Beyond Island Biogeography Theory

UNDERSTANDING HABITAT FRAGMENTATION

IN THE REAL WORLD

William F. Laurance

ISLAND BIOGEOGRAPHY THEORY (IBT; MacArthur and Wilson 1963, 1967) has profoundly influenced the study of biogeography, ecology, and even evolution (Janzen 1968, Losos 1996, Heaney 2000), and has also had an enormous impact on conservation biology. The theory has inspired much thinking about the importance of reserve size and connectivity in the maintenance of species diversity, and stimulated an avalanche of research on fragmented ecosystems. But, like all general models, IBT is a caricature of reality, capturing just a few important elements of a system while ignoring many others. Does it provide a useful model for understanding contemporary habitat fragmentation?

Here I critically evaluate the conceptual utility and limitations of IBT for the study of fragmented ecosystems. I briefly encapsulate the historical background, considering how IBT has helped to shape our thinking about habitat fragmentation over the past forty years. I then describe how fragmentation research has transcended the theory, using findings from tropical and other ecosystems.

The Impact of IBT

Prior to MacArthur and Wilson's (1967) seminal book, habitat fragmentation was not high on the radar screen of most ecologists, land managers, and politicians. That all changed with IBT (Powledge 2003). The theory has helped to revolutionize the thinking of mainstream ecologists about habitat fragmentation and stimulated literally thousands of studies of fragmented and insular ecosystems (figure 8.1).

Before summarizing some key conceptual advances linked to IBT, I have two caveats. First, in discussing the impact of IBT on fragmentation research, it can be difficult to distinguish between the contributions of

Figure 8.1. Experimentally isolated forest fragments in central Amazonia, part of the Biological Dynamics of Forest Fragments Project (photo by R. O. Bierregaard). This long-term experiment was inspired by a heated debate over the relevance of Island Biogeography Theory to nature conservation.

the original theory itself—*sensu stricto*—versus the ancillary contributions of the many investigations it has helped to spawn. Rather than worrying overly about this, I have listed as many conceptual advances as occurred to me, and tried (no doubt inadequately) to give credit where credit is due. Second, an inherent problem with the burgeoning IBT literature is that it is a little like the Bible: so large, diverse, and eclectic that one can seemingly draw any lesson one wants. Casting such concerns aside I stride incautiously ahead.

Perhaps more than anything, IBT opened people's eyes to the importance of bigness for nature conservation (see also Preston 1960). Big reserves contain more species, lose species more slowly (MacArthur and Wilson 1967, Burkey 1995), and suffer fewer of the deleterious effects of habitat isolation than do smaller reserves (Terborgh 1974, Diamond 1975, May 1975, Diamond and May 1976). The main advantage of bigness, according to IBT, is that individual species can maintain bigger populations than in small areas, and that big populations go locally extinct less often than do small populations (Shafer 1981). Big reserves should also be better at preserving the full range of successional communities and patch dynamics within ecosystems (Pickett and Thompson 1978). The presumed importance of area-dependent extinctions has given rise to evocative terms such as "supersaturation," "species relaxation," "faunal collapse," and "ecosystem decay" that have collectively helped to cement the importance of bigness in the scientific and popular imaginations (e.g., Diamond 1972, Lovejoy et al. 1984, Quammen 1997). Indeed, the pendulum of thought has swung so far in favor of bigness that some authors have found it necessary to remind us that small reserves can be important too (Shafer 1995, Turner and Corlett 1996).

Of course, IBT helped to refine people's thinking about habitat isolation as well. Isolation is bad, connectivity is good. If a little isolation is a bad thing, then a lot of isolation is even worse. Hence, reserves that are isolated from other areas of habitat by large expanses of degraded, hostile landscape will sustain fewer species of conservation concern than those nearer to intact habitat (Lomolino 1986, Watling and Donnelly 2006). This occurs for two reasons: weakly isolated reserves are easily colonized by new species, and they receive immigrants whose genetic and demographic contributions can reduce local extinction rates within the reserve (Brown and Kodric-Brown 1977).

IBT has also spawned a highly dynamic view of fragmented ecosystems. A key prediction of IBT is that insular biota should be inherently dynamic, with species disappearing (from local extinction) and appearing (from colonization) relatively often. If extinction and colonization are largely governed by fragment size and isolation, respectively, then big, isolated fragments should have slower species turnover than do

small, weakly isolated fragments. Demonstration of such relationships is a litmus test for IBT (Gilbert 1980, Abbott 1983) because other biogeographic phenomena, such as the species-area relationship, can arise for reasons aside from those hypothesized by IBT (for example, higher habitat diversity, rather than lower extinction rates, can cause species richness to increase on larger islands; Boecklen and Gotelli 1984, Ricklefs and Lovette 1999). Given its central importance, it is perhaps surprising that only a modest subset of all IBT studies has demonstrated elevated turnover (e.g., Diamond 1969, Wright 1985, Honer and Greuter 1988, Schmigelow et al. 1997—and even these have often been controversial (Simberloff 1976, Diamond and May 1977, Morrison 2003; reviewed in Schoener, this volume). As discussed below, population and community dynamics are often greatly amplified in habitat fragments relative to natural conditions (Laurance 2002), but a number of factors aside from those hypothesized by IBT can be responsible.

Habitat fragmentation affects different species in different ways. Some species decline sharply or disappear in fragments (figure 8.2), others remain roughly stable, and yet others increase, sometimes dramatically. Although IBT *sensu stricto* provides little understanding of the biological reasons for such differences, some insights have come from interpreting the slope (z) of species-area relationships in insular communities (Connor and McCoy 1979, Ricklefs and Lovette 1999). For instance, species at higher trophic levels (Holt et al. 1999), with lower volancy (Wright 1981), with greater ecological specialization (Krauss et al. 2003; Holt, this volume), and with greater taxonomic age (Rickefs and Cox 1972, Rickefs and Bermingham 2004) generally have steeper slopes, and thus respond more negatively to insularization than do those with opposite characteristics. Characteristics of fragmented landscapes can also affect species-area slopes (Wright 1981). For example, slopes are on average steeper for fauna on true islands than terrestrial fragments, presumably because agricultural or urban lands are less hostile to faunal movements than are oceans and lakes (Watling and Donnelly 2006).

Early proponents of IBT were keen to apply its principles to the design of protected areas, and used the theory (among other things) to advance the notion that a single large reserve was better for ensuring long-term species persistence than were several small reserves of comparable area (Terborgh 1974, Diamond 1975, May 1975, Wilson and Willis 1975). This idea, encapsulated in the famous acronym SLOSS (single large or several small reserves), became a remarkable flashpoint of controversy, following a pointed attack by Simberloff and Abele (1976a). Although of theoretical interest, the ensuing debate (e.g., Diamond 1976, Simberloff and Abele 1976b, Terborgh 1976, Whitcomb et al. 1976, Abele and
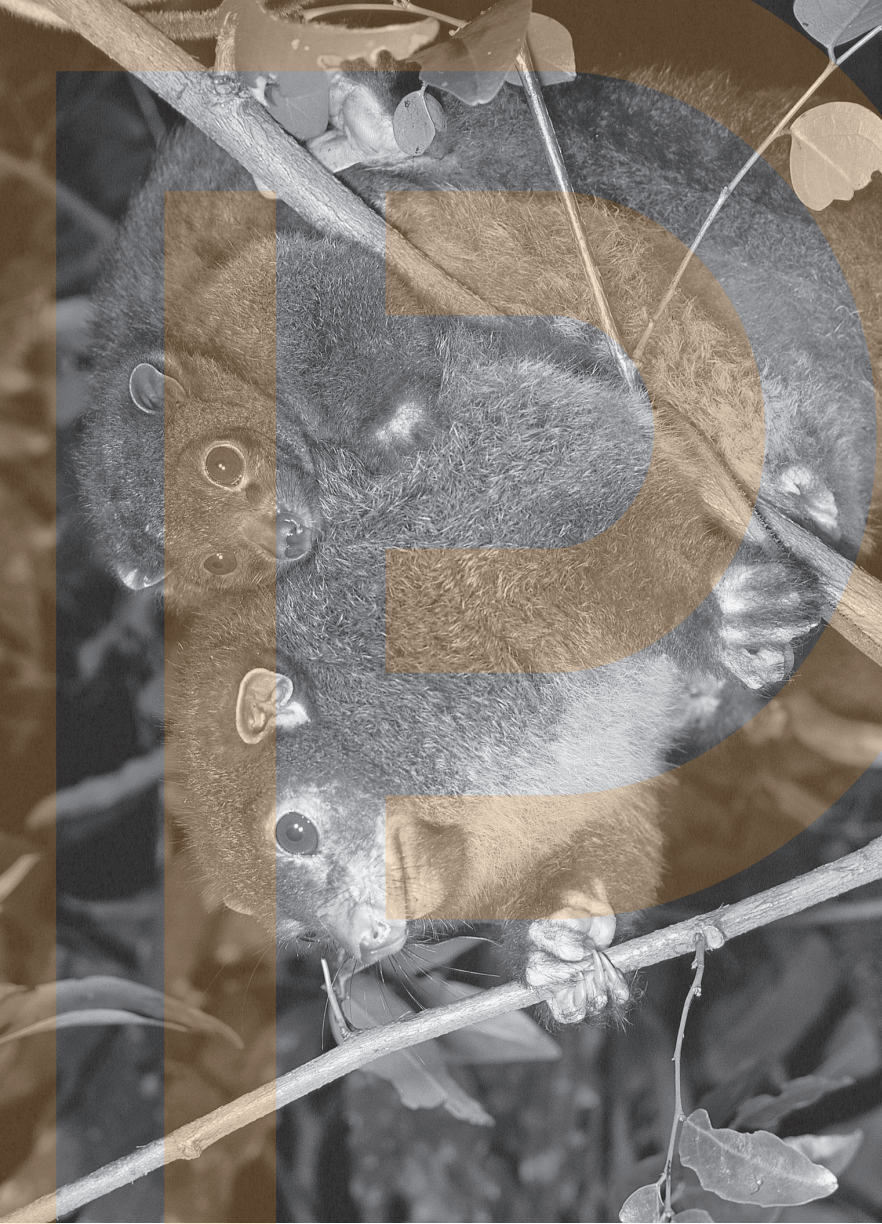
Figure 8.2. Forest specialists such as the lemuroid ringtail possum (*Hemibelideus lemuroides*), a restricted endemic in tropical Queensland, are often highly vulnerable to habitat fragmentation (photo by M. Trenerry).

Connor 1979, Higgs and Usher 1980) provided only a limited list of practical lessons for reserve managers (Soulé and Simberloff 1986, Zimmerman and Bierregaard 1986, Saunders et al. 1991). Perhaps the most important conclusion was that SLOSS depended on the degree of nestedness exhibited by an ecosystem (the extent to which the biota of small reserves was a proper subset of those in larger reserves; Patterson and Atmar 1986, Patterson 1987). The most extinction-prone species are often found only in large reserves, favoring the single-large-reserve strategy, although small reserves scattered across a region can sustain certain locally endemic species that would otherwise remain unprotected (see Ovaskainen 2002 and references therein). Thus, the answer to SLOSS is, "it depends."

Habitat Fragmentation in the Real World

By stimulating an avalanche of research on insular ecosystems, IBT has helped to teach us a great deal about habitat fragmentation. In a strict sense, however, IBT itself has only limited relevance to fragmentation because it fails to consider some of the most important phenomena in fragmented landscapes. Here I summarize some of the key lacunae.

Nonrandom Habitat Conversion

Habitat conversion is a highly nonrandom process. Farmers preferentially clear land in flatter lowland areas (Winter et al. 1987, Dirzo and Garcia 1992) and in areas with productive, well-drained soils (Chatelain et al. 1996, Smith 1997). Habitat loss also tends to spread contagiously, such that areas near highways, roads, and towns are cleared sooner than those located further from human settlements. In the Brazilian Amazon, for example, over 90% of all deforestation occurs within 50 km of roads or highways (Laurance et al. 2001a, Brandão et al. 2007).

As a consequence of nonrandom clearing, habitat remnants are often a highly biased subset of the original landscape. Remnants frequently persist in steep and dissected areas, on poorer soils, at higher elevations, and on partially inundated lands. In addition, habitat fragments near roads and townships are often older, more isolated, and smaller than those located further afield, where habitat destruction is more recent (Laurance 1997). The influence of nonrandom habitat loss on fragmented communities has been little studied, although Seabloom et al. (2002) concluded that species-area curves underestimate the magnitude of species extinctions when habitat destruction is contagious, as is typically the case. Regardless, it is important to recognize that the biota of

habitat fragments are likely to have been influenced by nonrandom habitat loss long before the effects of fragmentation per se are manifested.

Distinguishing Habitat Loss and Fragmentation Effects

The process of habitat fragmentation involves two distinct but interrelated processes. First, the total amount of original habitat in the landscape is reduced. Second, the remaining habitat is chopped up into fragments of various sizes and degrees of isolation. Distinguishing the impacts of these two processes on biodiversity is challenging because they generally covary. For example, in forested landscapes in which most of the original habitat has been destroyed, the surviving fragments tend to be small and isolated from other forest areas, and the opposite is true in landscapes with little forest loss. Hence, strong declines of biodiversity reported for many fragmented landscapes might actually be mostly a consequence of habitat loss, rather than habitat fragmentation per se (Fahrig 2003).

IBT emphasizes analyses at the individual-fragment scale, but the best way to quantify the relative importance of habitat loss versus fragmentation is to conduct comparative analyses at the landscape scale. In a meta-analysis, Fahrig (2003) concluded that habitat loss generally had much stronger effects on biodiversity than did fragmentation per se, although she emphasized that much is uncertain, especially for tropical forests. Others have tried to distinguish effects of habitat loss and fragmentation, either by experimentally controlling for habitat amount while varying fragmentation (e.g., Collins and Barrett 1997, Caley et al. 2001) or by comparing many different landscapes and extracting indices of fragmentation that are not correlated with the amount of habitat in each landscape (e.g., McGarigal and McComb 1995, Villard et al. 1999). Results have varied, and disentangling the often confounded effects of habitat loss and fragmentation remains a challenge for those attempting to discern the mechanisms of biodiversity loss in fragmented landscapes.

Edge Effects

Edge effects are diverse physical and biological phenomena associated with the abrupt, artificial boundaries of habitat fragments (figure 8.3). They include the proliferation of shade-intolerant vegetation along fragment margins (Ranney et al. 1981, Lovejoy et al. 1986) as well as changes in microclimate and light regimes that affect seedling germination and survival (Ng 1983, Bruna 1999). Forest interiors often are bombarded by a "seed rain" of weedy propagules (Janzen 1983, Nascimento et al. 2006) and by animals originating from outside habitats (Buechner 1987).

Figure 8.3. Edge effects documented in Amazonian forest fragments, showing the great diversity of edge phenomena and the varying distances they penetrate into forest interiors (after Laurance et al. 2002).

Increased windshear forces near edges can cause elevated rates of tree mortality that alter forest structure and composition (Chen et al. 1992, Laurance et al. 1997, 2000). Abundant generalist predators, competitors, or brood parasites in the vicinity of edges often impact forest-interior birds (Gates and Gysel 1978, Wilcove 1985) and mammals (Sievert and Keith 1985).

Edge effects can alter many aspects of the structure, microclimate, dynamics, and species composition of fragmented ecosystems (Lovejoy et al. 1986, Laurance et al. 2002, Lehtinen et al. 2003, Ries et al. 2004). Crucially, they are not addressed by IBT, which assumes that biota in

fragments are influenced solely by the opposing forces of colonization and extinction. Edge effects may be especially important in fragmented rainforests, where the dense forest with its stable temperatures and dark, humid, nearly windless conditions contrasts starkly with the dry, harsh, windy conditions of surrounding pastures or croplands.

It can be challenging to discriminate edge and area effects in fragmentation studies. Edge phenomena tend to increase in intensity as fragment size diminishes, and this creates a confounding intercorrelation between edge and area effects in fragmented landscapes (Laurance and Yensen 1991). In fact, many putatively "area-related" species losses in habitat fragments probably have been caused by edge effects (Schonewald-Cox and Bayless 1986, Temple 1986) or a synergism between edge and area effects (Ewers et al. 2007).

Understanding the role of edge effects is important, because edge models yield different predictions than does IBT about the effects of fragmentation on ecosystems and biota. For example, unlike IBT, edge-effect models predict large ecological changes (1) in irregularly shaped as well as in small fragments, (2) along the margins of even very large fragments, and (3) especially in areas affected by two or more nearby edges (Laurance and Yensen 1991, Malcolm 1994, Laurance et al. 2006a). Edge models also provide useful predictions about species responses to fragmentation. For instance, (1) the abundances of individual forest-interior species should be positively correlated with the unaltered core areas of fragments (Temple 1986, Ewers and Didham 2007), (2) edge specialists should be correlated with the total length of fragment edges, and (3) edge-insensitive species that depend on primary habitat should be correlated with the total areas of fragments (Laurance and Yensen 1991). IBT yields none of these insights.

Matrix Effects

For all its conceptual utility, IBT has had a huge downside for understanding forest fragmentation: it ignores the matrix of modified lands surrounding fragments. Whether surrounded by corn fields, strip malls, water, or secondary forest, all fragments (including isolated nature reserves) are treated equally by IBT. Such fragments are not equivalent, of course—the matrix matters.

The matrix has a big influence on fragment connectivity (Ricketts 2001). Matrices that differ dramatically in structure and microclimate from the primary habitat tend to be most hostile to native species (Laurance and Bierregaard 1997). In the Amazon, forest fragments surrounded by cattle pastures suffer considerably greater species losses than do those

surrounded by regrowth forest, and a variety of species—including certain primates, antbirds, obligate flocking birds, and euglossine bees—have been shown to recolonize fragments as young secondary forest regenerates around them (Becker et al. 1991, Stouffer and Bierregaard 1995, Gilbert and Setz 2001). Where hunting is pervasive, the matrix can become a population sink for exploited species (Woodroffe and Ginsberg 1998). By acting as a selective filter for animal and propagule movements, the matrix has pervasive effects on species composition in fragments.

The matrix can also influence the nature and magnitude of edge effects in fragments. In the Amazon, forest fragments surrounded by young regrowth forest experience less intensive changes in microclimate (Didham and Lawton 1999) and have lower edge-related tree mortality (Mesquita et al. 1999) than do similar fragments adjoined by cattle pastures. Edge avoidance by forest-interior birds is also reduced when fragments are adjoined by regrowth forest (Stouffer and Bierregaard 1995, S. G. Laurance 2004). Because fragments can receive a heavy seed rain from the nearby matrix, patterns of plant regeneration in forest fragments can be strongly influenced by the species composition of the matrix (Janzen 1983, Nascimento et al. 2006).

Correlates of Extinction Proneness

Whether on islands or habitat fragments, species vary enormously in their vulnerability to local extinction: some vanish rapidly, others more slowly, and yet others persist almost indefinitely. Why? Much effort has been expended in attempting to predict why certain species are especially extinction prone in insular habitats (e.g., Terborgh 1974, Pimm et al. 1989, Laurance 1991).

The traits associated with vulnerability may well differ between islands and habitat fragments. Studies of fauna on islands have often emphasized the importance of local rarity or its correlates, such as body size and trophic status, in determining species vulnerability (e.g., Terborgh 1974, Willis 1974, Wilcox 1980, Diamond 1984, Holt, this volume). Unlike islands, however, habitat fragments are surrounded by a matrix of modified habitats that permit dispersal or survival for species that can use the matrix, and matrix tolerance is often identified as a key predictor of vulnerability (Laurance 1990, 1991, Gascon et al. 1999, Nupp and Swihard 2000, Pires et al. 2002). On islands, or on other isolates surrounded by completely inhospitable habitat, matrix tolerance is necessarily a nonexistent predictor of extinction proneness, and effects of other predictors, such as rarity and its correlates, are likely to become more apparent.

Thus, as a model for predicting faunal extinctions in habitat fragments, studies of oceanic or land-bridge islands may (1) underestimate the importance of overland vagility and tolerance of modified habitats, and (2) overestimate the significance of factors such as rarity, body size, and trophic status. Insofar as IBT emphasizes true islands, its lessons for understanding species vulnerability in habitat fragments might be weak and even misleading.

Altered Ecosystem Processes

As a prism for understanding habitat fragmentation, IBT is woefully limited in scope: it concerns only the factors that affect species diversity. But habitat fragmentation has far broader effects on ecosystems, altering such diverse processes as forest dynamics, nutrient cycling, carbon storage, and forest-climate interactions.

In many forested landscapes, for example, habitat fragmentation leads to sharply elevated tree mortality, because trees near forest edges are particularly vulnerable to wind turbulence and increased desiccation (Chen et al. 1992, Laurance et al. 1997, 1998a). This fundamentally alters canopy-gap dynamics, forest structure, microclimate (Kapos 1989, Malcolm 1998), and the relative abundance of different plant functional groups (Laurance et al. 2001b, 2006a,b, Nascimento et al. 2006). Forest carbon storage is also reduced (figure 8.4) because large canopy and emergent trees, which contain a high proportion of forest biomass, are particularly vulnerable to fragmentation (Laurance et al. 2000). As the biomass from the dead trees decomposes, it is converted into greenhouse gases such as carbon dioxide and methane. In fragmented forests worldwide, many millions of tons of atmospheric carbon emissions are released each year by this process (Laurance et al. 1998b).

Fragmentation alters many aspects of the physical environment. Large-scale clearing of native vegetation can cause major changes in water and nutrient cycles, radiation balance, and wind regimes, which in turn affect communities in habitat remnants (Saunders et al. 1991, Laurance 2004). In Western Australia, the removal of most native vegetation for wheat production has reduced evapotranspiration and altered soil water flows. This has increased local flooding, brought the water table with its dissolved salts closer to the soil surface, and caused chronic waterlogging and salinization of the remaining vegetation (Hobbs 1993). Wind- or waterborne fluxes of agricultural chemicals (fertilizers, herbicides, pesticides) and other pollutants into habitat remnants (Cadenasso et al. 2000, Weathers et al. 2001) can also have long-term effects on ecosystems.

Fragmentation often drastically alters natural fire regimes. In some cases, burning declines sharply because fires are suppressed in the sur-
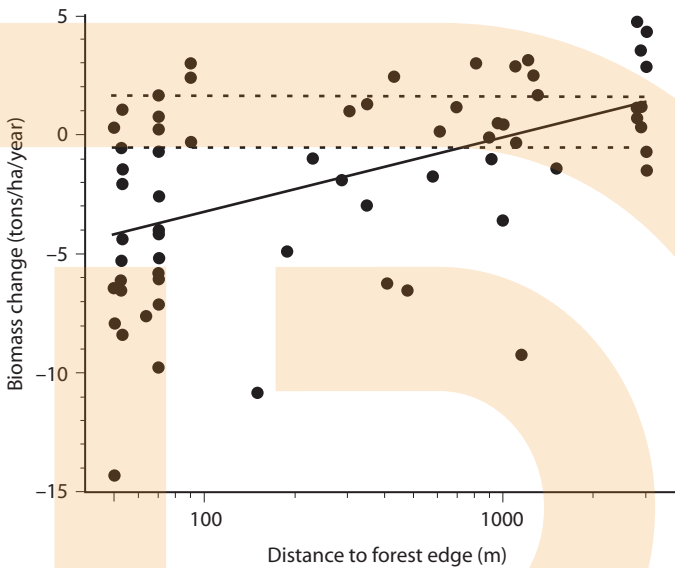
Figure 8.4. Collapse of aboveground biomass in Amazonian forest fragments. Shown is the annual loss of live tree biomass in 1 ha plots as a function of distance from forest edge. The dotted lines show the 95% confidence intervals for forest-interior plots (>500 m from edge) (after Laurance et al. 1997).

rounding matrix, leading to long-term changes in the composition and structure of remnant vegetation (Baker 1994). In other cases, fragmentation promotes burning in ecosystems that are highly vulnerable to fire, such as tropical rainforests (Cochrane et al. 1999, Gascon et al. 2000). In the Amazon, for example, fire frequency rises drastically in fragmented landscapes (figure 8.5) because forest remnants are juxtaposed with frequently burned pastures. These recurring burns have severe effects because the rainforest vegetation is poorly adapted for fire, and forest fragments can literally implode over time from recurring fires (Cochrane and Laurance 2002, 2008).

Environmental Synergisms

In the real world, habitat fragments are not merely reduced and isolated; they are also frequently affected by other perturbations that may interact additively or synergistically with fragmentation (Laurance and Cochrane 2001). Forest fragments in the tropics, for example, are often selectively logged, degraded by ground fires, and overhunted—changes that can dramatically alter fragment ecology (Peres 2001, Cochrane and Laurance
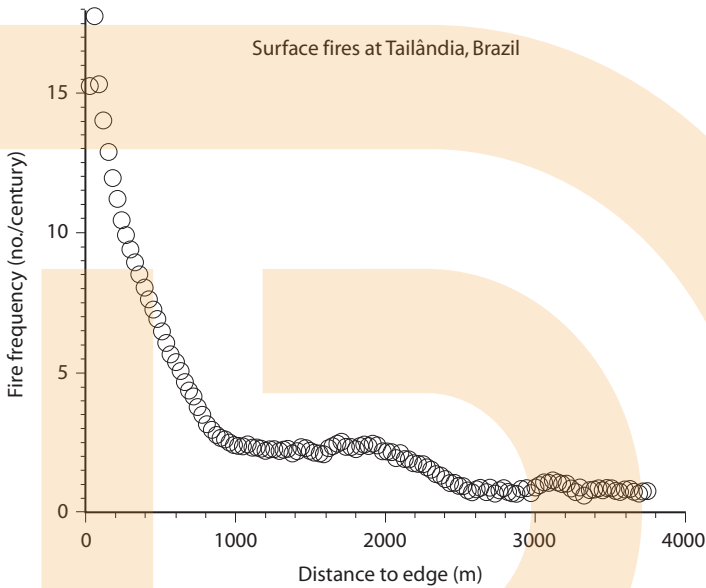
Figure 8.5. Fires can increase dramatically in fragmented forests. Shown here is the mean fire frequency (number per century) as a function of distance to forest edge for several hundred forest fragments in eastern Amazonia. Analyses were based on 14 years of satellite observations (adapted from Cochrane and Laurance 2002).

2002, Peres and Michalski 2006). In agricultural and urban areas, acid rain, pesticides and herbicides, hydrological changes, livestock grazing, and pressure from invading species can severely degrade fragments (Myers 1988, Apensperg-Traun et al. 1996, Hobbs and Huenneke 1992). In coming decades, anthropogenic climate change may emerge as an increasingly important threat to fragmented ecosystems, especially if droughts, storms, and other rare weather events increase in frequency or severity (Timmerman et al. 1999, Laurance and Curran 2008).

Thus, forest fragments and their biota are sometimes subjected to a withering array of environmental pressures that may be episodic or chronic in nature. A paradigm like IBT that considers only changes in fragment size and isolation while ignoring other anthropogenic effects (e.g., Curran et al. 1999, Laurance 2000) is dangerously inadequate for conservation purposes. It is also inadequate from a scientific perspective. A more realistic view of fragmented landscapes is one that explicitly recognizes the potential for interacting environmental changes to amplify and alter the ecological impacts of habitat fragmentation.

Elevated Dynamics

Finally, IBT postulates that fragmented ecosystems will be more dynamic than intact habitat, but only because of species relaxation and increased species turnover. In fact, a far wider range of phenomena promotes dynamism in fragmented landscapes, even to the extent that many fragments can be described as "hyperdynamic" (Laurance 2002).

Being a small resource base, a habitat fragment is inherently vulnerable to stochastic effects. Species abundances can fluctuate wildly in small communities, especially when immigration is low and disturbances are frequent (Hubbell 2001). The dynamics of plant and animal populations can be dramatically altered in fragmented habitats in response to edge effects, reduced dispersal, altered disturbance regimes, and changing herbivore or predation pressure (Lidicker 1973, Karieva 1987, Quintana-Ascencio and Menges 1996). Fragmented animal communities often pass through unstable transitional states that do not otherwise occur in nature (Terborgh et al. 2001). These can cause serious ecological distortions, such as a collapse of predator and parasite populations and a hyperabundance of herbivores (Mikkelson 1993, Terborgh et al. 2001, Holt, this volume, Terborgh, this volume). These and other instabilities plague small, dwindling populations in fragments.

As discussed above, habitat fragments are often strongly affected by external vicissitudes and disturbances in the human-dominated lands that surround it. For example, forest species that exploit edge or disturbed habitats often increase dramatically in fragmented landscapes (Margules and Milkovits 1994, Laurance et al. 2002). As habitat loss proceeds, displaced animals from surrounding degraded lands can flood into remaining habitat fragments, leading to sudden increases in local population densities (Lovejoy et al. 1986, Hagan et al. 1996, Curran et al. 1999, Holt, this volume). Modified landscapes can be a major source of recurring disturbances, with hunters, livestock, fires, smoke, and large abiotic fluxes penetrating into and destabilizing fragments.

Conclusions

If ideas were mountains, IBT would be a Mount Everest, towering above thousands of lesser ideas and concepts. The theory has provided a conceptual framework for understanding habitat fragmentation that continues to inform researchers today. The avalanche of research stimulated by IBT has dramatically advanced the study of fragmented and insular habitats.

That having been said, the study of fragmented ecosystems has now far transcended IBT. With perfect hindsight, the theory seems simplistic to the point of being cartoonish, and fails to address some of the most important phenomena affecting fragmented landscapes. Yet it would be churlish not to herald a theory of this importance, and unfair to expect it to do everything. Fragmentation research today has diversified enormously, touching on subdisciplines ranging from landscape ecology to metapopulation dynamics, and from conservation genetics to population viability analysis. Everyone working in these fields owes some allegiance to the original inspiration provided by IBT.

Acknowledgments

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