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# The Biological Dynamics of Tropical Rainforest Fragments

*A prospective comparison of fragments and continuous forest*

Richard O. Bierregaard Jr., Thomas E. Lovejoy, Valerie Kapos, Angelo Augusto dos Santos, and Roger W. Hutchings

**T**ropical rainforests may well be the most diverse ecosystem on the planet. Even though they cover less than 7% of the planet's land mass, they are home to half to two thirds of the species of plants and animals on the earth (Raven 1988, Wilson 1988).

In the latter half of the current

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**A mosaic of small forest remnants would suffer significant alteration by edge effects and would lose species**

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century, the advent of agribusiness, industrial forestry, and waves of colonization have led to large-scale tropical deforestation with clearings on the scale of  $10^2$ – $10^5$  ha. Forest clearing increased exponentially during the 1970s and 1980s in Brazil (Fearnside 1987) and continues at alarming rates around the world (Myers 1991). The speed of this clearing is unprecedented in the evolutionary history of tropical rainforests and thus may have profound effects on the ecosystem.

Inevitably, deforestation results in fragmentation of the rainforests (or any forests) that are retreating in the face of regional development and colonization. Either by chance or by design, islands of forest are left amidst a sea of nonforest habitat. This process, which has largely run its course in developed countries as well as a few tropical ones, is just beginning in the Amazon basin and looms as a key environmental issue over the next several decades.

The biological and physical effects of forest fragmentation are poorly understood. Certain changes are easy to predict, at least qualitatively. Popu-

lation sizes will be reduced, which may have deleterious genetic consequences. Because some species' distributions are not homogeneous, some species will be absent from certain fragments simply because they were not in the patches of forest before the fragments were isolated. Species requiring large home ranges will not survive in small fragments. Microclimate may change within fragments, especially along the edges. Local macroclimatic patterns may be altered.

We are only beginning to learn how such changes affect ecosystem function and structure. For example, as Terborgh (1992) has recently pointed out, the loss of large predators may have a destabilizing effect on populations of seed predators, which in turn may affect the composition of tree species in the forest. Understanding the implications of the fragmentation of tropical rainforests is essential to rational government planning of human settlements and land use in these regions if development is to proceed with minimal disturbance of the natural ecosystem. Such basic questions as "How large should a reserve be?" or "What shape should a reserve be?" have been discussed at length (e.g., Schafer 1990, Wilson and Willis 1975) but remain largely unanswered by experimental data. Additionally, regional planning must consider what happens to forest remnants too small to be deemed wildlife refuges.

MacArthur and Wilson (1963, 1967) formulated a simple model to explain the number of species found on islands as an equilibrium between

immigration and extinction rates. The model fit reasonably well the empirical data on species number on true islands as well as habitat islands such as forest fragments. It predicted that larger islands should support more species than smaller ones and that an island close to the mainland should support more species than an island of similar size farther from the mainland. Attempts to document the model's predicted turnover of species (immigration and extinction), however, have been controversial (e.g., Diamond 1969, Diamond and May 1977, Lynch and Johnson 1974).

The MacArthur-Wilson model was used by conservationists to argue for the creation of large reserves. However, in a seminal article, Simberloff and Abele (1976) pointed out that MacArthur and Wilson's theory of island biogeography is neutral regarding the question of the comparative efficacy of a single large reserve or a series of smaller reserves of similar total area. The article inspired a heated response from conservation biologists concerned that such a position would discourage the creation of large parks and spur developers to deforest large areas, leaving small tracts of forest as their contribution to conservation (Diamond 1976, Terborgh 1976). After a decade and a half, the debate continues in the scientific literature (e.g., Deshayne and Morrisset 1989) and detailed information about the processes of ecosystem change in forest areas of different sizes remains scarce.

### The Biological Dynamics of Forest Fragments Project

In 1979, the World Wildlife Fund and Brazil's National Institute for Research in Amazonia (INPA) launched the Biological Dynamics of Forest Fragments Project (BDFFP, also known as the Minimum Critical Size of Ecosystems Project) to address some of these issues. Since 1989, the National Museum of Natural History of the Smithsonian Institution has administered the project, which operates in Brazil under a cooperative research agreement between INPA and the Smithsonian.

The project was designed specifically to investigate the relationship between the size of a forest fragment



**Figure 1.** Aerial view of a 10-hectare and a 1-hectare isolated forest reserve of the Biological Dynamics of Forest Fragments Project in Manaus, Amazonas, Brazil.

and both the stability and species carrying capacity of that forest fragment. Other factors that affect forest fragments—in particular edge effects and forest regeneration around the fragments—have been incorporated into the research activities.

The many studies that have compared species/area relationships on true islands and in habitat islands have, with few exceptions, only compared species number in a series of islands after the islands were formed and some changes in the relative abundances of species had occurred. In contrast, BDFFP researchers have access to quantitative pre-isolation surveys of organisms in the habitat islands and have monitored changes in ecosystem structure from the moment of isolation. In addition, BDFFP is the only experimental investigation of the effects of tropical forest fragmentation.

The experimental design of BDFFP is based on comparisons of a replicated series of forest fragments, or reserves, of different sizes before and after they were isolated from continuous forest. The most basic studies consist of inventories through time of selected groups of plants and animals in the experimental plots. More detailed studies of the behavior and ecol-

ogy of selected groups of species, as well as the physical changes in the forest isolates, have also been performed.

The forest being studied is mature, terra firme, evergreen, tropical moist forest (Holdridge 1967), receiving approximately 2.3 m of rain annually (MME 1978). Soils are clayey and sandy yellow latosols (see Lovejoy and Bierregaard 1990 for a more detailed description of the study area and ongoing research projects).

The isolation of the experimental reserves was effected by cattle ranchers clear-cutting to create pastures. Based on a Brazilian law that requires that 50% of any landholding under development in the Amazon basin be left in forest, agreements were reached with the managers of five 15,000-hectare cattle ranches in an agricultural research and development district 30–90 km north of Manaus, Brazil (approximately 2° S x 60° W), to leave some of their forest reserve in the middle of their pastures (Figure 1). In addition, a 1000-hectare area in continuous forest not slated for clearing serves as a control site where populations of organisms being studied in the experimental fragments are also monitored. The control area is in forest that stretches unbroken for hundreds of

kilometers to the north and east.

One reserve was isolated in 1979, two in 1980, five in 1983, three in 1984, and finally one in 1990. Pre-isolation data are available for all but one reserve, the roughly 200-hectare forest reserve isolated in 1979. Of the isolated reserves, three are separated from adjacent forest by approximately 100 m, seven by roughly 250 m, and two by 500–700 m. We had expected 12 other reserves to be isolated, but shortfalls in, and eventual discontinuation of, fiscal incentives to the cattle ranchers have left these areas in continuous forest. Therefore, these 12 reserves serve as control plots, in addition to the 1000-hectare site originally planned as a control (Table 1).

Maintenance of the pastures around the experimental reserves varied substantially through time and space. Repeatedly, second-growth vegetation grew up around the reserves and was cut back to re-establish pasture, changing the degree to which the reserves behaved as islands. With increasing complexity and height of the second-growth vegetation, immigration to the reserves became more or less likely for different taxa. Thus, the project is able to ask, among other questions, How great a distance of separation from continuous forest effectively isolates a forest fragment? What is the effect of fragment size on the degree to which the forest community is preserved? What is the role of edge effects? How important is the vegetation matrix surrounding a forest fragment?

### Distance effects

At what distance from continuous forest is a patch of rainforest truly isolated? Our studies indicate that a break of as little as 80 m is a strong barrier to movement to an isolated forest fragment by some insects and mammals and the vast majority of understory birds.

Powell and Powell (1987) used chemical attractants (vanillin, methyl salicylate, and cineole) to study the response of euglossine bees to forest fragmentation. Euglossine bees are important pollinators for species in as many as 30 plant families, and many species of orchids are obligatorily pollinated by only one species of bee (Williams and Dodson 1972).

Table 1. Number of study areas.

Area	Size (ha)				
	1	10	100	200	1000
Fragment	5	4	2	1	0
Undisturbed forest	3	4	3	0	3

The Powells sampled 15 species of euglossine bees in continuous forest, in isolated reserves of 1, 10, and 100 ha, and in the 100-meter clearing that separated the 10-hectare isolate from adjacent continuous forest. They found declines in visitation rates by male bees in all forest isolates; male bees of four deep-forest species did not cross the 100-meter clearing that separated the reserve from continuous forest. Absence of these bees may be expected to decrease pollination rates in some plant species in the reserve and suggests that a mosaic of forest fragments surrounded by pasture will not support populations of certain species of these important pollinators.

Klein (1989) showed that movement of dung- and carrion-feeding beetles was also affected by a break in continuous forest of only 100 m. Malcolm (1991a) studied the small-mammal community (excluding bats) in continuous forest, forest fragments, and the pasture and second growth around the forest isolates. Nineteen species of marsupials and rodents were trapped on the forest floor and in arboreal traps, approximately 15 m above the ground (Malcolm 1991b).

When Malcolm performed his study, all but one of the 1- and 10-hectare isolates were surrounded by second-growth vegetation. The 1-hectare isolate that was surrounded by pasture was only 80 m from continuous forest and also the only one still structurally intact, having suffered far fewer tree falls than other 1-hectare reserves. Despite a vegetation structure similar to continuous forest and the proximity of continuous forest, this reserve showed the lowest number of species, biomass, and individuals of any area sampled, including all other isolates, the second-growth vegetation around the other reserves, and continuous forest. Because there was no replication of these particular conditions, this result remains anecdotal but nonetheless suggests that most small mammals find an 80-meter expanse of sparsely vegetated landscape

a formidable barrier to dispersal.

Using radio telemetry and translocation of trapped individuals of two small marsupials, Malcolm (1991a) confirmed this barrier effect and showed that it differs among species. He found that a 250-meter strip of pasture significantly inhibited homing in *Caluromys philander*, but it had no effect on the apparent habitat generalist *Marmosa cinerea*.

Understory birds show a similar reluctance to cross narrow gaps of clear-cut forest or pasture. On a well-sampled transect in continuous forest, more than half the birds caught are unbanded (Bierregaard and Lovejoy 1988). Most of these unbanded birds are neighbors from adjacent territories or birds with no territories seeking an uninhabited patch of suitable forest. Comparisons of recapture rates among all nine 1-hectare and 10-hectare isolated reserves (including those isolated by only 80 m and 100 m) and continuous forest show that fewer unbanded birds are trapped in the nets in the isolates (Figure 2a). Within several months of isolation, the percentage of a day's captures that are unbanded birds drops to approximately 25%, demonstrating that birds rarely cross a gap to get to an isolate from adjacent continuous forest.

### Fragment size

How does the size of a forest fragment affect animal communities isolated therein? The MacArthur-Wilson model predicts that small forest remnants will support smaller populations and fewer species than larger ones. Our censuses of beetles, birds, and primates in 1-, 10-, and 100-hectare reserves indicate that the number of species, and in some cases population sizes, in these groups varies with the size of the reserve.

Carrion- and dung-feeding beetle communities in 1- and 10-hectare forest fragments isolated by more than 350 m for 2–6 years were represented by fewer species, sparser populations, and smaller individuals than in nearby continuous forest (Klein 1989). Klein also was able to correlate the reduced densities of carrion and dung beetles with lower rates of decomposition of dung in 1-hectare isolates, thereby demonstrating a change in ecosystem process associated with the restricted

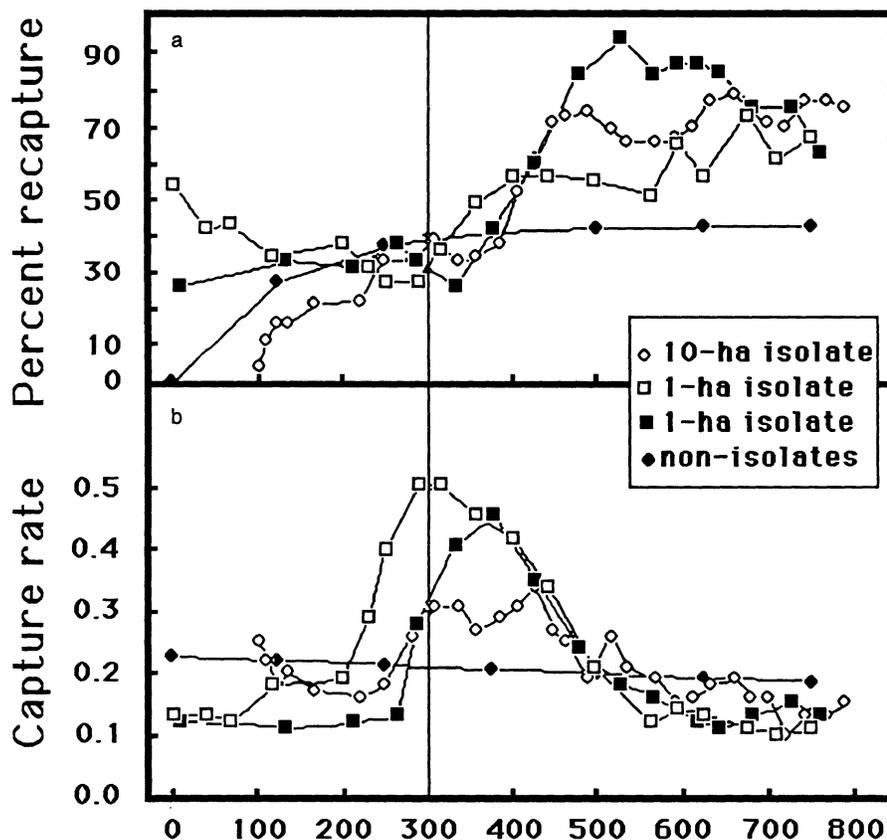


Figure 2. Recapture percentages (a) and capture rates (b), measured in captures per net hour, as a function of time in isolated reserves and continuous forest. Three-point running means of the data from three representative isolated reserves are plotted along with control data from all nonisolated net lines. Isolation is a prolonged process, which was completed approximately 300 days after sampling began, as indicated by the vertical line in both graphs (after Bierregaard and Lovejoy 1988).

forest area.

As forest is felled around a reserve, many birds find sanctuary in the remnant patch of forest (Bierregaard and Lovejoy 1989). After isolation, capture rates increased dramatically in newly isolated forest fragments, indicating both increased activity (movement) of birds in the reserves as well as an increased number of individuals present (Figure 2b). These elevated numbers, which are inversely correlated with fragment size, persist for approximately 200 days, at which point the number of birds in the reserves falls sharply to levels below pre-isolation values. The rate and extent of this faunal collapse are greater in smaller reserves than in larger ones (Bierregaard and Lovejoy 1988).

Avian community structure is most drastically altered in the smallest fragments. Two important ecological guilds, army-ant followers and mixed-species flocks, which represent more than 41% of all mist-net captures in

continuous forest, were dramatically reduced in all 1- and 10-hectare isolates. Three species of birds that obligatorily feed on insects fleeing from swarming army ants (*Eciton burchelli*) disappeared immediately upon isolation from all 1- and 10-hectare fragments (Harper 1987). Over a longer period (1–2 years), the majority of a larger suite of 13 insectivorous species—which forage in complex social units referred to as mixed species flocks (see review by Powell 1985)—disappeared from all the 1- and 10-hectare fragments (Bierregaard and Lovejoy 1989).

Changes in the relative abundances of birds captured in the 100-hectare reserve isolated in 1983 were not as dramatic. During the first year after isolation, the reserve remained connected to continuous forest by a 2-kilometer-long corridor of gallery forest along a small stream, whose headwaters lie within the reserve. The forest corridor varies in width from

100 to 300 m. While the reserve was connected by the corridor, the community structure of understory birds, as measured by our netting program, was indistinguishable from control plots in continuous forest. The three obligate ant-following species disappeared from the reserve almost immediately after we cleared a 250-meter break in the corridor (1.6 km from the reserve) a year after isolation, indicating that not all 100-hectare forest reserves will support populations of army-ant-following birds.

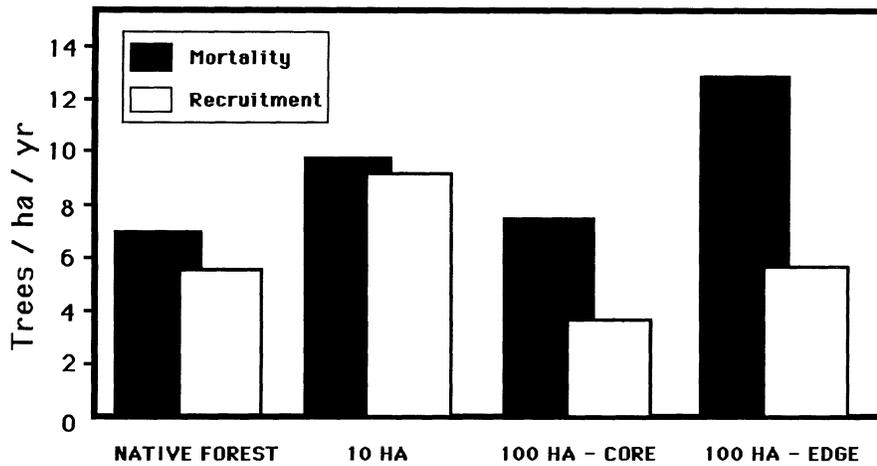
The number of species of primates that persisted in four 10-hectare experimental isolates was lower than in a single 100-hectare isolate (Rylands and Keuroghlian 1988). Additional, casual observations by BDFFP researchers in 1-hectare isolates and the second 100-hectare isolate confirm that primates conform to the predictions of the MacArthur-Wilson model; species number varies directly with fragment size, at least before the regrowth of substantial second growth around the isolates.

### Edge effects and other physical changes

By definition, the periphery of a forest fragment is an edge between forest and nonforest habitat. Changes, both physical and biological, that occur along these edges may affect both form and function of the isolated ecosystem. Increased insolation and wind penetration along a newly formed forest edge can be expected to change temperature and relative humidity in the reserve. Structural damage is likely to occur when storms buffet trees along a forest edge.

Kapos (1989) quantified penetration of microenvironmental changes into recently isolated forest reserves to assess their importance for understory plant water relations and changing evapotranspiration balances. Patterns of temperature, humidity, photosynthetically active radiation (PAR), and soil moisture were measured in transects across 1-hectare isolates and from edge to core of a partially isolated (two sides exposed by clear-cutting) 100-hectare reserve.

Compared to the core of the 100-hectare reserve, temperatures and vapor pressure deficits (VPDs) were higher up to 40 m into the reserves from the edges studied and were also higher in the cores



**Figure 3.** Mortality and recruitment of canopy trees with diameter at breast height of at least 10 cm in native forest and isolated forest fragments. Data from 3 ha along the edge and 3 ha from the core of an isolated 100-hectare reserve and 5 ha from a 10-hectare isolate are compared with control data from native forest (after Rankin-de Mérona et al. 1990).

of 1-hectare isolates. PAR in the understory was higher up to 40 m in from a 100-hectare reserve edge, and soil moisture was lower in the outer 20 m of large and small reserves than in their centers. The depletion of soil water near the edge suggested increased evapotranspiration, which may have been triggered in part by the increase in PAR near the reserve edge. However, no ecophysiological evidence indicated that understory plants suffered a shortage of available water.

Subsequent studies on gradients in relation to older edges (more than 5 years after clear-cut) have shown much more complicated patterns. Air temperature and VPD bore no relation to distance from the edge, and the edge effect on soil moisture was complex.<sup>1</sup> Changes in vegetation structure caused by edge-related tree mortality are likely the major cause of increasing complexity of these microenvironmental gradients. Altered forest structure may also influence regional evapotranspiration budgets and their contribution to rainfall (cf. Salati et al. 1978).

### Biotic changes

Because plants are long-lived and cannot flee changing microclimatic conditions, the first changes in the plant community are expected to be mani-

fested through differential mortality and growth of established individuals and through differential recruitment of seedlings. Through continued monitoring of growth and mortality of individual trees in two isolated reserves (10 and 100 ha) and comparisons with control data from five 1-hectare sample plots in continuous forest (Rankin-de Mérona et al. 1990), the effects of edge formation by forest fragmentation on the community of canopy trees are being assessed. Three separate 1-hectare plots in the core of a 100-hectare isolate, three 1-hectare plots along its edge, and the eastern half of a 10-hectare reserve isolated in 1980 are included in these analyses. Control and 100-hectare reserve samples cover a five-year period, whereas the 10-hectare isolate has been studied for ten years.

Demographic trends indicate a greater flux occurring on the edges of plots in comparison with continuous forest. In the two years after isolation of the 10-hectare fragment, many broken, dead trees were concentrated almost exclusively on the windward margin of the reserve (Lovejoy et al. 1984). Mortality of trees was greatest in the edge plots of the 100-hectare reserve than in the 10-hectare isolate, which in turn showed greater mortality than either the core samples from the 100-hectare isolate or continuous forest (Figure 3). Within the edge plots, the incidence of trees damaged by wind and by other trees was greatest in the

60 m nearest the edge. In another 100-hectare reserve, the proportion of forest area occupied by tree-fall gaps was greatest up to 160 m from a four-year-old edge than in undisturbed forest (Wandelli 1991).

Recruitment (growth) into the smallest size class of trees (10–15 cm diameter at breast height) was greatest in the 10-hectare fragment and lowest in the core of the 100-hectare reserve and continuous forest (Figure 3). There was a net loss of live trees along the edge and in the core of the 100-hectare reserve, where recruitment was significantly less than the total mortality over the five years studied (Figure 3).

The plant community in the lower strata of the forest is also subject to edge-related changes. For example, an understory palm, *Astrocaryum sociale*, was significantly less common near five- to eight-year-old edges than in undisturbed forest (Wandelli 1991). This pattern was probably due to the changes in forest structure near edges; individuals of *A. sociale* near edges were less vigorous than those in undisturbed understory.

Sizer<sup>2</sup> compared the regeneration of woody species along newly created edges of a 100-hectare reserve isolated in 1990 to that in the core of the reserve. All woody seedlings in plots at different distances from the edge of the reserve were tagged and were measured periodically from nine months before until two years after isolation. No edge effect on mortality rates was apparent, but seedling growth increased significantly up to 25 m into the forest. Plants  $\leq 50$  cm tall and those recruited close to the time of edge creation responded most strongly. Growth rates declined exponentially with increased distance from the edge, suggesting that the seedlings are using a resource (such as light) that also declines exponentially with distance from the edge.

Statistically significant changes in seedling recruitment patterns were documented up to 25 m into the forest, with similar, although not significant, tendencies to more than 50 m. Recruitment of pioneer species such as *Cecropia* spp. increased up to 10 m from the edge.

Sizer also showed that litterfall rates

<sup>1</sup>José Luiz Camargo, 1992, personal communication. Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil.

<sup>2</sup>Nigel Sizer, 1992, Ph.D. dissertation in preparation. Cambridge University, Cambridge, UK.

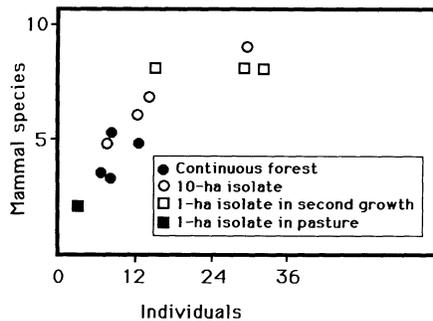
increased dramatically up to 50 m into the reserve after edge creation. The phosphorus content of falling leaves increased up to 10 m from the reserve edge. Very high leaf-fall rates were recorded near the edge after the adjacent felled forest was burned. A year later, the pattern was reversed, with litterfall 100 m into the forest exceeding that near the edge. The sudden loss of large numbers of leaves with high phosphorus content suggests that the adult trees did not have time to mobilize and retract nutrients before dropping their leaves, apparently in response to the proximity of the fire in the adjacent clear-cut. Such a loss of nutrients may play a significant role in the increased mortality of adult trees reported by Lovejoy et al. (1984).<sup>3</sup>

Current models of edge effects are too simplistic, generally describing little more than the ratio of the size of a core area unaffected by edge effects to the size of a peripheral area modified by its exposure to an adjacent, altered habitat (Laurance 1989 in Malcolm 1991a, Temple and Cary 1988). Malcolm (1991a) has proposed a more realistic model that assumes the edge effect decreases curvilinearly with increasing distance from the edge to a point  $D_{MAX}$  where it becomes zero. The total edge effect at any given point less than  $D_{MAX}$  from the edge is the sum of "point" edge effects—not only of the edge closest to the point in question but also, to a decreasing extent, that from all points along the edge  $\leq D_{MAX}$  from the point in question. Therefore, edge effects at corners of reserves are greater than along an external edge because a point near a reserve center is in close proximity to more edge.

Malcolm's measures of vegetation structure in both understory and the canopy of forest fragments fit the model well. Kapos (1989) showed that the relationship between distance from the nearest edge and air temperature and vapor-pressure deficit differed between 1-hectare and 100-hectare fragments, as would be predicted by Malcolm's model.

## Surrounding vegetation

Habitat islands are not strictly comparable to true islands. The surround-



**Figure 4.** Number of species versus number of individuals of small mammals trapped in forest isolates and adjacent continuous forest. Both average species number and number of individuals are greater in 1-hectare isolated reserves surrounded by second growth than in 10-hectare isolates and greater in both sizes of isolates than in continuous forest. The 1-hectare isolate with low species number and low number of individuals is the only one surrounded by pasture with little second growth (after Malcolm 1991a).

ing sea of vegetation is dynamic, changing with natural succession and pasture maintenance, and not completely inhospitable to many of the organisms in the habitat island. Whereas the community structure of primates, understory birds, and some insects seems strongly affected by patch size, small nonvolant mammals and some butterflies are apparently more sensitive to the vegetation structure around the forest fragments than to island size.

Two years after isolation, the relative abundances of species of small mammals in four 1-hectare and four 10-hectare fragments were quite different from those in adjacent continuous forest (Malcolm 1991a). In contrast to the response of understory birds, where population sizes and species numbers declined most dramatically in the smallest fragments, species richness, biomass, and abundances of most small mammal species were greater in 1-hectare than in 10-hectare fragments and higher in both than in continuous forest (Figure 4). In addition, the communities in fragments showed a shift in the vertical distribution of mammalian biomass. In continuous forest, arboreal biomass was slightly greater than terrestrial, whereas the reverse was true in fragments.

Malcolm's (1991a) measurements of foliage structure and insect abundance showed changes parallel to those exhib-

ited by the small-mammal communities; the foliage density and insect abundance were greater in the understory of fragments than in the canopy, whereas the reverse was true in continuous forest. Malcolm related the changes in mammal community structure to these habitat changes and was able to show that a model based on the effects of the creation of forest edge and the vegetation structure of the matrix surrounding the forest accurately explained changes in the mammal community in forest fragments. Insularization effects as such (fragment size and distance to adjacent forest) played no significant role in structuring the communities. Malcolm suggested that the fragments were small enough (10 ha or less) and close enough (1000 m or less) to continuous forest that, for some species, they did not function as true islands, where small mammal communities tend to conform to the predictions of the MacArthur-Wilson model (e.g., Brown 1986 and other references in Heaney and Patterson 1986).

Brown (1991) and Hutchings (1991) have shown that both the size of a forest fragment and the treatment of the surrounding forest after felling affect butterfly communities in forest fragments. The intensity of the fire used to clear the felled forest and the vegetation around the isolate are important determinants of post-isolation community structure. If the fire around a forest fragment was intense, butterfly species number were depressed, perhaps due to fumigation of the reserve by smoke and the subsequent scarcity of regrowth around the reserve. A year later, species numbers returned to pre-isolation levels and continued to increase, with more species found in 10-hectare than in 1-hectare reserves. In reserves where the surrounding forest was felled and not burned or only lightly burned, an exuberant second-growth vegetation began to surround the reserves within months and total butterfly species numbers in 1- and 10-hectare isolates exceeded those encountered in similar areas of continuous forest. Many of the species encountered, however, represented light-loving species that are rare or absent from continuous forest, although sometimes found in large clearings. The complement of some larger or more specialized deep-forest species decreases over several years in 1- and 10-hectare fragments (Brown and Hutchings in press).

<sup>3</sup>Edmund Tanner, 1989, personal communication. Cambridge University, Cambridge, UK.

Although the number of species of birds and euglossine bees in 1- and 10-hectare reserves declined after isolation, both groups increased somewhat from postisolation lows when the surrounding second-growth vegetation around the isolates grew tall enough to have a relatively open understory (Becker et al. 1992, Bierregaard and Lovejoy 1988). The MacArthur-Wilson model predicts such a change; dense second-growth vegetation can be expected to increase colonization, as if the island had moved closer to the mainland.

## Conservation implications

How then can the results of BDFFP be applied to regional conservation planning and ecosystem management? What practical results have we to show after 12 years of research?

Certain limitations in the BDFFP experiment must be recognized from the outset. Both the size range represented by the experimental reserves and the number of replicates are small. Logistical considerations made it impossible to plan to sample a series of reserves larger than 1000 ha, and changes in such reserves would probably be undetectable in normal research time spans. As a result of unforeseeable changes in government policy, only half of the experimental reserves, including neither of the 1000-hectare reserves, have been isolated, and the second 100-hectare reserve was only isolated in 1990.

Because the experimentally isolated reserves of BDFFP are three to four orders of magnitude smaller than the size generally accepted as adequate for national parks in the Amazon ( $10^5$ – $10^6$  ha; Terborgh 1974, Thiollay 1989), we cannot extrapolate our species/area results quantitatively to issues associated with such large protected areas. However, because it is safe to assume that the vast majority of the Amazon basin will be subjected to development rather than being set aside in large, protected areas, we can expect much of the currently extensive rainforest to be changed to the landscape mosaic typically created by organized or spontaneous colonization, replete with forest fragments of the size under study by BDFFP.

Given this scenario, data from BDFFP on the mechanisms by which

fragmentation affects the rainforest ecosystem become directly relevant to the future of vast areas of Amazonia. There is no other body of data being generated on the biotic and abiotic changes that are caused by fragmentation of Amazonian rainforests. For all their shortcomings, these are the only regionally collected data available with which to address habitat fragmentation issues in the Amazon basin.

Is the MacArthur-Wilson island biogeography model appropriate when discussing habitat islands of 1–100 ha? A major weakness of the MacArthur-Wilson model is that all species are treated equally; immigration and extinction probabilities are the same for all species (Lovejoy and Oren 1981). In nature, the different species have different tendencies to disperse (e.g., migratory versus nonmigratory species) and require different-sized home ranges or territories. Such differences should affect the likelihood that certain species will arrive and persist on an island or in an isolated, protected area. For example, obligate army-ant-following birds are far more susceptible to extinction in small reserves than are closely related species that require far smaller home ranges (Bierregaard and Lovejoy 1988, Harper 1987).

Reserve planning requires this type of detailed knowledge of the ecology and specific habitat requirements of target species. For example, Zimmerman and Bierregaard (1986) pointed out that because critical breeding habitat for several species of frogs is not randomly distributed in undisturbed forest, a prediction of the minimal size of a forest reserve necessary to preserve these species cannot be based on the simple paradigms of the MacArthur-Wilson model.

How might BDFFP data be applied in government-controlled colonization projects? Is the current scenario—of giving out 100- to 200-hectare lots to colonists and requiring that each leave half of the lot in forest reserve—an adequate model to preserve forest-dwelling flora and fauna? BDFFP data confirm that the forest remnants in such a mosaic would suffer significant alteration by edge effects and lose certain species of birds, monkeys, and perhaps important insect pollinators and coprophagous insects. Nonetheless, a landscape with such impoverished remnants

would clearly be better than one with none at all.

A high percentage (approximately 90%) of forest tree species in Paragominas, Brazil, depends on animals to disperse their seeds, and few potential dispersal agents are likely to carry seeds far into large open tracts (Uhl et al. 1988). Consequently, forest remnants would serve as important catalysts for forest regeneration.

Ideally, smaller fragments should be connected by forest corridors and the landscape should include one or more forest tracts larger than 1000 ha. Plantation forests for the harvest of fruits or other forest products would protect the edges of preserved areas and eventually encourage seed dispersal from the forest reserves.

Studies of habitat fragmentation have taken on an undeniable urgency. Ability to strike a balance between the need of tropical countries to use their forested land and the need to preserve their forests will depend in no small part on the understanding of forest fragments. The established infrastructure of forest fragments under long-term study as well as the control areas in undisturbed forest, both with easy access to Manaus and the researchers and facilities of INPA, make BDFFP a unique opportunity for the study of the natural history, dynamics, and conservation of tropical rainforest ecosystems.<sup>4</sup>

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<sup>4</sup>The BDFFP directors are eager to include new research initiatives under the auspices of the program and welcome inquiries addressed to the senior author of this article.

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