

## 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 (~1000 km<sup>2</sup>) experimental landscape, with forest fragments ranging from 1 to 100 ha in area.

Prior to forest fragmentation, successional trees were uncommon, typically comprising 2–3% of all trees (≥10 cm diameter at breast height [1.3 m above the ground surface]) 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. Fragment age had strong, positive effects on the density and basal area of successional trees, with no indication of a plateau in these variables, suggesting that successional species could become even more abundant in fragments over time.

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 nearby intact forest, suggesting that faster-growing species have a strong advantage in forest fragments.

An ordination analysis revealed three main gradients in successional-species composition across our study area. Species gradients were most strongly influenced by the stand-level rate of tree mortality on each plot and by the number of nearby forest edges. Species composition also varied significantly among different cattle ranches, which differed in their surrounding matrices and disturbance histories. These same variables were also the best predictors of total successional-tree abundance and species richness. Successional-tree assemblages in fragment interior plots (>150 m from edge), which are subjected to fragment area effects but not edge effects, did not differ significantly from those in intact forest, indicating that area effects per se had little influence on successional trees. Soils and topography also had little discernable effect on these species.

Collectively, our results indicate that successional-tree species proliferate rapidly in fragmented Amazonian forests, largely as a result of chronically elevated tree mortality near forest edges and possibly an increased seed rain from successional plants growing in nearby degraded habitats. The proliferation of fast-growing successional trees and correlated decline of old-growth trees will have important effects on species composition, forest dynamics, carbon storage, and nutrient cycling in fragmented forests.

**Key words:** Amazon; carbon storage; edge effects; floristic composition; forest dynamics; habitat fragmentation; permanent plots; pioneers; tree communities; tropical forest.

### INTRODUCTION

The Amazon Basin sustains some of the world's most biologically diverse forests (Gentry 1988, Valencia et

al. 1994, de Oliveira and Mori 1999). Unfortunately, these forests are being destroyed at an alarming pace: deforestation rates in Brazilian Amazonia currently average  $2.4 \times 10^6$  ha per year, equivalent to 11 football fields per minute (Laurance et al. 2004). Forests in southern and eastern Amazonia have already been severely reduced and fragmented (Skole and Tucker

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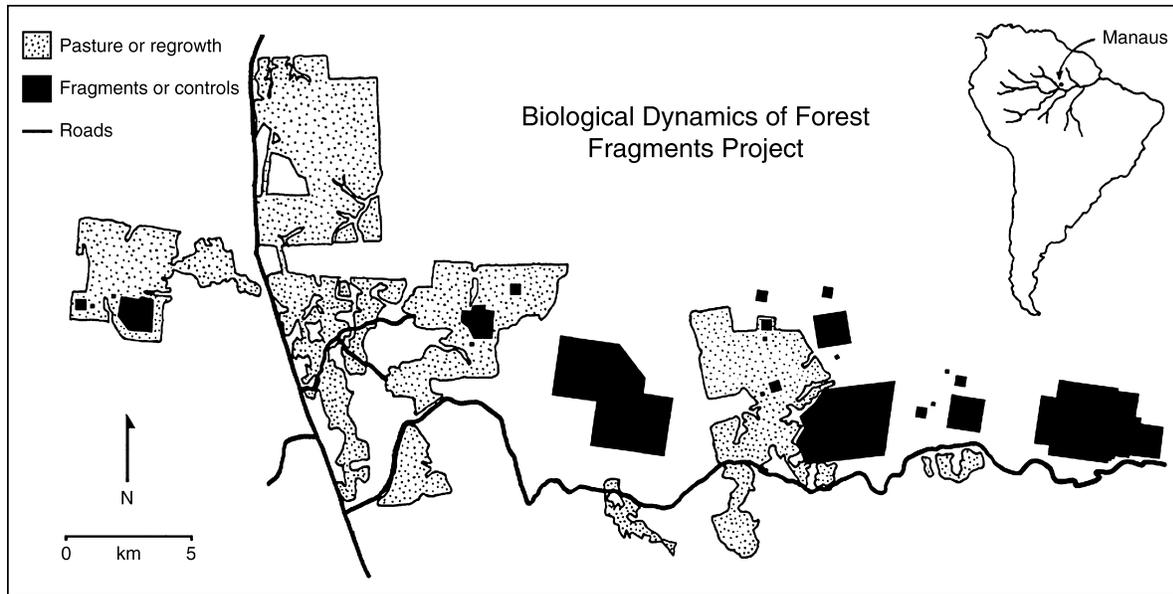


FIG. 1. The study area in central Amazonia, showing locations of forest fragments and control sites in intact forest.

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 (da 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, Oliveira-Filho et al. 1997, Laurance et al. 1998a, Tabarelli et al. 1999) 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 1983, 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 small but detectable increases up to 300 m from

edges (Laurance et al. 1998a, 2000). Additional disturbances, such as logging and surface fires, can further exacerbate tree mortality in fragmented landscapes (Cochrane and Laurance 2002).

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 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 durations (Crome 1997). Here we present findings from a long-term study that largely circumvents 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 response of successional trees to soil, topographic, forest dynamic, and landscape features in order 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 ~1000 km<sup>2</sup> (Fig. 1) and is located 80 km north 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 1900 to 3500 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 [1.3 above the ground surface; dbh]) per hectare (de 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 70–1000 m) from the surrounding forest by clearing the intervening vegetation to establish pastures in three large ( $\sim 5000$  ha) cattle ranches. Fragments were fenced to prevent encroachment by cattle. Reserves ranging from 1 to 1000 ha in area were delineated in nearby continuous forest to serve as experimental controls. Parts of the three ranches were soon abandoned, with *Cecropia*-dominated regrowth proliferating in areas that were cleared but not burned and *Vismia*-dominated regrowth regenerating on pastures that were repeatedly burned (Mesquita et al. 2001).

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 are generally 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. More than 60 000 trees ( $\geq 10$  cm dbh) are being monitored at regular (typically 4–6 yr) intervals within 66 permanent, square 1-ha plots spanning the study area. Thirty-nine of the plots are located within fragments: four 1-ha fragments (four 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 both edge and interior areas are 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.

We included in our analysis all identified species and morphospecies within nine of the most important successional genera in our study area. Our criteria for selecting these genera is that they were (1) relatively common within 2–15 year-old regenerating forests near our forest fragments (Mesquita et al. 2001, Moreira 2003, Grau 2004) and (2) present in at least some of our 66 study plots in fragmented and intact forests. The only major exception was the diverse legume genus *Inga*, which contains a mix of successional and old-growth species but was not included because of a general lack of knowledge about the ecology of individual species and difficulty in identifying some species. Some other successional treelets (e.g., certain *Vismia* spp.) rarely reach 10 cm dbh even when mature and thus were too small to be included in our study.

#### *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, describe 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 was determined for each plot by dividing it into 25 quadrats of  $20 \times 20$  m each, measuring the maximum slope in each quadrat with a clinometer, and 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 (Fearnside and Leal-Filho 2001). Within each quadrat, 15 surface samples (top 20 cm below litter layer) were collected at haphazard locations using a soil auger and then bulked and subsampled. Composite samples were oven-dried, cleaned, and passed through 20- and 2-mm sieves. Textural analyses, using the pipette method, were used to determine the percentage

of 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.

An index of forest disturbance, the mean stand-level rate of tree mortality (mean percentage of all trees dying annually), was determined for each plot (Nascimento and Laurance 2004) using a standard logarithmic model (cf. Sheil et al. 1995). 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 the amount and type of regrowth forest present (Bierregaard and Stouffer 1997; Nascimento et al., *in press*) and in the intensity of past windstorms, which can cause sharply elevated tree mortality in fragments (Laurance et al. 1998a).

Finally, we gleaned data on six ecological traits for many of our successional species to help predict their responses to forest fragmentation. Three demographic variables (initial population density, median and maximum growth rates in intact forest) were generated from our long-term forest dynamics study. Data on three other species traits, their regeneration capacities in pasture and regrowth forest, seed dispersal mode, and wood density (specific gravity of dry wood, which is correlated with traits such as growth rate, stem strength, and possibly drought tolerance; Borchert 1994, Hacke et al. 2001, ter Steege and Hammond 2001), were collected from a review of >130 publications and theses (W. F. Laurance and S. D'Angelo, *unpublished data*) and from colleagues (J. Chave and H. Muller-Landau, *personal communication*).

#### Data analysis

To quantify the change in population density of each successional species over time in fragmented forests, we calculated the intrinsic rate of population change ( $\log[\text{final density}/\text{initial density}]$ ), which was approximately normally distributed. Because the density of successional trees varied considerably among plots, we estimated successional-tree diversity using Fisher's log series  $\alpha$ , an index of species diversity that is insensitive to sample size (Magurran 1988).

When using parametric statistical tests, appropriate transformations were used to improve normality and stabilize variances of response variables and to help linearize relationships between response and predictor variables. Wilk-Shapiro tests (Zar 1999) were used to assess data normality. Data on tree density, basal area, stand-level mortality rates, median growth rates, wood density, and distance to forest edge were log transformed; percentage of sand data were arcsine square-root transformed; and slope data and maximum growth

rates were square-root transformed. The area of each fragment (1, 10, or 100 ha) and control site in intact forest was log transformed, with control sites assumed to have an area of 100 000 ha. A categorical variable was used to discriminate the three cattle ranches in our study area.

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 general linear models (GLM) in Systat version 10 (SPSS 2000). Our GLM model assumed a normal error structure and hence appropriate data transformations were used. Prior to analysis, Pearson correlations were used to test for strong intercorrelations among predictor variables, which can cause collinearity effects (Zar 1999). Performance of the final GLM models was assessed by comparing the standardized residuals to the fitted values and to each significant predictor (cf. Crawley 1993).

## RESULTS

### *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 to mid-1980s), there was no significant difference between the two treatments ( $t = 1.44$ ,  $df = 64$ ,  $P = 0.15$ ; two-sample  $t$  test), with interior plots and those that would later be edge plots having similar successional-tree densities ( $14.3 \pm 10.7$  and  $16.9 \pm 9.9$  stems/ha, respectively [mean  $\pm$  SD]). 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), whereas interior plots showed no significant change over time ( $t = 1.68$ ,  $df = 32$ ,  $P = 0.104$ ; paired  $t$  tests contrasting the same plots pre- vs. post-fragmentation).

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% successional trees and the remainder having substantially higher proportions (10–26%) of these trees.

In the forest interior plots, there was no change in mean species richness of successional trees between

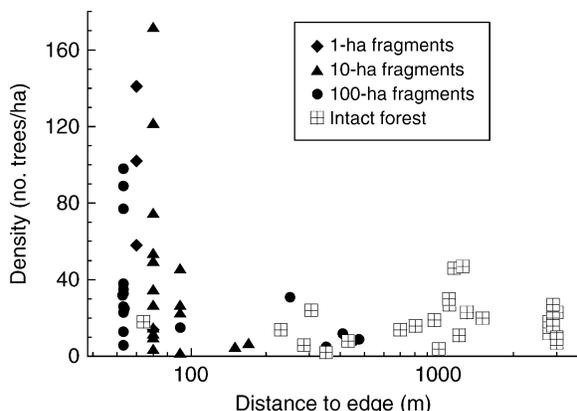


FIG. 2. Density of successional trees as a function of distance from forest edge (note the log scale), in 66 1-ha plots in intact forest and in nine forest fragments ranging from 13 to 17 years old. The relationship is highly significant ( $r_s = -0.393$ ,  $n = 66$ ,  $P = 0.001$ ; Spearman rank correlation).

the pre-fragmentation census and that 13–17 years after fragmentation ( $t = -1.74$ ,  $df = 32$ ,  $P = 0.092$ ). On edge plots, however, successional-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 result of increasing successional-tree density on edge plots, as there was no significant difference in Fisher's  $\alpha$  values between the pre- ( $10.15 \pm 4.80$ ) and post-fragmentation ( $8.82 \pm 4.22$ ) censuses of the edge plots ( $t = 0.90$ ,  $df = 29$ ,  $P = 0.38$ ; paired  $t$  test), nor between the edge ( $8.82 \pm 4.22$ ) and interior ( $10.12 \pm 5.63$ ) plots 13–17 years after fragmentation ( $t = 0.99$ ,  $df = 55$ ,  $P = 0.32$ ; two-sample  $t$  test; sample sizes varied because a few plots had too few individuals to calculate  $\alpha$  values).

#### Ecological differences among species

The 52 tree species we examined exhibited great variability in their response to fragmentation and forest edges (Appendix A). Nearly two-thirds of these 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 (seven species) or declined in density (12 species).

We tested the efficacy of six ecological traits to predict the population responses ( $\log[\text{final density}/\text{initial density}]$ ) of the tree species to edge effects, using available data (Appendix A). 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 and found no significant effect ( $F_{1,50} = 0.05$ ,  $R^2 = 0.1\%$ ,  $P = 0.83$ ; linear regression). Second, we evaluated species regeneration capacities, contrasting 10 early successional species

that frequently regenerate in cattle pastures vs. 16 mid-successional species that normally occur in regrowth forest or treefall gaps in primary forest. The responses of these two groups to forest edges did not differ significantly ( $t = -0.10$ ,  $df = 24$ ,  $P = 0.92$ ; two-sample  $t$  test). Third, we tested 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 ( $F_{1,13} = 0.97$ ,  $R^2 = 6.3\%$ ,  $P = 0.37$ ; linear regression). Fourth, we assessed the effect of seed-dispersal mode, contrasting eight species that are entirely animal dispersed with seven species that are partially or completely dispersed abiotically. Although animal-dispersed species generally had larger population increases ( $701 \pm 1084\%$ ) in edge plots than did abiotically dispersed species ( $206 \pm 418\%$ ), the difference was nonsignificant ( $t = 1.71$ ,  $df = 13$ ,  $P = 0.11$ ; two-sample  $t$  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 ( $F_{1,28} = 4.25$ ,  $R^2 = 13.2\%$ ,  $P = 0.049$ ) and median growth rate was a highly significant predictor ( $F_{1,28} = 36.90$ ,  $R^2 = 56.9\%$ ,  $P < 0.00001$ ) of their responses to forest edges (linear regressions). 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. 3).

#### Ecological gradients in species composition

The NMS ordination revealed three major gradients in species composition among plots (Appendix B), based on the 24 most abundant successional species (each detected in  $\geq 10$  plots) recorded 13–17 years after forest fragmentation. Axis 1, which explained 44.5% of the total variation in the data set, described variation

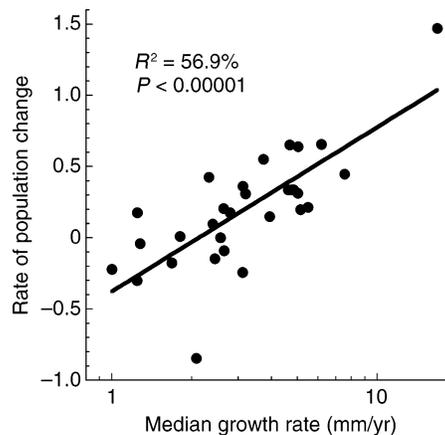


FIG. 3. The influence of median growth rates (log scale) on the intrinsic rate of population change ( $\log[\text{final density}/\text{initial density}]$ ) for 30 predominantly successional tree species near forest edges.

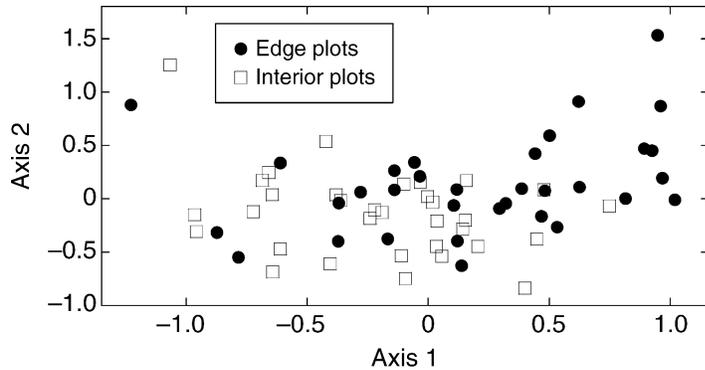


FIG. 4. Ordination of 24 common successional tree species in 66 1-ha plots in fragmented and continuous Amazonian forest. Edge plots are <100 m from the nearest forest edge, whereas interior plots are >100 m from forest edge. Axis lengths are scaled relative to the amount of variation explained by each axis.

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 *P. 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. 4). 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 dichotoma*, and *Miconia burchelli* all increased by >360%). Axis 1 was also strongly and positively correlated with the total species richness ( $r = 0.748$ ,  $P < 0.00001$ ) of successional trees on each plot, 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 1). Although a few predictors were moderately intercorrelated (e.g., stand-level tree mortality was positively correlated with the number of nearby forest edges and negatively correlated with distance to edge,  $R^2 = 32$ –44%), no correlation was strong enough to cause major collinearity effects ( $R^2 \leq 45\%$  in all cases).

Four predictors significantly influenced the total population density of successional trees: stand-level tree mortality and the number of nearby forest edges, both of which increased tree density; fragment area, which decreased tree density; and cattle ranch, with the eastern ranch (Fig. 1) having a lower tree density than the other two ranches (Table 1). Trends were similar for the species richness of successional trees, except that the effects of fragment area were nonsignificant.

The three ordination axes describing gradients in successional-tree community composition were correlated in individualistic ways with the predictors. Axis 1 was significantly associated with the stand-level rate of tree mortality and cattle ranch, with the eastern ranch differing significantly from the other two ranches. Axis 2 was correlated only with stand-level tree mortality. Axis 3 was significantly affected by the number of nearby forest edges and cattle ranch, with the western ranch differing in composition from the other two ranches.

TABLE 1. Influence of edaphic, landscape, and forest-dynamics predictors on successional tree communities in 66 1-ha plots in fragmented and continuous Amazonian forests, using general linear models.

Response variable	Slope	Sand content	Soil carbon	Tree mortality	Fragment area	Distance to edge	No. edges	Ranch	Multiple $R^2$ (%)
Density	0.407	0.900	0.697	<b>0.001</b>	<b>0.046</b>	0.765	<b>0.008</b>	<b>0.001</b>	53.1
Species	0.542	0.737	0.059	<b>0.038</b>	0.295	0.457	<b>0.003</b>	<b>0.014</b>	49.1
Axis 1	0.664	0.547	0.945	<b>0.001</b>	0.184	0.719	0.125	<b>0.007</b>	44.5
Axis 2	0.370	0.079	0.299	<b>0.014</b>	0.290	0.418	0.666	0.611	29.7
Axis 3	0.231	0.218	0.666	0.054	0.063	0.389	<b>0.015</b>	<b>0.035</b>	34.9

Notes: 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 (significant values appear in boldface type). 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, percentage of 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.

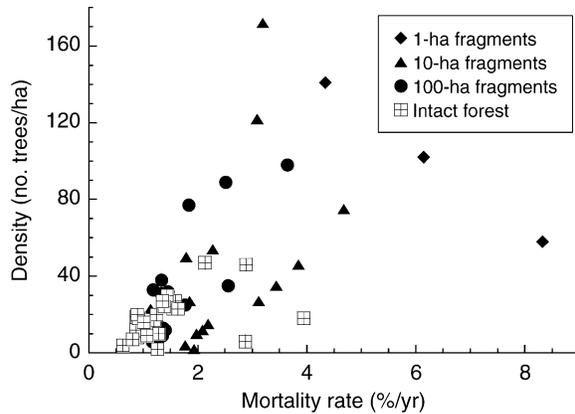


FIG. 5. Effects of forest disturbance (mean rate of stand-level tree mortality) on the density of successional tree species in fragmented and intact Amazonian forests. The relationship is highly significant ( $F_{1,64} = 32.71$ ,  $R^2 = 33.8\%$ ,  $P < 0.0001$ ; linear regression).

The overall conclusion from these GLM models is that the stand-level rate of tree mortality (Fig. 5), number of nearby forest edges (Fig. 6), and cattle ranch had the strongest effects on successional-tree communities in our study area. These same three predictors also generally had the strongest effects on tree species composition, as described by the three ordination axes. Soil and topographic variables had a weak influence on successional trees and fragment area only a modest influence, once effects of the other predictors were accounted for statistically (Table 1).

The conclusion that fragment area effects per se had only a limited influence on successional trees was reinforced by a comparison of forest interior plots (>150 m from edge) 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.

*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 (Fig. 7). We pooled data for all plots within each fragment and then, for each fragment, regressed successional-tree abundance against fragment age. As fragments became older, successional-tree density increased in most (8/9) fragments and basal area increased in all (9/9) fragments, both significant

deviations from chance expectation ( $P = 0.02$  and  $P = 0.0002$ , respectively; sign tests).

Slope coefficients for the regressions describe how successional-tree abundance changed with fragment age, so we used these coefficients as the response variable in an ANCOVA, with  $\log_{10}$  fragment area as a covariate and cattle ranch as a fixed factor (repeated-measures ANOVA was not feasible in this case because the nine fragments were not censused at identical intervals). For successional-tree density, both fragment area ( $F_{1,5} = 6.37$ ,  $P = 0.053$ ; slope negative) and cattle

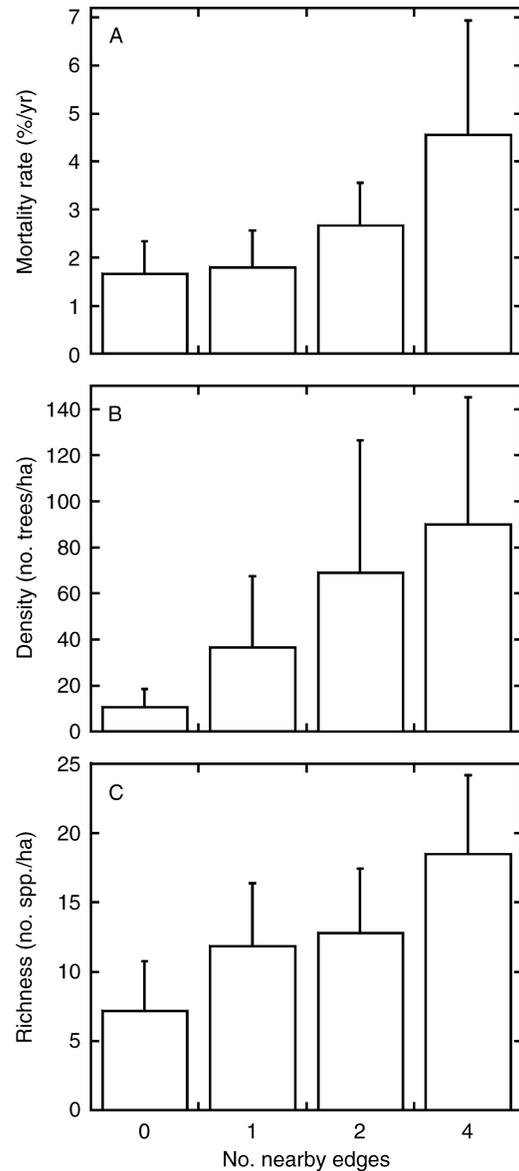


FIG. 6. Effects of number of nearby forest edges (<100 m from the plot center) on the (A) stand-level rate of tree mortality and on the (B) density and (C) species richness of successional trees. Values (means + SD) were adjusted to account for variation in the distance of plots to forest edge (using edge distance as a covariate in ANCOVA models).

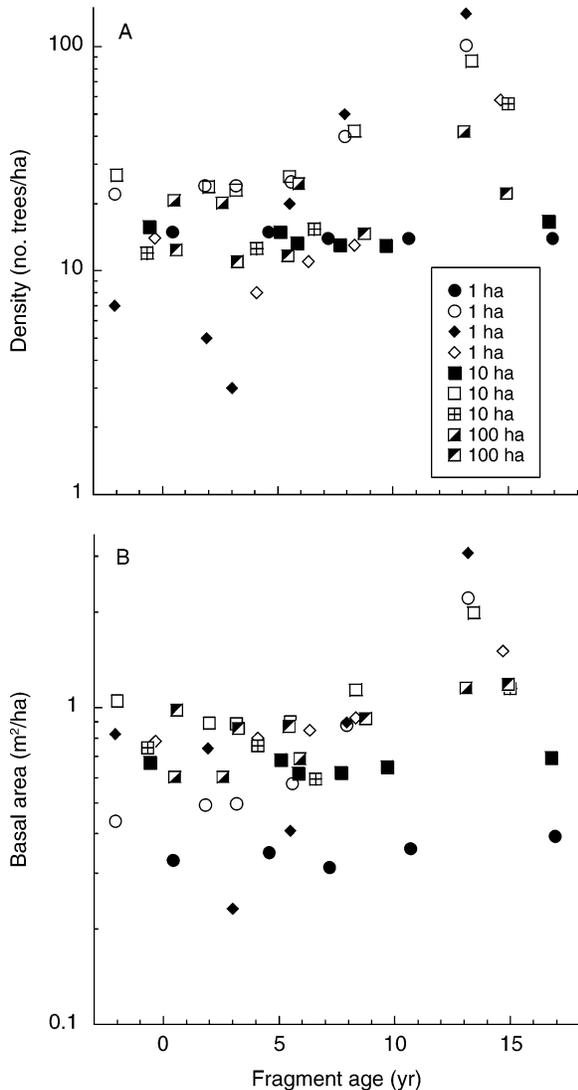


FIG. 7. Effects of fragment age on the (A) density and (B) basal area of successional trees in central Amazonia. Data are shown for 3–6 censuses of each fragment, with pooled data from all 1-ha plots within the same fragment.

ranch ( $F_{2,5} = 7.19$ ,  $P = 0.034$ ) had significant or nearly significant effects. As expected, successional trees increased faster over time (larger slope values) in smaller fragments. Slopes also differed among the ranches, with fragments in the western ranch having significantly ( $P = 0.03$ ) higher slopes than those in the eastern ranch and those in the middle ranch not differing significantly ( $P \geq 0.20$ ) from the other two (Tukey's honestly significant difference [hsd] tests). Results were similar for basal area of successional trees, with both fragment area ( $F_{1,5} = 10.04$ ,  $P = 0.025$ , slope negative) and cattle ranch ( $F_{2,5} = 14.71$ ,  $P = 0.008$ ) having significant effects; in this case the western ranch had significantly higher slopes than did the middle ( $P = 0.05$ ) and eastern ranches ( $P = 0.008$ , Tukey's hsd tests).

Thus, fragment area and cattle ranch both influenced the proliferation of successional trees, with smaller fragments and fragments in the western ranch showing faster rates of increase.

#### Additional edge effects

In addition to elevated stand-level tree mortality, other ecological changes that favor successional trees, such as an increased seed rain from successional plants growing in outside degraded lands and microclimatic alterations that promote germination of successional species, might also occur near forest edges. To test for these effects, we contrasted successional trees in paired edge and interior plots that had very similar stand-level mortality, reasoning that the edge plots should have more abundant and diverse successional-tree assemblages if the other edge effects were also important. Our pairs of plots were always within the same fragment to minimize substantial among-site differences, and in each case we selected the paired edge and interior plots that had the most similar stand-level mortality rate.

Seven pairs of nearby plots met our criteria, such that there was no significant difference ( $t = 0.86$ ,  $P = 0.42$ ) in stand-level tree mortality rates between edge ( $1.91 \pm 1.05\%/yr$ ) and interior ( $1.70 \pm 0.75\%/yr$ ) plots, nor did basal-area losses from tree mortality differ significantly ( $t = 0.75$ ,  $P = 0.48$ ) between edge ( $0.48 \pm 0.22$   $m^2/yr$ ) and interior ( $0.43 \pm 0.08$   $m^2/yr$ ) plots. 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 ( $20.4 \pm 8.3$  vs.  $7.4 \pm 2.3$  stems/ha). 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 ( $10.1 \pm 3.2$  vs.  $5.4 \pm 1.5$  species/ha). Thus, when compared to nearby forest interior plots with very similar stand-level tree mortality, edge plots had much more diverse and 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 striking changes in tree species composition can occur during the first two decades after fragmentation (Fig. 4). 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. These include microclimatic



PLATE 1. Dead and broken trees are common along the margins of Amazonian forest fragments. Photo credit: W. F. Laurance.

changes, increased wind shear and turbulence, elevated tree mortality (see Plate 1), higher liana abundances, altered litterfall and nutrient cycling, and a variety of other ecological changes near forest edges (see Laurance et al. 2002 and references therein). 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 exceptionally abundant in more than a quarter of all edge plots, comprising 10–26% of all trees ( $\geq 10$  cm dbh).

On average, successional trees proliferate more rapidly (Fig. 7) and achieve higher population densities (Fig. 2) in small than in large fragments. However, these patterns are likely driven by edge effects, not fragment area 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 1). 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 limited fragment area per se, such as the collapse of isolated tree populations from random demographic events or inbreeding (cf. Thomas 2004) or as a consequence of area-related declines of pollinators or seed dispersers (da Silva and Tabarelli 2000, Cordeiro and Howe 2003), might require more than two decades to become detectable. Nonetheless, remarkably rapid, seemingly 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 our fragments and often 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, forest canopy disturbance (as reflected in the mean stand-level rate of tree mortality) is a key factor for successional trees (Fig. 5), as most or all of these species are light-loving. Notably, the density of successional trees in our plots was strongly and positively correlated with the abundance of lianas ( $r_s = 0.489$ ,  $n = 66$ ,  $P = 0.00003$ ; Spearman rank correlation), another plant guild that responds positively to canopy disturbances (Laurance et al. 2001b). In addition to forest disturbance, the lateral penetration of light and wind along forest edges could 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). Finally, plots near forest edges probably receive a greater seed rain from successional plants that proliferate in outside modified habitats (Janzen 1983, Willson and Crome 1989, Grau 2004) and in abundant treefall gaps near edges. For many successional species, densities of viable seeds in the litter and soil decline sharply with increasing distance from parent trees, and the likelihood of successful gap colonization rises markedly when reproductive trees are nearby (Dalling 1998, Dalling and Denslow 1998, Grau 2004). The importance of an elevated seed rain and possibly other edge effects is suggested by the significantly greater species richness and density of successional trees in edge plots relative to nearby interior plots with very similar stand-level tree mortality.

As an edge effect, how far do elevated abundances of successional trees penetrate into forest fragments? We attempted to estimate this distance using nonlinear regression techniques (cf. Laurance et al. 1997, 1998a) but with limited success ( $R^2 < 11\%$  in all models and data transformations). The reason, evidently, is that, although successional trees clearly increase near edges (Fig. 2), other factors also strongly influence their local abundance. Key additional variables include the number of nearby forest edges, stand-level tree mortality

(which is somewhat patchy in space and time because of the random nature of windstorms), and the surrounding matrix vegetation, which strongly influences the seed rain into fragments (Janzen 1983, Grau 2004; Nascimento et al., *in press*). Indeed, differences among our three cattle ranches in successional-tree assemblages (Table 1) are substantially attributable to variation in their matrix vegetation and intensity of past windstorms (Nascimento et al., *in press*). Despite these complicating factors, it is apparent from visual inspection (Fig. 2) and calculation of running averages that successional trees are mainly elevated within the first 80–100 m of forest edges, which corresponds closely to the distance at which edge-related tree mortality is most strongly elevated in our fragments (Laurance et al. 1997, 1998a).

The results of our study clearly accord with “additive” edge models (Malcolm 1994, 1998), 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. 6). Given that the most important edge effects penetrate about 100 m inside Amazonian forests (Lovejoy et al. 1986, 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 altered 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. 7), 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 probably increases as edge permeability declines (Laurance 2004). The importance of wind disturbance 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, mean stand-level rates of mortality were very high in the first 3–5 years after fragment isolation, averaging  $3.43 \pm 1.92\%/yr$ , a rate nearly triple that in forest interiors ( $1.23 \pm 0.45\%/yr$ ). However, tree mortality also remained substantially elevated in subsequent years ( $2.70 \pm 1.70\%/yr$ ), 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, could promote a continued erosion of fragment floristic composition. Surrounding land uses will undoubtedly have a major influence on fragment dynamics (as demonstrated by significant differences in successional-tree abundance among our three cattle ranches). Tree mortality in fragments can be greatly exacerbated by selective logging or recurring surface fires (Cochrane and Laurance 2002, Alencar et al. 2004). The results from our experimental study are probably a best case scenario, as many fragments in anthropogenic tropical landscapes suffer from disturbances such as logging, fires, hunting, and fuel-wood gathering (Gascon et al. 2000, Laurance and Cochrane 2001, Peres and Michalski 2006).

### *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 significantly from those in forest interiors (Fig. 4). Some species that were absent or very rare in intact forest (e.g., *Vismia amazonica*, *V. bemerguii*, *V. cayennensis*, *V. duckei*, and *V. guianensis*) became established near edges, whereas other forest species (e.g., *Cecropia sciadophylla* and *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 were dominated by the fastest-growing successional species, whereas slower-growing species tended to decline in abundance (Fig. 3). A number of bat- and bird-dispersed species also increased in forest fragments, as has been observed in other tropical forests disturbed by fragmentation, logging, and ground fires (Guevara et al. 1992, Thiollay 1992, Galindo-González et al. 2000, Barlow et al. 2002). In our study area, some frugivorous bat and bird species commonly forage on successional trees in edge and regrowth habitats (Bierregaard and Stouffer 1997, Sampaio 2000).

Although species in our nine successional genera constituted less than 3% of all trees before forest fragmentation, they accounted for a fifth (19.7%) of all tree recruitment in edge plots after fragmentation. This total would have been even larger had we included all successional species (such as members of the diverse genus *Inga*, which were not considered because their successional status was uncertain) in our study. This pattern demonstrates that the dramatic proliferation in fragments of successional trees and lianas comes at the expense of many old-growth shade-tolerant species (Oliveira-Filho et al. 1997, Laurance et al. 1998b, 2000, 2001b, Tabarelli et al. 1999).

### *Implications*

The proliferation of fast-growing successional trees and lianas in tropical forest fragments and the correlated decline of many old-growth trees have 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 loss of live biomass and reduced 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 longevities 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 do old-growth species, given their small size and low wood density (Chambers et al. 2000).

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 (Oliveira-Filho et al. 1997, Viana et al. 1997).

Fourth, faunal communities often change in response to compositional and structural shifts in tree communities (e.g., Pearman 1997, Malcolm and Ray 2000). Some successional trees (e.g., *Cecropia* spp.) provide abundant food for frugivorous bats and birds, but a decline of old-growth trees would have deleterious effects on tree-cavity-dependent animals and on some specialized mutualists and herbivores (Gilbert 1980, Lindenmayer et al. 1997, Ødegaard et al. 2005). 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, a profusion 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 in our study area have higher rates of leaf turnover than do old-growth trees, and their fallen leaves tend to decompose slowly (because they have a lower initial concentration of N and higher C:N and lignin:N ratios, all of which deter decomposers; Vasconcelos and Laurance 2005). For these reasons, litter stocks increase near forest margins (Sizer et al. 2000, Vasconcelos and Luizão 2004), especially during periods of drought stress, when leaf shedding by plants increases (Laurance and Williamson 2001). Surface fires, which often originate in the frequently burned cattle pastures surrounding fragments, are extremely destructive to forests, typically killing 20–50% of all trees and all vines (Cochrane et al. 1999, Barlow et al. 2003). 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.

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#### LITERATURE CITED

- Alencar, A. A., L. Solórzano, and D. C. Nepstad. 2004. Modeling forest understory fires in an eastern Amazonian landscape. *Ecological Applications* **14**:S139–S149.
- Asquith, N. M., S. J. Wright, and M. J. Clauss. 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. *Ecology* **78**: 941–946.
- Barlow, J., T. Haugaasen, and C. A. Peres. 2002. Effects of ground fires on understory bird assemblages in Amazonian forests. *Biological Conservation* **105**:157–169.
- Barlow, J., C. A. Peres, B. O. Lagan, and T. Haugaasen. 2003. Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecology Letters* **6**:6–8.
- Benitez-Malvido, J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* **12**:380–389.
- Bierregaard, R. O., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. 2001. *Lessons from Amazonia: the ecology and conservation of a fragmented forest*. Yale University Press, New Haven, Connecticut, USA.
- Bierregaard, R. O., Jr., and P. C. Stouffer. 1997. Understory birds and dynamic habitat mosaics in Amazonian rainforest. Pages 138–155 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, Illinois, USA.
- Borchert, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* **75**:1437–1449.
- Bravard, S., and D. Righi. 1989. Geochemical differences in an oxisol-spodosol toposequence of Amazonia, Brazil. *Geoderma* **44**:29–42.
- Bruna, E. M. 1999. Seed germination in rainforest fragments. *Nature* **402**:139.
- Chambers, J. Q., N. Higuchi, and J. Schimel. 1998. Ancient trees in Amazonia. *Nature* **391**:135–136.
- Chambers, J. Q., N. Higuchi, J. P. Schimel, L. V. Ferreira, and J. M. Melack. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia* **122**:380–388.
- Chauvel, A., Y. Lucas, and R. Boulet. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experientia* **43**:234–240.
- Cochrane, M. A., A. Alencar, M. D. Schulze, C. M. Souza, D. C. Nepstad, P. Lefebvre, and E. Davidson. 1999. Positive feedbacks in the fire dynamics of closed canopy tropical forests. *Science* **284**:1832–1835.
- Cochrane, M. A., and W. F. Laurance. 2002. Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology* **18**:311–325.
- Cordeiro, N. J., and H. F. Howe. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences (USA)* **100**:14052–14056.
- Crawley, M. J. 1993. *GLIM for ecologists*. Blackwell Scientific, London, UK.
- Crome, F. H. J. 1997. Researching tropical forest fragmentation: shall we keep on doing what we're doing? Pages 485–501 in W. F. Laurance and R. O. Bierregaard, editors. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago, Illinois, USA.
- Dalling, J. W. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology* **79**:564–578.
- Dalling, J. W., and J. S. Denslow. 1998. Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest, Panama. *Journal of Vegetation Science* **9**: 669–678.
- D'Angelo, S., A. Andrade, S. G. Laurance, W. F. Laurance, and R. Mesquita. 2004. Inferred causes of tree mortality in fragmented and intact Amazonian forests. *Journal of Tropical Ecology* **20**:243–246.
- da Silva, J. M. C., and M. Tabarelli. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeastern Brazil. *Nature* **404**:72–74.
- de Oliveira, A. A., and S. A. Mori. 1999. A central Amazonian terra firme forest. I. High tree species richness on poor soils. *Biodiversity and Conservation* **8**:1219–1244.
- Didham, R. K., and J. H. Lawton. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* **31**:17–30.
- Fearnside, P. M., and N. Leal-Filho. 2001. Soil and development in Amazonia: lessons from the Biological Dynamics of Forest Fragments Project. Pages 405–422 in R. O. Bierregaard, C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. *Lessons from Amazonia: the ecology and conservation of a fragmented forest*. Yale University Press, New Haven, Connecticut, USA.
- Galindo-González, J., S. Guevara, and V. J. Sosa. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conservation Biology* **14**:1693–1703.
- Gascon, C., G. B. Williamson, and G. A. B. Fonseca. 2000. Receding edges and vanishing reserves. *Science* **288**:1356–1358.
- Gentry, A. H. 1988. Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences (USA)* **85**:156–159.
- Gilbert, L. E. 1980. Food web organization and the conservation of Neotropical diversity. Pages 11–33 in M. E. Soulé and B. A. Wilcox, editors. *Conservation biology: an evolutionary-ecological perspective*. Sinauer, Sunderland, Massachusetts, USA.
- Grau, H. R. 2004. Landscape context and local-scale environment influence regeneration of pioneer tree species in treefall gaps. *Biotropica* **36**:52–59.
- Guevara, S., J. Meave, P. Moreno-Casasola, and J. Laborde. 1992. Floristic composition and structure of vegetation under isolated trees in neotropical pastures. *Journal of Vegetation Science* **3**:655–664.
- Hacke, U. G., J. S. Sperry, W. Pockman, S. Davis, and K. McCulloh. 2001. Trends in wood density and structure linked to prevention of xylem implosion by negative pressure. *Oecologia* **126**:457–461.
- 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.

- Kapos, V., G. Ganade, E. Matsui, and R. L. Victoria. 1993.  $\delta^{13}\text{C}$  as an indicator of edge effects in tropical rainforest reserves. *Journal of Ecology* **81**:425–432.
- 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, Illinois, USA.
- Laurance, W. F. 2004. Forest–climate interactions in fragmented tropical landscapes. *Philosophical Transactions of the Royal Society B* **359**:345–352.
- Laurance, W. F., A. K. M. Albernaz, P. M. Fearnside, H. L. Vasconcelos, and L. V. Ferreira. 2004. Deforestation in Amazonia. *Science* **304**:1109.
- Laurance, W. F., and R. O. Bierregaard, Jr., editors. 1997. *Tropical forest remnants: ecology, management and conservation of fragmented communities*. University of Chicago Press, Chicago, Illinois, USA.
- Laurance, W. F., and M. A. Cochrane, editors. 2001. Synergistic effects in fragmented landscapes. *Conservation Biology* **15**:1488–1535.
- Laurance, W. F., M. A. Cochrane, S. Bergen, P. M. Fearnside, P. Delamonica, C. Barber, S. D'Angelo, and T. Fernandes. 2001a. The future of the Brazilian Amazon. *Science* **291**:438–439.
- Laurance, W. F., P. Delamonica, S. G. Laurance, H. L. Vasconcelos, and T. E. Lovejoy. 2000. Rainforest fragmentation kills big trees. *Nature* **404**:836.
- Laurance, W. F., P. M. Fearnside, S. G. Laurance, P. Delamonica, T. E. Lovejoy, J. M. Rankin-de Merona, J. Q. Chambers, and C. Gascon. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management* **118**:127–138.
- Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, and S. G. Laurance. 1998a. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* **79**:2032–2040.
- Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, S. G. Laurance, R. Hutchings, and T. E. Lovejoy. 1998b. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* **12**:460–464.
- Laurance, W. F., and C. Gascon, editors. 1999. Ecology and management of fragmented tropical landscapes. *Biological Conservation* **91**:101–247.
- Laurance, W. F., S. G. Laurance, and P. Delamonica. 1998c. Tropical forest fragmentation and greenhouse gas emissions. *Forest Ecology and Management* **110**:173–180.
- Laurance, W. F., S. G. Laurance, L. V. Ferreira, J. Rankin-de Merona, C. Gascon, and T. E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. *Science* **278**:1117–1118.
- Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* **16**:605–618.
- Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, R. Condit, S. D'Angelo, and A. Andrade. 2004. Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *Forest Ecology and Management* **190**:131–143.
- Laurance, W. F., D. Perez-Salicrup, P. Delamonica, P. M. Fearnside, S. D'Angelo, A. Jerzolinski, L. Pohl, and T. E. Lovejoy. 2001b. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* **82**:105–116.
- Laurance, W. F., and G. B. Williamson. 2001. Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conservation Biology* **15**:1529–1535.
- Leigh, E. G., S. J. Wright, E. Herre, and F. E. Putz. 1993. The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evolutionary Ecology* **7**:76–102.
- Lindenmayer, D. B., R. B. Cunningham, and C. F. Donnelly. 1997. Decay and collapse of trees with hollows in eastern Australian forests: impacts on arboreal marsupials. *Ecological Applications* **7**:625–641.
- Lovejoy, T. E., R. O. Bierregaard, Jr., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, Jr., A. H. Powell, G. V. N. Powell, H. O. Schubart, and M. B. Hays. 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, Sunderland, Massachusetts, USA.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey, USA.
- Malcolm, J. R. 1994. Edge effects in central Amazonian forest fragments. *Ecology* **75**:2438–2445.
- Malcolm, J. R. 1998. A model of conductive heat flow in forest edges and fragmented landscapes. *Climatic Change* **39**:487–502.
- Malcolm, J. R., and J. C. Ray. 2000. Influence of timber extraction routes on central African small-mammal communities, forest structure, and tree diversity. *Conservation Biology* **14**:1623–1638.
- McCune, B., and M. J. Mefford. 1999. PC-ORD: multivariate analysis of ecological data. Version 4.17. MjM Software, Gleneden Beach, Oregon, USA.
- Mesquita, R., K. Ickes, G. Ganade, and G. B. Williamson. 2001. Alternative successional pathways in the Amazon basin. *Journal of Ecology* **89**:528–537.
- Metzger, J. P. 2000. Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. *Ecological Applications* **10**:1147–1161.
- Moreira, M. P. 2003. *Uso do sensoriamento remoto para avaliar a dinâmica de sucessão secundária na Amazônia central*. Thesis. National Institute for Amazonian Research (INPA), Manaus, Brazil.
- Nascimento, H. E. M., A. C. S. Andrade, J. L. C. Camargo, W. F. Laurance, S. G. Laurance, and J. E. L. Ribeiro. *In press*. Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conservation Biology*.
- Nascimento, H. E. M., and W. F. Laurance. 2004. Biomass dynamics in Amazonian forest fragments. *Ecological Applications* **14**:S127–S138.
- Ødegaard, F., O. H. Diserud, and K. Østbye. 2005. The importance of plant relatedness for host utilization among phytophagous insects. *Ecology Letters* **8**:612–617.
- Oliveira-Filho, A. T., J. M. de Mello, and J. R. S. Scolforo. 1997. Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987–1992). *Plant Ecology* **131**:45–66.
- Pearman, P. B. 1997. Correlates of amphibian diversity in an altered landscape of Amazonian Ecuador. *Conservation Biology* **11**:1211–1225.
- Pearson, T. R. H., D. F. R. P. Burslem, C. E. Mullins, and J. W. Dalling. 2002. Germination ecology of Neotropical pioneers: interacting effects of environmental conditions and seed size. *Ecology* **83**:2798–2807.
- Peres, C. A., and F. Michalski. 2006. Synergistic effects of habitat disturbance and hunting in Amazonian forests. *In*

- W. F. Laurance and C. A. Peres, editors. Emerging threats to tropical forests. University of Chicago Press, Chicago, Illinois, USA.
- Richter, D. D., and L. I. Babbar. 1991. Soil diversity in the tropics. *Advances in Ecological Research* **21**:315–389.
- Sampaio, E. 2000. The effects of fragmentation on structure and diversity of bat communities in a central Amazonian tropical rain forest. Dissertation. University of Tuebingen, Tuebingen, Germany.
- Schelhas, J., and R. Greenberg, editors. 1996. Forest patches in tropical landscapes. Island Press, Washington, D.C., USA.
- Sheil, D., D. Burslem, and D. Alder. 1995. The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* **83**:331–333.
- Sizer, N., and E. V. J. Tanner. 1999. Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biological Conservation* **91**:135–142.
- Sizer, N. C., E. V. J. Tanner, and I. D. Kossman Ferraz. 2000. Edge effects on litterfall mass and nutrient concentrations in forest fragments in central Amazonia. *Journal of Tropical Ecology* **16**:853–863.
- Skole, D., and C. J. Tucker. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* **260**:1905–1910.
- SPSS. 2000. Systat. Version 10. SPSS, San Francisco, California, USA.
- Tabarelli, M., W. Mantovani, and C. A. Peres. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* **91**:119–128.
- Terborgh, J., L. Lopez, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. Adler, T. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**:1923–1926.
- Terborgh, J., and J. S. Weske. 1969. Colonization of secondary habitats by Peruvian birds. *Ecology* **50**:765–782.
- ter Steege, H., and D. S. Hammond. 2001. Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology* **82**:3197–3212.
- Thiollay, J.-M. 1992. Influence of selective logging on bird species diversity in a Guianan rain forest. *Conservation Biology* **6**:47–63.
- Thomas, S. E. 2004. Ecological correlates of tree species persistence in tropical forest fragments. Pages 279–314 in E. Losos and E. G. Leigh, editors. Forest diversity and dynamism: findings from a large-scale plot network. University of Chicago Press, Chicago, Illinois, USA.
- Valencia, R., H. Balslev, and C. G. Paz y Miño. 1994. High tree alpha-diversity in Amazonian Ecuador. *Biodiversity and Conservation* **3**:21–28.
- Vasconcelos, H. L., and W. F. Laurance. 2005. Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape. *Oecologia* **144**:456–462[doi 10.1007/s00442-005-0117-1].
- Vasconcelos, H. L., and F. J. Luizão. 2004. Litter production and litter nutrient concentrations in a fragmented Amazonian landscape. *Ecological Applications* **14**:884–892.
- Viana, V. M., A. 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, editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, Illinois, USA.
- 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.
- Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

#### APPENDIX A

Available ecological, demographic, and life history data for 52 predominantly successional tree species in Amazonia (*Ecological Archives* E087-025-A1).

#### APPENDIX B

Pearson correlations of individual species densities with three ordination axes describing major gradients in successional tree communities (*Ecological Archives* E087-025-A2).