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Please cite as:

Laurance, W.F., H.E.M. Nascimento, S.G. Laurance, A.C. Andrade, P.M. Fearnside, J.E.L. Ribeiro and R.L. Capretz. 2006. Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87(2): 469-482.

ISSN: 0012-9658

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The original publication is available from <http://www.esa.org>

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## RAIN FOREST FRAGMENTATION AND THE PROLIFERATION OF SUCCESSIONAL TREES

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*Abstract.*—The effects of habitat fragmentation on diverse tropical tree communities are poorly understood. Over a 20-year period, we monitored the density of 52 tree species in nine predominantly successional genera (*Annona*, *Bellucia*, *Cecropia*, *Croton*, *Goupia*, *Jacaranda*, *Miconia*, *Pourouma*, *Vismia*) in fragmented and continuous Amazonian forests. We also evaluated the relative importance of soil, topographic, forest-dynamic, and landscape variables in explaining the abundance and species composition of successional trees. Data were collected within 66 permanent 1-ha plots within a large (ca. 1,000 km<sup>2</sup>) experimental landscape, with forest fragments ranging from 1-100 ha in area.

Prior to forest fragmentation, successional trees were uncommon, typically comprising 2-3% of all trees ( $\geq 10$  cm diameter-at-breast-height) in each plot. Following fragmentation, the density and basal area of successional trees increased rapidly. By 13-17 years after fragmentation, successional trees had tripled in abundance in fragment and edge plots, and constituted more than a quarter of all trees in some plots.

Nonetheless, the 52 species differed greatly in their responses to fragmentation and forest edges. Some disturbance-favoring pioneers (e.g. *Cecropia sciadophylla*,

*Vismia guianensis*, *V. amazonica*, *V. bemerguii*, *Miconia cf. crassinervia*) increased by >1000% in density on edge plots, whereas over a third (19 of 52) of all species remained constant or declined in numbers. Species responses to fragmentation were effectively predicted by their median growth rate in intact forest, and to some extent by their seed-dispersal mechanism, suggesting that fast-growing, animal-dispersed species are strongly advantaged in forest fragments.

An ordination analysis revealed three main gradients in successional-species composition across our study area. These species gradients were most strongly influenced by the average rate of tree mortality on each plot and by the proximity and number of nearby forest edges. These same variables were also the best predictors of total successional-tree abundance and species richness. Soils and topography had little effect on successional trees. Collectively, our results indicate that successional tree species proliferate rapidly in fragmented Amazonian forests, largely as a result of chronically elevated tree mortality and possibly an increased seed rain from successional plants near forest edges. The proliferation of fast-growing successional trees, and the correlated decline of old-growth trees, will affect species composition, carbon storage, forest dynamics, and nutrient cycling in fragmented forests.

## INTRODUCTION

The Amazon Basin sustains some of the world's most biologically diverse forests (Gentry 1988, 1990, Valencia et al. 1994, Oliveira and Mori 1999, Bierregaard et al. 2001), which are being destroyed at an alarming pace. Deforestation rates in Brazilian Amazonia now average 2.4 million ha per year, equivalent to 11 football fields a minute (Laurance et al. 2004). Forests in southern and eastern Amazonia have already been severely reduced and fragmented (Skole and Tucker 1993), and major new highways and transportation projects are penetrating into central and northern Amazonia, where they could promote unprecedented forest loss and fragmentation (Laurance et al. 2001a).

Many effects of forest fragmentation on tropical communities are poorly understood, especially for diverse, long-lived organisms like trees (Schelhas and Greenberg 1996, Laurance and Bierregaard 1997, Laurance and Gascon 1999, Bierregaard et al. 2001). Fragmentation is known to increase tree mortality and turnover (Laurance et al. 1998a, 2000), reduce live tree biomass, and increase atmospheric carbon emissions (Laurance et al. 1997, Nascimento and Laurance 2004). For some species, seed and seedling survival are reduced in fragments because of altered microclimatic conditions (Benitez-Malvido 1998, Bruna 1999), a decline of animal seed-dispersers (Silva and Tabarelli 2000, Cordeiro and Howe 2003), and elevated seed predation (Terborgh et al. 2001).

A potentially critical consequence of habitat fragmentation is an increase in disturbance-favoring, early successional trees (Laurance 1991, 1997, Laurance et al. 1998a, Tabarelli et al. 1999, Oliveira-Filho et al. 1997) and lianas (Viana et al. 1997, Laurance et al. 2001b), and a correlated decline of old-growth trees (Laurance et al. 1998b, Tabarelli et al. 1999, Metzger 2000). These changes are at least partly driven by edge effects, the diverse physical and biotic changes associated with the abrupt, artificial boundaries of habitat fragments (Janzen 1986, Lovejoy et al. 1986, Laurance et al. 2002).

In central Amazonia, increased desiccation and wind turbulence near forest margins cause sharply elevated tree mortality within 100 m of fragment edges and smaller but detectable increases up to 300 m from edges (Laurance et al. 1998a, 2000). Other disturbances, such as logging and surface fires, can further exacerbate tree mortality in fragmented forests (Cochrane and Laurance 2002). An increased seed rain from disturbance-adapted plants proliferating in outside modified habitats could also promote regeneration of successional trees in fragments (Janzen 1986).

Although fragmented forests can experience large changes in floristic composition, including an increase in disturbance-adapted plants, the details of such changes, and their underlying causes, are poorly understood. This is so because most fragmentation studies suffer from a lack of knowledge about species distributions prior to fragmentation, and often from small sample sizes, inadequate replication of fragments, complex land-use histories, and short study duration (Crome 1997). Here we present findings from a long-term study that largely circumvent these problems. Working within a spatially extensive network of permanent plots in an experimentally fragmented landscape in central Amazonia, we quantify changes in the distribution and abundance of 52 successional-tree species before fragmentation and for the first 13-17 years after fragmentation. We also assess the effects on successional trees of soil, topographic, forest-dynamic, and landscape features, to better understand the factors structuring tree communities in fragmented forests.

## METHODS

### *Study area*

This study is part of the Biological Dynamics of Forest Fragments Project (BDFFP), a long-term experimental study of Amazonian forest fragmentation (Lovejoy et al. 1986, Laurance et al. 2002). The study area spans about 1,000 km<sup>2</sup> (Fig. 1) and is located 80 km N of Manaus, Brazil (2° 30' S, 60° W), at 50-100 m elevation (Lovejoy et al. 1986). The topography consists of flat or undulating plateaus interspersed by many steeply eroded gullies. Rain forests in the area are not seasonally inundated. Rainfall ranges from 1,900-3,500 mm annually with a pronounced 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 280 species ( $\geq 10$  cm diameter-at-breast-height [dbh]) per hectare (Oliveira and Mori 1999).

The study area (Fig. 1) is surrounded by large expanses (>200 km) of continuous forest to the west, north, and east. In the early to mid 1980s, a series of forest fragments were isolated (by distances of 70-1,000 m) from surrounding forest by clearing the intervening vegetation to establish pastures in three large (ca. 5,000 ha) cattle ranches. Fragments were fenced to prevent encroachment by cattle. Reserves ranging from 1-1,000 ha in area were delineated in nearby continuous forest to serve as experimental controls. Regrowth forests have regenerated in some previously cleared areas and are dominated by *Cecropia* spp. or *Vismia* spp.

The dominant soils in the study area are xanthic ferralsols. Ferralsols are widespread in the Amazon Basin, heavily weathered, and usually have a low base saturation. They often are well aggregated, porous, and friable, with variable clay contents. Clay particles in ferralsols can form very durable aggregations, giving the soil poor water-holding characteristics, even with high clay contents (Richter and Babbar

1991). Xanthic ferralsols in the Manaus area are derived from Tertiary deposits and are typically acidic and very poor in nutrients such as P, Ca, and K (Chauvel et al. 1987).

#### *Network of permanent plots*

Since 1980, a long-term study of tree-community dynamics and composition has been conducted in fragmented and continuous forests in the study area. Over 60,000 trees ( $\geq 10$  cm diameter-at-breast-height [dbh]) are being monitored at regular (typically 4-6-year) intervals within 66 permanent, square, 1-ha plots spanning the study area. Thirty-nine of the plots are located within four 1-ha fragments (4 plots), three 10-ha fragments (17 plots), and two 100-ha fragments (18 plots). The remaining 27 control plots are arrayed in nine reserves that roughly mimic the spatial arrangement of fragment plots, but in continuous forest. Plots within fragments and continuous forest are stratified so that edge and interior areas are both sampled.

All plots were initially censused between January 1980 and January 1987, then recensused 3-5 times, with the most recent recensus completed in June 1999 (mean=4.0 censuses/plot). During the initial census, trees in each plot were marked with numbered aluminum tags and mapped. During recensuses, all new trees ( $\geq 10$  cm dbh) were mapped and marked, and all dead or severely damaged trees (with broken crowns or snapped boles) were recorded. On average, 95.3% of all trees in each plot, including virtually all individuals of the successional taxa examined in this study, have been identified to species or morphospecies level, using sterile or fertile material collected from each tree. Voucher specimens for each tree are maintained in the BDFFP Plant Collection, Manaus, Brazil.

#### *Predictor variables*

We evaluated the efficacy of eight soil, topographic, forest-dynamic, and landscape variables to explain the abundance and species composition of successional trees. Two variables, soil organic-carbon content and sand fraction, described potentially important attributes of forest soils, whereas slope is a key topographic variable (Laurance et al. 1999). In our study area, flat areas tend to have high clay and organic-carbon contents (typically 45-75%), which are associated with relatively high (although still very modest) concentrations of important nutrients such as nitrogen and exchangeable bases. On sloping terrain, however, a "podzolization" process occurs over time because lateral water movement results in the gradual destruction of clay-rich upper soil horizons. This ultimately leads to the creation of dendritic valley systems with increasing sand on lower slopes and valley bottoms (Chauvel et al. 1987, Bravard and Righi 1989).

The mean slope for each plot was determined by dividing the plot into 25 quadrats of 20 x 20 m each, measuring the maximum slope in each quadrat with a clinometer, then averaging these values. For the soil samples, 9-13 quadrats were selected for sampling, using an alternating pattern to provide good coverage of the plot. Within each quadrat, 15 surface samples were collected at haphazard locations using a soil auger, then bulked and subsampled. Composite samples were oven-dried, cleaned, and passed through 20 mm and 2 mm sieves. Textural analyses, using the pipette method, were used to determine percent sand content, whereas total organic carbon was determined by dry combustion (Fearnside and Leal-Filho 2001). Data from the different quadrats were averaged for each plot.

A key index of forest dynamics, the mean annualized rate of tree mortality, was determined for each plot using logarithmic models (Laurance et al. 1998a). Three landscape variables, fragment area, the distance of each plot to the nearest forest edge (measured from the center of the plot), and the number of nearby forest edges (<100 m from the plot center), describe the vulnerability of forests to edge and area effects (cf. Laurance et al. 1997, 1998a, 2002). The final variable discriminated among the three cattle ranches, which differed somewhat in land-use history, the amount and type of regrowth forest on abandoned pastures, and the intensity of past windstorms (Bierregaard and Stouffer 1997).

#### *Data analysis*

When using parametric statistical tests, appropriate transformations were used to stabilize variances and improve normality of data. Data on tree density, basal area, annualized mortality rates, and distance to forest edge were log transformed; percent sand data were arcsine-square-root transformed, and slope data were square-root transformed. All other variables were approximately normal.

Nonmetric multidimensional scaling (NMS), an ecological ordination technique on the PC-ORD package (McCune and Mefford 1999), was used to identify major gradients in successional-tree species composition across the study area. For these analyses we used raw data on species densities in each plot, excluding rare species (detected at <10 plots), with Sorensen's distance metric. Randomization tests ( $n=50$ ) were used to determine the number of ordination axes that explained significantly more variation than expected by chance.

The effects of soil, topographic, landscape, and forest-dynamic predictors on successional trees were assessed using generalized linear models (GLM) on Systat Version 10 (SPSS 2000). Our GLM model assumed a normal error structure and hence appropriate data transformations were used. Fragment area, the number of nearby forest edges, and the cattle ranch, which each had only 3-4 classes, were treated as categorical variables.

## RESULTS

### *Overall changes in edge and interior plots*

We initially compared the overall density of the 52 successional species between edge (<100 m from forest edge) and forest-interior (>100 m from edge) plots. Prior to fragmentation (in the early-mid 1980s), there was no significant difference between the two treatments ( $t=1.44$ ,  $df=64$ ,  $P=0.15$ ; two-sample  $t$ -test), with edge and interior plots having similar successional-tree densities ( $16.9\pm 9.9$  and  $14.3\pm 10.7$  stems  $ha^{-1}$ , respectively). By 13-17 years after fragmentation, however, successional-tree density had risen sharply on edge plots ( $t=4.55$ ,  $df=32$ ,  $P=0.0001$ ; Fig. 2), roughly tripling on average ( $46.0\pm 41.9$  stems  $ha^{-1}$ ), whereas interior plots showed no significant change over time ( $t=1.68$ ,  $df=32$ ,  $P=0.104$ ; paired  $t$ -tests).

In percentage terms, by 13-17 years after fragmentation, successional trees constituted just  $2.8\pm 2.0\%$  of all trees on interior plots, but  $7.6\pm 6.9\%$  of all trees on edge plots. Successional trees were, however, patchily distributed on edge plots, with 73% of plots having <10% pioneer trees and the remainder having substantially higher proportions (10-26%) of successional trees.

In the forest-interior plots, there was no change in species richness of successional trees between the pre-fragmentation census and that 13-17 years after fragmentation ( $t = -1.74$ ,  $df=32$ ,  $P=0.092$ ). On edge plots, however, species richness rose significantly over the same interval ( $t = -4.17$ ,  $df=32$ ,  $P=0.0002$ ; paired  $t$ -tests), from an average of  $9.1 \pm 3.8$  to  $12.5 \pm 5.2$  species per plot. This increase was a direct consequence of increasing successional-tree density on edge plots, as there was a strong linear relationship between species richness and log-tree density per plot during both the pre-fragmentation ( $F_{1,64}=243.7$ ,  $R^2=79.2\%$ ,  $P<0.0001$ ) and post-fragmentation ( $F_{1,64}=179.9$ ,  $R^2=73.8\%$ ,  $P<0.0001$ ) censuses (linear regressions).

#### *Effects of fragment age*

Did the abundance of successional-tree species increase progressively with fragment age, remain roughly stable, or decline over time following an initial pulse of recruitment? To test these alternative hypotheses we used data from the repeated censuses of each fragment. We pooled data for all plots within each fragment and then used ANCOVAs, with fragment age as a covariate and fragment area as a fixed effect (repeated-measures ANOVA was not feasible in this case because the nine fragments were not censused at identical intervals). Fragment age had a highly significant, positive effect on the overall density of successional trees ( $F_{1,43}=12.92$ ,  $P=0.0008$ ), whereas the effect of fragment area was nonsignificant ( $F_{2,43}=0.17$ ,  $P=0.85$ ). Fragment age had a similar effect on the basal area of successional trees ( $F_{1,43}=7.02$ ,  $P=0.011$ ), while fragment area was again nonsignificant ( $F_{2,43}=1.71$ ,  $P=0.19$ ). Thus, fragment age, but not fragment area, had strong and positive effects on the abundance and dominance of successional trees (Fig. 3).

#### *Ecological differences among species*

The 52 tree species we examined exhibited great variability in their response to fragmentation and forest edges (Appendix 1). Nearly two-thirds of all species (33) increased in density on edge plots, with 15 species, especially *Cecropia sciadophylla* (3140% increase), *Vismia guianensis* (1400%), *V. amazonica* (1200%), and *Miconia cf. crassinervia* (1100%), showing large population increases (>200%). The remaining 19 species either remained constant (7 species) or declined in density (12 species).

We tested the efficacy of six ecological traits to predict tree species responses to edge effects, using available data (Appendix 1). First, we assessed whether the initial population density of each species (in edge plots but before fragmentation) influenced their subsequent population response to forest edges, but there was no significant effect ( $r_s=0.011$ ,  $n=52$ ,  $P=0.94$ ; Spearman rank test). Second, we evaluated species regeneration capacities, contrasting 10 early successional species that frequently regenerate in cattle pastures, versus 16 mid-successional species that normally occur in regrowth forest or treefall gaps in primary forest. These two groups did not differ in terms of their percent change in density in edge plots ( $P=0.33$ ; Mann-Whitney  $U$ -test). Third, we assessed the influence of wood specific gravity on species responses, but found no significant effect, at least for the 15 species for which data were available ( $r_s = -0.196$ ,  $P=0.48$ ; Spearman rank test). Fourth, we assessed the effect of seed-dispersal mode, contrasting 8 species that are entirely animal dispersed with 7 species that are partially or completely dispersed abiotically. Animal-dispersed species generally had larger

population increases ( $701 \pm 1084\%$ ) in edge plots than did abiotically dispersed species ( $206 \pm 418\%$ ), and this difference was nearly significant ( $P=0.053$ ; Mann-Whitney  $U$ -test). Finally, we examined the influence of median and maximum growth rates of each species on their edge responses (to avoid circularity we used growth data only from trees in forest-interior plots). For the 30 species for which data were available, maximum growth rate was a significant predictor ( $r_s=0.457$ ,  $P=0.011$ ) and median growth rate a highly significant predictor ( $r_s=0.726$ ,  $P=0.00001$ ) of their responses to forest edges (Spearman rank tests). Thus, the most effective predictor of species responses was their median growth rate, with the fastest-growing species exhibiting dramatic population increases near forest edges (Fig. 4). There was also a tendency for strictly animal-dispersed species to increase more in edge plots than those with complete or partial abiotic dispersal, although this difference was marginally nonsignificant.

#### *Ecological gradients in species composition*

The NMS ordination revealed three major gradients in species composition among plots (Table 1), based on the 24 most abundant successional species (each detected at  $\geq 10$  plots) recorded 13-17 years after forest fragmentation. Axis 1, which explained 44.5% of the total variation in the dataset, described variation in some of the most abundant species, including *Pourouma tomentosa* ( $n=215$ ), *Miconia burchelli* ( $n=238$ ), and *Cecropia sciadophylla* ( $n=337$ ). Axis 2 explained 16.5% of the total variation and was significantly correlated with only three species, *Cecropia sciadophylla*, *C. purpurascens*, and *Pourouma villosa*. Axis 3 explained 10.0% of the variation and was correlated with only two species, *Goupia glabra* and *P. minor*.

The scores on all three ordination axes differed significantly between forest edge and interior plots (Axis 1:  $t=-3.15$ ,  $P=0.0025$ ; Axis 2:  $t=-2.65$ ,  $P=0.01$ ; Axis 3:  $t=-2.29$ ,  $P=0.025$ ; two-sample  $t$ -tests,  $df=64$  in all cases), indicating that edge effects had a major influence on species composition (Fig. 5). The species that were strongly correlated with Axis 1 often increased very sharply near forest edges (e.g. *Cecropia sciadophylla*, *C. purpurascens*, *Vismia cayennensis*, *Bellucia dichotima*, *Miconia burchelli* all increased by  $>360\%$ ). Axis 1 was also positively correlated with successional-tree species richness ( $r=0.748$ ,  $df=64$ ,  $P<0.0001$ ), whereas neither of the other two axes was correlated with species richness ( $r<0.16$ ,  $df=64$ ,  $P>0.20$ ; Pearson correlations).

#### *Factors influencing successional-tree communities*

We used GLM models to assess the influence of combinations of edaphic, forest-dynamic, and landscape predictors on successional-tree communities 13-17 years after forest fragmentation (Table 2). The strongest predictors of successional-tree density were the rate of tree mortality and the number of nearby forest edges, both of which increased tree density. Tree density also varied among the three cattle ranches in our study area. Trends were similar for species richness of successional trees, except that there was no significant difference among the three ranches.

The ordination axes describing gradients in successional-tree community composition were influenced in individualistic ways by the predictors (Table 2). Axis 1 was strongly affected by the rate of tree mortality, whereas Axis 2 was influenced by fragment area, distance to edge, and cattle ranch. Axis 3 was most strongly influenced by



the number of nearby forest edges, followed by cattle ranch and the distance to forest edge.

The overall conclusion from these GLM models is that the rate of tree mortality (Fig. 6) and number of nearby forest edges (Fig. 7) had the strongest effects on successional-tree communities in our study area. Notably, these two variables are interrelated, because the number of nearby edges strongly influenced tree mortality (Fig. 7). Distance to forest edge had significant or near-significant effects on species composition (NMS Axes 2 and 3), whereas tree density and species composition (Axes 2 and 3) varied among the cattle ranches. Fragment area and the soil and topographic variables had generally weak effects on successional trees, once effects of the other predictors were removed statistically.

The notion that fragment area had surprisingly little direct influence on successional trees was reinforced by a comparison of forest-interior plots in 10- and 100-ha fragments ( $n=7$ ) with the plots in intact-forest interiors ( $n=26$ ). In this comparison, there was no significant difference in successional-tree density ( $t= -1.62, P=0.11$ ), species richness ( $t= -1.23, P=0.23$ ), or the three NMS axes describing gradients in species composition ( $t<1, P>0.35$ ; all two-sample  $t$ -tests with  $df=31$ ). Thus, successional-tree communities in fragment-interior plots, which are subjected to area effects but not edge effects, did not differ significantly from those in intact forest.

#### *Edge-related seed rain*

In addition to experiencing elevated tree mortality, do edge plots receive a greater seed rain from successional plants, which often proliferate in the degraded lands surrounding fragments? To test this hypothesis we contrasted successional trees in paired edge and interior plots that had very similar tree mortality, reasoning that the edge plots should have more abundant and diverse successional-tree assemblages if the seed rain near edges is important. Our pairs of plots were always within the same fragment to minimize substantial among-site differences (Table 2), and in each case we selected the paired edge and interior plots that had the most similar tree-mortality rate.

Seven pairs of nearby plots met our criteria. As expected, there was no significant difference in tree-mortality rates between edge and interior plots ( $t=0.86, P=0.42$ ). The density of successional trees was significantly higher in edge than interior plots ( $t=3.05, P=0.022$ ), with edge plots averaging nearly three times as many trees as interior plots ( $20.4\pm 8.3$  versus  $7.4\pm 2.3$  stems  $ha^{-1}$ ). Species richness of successional trees was also significantly higher in edge than interior plots ( $t=2.92, P=0.027$ ; all paired  $t$ -tests with  $df=6$ ), with edge plots having nearly twice as many species on average ( $10.1\pm 3.2$  versus  $5.4\pm 1.5$  species  $ha^{-1}$ ). Thus, when compared to nearby forest-interior plots with very similar tree mortality, edge plots had more diverse and more abundant assemblages of successional trees.

## DISCUSSION

### *Edge effects and tree communities*

Because many tropical trees are long-lived, persisting for centuries and even millennia (Chambers et al. 1998, Laurance et al. 2004), one might expect that the effects of habitat fragmentation on tree communities would require a long time to become manifest. Our study demonstrates, however, that large changes in tree species

composition occur during the first two decades after fragmentation (Fig. 5). During this interval, edge effects appear to be the dominant force structuring fragmented tree communities.

Edge effects in fragmented rainforests are remarkably diverse, affecting many aspects of forest functioning and composition (Lovejoy et al. 1986, Laurance et al. 2002). These include microclimatic changes, increased wind shear and turbulence, elevated tree mortality, higher liana abundances, altered litterfall and nutrient cycling, and a variety of other ecological changes near forest edges (Laurance et al. 2002). In response to these changes, successional trees near edges increased sharply in density (Fig. 2), basal area, and species richness. On average, the population density of the 52 predominantly successional species we studied tripled within 100 m of fragment edges. Despite being uncommon in intact forest, these species became super-abundant in more than a quarter of all edge plots, comprising 10-26% of all trees ( $\geq 10$  cm dbh).

For successional trees, fragment-area effects were far less important than edge effects. Fragment area was generally a weak predictor of changes in successional-tree communities when the effects of other landscape and forest-dynamic variables were removed statistically (Table 2). Moreover, when plots located in the interiors of larger (10-100 ha) forest fragments—which are subject to area effects but not edge effects—were compared with those in the interiors of intact forest, there was no significant difference in successional-tree assemblages. Changes attributable to fragment area per se, such as the collapse of isolated tree populations from random demographic events or inbreeding, or as a consequence of declining pollinators or seed dispersers (Silva and Tabarelli 2000, Cordeiro and Howe 2003), may require more than two decades to become detectable. Nonetheless, remarkably rapid, area-related changes have been observed in tree communities on small (<5 ha) land-bridge islands (Terborgh et al. 2001), which are more strongly isolated than fragments and can experience dramatic distortions of herbivore and seed-predator assemblages (Leigh et al. 1993, Asquith et al. 1997, Terborgh et al. 2001).

Edge-related alterations cause rapid changes in tree communities, but which specific ecological changes are most important? Clearly, the rate of forest-canopy disturbance (as reflected in the mean rate of tree mortality on each plot) is a critical variable for successional trees (Fig. 6), as all of these species require the increased light and microclimatic conditions of treefall gaps for germination and survival. The lateral penetration of light and wind along forest edges could also help to increase soil irradiance and temperature fluctuations (Kapos 1989, Malcolm 1998, Didham and Lawton 1999, Laurance 2004), which are cues for germination of many pioneer species (Pearson et al. 2002). In addition, plots near edges probably receive a greater seed rain from successional plants growing in outside modified habitats (Janzen 1986, Willson and Crome 1989, Grau 2004). In our study, this was evidenced by the significantly greater species richness and density of successional trees in edge plots, compared to nearby interior plots with very similar tree mortality. For many successional species, densities of viable seeds in the litter and soil decline sharply with increasing distance from parent trees, and for this reason the likelihood of successful gap colonization rises markedly when reproductive trees are nearby (Dalling 1998, Dalling and Denslow 1998).

The results of our study clearly accord with “additive” edge models (e.g. Malcolm 1994), in which a forest adjoined by two or more nearby edges is subjected to stronger

edge effects than one adjoined by a single nearby edge. For example, during our 20-year study, the population density of successional trees increased far more in edge plots with four nearby edges ( $658 \pm 850\%$ ) than in those with two ( $264 \pm 353\%$ ) or one ( $129 \pm 225\%$ ) nearby edges. Species richness of successional trees and stand-level tree mortality were also much higher in plots with 2-4 nearby edges than in those with a single nearby edge (Fig. 7). Given that the most important edge effects penetrate about 100 m inside Amazonian forests (Laurance et al. 1997, 1998a, 2002), small (<5 ha) forest fragments and narrow (<200 m wide) forest corridors are likely to be severely degraded by edge effects. Moreover, because most forest fragments in human-dominated landscapes are irregularly shaped (Cochrane and Laurance 2002), even much larger (100-400 ha) fragments can be substantially influenced by edge-related tree mortality (Laurance et al. 1998a).

#### *Effects of fragment age*

In our nine forest fragments, the density and basal area of successional trees increased significantly over time following fragment isolation (Fig. 3), and there is no evidence that successional-tree populations had stabilized by the time fragments were 13-17 years old. There are at least two possible explanations for these results. The first is that these trends are simply time-lag effects, which arise because even the fastest-growing successional trees will require 5-10 years to reach the minimum 10 cm-dbh size class used in our study. Undoubtedly, this at least partially explains the observed increase. The second possibility is that successional trees (and probably other disturbance-adapted plants, such as lianas; Viana et al. 1997, Laurance et al. 2001b) will continue to increase in fragments over time. This seems especially likely if stand-level tree mortality remains chronically elevated near fragment margins.

Does tree mortality remain high in fragments, or is it a short-term phenomenon? Clearly, there is a strong pulse of edge-related tree mortality in the first few years after fragmentation (Lovejoy et al. 1986, Sizer and Tanner 1999, Laurance et al. 2002). This likely occurs because microclimatic alterations are very strong near newly formed fragment edges, which are structurally open and thereby permeable to the penetration of heat, light, and wind from outside degraded lands (Kapos et al. 1993, Didham and Lawton 1999). Trees along newly formed edges are presumably not physiologically acclimated to the sudden heat and desiccation stress, and many simply drop their leaves and die standing (Lovejoy et al. 1986). Over time, the edge is gradually sealed by proliferating vines and second-growth, and microclimatic gradients lessen in intensity (Kapos et al. 1993). Tree death from physiological stress probably declines over time, both because older edges are less permeable and because trees that are poorly adapted for edge conditions tend to die and be replaced by more desiccation-tolerant species (Laurance 2004).

However, tree mortality from elevated wind turbulence near forest edges is unlikely to decline with fragment age. This is because (as suggested by wind-tunnel models) downwind turbulence is likely to increase as edge permeability declines (Laurance 2004). The continued importance of wind disturbance over time is demonstrated by the fact that, among all dead trees, plots near 13-17 year-old forest edges had relatively fewer standing dead trees, and relatively more uprooted trees, than did plots in forest interiors (D'Angelo et al. 2004). Among our nine fragments, average rates

of tree mortality were very high in the first 3-5 years after fragment isolation, averaging  $3.43 \pm 1.92\% \text{ yr}^{-1}$ , a rate nearly triple that in forest interiors ( $1.23 \pm 0.45\% \text{ yr}^{-1}$ ). However, tree mortality remained quite high in subsequent years ( $2.70 \pm 1.70\% \text{ yr}^{-1}$ ) and the difference in mortality rates was nonsignificant ( $t=1.16$ ,  $df=8$ ,  $P=0.28$ ; paired  $t$ -test).

Thus, it seems likely that older fragments will continue to suffer elevated tree mortality, and this, in concert with the demographic and genetic isolation of fragment populations, may well promote a progressive erosion of fragment floristic composition. Surrounding land uses will undoubtedly have a major influence on fragment dynamics. For example, tree mortality in fragments can be greatly exacerbated by selective logging or recurring surface fires (Cochrane and Laurance 2002). In fact, the results from our experimental study are probably a best-case scenario, as many fragments in anthropogenic tropical landscapes suffer from additional disturbances such as logging, fires, hunting, and fuel-wood gathering (Gascon et al. 2000, Laurance and Cochrane 2001, Peres and Michalski, in press).

#### *Compositional changes in successional trees*

In less than two decades after isolation, assemblages of successional trees in forest fragments and edges deviated markedly from those in intact forest. In addition to being more abundant and species rich, the species composition of successional trees in edge plots differed from those in forest interiors (Fig. 5). Some species that were absent or very rare in intact forest (e.g. *Vismia amazonica*, *V. bemerguii*, *V. cayennensis*, *V. duckei*, *V. guianensis*) became established near edges, whereas other forest species (e.g. *Cecropia sciadophylla*, *Miconia cf. crassinervia*) increased dramatically (by  $>1000\%$ ) in density.

Ecological traits such as wood density, regeneration strategy, and their natural density in intact forest were poor predictors of successional species' responses to fragmentation. Rather, edge plots became increasingly dominated by the fastest-growing successional species, whereas slower-growing species tended to decline in abundance (Fig. 4). The abundance of bat- and bird-dispersed species may also have increased relative to those with abiotic dispersal modes. Notably, frugivorous bats that forage on successional trees along forest edges and in nearby regrowth are very common in our study area (Sampaio 2000).

Although species in our nine successional genera constituted less than 3% of all trees before forest fragmentation, they accounted for about a quarter of all tree recruitment in edge plots after fragmentation. This total would have been even larger had we included all successional species in our study area. The diverse legume genus *Inga*, in particular, contains many successional species and may well have increased in abundance on edge plots, but these were not included in our study because of a general lack of knowledge about the ecology of individual species. Other successional trees (e.g. many *Vismia* spp.) rarely reach 10 cm in diameter, and thus were too small to be included in our study. These trends illustrate that the dramatic increase in abundance of successional trees and lianas comes at the expense of many old-growth, shade-tolerant species in forest fragments (Oliveira-Filho et al. 1997, Tabarelli et al. 1999, Laurance et al. 1998b, 2001b).

### *Implications*

The proliferation of fast-growing successional trees and lianas in tropical forest fragments, and the correlated decline of many old-growth trees, has important implications for forest ecosystems. First, fast-growing trees and lianas have substantially lower wood density, and hence lower carbon storage, than do large, old-growth trees. These compositional shifts will probably exacerbate the decline of live biomass and the reduction in carbon storage in forest fragments caused by chronically elevated canopy-tree mortality (Laurance et al. 1997, Nascimento and Laurance 2004). Given the rapid pace of forest fragmentation in the tropics, such changes could be a potentially significant source of greenhouse gas emissions (Laurance et al. 1998c).

Second, because successional trees have considerably shorter longevity than do old-growth trees (Laurance et al. 2004), forest dynamics and tree-population turnover will both increase in fragments. This can influence diverse aspects of forest ecology, such as canopy-gap dynamics and the residence time of forest carbon stocks. Nutrient cycling is also expected to accelerate, both because successional trees have faster population turnover and because they decompose more rapidly than old-growth species, given their small size, low wood density (Chambers et al. 2000), and generally low concentrations of secondary compounds that inhibit decomposers (Coley 1983).

Third, the architecture of fragmented forests will change as they become increasingly dominated by successional trees and vines. Because successional trees are usually smaller in girth and height than old-growth canopy and emergent trees, forest volume will decline and the size-distributions of trees will shift toward smaller individuals. In some cases, forest fragments can be reduced to degraded, vine-dominated scrub in which canopy-tree regeneration is severely impeded (Viana et al. 1997).

Fourth, faunal communities are likely to change in response to compositional and structural shifts in tree communities. Some successional trees (e.g. *Cecropia* spp.) provide abundant food for frugivorous bats and birds, but a decline of old-growth trees would likely have deleterious effects on tree-cavity-dependent animals and on specialized mutualists and herbivores (Gilbert 1980, Laurance, in press). Birds and other species that rely on fine vertical partitioning of forest strata may be especially sensitive to reduced forest volume (Terborgh and Weske 1969).

Finally, large numbers of successional trees near fragment margins may increase forest vulnerability to surface fires, which can propagate only when dense litter is present on the forest floor (Cochrane et al. 1999). Successional species have higher rates of leaf turnover than do old-growth trees, and their fallen leaves tend to decompose slowly, as they have a lower initial concentration of N and higher C:N and lignin:N ratios, all of which deter decomposers (Vasconcelos and Laurance, in press). For these reasons, litter stocks tend to increase near forest margins, especially during periods of drought stress when leaf-shedding by plants increases (Sizer et al. 2000, Laurance and Williamson 2001). Surface fires, which often originate in the cattle pastures surrounding fragments, are extremely destructive to forests, typically killing all vines and 20-50% of all trees. Once burned, forests become far more vulnerable to subsequent, hotter fires because the protective canopy cover is thinned and dead fuel accumulates (Cochrane et al. 1999). By contributing to the alarming synergism between forest fragmentation and fire (Gascon et al. 2000, Cochrane and Laurance 2002), proliferating successional trees could actually help to facilitate forest destruction.

## ACKNOWLEDGEMENTS

We thank the many taxonomic experts who identified plant material in this study, and [Jim Dalling, Joe Wright, Rick Condit, Chris Dick, Ken Feeley, Rob Ewers, Heraldo Vasconcelos] for commenting on the manuscript. Support was provided by the NASA-LBA Program, A. W. Mellon Foundation, Conservation, Food and Health Foundation, World Wildlife Fund-U.S., MacArthur Foundation, National Institute for Amazonian Research, and Smithsonian Institution. This is publication number --- in the BDFFP technical series.

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Table 1. Pearson correlations of 24 common successional-tree species with three ordination axes produced by Nonmetric Multidimensional Scaling. Significant correlations are indicated by asterixes, using a Bonferroni-corrected alpha value ( $P=0.002$ ).

<u>Species</u>	<u>Axis 1</u>	<u>Axis 2</u>	<u>Axis 3</u>
<i>Bellucia dichotoma</i>	0.389*	0.096	0.084
<i>Cecropia purpurascens</i>	0.492*	0.518*	-0.116
<i>Cecropia sciadophylla</i>	0.456*	0.629*	0.021
<i>Croton lanjouwensis</i>	0.360	0.242	0.165
<i>Goupia glabra</i>	-0.061	-0.085	-0.435*
<i>Jacaranda aff. copaia</i>	-0.011	0.290	-0.077
<i>Jacaranda copaia</i>	0.100	0.209	-0.026
<i>Miconia burchellii</i>	0.616*	0.105	-0.108
<i>Miconia cf. tetrasperma</i>	0.097	-0.084	0.018
<i>Miconia elaeagnoides</i>	0.202	-0.295	0.015
<i>Miconia phanerostila</i>	0.391*	0.100	0.151
<i>Miconia punctata</i>	0.118	-0.230	0.269
<i>Miconia pyrifolia</i>	0.284	-0.039	-0.225
<i>Miconia regelii</i>	0.078	-0.069	0.076
<i>Pourouma bicolor</i>	0.529*	0.368	0.229
<i>Pourouma cucura</i>	0.467*	0.113	0.158
<i>Pourouma guianensis</i>	0.504*	0.117	0.193
<i>Pourouma melinonii</i>	0.367	0.095	0.216
<i>Pourouma minor</i>	0.325	-0.303	0.408*
<i>Pourouma ovata</i>	0.146	-0.367	0.361
<i>Pourouma tomentosa</i>	0.667*	0.178	0.431
<i>Pourouma velutina</i>	0.442*	0.059	0.027
<i>Pourouma villosa</i>	0.280	0.509*	0.057
<i>Vismia cayennensis</i>	0.375*	0.191	0.177
Variation explained <sup>a</sup> (%)	44.5	16.5	10.0

<sup>a</sup> Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space.

Table 2. Influence of edaphic, landscape, and forest-dynamics predictors on successional tree communities in 66 1-ha plots in fragmented and continuous Amazonian forests, using generalized linear models. Data on trees were recorded 13-17 years after forest fragmentation. The *P* value for each predictor is for a complete model that includes all predictors. Response variables include the overall density of all successional trees in each plot (Density), the number of successional species in each plot (Species), and three ordination axes describing successional-tree assemblage structure. Predictors for each plot include mean slope, percent sand content, soil-carbon content, annual tree mortality, fragment (or reserve) area, the distance to the nearest forest edge, the number of nearby forest edges, and the cattle ranch in which fragments were located.

Response Variable	Slope	Sand Content	Soil Carbon	Tree Mortality	Fragment Area	Distance to Edge	Number of Edges	Ranch	Multiple $R^2$ (%)
Density	0.659	0.658	0.467	<b>0.001</b>	0.268	0.187	<b>0.018</b>	<b>0.023</b>	57.0
Species	0.490	0.944	0.078	<b>0.047</b>	0.924	0.151	<b>0.032</b>	0.110	51.1
Axis 1	0.695	0.464	0.986	<b>0.001</b>	0.546	0.270	0.337	0.108	45.9
Axis 2	0.738	0.130	0.537	0.112	<b>0.022</b>	0.053	0.610	0.063	41.2
Axis 3	0.221	0.068	0.752	0.070	0.288	<b>0.025</b>	<b>&lt;0.001</b>	<b>0.012</b>	48.9

**FIGURE CAPTIONS**

Fig. 1. The study area in central Amazonia, showing locations of forest fragments and control sites in intact forest.

Fig. 2. Density of successional trees as a function of distance from forest edge, in 66 1-ha plots in intact forest and in nine forest fragments ranging from 13-17 years old. The relationship is highly significant ( $r_s = -0.393$ ,  $n=66$ ,  $P=0.001$ ; Spearman rank correlation).

Fig. 3. Effects of fragment age on the (A) density and (B) basal area of successional trees in central Amazonia. Data are shown for 3-6 censuses of each fragment, with pooled data from all 1-ha plots within the same fragment.

Fig. 4. The influence of median growth rates for 30 predominantly successional tree species on their relative population change near forest edges. Data are not shown for *Cecropia sciadophylla*, which had the fastest growth rate ( $15.9 \text{ mm yr}^{-1}$ ) and by far the largest population increase in edge plots (3140%).

Fig. 5. Ordination of 24 common successional tree species in 66 1-ha plots in fragmented and continuous Amazonian forest. Edge plots are <100 m from the nearest forest edge, whereas interior plots are >100 m from forest edge. Axis lengths are scaled relative to the amount of variation explained by each axis.

Fig. 6. Effects of forest disturbance (long-term average rate of tree mortality) on the density of successional tree species in fragmented and intact Amazonian forests. The relationship is highly significant ( $F_{1,64}=31.14$ ,  $R^2=32.7\%$ ,  $P<0.0001$ ; linear regression with log-transformed axes).

Fig. 7. Effects of number of nearby forest edges (<100 m from the plot center) on the (A) stand-level rate of tree mortality and on the (B) density and (C) species richness of successional trees. Values ( $X \pm \text{SD}$ ) were adjusted to account for variation in the distance of plots to forest edge (using edge distance as a covariate in ANCOVA models).

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Fig. 1

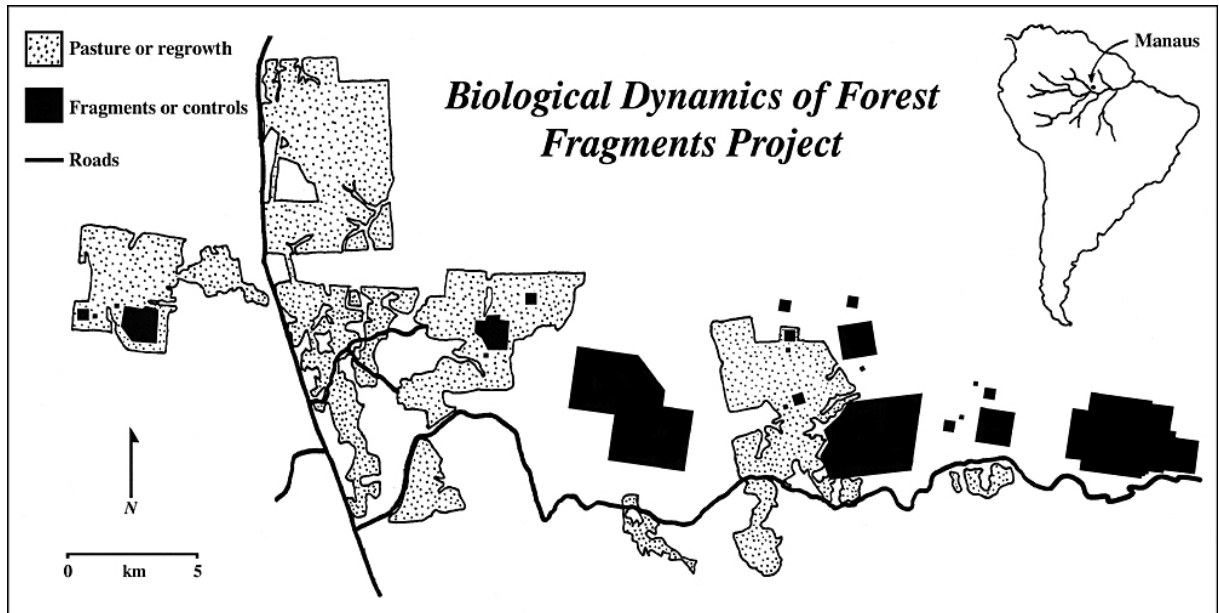


Fig. 2

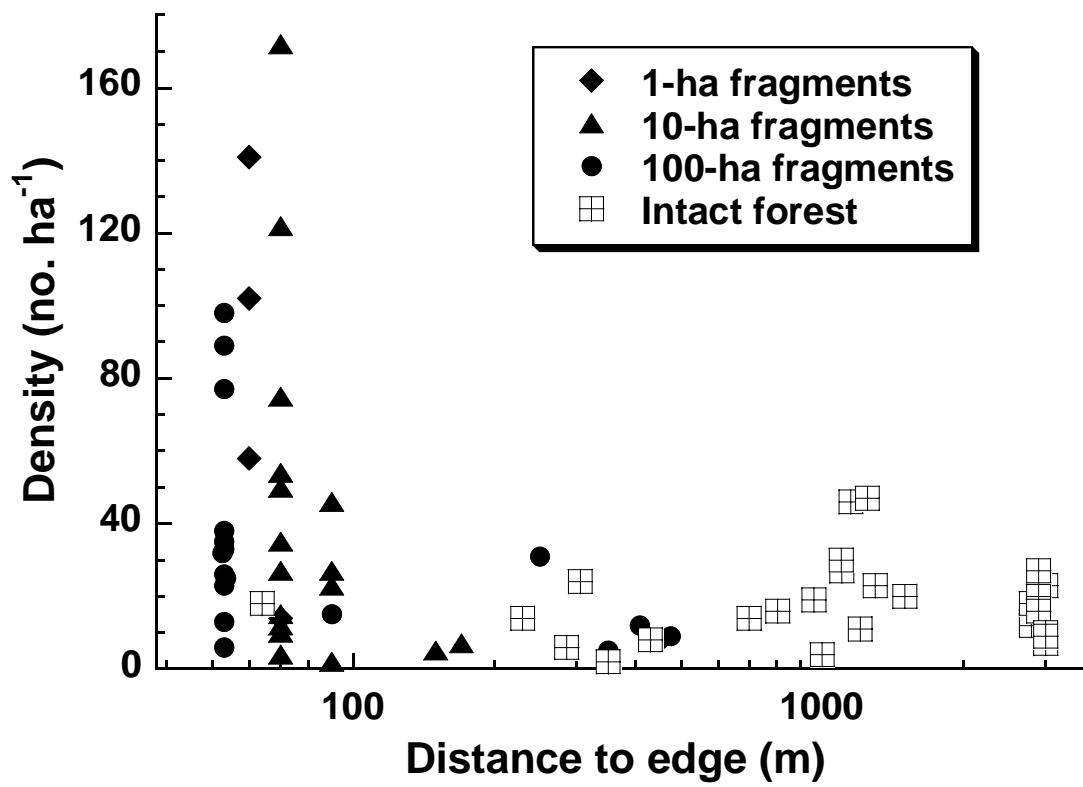


Fig. 3

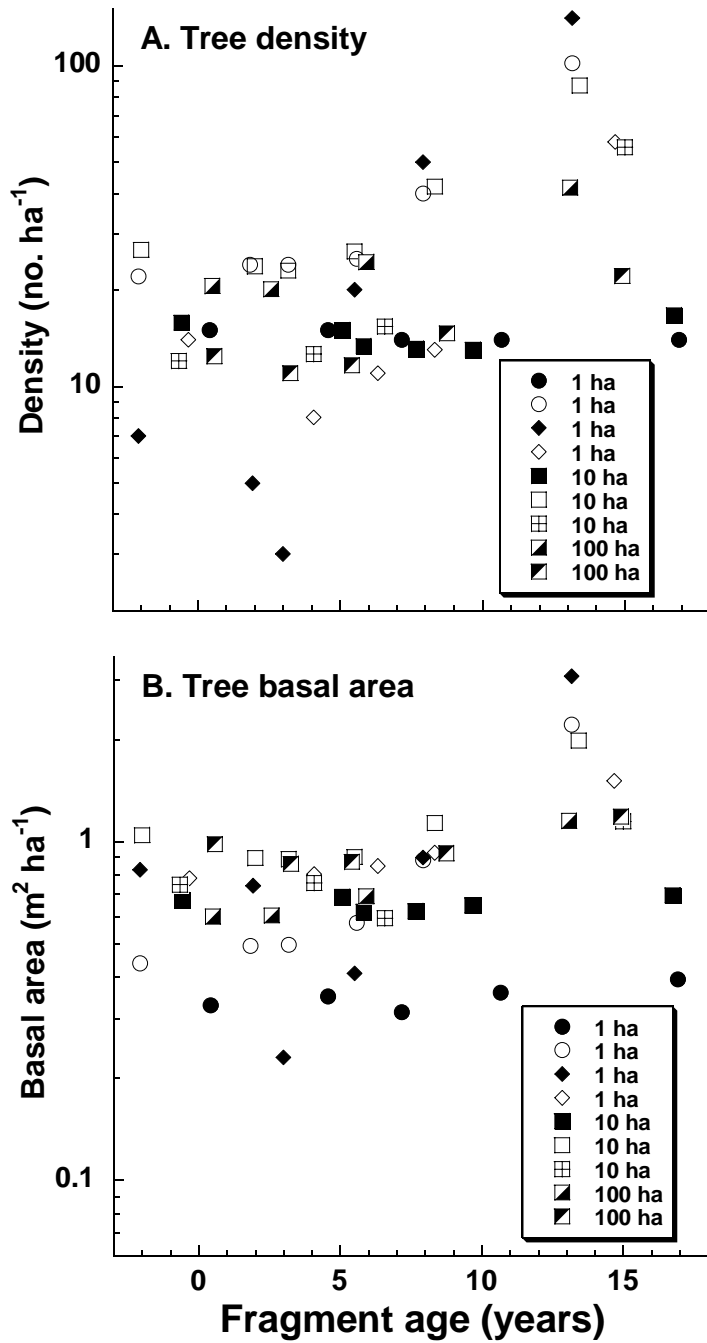




Fig. 4

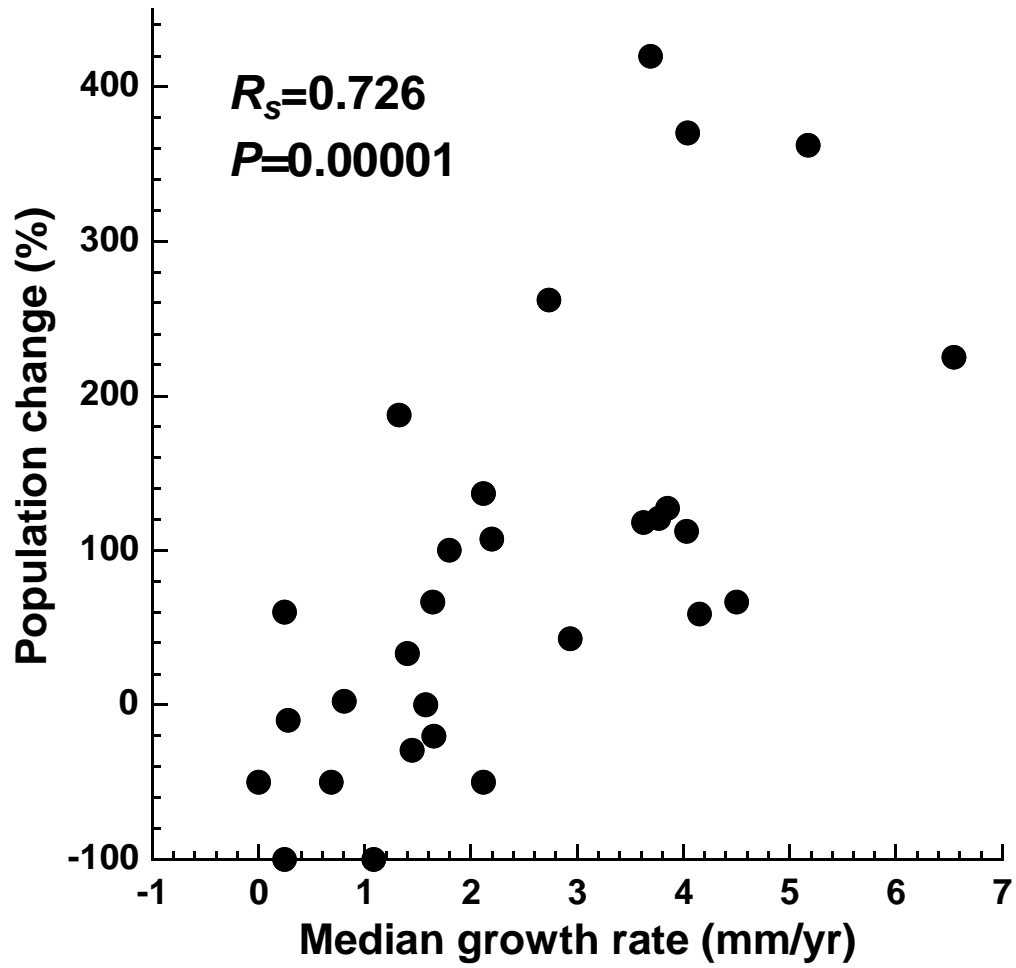


Fig. 5

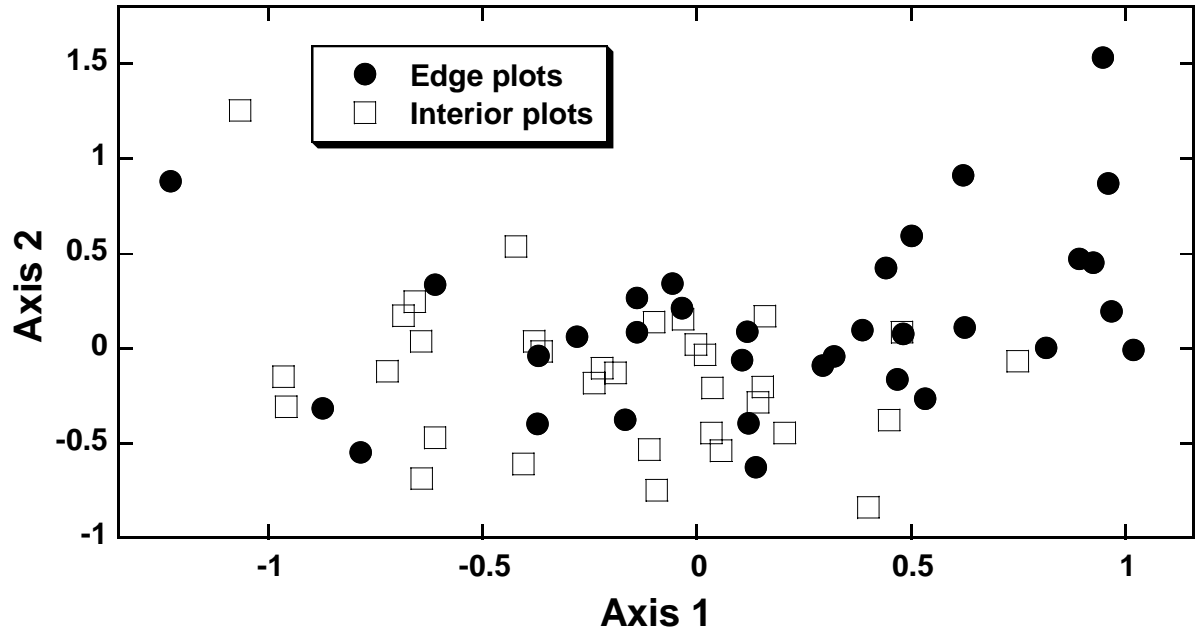


Fig. 6

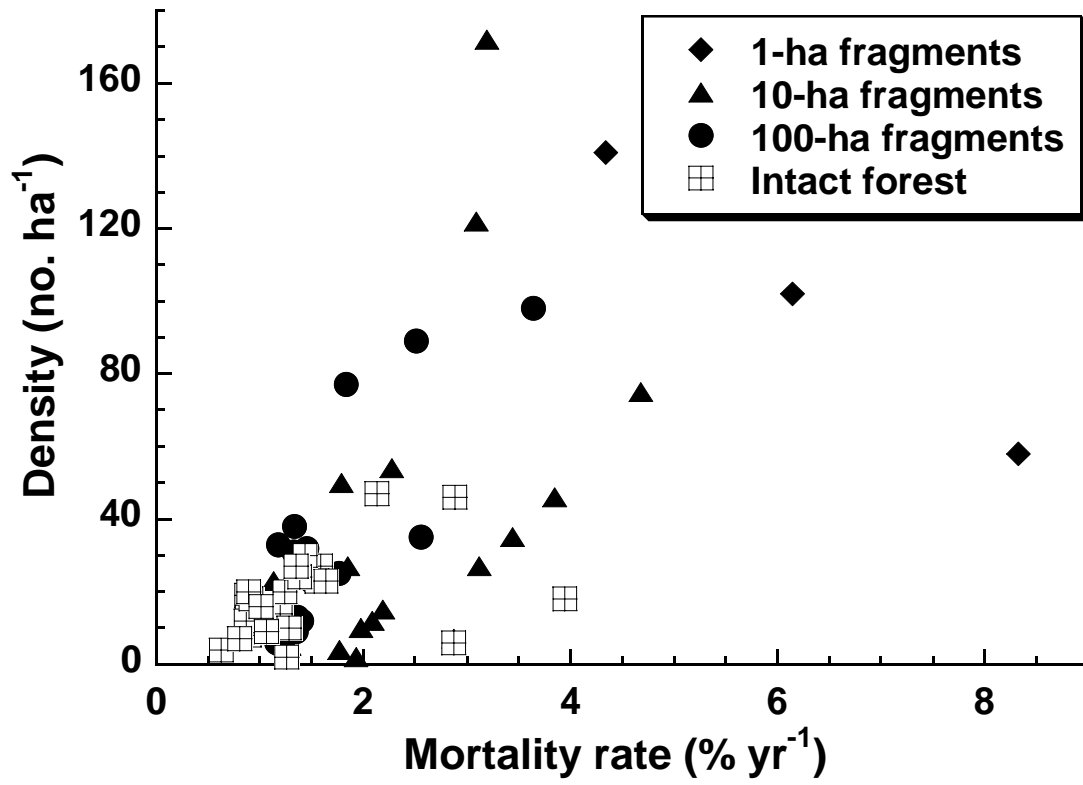
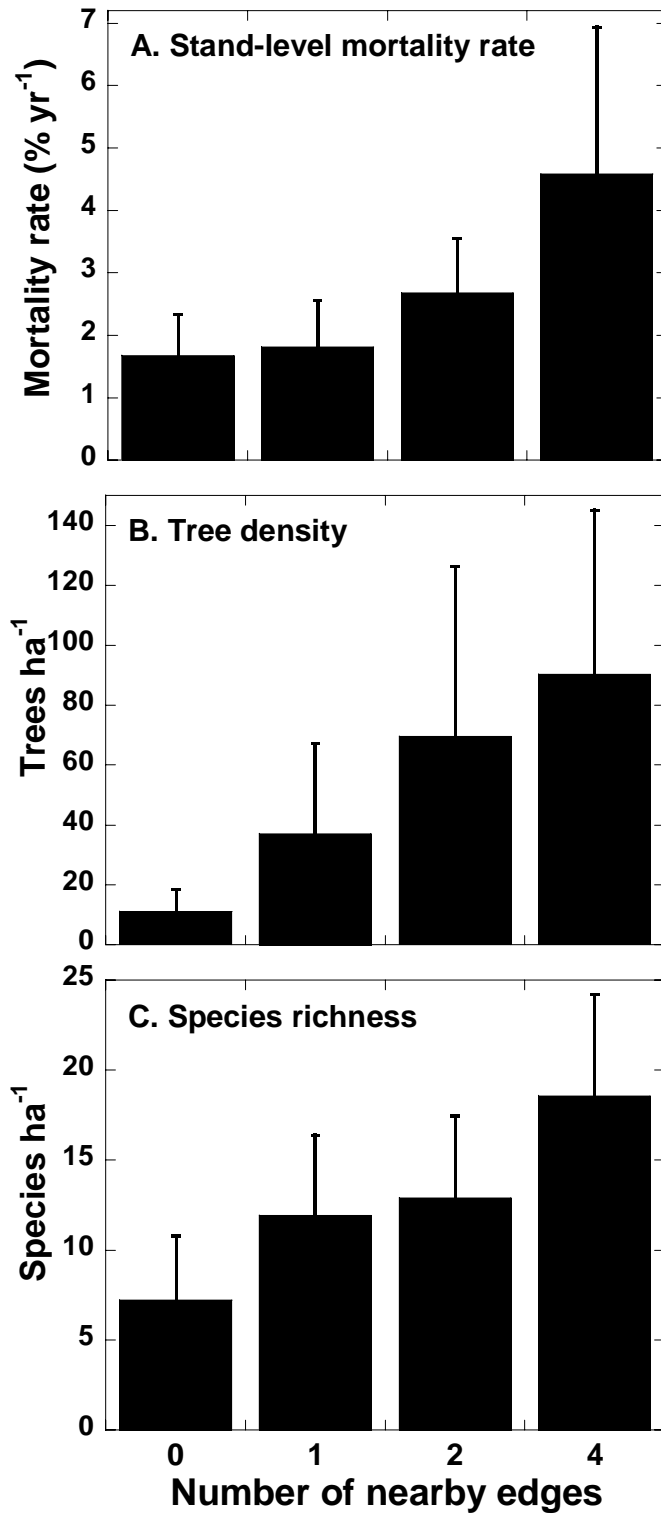


Fig. 7



Appendix 1 (to be lodged online). Available data on initial population density, regeneration capacity, wood specific gravity (wood density), seed-dispersal mode, and median and maximum growth rates for 52 successional tree species or morphospecies in central Amazonia. Also shown is the percentage change in population density for each species near forest edges. Data on regeneration capacities (E=early successional species that can regenerate in pastures; M=mid-successional species normally found in regrowth forest or treefall gaps in primary forest) and seed-dispersal mode (AN=animal dispersed species; AB=abiotically dispersed species; AB/AN=partially abiotically dispersed species) were gleaned from publications and graduate theses. Data on wood density are from publications or from tree cores in our study area.

Species	Density change (%) <sup>a</sup>	Initial density (no. ha <sup>-1</sup> )	Regen. capacity	Wood density (g cm <sup>-3</sup> )	Dispers. mode	Median growth rate (mm yr <sup>-1</sup> )	Maximum growth rate (mm yr <sup>-1</sup> ) <sup>b,c</sup>
<i>Annona amazonica</i>	0	0	0			0	0.51
<i>Annona ambotay</i>	-50	0.12	M		AB		
<i>Annona foetida</i>	33.3	0.09	M			4.04	5.27
<i>Bellucia dichotoma</i>	370	0.3	M		AN		
<i>Bellucia grossularioides</i>	-100	0.06	E			1.57	15.29
<i>Cecropia distachya</i>	0	0.06	E		AB/AN	3.69	6.19
<i>Cecropia purpurascens</i>	420	0.15	M	0.36	AN	15.88	16.04
<i>Cecropia sciadophylla</i>	3140	0.3	E	0.39	AN		
<i>Cecropia ulei</i>	100	0.06	M				
<i>Cecropia vs. ficifolia</i>	-100	0.03					
<i>Croton draconoides</i>	-25	0.12				2.73	8.05
<i>Croton lanjouwensis</i>	262.2	1.36	E	0.62		1.44	3.43
<i>Goupia glabra</i>	-29.4	1.55	E	0.72	AB/AN	1.4	4.95
<i>Jacaranda aff. copaia</i>	33.3	0.09				0.81	3.95
<i>Jacaranda copaia</i>	2.3	1.3	E	0.35	AB		
<i>Miconia aff. hypoleuca</i>	100	0.06				5.17	8.78
<i>Miconia burchellii</i>	362.2	1.12	M		AB		
<i>Miconia cf. crassinervia</i>	1000	0.03					
<i>Miconia cf. navioensis</i>	-100	0.03				1.64	1.88
<i>Miconia cf. tetrasperma</i>	66.7	0.27					
<i>Miconia dispar</i>	400	0	M			4.5	7.31
<i>Miconia elaeagnoides</i>	66.7	0.64	M				
<i>Miconia gratissima</i>	0	0					
<i>Miconia holosericea</i>	0	0.03				1.79	4.42
<i>Miconial ongispicata</i>	100	0.03					
<i>Miconia minutiflora</i>	0	0.03	M		AN	1.32	1.73
<i>Miconia phanerostila</i>	187.5	0.24				0.25	4.03
<i>Miconia punctata</i>	60	0.15				4.03	11.74
<i>Miconia pyrifolia</i>	112.5	0.48				0.28	0.56

<i>Miconia regelii</i>	-10	0.3 M		0.25	1.33
<i>Miconia splendens</i>	-100	0.03 M			
<i>Miconia sp. nov. aff lepidota/punctata</i>	0	0			
<i>Miconia tetraspermoides</i>	200	0.03		0.69	1.41
<i>Miconia tomentosa</i>	-50	0.06	0.71	4.15	10.74
<i>Pourouma bicolor</i>	59	1.18 M	0.36 AB		
<i>Pourouma cf. cucura</i>	200	0		3.85	9.83
<i>Pourouma cucura</i>	127.3	0.33		3.77	9.52
<i>Pourouma guianensis</i>	120.7	0.88 M	0.38 AN	6.54	10.27
<i>Pourouma melinonii</i>	225	0.12	0.32	2.94	5.27
<i>Pourouma minor</i>	42.9	0.64 M	0.44 AN		
<i>Pourouma myrmecophyla</i>	0	0 M		1.65	4.04
<i>Pourouma ovata</i>	-20	0.61		3.63	7.49
<i>Pourouma tomentosa</i>	118.3	2.15	0.4 AN	2.12	10.31
<i>Pourouma velutina</i>	136.8	0.58		2.2	6.73
<i>Pourouma villosa</i>	107.4	0.82	0.34		
<i>Vismia amazonica</i>	1200	0			
<i>Vismia bemerguii</i>	1100	0.03 M	AB/AN		
<i>Vismia cayennensis</i>	950	0.06 E	0.5		
<i>Vismia duckei</i>	500	0.03			
<i>Vismia guianensis</i>	1400	0 E	0.48 AN	2.12	24.92
<i>Vismia japurensis</i>	-50	0.18 E		1.08	5.14
<i>Vismia macrophylla</i>	-100	0.18 E	0.49		

<sup>a</sup> Based on data from 33 1-ha plots that were <100 m from the nearest forest edge, contrasting densities from before fragmentation vs. 13-17 years after forest fragmentation. For species with an initial density of 0 individuals ha<sup>-1</sup>, data from pre- and post-fragmentation censuses were (X+1)-transformed prior to calculating percentages.

<sup>b</sup> Growth-rate data were generated only for species with ≥3 individuals in forest-interior plots (>100 m from the nearest edge).

<sup>c</sup> To avoid possible bias from outliers, maximum growth rates are the upper decile of values for each species.