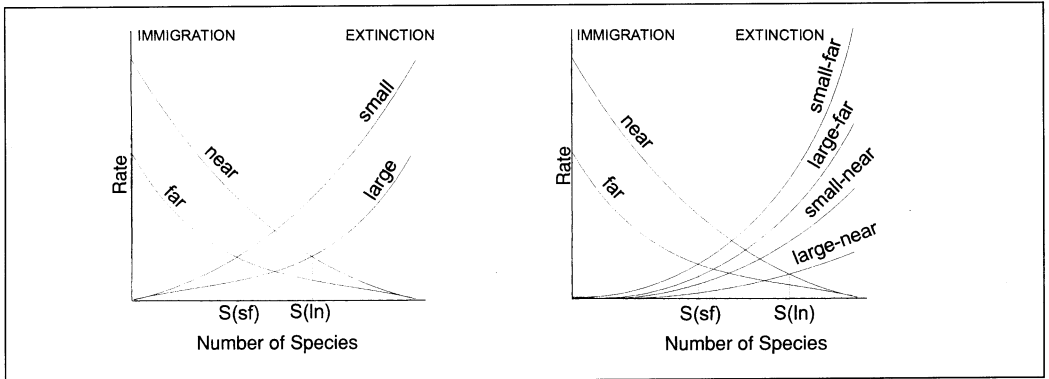
Fig. 2.1. Models of insular biogeography. At left, MacArthur and Wilson's (1967) model, representing the number of species in an island (S) being determined by a balance between extinction and immigration rates, which depend on the island's size and its distance from the source of colonizers. At right is Brown and Kodric-Brown's (1977) modification of the model, incorporating the "rescue effect" of immigration on extinction.

a given island would vary with time. On any island, the immigration rate (i.e., the number of new species arriving per unit time) falls as more species become established, because fewer immigrants will belong to new species. Simultaneously, the extinction curve rises, because the more species that are present, the more there are to become extinct, and the more likely any given one will become extinct because of ecological and genetic accidents related to small population sizes. The intersection of these curves represents the equilibrial species numbers and turnover rate (fig. 2.1 left).

Immigration rates depend on the proximity to a continent or other source of dispersing species, so that islands near the continent would present higher immigration curves than would isolated islands. Extinction rates depend on island size to the extent that the smaller the area, the stronger the detrimental effect promoted by the combination of diminishing population size and increasing probability of interference among species. Extinction rates, however, are also dependent on island isolation, because the same parameters that affect colonization by species new to the community also affect

the arrival of individuals belonging to the species already on the island. Providing that this immigration rate is sufficiently high, it will reduce the extinction rate because demographic and genetic contributions of immigrants tend to increase the size and fitness of insular populations, through what has been termed the "rescue effect" (Brown and Kodric-Brown 1977). High immigration rate also will have a statistical effect in reducing the apparent extinction rate simply by decreasing the probability that a given species will be absent during any census. Consequently, the extinction curves should be higher for islands that are small and distant, and lower for large and near ones. The equilibrial species number increases from small and distant islands to large and near ones (fig. 2.1 right).

These effects of the species-area relationship must be considered when analyzing the consequences of habitat fragmentation. One of the most universal relationships observed in biological communities is that between species and area—large areas will have more species than smaller ones. This relationship may be linked to effects of area per se or to an increased variety of habitats in

larger areas. For a more complete discussion of species-area relationships, see, for example, Rosenzweig (1995).

Researchers using the theoretical framework derived for island situations in the study of ecosystem fragmentation must consider, for terrestrial ecosystems, that colonizers may also come *from,* rather than just pass over, the "sea of inhospitable habitats" surrounding the fragment. This changes how one should analyze immigration rates, because two types of sources of dispersing species must be considered: immigrants can come both from the "continent" (the nearest block of undisturbed habitat) and from the "sea." Moreover, ecosystem fragmentation promotes drastic and sudden changes in habitat, reducing its size and possibly, via sampling effects, the number of habitats in a given area. Some species, however, will survive this process, adding a confusing factor to the predictions of the theory of island biogeography, which assumes that an island is initially a species-empty environment.

Pursuing the island analogy, habitat fragments have been likened to "land-bridge" islands, which were once part of a more extensive habitat before becoming isolated by rising water levels and began with a full complement of the regional flora and fauna. In contrast, true "oceanic" islands, created by volcanos, for example, began as barren rocks devoid of life. In the latter case, immigration will initially be the dominant force, whereas in the case of land-bridge islands, extinction will predominate as ecosystems restricted to small areas "shed" species for the reasons outlined above. These extant species, present at the moment of isolation, may affect extinction and colonization rates in a way that may make these rates appear independent of fragment size and isolation. Therefore, although very useful, the equilibrium theory of island biogeography and associated species-area rela-

tions provide only a framework for the study of the biological dynamics of fragments (Forman 1995).

A number of factors in addition to fragment size and isolation must be considered in making predictions regarding the effects of fragmentation on terrestrial ecosystems. Most important, as Zimmerman and Bierregaard (1986) and others have pointed out, different species have different ecological requirements and therefore do not have equal probabilities of immigration or extinction on a real or habitat island.

In the three decades since MacArthur and Wilson developed their theory of island biogeography, ecologists and conservation biologists have adopted a much broader view and begun to look not just at individual fragments but at how the fragments interact with communities in the surrounding landscape. Indeed, an entire discipline, landscape ecology, has arisen as researchers began to question how populations interact with one another in fragmented landscape mosaics (e.g., Wiens and Moss 1999). Levins (1970) coined the term "metapopulations" to recognize that populations in a heterogeneous environment interact with each other, exchanging genetic material through emigration and immigration. Fahrig and Merriam (1994) argued that we should be focused on the spatial structure of fragmented habitats, because often the most important source of immigrants to a habitat fragment will be another fragment rather than a nearby "mainland" (continuous habitat) source with continuous habitat. To this end we have begun to measure our landscape mosaics from as far away as possible—via satellites—and have developed geographical information systems to quantify the structure and processes that are occurring at the landscape level (see Chapter 28).

Again, it is outside the scope of this chapter to synthesize this enormous and bur-

geoning discipline. Throughout the rest of this volume readers will encounter the reports of many studies dealing with landscape-level issues—from the genetics of rare species (Chapter 8) to metapopulations (Chapter 15) to spatial analyses of remotely sensed data describing the entire study area (Chapter 28). Here we shall focus on the processes in individual fragments that affect population levels.

## The Biological Dynamics of a Fragmented Ecosystem

With habitat fragmentation, as opposed to oceanic island-based systems, there are three possible results following a fragmentation event: increment, diminishment, or maintenance of the species number of the community concerned (fig. 2.2). Once an ecosystem is fragmented, structural and biological changes are observed, with a consequent effect on the ecological processes operating in the fragment. Structural changes involve isolation of the remnant from its original matrix and increased proximity of its core to the bordering environment. Biological changes involve losses of individuals, species, and habitats. Structural changes are, therefore, linked to regional processes, such as immigration, whereas biological changes refer to local processes, such as species interactions. This dichotomy, however, is not as clear as we might like. Edge creation, for instance, is primarily a structural change, but it will affect habitat suitability (a local process) as well as immigration (a regional process). Thus, edge effects lie in a gray zone between local mechanisms that operate in the community living within the fragment, and large-scale processes related to the ensemble of local communities connected by dispersal. As such, edge effects deal with species interactions at local and regional

scales simultaneously. Mechanisms addressing such a broader geographical context of species interactions are referred to by some authors as operating at the "mesoscale" (Holt 1993).

The proximate consequence of these changes is local extinction, which is the most frequently reported effect of habitat fragmentation (e.g., DeSouza and Brown 1994; Bierregaard and Stouffer 1997; Stratford and Stouffer, 1999). Some researchers have reported that the number of species in the fragment relative to sites in the continuous forest may be maintained—or might even increase—after fragmentation (e.g., Malcolm 1997a; Tocher, Gascon, and Zimmerman 1997).

Interestingly enough, no matter whether species richness increases, decreases, or is kept constant after fragmentation, the ecological processes involved have many mechanisms in common (Gascon et al. 1999). What characterizes a particular process is, to a large extent, the number of mechanisms involved and the pathways linking such mechanisms. The dynamic equilibrium postulated by island biogeography theory is achieved by loops and feedbacks performed by these chains of mechanisms (see fig. 2.2).

Some immediate changes are promoted by ecosystem fragmentation (boxes in top row of fig. 2.2). These changes are the trigger mechanisms that will lead to the three possible outcomes: reduction, increase, or maintenance of species richness. As discussed above, the changes are related to local, mesoscale, and regional processes that, although they share several mechanisms, will be discussed separately.

Local Processes

Local processes are represented by losses of individuals and habitats (fig. 2.2, top boxes on the right). Losses of individuals may lead
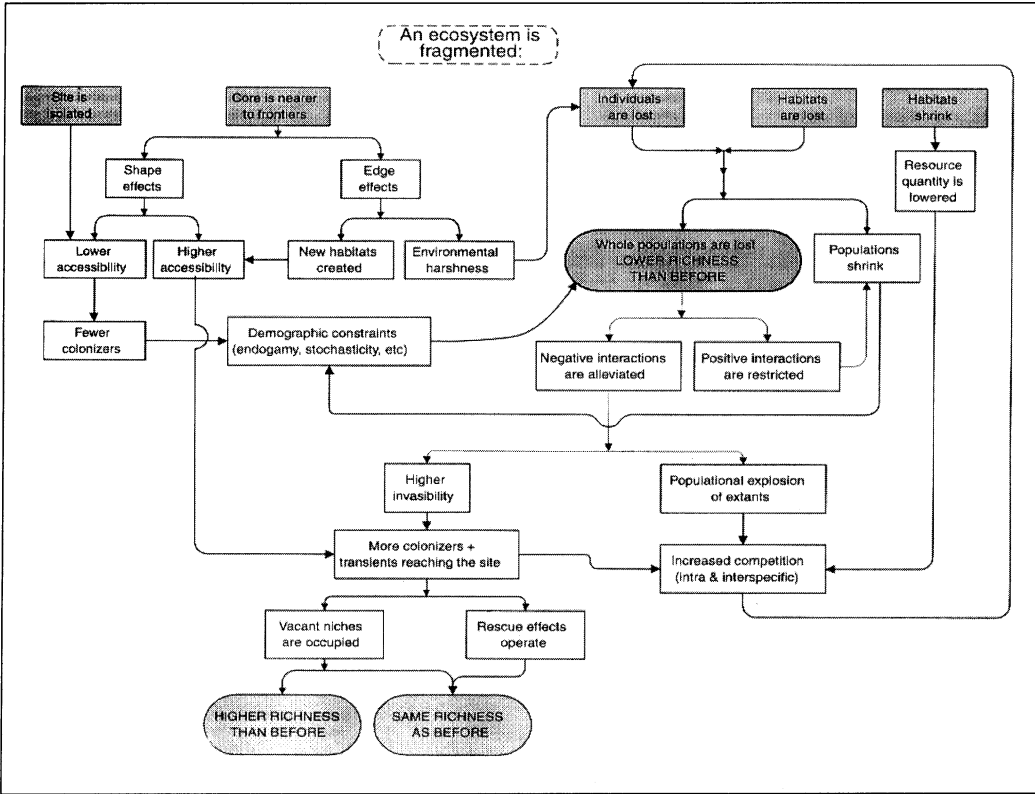
Fig. 2.2. Ecological processes determining species richness upon a fragmentation event. The boxes at top represent the immediate changes caused by habitat fragmentation. Rounded, shaded boxes represent the three possible outcomes of ecosystem fragmentation regarding species richness. Loops are indicated to make it clear that an observed value of species richness may not represent a static result but can be part of a dynamic equilibrium.

to local extinction if the individuals missed represent a whole population. This is likely to happen either to small populations or to species with high levels of spatial aggregation. Local extinction may be caused by other mechanisms, such as the loss of habitat, for species restricted to the lost habitat. It is often difficult to isolate the effects of each of the above mechanisms because they probably occur together. In areas with high beta (habitat-specific) and gamma (regional-turnover) diversity patterns, some species may be missed by the fragmentation event simply because of an incomplete sampling of all local habitats or of all regional subsets (see Schluter and Ricklefs [1993]). This is particularly true for highly patchy environments, such as tropical forests, as shown by Zimmerman and Bierregaard (1986) for central Amazonian forest frogs.

Sampling effects also operate frequently in agricultural landscapes, where the preserved areas are normally spared because of their agricultural unsuitability (Usher 1987). That is, habitat remnants will represent only poor soils, steep topography, and so forth, thereby preserving only the community adapted to such situations. Local extinction may then be the final product of ecosystem fragmentation, specifically as a result of sampling effects, habitat loss, or any other factors. In such cases, the "species compris-

ing a depauperate fauna should constitute a subset of those in richer faunas," the so-called nested subset hypothesis of Patterson (1987).

It is often difficult to isolate the importance of sampling effects (if, by chance, the fragment does not contain some of the original species) from habitat loss (the fragment does not contain some of the original species because they were restricted to one or more lost habitats not found in the fragment—which is itself a sampling effect at the habitat level). If one aims to verify the importance of these factors in the reduction of species richness, it is necessary to conduct rigorous sampling to estimate the heterogeneity of habitats in both pristine and fragmented ecosystems.

Missing individuals or habitats may not necessarily lead directly to local extinction but simply to reduction in population sizes ("Populations shrink" box in fig. 2.2) of some or all of the populations in the community. This reduction may in turn lead to demographic constraints, impairment of positive interactions, or alleviation of pressure from negative interactions. Small populations are more prone to extinction caused by chance events than are large populations (stochastic effects) and are likely to face important genetic constraints (Templeton et al. 1990). The smaller the population, the higher the chance that individuals will mate with close relatives, which may produce few offspring and offspring that are weak or sterile. This is called inbreeding depression, or endogamy. Outbreeding depression is the opposite trend: the paucity of mates may lead to hybridization with nearly genetically incompatible individuals (say, different species from the same genus, which often produces vigorous but sterile hybrids).

Small populations may also have their fitness severely affected by genetic drift (Nei, Maruyamo, and Chakraborty 1975), which is

the chance increase or decrease of alleles. Stochastic and genetic constraints may lead to extinction of some populations in the fragmented ecosystem, lowering species richness of the community. It is important to notice that this extinction is secondary, induced by the decrease in population density and not directly by the loss of species or habitats. Such a decrease in species richness would not happen for some generations after a fragmentation event and would not be detected by sampling an area soon after its isolation.

Reductions in population sizes can adversely affect positive interactions if lost individuals belong to species playing mutualistic roles in the remnant (see Chapter 12). This would cause, ultimately, a decrease in the reproductive success of individuals in the remnants, reducing even further their population sizes.

A decrease in population densities may, on the other hand, lead to the reduction of competitive interactions, if resources have been unaffected by fragmentation. Similarly, predation pressures may be also diminished when predators' populations decline or disappear. This reduction of interactions may either ease the increment of population size of resident species through density compensation (Case 1975) or increase the invasibility of the remnant by immigrants (Tilman 1997). Density compensation occurs when extant populations grow in such a way that the community in the fragment will present the same total number of individuals as before fragmentation, but these individuals will be distributed over fewer species (see M. Williamson [1981] for a further discussion of density compensation and Terborgh, Lopez, et al. [1997] for a report on hyperabundant species in ecosystem fragments).

It may be difficult to identify the mechanisms leading to an increase in populations

surviving in a habitat fragment, because, for example, two prey species whose populations are limited by a predator are, in essence, indistinguishable from two species competing for a resource. Populations may increase when predation pressure is reduced through an effect known as apparent competition (Holt 1977) or competition for enemy-free space (Jefferies and Lawton 1984), which may strongly affect the structure of ecological assemblages in fragments (Namba, Umemoto, and Minami 1999).

Density compensation may lead to a secondary increase in either intra- or interspecific competition, which, in turn, may lead to elimination of individuals from the remnant. If, on the other hand, reduction of interactions increases the invasibility of the remnant by immigrants, three possible outcomes may be observed, depending on the number and identity of immigrant species arriving in the fragment. First, the ecological niche of an invading species may overlap that of resident species, with the resulting competition leading to the elimination of individuals from the remnant, as discussed above. Second, an invading species may occupy niches that have been emptied totally by local extinction or partially by population shrinkage. Alternatively, if an immigrant belongs to a resident species, its arrival will increase population densities, thereby decreasing the strength of demographic constraints. The first event above is an adverse effect of higher invasibility, because it will feed back via the loop to local extinctions, leading to lower species richness. The second event may either maintain the same species richness as before fragmentation, when the invading species occupies niches freed by local extinction, or increase species richness, when the invader occupies niches partially freed by a reduction in population of residents. Species richness in the fragment may also increase when vacant niches are occupied by more than one invader species. The third event (the invader belongs to a resident species) can lead to restoration of original species richness, through "rescue effects" (Brown and Kodric-Brown 1977). It is important to realize that different processes may cause species richness to remain constant. Therefore, when species richness is deemed unchanged after fragmentation, it does not necessarily mean that the community is "immune" to the disturbance in question.

Whereas fragmentation often leads to a reduction in species richness through sampling effects for both species and habitat, fragmentation can preserve the original variety of habitats with nothing more than a reduction in their extent ("Habitats shrink" box). Residents would then be expected to experience resource shortages and a consequent increase in competition. Again the loop to local extinction is fed back as a secondary step induced by the increase in competition pressures and its consequential exclusion of individuals from the site.

## MESOSCALE PROCESSES

Structural changes (top left boxes of fig. 2.2) can also trigger processes determining the species richness of fragments. By cutting down surrounding environments, one brings the core of a fragment closer to its borders, creating edges where they previously did not exist. Edges can be important determinants of habitat quality (Kapos 1989; Malcolm 1994), because the smaller the site, or the more linear (LaGro 1991), the greater the proportion of its area is exposed to winds, solar radiation, and the like. In such a scenario, more sensitive species would tend to disappear. Whereas such changes represent increased environmental harshness for some species, for others they may be seen as creating new habitats. These species would
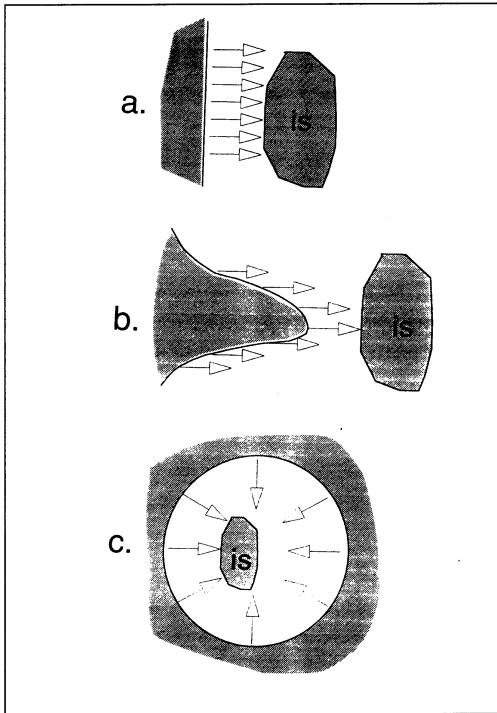
Fig. 2.3. Shape effects in colonization rates for passive dispersers.

distant margin (fig. 2.3c). The same can be true for the shape of the fragment: the number of propagules "hitting" the fragment should increase when the side of the site facing the source population expands and its position approaches a perpendicular to the main direction of colonists' travel (fig. 2.3a). Therefore, shape effects may promote both lower and higher accessibility of the site by immigrants, as compared to its original status within the forest. Higher accessibility implies the arrival of more immigrants, with consequences discussed above. Lower accessibility implies that fewer immigrants reach the site, which may lead to local extinction through inbreeding depression and demographic stochasticity (Jaenike 1978; Jennersten 1988; Klein 1989; Harrison 1991; Pease and Fowler 1997). A similar process can be triggered purely by isolating the remnant from its original matrix, which also reduces accessibility of the site.

gain easier access to the site, feeding the loops to maintenance, impoverishment, or enhancement of species richness in fragments.

REGIONAL PROCESSES

Immigration rates can also be affected by the shape of both the fragment and the potential source population, as proposed by Taylor (1987a, b) (fig. 2.3). According to this model, straight-line shores should "release" more colonizers than do pointed peninsulas (fig. 2.3b), at least for passive dispersers. Similarly, an island in the center of a circular lake should receive more immigrants than if it were located eccentrically, close to the shore. An island in the center of a lake can receive colonizers from the entire lake's perimeter, whereas an island near one shore might not receive colonizers from the more

## Final Remarks

In this chapter we have presented an overview of the theoretical pathways by which ecological processes affect species richness after fragmentation. Using such an overview, the reader should be able to build a global picture of these intricate biological dynamics and be less likely to misinterpret results obtained in the field. Precise interpretation of field data is essential not only to the development of a sound theoretical framework with which to understand ecosystem fragmentation but also to the definition of sensible technical and political guidelines for conservation. In this regard, our flowchart (fig. 2.2) provides a checklist of the possible explanations for an empirically observed maintenance, increase, or decrease of species richness in a fragmented ecosystem. Possible explanations of the pattern may be tested individually, using sam-

pling procedures or experiments designed for such aims.

## Conservation Lessons

1. Ecosystem fragmentation may increase, diminish, or maintain the original number of species in the site concerned.
2. Maintenance of the original number of species does not necessarily mean that the community is immune to fragmentation effects.
3. Local extinction may be either a final product of ecosystem fragmentation or an intermediate step to an increase *or* decrease of species richness in the fragment.
4. Along with determining the best site to preserve, it is imperative to decide the best shape and geographical location of the fragment to be created, because species richness in the fragment depends strongly on these features.

## Acknowledgments