
Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation

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Abstract: *We synthesized key findings from the Biological Dynamics of Forest Fragments Project, the world's largest and longest-running experimental study of habitat fragmentation. Although initially designed to assess the influence of fragment area on Amazonian biotas, the project has yielded insights that go far beyond the original scope of the study. Results suggest that edge effects play a key role in fragment dynamics, that the matrix has a major influence on fragment connectivity and functioning, and that many Amazonian species avoid even small (<100-m-wide) clearings. The effects of fragmentation are highly eclectic, altering species richness and abundances, species invasions, forest dynamics, the trophic structure of communities, and a variety of ecological and ecosystem processes. Moreover, forest fragmentation appears to interact synergistically with ecological changes such as hunting, fires, and logging, collectively posing an even greater threat to the rainforest biota.*

Descomposición del Ecosistema en Fragmentos de Bosque Amazónico, Una Investigación de 22 Años

Resumen: *Sintetizamos resultados clave del proyecto sobre Dinámicas Biológicas de Fragmentos de bosque, el estudio experimental sobre fragmentación del hábitat más largo y de mayor trayectoria del mundo. A pesar de que inicialmente el proyecto se diseñó para evaluar la influencia del área de fragmentos en biotas del Amazonas, ha proporcionado un entendimiento que va más allá del propósito original del estudio. Los resultados sugieren que los efectos de borde juegan un papel clave en las dinámicas de los fragmentos, que la matriz tiene una influencia mayor sobre la conectividad y el funcionamiento del fragmento y que muchas de las especies del Amazonas evitan áreas taladas pequeñas (de hasta < 100 m de ancho). Los efectos de la fragmentación son altamente eclécticos, alterando la riqueza y abundancia de especies, las invasiones de especies, las dinámicas del bosque, la estructura trófica comunitaria y una variedad de procesos ecológicos y del ecosistema. Mas aún, la fragmentación del bosque aparentemente interactúa sinérgicamente con cambios ecológicos como lo son la caza, los incendios y la tala, representando colectivamente una gran amenaza sobre la biota del bosque lluvioso.*

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Introduction

The Amazon Basin contains over half the Earth's remaining tropical rainforests and is experiencing the world's highest absolute rate of deforestation (Instituto Nacional de Pesquisas Espaciais [INPE] 2000; Laurance et al. 2001a). Because rapid forest conversion is causing widespread habitat fragmentation (Skole & Tucker 1993; Laurance 1998), the fate of many Amazonian species ultimately will depend on their capacity to persist in fragmented landscapes or isolated nature reserves.

The Biological Dynamics of Forest Fragments Project (BDFFP) was initiated in 1979 as a large-scale experiment to assess the effects of fragmentation on Amazonian biotas (Lovejoy et al. 1983, 1986; Bierregaard et al. 1992). It is the world's largest and longest-running experimental study of habitat fragmentation (cf. Debinski & Holt 2000). Originally, the project's main goals were to assess the influence of fragment size on Amazonian animal and plant communities, to identify a minimum critical size for rainforest reserves, and to help resolve the heated SLOSS (single large versus several small reserves) debate (e.g., Simberloff & Abele 1976; Wilcox & Murphy 1985). Over time, however, many additional research aims have been added as new insights have developed.

A key feature of the BDFFP is that standardized abundance data were collected for trees, understory birds, mammals, amphibians, and various invertebrate groups prior to experimental isolation of the forest fragments. This permitted a far more rigorous assessment of frag-

mentation effects than would have been possible with only comparisons of fragmented versus intact forest. In addition, the long-term nature of the BDFFP and its synthetic approach, integrating studies of many taxa and numerous ecological and ecosystem processes, have provided insights impossible in most other fragmentation studies.

We synthesized key BDFFP findings from the past 22 years based on a survey of over 340 publications and theses and herein highlight their implications for forest conservation. The first part of our review focuses on extrinsic factors that influence fragment biotas—particularly area, edge, matrix, isolation, and sample effects. The second part identifies key community- and ecosystem-level effects of fragmentation on tropical forests.

Study Area

The 1000-km² study site is located 80 km north of Manaus, Brazil, in central Amazonia (lat. 2°30'S, long. 60°W) at 50- to 100-m elevation (Fig. 1). Local soils are nutrient-poor sandy or clay-rich ferrasols, which are widespread in the Amazon Basin (Brown 1987). As is typical of the basin, the topography is relatively flat but dissected by many stream gullies. Rainfall ranges from 1900 to 3500 mm annually, with a dry season from June to October (Laurance 2001). The climate regime is intermediate between that of the very wet western Amazon and the drier, more seasonal areas in the southeastern and north-central basin

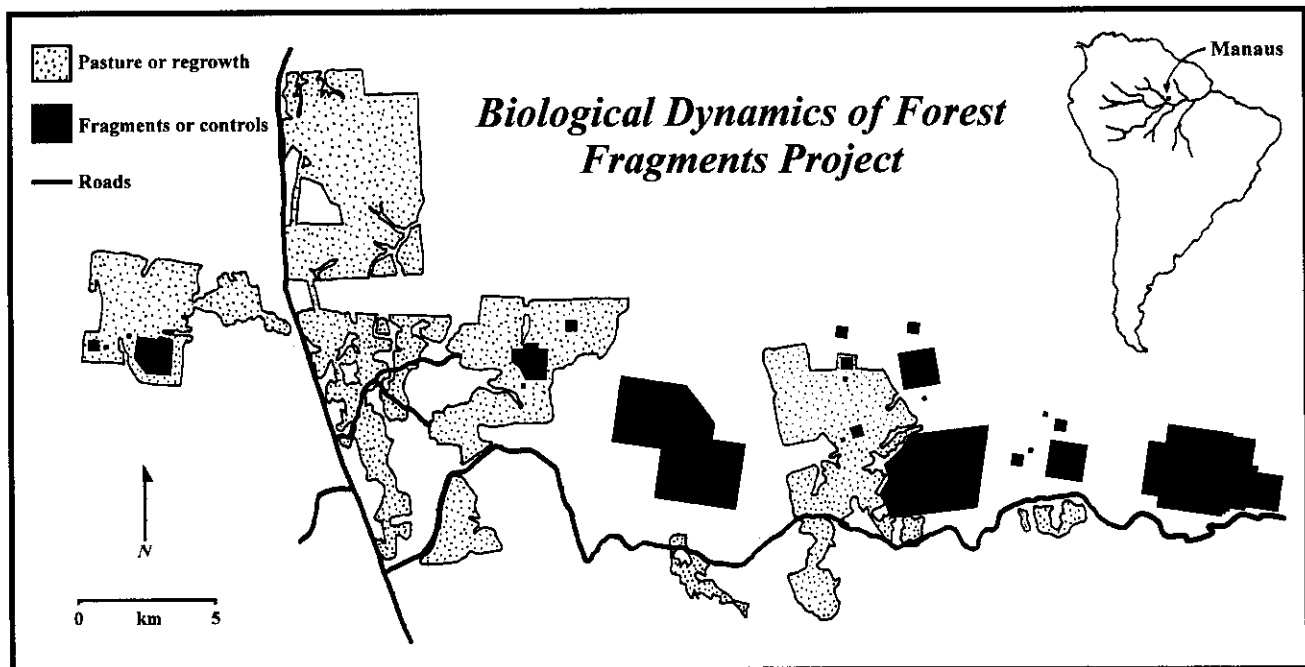


Figure 1. The Biological Dynamics of Forest Fragments Project study area in central Amazonia, showing locations of forest fragments and control sites in intact forest.

(Nepstad et al. 1994). The forest canopy is 30–37 m tall, with emergents reaching 55 m. Species richness of trees is very high and can exceed 280 species (≥ 10 cm diameter) per ha (Oliveira & Mori 1999).

The study area is surrounded by large expanses (>200 km) of continuous forest to the west, north, and east. In the early 1980s, five 1-ha fragments, four 10-ha fragments, and two 100-ha fragments were isolated by distances of 80–650 m from surrounding forest by clearing the intervening vegetation to establish cattle pastures. Fragments were fenced to prevent encroachment by cattle. Twelve reserves ranging from 1 to 1000 ha in area (three of 1 ha, four of 10 ha, two of 100 ha, and three of 1000 ha) were delineated in nearby continuous forest to serve as experimental controls. Because of low pasture productivity, the ranches were gradually abandoned, and 3- to 15-m-tall secondary forests (dominated by *Cecropia* spp. or *Vismia* spp.) proliferated in many formerly cleared areas. To help maintain fragment isolation, 100-m-wide strips of regrowth were cleared and burned around each fragment on two or three occasions. Detailed descriptions of the study area, including the history of each fragment and its surrounding vegetation, are provided elsewhere (Lovejoy et al. 1986; Bierregaard & Stouffer 1997).

Extrinsic Factors Affecting Fragment Biotas

Sample Effects

Forest fragments contain a limited subset of any regional biota, in part because small patches inevitably sample fewer species and less habitat diversity than larger patches (e.g., Wilcox & Murphy 1985; Haila et al. 1993). Results from the BDFFP suggest that such sample effects could be especially important for Amazonian species, which often have patchy distributions at varying spatial scales and complex patterns of endemism (e.g., Zimmerman & Bierregaard 1986; Vasconcelos 1988; Allmon 1991; Rankin-de Merona et al. 1992; de Souza & Brown 1994; Didham et al. 1998a; Laurance et al. 1998a). Pronounced clumping means that many species will be missing from any particular fragment or reserve simply because they never occurred there in the first place.

Another key factor is that, in tropical rainforests, most species are locally rare throughout all or much of their geographic range (Hubbell & Foster 1986; Pittman et al. 1999). The acidic, nutrient-poor soils prevalent in much of Amazonia (Brown 1987) appear to promote animal rarity by limiting fruit and flower production and reducing the nutrient content of foliage (reviewed by Laurance 2001). As a result, many invertebrates (Vasconcelos 1988; Becker et al. 1991) and vertebrates (Emmons 1984; Rylands & Keuroghlian 1988; Stouffer & Bierregaard 1995a; Kalko 1998; Spironello 2001) are consid-

erably less abundant in forests overlaying nutrient-poor Amazonian soils than they are in more-productive areas of the Neotropics. Intrinsic rarity is a critical feature, as demonstrated by studies of Amazonian trees. Even if a species is present when a fragment is initially isolated, its population may be so small that it has little chance of persisting in the long term (Laurance et al. 1998a).

Area Effects

As expected, BDFFP researchers have often found that species richness is positively correlated with fragment size and that intact forest contains more species per unit area than fragments (e.g., Fig. 2). This occurs because many large mammals (Lovejoy et al. 1986), primates (Rylands & Keuroghlian 1988; Schwartzkopf & Rylands 1989; Gilbert & Setz 2001), understory birds (Stouffer & Bierregaard 1995b; Stratford & Stouffer 1999), and even certain beetle, ant, bee, termite, and butterfly species (Powell & Powell 1987; Vasconcelos 1988; Klein 1989; Souza & Brown 1994; Brown & Hutchings 1997; Didham 1997a) are highly sensitive to fragment area. A number of these species have disappeared from even the largest (100 ha) fragments in the study area.

The prediction that extinction rates will be negatively correlated with fragment area (MacArthur & Wilson 1967) is also supported by the BDFFP results. Once isolated, small (1–10 ha) fragments initially lose species at a remarkably high rate; for example, dung and carrion

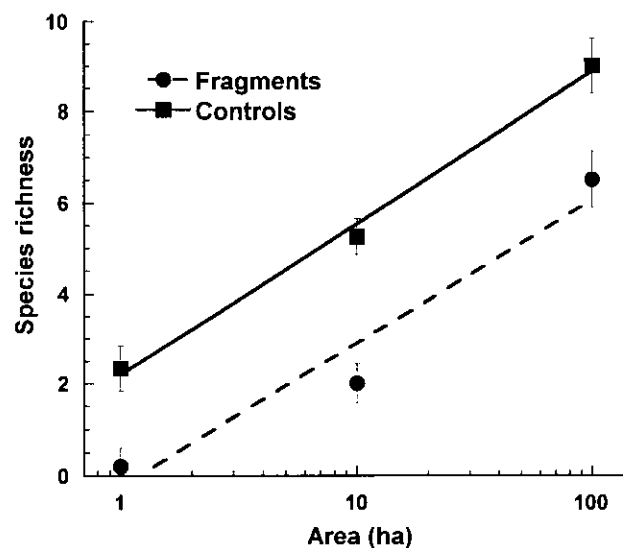


Figure 2. Species-area relationships for nine species of terrestrial insectivorous birds (mean \pm SE) in the Biological Dynamics of Forest Fragments Project study area. Regression lines are fitted separately for fragments ($R^2 = 94.3\%$) and control sites ($R^2 = 99.4\%$) (after Stratford & Stouffer 1999).

beetle assemblages were markedly altered only 2–6 years after fragment isolation (Klein 1989). Local extinctions of birds (Harper 1989; Stouffer & Bierregaard 1995b; Stratford & Stouffer 1999), primates (Lovejoy et al. 1986; Schwartzkopf & Rylands 1989; Gilbert & Setz 2001), and butterflies (Brown & Hutchings 1997) have also occurred more rapidly in small (1–10 ha) than in large (100 ha) fragments.

In contrast, a few taxa have remained stable or even increased in species richness after fragment isolation. Frog richness increased because of an apparent resilience of most rainforest frogs to area and edge effects and an influx of nonrainforest species from the surrounding ma-

trix (Gascon 1993; Tocher et al. 1997). Butterfly richness also rose after fragment isolation, largely from an invasion of generalist matrix species at the expense of forest-interior butterflies (Brown & Hutchings 1997). Small-mammal richness has not declined in the BDFFP fragments, because most species readily use edge and regrowth habitats (Malcolm 1997). Collectively, BDFFP results reveal that the responses of different species and taxonomic groups to fragmentation are highly individualistic and suggest that species with small area needs which tolerate matrix and edge habitats are the least vulnerable (e.g., Offerman et al. 1995; Stouffer & Bierregaard 1995b; Didham et al. 1998a; Gascon et al. 1999).

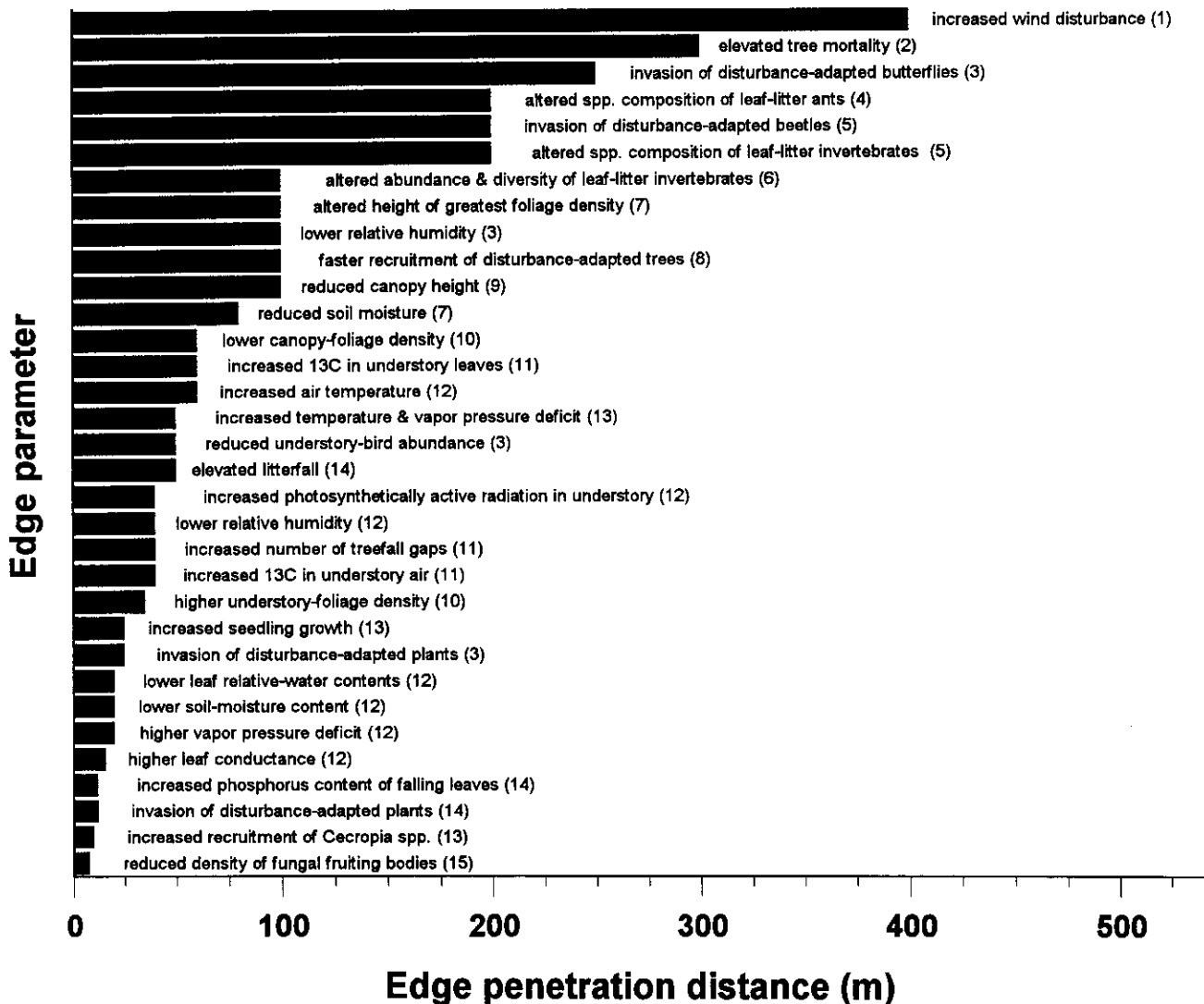


Figure 3. Penetration distances of different edge effects into the forest remnants of the Biological Dynamics of Forest Fragments Project (data sources: 1, Lewis 1998; 2, Laurance et al. 1998b, 2000; 3, Lovejoy et al. 1986; 4, Carvalho & Vasconcelos 1999; 5, Didham 1997b; 6, Didham 1997a; 7, Camargo & Kapos 1995; 8, Laurance et al. 1998c; 9, Camargo 1993; 10, Malcolm 1994; 11, Kapos et al. 1993; 12, Kapos 1989; 13, Sizer & Tanner 1999; 14, Bierregaard et al. 1992; 15, R. K. Didham, unpublished data).

Edge Effects

The BDFFP has helped reveal the remarkable diversity of edge effects in fragmented rainforests, effects that alter physical gradients, species distributions, and many ecological and ecosystem processes (Fig. 3). Microclimatic changes near edges, such as reduced humidity, increased light, and greater temperature variability, penetrate up to 60 m into fragment interiors (Kapos 1989) and can negatively affect species adapted for humid, dark forest interiors (Lovejoy et al. 1986; Benitez-Malvido 1998). Leaf litter accumulates near edges (Carvalho & Vasconcelos 1999; Didham & Lawton 1999) because drought-stressed trees shed leaves and possibly because drier edge conditions slow litter decomposition (Kapos et al. 1993; Didham 1998). Accumulating litter may negatively affect seed germination (Bruna 1999) and seedling survival (Scarlet 2001) and makes forest edges vulnerable to surface fires during droughts (Cochrane et al. 1999).

One of the most striking edge effects is a sharp increase in rates of tree mortality and damage (Ferreira & Laurance 1997; Laurance et al. 1998b). When an edge is created, some trees simply drop their leaves and die standing (Lovejoy et al. 1986), apparently because abrupt changes in light, temperature, or moisture exceed their physiological tolerances. Other trees are snapped or felled by winds, which accelerate over cleared land and then strike forest edges, creating strong turbulence (Laurance 1997). Finally, lianas (woody vines)—important structural parasites that reduce tree growth, survival, and reproduction—increase markedly near edges and may further elevate tree mortality (Laurance et al. 2001b).

The abrupt rise in tree mortality fundamentally alters canopy-gap dynamics (Ferreira & Laurance 1997; Laurance et al. 1998b), which can influence forest structure, composition, and diversity (Brokaw 1985; Hubbell & Foster 1986; Denslow 1987). Smaller fragments often become hyperdisturbed, leading to progressive changes in floristic composition. New trees regenerating within 100 m of forest edges are significantly biased toward disturbance-loving pioneer and secondary species and against old-growth, forest-interior species (Laurance et al. 1998c). The pioneer tree *Cecropia sciadophylla*, for example, has increased 33-fold in density since the BDFFP fragments were isolated (Laurance et al. 2001b).

Some animals respond positively to edges. Certain termites, leafhoppers, scale insects, aphids, aphid-tending ants (Fowler et al. 1993), and light-loving butterflies (Brown & Hutchings 1997) increase near edges. Birds that forage in treefall gaps, such as some arboreal insectivores, hummingbirds, and habitat generalists, often become abundant near edges (Bierregaard & Lovejoy 1989; Bierregaard 1990; Stouffer & Bierregaard 1995a, 1995b). Frugivorous bats increase in number near edges, probably because such areas have higher fruit abundance than forest interiors (Kalko 1998). The insectivorous marsu-

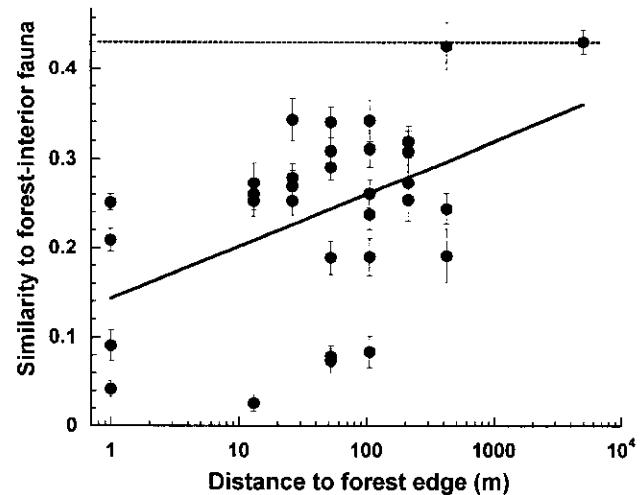


Figure 4. Changes in the composition of leaf-litter beetle assemblages as a function of distance from forest edge. For each sample, the mean percentage similarity (\pm SE) to forest-interior samples (approximately 5000 m from edge) is shown. Dotted line shows the average background level of similarity among different forest-interior samples. The regression was highly significant ($R^2 = 23.2\%$, $p = 0.005$) (after Didham 1997b).

pial *Metachirus nudicaudatus* apparently increases in fragments because dead trees and ground cover, which provide favored foraging microhabitats, increase near edges (Malcolm 1991).

Many other animal species respond negatively to edges and thus are likely to be vulnerable to fragmentation. Numerous flies, bees, wasps (Fowler et al. 1993), beetles (Didham et al. 1998a, 1998b), ants (Carvalho & Vasconcelos 1999), and butterflies (Brown & Hutchings 1997) decline in abundance near edges. A number of insectivorous understory birds avoid edges (Quintela 1985), particularly solitary species, obligatory ant followers, and those that forage in mixed-species flocks (S. G. Laurance 2000). Some frog species use breeding habitat independent of its proximity to edges (Gascon 1993), whereas others may be edge avoiders (e.g., Pearman 1997).

The most striking edge effects in the BDFFP study area occur within 100 m of forest edges (Fig. 3). However, wind damage to forests can penetrate 300–400 m from edges (Laurance et al. 1998b, 2000; Lewis 1998), and changes in beetle, ant, and butterfly communities can be detected as far as 200–400 m from edges (Fig. 4; Brown & Hutchings 1997; Didham 1997b; Carvalho & Vasconcelos 1999). Notably, some edge effects occur over even larger spatial scales in more seasonal areas of the Amazon: ground fires in two fragmented landscapes of eastern Amazonia were sharply elevated in frequency within at least 2400 m of forest edges (Cochrane & Laurance 2002).

Edge Evolution

Another important finding is that rapid changes in the physical permeability of edges occur in the initial years after fragmentation. Newly created edges are structurally open and thereby permeable to lateral light penetration and hot, dry winds from adjoining cattle pastures. After a few years, these microclimatic alterations decline in intensity as edges are partially sealed by a profusion of second growth (Kapos 1989; Camargo & Kapos 1995; Kapos et al. 1997). Desiccation-related plant mortality may also decline over time because of an increase in drought-tolerant species or physiological acclimation of plants near edges. Unlike microclimatic changes, however, wind damage to forests is unlikely to lessen as fragment edges become older and less permeable, because downwind turbulence usually increases as edge permeability is reduced (Savill 1983). In terms of edge permeability, three phases of edge evolution can be identified: initial isolation, edge-closure, and post-closure.

In the initial isolation phase (<1 year after edge formation), the gradient between the forest interior and edge is steepest, with hot, dry conditions and increased light and wind penetrating into the fragment. There is a dramatic pulse in tree mortality; many trees die standing (Laurance et al. 1998b). Leaf-litter accumulates as drought-stressed trees shed leaves to conserve water, or replace shade-adapted leaves with sun-adapted leaves (Didham 1998). Abundances of many animals fluctuate sharply. The most sensitive species decline almost immediately.

During the edge-closure phase (1–5 years after edge formation), a proliferation of secondary vegetation and lateral branching by edge trees progressively seals the edge. Edge gradients in microclimate become more complex but do not disappear entirely (Kapos et al. 1997). Plants near the edge die or become physiologically acclimated to edge conditions. Treefall gaps proliferate within the first 100–300 m of edges, partly as a result of increased windthrow. Additional animal species disappear from fragments. Edge-favoring plants and animals sometimes increase dramatically in abundance (Laurance & Bierregaard 1997).

In the post-closure phase (>5 years after edge formation), edge-related changes are largely stabilized, although external land-use changes (such as fires or the development of adjoining regrowth) can disrupt this equilibrium (Gascon et al. 2000). Windthrow remains elevated near edges, despite the fact that the edge is partially sealed by secondary growth. Proliferating lianas near edges probably contribute to increased tree mortality. Turnover rates of trees increase near edges because of elevated tree mortality and recruitment and increasing numbers of short-lived pioneer species. Pioneer plants replace leaves rapidly, contributing to the accumulation of leaf litter near edges. Although edge closure occurs relatively quickly in tropical rainforests because

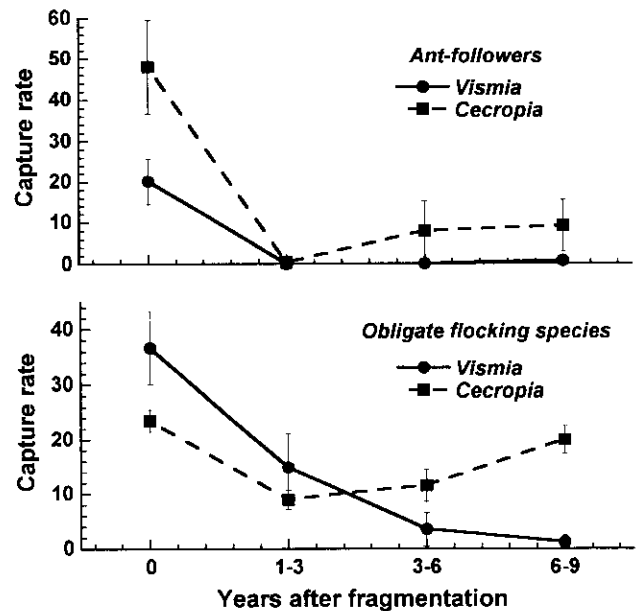


Figure 5. Changes in capture rates (mean \pm SE captures/1000 mist-net hours) over time for two guilds of rainforest birds in 10-ha forest fragments that gradually became surrounded by *Vismia*-dominated and *Cecropia*-dominated regrowth (after Stouffer & Bierregaard 1995b).

of rapid plant growth, edges are still more dynamic and vulnerable to climatic vicissitudes than are forest interiors (Laurance et al. 2002).

Matrix Effects

Successional changes in the BDFFP landscape reveal that surrounding matrix habitats strongly influence fragment ecology. For example, fragments surrounded by regrowth forest 5–10 m tall experienced less-intensive changes in microclimate (Didham & Lawton 1999) and had lower edge-related tree mortality (Mesquita et al. 1999) than did similar fragments adjoined by cattle pastures. Edge avoidance by mixed-species bird flocks was also reduced when fragments were surrounded by regrowth rather than cattle pastures (Stouffer & Bierregaard 1995b).

Of even more significance is that the matrix influences fragment connectivity. Several species of primates (Gilbert & Setz 2001), antbirds, obligate flocking birds (Fig. 5; Stouffer & Bierregaard 1995b), and euglossine bees (Becker et al. 1991) that disappeared soon after fragment isolation recolonized fragments when regrowth regenerated in the surrounding landscape. Among rainforest frogs, birds, small mammals, and bats, matrix-avoiding species were much more likely to decline or disappear in the BDFFP fragments than were those that use the matrix (Offerman et al. 1995; Stouffer & Bierregaard 1995a,

1995b; Kalko 1998; Borges & Stouffer 1999; Gascon et al. 1999; Stratford & Stouffer 1999).

Some matrix habitats are more suitable for rainforest fauna than others. Regrowth dominated by *Cecropia* trees, which tends to be tall and floristically diverse with a relatively closed canopy (Williamson et al. 1998), is used by more rainforest bird, frog, and ant species than is more open *Vismia*-dominated regrowth (Stouffer & Bierregaard 1995b; Tocher 1998; Borges & Stouffer 1999; Vasconcelos 1999; Stouffer & Borges 2001). Virtually any kind of regrowth is better than cattle pastures; for example, forest-dependent dung and carrion beetles are far more likely to cross a matrix of regrowth than one that has been clearcut (Klein 1989). In general, the more closely the matrix approximates the structure and microclimate of primary forest, the more likely that fragmentation-sensitive species can use it.

The matrix can have both positive and negative effects on fragmented populations. Because game in farmland mosaics is often intensively hunted (Robinson & Redford 1991; Rabinowitz 2000), the matrix can become a population sink for exploited species (Woodroffe & Ginsberg 1998). The matrix can also be a source of fruits, flowers, and other resources that help maintain fragment populations (Bierregaard et al. 1992; Brown & Hutchings 1997). Finally, the matrix supports many nonforest species; for example, from 8% to 25% of all frog, bird, small mammal, and ant species in the BDFFP study area are associated exclusively with the matrix (Gascon et al. 1999).

Distance Effects

A key finding of the BDFFP is that even small clearings are barriers for many rainforest organisms. Many terrestrial insectivorous birds have disappeared from the BDFFP fragments and failed to recolonize even those isolated by only 80 m, despite a proliferation of regrowth around many fragments (Stratford & Stouffer 1999). Clearings of just 15–100 m are insurmountable barriers for certain dung and carrion beetles (Klein 1989), euglossine bees (Powell & Powell 1987), and arboreal mammals (Malcolm 1991; Gilbert & Setz 2001). Peccaries (Offerman et al. 1995) and many insect-gleaning bats (Kalko 1998) are also highly reluctant to enter clearings. Even an unpaved road only 30–40 m wide dramatically alters the community structure of understory birds and inhibits the movements of many species (S. G. Laurance 2000).

Some species will cross small clearings but are inhibited by larger expanses of degraded land. Woodcreepers (Dendrocolaptidae) were induced by translocation to move between the BDFFP fragments and nearby areas (80–150 m) of mainland forest (Harper 1989), but they have disappeared from slightly more isolated areas such as Barro Colorado Island in Panama (Robinson 1999). Large predators such as jaguars (*Panthera onca*) and pu-

mas (*Puma concolor*) traverse pastures and regrowth in the BDFFP study area but would likely avoid these areas if hunters were present or human density was higher (Rabinowitz 2000). Some ant-following birds (*Pithys albifrons*, *Gymnopithys rufigula*, *Dendrocincla merula*) translocated into forest fragments where army ants are absent will cross clearings of 100–320 m to return to primary forest (Lovejoy et al. 1986; Harper 1989), although clearings of only 100 m preclude such movement under normal circumstances (Bierregaard & Lovejoy 1989; Stouffer & Bierregaard 1995b).

Amazonian animals avoid clearings for many reasons. Most understory species have had little reason to traverse clearings in their evolutionary history, so the avoidance of such areas is probably an innate response (Greenberg 1989). Other species are constrained by morphology or physiology; strictly arboreal species, for instance, will find even a small pasture an impenetrable barrier. Specialized habitat needs probably limit yet others; for example, rainforest birds that flip over dead leaves in order to find insects, such as the antbird *Myrmornis torquata*, probably cannot manipulate the large leaves of *Cecropia* trees, and therefore avoid *Cecropia*-dominated regrowth (Stratford & Stouffer 1999). A final limit on interfragment movements, at least in Amazonian birds, is that few species are migratory. In temperate forests, even truly isolated fragments can be colonized in the breeding season by migratory species (e.g., Blake & Karr 1987), but Amazonian birds appear less likely to do so.

Ecological Changes in Fragmented Communities

Hyperdynamism

The BDFFP results suggest that, for many organisms, fragmentation alters population and community dynamics. At the outset, deforestation causes recurring disturbances. Surface fires, loggers, hunters, miners, fuelwood gatherers, and livestock can all penetrate into forest remnants and cause a diversity of ecological changes (Schelhas & Greenberg 1996; Laurance & Bierregaard 1997; Curran et al. 1999). For instance, smoke from nearby forest burning strongly disturbed butterfly communities in the BDFFP fragments, accelerating the loss of forest-interior species (Brown & Hutchings 1997).

The proliferation of forest edges also has important effects, because edges are intrinsically less stable than forest interiors. For example, insect activity is highly variable near edges and is influenced more strongly than forest interiors by daily weather variation (Fowler et al. 1993). Tree-mortality rates are sharply elevated near edges and vary markedly over time because of periodic windstorms, droughts, and successional changes in edge structure (Laurance et al. 1998b, 2002; Mesquita et al. 1999).

In addition, small populations in fragments may be less stable than those in continuous forest. Bat communities in the BDFFP fragments appear to exhibit an unusually rapid turnover of species, apparently because of high rates of disappearance of forest-interior species, coupled by an influx of opportunistic frugivores that feed along forest edges and in nearby regrowth (Sampaio 2000). Population turnover in the social spider *Anelosimus eximius* was much higher near forest edges than in forest interiors, suggesting that small fragment populations are unstable (Ventincinque et al. 1993). Small-mammal abundances fluctuated dramatically in the BDFFP fragments, especially in the first few years after isolation, relative to populations in intact forest (Malcolm 1991).

Finally, fluxes of animals and plant propagules to and from the surrounding matrix can sometimes destabilize fragment populations. When the forest surrounding the BDFFP fragments was initially felled, displaced birds flooded into the fragments, leading to sharply elevated densities and increased territorial behavior by resident birds (this increase was temporary; total bird numbers fell to pre-fragmentation levels within 200 days of fragment isolation) (Bierregaard & Lovejoy 1989). Dramatic irruptions of some Heliconine and Ithomiine butterflies occurred in the BDFFP fragments when their weedy food plants (*Passiflora* vines and *Solanum* bushes) proliferated near fragment margins (Brown & Hutchings 1997).

Hyperabundance

Many species decline or disappear in fragmented forests, but others can increase dramatically, especially if they favor disturbed or edge habitats or readily tolerate the surrounding matrix. Examples of edge- and disturbance-favoring groups include certain rodents and marsupials (Malcolm 1997), gap-favoring and nectarivorous birds (Stouffer & Bierregaard 1995a, 1995b; S. G. Laurance 2000), frugivorous bats (Kalko 1998), some understory insects (Malcolm 1991, 1994), pioneer trees (Laurance et al. 1998c), and lianas (Laurance et al. 2001b). Species that thrive in fragments because they can exploit the adjoining matrix include shrub-frugivorous bats (Kalko 1998) and the tamarin *Sanguinus midas* (Rylands & Keuroghlian 1988).

Other species may increase in fragments when their competitors or predators disappear or because they have flexible behavioral repertoires. Howler monkeys (*Alouatta seniculus*), for instance, can achieve high densities in small forest fragments where only a few other monkeys are present (Gilbert & Setz 2001). The woodcreeper (*Xiphorhynchus pardalotus*) often forages with mixed-species and canopy flocks in intact forest, but in fragments it will forage alone and even on edges abutting pastures (Bierregaard 1990). Some canopy-feeding hum-

mingbirds will also forage along forest edges and in tree-fall gaps and thereby increase in fragments (Stouffer & Bierregaard 1995a).

Species Invasions

Species-rich rainforests are relatively resistant to invasions (Laurance & Bierregaard 1997). Although many nonrainforest species have colonized matrix habitats in the BDFFP landscape, incursions into fragments have been more limited. The most conspicuous invaders of fragments are generalist frogs (Tocher et al. 1997) and light-loving butterflies (Brown & Hutchings 1997), although many other taxa have been detected, including open-forest bats (Kalko 1998), exotic and generalist palms (Scariot 1998), Africanized honeybees (Dick 2001), *Glaphrocantbon* beetles (Klein 1989), generalist fruitflies (*Drosophila* spp.; Martins 1989), and leaf-cutting ants native to tropical savannas (*Atta laevigata* and *Acromyrmex laticeps*; Vasconcelos & Cherrett 1995). Incursions of nonrainforest birds (e.g., *Troglodytes aedon*, *Ramphocelus carbo*) into the BDFFP fragments have been surprisingly limited, despite widespread local extinctions of many native insectivorous birds (Stouffer & Bierregaard 1995b; Stouffer & Borges 2001). Likewise, exotic lianas are apparently uncommon in the BDFFP fragments (Laurance et al. 2001b), unlike forest remnants in some other tropical regions (reviewed in Laurance 1997).

However, the BDFFP study area is relatively young (forest clearing began only in 1980) and still largely isolated from other human-dominated landscapes. Many non-native species, such as generalist frogs, probably arrived from settled areas by traversing road verges and powerline clearings (Tocher et al. 1997; Gascon et al. 1999). As degraded lands draw nearer, the pressure from invading species is likely to increase. In this sense, older Amazonian frontiers are likely to be more severely degraded by invaders than are landscapes that have only recently been colonized and fragmented.

Changes in Trophic Structure

Because they have high area and energy requirements, predators and large-bodied species are predicted to decline in habitat fragments, whereas smaller species at lower trophic levels—such as generalist herbivores and omnivores—should increase (Holt 1996). Such changes have been hypothesized to cause ecological distortions that help drive the process of species impoverishment in fragments (Terborgh et al. 1997, 2001).

Results from the BDFFP partially support these hypotheses. Among birds and forest-interior bats, insectivores have been especially vulnerable to fragmentation, whereas many omnivores and nectarivores have remained stable or increased in fragments (Bierregaard &

Stouffer 1997; Kalko 1998; Sampaio 2000). There is also a decline of large mammals in fragments, including predators (Lovejoy et al. 1986; Bierregaard et al. 1992), but because the BDFFP landscape is protected from hunting, the reductions are less dramatic than typically occur in other tropical areas (Robinson & Redford 1991; Peres 2001).

Patterns among insects are more complex and may partly reflect shifts in resource abundance in fragmented forests. The guild composition of termites is altered in fragments, with lower species richness and an increase in litter feeders and those intermediate between soil-feeding and wood-feeding types (Souza & Brown 1994). Such changes could result to some extent from increased litter and wood debris in fragments. Dung and carrion beetles are less abundant and diverse in fragments, in part because many vertebrates on which they rely have declined or disappeared (Klein 1989). Among leaf-litter beetles, there are proportionally more predator species and fewer wood-boring species in fragments and near edges (Didham et al. 1998b). Of these patterns, the relative increase in fragments of predatory beetle diversity (Didham et al. 1998b) and the declines in diversity of decomposer beetles (Klein 1989) and termites (Souza & Brown 1994) seem contrary to the simple expectation that fragments should be biased toward taxa at lower trophic levels.

Changes in Ecological Processes

Tropical rainforests are renowned for their ecological complexity (Janzen 1969; Gilbert 1980). Fragmentation clearly alters some ecological processes, but the generality of these effects is not yet known (Harrison & Bruna 1999). For example, fragmentation has a strong positive effect on pollination or fecundity in the emergent tree *Dinezia excelsia* (Dick 2001), but no detectable effect on the understory herb *Heliconia acuminata* (Bruna 2001). Hypothetically at least, the disappearance of many euglossine bees in the BDFFP fragments could reduce the fecundity of orchids, which rely entirely on euglossines for pollination (Powell & Powell 1987). Likewise, the decline in fragments of dung beetles, which bury dung for their larvae that often contains seeds, might reduce seed survival and germination for some plant species (Klein 1989; Andresen 2001).

Predation intensity is almost certainly altered in Amazonian fragments. Predation on understory and litter arthropods has likely declined because of a collapse of assemblages of insectivorous birds (Stouffer & Bierregaard 1995b; Stratford & Stouffer 1999), bats (Kalko 1998; Sampaio 2000), and army ants (Harper 1989; Bierregaard et al. 1992). It seems plausible that these declines could be partly responsible for increased insect abundance near forest edges (Lovejoy et al. 1986; Fowler et al. 1993) and might even promote increased herbivory in fragments

(Benitez-Malvido et al. 1999). The decline of large carnivores may reduce predation on some vertebrates, but there is no indication of mesopredator release (Crooks & Soulé 1999) in the BDFFP fragments (Meyer 1999).

Because tropical rainforests sustain myriad species with coevolved interdependencies, they may be vulnerable to secondary extinctions (Gilbert 1980), although such losses might be limited by ecological redundancy in some mutualisms (e.g., Horvitz & Schemske 1990). An example from the BDFFP involves several species of obligatory ant-following birds, which accompany marauding swarms of army ants to capture fleeing insects. Each ant colony raids over areas of up to 100 ha, and the birds' home ranges must encompass two or three colonies because each colony spends several weeks per month in an inactive phase (Harper 1989). Because army ants need such large areas, the ant-followers are highly prone to extinction in fragments (Stouffer & Bierregaard 1995b). In addition, the decline of peccaries in BDFFP fragments has led to reduced abundances of at least four frog species (*Phyllomedusa* spp. and *Colostethus* sp.) that breed only in peccary wallows (Zimmerman & Bierregaard 1986). Understanding the effects of fragmentation on such interdependent species is a priority for future research.

Changes in Ecosystem Processes

Tropical forests have a major influence on the global climate, in part by storing large quantities of terrestrial carbon. The rapid destruction of these forests probably ac-

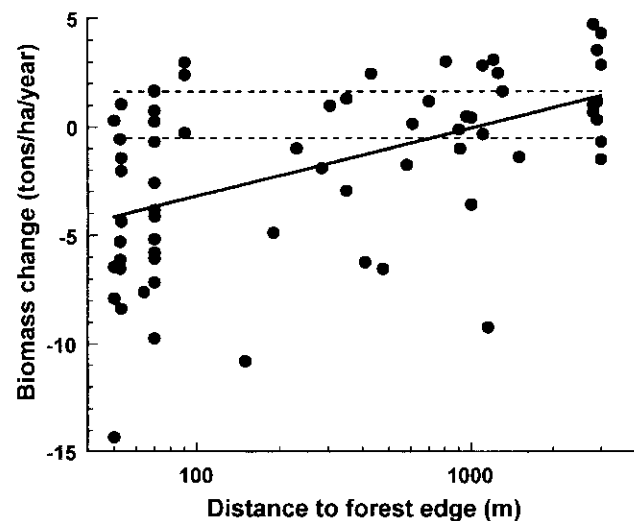


Figure 6. Annual change in aboveground tree biomass in the Biological Dynamics of Forest Fragments Project study area as a function of distance from forest edge. Each data point represents a 1-ha plot that was studied for up to 18 years. The dotted lines show the 95% confidence intervals for forest-interior plots (>500 m from edge) (after Laurance et al. 1997).

counts for at least a quarter of all greenhouse-gas emissions, contributing significantly to global warming (Houghton 1991; Fearnside 2000). An unexpected finding is the degree to which fragmentation alters carbon storage. Elevated tree mortality leads to a decline of living biomass near edges (Fig. 6; Laurance et al. 1997, 1998*d*), especially 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. This loss of living biomass is not offset by increased numbers of lianas and small successional trees (Laurance et al. 1998*d*, 2001*b*), which have lower wood densities and therefore store less carbon than the old-growth species they replace (Laurance et al. 1998*d*). In tropical forests worldwide, millions of tons of atmospheric carbon may be released each year by this process (Laurance et al. 1998*e*). Edge-related losses of biomass are predicted to increase sharply once fragments fall below 100–400 ha in area, depending on fragment shape (Laurance et al. 1998*b*).

The rate of carbon cycling is also altered. In intact forests, carbon can be stored for very long periods in large trees, some of which can live for more than a thousand years (Chambers et al. 1998). In fragments, the residence time for carbon will surely decrease as smaller, short-lived plants replace large old-growth trees and rates of litter deposition increase near edges. The dynamics of this cycle can have major effects on carbon storage in vegetation and soils and the rate of input of organic material into tropical rivers and streams (Wissmar et al. 1981).

Caveats and Conclusions

The BDFFP has yielded scores of insights into the effects of habitat fragmentation on rainforest biotas. Results suggest that edge effects and area-related extinctions will rapidly degrade smaller (<100 ha) fragments, which are predominant in anthropogenic landscapes (Laurance & Bierregaard 1997; Gascon et al. 2000). Species' abundances in fragments will differ from those in intact forest, with some declining and others becoming hyperabundant. Fundamental processes such as canopy-gap dynamics, predation, and carbon storage will be altered or disrupted. Fragments will be strongly influenced by the surrounding matrix, which affects landscape connectivity, the intensity of edge effects, species invasions, and the frequency or intensity of disturbances such as windstorms and fire. Over time, fragmented communities will become increasingly dominated by matrix-tolerant generalists, disturbance-adapted opportunists, and species with small area requirements.

The BDFFP is a controlled experiment, and the ecological effects of fragmentation should be even greater in other tropical landscapes. First, the BDFFP fragments are primarily square, which makes them less vulnerable to edge effects than more irregularly shaped fragments. Second, the BDFFP fragments are located near large tracts of continuous forest, which facilitates rescue effects (Brown & Kodric-Brown 1977) and recolonization for some species and may help maintain natural rainfall and hydrological cycles (Shukla et al. 1990). Third, many of the BDFFP fragments have become surrounded by regrowth, which increases fragment connectivity while reducing the intensity of some edge effects. Finally, the BDFFP study area is protected from hunters, loggers, miners, and recurring surface fires that have dramatically exacerbated the effects of fragmentation in other tropical landscapes (Curran et al. 1999; Cochrane & Laurance 2002).

The BDFFP findings have not identified a single "minimum critical size" for tropical nature reserves. Results have helped demonstrate, however, that such reserves should be both large and numerous. The low densities and patchy distributions of most Amazonian species, the large spatial scale of some edge effects, the irregular shapes of many nature reserves, and the synergistic interactions of fragmentation with other human effects all indicate that Amazonian reserves should be as large as possible—ideally on the order of tens to hundreds of thousands of square kilometers (cf. Peres & Terborgh 1995; W. F. Laurance 2000; Cochrane & Laurance 2002). Moreover, the high turnover of many taxa at regional scales (high gamma diversity) implies that multiple reserves should be stratified along major environmental gradients to capture a large fraction of the regional biota. Finally, the extreme sensitivity of many species to forest clearings and edge effects suggests that relatively wide, continuous corridors of primary forest must be maintained—with limited hunting pressure—to permit faunal movement, plant dispersal, and gene flow among reserves.

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