
Effects of the Surrounding Matrix on Tree Recruitment in Amazonian Forest Fragments

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Abstract: Little is known about how the surrounding modified matrix affects tree recruitment in fragmented forests. We contrasted effects of two different matrix types, *Vismia*- and *Cecropia*-dominated regrowth, on recruitment of pioneer tree species in forest fragments in central Amazonia. Our analyses were based on 22, 1-ha plots in seven experimental forest fragments ranging in size from 1 to 100 ha. By 13 to 17 years after fragmentation, the population density of pioneer trees was significantly higher in plots surrounded by *Vismia* regrowth than in plots surrounded by *Cecropia* regrowth, and the species composition and dominance of pioneers differed markedly between the two matrix types. *Cecropia sciadophylla* was the most abundant pioneer in fragments surrounded by *Cecropia* regrowth (constituting nearly 50% of all pioneer trees), whereas densities of species in *Vismia*-surrounded fragments were distributed more evenly. Thus the surrounding matrix had a strong influence on patterns of tree recruitment in Amazonian forest fragments.

Keywords: Amazon, edge effects, forest fragmentation, pioneer species, rain forest

Efectos de la Matriz Circundante sobre el Reclutamiento de Árboles en Fragmentos de Bosque Amazónicos

Resumen: Se conoce poco del efecto de la matriz modificada circundante sobre el reclutamiento de árboles en bosques fragmentados. Contrastamos los efectos de dos tipos diferentes de matriz, vegetación secundaria dominada por *Vismia*- y *Cecropia*-, sobre el reclutamiento de especies de árboles pioneros en fragmentos de bosque en la Amazonia central. Nuestros análisis se basaron en 22 parcelas de 1 ha en siete fragmentos de bosque experimentales que varían entre 1 y 1000 ha. Entre 13 y 17 años después de la fragmentación, la densidad poblacional de árboles pioneros era significativamente mayor en parcelas rodeados por *Vismia* que en las parcelas rodeadas por *Cecropia*, y la composición y dominancia de especies pioneras fueron marcadamente diferentes en cada tipo de matriz. *Cecropia sciadophylla* fue la pionera más abundante en fragmentos rodeados por *Cecropia* (constituyó casi 50% de todos los árboles pioneros), mientras que las densidades de especies en los fragmentos rodeados por *Vismia* se distribuyeron más homogéneamente. Por lo tanto, la matriz circundante tiene una fuerte influencia sobre los patrones de reclutamiento de árboles en fragmentos de bosque Amazónicos.

Palabras Clave: efectos de borde, especies pioneras, fragmentación de bosques, bosque lluvioso

Introduction

Many consequences of tropical forest fragmentation are poorly understood, especially for long-lived organisms

such as trees. Previous studies of forest fragmentation in central Amazonia have emphasized changes in forest structure and dynamics in relation to forest edges. Such edge effects result from alterations of microenvironmental

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conditions and increased wind turbulence near abrupt forest borders between cleared land and remnant forest habitat (Lovejoy et al. 1986; Kapos 1989). The most striking consequence of these changes is sharply elevated tree mortality and associated formation of gaps in the canopy near forest edges (Ferreira & Laurance 1997; Laurance et al. 1998a, 2000). Tree mortality and canopy gaps in turn influence the recruitment of regenerating plants near edges and changes in floristic composition due to the initial disturbance events. Light-demanding, gap-dependent pioneer trees (Laurance et al. 1998b, 2006; Sizer & Tanner 1999) and lianas (Laurance et al. 2001) proliferate in fragments, especially in the vicinity of forest edges, whereas the densities of shade-tolerant, forest-interior seedlings (Benitez-Malvido 1998) and trees (Laurance et al. 1998b) decline.

The importance of edge effects may vary over time in fragmented landscapes (Murcia 1995; Gascon et al. 2000; Laurance et al. 2002). In the first few years after fragmentation, forest edges tend to be structurally open and therefore permeable to fluxes of heat, light, and wind. Over time, however, these physical edge effects may become more buffered, either because fragment edges gradually become "sealed" by proliferating successional trees and lianas or because the fragment is surrounded by regenerating secondary forests. An increasing body of evidence suggests that such changes in edge and surrounding vegetation can have a substantial influence on the microclimate, structure, and dynamics of forest fragments (e.g., Camargo & Kapos 1995; Didham & Lawton 1999; Mesquita et al. 1999).

In the Amazon, as in other parts of Latin America, vast areas of land initially deforested for farming and cattle ranching have been abandoned, resulting in various states of secondary succession. Land abandonment has been promoted by rapid declines in soil productivity (Serrão et al. 1993), increases in migration to urban areas, and the expansion of high-yield agriculture (Lugo 2002; Aide & Grau 2004). By 1990 approximately 47% of deforested land in the Brazilian Amazon was occupied by regrowth forest > 3 years old, and more than one-third of this amount was > 20 years old (Fearnside 1996). In Caribbean islands, changes in land-use systems have led to substantial increases in forest recovery over the past 50 years (Lugo 2002; Aide & Grau 2004). On such lands the type and intensity of land use before abandonment and the proximity of seed sources have been identified as key factors driving successional patterns (e.g., Uhl et al. 1988; Guariguata et al. 1997; Mesquita et al. 2001). Although a seed rain from remnant forests potentially influences regeneration patterns in cleared areas (i.e., the mass effect; Shmida & Wilson 1985), the opposite may also occur: a seed rain from secondary trees growing in the surrounding matrix might affect tree recruitment in forest fragments. Few studies (e.g., Janzen 1983; Grau 2004), however, have assessed whether and how the surrounding matrix vegetation affects floristic composition in forest fragments.

We evaluated recruitment of pioneer tree species in Amazonian forest fragments surrounded by two different types of secondary forest. Specifically, we asked how the two secondary-forest types influence the density, richness, and floristic composition of trees regenerating in fragments. We hypothesized that regenerating pioneers differ among fragments with differing matrix types and that these differences partially reflect the floristic composition of the adjoining matrix.

Methods

Study Site

The Biological Dynamics of Forest Fragments Project (BDFFP) is the world's largest and longest-running experimental study of habitat fragmentation (Lovejoy et al. 1986; Laurance et al. 2002). Located approximately 80 km north of Manaus, Brazil (2° 30' S, 60° W), the BDFFP is composed of replicated forest fragments of 1, 10, and 100 ha that were isolated originally in the early to mid-1980s by the establishment of cattle pastures. Reserves ranging from 1 to 1000 ha were delineated in nearby continuous forest to serve as experimental controls (Lovejoy et al. 1986; Bierregaard et al. 1992).

We assessed forest fragments within two nearby experimental areas, the Dimona and Porto Alegre farms. These farms are approximately 20 km apart and were first clearcut in the early 1980s. Dimona contains two 1-, one 10-, and one 100-ha fragments, whereas Porto Alegre has one each of the 1-, 10-, and 100-ha fragments. The two farms have similar elevation, topography, soils, and climate and experience comparable disturbances from occasional windstorms and small-scale floods in the wet season. The farms, however, have quite different land-use histories. At Dimona the mature forest was initially clearcut and subsequently burned for pasture establishment. After 4–5 years of use, the pastures were gradually abandoned and forest regrowth dominated by *Vismia* spp. (mainly *V. guianensis*, *V. japurensis*, and *V. cayennensis*). At Porto Alegre land was abandoned immediately after the mature forest was felled because an early onset of the 1983 wet season precluded forest burning. The matrix surrounding fragments at Porto Alegre is now dominated by *Cecropia* spp. Because the regrowth on each farm differs so characteristically, the Dimona and Porto Alegre farms are hereafter referred to as the *Vismia* and *Cecropia* sites, respectively. Both regrowth types are typical of the central Amazon region (Mesquita et al. 1999).

Vismia regrowth and *Cecropia* regrowth differ in both species diversity and composition. In *Cecropia* stands, species richness of trees ≥ 20 cm tall is nearly twice that in *Vismia* stands (300 vs. 147 species/ha), and floristic similarity between different *Cecropia* stands is generally lower than that between different *Vismia* stands

(Mesquita et al. 2001). In our study area, plant regeneration in *Vismia* regrowth was dominated by small *Vismia* individuals (comprising approximately 25% of plants <2 cm basal diameter), whereas regeneration under a *Cecropia* canopy was more diverse floristically and did not include a single young *Cecropia*. These genera differ markedly in their life histories and structural characteristics. *Cecropia* species can reach 20–25 m tall and have low wood density, rapid growth in diameter and height, and low height:crown ratios, whereas *Vismia* species are much shorter (8–12 m tall), with slower diameter and height growth, higher wood density, and higher height:crown ratios (Williamson et al. 1998).

Field Sampling

Between 1980 and 1985, before the BDFFP fragments were isolated, 29 square, 1-ha plots were established in the Dimona and Porto Alegre fragments. We focused on plots within 100 m of forest edges (measured from the plot center) because they have markedly elevated tree mortality and turnover (Laurance et al. 1998a, 1998b), exhibit striking changes in pioneer tree communities (Laurance et al. 2006), and are most likely to be influenced by the surrounding secondary vegetation. Twenty-two plots at Dimona and Porto Alegre (11 in each site) are located within 100 m of forest edges. These include three 1-ha fragments (two at Dimona and one at Porto Alegre), each with one plot; two 10-ha fragments (one each at Dimona and Porto Alegre), with three and four plots, respectively; and two 100-ha fragments (one each at Dimona and Porto Alegre), each with six plots.

During the initial census and before fragmentation (between July 1980 and April 1985), all trees (≥ 10 cm diameter at breast height [dbh]) in each plot were marked with numbered aluminum tags, mapped, and measured to determine dbh. These plots were recensused 13 to 17 years later (between October 1997 and May 1998), during which all new trees ≥ 10 cm dbh were tagged, measured, and identified. On average, 95.3% of all trees in each plot, including all individuals of the successional taxa we examined, have been identified to species or morphospecies level based on sterile or fertile material collected from each tree and lodged in the BDFFP herbarium collection.

We selected 27 pioneer species for analysis based on their known regeneration requirements and presence in secondary forests in our study area (Moreira 2003). These species represent 10 genera: *Bellucia* (Melastomataceae, one species), *Cecropia* (Cecropiaceae, five species), *Croton* (Euphorbiaceae, two species), *Guatteria* (Annonaceae, two species), *Mabea* (Euphorbiaceae, one species), *Miconia* (Melastomataceae, four species), *Pourouma* (Cecropiaceae, five species), *Stryphnodendron* (Fabaceae, one species), *Tapirira* (Anacardiaceae, one species), and *Vismia* (Clusiaceae, five species). Collectively, these species accounted for 29.1% of all individ-

uals recruited over the study period within the 22 edge plots.

Data Analysis

We compared stem density and species richness per plot between sites in the initial (before fragmentation) and final (by 13–17 years after fragmentation) censuses by performing unpaired *t* tests with log-transformed data. Because the number of pioneer trees varied among plots, we also used both individual- and sample-based rarefactions to assess differences in pioneer species richness between *Cecropia*- and *Vismia*-surrounded fragments. We used individual-based rarefaction to minimize the confounding effects of varying stem number on species-richness estimates and sample-based rarefaction to assess the level of sample heterogeneity (patchiness) in the data (Gotelli & Colwell 2001). Both rarefaction curves were created in the software EstimateS (Colwell 1997). We also used Fisher's alpha, which is derived from the log series species-abundance model, as another measure of α diversity because it is insensitive to sample size (Magurran 1988).

We used ordination methods to describe major gradients in pioneer species composition among plots. Results of initial analyses with nonmetric multidimensional scaling (Sorensen similarity index) suggested that gradients in species composition were short, generally resulting in linear responses between species abundances. In such situations, principal component analysis (PCA) is recommended because it assumes that species vary monotonically along sampled gradients (ter Braak & Prentice 1988). We performed the PCA in the PC-ORD package (McCune & Mefford 1999) with log-transformed data on species densities in each plot and sampling interval. Because stand-level rates of tree mortality vary among plots and can influence pioneer tree regeneration (Laurance et al. 2006), we correlated the mean mortality rate in each plot with absolute changes in axis ordination scores between census intervals. We also compared the densities of each of the 10 most abundant tree species between the initial and final plot censuses with nonparametric Wilcoxon tests.

Results

Before fragmentation, neither the density nor species richness of pioneer trees differed significantly between forest fragments surrounded by *Cecropia* and *Vismia* regrowth ($t < 0.99$, $df = 20$, $p > 0.33$; two-sample *t* tests). Pioneer density in the *Vismia* and *Cecropia* sites was 15.3 ± 12.3 and 11.1 ± 4.9 stems/ha, respectively, whereas species richness was 7.1 ± 4.2 and 5.7 ± 2.5 species/ha, respectively. By 13–17 years after fragmentation, however, these patterns changed markedly. Pioneer density and

species richness were both significantly higher in *Vismia*-than in *Cecropia*-surrounded fragments, averaging 82.3 ± 57.7 versus 36.6 ± 33.3 stems/ha ($t = 2.27$, $df = 20$, $p = 0.03$) and 14.1 ± 4.2 versus 8.5 ± 2.5 species/ha ($t = 2.81$, $df = 20$, $p = 0.01$), respectively. The higher species richness in *Vismia*-surrounded fragments was mainly a consequence of greater tree density, as demonstrated by the species-individual and species-area accumulation curves (Fig. 1). Moreover there was no significant difference in Fisher's α diversity values between fragments surrounded by *Vismia* (5.4 ± 1.7) and *Cecropia* (5.6 ± 2.9) regrowth ($t = -0.11$, $df = 20$, $p = 0.91$).

The PCA ordination showed that pioneer species composition varied over time of sampling (before vs. 13–17 years after fragmentation) and plot location (*Vismia*- vs.

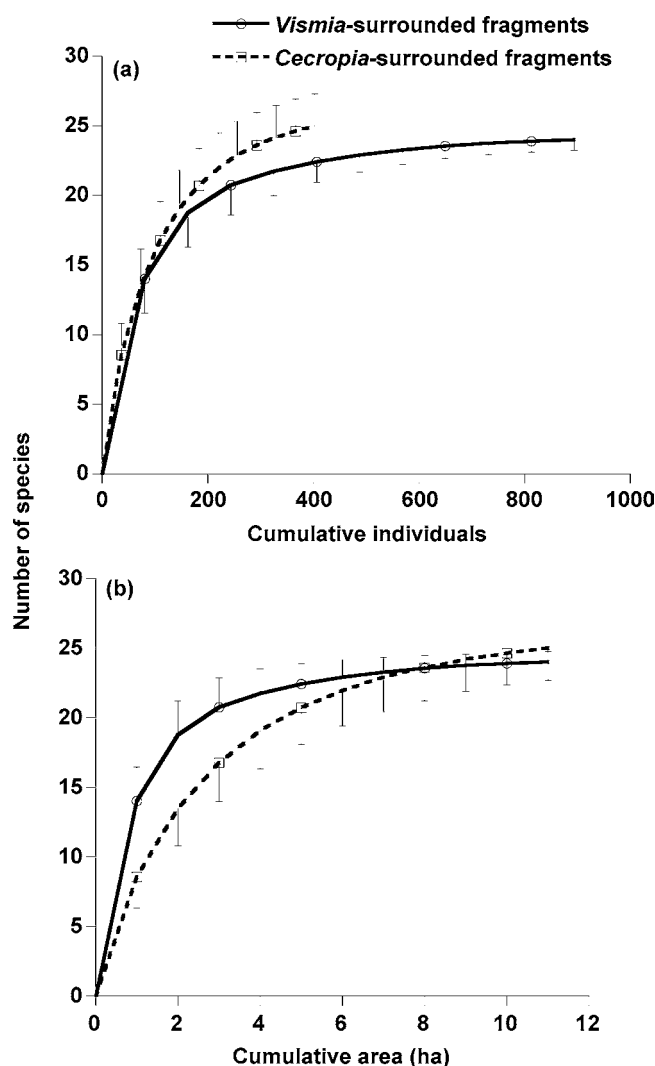


Figure 1. Species-individual (a) and species-area (b) accumulation curves (mean \pm 95% confidence intervals) for pioneer tree species recruited into forest fragments surrounded by *Cecropia*- and *Vismia*-dominated forest regrowth.

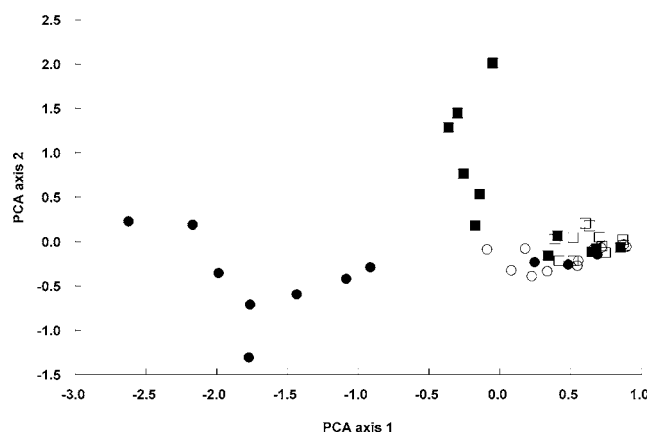


Figure 2. Ordination of 22, 1-ha plots based on 27 pioneer tree species in forest fragments surrounded by *Cecropia*- and *Vismia*-dominated regrowth forest. Circles indicate *Vismia*-surrounded plots and squares indicate *Cecropia*-surrounded plots. Open symbols correspond to the initial census, and closed symbols correspond to the final census. Axis lengths are scaled relative to the amount of variation explained by each axis.

Cecropia-surrounded plots; Fig. 2). The ordination was best fit by a two-axis solution because the broken-stick eigenvalues for axes 1 and 2 were lower than the actual eigenvalues (axis 1 = 14.1 vs. 37.8 and axis 2 = 8.3 vs. 12.8, respectively). The first two axes accounted for 68.3% of the variability in the data (axis 1 = 42.5% and axis 2 = 24.8%). Before fragmentation all 22 plots were clustered in ordination space, revealing high floristic similarity among fragments. When ordination scores were compared for *Vismia* versus *Cecropia* plots 13–17 years after fragmentation, however, there were highly significant differences in ordination scores on both axes (MANOVA, $F_{2,19} = 13.5$, $p = 0.0002$), indicating that plots surrounded by each regrowth followed a different successional trajectory. In addition, tree mortality was a strong predictor of changes in floristic composition between the initial and final censuses, as revealed by strong, positive relationships between mean tree mortality and changes in axis-1 scores for both the *Vismia* ($r_s = 0.91$, $p = 0.0001$) and *Cecropia* ($r_s = 0.81$, $p = 0.002$; Fig. 3) plots and changes in axis-2 scores for the *Cecropia* plots ($r_s = 0.89$, $p = 0.003$; Spearman rank correlations). By 13–17 years after fragmentation, floristic composition varied more among plots in *Cecropia*- than among *Vismia*-surrounded fragments, as demonstrated both by the ordination analysis (Fig. 2) and by the flatter rarefaction curves in the *Vismia*-surrounded fragments (Fig. 1).

In the *Vismia*-surrounded fragments 7 of the 10 most abundant tree species showed significant changes in abundance between the initial and final censuses of each plot (Table 1). In the *Cecropia*-surrounded fragments,

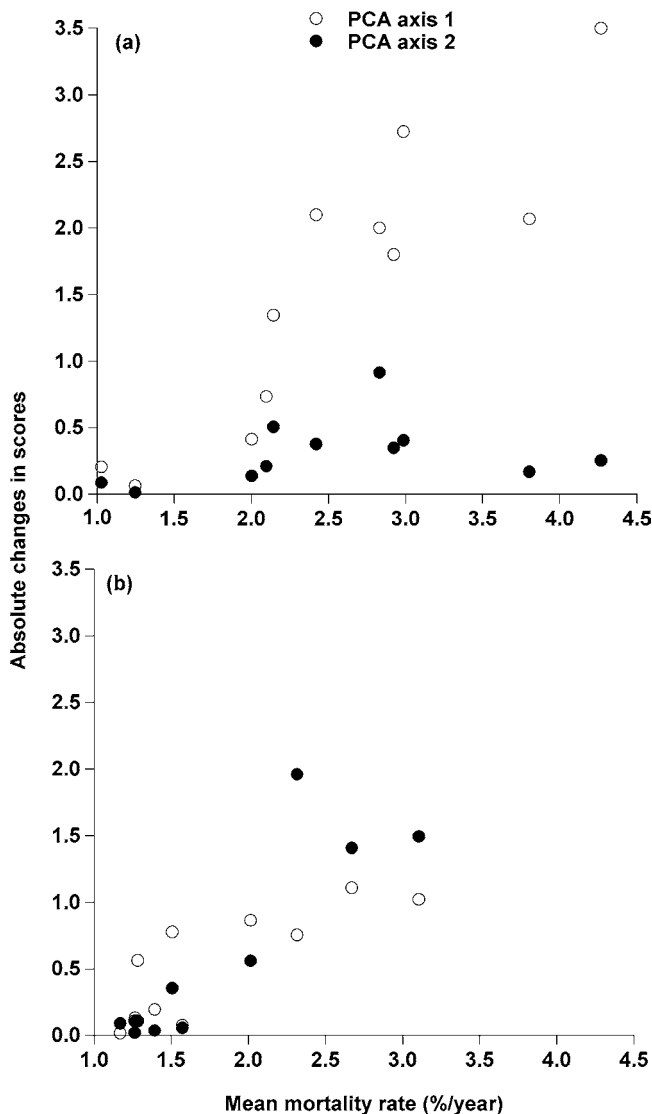


Figure 3. Relationships between changes in principal component analysis scores from the initial to final censuses and mean mortality rates for fragments surrounded by (a) *Vismia* and (b) *Cecropia* secondary forests.

however, only *Cecropia sciadophylla* changed significantly in abundance. In percentage terms (Fig. 4) *C. sciadophylla* accounted for nearly half (49%) of the pioneers in *Cecropia*-surrounded fragments, with the remaining species having low density and dominance. Pioneer species were more evenly distributed in abundance in the *Vismia*-surrounded fragments.

Discussion

Matrix Effects in Forest Fragments

Our findings suggest that the type of secondary vegetation surrounding rainforest fragments had marked influ-

ences on patterns of tree regeneration within the fragments. Fragments surrounded by *Cecropia*-dominated forests harbored a very high proportion of *Cecropia sciadophylla* trees among their regenerating pioneers, whereas those surrounded by *Vismia*-dominated forests supported a more even assemblage of pioneers. This assemblage included species of *Bellucia*, *Croton*, *Guatertia*, and *Miconia*, which were abundant in *Vismia*-dominated regrowth and that can evidently tolerate the drier and more open conditions there. Such trends are expected to lead to long-term changes in the floristic composition of forests, at least for fragments surrounded by certain types of matrices, because fragments may increasingly mirror the composition of their surrounding regrowth (Janzen 1983).

In our study area, fragment size is not a strong predictor of pioneer tree density and species richness; rather, the number of nearby forest edges and the stand-level rate of tree mortality are the key factors (Laurance et al. 2006). This most likely reflects the fact that edge effects (such as increased tree mortality and a greater seed rain from pioneer trees proliferating in nearby secondary vegetation) are the main drivers of floristic change in our fragments. Our fragments are only 2–3 decades old, and over longer time scales it is possible that area-related phenomena (such as local extinctions of rare tree species from random demographic and genetic effects) could become increasingly important. Hence, for long-lived organisms such as trees, the consequences of fragment area per se may require quite a long time to become manifest, but the impacts of edge effects are felt almost immediately.

Unlike fragments surrounded by *Cecropia* regrowth, those encircled by *Vismia* regrowth were initially maintained as cattle pastures via repeated burning. This created strong microclimatic gradients between the fragments and surrounding pastures and led to higher rates of tree mortality near the edges of *Vismia*-surrounded fragments (Mesquita et al. 1999). In our study area, tree mortality is an important predictor of the density and species richness of pioneer trees, although other factors such as the proximity and number of nearby edges also have a strong influence (Laurance et al. 2006). In addition, as our findings show, the type of surrounding forest regrowth influences the species composition of pioneer trees, evidently as a result of an increased seed rain into fragments from pioneer species in the nearby matrix (Janzen 1983; Grau 2004). Among pioneer trees, seeds and seedlings tend to be much more abundant near reproductive conspecifics, suggesting that seed-rain effects are important (Álvarez-Buylla & Martínez-Ramos 1990; Dalling et al. 1998a, 1998b). Thus the type of surrounding regrowth can affect both forest dynamics (tree mortality and turnover rates) and the floristic composition of trees regenerating in forest fragments.

Before our experimental study area was fragmented our plots had few pioneers, and there was no significant

Table 1. Mean density (\pm SE stems/ha) of the 10 pioneer tree species that were most abundant by 13–17 years after fragmentation, contrasting their initial and final densities in forest fragments surrounded by *Vismia*- and *Cecropia*-dominated regrowth (significant differences based on Wilcoxon tests).

Species	Vismia site		Cecropia site	
	initial	final	initial	final
<i>Cecropia sciadophylla</i>	1.4 ^a (0.2)	11.8 ^a (4.4)	1.4 ^a (0.1)	18.7 ^a (6.6)
<i>Croton lanjouensis</i>	2.5 ^a (0.4)	12.4 ^a (3.1)	1.8 (0.2)	2.0 (0.6)
<i>Miconia burchellii</i>	2.4 ^a (0.8)	12.1 ^a (3.5)	1.7 (0.2)	1.9 (0.3)
<i>Pourouma tomentosa</i>	3.5 (0.7)	6.2 (1.4)	4.0 (0.6)	4.9 (0.6)
<i>Mabea angularis</i>	1.4 ^b (0.1)	7.1 ^b (1.6)	1.0 (0.0)	1.0 (0.0)
<i>Gauteria olivacea</i>	2.3 ^b (0.6)	6.5 ^b (1.2)	1.9 (0.2)	1.6 (0.2)
<i>Pourouma guianensis</i>	2.3 (0.5)	4.7 (1.2)	1.6 (0.3)	3.9 (0.7)
<i>Tapirira guianensis</i>	1.6 ^b (0.4)	5.5 ^b (1.4)	1.3 (0.1)	1.6 (0.3)
<i>Bellucia dichotoma</i>	1.4 ^a (0.2)	4.7 ^a (1.7)	1.0 (0.0)	1.5 (0.2)
<i>Porouma velutina</i>	1.6 (0.3)	3.2 (0.9)	1.7 (0.2)	2.9 (0.5)

^ap < 0.05.

^bp < 0.01.

difference in pioneer density, species richness, and floristic composition between plots that were later surrounded by *Cecropia* and *Vismia* regrowth. This suggests that differences observed 13–17 years after fragmentation resulted not from any local site effects (such as systematic differences in soil types or soil seed banks) but from differences in tree mortality rates and surrounding regrowth that occurred after the forests were fragmented. Our results also indicated that different light-demanding pioneer species varied considerably in their life histories and physiological characteristics and that these differences had a large influence on their recruitment success in forest fragments. Establishment success in pioneer species is evidently influenced by many factors, including their abiotic requirements for seed germination, their seedling and sapling growth rates, and their gap-size preferences (Brokaw 1987; Pearson et al. 2003; Dalling et al. 2004).

Two aspects of our study were surprising. First, forest fragments surrounded by *Vismia*-dominated regrowth had a greater abundance and evenness of regenerating pioneer species than did those encircled by *Cecropia*-dominated regrowth, despite the fact that floristic diversity is actually higher in *Cecropia*- than *Vismia*-dominated regrowth (Mesquita et al. 2001). This suggests that one cannot easily predict the effects of different types of surrounding matrices on forest fragments, at least in terms of plant regeneration. One factor that might contribute to this trend is that heavy litterfall and greater shading in *Cecropia* regrowth tend to inhibit seedling establishment (Mesquita 1995), whereas many seedlings perform well in *Vismia* regrowth (Ganade 1996). Hence, in *Vismia* regrowth, other pioneer species may more easily reach adulthood and thus become a seed source for nearby forest fragments.

Second, forest fragments surrounded by *Cecropia*-dominated regrowth had a very large number of regenerating *C. sciadophylla* trees, but those surrounded by *Vismia* regrowth had few regenerating *Vismia* species.

Although the paucity of *Vismia* trees in fragments might conceivably have arisen from a sampling artifact (*Vismia* trees rarely reach 10 cm in diameter even as adults and thus were rarely recorded in our censuses), in a separate study we found only a small, nonsignificant increase in small *Vismia* individuals near fragment edges (for trees 1.0–9.9 cm in diameter, the mean density was 0.9 ± 0.6 stems/ha in plots within 100 m of edges, vs. 0.5 ± 0.4 stems/ha in forest interiors; H.N., unpublished data). A more likely explanation is that seed production by *Vismia* trees is relatively low, reducing their seed rain into forest fragments (in *Vismia* regrowth, most *Vismia* seedlings are clonal sprouts from adult trees; Williamson et al. 1998). Moreover, *Vismia* seedlings appear less competitive than other pioneers in the relatively shaded conditions of forest fragments (although they germinate readily in previously burned pastures, where they are favored by direct sunlight and ash beds; Ludewigs et al. 1997; Adkins et al. 2000). *Cecropia* trees, however, have high fecundity (10^4 to 10^7 seeds per tree; Álvarez-Buylla & Martínez-Ramos 1990), are readily dispersed by frugivorous bats

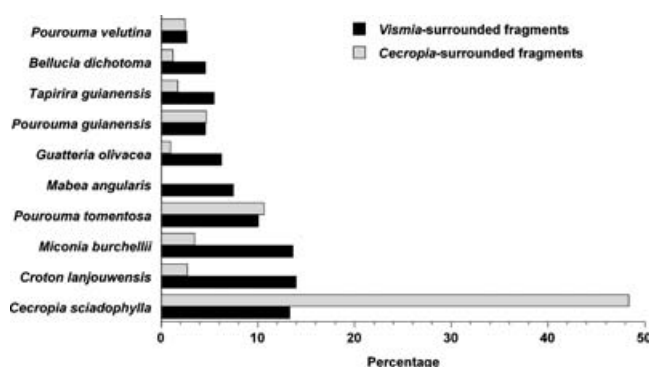


Figure 4. Percentage of the 10 most abundant pioneer species in Amazonian forest fragments surrounded by *Vismia*- and *Cecropia*-dominated regrowth.

(Sampaio 2000) and birds, and have high absolute rates of stem growth in primary forest (Laurance et al. 2006), a suite of traits that evidently favors their establishment in fragmented forests.

Conservation Implications

Our study is part of a larger body of work demonstrating that the species composition, dynamics, and connectivity of forest fragments can be markedly influenced by their surrounding modified vegetation (Laurance & Bierregaard 1997; García & Bañuelos 2003; Jules & Shani 2003). In general, forest fragments encircled by hostile matrices are likely to experience less immigration and gene flow, a higher incidence of local extinctions, and stronger declines of animal-dispersed plant species (Silva & Tabarelli 2000; Cordeiro & Howe 2001, 2003; Benitez-Malvido & Martínez-Ramos 2003) than fragments surrounded by well-developed regrowth (Bierregaard & Stouffer 1997; Borges & Stouffer 1999; S.G. Laurance et al. 2004). Moreover, regrowth adjoining fragments can act as a buffer zone against abiotic edge effects (Camargo & Kapos 1995; Didham & Lawton 1999), reducing tree mortality (Mesquita et al. 1999; Gascon et al. 2000) and the probability of destructive surface fires (Gascon et al. 2000; Cochrane & Laurance 2002).

Nonetheless, different kinds of regrowth forests may affect forest fragments in different ways. Regrowth dominated by exotic species such as tree plantations may promote invasions of foreign species into forest fragments (Fine 2002). In our study area, *Cecropia*-dominated regrowth, which tends to be tall and floristically diverse with a relatively closed canopy, is used by more rainforest bird, frog, and ant species than is the more-open *Vismia*-dominated regrowth (Laurance et al. 2002). For this reason *Cecropia* regrowth is generally superior from a conservation perspective. Virtually any kind of regrowth is better than cattle pastures; for example, forest-dependent dung and carrion beetles are far more likely to cross a matrix of regrowth than one that has been completely clearcut (Klein 1989). In general, the more closely the matrix approximates the structure and microclimate of primary forest, the more likely that fragmentation-sensitive species can use it.

Collectively these findings indicate that efforts to mitigate the impacts of habitat fragmentation should focus not only on the important goal of establishing faunal corridors (Beier 1993; Laurance & Laurance 1999; Lima & Gascon 1999), but also more broadly on managing the entire surrounding matrix. In the Amazon and elsewhere in the tropics, simply preventing recurring fires will often facilitate forest regeneration in degraded lands (Uhl et al. 1988), and this could go a long way toward reducing the deleterious consequences of habitat fragmentation.

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