

RAIN FOREST FRAGMENTATION AND THE DYNAMICS OF AMAZONIAN TREE COMMUNITIES

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Abstract. Few studies have assessed effects of habitat fragmentation on tropical forest dynamics. We describe results from an 18-yr experimental study of the effects of rain forest fragmentation on tree-community dynamics in central Amazonia. Tree communities were assessed in 39 permanent, 1-ha plots in forest fragments of 1, 10, or 100 ha in area, and in 27 plots in nearby continuous forest. Repeated censuses of >56 000 marked trees (≥ 10 cm diameter at breast height) were used to generate annualized estimates of tree mortality, damage, and turnover in fragmented and continuous forest.

On average, forest fragments exhibited markedly elevated dynamics, apparently as a result of increased windthrow and microclimatic changes near forest edges. Mean mortality, damage, and turnover rates were much higher within 60 m of edges (4.01, 4.10, and 3.16%, respectively) and moderately higher within 60–100 m of edges (2.40, 1.96, and 2.05%) than in forest interiors (1.27, 1.48, and 1.15%). Less-pronounced changes in mortality and turnover rates were apparently detectable up to ~ 300 m from forest edges. Edge aspect had no significant effect on forest dynamics. Tree mortality and damage rates did not vary significantly with fragment age, suggesting that increased dynamics are not merely transitory effects that occur immediately after fragmentation, while turnover rates increased with age in most (8/9) fragments.

These findings reveal that fragmentation causes important changes in the dynamics of Amazonian forests, especially within ~ 100 m of habitat edges. A mathematical “core-area model” incorporating these data predicted that edge effects will increase rapidly in importance once fragments fall below ~ 100 –400 ha in area, depending on fragment shape. Accelerated dynamics in fragments will alter forest structure, floristic composition, biomass, and microclimate and are likely to exacerbate effects of fragmentation on disturbance-sensitive species.

Key words: Amazon rain forest; deforestation; edge effects; forest dynamics; habitat fragmentation; tree mortality and turnover; wind disturbance.

INTRODUCTION

The rate of tropical deforestation exceeds 15×10^6 ha annually, resulting in extensive fragmentation of forest landscapes (Whitmore 1997). Although research on fragmented tropical forests is increasing (Schelhas and Greenberg 1996, Laurance and Bierregaard 1997), few studies have assessed effects of fragmentation on the dynamics of tree communities. Trees largely determine the architecture and microclimatic conditions of the forest, and hence changes in tree-community dynamics may strongly affect other forest species (Brokaw 1985, Levey 1988, Clark 1990) and ecological processes (Powell and Powell 1987, Klein 1989, Didham et al. 1996).

In recently fragmented forests, edge effects appear to be a major cause of change in plant communities. In rain forests the harsh external climate is buffered by

dense canopy cover, but this buffering breaks down near forest edges (Kapos 1989, Williams-Linera 1990) and may lead to higher mortality of desiccation-sensitive plants (Lovejoy et al. 1986, Sizer 1992, Kapos et al. 1997). Strong turbulence can result when winds strike abrupt forest edges, increasing rates of windthrow and forest structural damage (Laurance 1991, 1997, Ferreira and Laurance 1997). Fragmented rain forests often exhibit a proliferation of vines, lianas, and secondary vegetation near edges (Laurance 1991, Turner and Tan 1992, Malcolm 1994, Viana et al. 1997), and some seasonal forests appear highly prone to invasions of exotic plants (Fensham et al. 1994, Laurance 1997).

In central Amazonia, a long-term study of rain forest fragments experimentally isolated in the early 1980s (Lovejoy et al. 1986, Bierregaard et al. 1992) has begun to yield insights into the dynamics of fragmented tree communities. Working with a single tree family (Myrtaceae), Ferreira and Laurance (1997) found sharply elevated rates of tree mortality and damage within ~ 100 m of forest-pasture edges. Laurance et al.

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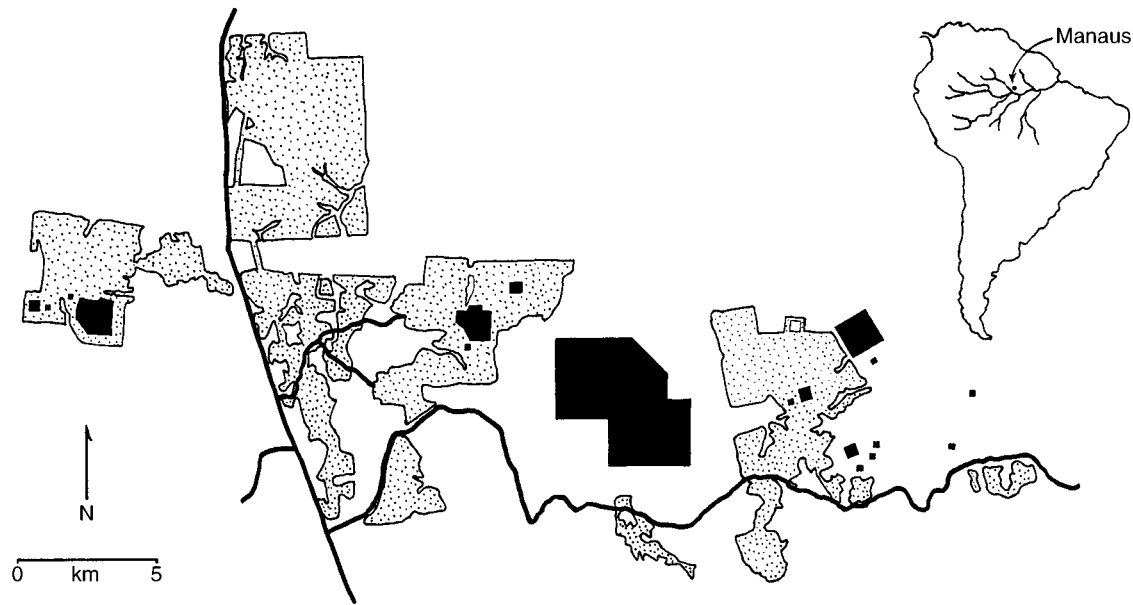


FIG. 1 Study area in central Amazonia, showing locations of forest fragments and controls (shaded blocks) used in the study. Stippled areas are cattle pastures or regrowth forest, while unstippled areas are rain forest. Thick, solid lines are roads.

(1998a) detected a marked increase in tree recruitment rates within ~ 100 m of edges, and found that regenerating trees in study plots with high recruitment were biased toward families with many pioneer and secondary species, and against families of old-growth, forest-interior species.

Here we present a large-scale analysis of tree-community dynamics in recently fragmented rain forests, using data collected over an 18-yr period. We focus on three vital rates, tree mortality, tree damage, and tree turnover, which we compare in fragments of various sizes to adjacent continuous forest.

METHODS

Study area

The study area is located ~ 80 km N of Manaus, Brazil in central Amazonia ($2^{\circ}30'$ S, 60° W), at 100–150 m elevation. Local soils are nutrient poor. Rainfall ranges from 1900–2500 mm annually with a dry season from June to October. The forest canopy is 30–37 m tall, with emergents to 55 m. Species richness of trees is very high and can exceed 250 species (≥ 10 cm dbh) per hectare (Rankin-de Merona et al. 1992).

The study area is surrounded by large expanses (>200 km) of continuous forest to the west, north, and east. In the early 1980s, a series of 1-, 10-, and 100-ha fragments (Fig. 1) were isolated by distances of 70–1000 m from surrounding forest by clearing the intervening vegetation to establish cattle pastures. Fragments were fenced to prevent encroachment by cattle. Reserves ranging from 1–1000 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/or *Vismia* spp.

Study design

From 1980 to 1986, inventories of all trees of ≥ 10 cm dbh were conducted in 66 square 1-ha plots in the study area (Rankin-de Merona et al. 1992). Trees in each plot were marked with numbered aluminum tags and mapped. All trees were identified to family, genus, or species level using sterile or fertile material from each tree. Each plot was recensused two to five times between 1985 and 1997, during which all new trees of ≥ 10 cm dbh were marked, mapped, and identified to at least family level. All dead or severely damaged trees (living trees with broken crowns or snapped boles) of ≥ 10 cm dbh also were recorded during recensuses.

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), while the control plots were in six 1-ha (6 plots), one 10-ha (3 plots), one 100-ha (9 plots), and one 1000-ha reserves (9 plots). Control plots were lumped into a single sample for most analyses, not treated as separate reserves. Plots within fragments were stratified so that edge and interior areas were both sampled.

We recorded three landscape variables for each plot: (1) distance to the nearest forest edge (measured from the center of the plot); (2) fragment area; and (3) fragment age (number of years since isolation). Plots were pooled into treatment classes to assess effects of edge distance and area, given that the number of plots was limited (distance to edge: ≤ 60 , 61–100, 101–500,

>500 m; fragment area: 1, 10, 100 ha, controls). The distance-to-edge categories were based on previous studies showing that microclimatic changes in the study area can occur within 60 m of forest edges (Kapos 1989), while wind disturbance increases markedly within ~100 m of edges (Kapos 1989, Ferreira and Laurance 1997, Laurance et al. 1997) and may be detectable up to 500 m from edges, at least in some Australasian forests (Laurance 1991).

Because our study area receives convectional windstorms and prevailing easterly winds (B. Nelson, *personal communication*), which could increase rates of forest disturbance, we assessed effects of edge aspect for plots within 100 m of edges. Forest dynamics were compared among edges with four types of aspects, eastern (45–135°), northern (315–45°), western (225–315°), and southern (135–225°), and also between eastern edges and those with all other aspects.

Statistical analysis

For each plot and census interval, mean annual rates of tree mortality and damage were calculated as $r = 1 - (N_t/N_0)^{1/t}$, where N_0 = number of trees at beginning of interval, N_t = number of living or undamaged trees at end of interval, and t = number of years (Sheil et al. 1995). Following the procedure of Philips and Gentry (1994), annual turnover rates for each plot and census were calculated as (mortality rate + recruitment rate)/2, using recruitment-rate data for 1980–1992 presented in Laurance et al. (1998), augmented with unpublished data for 1993–1997. Half-lives of tree communities (the time required for 50% of the stems to die) were estimated as $t(0.5) = -\ln(2)/\ln(1 - m)$, where m is annualized mortality rate (Sheil et al. 1995).

Estimates of forest dynamics (mortality, damage, recruitment, and turnover rates) from permanent plots may not be independent of the length of census interval (Sheil and May 1996). We therefore tested for associations between census interval (number of months between successive censuses) and forest dynamics with Spearman rank correlations, using data from plots in forest interiors (>500 m from forest edge).

To assess effects of fragment age, we used linear regressions to determine whether dynamics indices increased or declined over time in each fragment. For 10- and 100-ha fragments, data from multiple plots were averaged, using only plots within 100 m of edges, which were most prone to fragmentation effects. For each index, the ratio of positive to negative regression-slope coefficients from the nine fragments was compared using sign tests.

To assess effects of fragment area, proximity to edge, and edge aspect, we pooled data from repeated censuses of each plot to derive an overall mean for each dynamics index (to calculate means, census values were weighted by census duration, so that longer intervals were given proportionately greater weight). We then used one-way ANOVAs to assess treatment effects, fol-

lowed where appropriate by Tukey's HSD tests to contrast sample means. Dynamics indices were $\log(X + 1)$ -transformed prior to analysis to help normalize data and reduce heteroscedasticity. Bartlett's tests were used to test for homogeneity of variances. The one-way ANOVAs were probably conservative tests of our null hypothesis of no treatment effects because the error term for each test was probably inflated by between-site (fragment) variation, which would tend to depress the F statistics. However, two-way ANOVAs, with treatment and site as random factors, were inadvisable because it was impossible with our unbalanced study design to test for interactions between factors; consequently, post hoc comparisons of treatment effects could be contingent upon the site variables (Sokal and Rohlf 1995).

The maximum detectable distance to which edge effects penetrate into forest interiors was estimated by plotting each dynamics index against distance to forest edge, using double-log axes, then fitting a three-parameter negative exponential equation:

$$\begin{aligned} \log(\text{dynamics index}) \\ = B1 + B2 \exp[B3 \log(\text{distance to edge})] \end{aligned} \quad (1)$$

where B1 is the baseline value of the index in forest interiors, B2 is the maximum value for the index, just at the forest edge, and B3 indicates how fast the edge effect attenuates with increasing distance from edge. Fitted values were derived using a maximum-likelihood procedure for nonlinear models in Systat (Wilkinson 1986). A curve was generated for each dynamics index, then compared to 95% confidence limits for the index based on forest-interior plots (>500 m from edge). The point at which the curve exceeded the upper 95% limit for forest-interior plots was defined as the maximum penetration-distance for the edge effect.

A mathematical core-area model (Laurance 1991, Laurance and Yensen 1991) was used to predict the impacts of edge effects on fragments of varying sizes and shapes. The model generates accurate (>99%) predictions of the size of unaffected core area for any fragment, using three parameters: a fragment shape-index (SI), fragment area (TA), and empirical knowledge of the distance (d) to which edge effects penetrate into fragments.

RESULTS

Landscape variables and forest dynamics

Length of census interval had no significant effect on tree mortality ($r_s = 0.133$, $P = 0.29$), damage ($r_s = -0.183$, $P = 0.15$), and turnover ($r_s = -0.237$, $P = 0.06$) in continuous forest (Spearman rank tests, $n = 65$). Therefore, no attempt was made to partial out effects of variation in census interval prior to comparing treatments.

Fragment age did not significantly affect mortality and damage rates (Fig. 2), although in both cases more

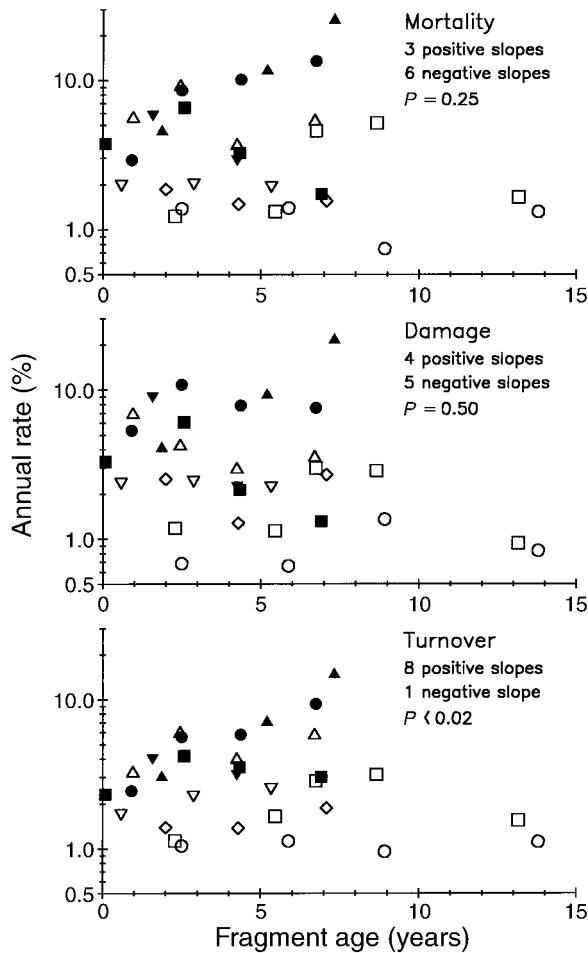


FIG. 2. Effects of fragment age on annualized tree mortality, damage, and turnover rates in nine forest remnants in central Amazonia. Values for fragment age are the means of each census interval. Key to symbols: 1-ha fragments, open circles (fragment no. 1104), filled circles (no. 2107), open triangles (no. 2108), filled triangles (no. 3114); 10-ha fragments, open squares (no. 1202), filled squares (no. 2206), open inverted triangles (no. 3209); 100-ha fragments, filled inverted triangles (no. 2303), open diamonds (no. 3304).

fragments had negative than positive slopes, indicating a weak tendency for mortality and damage rates to decline with fragment age. Turnover, however, increased with age in eight of the nine fragments (Fig. 2); this ratio deviated significantly from chance expectation ($P < 0.02$, sign test).

Fragments in the 1- and 10-ha size classes had higher mortality than controls (Table 1, Fig. 3), and 1-ha fragments also had greater mortality than 10- and 100-ha fragments. Damage rates were higher in 1-ha fragments than in larger fragments and controls, and in 100-ha fragments than controls. Turnover rates were higher in both 1- and 10-ha fragments than controls.

Mortality was significantly greater within 100 m of edges than in controls, and also higher within 60 m of edges than 101–500 m of edges (Table 1, Fig. 3). Dam-

age rates were higher within 60 m of edges than in all other edge-distance categories. Turnover rates were higher within 100 m of edges than controls, and within 60 m of edges than 60–100 and 101–500 m of edges.

To determine whether differences between fragmented and continuous forest were principally due to edge effects (Fig. 4), we excluded all plots within <150 m of forest edges, then compared dynamics indices between the interiors of fragments ($n = 7$) and controls ($n = 26$). Although indices were somewhat higher in fragment interiors, none of the differences was significant (mortality: $F_{1,31} = 3.59$, $P = 0.07$; damage: $F_{1,31} = 1.47$, $P = 0.14$; turnover: $F_{1,31} = 1.34$, $P = 0.26$; one-way ANOVAs).

Among plots near edges, edge aspect had no significant effect on forest dynamics, both when the four cardinal aspects were compared and when eastern edges were compared to all other aspects (Table 2). Results were similar when edge distance was included as a covariate for each plot.

Correlations among indices

At the level of individual plots, annualized rates of tree mortality and damage were only moderately correlated ($r_s = 0.452$, $P = 0.0001$). The rate of tree recruitment was also moderately correlated with mortality ($r_s = 0.538$, $P < 0.0001$), and more strongly correlated with damage ($r_s = 0.725$, $P < 0.0001$). Turnover was much more strongly correlated with mortality ($r_s = 0.935$, $P < 0.0001$) than with either recruitment ($r_s = 0.769$, $P < 0.0001$) or damage ($r_s = 0.588$, $P < 0.0001$; Spearman rank correlations; $n = 66$ in all cases).

Maximum penetration of edge effects

While the strongest edge effects occurred within ~100 m of fragment edges, less-pronounced effects could apparently be detected at greater distances (Fig. 5). Negative exponential curves describing the attenuation of edge effects with increasing edge distance explained 31–45% of the variation in each index. The curves for mortality, damage, and turnover rates exceeded the upper 95% confidence limits for forest-interior plots at ~335, 85, and 280 m, respectively.

Core-area model

The core-area model (Fig. 6) was generated for two edge penetration distances: 60 and 100 m, based on the results where strong edge effects were evident within 60 m of edges and moderate effects were detected within 100 m of edges (Fig. 3). Predictions also were derived for two realistic fragment shapes: moderately circular (SI = 1.5) and irregular (SI = 3.0). Much higher SI values are possible for fragments with highly irregular shapes.

The model yielded three general predictions (Fig. 6). First, strong edge effects are expected to increase sharply (influencing >50% of the fragment's area) once

TABLE 1. Summary of one-way ANOVAs used to test effects of fragment area and proximity to forest edge on the dynamics of Amazonian tree communities.

Variable†	$F_{3,62}$	P	Tukey's tests
Mortality			
Area	14.53	<0.0001	1-ha fragments > controls ($P < 0.01$) 10-ha fragments > controls ($P < 0.01$)
Edge	11.53	<0.0001	1-ha fragments > 10- and 100-ha fragments ($P < 0.01$) <60 m from edge > >500 m from edge ($P < 0.01$) 60–100 m from edge > >500 m from edge ($P < 0.01$) <60 m from edge > 101–500 m from edge ($P < 0.01$)
Damage			
Area	10.43	<0.0001	1-ha fragments > controls ($P < 0.01$) 100-ha fragments > controls ($P < 0.01$) 1-ha fragments > 10-ha fragments ($P < 0.01$) 1-ha fragments > 100-ha fragments ($P < 0.05$)
Edge	14.50	<0.0001	<60 m from edge > >500 m from edge ($P < 0.01$) <60 m from edge > 101–500 m from edge ($P < 0.01$) <60 m from edge > 60–100 m from edge ($P < 0.01$)
Turnover			
Area	14.06	<0.0001	1-ha fragments > controls ($P < 0.01$) 10-ha fragments > controls ($P < 0.01$) 1-ha fragments > 10- and 100-ha fragments ($P < 0.01$)
Edge	16.73	<0.0001	<60 m from edge > >500 m from edge ($P < 0.01$) 60–100 m from edge > >500 m from edge ($P < 0.01$) <60 m from edge > 101–500 m from edge ($P < 0.01$) <60 m from edge > 60–100 m from edge ($P < 0.05$)

Note: Annualized mortality, damage, and turnover rates of trees were $\log(X + 1)$ -transformed prior to analysis.

† Sample sizes: 4 (fragment area = 1 ha), 17 (10 ha), and 18 (100 ha); 12 (distance to edge <60 m), 18 (60–100 m), 11 (101–500 m), and 25 (>500 m).

fragment size falls below 30–140 ha, depending on fragment shape. Second, moderate edge effects should rise rapidly (influencing >50% of fragment area) once fragment size falls below 90–380 ha, again depending on fragment shape. Finally, if irregularly shaped, even large fragments can be markedly influenced by edge effects; an irregularly shaped fragment of 1000 ha, for example, is predicted to have nearly a third (32%) of its area influenced by moderate to strong edge effects.

Significantly, the core-area predictions in Fig. 6 apply only to relatively dramatic edge effects within the first 100 m of fragment boundaries. For modest but detectable effects, which may penetrate up to ~300 m (Fig. 5), the model suggests that a 1000-ha fragment would have 45–85% of its area influenced by edge effects, depending on fragment shape.

DISCUSSION

Edge effects and forest dynamics

Our results reveal that fragmentation causes a pronounced acceleration of tree-community dynamics in Amazonian rain forests. The most important proximate cause of elevated tree mortality, damage, and turnover in recently created fragments is probably edge effects, particularly alterations in forest microclimate and greater wind turbulence near edges. In the same study area, Kapos (1989) demonstrated that hotter, drier conditions of adjacent deforested areas penetrated at least 40–60 m into fragment interiors. Large numbers of

standing dead trees observed near new edges (Lovejoy et al. 1986, Ferreira and Laurance 1997) may have been killed by sudden shifts in temperature, relative humidity, or soil moisture, which exceeded their physiological tolerances. The observation that leaf fall increased dramatically near recent edges (Lovejoy et al. 1986, Sizer 1992) suggests affected trees either experienced severe water stress or shed shade-adapted subcanopy leaves (Bazazz 1991) that were suddenly exposed to direct sunlight near edges. Over time, however, edge-induced changes in light and forest microclimate may decline as older edges become “sealed” by a profusion of new leaf growth (Williams-Linera 1990, Matlack 1994, Kapos et al. 1997).

Winds striking an abrupt forest edge can cause increased turbulence and vorticity, leading to elevated windthrow and forest structural damage (Laurance 1991, 1997, Chen et al. 1992). As an edge effect, wind damage probably occurs over larger spatial scales than changes in forest microclimate. Wind-tunnel models demonstrate that pronounced turbulence can persist downwind for at least 2–10 times the height of the forest edge (Savill 1983). In this study, modest changes in mortality and turnover rates could apparently be detected within ~300 m of forest edges (Fig. 5), which is 8–10 times the typical canopy height (30–37 m) of these forests. The value of 300 m should be interpreted cautiously, however, because only 10 of our 66 plots were located at intermediate distances (100–500 m)

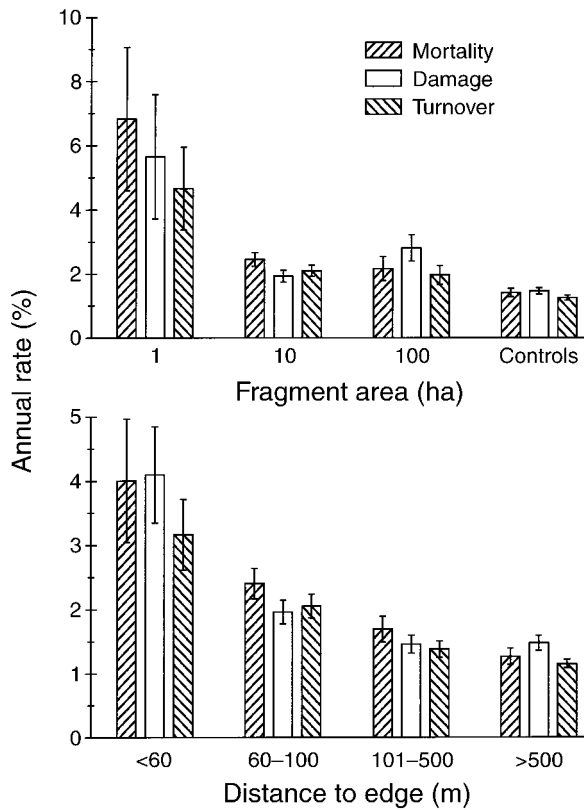


FIG. 3. Annualized rates ($\bar{X} \pm 1$ SE) of forest dynamics as a function of fragment area and distance of study plots to forest edge.

from forest edge. The most striking changes in forest dynamics occurred within 100 m of edges, and the sharp increase in edge effects near forest margins is illustrated by the fact that, even with double-log axes, curvilinear models were needed to describe changes in forest dynamics as a function of edge distance (Fig. 5). It is apparent, nevertheless, that edge effects from wind can penetrate considerable distances into forest interiors. In cyclonic rain forests in tropical Queensland, Australia, elevated wind disturbance was detectable within several hundred meters of fragment edges, with the greatest increases occurring within 150–200 m of edges (Laurance 1991, 1997). Unlike microclimatic changes, wind damage is unlikely to lessen as fragment edges become older and less permeable because downwind turbulence usually increases as edge permeability is reduced (Bull and Reynolds 1968, Savill 1983).

Although our study area receives easterly prevailing winds, edge aspect had no significant effect on forest dynamics. This may occur because convective thunderstorms that damage trees and cause occasional large blowdowns (Nelson et al. 1994) can come from virtually any direction (V. Kapos, *personal communication*), and may cause complex patterns of forest disturbance (Boose et al. 1994) that obviate any simple

relationship between edge aspect and tree mortality. In addition, at the equatorial latitude of this study (2° S), microclimatic changes that kill trees may not vary greatly among edges with differing aspects.

Effects of fragment age and area

In this study, tree mortality and damage rates did not vary significantly as a function of fragment age (Fig. 2), suggesting these are not merely short-term responses to fragmentation but rather the result of recurring wind disturbances or microclimatic alterations. The significant increase in turnover rates with fragment age (Fig. 2) was partly attributable to the fact that recruitment rates of trees increased with age in all nine of our fragments. Although this trend may have been partly caused by a time lag before new trees reached the 10-cm minimum size limit used in this study, it clearly suggests that fragmentation is not merely having a temporary effect on forest dynamics.

Edge and area effects are rarely discriminated in studies of fragmented ecosystems (Temple 1986, Laurance and Yensen 1991, Didham 1997, Ferreira and Laurance 1997), but in our study, area effects per se appeared to have relatively minor effects on forest dynamics, as indicated by a comparison of plots in forest and fragment interiors (Fig. 4). Area effects that could influence tree species persistence in fragments include population-level processes, such as the collapse of small populations via random genetic or demographic events (Shafer 1981), and community-level phenomena, such as declines in reproduction following losses of specialized pollinators or seed dispersers (Powell and Powell 1987, Aizen and Feinsinger 1994). These processes are more akin to island biogeographic questions of extinction and colonization (e.g., MacArthur and Wilson 1967, Bush and Whittaker 1991), which probably require longer time scales to become manifested (e.g., Turner et al. 1996) than the largely edge-driven dynamics of recently created fragments examined in this study.



FIG. 4. Annualized rates ($\bar{X} \pm 1$ SE) of forest dynamics in the interiors of forest fragments and continuous forest (all sites are ≥ 150 m from the nearest forest edge).

TABLE 2. Effects of edge aspect on annualized rates of tree mortality, damage, and turnover in central Amazonia, using one-way ANOVAs.

Variable	Comparison among four aspects†		Eastern vs. other aspects‡	
	$F_{3,13}$	P	$F_{1,25}$	P
Mortality	0.32	0.82	0.09	0.77
Damage	0.40	0.75	0.01	0.94
Turnover	0.92	0.46	0.17	0.68

Notes: All study plots were within 100 m of forest edges. Annualized rates were $\log(X + 1)$ -transformed prior to analysis.

† Sample sizes: 5 (eastern edges), 2 (northern edges), 7 (western edges), and 3 (southern edges). Edges on fragment corners were not considered in this analysis.

‡ Sample sizes: 9 (eastern edges) and 18 (other edges). Plots on northeastern or southeastern corners of fragments were considered to have eastern aspects in this analysis.

Ecological effects of accelerated forest dynamics

Inside tropical forest remnants, edge effects that influence forest dynamics are patchy due to the distribution of treefall gaps. Because of elevated tree mortality and damage near edges, forest fragments will tend to have high proportions of their area in gap and building phases of forest dynamics. These effects will obviously be greatest in small, irregularly shaped fragments, which have the highest ratios of edge to area. For example, based on mean mortality rates (Fig. 3), the half-lives of tree communities (time for 50% of all measured stems to die) would be only 9.8 yr for 1-ha fragments and 28–32 yr for larger (10–100 ha) fragments, compared to 54 yr for forest interiors (the mean mortality rate for continuous forest in this study [1.27%/yr] falls well within the range of values recorded for other, non-inundated Neotropical forests [$\bar{X} \pm 1 \text{ SD} = 1.66 \pm 0.46\%$, $n = 16$ studies; cf., Philips and Gentry 1994]). Local factors such as topography and structure of the adjoining matrix habitat may also influence rates of fragment disturbance (Laurance 1997).

Substantially elevated rates of gap formation will alter the structure, floristic composition (Clark 1990, Denslow 1995), and microclimate (Kapos et al. 1997) of forest remnants. Smaller fragments can be devastated by wind disturbance, while larger fragments may exhibit increased disturbance and a general shift toward pioneer and secondary vegetation, with a concomitant decline in old-growth species of the forest interior (Laurance et al. 1998a). Many animal species are strongly influenced by forest structure and microclimate (Schemske and Brokaw 1987, Crome and Richards 1988, Levey 1988, Laurance 1994), and a sudden increase in edge and gap-phase vegetation could help drive local extinctions of disturbance-sensitive species in fragments. Changes in forest dynamics may even have regional or global effects: because large trees are often killed and replaced by much smaller trees, fragmentation of Amazonian forests leads to a marked loss

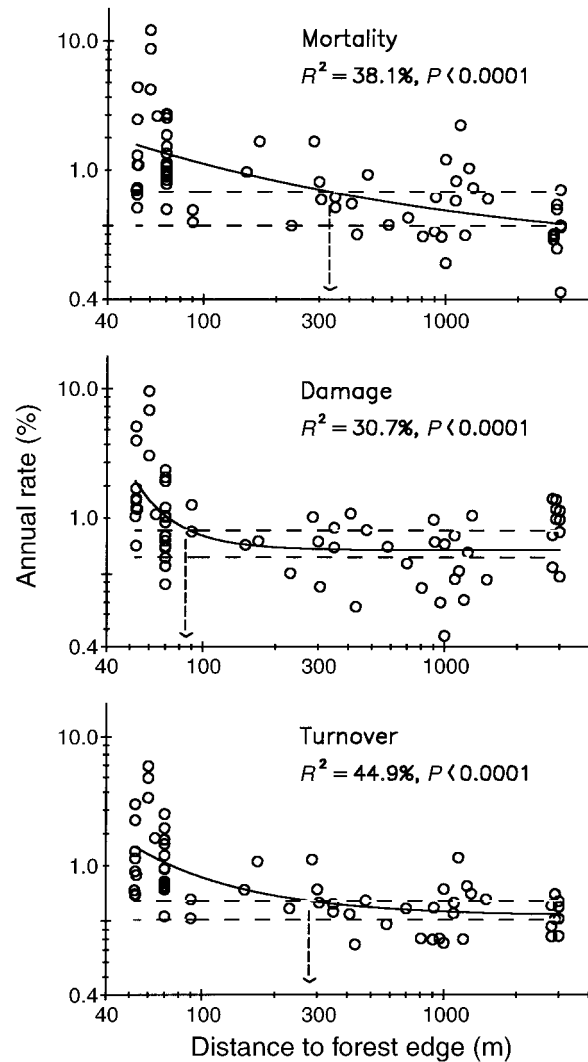


FIG. 5. Estimates of the maximum detectable distance to which edge effects penetrate into forest interiors, based on 66 study plots in fragmented and continuous forest. Solid lines show negative exponential curves fitted to each forest-dynamics index, while horizontal dashed lines are 95% confidence intervals for forest-interior plots (>500 m from forest edge). For each index, the vertical dashed line indicates the point at which the curve exceeds forest-interior values, suggesting that edge effects can be detected up to that distance from forest edge. (Formulas for curves and F statistics for comparisons of fitted and actual values: $\log(\text{mortality}) = -0.19 + 1.94 \times \exp[-0.66 \times \log(\text{edge-distance})]$, $F_{1,64} = 39.37$; $\log(\text{damage}) = 0.13 + 5528.4 \times \exp[-5.58 \times \log(\text{edge-distance})]$, $F_{1,64} = 28.33$; $\log(\text{turnover}) = 0.03 + 14.51 \times \exp[-2.12 \times \log(\text{edge-distance})]$, $F_{1,64} = 52.15$.)

of aboveground tree biomass, which may increase production of greenhouse gases such as CO_2 above and beyond that caused by deforestation per se (Laurance et al. 1997, 1998b).

These findings have important implications for landscape management and the design of tropical nature reserves. The core-area model (Fig. 6) suggests that

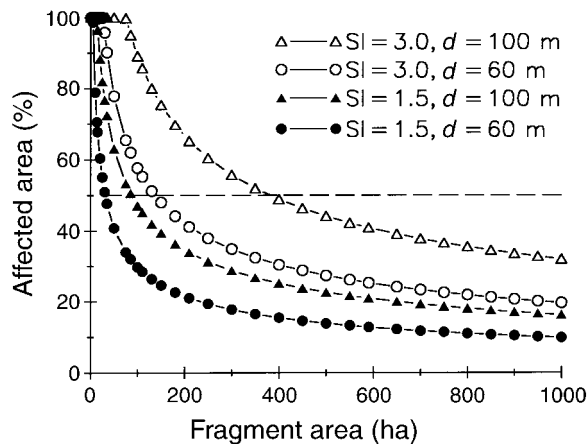


FIG. 6. A core-area model for rain forest fragments in central Amazonia, using empirical data for strong ($d = 60$ m) and moderate ($d = 100$ m) edge effects. Curves are generated for both moderately circular ($SI = 1.5$) and irregular ($SI = 3$) fragment shapes. The dotted line indicates the point at which 50% of the fragment's area is influenced by edge effects.

edge effects should have a rapidly increasing impact on Amazonian forest dynamics once fragment area falls below 100–400 ha, depending on fragment shape. Striking changes in dynamics are expected in smaller (<100 ha) fragments. Fragments in these size ranges may still have important conservation values (Turner and Corlett 1996, Laurance and Bierregaard 1997), but their ecological characteristics are likely to differ markedly from those of intact forest. Detectable changes in forest dynamics may be evident in much larger (e.g., 1000 ha) fragments, especially if they are irregularly shaped.

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