

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Review

Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory

William F. Laurance*

Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama

Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), C.P. 478, Manaus, AM 69011-970, Brazil

ARTICLE INFO

Article history:

Received 2 May 2008

Received in revised form

14 May 2008

Accepted 17 May 2008

Available online 30 June 2008

Keywords:

Area effects

Edge effects

Extinction

Fragmentation

Island biogeography theory

Matrix effects

Species turnover

ABSTRACT

Island biogeography theory (IBT) provides a basic conceptual model for understanding habitat fragmentation. Empirical studies of fragmented landscapes often reveal strong effects of fragment area and isolation on species richness, although other predictions of the theory, such as accelerated species turnover in fragments, have been tested less frequently. As predicted by IBT, biota in fragments typically ‘relax’ over time towards lower species richness. Beyond these broad generalizations, however, the relevance of IBT for understanding fragmented ecosystems is limited. First, IBT provides few predictions about how community composition in fragments should change over time, and which species should be most vulnerable. Second, edge effects can be an important driver of local species extinctions and ecosystem change, but are not considered by IBT. Third, the matrix of modified vegetation surrounding fragments—also ignored by IBT—can strongly influence fragment connectivity, which in turn affects the demography, genetics, and survival of local populations. Fourth, most fragmented landscapes are also altered by other anthropogenic changes, such as hunting, logging, fires, and pollution, which can interact synergistically with habitat fragmentation. Finally, fragmentation often has diverse impacts on ecosystem properties such as canopy-gap dynamics, carbon storage, and the trophic structure of communities that are not considered by IBT. I highlight these phenomena with findings from fragmented ecosystems around the world.

Published by Elsevier Ltd.

Contents

1. Introduction	1732
2. The Impact of IBT	1732
3. Habitat fragmentation in the real world	1734
3.1. Nonrandom habitat conversion	1734
3.2. Distinguishing habitat loss and fragmentation effects	1734
3.3. Edge effects	1735

* Address: Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama. Tel.: +507 212 8252; fax: +507 212 8148.

E-mail address: laurancew@si.edu

0006-3207/\$ - see front matter Published by Elsevier Ltd.

doi:10.1016/j.biocon.2008.05.011

3.4. Matrix effects	1736
3.5. Correlates of extinction proneness	1736
3.6. Community-level changes	1736
3.7. Altered ecosystem processes	1737
3.8. Environmental synergisms	1738
3.9. Elevated dynamics	1739
4. Conclusions	1739
Acknowledgements	1739
References	1739

1. Introduction

Island biogeography theory (MacArthur and Wilson, 1963, 1967) has profoundly influenced the study of biogeography, ecology, and even evolution (Janzen, 1968; Losos, 1996; Heaney, 2000). It has also had an enormous impact on conservation biology. The theory (hereafter ‘IBT’) 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. Like all general models, however, 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 to 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 four decades. I then describe how fragmentation research has transcended the theory, using findings from a wide variety of terrestrial ecosystems.

2. 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 (Fig. 1). Here I summarize some key conceptual advances linked to IBT, including those from the many investigations it helped to spawn, as well as from the original theory itself.

Perhaps more than anything, IBT opened people’s eyes to the importance of vastness for nature conservation (see also Preston, 1960). Big reserves contain more species, lose species more slowly (MacArthur and Wilson, 1967; Burkey, 1995; Sodhi et al., 2005a), and suffer fewer of the deleterious effects of habitat isolation, than do smaller reserves (Terborgh, 1974; Diamond, 1975a; May, 1975; Diamond and May, 1976). The main advantage of vastness, according to IBT, is that individual species can maintain larger populations than in small



Fig. 1 – An experimentally isolated forest fragment 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.

areas, and that large populations go locally extinct less often than do small populations (Shaffer, 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 vastness 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 vastness 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; Koh and Sodhi, 2004; 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. Demonstrating 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 to the theory, it is perhaps surprising that relatively few IBT studies have demonstrated elevated turnover (e.g. Diamond, 1969; Wright, 1985; Honer and Greuter, 1988; Schmigelow et al., 1997; Sodhi et al., 2005a)—and even these have often been controversial (Simberloff, 1976; Diamond and May, 1977; Morrison, 2003). As discussed below, population and community dynamics are often greatly amplified in habitat fragments relative to natural conditions (Laurance, 2002), but a variety 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 (Fig. 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 (aside from small population size; Ale and Howe, in press), 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,



Fig. 2 – Ecological specialists such as the scaled-backed antbird (*Hylophylax poecilonota*), Boyd’s forest dragon (*Hypsilurus boydii*), and lemuroid ringtail possum (*Hemibelideus lemuroides*) decline precipitously in fragmented forests (photos by A.M. Dennis, S. Williams, and W.F. Laurance, respectively).

species at higher trophic levels (Holt et al., 1999), with lower mobility (Wright, 1981), with greater ecological specialization (Krauss et al., 2003), and with greater taxonomic age (Ricklefs and Cox, 1972; Ricklefs and Bermingham, 2001) 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 to (among other things) 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, 1975a; May, 1975; Wilson and Willis, 1975). This idea, encapsulated in the famous acronym ‘SLOSS’ (single large or several small reserves), became a remarkably heated 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 Connor, 1979; Higgs and Usher, 1980) had only limited practical relevance 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).

Beyond the SLOSS debate, IBT has promoted the wide use of species–area curves for conservation applications (see Rosenzweig, 1995; Lomolino, 2000; Haila, 2002). These include predicting species endangerment (Pimm et al., 1995; Brooks and Balmford, 1996) and local extinctions (Tilman et al., 1994; Newmark, 1996; Magura et al., 2001) in fragmented landscapes, devising general reserve-design principles (Diamond, 1975a; Wilson and Willis, 1975; Faaborg, 1979), and identifying conservation targets for specific habitat types (Desmet and Cowling, 2004). Among the most controversial uses involve projecting global species extinctions, such as from tropical deforestation. Results have varied dramatically, ranging from alarming (Ehrlich and Wilson, 1991; Reid, 1992; Dirzo and Raven, 2003) to far more modest (Wright and Muller-Landau, 2006) projections of future species losses. Such differences arise from the high sensitivity of predictions to uncertainty or errors in species–area slopes (Rosenzweig, 1995; Pereira and Daily, 2006; Ale and Howe, in press), from differing assumptions about species persistence in degraded habitats (Pereira and Daily, 2006; Wright and Muller-Landau, 2006; Laurance, 2007), and from large uncertainties about the geographic distribution of biodiversity. Clearly, the species–area curve is a blunt tool in many contexts.

3. Habitat fragmentation in the real world

By stimulating a broad array of research on insular ecosystems, IBT has helped to teach us much about habitat fragmentation. In a strict sense, however, IBT itself has only narrow relevance to fragmentation because it fails to consider some of the most important phenomena in fragmented landscapes. Here I summarize some key limitations.

3.1. 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., 2001; Brandão et al., 2007).

Because 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; Fahrig, 2003). 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.

3.2. Distinguishing habitat loss and fragmentation effects

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 co-vary. For example, in forested landscapes in which most of the original habitat has been destroyed, the surviving fragments are often small and isolated from other forest areas, whereas the opposite is true in landscapes with little forest loss. Hence, strong declines of biodiversity reported for many fragmented landscapes might actually be largely 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 typically 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 (Colins 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 (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 understand the mechanisms of biodiversity loss in fragmented landscapes.

3.3. Edge effects

Edge effects are diverse physical and biological phenomena associated with the abrupt, artificial boundaries of habitat fragments (Fig. 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). 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 birds (Gates and Gysel, 1978; Wilcove, 1985) and mammals (Sievert and Keith, 1985).

Edge effects 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; Wirth et al., 2007). 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 fragments of dense forest, where the dark, humid microclimate contrasts starkly with the dry, harsh, windy conditions of surrounding open habitats (Harper et al., 2005).

It can be challenging to discriminate edge and area effects in fragmentation studies. Edge phenomena tend to increase in intensity as fragment size diminishes, creating 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; Woodroffe and Ginsberg, 1998) or by 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 major

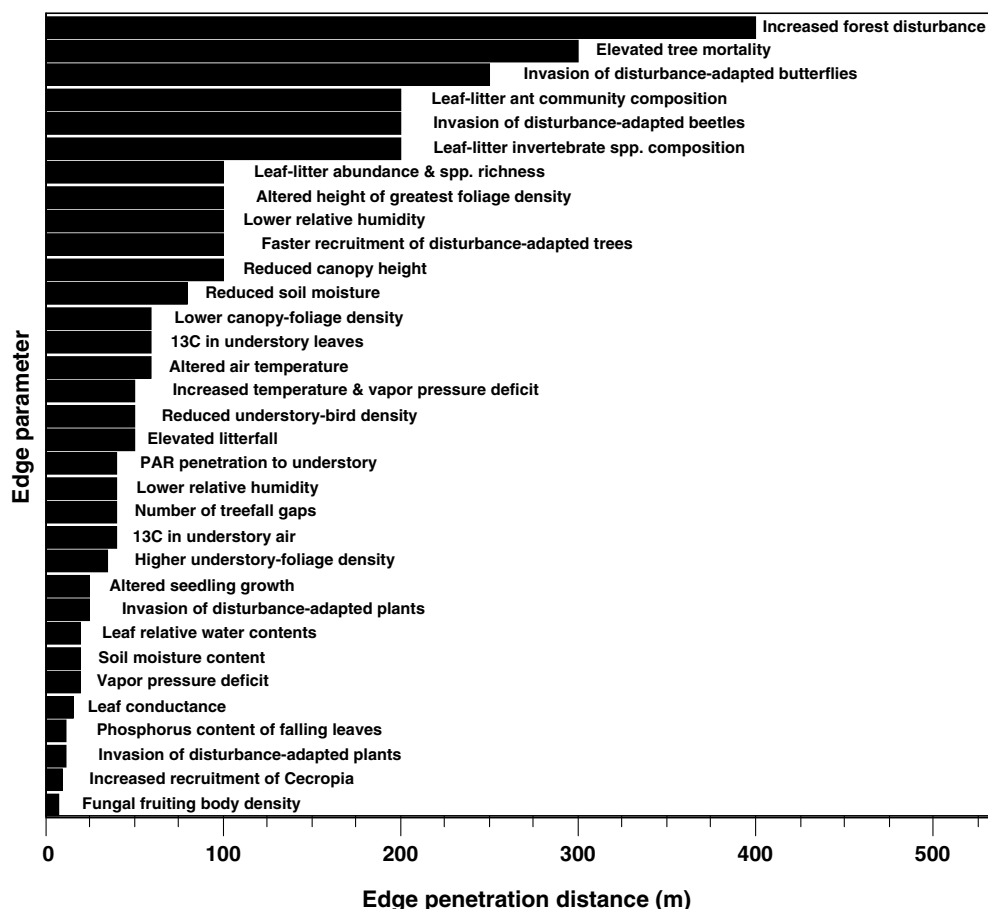


Fig. 3 – Edge effects documented in Amazonian forest fragments, showing the great diversity of edge phenomena and the varying distances they penetrate into forest interiors (after Laurance et al., 2002).

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, the abundances of forest-interior species should be positively correlated with the unaltered core-areas of fragments (Temple, 1986; Ewers and Didham, 2007), edge specialists should be correlated with the total length of fragment edges, and 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.

3.4. Matrix effects

For all its conceptual utility, IBT has had a striking downside for understanding forest fragmentation: it ignores the matrix of modified lands surrounding fragments. Whether surrounded by soy fields, suburbia, 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 major 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; Sodhi et al., 2005b). 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 or persecuted species (Newmark, 1996; Woodroffe and Ginsberg, 1998; Brashares et al., 2001). 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; Grau, 2004; Nascimento et al., 2006).

3.5. Correlates of extinction proneness

Whether on islands or habitat fragments, species can differ enormously in their vulnerability to local extinction: some vanish rapidly, others more slowly, and yet others persist

almost indefinitely. Why? Many researchers have attempted to predict why certain species are especially extinction prone in insular habitats (e.g. Terborgh, 1974; Pimm et al., 1989; Laurance, 1991; Henle et al., 2004; Koh et al., 2004).

Importantly, 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). 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 and its correlates (such as high dietary specialization) are often identified as key predictors of vulnerability (Fig. 4) (Laurance, 1990, 1991; Gascon et al., 1999; Nupp and Swihart, 2000; Pires et al., 2002; Sekercioglu et al., 2002; Brashares, 2003; Koh et al., 2004; Antongiovanni and Metzger, 2005). 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.

Hence, 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.

3.6. Community-level changes

IBT treats species as non-interacting entities, assuming that their responses to fragmentation are governed solely by their

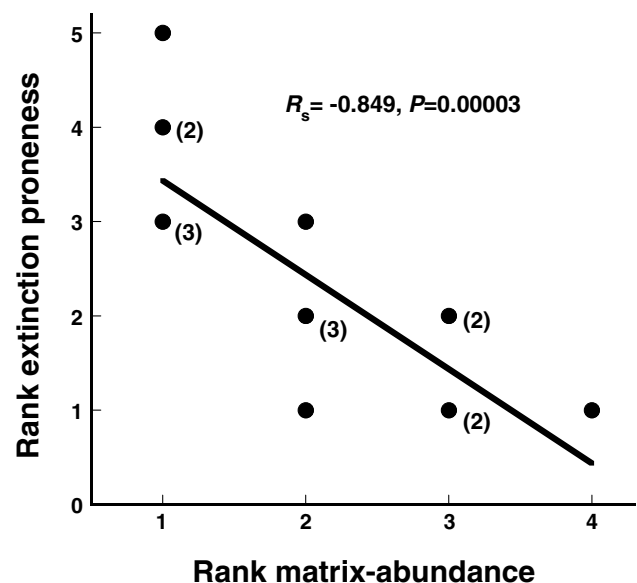


Fig. 4 – Relationship between matrix tolerance and local extinction proneness in 16 mammal species in Australian rainforest fragments (after Laurance, 1991).

population size (Harrison and Bruna, 1999; Ale and Howe, in press). In reality, species interact with one another in myriad ways via competition, predation, parasitism, disease, and mutualisms, and distortions in such interactions can markedly affect species survival and community composition in fragments.

For instance, large predators often disappear from habitat fragments and in their absence generalist omnivores, such as raccoons, coatis, opossums, and baboons (Fig. 5), can explode in abundance, a phenomenon termed ‘mesopredator release’ (Soulé et al., 1988; Terborgh, 1992). Omnivores also invade fragments from surrounding agricultural lands (Gates and Gysel, 1978; Andren and Angelstam, 1988; Paton, 1994; Galetti and Sazima, 2006). When hyperabundant, such omnivores can have important impacts on nesting birds (Crooks and Soulé, 1999; Schmidt, 2003), large-seeded plants (Wright and Duber, 2001), and other species (Dirzo and Miranda, 1991; Laurance, 1997). A related phenomenon is the proliferation in fragments of certain herbivorous insects, such as leaf-cutter ants, in the absence of their predators (Rao, 2000; Terborgh et al., 2001).

Fragmentation can also distort competitive interactions. In the restricted universe of a habitat fragment, interspecific competition may well be intensified because resources such as space, food, and shelter are more limited. ‘Checkerboard’ distribution patterns, in which closely related, ecologically similar species have nearly mutually exclusive distributions on islands or fragments, are thought to result from such

intensified competition (Diamond, 1975b; Fox and Fox, 2000; Laurance, 1997). Ecological changes in fragments such as edge (Fagan et al., 1999) and matrix (Cantrell et al., 1999) effects can favor certain competitors over others and thereby change competitive interactions and species survival.

Species with strong ecological linkages may be especially vulnerable in fragments. For example, the decline of key seed dispersers or pollinators in fragments can reduce reproduction, dispersal, and establishment of dependent plant species (e.g. Aizen and Feinsinger, 1994; Chapman et al., 2003; Cordeiro and Howe, 2003; Wright et al., 2007). In the Amazon, obligate ant-following birds, which accompany marauding swarms of army ants to capture fleeing insects, disappear from forest fragments too small to sustain army-ant colonies (Lovejoy et al., 1986; Stouffer and Bierregaard, 1995). In addition, the decline of peccaries in Amazon fragments has reduced the abundance of frogs that require peccary wallows for breeding (Zimmerman and Bierregaard, 1986).

In these and other ways, habitat fragmentation alters species interactions, with far-reaching impacts on community composition and functioning. Such changes fall entirely outside the scope of IBT.

3.7. Altered ecosystem processes

As a prism for understanding habitat fragmentation, IBT is woefully limited: it focuses only on species diversity. But habitat fragmentation has far broader effects on ecosystems,



Fig. 5 – Opportunistic omnivores, such as coatis (*Nasua nasua*), chacma baboons (*Papio cynocephalus*), bearded pigs (*Sus barbatus*), and giant white-tailed rats (*Uromys caudimaculatus*), can explode in abundance following the loss of large, regulating predators in fragmented habitats (photos by W.F. Laurance).

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; Harper et al., 2005). This fundamentally alters canopy-gap dynamics, forest structure, microclimate (Kapos, 1989; Malcolm, 1998), and the relative abundance of different plant functional groups (Tabarelli et al., 1999; Metzger, 2000; Laurance et al., 2006a, 2006b; Nascimento et al., 2006). Forest carbon storage is also reduced (Fig. 6) 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.

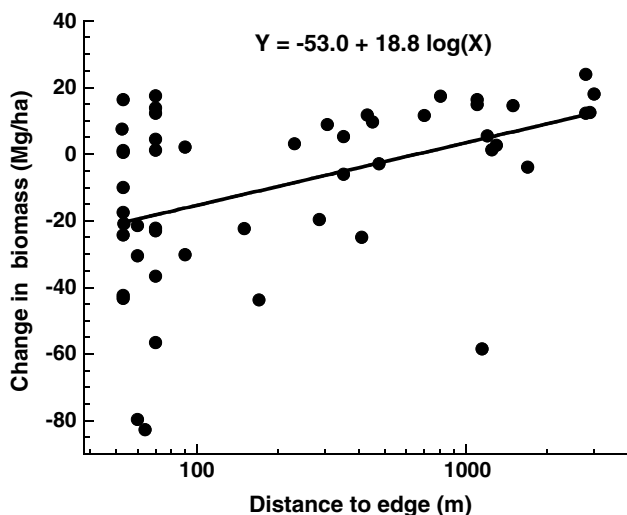


Fig. 6 – Collapse of aboveground biomass in Amazonian forest fragments. Shown is the net change in aboveground tree biomass in 1-ha plots as a function of distance from forest edge, during the first 1–2 decades after forest fragmentation (after Nascimento and Laurance, 2004).

Fragmentation often drastically alters natural fire regimes. In some cases, burning declines sharply because fires are suppressed in the surrounding 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 (Fig. 7) 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, in press).

3.8. 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 are often selectively logged, degraded by ground fires, and overhunted—changes that can dramatically alter fragment ecology (Cullen et al., 2000; Peres, 2001; Cochrane and Laurance, 2002; Galetti et al., 2006; 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; Hobbs and Huenneke, 1992; Abensperg-Traun et al., 1996; Suarez et al., 1998; Cumming, 2002). In coming decades, anthropogenic climate change may emerge as an increasingly important threat to fragmented ecosystems (Travis, 2003; Opdam and Wascher, 2004; Laurance and Curran, 2008), especially if droughts, storms, and other rare weather events increase

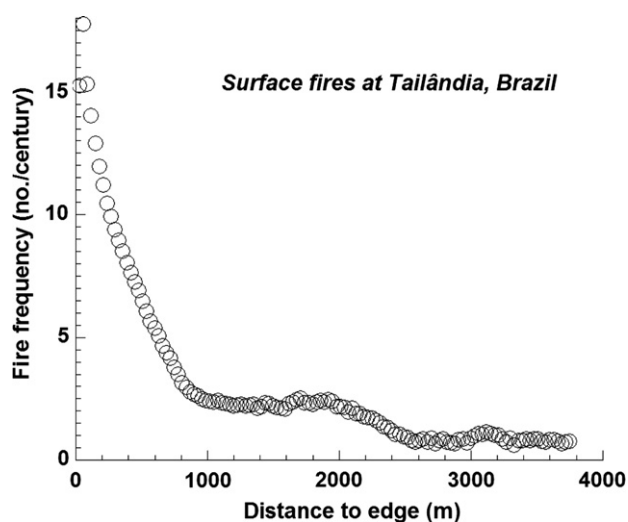


Fig. 7 – Fires can increase dramatically in fragmented forests. Shown is the mean fire frequency (number per century) as a function of distance to forest edge for several hundred forest fragments in eastern Amazonia. Analyses were based on 14 years of satellite observations (adapted from Cochrane and Laurance, 2002).

in frequency or severity (Timmerman et al., 1999; Webster et al., 2005).

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.

3.9. 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; Casagrande and Gatto, 2002). 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; Wirth et al., 2007). 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 and ecological generalists (Mikkelsen, 1993; Didham et al., 1998; Terborgh et al., 2001; Sekercioglu et al., 2002; Feeley and Terborgh, 2006), with cascading impacts on plant communities (Dirzo and Miranda, 1991; Terborgh, 1992; Leigh et al., 1993; Rao et al., 2001; Asquith and Meija-Chang, 2005; Feeley and Terborgh, 2005). 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). Modified landscapes can be a major source of recurring disturbances, with hunters, livestock, fires, smoke, and large abiotic fluxes penetrating into and destabilizing fragments.

4. Conclusions

IBT is one of the most elegant and important theories in contemporary ecology, towering above thousands of lesser ideas and concepts. The theory provides 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.

This having been said, the study of fragmented ecosystems has now greatly 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. Fragmentation research today has diversified enormously, touching on sub-disciplines ranging from landscape ecology to metapopulation dynamics, and from conservation genetics to population viability analysis. Although everyone working in these fields owes some allegiance to the initial insights of IBT, fragmentation research has advanced far beyond the original scope of the theory.

Acknowledgements

I thank J. Losos, R. Ricklefs, R. Ewers, S. Laurance, N. Sodhi, and two anonymous reviewers for many useful comments. This paper is modified and expanded from a book chapter (Laurance, in press) but retains much of the original structure. This is publication number 513 in the technical series of the Biological Dynamics of Forest Fragments Project.

REFERENCES

- Abbott, I., 1983. The meaning of z in species/area regressions and the study of species turnover in island biogeography. *Oikos* 41, 385–390.
- Abele, L.G., Connor, E.F., 1979. Application of island biogeography theory to refuge design: making the right decision for the wrong reasons. In: Linn, R.M. (Ed.), *Proceedings of the First Conference on Scientific Research in the National Parks*. US Department of the Interior, Washington, DC, pp. 89–94.
- Abensperg-Traun, M., Smith, G.T., Arnold, G., Steven, D., 1996. The effects of habitat fragmentation and livestock-grazing on animal communities in remnants of gimlet *Eucalyptus salubris* woodland in the Western Australian wheatbelt. I. *Arthropods*. *J. Appl. Ecol.* 33, 1281–1301.
- Aizen, M.A., Feinsinger, P., 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest. *Ecology* 75, 330–351.
- Ale, S., Howe, H.F., in press. What do ecological paradigms offer to conservation? *Conserv. Biol.*
- Andren, H., Angelstam, P., 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69, 544–547.
- Antongiovanni, M., Metzger, J.P., 2005. Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. *Biol. Conserv.* 122, 441–451.
- Asquith, N.M., Meija-Chang, M., 2005. Mammals, edge effects, and the loss of tropical forest diversity. *Ecology* 86, 379–390.
- Baker, W.L., 1994. Restoration of landscape structure altered by fire suppression. *Conserv. Biol.* 8, 763–769.

- Becker, P., Moure, J.B., Peralta, F.J.A., 1991. More about euglossine bees in Amazonian forest fragments. *Biotropica* 23, 586–591.
- Boecklen, W.J., Gotelli, N., 1984. Island biogeographic theory and conservation practice: species–area or specious–area relationships? *Biol. Conserv.* 29, 63–80.
- Brandão, A.O., Souza, C.M., Ribeiro, J.G., Sales, M., 2007. Desmatamento e estradas não-oficiais da Amazônia. In: *Anais XIII Simpósio Brasileiro de Sensoriamento Remoto*, April, pp. 2357–2364.
- Brashares, J.S., 2003. Ecological, behavioral, and life-history correlates of mammal extinctions in West Africa. *Conserv. Biol.* 17, 733–743.
- Brashares, J.S., Arcese, P., Sam, M.K., 2001. Human demography and reserve size predict wildlife extinction in West Africa. *Proc. Royal Soc. London B* 268, 2473–2478.
- Brooks, T., Balmford, A., 1996. Atlantic forest extinctions. *Nature* 380, 115.
- Brown, J.H., Kodric-Brown, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58, 445–449.
- Bruna, E.M., 1999. Seed germination in rainforest fragments. *Nature* 402, 139.
- Buechner, M., 1987. Conservation in insular parks: simulation models of factors affecting the movement of animals across park boundaries. *Biol. Conserv.* 41, 57–76.
- Burkey, T.V., 1995. Extinction rates in archipelagoes: implications for populations in fragmented habitats. *Conserv. Biol.* 9, 527–541.
- Cadenasso, M., Pickett, S., Weathers, K., 2000. Effects of edges and boundaries on the flux of nutrients, detritus, and organisms. In: Polis, G., Power, M. (Eds.), *Food Webs at the Landscape Level*. University of Chicago Press, Chicago, pp. 128–135.
- Caley, M.J., Buckley, K.A., Jones, G.P., 2001. Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. *Ecology* 82, 3435–3448.
- Cantrell, R.S., Cosner, C., Fagan, W.F., 1999. Competitive reversals inside ecological reserves: the role of external habitat degradation. *J. Math. Biol.* 37, 491–533.
- Casagrande, R., Gatto, M., 2002. Habitat destruction, environmental catastrophes, and metapopulation extinction. *Theor. Popul. Biol.* 61, 127–140.
- Chapman, C.A., Chapman, L.J., Vulinec, K., Zanne, A., Lawes, M.J., 2003. Fragmentation and alteration of seed dispersal processes: an initial evaluation of dung beetles, seed fate, and seedling diversity. *Biotropica* 35, 382–393.
- Chatelain, C., Gautier, L., Spichiger, R., 1996. A recent history of forest fragmentation in southwestern Ivory Coast. *Biodiv. Conserv.* 5, 37–53.
- Chen, J., Franklin, J.F., Spies, T.A., 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecol. Appl.* 2, 387–396.
- Cochrane, M.A., Laurance, W.F., 2002. Fire as a large-scale edge effect in Amazonian forests. *J. Trop. Ecol.* 18, 311–325.
- Cochrane, M.A., Laurance, W.F., in press. Synergisms among fire, land use, and climate change in the Amazon. *Ambio*.
- Cochrane, M.A., Alencar, A., Schulze, M., Souza, C., Nepstad, D., Lefebvre, P., Davidson, E., 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* 284, 1832–1835.
- Collins, R.J., Barrett, G.W., 1997. Effects of habitat fragmentation on meadow vole (*Microtus pennsylvanicus*) population dynamics in experiment landscape patches. *Landscape Ecol.* 12, 63–76.
- Connor, E.R., McCoy, E.D., 1979. The statistics and biology of the species–area relationship. *Am. Nat.* 113, 791–833.
- Cordeiro, N., Howe, H.F., 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proc. Natl. Acad. Sci. USA* 100, 14052–14054.
- Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400, 563–566.
- Cullen, L., Bodmer, R.E., Padua, C.V., 2000. Effects of hunting in habitat fragments of the Atlantic forest, Brazil. *Biol. Conserv.* 95, 49–56.
- Cumming, G.S., 2002. Habitat shape, species invasions, and reserve design: insights from simple models. *Conserv. Ecol.* 6, 3. <<http://www.consecol.org/vol6/iss1/art3>>.
- Curran, L.M., Caniogo, I., Paoli, G., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C., Haeruman, H., 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* 286, 2184–2188.
- Desmet, P., Cowling, R., 2004. Using the species–area relationship to set baseline targets for conservation. *Ecol. Soc.* 9, 11. <<http://www.ecologyandsociety.org/vol9/iss2/art11>>.
- Diamond, J.M., 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proc. Natl. Acad. Sci. USA* 64, 57–63.
- Diamond, J.M., 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. *Proc. Natl. Acad. Sci. USA* 69, 3199–3203.
- Diamond, J.M., 1975a. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* 7, 129–146.
- Diamond, J.M., 1975b. Assembly of species communities. In: Cody, M.L., Diamond, J.M. (Eds.), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, Massachusetts, pp. 342–444.
- Diamond, J.M., 1976. Island biogeography and conservation: strategy and limitations. *Science* 193, 1027–1029.
- Diamond, J.M., 1984. “Normal” extinctions of isolated populations. In: Nitecki, M.H. (Ed.), *Extinctions*. University of Chicago Press, Chicago, pp. 191–246.
- Diamond, J.M., May, R.M., 1976. Island biogeography and the design of natural reserves. In: May, R.M. (Ed.), *Theoretical Ecology: Principles and Applications*. Blackwell Scientific, Oxford, pp. 163–186.
- Diamond, J.M., May, R.M., 1977. Species turnover rates on islands: dependence on census interval. *Science* 197, 266–270.
- Didham, R.K., Lawton, J.H., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31, 17–30.
- Didham, R.K., Lawton, J.H., Hammond, P.M., Eggleton, P., 1998. Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Philos. Trans. Royal Soc. London B* 353, 437–451.
- Dirzo, R., Garcia, M.C., 1992. Rates of deforestation in Los Tuxtlas, a neotropical area in southern Mexico. *Conserv. Biol.* 6, 84–90.
- Dirzo, R., Miranda, A., 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. In: Price, P.W., Lewinsohn, T., Fernandes, G., Benson, W. (Eds.), *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. John Wiley & Sons, New York, pp. 273–287.
- Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. *Ann. Rev. Environ. Resour.* 28, 137–167.
- Ehrlich, P.R., Wilson, E.O., 1991. Biodiversity studies: science and policy. *Science* 253, 758–762.
- Ewers, R.M., Didham, R.K., 2007. The effect of fragment shape and species’ sensitivity to habitat edges on animal population size. *Conserv. Biol.* 21, 926–936.
- Ewers, R.M., Thorpe, S., Didham, R.K., 2007. Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* 88, 96–106.
- Faaborg, J., 1979. Qualitative patterns of avian extinction on neotropical land-bridge islands: lessons for conservation. *J. Appl. Ecol.* 16, 99–107.

- Fagan, W.F., Cantrell, R.S., Cosner, C., 1999. How habitat edges change species interactions. *Am. Nat.* 153, 165–182.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Ann. Rev. Ecol. Syst.* 34, 487–515.
- Feeley, K.J., Terborgh, J.W., 2005. Elevated densities of herbivores (*Alouatta seniculus*) affect soil nutrient concentrations and tree growth on islands in Lago Guri, Venezuela. *Ecology* 86, 116–124.
- Feeley, K.J., Terborgh, J.W., 2006. Habitat fragmentation and effects of herbivore (howler monkey) abundances on bird species richness. *Ecology* 87, 144–150.
- Fox, B.J., Fox, M.D., 2000. Factors determining mammal species richness on habitat islands and isolates: habitat diversity, disturbance, species interactions and guild assembly rules. *Global Ecol. Biogeogr.* 9, 19–37.
- Galetti, M., Sazima, I., 2006. Impact of feral dogs in an urban Atlantic forest fragment in southeastern Brazil. *Natur. Conserv.* 4, 146–151.
- Galetti, M., Donatti, C.I., Pires, A.S., Guimarães, P.R., Jordano, P., 2006. Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Bot. J. Linn. Soc.* 151, 141–149.
- Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P., Vasconcelos, H., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S., 1999. Matrix habitat and species persistence in tropical forest remnants. *Biol. Conserv.* 91, 223–229.
- Gascon, C., Williamson, G.B., Fonseca, G., 2000. Receding edges and vanishing reserves. *Science* 288, 1356–1358.
- Gates, J.E., Gysel, L.W., 1978. Avian nest dispersion and fledgling outcome in field-forest edges. *Ecology* 59, 871–883.
- Gilbert, F.S., 1980. The equilibrium theory of island biogeography, fact or fiction? *J. Biogeogr.* 7, 209–235.
- Gilbert, K.A., Setz, E., 2001. Primates in a fragmented landscape: six species in central Amazonia. In: Bierregaard, R.O., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), *Lessons from Amazonia: Ecology and Conservation of a Fragmented Forest*. Yale University Press, New Haven, Connecticut, pp. 262–270.
- Grau, H.R., 2004. Landscape context and local-scale environment influence regeneration of pioneer tree species in treefall gaps. *Biotropica* 36, 52–59.
- Hagan, J.M., Vander, H., Matthew, W., McKinley, P., 1996. The early development of forest fragmentation effects on birds. *Conserv. Biol.* 10, 188–202.
- Haila, Y., 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecol. Appl.* 12, 321–334.
- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosnokske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., Esseen, P.-A., 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conserv. Biol.* 19, 768–782.
- Harrison, S., Bruna, E., 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22, 225–232.
- Heaney, L.R., 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecol. Biogeogr.* 9, 59–74.
- Henle, K., Davies, K.F., Kleyer, M., Margules, C., Settele, J., 2004. Predictors of species sensitivity to fragmentation. *Biodiv. Conserv.* 13, 207–251.
- Higgs, A.J., Usher, M.B., 1980. Should nature reserves be large or small? *Nature* 285, 568–569.
- Hobbs, R.J., 1993. Effects of landscape fragmentation on ecosystem processes in the Western Australian wheatbelt. *Biol. Conserv.* 64, 193–201.
- Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.* 6, 324–337.
- Holt, R.D., Lawton, J.H., Polis, G., Martinez, N.D., 1999. Trophic rank and the species–area relationship. *Ecology* 80, 1495–1504.
- Honer, D., Greuter, W., 1988. Plant population dynamics and species turnover on small islands near Karpathos (South Aegean, Greece). *Vegetatio* 77, 129–137.
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey.
- Janzen, D.H., 1968. Host plants as islands in evolutionary and contemporary time. *Am. Nat.* 102, 592–595.
- Janzen, D.H., 1983. No park is an island: increase in interference from outside as park size decreases. *Oikos* 41, 402–410.
- Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* 5, 173–185.
- Karieva, P., 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature* 326, 388–390.
- Koh, L.P., Sodhi, N.S., 2004. Importance of reserves, fragments, and parks for butterfly conservation in a tropical urban landscape. *Ecol. Appl.* 14, 1695–1708.
- Koh, L.P., Sodhi, N.S., Brook, B.W., 2004. Ecological correlates of extinction proneness in tropical butterflies. *Conserv. Biol.* 18, 1571–1578.
- Krauss, J., Stefan-Dewenter, I., Tschamntke, T., 2003. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. *Oecologia* 137, 591–602.
- Laurance, S.G., 2004. Responses of understory rainforest birds to road edges in central Amazonia. *Ecol. Appl.* 14, 1344–1357.
- Laurance, W.F., 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. *J. Mammal.* 71, 641453.
- Laurance, W.F., 1991. Ecological correlates of extinction processes in Australian tropical rainforest mammals. *Conserv. Biol.* 5, 79–89.
- Laurance, W.F., 1997. Responses of mammals to rainforest fragmentation in tropical Queensland: a review and synthesis. *Wildlife Res.* 24, 603–612.
- Laurance, W.F., 2000. Do edge effects occur over large spatial scales? *Trends Ecol. Evol.* 15, 134–135.
- Laurance, W.F., 2002. Hyperdynamism in fragmented habitats. *J. Veg. Sci.* 13, 595–602.
- Laurance, W.F., 2004. Forest–climate interactions in fragmented tropical landscapes. *Philos. Trans. Royal Soc. B* 359, 345–352.
- Laurance, W.F., 2007. Have we overstated the tropical biodiversity crisis? *Trends Ecol. Evol.* 22, 65–70.
- Laurance, W.F., in press. Beyond island biogeography theory: understanding habitat fragmentation in the real world. In: Losos, J.B., Ricklefs, R.E. (Eds.), *The Theory of Island Biogeography at 40: Impacts and Prospects*. Princeton University Press, Princeton, New Jersey.
- Laurance, W.F., Bierregaard, R.O. (Eds.), 1997. *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago.
- Laurance, W.F., Cochrane, M.A., 2001. Synergistic effects in fragmented landscapes. *Conserv. Biol.* 15, 1488–1489.
- Laurance, W.F., Curran, T.J., 2008. Impacts of wind disturbance on fragmented tropical forests: a review and synthesis. *Austral. Ecol.* 33, 399–408.
- Laurance, W.F., Yensen, E., 1991. Predicting the impacts of edge effects in fragmented habitats. *Biol. Conserv.* 55, 77–92.
- Laurance, W.F., Laurance, S.G., Ferreira, L., Rankin-de Merona, J., Gascon, C., Lovejoy, T.E., 1997. Biomass collapse in Amazonian forest fragments. *Science* 278, 1117–1118.
- Laurance, W.F., Ferreira, L., Rankin-de Merona, J., Laurance, S.G., 1998a. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79, 2032–2040.

- Laurance, W.F., Laurance, S.G., Delamonica, P., 1998b. Tropical forest fragmentation and greenhouse gas emissions. *For. Ecol. Manage.* 110, 173–180.
- Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos, H., Lovejoy, T.E., 2000. Rainforest fragmentation kills big trees. *Nature* 404, 836.
- Laurance, W.F., Cochrane, M.A., Bergen, S., Fearnside, P.M., Delamonica, P., Barber, C., D'Angelo, S., Fernandes, T., 2001. The future of the Brazilian Amazon. *Science* 291, 438–439.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H., Bruna, E., Didham, R., Stouffer, P., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* 16, 605–618.
- Laurance, W.F., Nascimento, H., Laurance, S.G., Andrade, A., Fearnside, P.M., Ribeiro, J., 2006a. Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87, 469–482.
- Laurance, W.F., Nascimento, H., Laurance, S.G., Andrade, A., Ribeiro, J., Giraldo, J., Lovejoy, T.E., Condit, R., Chave, J., D'Angelo, S., 2006b. Rapid decay of tree-community composition in Amazonian forest fragments. *Proc. Natl. Acad. Sci. USA* 103, 19010–19014.
- Lehtinen, R.M., Ramanamanjato, J., Raveloarison, J.G., 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar. *Biodiv. Conserv.* 12, 1357–1370.
- Leigh Jr., E.G., Wright, S.J., Herre, E., Putz, F.E., 1993. The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evol. Ecol.* 7, 76–102.
- Lidicker Jr., W.Z., 1973. Regulation of numbers in an island population of the California vole, a problem in community dynamics. *Ecol. Monogr.* 43, 271–302.
- Lomolino, M.V., 1986. Mammalian community structure on islands: immigration, extinction and interactive effects. *Biol. J. Linn. Soc.* 28, 1–21.
- Lomolino, M.V., 2000. Ecology's most general, yet Protean pattern: the species–area relationship. *J. Biogeogr.* 27, 17–26.
- Losos, J.B., 1996. Ecological and evolutionary determinants of the species–area relation in Caribbean anoline lizards. *Philos. Trans. Royal Soc. B* 351, 847–854.
- Lovejoy, T.E., Rankin, J., Bierregaard, R.O., Brown, K., Emmons, L., Van der Voort, M., 1984. Ecosystem decay of Amazon forest fragments. In: Nitecki, M.H. (Ed.), *Extinctions*. University of Chicago Press, Chicago, pp. 295–325.
- Lovejoy, T.E., Bierregaard, R.O., Rylands, A., Malcolm, J., Quintela, C., Harper, L., Brown, K., Powell, A., Powell, G., Schubart, H., Hays, M., 1986. Edge and other effects of isolation on Amazon forest fragments. In: Soulé, M.E. (Ed.), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer, Sunderland, Massachusetts, pp. 257–285.
- MacArthur, R.H., Wilson, E.O., 1963. An equilibrium theory of insular zoogeography. *Evolution* 17, 373–387.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Magura, T., Kodobocz, V., Tothmeresz, B., 2001. Effects of habitat fragmentation on carabids in forest patches. *J. Biogeogr.* 28, 129–138.
- Malcolm, J.R., 1994. Edge effects in central Amazonian forest fragments. *Ecology* 75, 2438–2445.
- Malcolm, J.R., 1998. A model of conductive heat flow in forest edges and fragmented landscapes. *Clim. Change* 39, 487–502.
- Margules, C.R., Milkovits, G.A., 1994. Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and an amphipod. *Ecology* 75, 2033–2042.
- May, R.M., 1975. Island biogeography and the design of wildlife preserves. *Nature* 254, 177–178.
- McGarigal, K., McComb, W.C., 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecol. Monogr.* 65, 235–260.
- Mesquita, R., Delamônica, P., Laurance, W.F., 1999. Effects of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biol. Conserv.* 91, 129–134.
- Metzger, J.P., 2000. Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. *Ecol. Appl.* 10, 1147–1161.
- Mikkelsen, G.M., 1993. How do food webs fall apart? A study of changes in trophic structure during relaxation on habitat fragments. *Oikos* 67, 539–547.
- Morrison, L.W., 2003. Plant species persistence and turnover on small Bahamian islands. *Oecologia* 136, 51–62.
- Myers, N., 1988. Synergistic interactions and environment. *BioScience* 39, 506.
- Nascimento, H., Laurance, W.F., 2004. Biomass dynamics in Amazonian forest fragments. *Ecol. Appl.* 14, S127–S138.
- Nascimento, H., Andrade, A., Camargo, J., Laurance, W.F., Laurance, S.G., Ribeiro, J., 2006. Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conserv. Biol.* 20, 853–860.
- Newmark, W.D., 1996. Insularization of Tanzanian parks and the local extinction of large mammals. *Conserv. Biol.* 10, 1549–1556.
- Ng, F.S.P., 1983. Ecological principles of tropical lowland rain forest conservation. In: Sutton, S.L., Whitmore, T.C., Chadwick, A.C. (Eds.), *Tropical Rain Forest: Ecology and Management*. Blackwell, Oxford, UK, pp. 359–376.
- Nupp, T.E., Swihart, R.K., 2000. Landscape-level correlates of small mammal assemblages in forest fragments surrounded by farmland. *J. Mammal.* 81, 512–526.
- Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biol. Conserv.* 117, 285–297.
- Ovaskainen, O., 2002. Long-term persistence of species and the SLOSS problem. *J. Theor. Biol.* 218, 419–433.
- Paton, P.W.C., 1994. The effect of edge on avian nest success: how strong is the evidence? *Conserv. Biol.* 8, 17–26.
- Patterson, B.D., 1987. The principle of nested subsets and its implications for biological conservation. *Conserv. Biol.* 1, 323–334.
- Patterson, B.D., Atmar, U., 1986. Nested subsets and the structure of insular mammalian faunas and archipelagoes. *Biol. J. Linn. Soc.* 28, 65–82.
- Pereira, M.P., Daily, G.C., 2006. Modeling biodiversity dynamics in countryside landscapes. *Ecology* 87, 1877–1885.
- Peres, C.A., 2001. Synergistic effects of subsistence hunting and forest fragmentation on Amazonian forest vertebrates. *Conserv. Biol.* 15, 1490–1505.
- Peres, C.A., Michalski, F., 2006. Synergistic effects of habitat disturbance and hunting in Amazonian forest fragments. In: Laurance, W.F., Peres, C.A. (Eds.), *Emerging Threats to Tropical Forests*. University of Chicago Press, Chicago, pp. 105–127.
- Pickett, S.T.A., Thompson, J.N., 1978. Patch dynamics and the design of nature reserves. *Biol. Conserv.* 13, 27–37.
- Pimm, S.L., Jones, H.L., Diamond, J.M., 1989. On the risk of extinction. *Am. Nat.* 132, 757–785.
- Pimm, S.L., Russell, G.J., Gittleman, J., Brooks, T.M., 1995. The future of biodiversity. *Science* 269, 347–350.
- Pires, A.S., Lira, P., Fernandez, F., Schittini, G., Oliveira, L., 2002. Frequency of movements of small mammals among Atlantic coastal forest fragments in Brazil. *Biol. Conserv.* 108, 229–237.
- Powledge, F., 2003. Island biogeography's lasting impact. *BioScience* 53, 1032–1038.
- Preston, F.W., 1960. Time and space and the variation of species. *Ecology* 41, 611–627.
- Quammen, D., 1997. *The Song of the Dodo: Island Biogeography in an Age of Extinctions*. Scribner, New York.
- Quintana-Ascencio, P.F., Menges, E.S., 1996. Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. *Conserv. Biol.* 10, 1210–1219.

- Ranney, J.W., Bruner, M., Levenson, J., 1981. The importance of edge in the structure and dynamics of forest islands. In: Burgess, R., Sharpe, D. (Eds.), *Forest Island Dynamics in Man-dominated Landscapes*. Springer-Verlag, New York, pp. 67–95.
- Rao, M., 2000. Variation in leaf-cutter ant (*Atta* sp.) densities in forest isolates: the potential role of predation. *J. Trop. Ecol.* 16, 209–225.
- Rao, M., Terborgh, J., Nuñez, P., 2001. Increased herbivory in forest isolates: implications for plant community structure and composition. *Conserv. Biol.* 15, 624–633.
- Reid, W.V., 1992. How many species will there be? In: Whitmore, T.C., Sayer, J.A. (Eds.), *Tropical Deforestation and Species Extinction*. Chapman & Hall, London, UK, pp. 53–73.
- Ries, L., Fletcher, R.J.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models and variability explained. *Ann. Rev. Ecol. Evol. Syst.* 35, 491–522.
- Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 158, 87–99.
- Ricklefs, R.E., Bermingham, E., 2001. Nonequilibrium diversity dynamics of the lesser Antillean avifauna. *Science* 294, 1522–1524.
- Ricklefs, R.E., Cox, G.W., 1972. Taxon cycles in the West Indian avifauna. *Am. Nat.* 106, 195–219.
- Ricklefs, R.E., Lovette, I.J., 1999. The roles of island area per se and habitat diversity in the species–area relationships of four lesser Antillean faunal groups. *J. Anim. Ecol.* 68, 1142–1160.
- Rosenzweig, M., 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.
- Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* 5, 18–32.
- Schmidt, K.A., 2003. Nest predation and population declines in Illinois songbirds: a case for mesopredator effects. *Conserv. Biol.* 17, 1141–1150.
- Schmigelow, F.K.A., Machtans, C., Hannon, S.J., 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* 78, 1914–1932.
- Schonewald-Cox, C.M., Bayless, J.W., 1986. The boundary model: a geographical analysis of design and conservation of nature reserves. *Biol. Conserv.* 38, 305–322.
- Seabloom, E.W., Dobson, A.P., Stoms, D.M., 2002. Extinction rates under nonrandom patterns of habitat loss. *Proc. Natl. Acad. Sci. USA* 99, 1129–11234.
- Sekercioglu, C.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Figeroa-Sandi, R., 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proc. Natl. Acad. Sci. USA* 99, 263–267.
- Shafer, C.L., 1995. Values and shortcomings of small reserves. *BioScience* 45, 80–88.
- Shaffer, M.L., 1981. Minimum population sizes for species conservation. *BioScience* 31, 131–134.
- Sievert, P.R., Keith, L., 1985. Survival of snowshoe hares at a geographic range boundary. *J. Wildlife Manage.* 49, 854–866.
- Simberloff, D.S., 1976. Species turnover and equilibrium island biogeography. *Science* 194, 572–578.
- Simberloff, D.S., Abele, L.G., 1976a. Island biogeography theory and conservation practice. *Science* 191, 285–286.
- Simberloff, D.S., Abele, L.G., 1976b. Island biogeography and conservation: strategy and limitations. *Science* 193, 1032.
- Smith, A.P., 1997. Deforestation, fragmentation, and reserve design in western Madagascar. In: Laurance, W.F., Bierregaard, R.O. (Eds.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, pp. 415–441.
- Sodhi, N.S., Lee, T.M., Koh, L.P., Dunn, R.R., 2005a. A century of avifaunal turnover in a small tropical rainforest fragment. *Anim. Conserv.* 8, 217–222.
- Sodhi, N.S., Koh, L.P., Prawiradilaga, D.M., Tinulele, D.I., Dargano, I., Putra, D., Tan, H., 2005b. Land use and conservation value for forest birds in Central Sulawesi (Indonesia). *Biol. Conserv.* 122, 547–558.
- Soulé, M.E., Simberloff, D.S., 1986. What do genetics and ecology tell us about the design of nature reserves? *Biol. Conserv.* 35, 19–40.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Sauvajot, R., Wright, J., Sorice, M., Hill, S., 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2, 75–92.
- Stouffer, P.C., Bierregaard, R.O., 1995. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76, 2429–2445.
- Suarez, A.V., Bolger, D.T., Case, T.J., 1998. The effects of fragmentation and invasion on the native ant community in coastal southern California. *Ecology* 79, 2041–2056.
- Tabarelli, M., Mantovani, W., Peres, C.A., 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biol. Conserv.* 91, 119–128.
- Temple, S.A., 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. In: Verner, J., Morrison, M., Ralph, C. (Eds.), *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison, pp. 301–304.
- Terborgh, J., 1974. Faunal equilibria and the design of wildlife preserves. In: Golley, F.B., Medina, E. (Eds.), *Tropical Ecological Systems*. Springer-Verlag, New York, pp. 369–380.
- Terborgh, J., 1976. Island biogeography and conservation: strategy and limitations. *Science* 193, 1029–1030.
- Terborgh, J., 1992. Maintenance of diversity in tropical forests. *Biotropica* 24, 283–292.
- Terborgh, J., Lopez, L., Nuñez, V.P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G., Lambert, T., Balbas, L., 2001. Ecological meltdown in predator-free forest fragments. *Science* 294, 1923–1926.
- Tilman, D., May, R., Lehman, C., Nowak, M., 1994. Habitat destruction and the extinction debt. *Nature* 371, 65–66.
- Timmerman, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M., Roeckner, E., 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398, 694–697.
- Travis, J.M.J., 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc. Royal Soc. London B* 270, 467–473.
- Turner, I.M., Corlett, R.T., 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends Ecol. Evol.* 11, 330–333.
- Villard, M.-A., Trzcinski, M., Merriam, G., 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conserv. Biol.* 13, 774–783.
- Watling, J.I., Donnelly, M.A., 2006. Fragments as islands: a synthesis of faunal responses to habitat patchiness. *Conserv. Biol.* 20, 1016–1025.
- Weathers, K., Cadenasso, M., Pickett, S.T.A., 2001. Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conserv. Biol.* 15, 1506–1514.
- Webster, P.J., Holland, G.J., Curry, J.A., Chang, H.-R., 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309, 1844–1846.
- Whitcomb, R.F., Lynch, J.F., Opler, P., Robbins, C.S., 1976. Island biogeography and conservation: strategy and limitations. *Science* 193, 1030–1032.
- Wilcove, D.S., 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66, 1212–1214.

- Wilcox, B.A., 1980. Insular ecology and conservation. In: Soulé, M.E., Wilcox, B.A. (Eds.), *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, Massachusetts, pp. 95–117.
- Willis, E.O., 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.* 44, 53–169.
- Wilson, E.O., Willis, E.O., 1975. Applied biogeography. In: Cody, M.L., Diamond, J.M. (Eds.), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, Massachusetts, pp. 522–534.
- Winter, J.W., Bell, F., Pahl, L., Atherton, R., 1987. Rainforest clearing in northeastern Australia. *Proc. Royal Soc. Queensland* 98, 41–57.
- Wirth, R., Meyer, S.T., Almeida, W.R., Araújo, M., Barbosa, V., Leal, I.R., 2007. Increasing densities of leaf-cutting ants with proximity to the edge in a Brazilian Atlantic forest. *J. Trop. Ecol.* 23, 501–505.
- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280, 2126–2128.
- Wright, S.J., 1981. Intra-archipelago vertebrate distributions: the slope of the species–area relation. *Am. Nat.* 118, 726–748.
- Wright, S.J., 1985. How isolation affects rates of turnover of species on islands. *Oikos* 44, 331–340.
- Wright, S.J., Duber, H.C., 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica* 33, 583–595.
- Wright, S.J., Muller-Landau, H.C., 2006. The future of tropical forest species. *Biotropica* 38, 287–301.
- Wright, S.J., Stoner, K.E., Beckman, N., Corlett, R.T., Dirzo, R., Muller-Landau, H.C., Nuñez-Iturri, G., Peres, C.A., Wang, B.C., 2007. The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica* 39, 289–291.
- Zimmerman, B.L., Bierregaard, R.O., 1986. Relevance of the equilibrium theory of island biogeography and species–area relations to conservation with a case from Amazonia. *J. Biogeogr.* 13, 133–143.