Effects of Forest Fragmentation on Recruitment Patterns in Amazonian Tree Communities

William F. Laurance; Leandro V. Ferreira; Judy M. Rankin-De Merona; Susan G. Laurance; Roger W. Hutchings; Thomas E. Lovejoy

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WILLIAM F. LAURANCE,* LEANDRO V. FERREIRA, JUDY M. RANKIN-DE MERONA,
SUSAN G. LAURANCE, ROGER W. HUTCHINGS, AND THOMAS E. LOVEJOY

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

Introduction

Fragmentation can alter the ecology of rain forest remnants in many ways, but its long-term effects on tree communities are poorly understood. One phenomenon that has received little attention is tree regeneration in fragmented forests (Janzen 1983; Viana et al. 1997). Patterns of regeneration are important because they will ultimately determine the floristic composition of the remnant. Janzen (1983) suggested that fragments of tropical dry forest in Costa Rica are prone to invasions of weedy, generalist plant species from the surrounding modified matrix, which could progressively alter the floristic composition of remnants. Laurance (1991, 1997) proposed that fragments in some tropical regions are chronically disturbed by winds and other factors and may exhibit a general shift toward successional trees, lianas, and vines adapted for recurring disturbance.

Using data collected over 13 years, we describe patterns of tree recruitment in a fragmented landscape in central Amazonia. We ask three questions: (1) Do rates of tree recruitment differ between fragmented and continuous forests? (2) Are recruitment rates influenced by fragment area, age, and proximity of forest edge? (3) Are regenerating trees in fragments biased toward successional species or against old-growth species?

Methods

Study Area

The study area (Fig. 1) is located 70 km north of Manaus in central Amazonia (2°30'S, 60°W) at 100–150 m eleva-

*email wfl@inpa.gov.br

tion. Local soils are poor in nutrients. Rainfall ranges from 1900 to 2500 mm annually, with a dry season from June to October. The forest canopy is 30–37 m tall, and tree diversity is very high (Rankin-de Mérona et al. 1992).

The study area is surrounded by large expanses of continuous forest. In the early 1980s a series of 1-, 10-, and 100-ha fragments were isolated by distances of 70–1000 m from surrounding forest by clearing and often burning the intervening vegetation to establish cattle pastures. Reserves ranging from 1 to 1000 ha in area were delineated in nearby continuous forest to serve as experimental controls. Regrowth forests have regenerated in some cleared areas and are dominated by *Cecropia* spp. and *Vismia* spp.

Study Design

From 1980 to 1986, inventories of all trees of 10 cm diameter at breast height (dbh) or more were conducted in 66 square, 1-ha plots in the study area (Rankin-de Merona et al. 1992). All trees were marked with numbered tags, mapped, and identified at least to family level using sterile or fertile material. Each plot was recensused two to five times between 1985 and 1992, during which all new trees of 10 cm dbh or more were marked, mapped, and identified to family level (Rankin-de Merona et al. 1992).

Of the 66 plots, 39 were located in forest fragments and 27 in continuous forest (controls). The fragment plots were in four 1-ha fragments (4 plots), three 10-ha fragments (17 plots), and two 100-ha fragments (18 plots), whereas the control plots were in six 1-ha (6 plots), one 10-ha (3 plots), one 100-ha (9 plots), and one 1000-ha (9 plots) reserves. Plots within fragments were stratified so that edge and interior areas were both sampled.

We devised three landscape predictors for each plot: (1) distance to the nearest forest edge (measured from
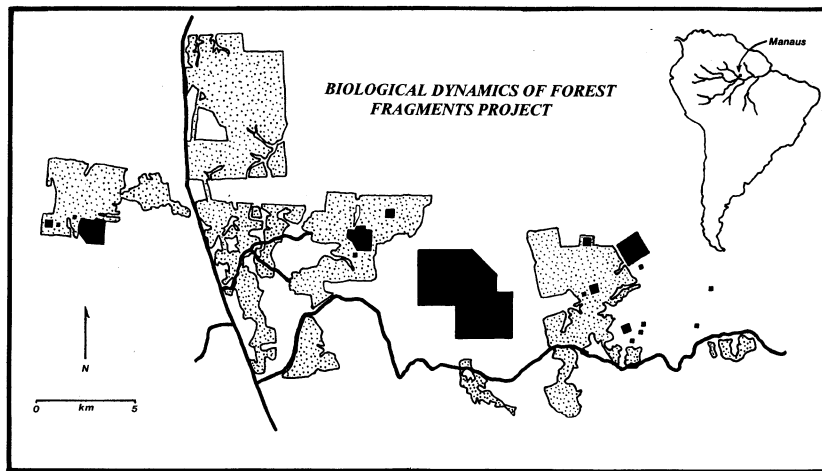
Figure 1. Study area in central Amazonia, showing locations of forest fragments and controls (shaded blocks) used in this study. Stippled areas are cattle pastures or regrowth forest, and unstippled areas are rain forest.

the center of the plot); (2) fragment area; and (3) fragment age (number of years since isolation). Plots were pooled into categories to simplify analysis. There were four categories for edge distance (1 = $\leq$60 m; 2 = 61–100 m; 3 = 101–500 m; 4 = >500 m) and fragment area (1 = 1 ha; 2 = 100 ha; 3 = 100 ha; 4 = controls) and three categories for fragment age (1 = controls; 2 = <5 years; 3 = >5 years). The rationale for the edge-distance categories is that microclimatic changes can occur within 60 m of edges in the study area (Kapos 1989), whereas wind disturbance may be pronounced within 100–200 m of edges and detectable up to 500 m from edges, at least in some Australasian forests (Laurance 1991).

Successional versus Old-Growth Trees

Several tree families in the study area are dominated by either pioneer and secondary species or old-growth species (Nee 1995; R. Mesquita, personal communication). We selected five major successional families (Annonaceae, Cecropiaceae, Clusiaceae, Euphorbiaceae, Malpighiaceae) and four major old-growth families (Burseraceae, Chrysobalanaceae, Lecythidaceae, Sapotaceae) to assess patterns of recruitment in our plots; these two groups represented 18% and 30% of all new trees, respectively. To avoid bias due to small sample sizes, only plots and census intervals with at least 20 trees were included in the analysis. Data were expressed as the percentage of new trees per plot and arcsine-transformed prior to analysis.

Statistical Analysis

The mean annual rate of tree recruitment was calculated using a logarithmic model: $r = (N_t/N_o)^{1/t}$, where N_o is the number of trees at beginning of interval, N_t is the number of trees at end of interval, and t is the number of

years (Sheil et al. 1995). Recruitment estimates are not independent of census interval, however, because during longer intervals a larger fraction of trees will enter the 10-cm dbh size class but die before being censused (Sheil & May 1996). To help compensate for this effect, we plotted the census interval and estimated recruitment rate for sites in natural forest (plots located >150 m from forest edge; Fig. 2). An exponential curve was fitted to these data and used to adjust all census intervals to 5 years, the recommended standard for permanent plots (Sheil et al. 1995). The adjustment was achieved by subtracting the predicted from the observed recruitment rate for each observation, then adding the predicted value for 5 years.

One-way analyses of variance (ANOVAs) were used to assess treatment effects on the adjusted recruitment rates. Rates were log-transformed prior to analysis to reduce heteroscedasticity among samples. Tukey's HSD tests were used to compare sample means, where appropriate. When performing the ANOVAs we assumed
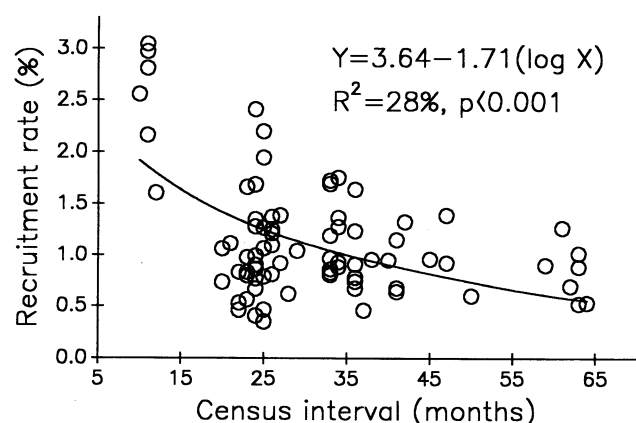

Figure 2. Relationship between length of census interval and estimates of annual recruitment rates of trees in continuous forest.

that treatment effects were greater than effects of plot or site, and we analyzed the repeated measures as independent samples. Use of repeated-measures ANOVA (Sokal & Rohlf 1995) was not possible because the experimental landscape we studied was dynamic, and variables describing fragment area and edge-distance frequently changed during repeated measures of the same study plot.

Results

Recruitment Rates

Mean recruitment rates were higher in forest fragments than in continuous forest (Fig. 3a). On average the rate in 1-ha fragments (2.60 ± 0.45%) was more than twice that in continuous forest (1.16 ± 0.07%), whereas those in 10-ha (1.74 ± 0.16%) and 100-ha (1.57 ± 0.17%) fragments were also markedly higher than in those continuous forest ($\overline{X}$ ± SE). Rates were significantly higher in 1-ha fragments than in controls ($p < 0.01$), 10-ha fragments ($p < 0.05$), and 100-ha fragments ($p < 0.05$), and they were higher in 10-ha fragments than in controls ($p < 0.10$; Table 1).

Recruitment rates also increased with fragment age (Fig. 3b). The mean rate in younger fragments (1.47 ± 0.13%) was 27% higher than in controls (1.16 ± 0.07%), whereas that in older fragments (1.95 ± 0.16%) was 68% higher than controls. The difference between older fragments and controls was highly significant ($p < 0.01$), whereas the other comparisons were nonsignificant (Table 1).

Recruitment rates were markedly elevated near forest edges (Fig. 3c). Plots within 100 m of edges (0–60 m: 2.13 ± 0.22%; 61–100 m: 1.75 ± 0.16%) had mean rates
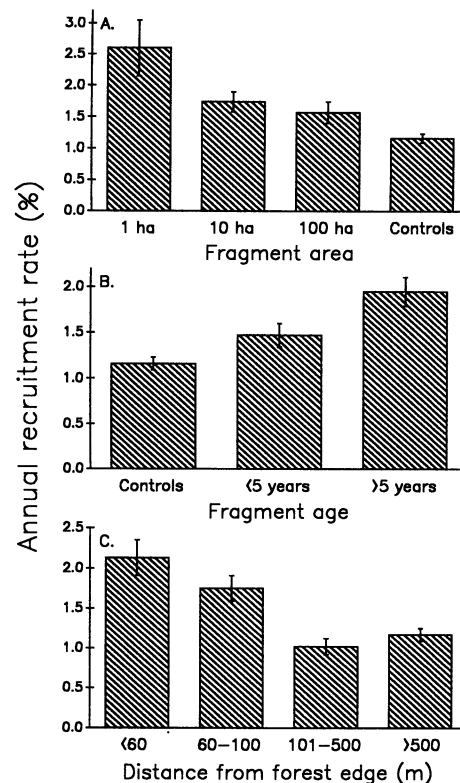
Figure 3. Effects of fragment area, age, and proximity of forest edge on annual tree recruitment rates ($\overline{X}$ ± SE).

about twice those further from edges (101–500 m: 1.02 ± 0.10%, >500 m: 1.17 ± 0.08%); these differences were highly significant (Table 1). Many edge plots had sharply elevated recruitment; for example, 18% (18/98) of the censuses within 100 m of edges yielded annual recruitment rates of 2–7%, whereas none (0/82) of the forest-interior censuses exceeded 2%.

Floristic Patterns

The proportions of successional and old-growth families varied roughly linearly with recruitment rate (Fig. 4). Samples with high rates tended to have many successional trees and fewer old-growth trees, and those with low rates exhibited opposite trends. These relationships were highly significant (successional trees: $F_{1,62} = 25.59$, $p < 0.0001$; old-growth trees: $F_{1,62} = 8.89$, $p = 0.004$).

In terms of landscape predictors, the proportion of successional trees was significantly higher in 1-ha fragments than controls, in older fragments than controls, and at sites less than 60 m from edges than controls (Table 2). For old-growth trees, area and proximity to edge had no significant effects, but older fragments had significantly lower proportions of old-growth trees than did younger fragments and controls (Table 2).

Table 1. Summary of one-way analysis of variance used to test the effects of fragment area, age, and proximity to edge on annual recruitment rates of trees in central Amazonia.

Factor*	F	p	Tukey's tests
Area	6.92	0.0002	1-ha fragments > controls ($p < 0.01$); 1-ha fragments > 10- and 100-ha fragments ($p < 0.05$); 10-ha fragments > controls ($p < 0.10$)
Age	8.24	0.0005	older fragments > controls ($p < 0.01$)
Edge	9.90	<0.0001	<60 -m from edges > 101–500 m and > 500 m from edges ($p < 0.01$); 60–100 m from edges 101–500 m and < 500 m from edges ($p < 0.05$)

*Recruitment rates were log-transformed prior to analyses. Sample sizes: fragment area, 1 ha = 14, 10 ha = 63, 100 ha = 33, controls = 70; fragment age, controls = 70, younger fragments = 34, older fragments = 76; disance from edge: <60 m = 38, 60–100 m = 60, 101–500 m = 21, >500 m = 61.
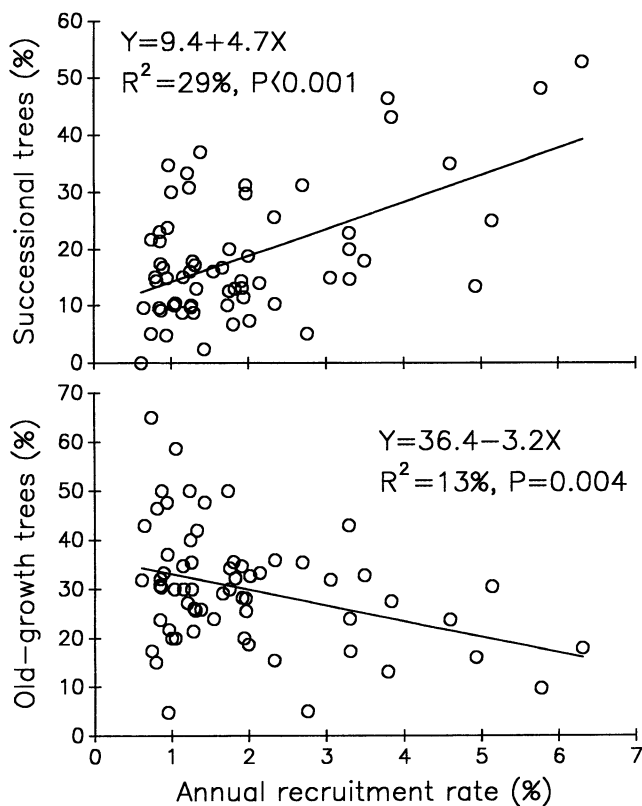
Figure 4. Relationships between annual recruitment rate and proportions of successional and old-growth tree families in study plots.

Table 2. Summary of one-way analysis of variance used to test the effects of fragment age, area, and proximity to edge on the proportions of trees in successional and old-growth categories regenerating in study plots.

Factor*	F	p	Tukey's tests
Successional trees			
Area	3.43	0.022	1-ha fragments > controls ($p < 0.05$)
Age	3.41	0.039	older fragments > controls ($p < 0.05$)
Edge	2.81	0.067	<60 m from edges > controls ($p < 0.10$)
Old-growth trees			
Area	0.97	0.414	—
Age	3.43	0.038	controls and younger fragments > older fragments ($p < 0.10$)
Edge	2.22	0.115	—

*Percentage data were arcsine-transformed prior to analyses. Sample sizes: fragment area, 1 ha = 10, 10 ha = 20, 100 ha = 17, controls = 17; fragment age; controls = 17, younger fragments = 13, older fragments = 34; distance to edge: <60 m = 24, 60-100 m = 22, >100 m = 18.

Discussion

Tree Recruitment Rates

Our results suggest that rates of tree recruitment are markedly elevated in Amazonian forest fragments. Relative to continuous forest, mean rates were sharply increased in 1-ha fragments (by 224%) and moderately increased in fragments of 10-100 ha (by 35-50%).

Recruitment rates were highest within 100 m of forest margins, which suggests that the growth of young trees is directly linked to increased tree mortality and canopy disturbance near edges. In the same study area, Ferreira and Laurance (1997) and Laurance et al. (1997, in press) showed that mortality and damage rates of large (≥10 cm dbh) trees were sharply elevated within 100 m of forest margins, apparently as a result of increased wind turbulence and microclimatic changes near edges. In closed-canopy forests, light is strongly limiting to small trees, and many species are adapted for growing rapidly in treefall gaps (Clark 1990). In this study, young trees may also have responded positively to lateral light penetration along fragment margins (Lovejoy et al. 1986).

Older fragments (>5 years) had much higher recruitment (68%) than continuous forest, whereas younger fragments had moderately higher recruitment (27%). This pattern may be partly an artifact of the study design; trees regenerating from seeds or saplings would require several years to reach the 10-cm dbh threshold used in this study. It is also possible that these fragments became increasingly disturbed over time. This could occur, for example, because winds form complex vortices in treefall gaps, which cause further forest damage (Reville et al. 1990), and because the lateral growth of tree crowns at gap margins makes trees lopsided and prone to falling (Young & Hubbell 1991).

Floristic Composition of Fragments

The regression models (Fig. 4) suggest that areas experiencing high tree recruitment were biased toward successional tree families and against old-growth families. These patterns must be interpreted cautiously, both because the selected families accounted for only half of all trees in the study area and because there may be substantial variation in life histories among species in a single family. Our findings nevertheless support our intuitive expectations: successional trees increased in older and smaller fragments and in plots near forest edges, whereas old-growth trees declined in older fragments. Successional trees may increase in fragments both because recurring disturbances provide light and microclimatic conditions that favor their germination and growth (Clark 1990) and because of a heavy seed rain from pioneer species growing in the surrounding matrix (Janzen 1983; Willson & Crome 1989). In our study area, pioneer trees such as *Cecropia* spp. and *Vismia* spp.,

which dominate local regrowth forest, increased sharply in rain forest near edges (Sizer 1992).

This study documents some short-term (<13 years) effects of fragmentation on tree communities. Over time, additional floristic changes will probably accumulate in fragments, such as the loss of vulnerable species like short-lived shrubs and epiphytes (Turner et al. 1996), a proliferation of lianas and vines (Laurance 1991; Viana et al. 1997), and invasions of exotic weeds (Turner et al. 1996; Laurance 1997). Studies of forest remnants isolated for a century or more are needed to provide insights into the longer-term effects of fragmentation on tropical floras (e.g., Turner et al. 1996).

Acknowledgments

Literature Cited

Clark, D. B. 1990. The role of disturbance in the regeneration of Neotropical moist forests. Pages 291–315 in K. S. Bawa and M. Hadley, editors. Reproductive ecology of tropical forest plants. United Nations Educational Scientific and Cultural Organization, Paris.

Ferreira, L. V., and W. F. Laurance. 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. Conservation Biology **11:**797–801.

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. Journal of Tropical Ecology **5:**173–185.

Laurance, W. F. 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. Biological Conservation **57:**205–219.

Laurance, W. F. 1997. Hyper-disturbed parks: edge effects and the ecology of isolated rainforest reserves in tropical Australia. Pages 71–83 in W. F. Laurance and R. O. Bierregaard, Jr., editors. Tropical forest remnants: ecology, management and conservation of fragmented communities. University of Chicago Press, Chicago.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, and S. G. Laurance. In press. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology.

Laurance, W. F., S. G. Laurance, L. V. Ferreira, J. M. Rankin-de Merona, C. Gascon, and T. E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. Science **278:**1117–1118.

Lovejoy, T. E., et al. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Nee, M. 1995. Preliminary flora for the Biological Dynamics of Forest Fragments Project. New York Botanical Garden, Bronx.

Rankin-de Merona, J. M., J. M. Prance, R. W. Hutchings, M. F. Silva, W. A. Rodrigues, and M. E. Uehling. 1992. Preliminary results of a large-scale inventory of upland rain forest in the Central Amazon. Acta Amazonica **22:**493–534.

Reville, B. J., J. D. Tranter, and H. D. Yorkston. 1990. Impact of forest clearing on the endangered seabird *Sula abbotti.* Biological Conservation **51:**23–38.

Sheil, D., D. Burslem, and D. Alder. 1995. The interpretation and misinterpretation of mortality rate measures. Journal of Ecology **83:**331–333.

Sheil, D., and R. M. May. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. Journal of Ecology **84:**91–100.

Sizer, N. C. 1992. The impact of edge formation on regeneration and litterfall in a tropical rain forest fragment in Amazonia. Ph.D. thesis. University of Cambridge, Cambridge, United Kingdom.

Sokal, R. R., and F. H. J. Rohlf. 1995. Biometry. 3rd edition. W. H. Freeman, San Francisco.

Turner, I. M., K. S. Chua, J. Ong, B. Soong, and H. Tan. 1996. A century of plant species loss from an isolated fragment of lowland tropical rain forest. Conservation Biology **10:**1229–1244.

Viana, V., A. Tabanez, and J. Batista. 1997. Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. Pages 351–365 in W. F. Laurance and R. O. Bierregaard, Jr., editors. Tropical forest remnants: ecology, management and conservation of fragmented communities. University of Chicago Press, Chicago.

Willson, M. F., and F. H. J. Crome. 1989. Patterns of seed rain at the edge of a tropical Queensland rain forest. Journal of Tropical Ecology **5:**301–308.

Young, T. P., and S. P. Hubbell. 1991. Crown asymmetry, treefalls, and repeat disturbance in a broad-leaved forest. Ecology **72:**1464–1471.