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Influence of Edge Exposure on Tree Seedling Species Recruitment in Tropical Rain Forest Fragments¹

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ABSTRACT

Edge creation has a pronounced influence on the understory vegetation, but the effects of edges on seedling species recruitment are still poorly understood. In Central Amazonia, 9–19 years after fragmentation, we recorded species richness and net seedling recruitment rate in 1 ha blocks exposed to none, one, or multiple edges within forest fragments. One-hectare blocks were located in the center (no edge), the edge (one edge), the corners (two edges) of 10 and 100 ha fragments, and in a 1 ha fragment (four edges). In 1991, we counted all tree seedlings 5–100 cm tall found within permanent 1 m² plots located within the 1 ha blocks. In May 1993, we manually removed all seedlings that were smaller than 1 m tall from the permanent plots. Six years and five months later (October 1999), all new seedlings recruited into the plots were counted and classified into distinct morphospecies. Species richness of recruited seedlings, scaled by total seedling density, declined from the center to the edge, the corner blocks, and then to the 1 ha fragment. Overall, the four-edged, 1 ha fragment had the poorest species richness and the non-edged 100 ha central block the highest. The total number of recruited individuals was 40 percent less than that previously present, with the 100 ha corner having the lowest recruitment. Pairwise comparisons showed that species similarity was related to edge number for the 100 and 1 ha fragments. Species rank/abundance curves showed that a subset of species was common in all blocks within the fragments, and that the 100 ha center held more rare species than any other 1 ha block. This study demonstrated that, in a given fragment patch, the number of tree seedling species recruited varied inversely with the number of edges.

RESUMO

A formação de bordas influencia drasticamente a vegetação de sub-bosque, mas os efeitos sobre o recrutamento de espécies de plântulas ainda são poucos conhecidos. A riqueza de espécies e a taxa de recrutamento de plântulas na Amazônia Central em um período de 9–19 anos depois da fragmentação foram quantificadas em parcelas de 1 ha expostas a uma, nenhuma e várias bordas dos fragmentos. Estas parcelas de 1 ha foram distribuídas no centro (sem borda), na borda (uma borda), na esquina (dois bordas) de fragmentos de 10 e 100 ha e em um fragmento de 1 ha (quatro bordas). Em 1991, contamos todas as plântulas de espécies arbóreas, de 5 a 100 cm de altura dentro das parcelas permanentes de 1 m². Seis anos e cinco meses depois (1999) todas as plântulas novas recrutadas foram contadas e classificadas em morfoespécies. A riqueza de espécies de plântulas recrutadas foi maior no centro, seguida de bordas e depois de parcelas de esquina de fragmentos de 10 e 100 ha. O fragmento de 1 ha apresentou a menor riqueza de espécies e a parcela central de 100 ha a maior. O número total de indivíduos recrutados foi 40 por cento menor que o quantificado anteriormente e o menor recrutamento foi observado na esquina do fragmento de 100 ha. Comparações pareadas evidenciaram que a similaridade de espécies se relaciona com o número de bordas para os fragmentos de 100 e 1 ha. As curvas de amplitude/abundância de espécies demonstrou que determinado grupo de espécies era comum em todas as parcelas de todos os fragmentos, sendo que o centro do fragmento de 100 ha apresentou, comparativamente, mais espécies raras. Este estudo demonstrou que quanto maior o número de bordas em um fragmento, menor o número de espécies de plântulas arbóreas recrutadas.

Key words: Amazon; edge effects; fragmentation; seedling recruitment; tropical rain forest.

THE CREATION OF HABITAT EDGES STRONGLY AFFECTS MANY FOREST SPECIES AS WELL AS ECOLOGICAL PROCESSES SUCH AS FOREST REGENERATION, LITTER PRODUCTION, AND

biotic interactions. These edge effects are among the major consequences of forest fragmentation (Murcia 1995). Edges are often the most altered zone of a fragment, but edge effects can propagate several hundred meters into the forest (Curran *et al.* 1999, Laurance 2000, Peters 2001). Fragment size, shape, position in the landscape, and the sur-

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rounding matrix may influence the magnitude of edge effects (Saunders *et al.* 1991, Malcolm 1994, Benítez-Malvido 1998, Didham & Lawton 1999).

Forest microenvironment is strongly modified at fragment edges (Kapos 1989, Camargo & Kapos 1995). Modifications of incident light, soil and air humidity and temperature, wind, and frequency of fires, can significantly impact the establishment and composition of plant species in the edge zone. In rectangular fragments, physical changes may be more dramatic at the corners of the fragment because the effect of two perpendicular edges is greater than the effect of a single linear edge (Malcolm 1994, 2001). Nevertheless, the effects of multiple edges on biotic communities have rarely been investigated (Milne & Forman 1986). Exposure to more than one edge can influence the abundance, performance, and levels of herbivory on tree seedlings (Benítez-Malvido 1998, 2001), foliage density (Malcolm 1994), mortality rates of trees (Lewis 1998), and microclimatic conditions (Kapos 1989) within the fragments.

Local extinction or invasion of several plant species is expected after habitat fragmentation (Leigh *et al.* 1993, Turner *et al.* 1996, Scariot 1999). The processes and mechanisms underlying plant species recruitment within fragments, however, are scarcely known (Turner *et al.* 1996, Benítez-Malvido & Martínez-Ramos 2003). Recent research has shown that rain forest fragmentation produces severe changes in the demography and community attributes of tree and palm seedlings. Seedling abundance and species richness are lower in forest fragments than in continuous forest, with the smallest fragments having the lowest abundance and richness (Benítez-Malvido 1998; Scariot 1999, 2001; Benítez-Malvido & Martínez-Ramos 2003). Reduction of local (produced by *in situ* fruiting mature trees) and external seed sources (seed rain produced by dispersal agents), and higher seed/seedling mortality due to adverse conditions have been proposed to cause poor regeneration within fragments (Benítez-Malvido 1998, 2001; Bruna 2002). We can expect these declines to increase at fragment edges and with increasing isolation time.

In this study, we assessed edge effects on tree seedling recruitment in forest fragments. We took advantage of an experimentally fragmented forest system (Gascon & Bierregaard 2001) that enabled us to (1) account for different numbers of exposed forest edges and forest areas not exposed to nearby edges and (2) assess edge effects on species richness of new recruited seedlings 9–19 years after fragmentation. In particular, we asked if species re-

cruitment of tree seedling is reduced near forest edges relative to forest interiors and if so, did the magnitude of the reduction depend on the number of exposed forest edges? We then compared seedling species composition in forest areas exposed to different numbers of forest edges to determine if some species were more prone to extinction than others at forest edges.

METHODS

STUDY AREA.—The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), 80 km north of Manaus, Brazil. The study area is composed of 11 square-shaped fragments of various sizes (1, 10, 100 ha), isolated between 1980 and 1990 (Bierregaard *et al.* 1992, Gascon & Bierregaard 2001). Average annual rainfall at the site is 1900–3500 mm (Laurance 2001). The mean annual temperature is 27°C and on rare occasions can drop to 17°C (Lovejoy & Bierregaard 1990). The soils are mostly nutrient-poor, Yellow Latosols of high clay content (Chauvel 1983).

The vegetation in the area is mature, *terra firme* tropical rain forest. The primary forest has a fairly even closed canopy that ranges from 35 to 40 m in height, with occasional emergent trees up to 55 m (Laurance 2001). The forest has remarkably high species richness coupled with low population densities of most species (Oliveira & Mori 1999). The understory is dominated by stemless palms (Klein 1989), and there is an extremely low density of herbs and shrubs (Gentry & Emmons 1987). Lianas are sparsely distributed and increase in abundance close to forest edges (Laurance *et al.* 2001).

EXPERIMENTAL DESIGN.—All woody trees from 5 to 100 cm tall were considered seedlings. We did not consider other life-forms (palms, herbs, vines, and shrubs) because preliminary analysis and previous studies have shown very low densities and recruitment of understory plants other than trees (Benítez-Malvido, pers. obs.; Benítez-Malvido & Martínez-Ramos 2003). In 1991, tree seedling density was sampled in three fragments: (1) 100 ha fragment (BDFFP reserve no. 2303), (2) 10 ha fragment (no. 1202), and (3) 1 ha fragment (no. 2107) in the area (*cf.* Lovejoy *et al.* 1986). Fragments of 100 ha and 1 ha were located within the Dimona site, and the 10 ha fragment was within the Colosso site. Fragments were sampled by 1 ha blocks, each of which contained 20 1 m² plots arranged in a stratified random manner, with 4 plots located

along each of five 100 m long, parallel transects spaced 20 m apart. For the 10 and 100 ha fragments, we placed one 1 ha block in the center, one 1 ha block at the edge, and one 1 ha block in the corner of each fragment, which allowed us to compare the variation between fragment edge and interior (Benítez-Malvido 1998, Benítez-Malvido *et al.* 1999).

The edges and corners of the 100 and 10 ha fragments were not chosen at random because fragments had different disturbance histories and to avoid the influence of the surrounding matrix (Gascon *et al.* 1999, Mesquita *et al.* 1999). Instead, we sampled edges and corners that were at least five years old with similar vegetation around them in 1991 (pasture), not considering compass orientation. The experimental design allowed us to assess seedling abundance within 1 ha blocks exposed to different number of edges: 100 and 10 ha central blocks with no edge (nearest edge >100 m away); fragment edge blocks with one edge; fragment corner blocks with two edges; and 1 ha fragment with four edges. We did not assess seedling recruitment at different distances from the edge in 100 and 10 ha fragments because of the low number of 1 m² sampling plots per distance from the edge ($N = 4$), and poor seedling recruitment did not permit statistical analysis of the data.

To assess net plant recruitment after isolation, in May 1993, we manually removed all understory plants smaller than 1 m tall from the 1 m² plots, taking care to minimize soil disturbance. This ensured that all seedlings were recruited after fragmentation. Seedling removal, however, could have influenced recruitment in several ways. The absence of small vegetation near the ground may have affected the microenvironment, seed predators, and herbivores. Plant litter, however, was not removed from the plots; thus, recruited seeds and seedlings were not completely exposed to predators and desiccation. Understory vegetation in the study area was sparse (very low density of herbs and vines; Gentry & Emmons 1987) and herbivory is reduced in forest fragments compared to unfragmented forest (Benítez-Malvido 2001). Generally, the density of naturally occurring seedlings in life-forms other than trees is less than 1 individual/m² (J. Benítez-Malvido, pers. obs.; Benítez-Malvido & Martínez-Ramos 2003); hence, the removal of broadleaved species such as palms and herbs was a rather uncommon event. If there were an effect of seedling removal on recruitment, it would have been similar throughout the experimental plots.

Six years and five months later (October 1999),

based on experience and with the help of a local parataxonomist, all new tree seedlings recruited into the plots were counted and classified into distinct morphospecies based on stem, leaf, and root traits. No new recruit was more than 50 cm tall and no seedling of the recognizable fast-growing pioneers *Cecropia* and *Vismia* was recorded, which indicated that we did not miss common, fast-growing pioneer species except for those that had died during the study period. Furthermore, experimental seedlings of three forest species (*Pouteria caimito*, *Micropholis venulosa*, and *Chrysophyllum pomiferum*) in our study plots have shown very low height increments or no growth at all in about ten years after transplantation (Benítez-Malvido, pers. obs.).

FRAGMENT DESCRIPTION.—Fragments of 100 and 1 ha at Dimona were partially or totally isolated in 1984 (100 ha, isolation completed in 1991), whereas the 10 ha fragment at Colosso was isolated in 1980. The linear distance between the 100 ha and 1 ha fragments was 0.3 km whereas the 10 ha fragment (Colosso) was *ca* 24 km from the 100 and 1 ha fragments (Dimona). The distance from the fragments to the nearest continuous forest was 700 m for the 10 ha and 150 m for the 100 and 1 ha fragments (Gascon & Bierregaard 2001). Old edges (≥ 5 yr) at our study fragments were characterized by abundant forest regrowth and dense foliage that “sealed” the edge and blocked light penetration (Camargo 1993, Malcolm 1994, Kapos *et al.* 1997). Benítez-Malvido (1995) found that photosynthetically active radiation (PAR) measurements 0.5 m above the 1 m² plots were similar at different positions (center, edge, and corner) within the fragments (Table 1). Furthermore, minimum and maximum temperatures at soil level were similar between 1 ha blocks, but were higher in the 1 ha fragment and the 10 ha corner (Table 1).

The fragments were surrounded by shrubby pasture when the experiment was initiated in 1991, but by 1999, this had become a 10–15 m tall regrowth forest dominated by *Cecropia* spp. and *Vismia* spp. During this study, fragments had been reisolated several times by slash-and-burn practices. In some cases, fire had penetrated the reserves (Gascon & Bierregaard 2001).

SPECIES RICHNESS.—Differences in species richness of recruited seedlings among different fragment positions were assessed by constructing mean individual-based species accumulation curves after 100

TABLE 1. *The microenvironment at different positions within 100 and 10 ha forest fragments and in a 1 ha fragment near Manaus, Brazil. Photosynthetic active radiation (% PAR) is expressed as the percentage of the open sky measurements (Benítez-Malvido, pers. obs.).*

Location of 1 ha blocks	% PAR ($\bar{x} \pm SE$)	Maximum and minimum	
		Temperatures °C	($\bar{x} \pm SE$)
100 ha center	1.35 \pm 0.32	28.37 \pm 1.50	22.77 \pm 0.37
100 ha edge	1.49 \pm 0.29	27.81 \pm 0.49	22.21 \pm 0.49
100 ha corner	2.94 \pm 1.18	27.81 \pm 0.49	21.84 \pm 0.32
1 ha	2.04 \pm 0.38	31.17 \pm 0.49	20.53 \pm 0.37
10 ha center	2.96 \pm 1.02	28.93 \pm 1.13	22.77 \pm 0.37
10 ha edge	1.68 \pm 0.34	28.74 \pm 0.74	22.77 \pm 0.37
10 ha corner	3.78 \pm 1.11	30.98 \pm 0.37	22.58 \pm 0.18

randomizations of the order of sampled individuals using the program EstimateS (Colwell 1997). To compare species richness among 1 ha blocks within fragments, we standardized the number of individuals sampled (and not the area sampled) to control for differences in individual density (Gotelli & Colwell 2001). Because the resulting curves underestimated species richness (Colwell & Coddington 1994), we used nonparametric methods provided by the EstimateS program to approach true species richness. We selected three methods that have been suggested to be the best estimators of species richness for seedling communities in tropical rain forests (Chazdon *et al.* 1998): Incidence-based coverage estimator (ICE), Chao-2, and Jackknife-2 (estimators are based on incidence [presence/absence] of species). For a complete description of these methods, see Colwell and Coddington (1994, 1995), Chazdon *et al.* (1998), and Gotelli and Colwell (2001). In all cases, we performed EstimateS, setting patchiness at 0 (Colwell & Coddington 1994). This procedure eliminates bias in the species-richness estimates due to species patchiness (Colwell & Coddington 1994).

SPECIES SIMILARITY AND DOMINANCE.—To estimate the proportion of species shared between block pairs, we used the Jaccard index of similarity (JI) based on species presence-absence data (Magurran 1988). The index is designed to equal 1 in cases of complete similarity (*i.e.*, when two sets of species are identical) and 0 if the sites have no species in common. For each site (Dimona and Colosso), average JI values were obtained after bootstrapping the data from the plot pool of each 1 ha block 100 times (*i.e.*, by pairwise comparisons of any pair of 1 m² plots). The JI results should be interpreted with caution because in some cases, two samples with substantially different numbers of individuals

were compared; however, by bootstrapping we have incorporated much of such variation in abundance.

To determine if species relative abundance is modified by edge exposure, we constructed rank/abundance plots for the tree-seedling community (Magurran 1988). For each 1 ha block, we plotted the relative abundance of each species on a logarithmic scale against the species' rank in order from the most abundant to the least abundant species following Magurran (1988).

STATISTICAL ANALYSIS.—Differences in the density of seedlings in 1991 and 1999 were analyzed with log-linear models for count data (Crawley 1993), using the GLIM statistical package (Green & Payne 1994). We evaluated the effect of edge exposure in the fragments (center, edge, corner, and 1 ha fragment) by comparing different positions within the 100 and 10 ha fragments at each individual site (Dimona and Colosso, respectively). For Poisson data, the deviance will be approximately distributed as a chi-square (Crawley 1993). The significance of each term was tested through the deviance that the term removed from the total. In those cases in which a term was found to be significant, the individual levels of the term were compared with *a posteriori* *t*-tests (Crawley 1993). Because each fragment size was not replicated, to assess seedling density differences among fragments and handle pseudoreplication (*sensu* Hurlbert 1984), we obtained a single density value per 1 ha block within different fragments (100, 10, and 1 ha). The proportion of seedlings found in 1999 with respect to that in 1991 was analyzed with chi-square tests. Species similarity among different 1 ha blocks was analyzed for each site by one-way analysis of variance of arcsine \sqrt{JI} values.

To test if differences in species similarity were related to geographic distances among 1 ha blocks,

TABLE 2. Density of tree seedlings (<1 m tall) in 20 m², at different positions within 10 and 100 ha forest fragments and in a 1 ha fragment north of Manaus, Brazil¹. The R:O² ratio defines the proportion of plants found in 1999 (R) with respect to those in 1991 (O).

Location of 1 ha blocks	Number of edges (distance to edge [m])	R:O		
		O	R	R:O
100 ha center	0 (500)	218 ^{b, c}	82 ^c	0.38*
100 ha edge	1	232 ^c	55 ^b	0.24*
100 ha corner	2	127 ^a	35 ^a	0.28*
1 ha	4	188 ^b	72 ^{b, c}	0.38*
10 ha center	0 (116.2)	208 ^a	64 ^a	0.31*
10 ha edge	1	226 ^a	80 ^a	0.35*
10 ha corner	2	220 ^a	63 ^a	0.29*

¹ Sites with different letters are significantly different ($P < 0.05$).

² With chi-square analysis, R:O values significantly different from 1.0 are indicated by * ($P < 0.05$).

we performed a Mantel test (Sokal & Rohlf 1995). Significant differences were set at 0.05 or below.

RESULTS

SEEDLING DENSITY.—In 1991, seedling density was significantly lower in the corner of the 100 ha fragment than in any other 1 ha block at the Dimona site ($X^2 = 36.3$, $df = 3$, $P < 0.001$). Seedling density did not differ among positions within the 10 ha fragment (Table 2). For seedlings recruited after 1993, the same pattern as in 1991 was observed for the 100 ha ($X^2 = 22.12$, $df = 3$, $P < 0.001$) and the 10 ha fragments. Density, however, did not differ between the 100 ha edge and the 1 ha fragment (Table 2). After more than six years, the initial abundance had not recovered for any 1 ha block. Tree seedlings recovered less than half of their initial density (Table 2).

SPECIES RICHNESS.—The results showed that fewer species established in blocks exposed to edges regardless of seedling abundance. The individual-based species accumulation curves showed that species richness was not completely recorded in the center of the 100 ha fragment with our sampling effort (Fig. 1). In contrast, with similar numbers of individuals (*ca* 40), blocks at the edge, corner, and the 1 ha fragment showed an asymptotic trend, and species richness was much lower in the 1 ha fragment. For the 10 ha fragment, all positions followed an asymptotic trend, with the central block having more species than the edge and corner.

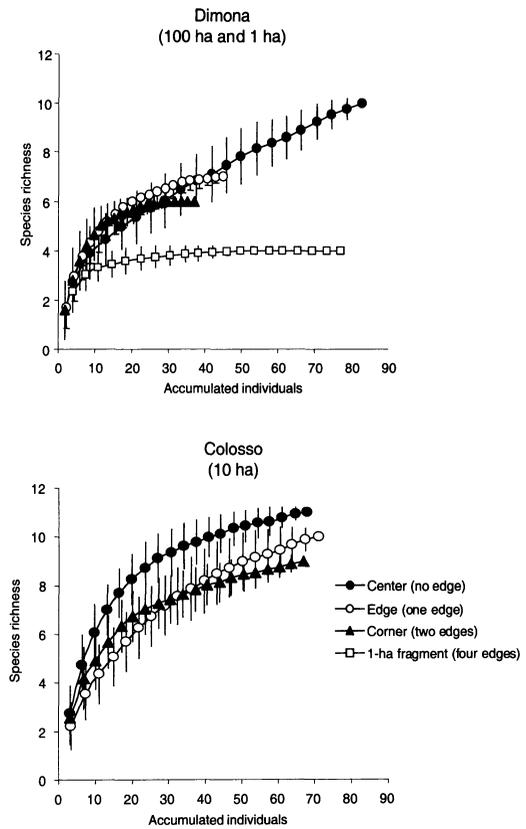


FIGURE 1. Individual-based species accumulation curves ($\bar{x} \pm 1$ SD) for tree seedlings recruited into different positions within 100 and 10 ha fragments and in a 1 ha fragment at two sites near Manaus, Brazil.

Considering the sampled area, nonparametric estimators magnified the differences in species richness among 1 ha blocks exposed to different number of edges; in most cases, species richness declined from the fragment center toward the edge, to the corner, and then to the 1 ha fragment (Fig. 2). This decline was less pronounced for the 10 ha fragment. For all estimators, the blocks within the 10 ha fragment, held greater species richness than the 100 ha fragment edge and corner blocks. Considering similar numbers of individuals (*ca* 40 per block), differences in species richness among blocks followed a similar pattern, with corners and the 1 ha fragment having the lowest number of species (Fig. 2).

SPECIES SIMILARITY.—Species similarity differed significantly among block pairs at Dimona ($F_{5, 594} = 19.4$, $P < 0.0001$) and Colosso ($F_{2, 297} = 32.5$, $P < 0.0001$). At Dimona, hectare blocks with the highest edge exposure showed higher similarity than blocks with lower or no exposure (Fig. 3). For

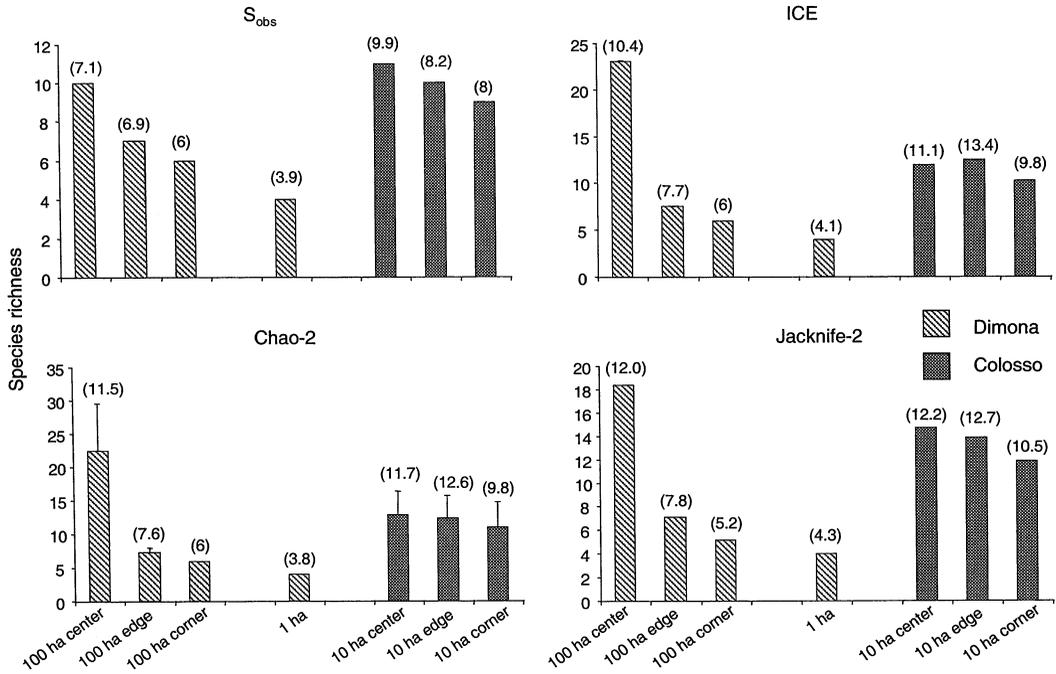


FIGURE 2. Species richness of tree seedlings recruited into different positions within 100 and 10 ha fragments and in a 1 ha fragment at two sites. Bars indicate the mean (± 1 SD) observed species richness (S_{obs}) and the three nonparametric estimators, where incidence-based coverage estimator (ICE), Chao-2, and jackknife-2 estimators are based on incidence (presence/absence) of species considering the sample area (20 m²). Number in parenthesis indicate the number of species per hectare block when the number of individuals was set at ca 40 (minimum number of individuals found in a hectare block).

the 100 ha fragment, the central block was more similar to the edge than to the corner and 1 ha fragment blocks, whereas the 1 ha fragment was more similar to the corner block than to the edge and central blocks. The greatest similarity at Dimona was observed between the edge and corner blocks within the 100 ha fragment (Fig. 3). In contrast, the central block at the Colosso 10 ha fragment showed higher similarity with the edge than with the corner blocks, whereas the edge and corner blocks showed the lowest similarity (Fig. 3). On average, blocks at Dimona shared 46 percent of the species, those at Colosso shared 43 percent, and both sites shared 35 percent of the species. The Mantel test showed that there was not a significant association between species similarity and geographic distances among hectare blocks ($t_x = -0.0725$, $P = 0.94$); *i.e.*, species were as likely to be found in blocks close together as in blocks far apart.

SPECIES DOMINANCE.—Overall, the newly recruited tree seedling community within most 1 ha blocks resembled a log-series model (*i.e.*, a small number

of abundant species and a large proportion of rare species; Magurran 1988). In contrast, the log-series function was less steep in the seedling community within the 10 ha fragment center. In the 10 ha fragment, the species in the community were distributed more uniformly. The dominant species throughout the study site was *Protium hebetatum* (Burseraceae sp.1). This species accounted for 42 percent of all tree seedlings recruited into the 1 ha blocks. The following patterns emerged in the rank abundance plots: (1) all 1 ha blocks had a similar subset of dominant seedling species regardless of edge exposure (particularly, sp. 1, sp. 40, and sp. 8); (2) rare species within the 100 ha center tended to be absent from the blocks at the edge and corner and from the 1 ha fragment; (3) some species were exclusive of particular 1 ha blocks; and (4) all species in the 1 ha fragment were present in more than one block (Fig. 5).

DISCUSSION

The lack of replication for any fragment size limits the generality and implications of our results to the

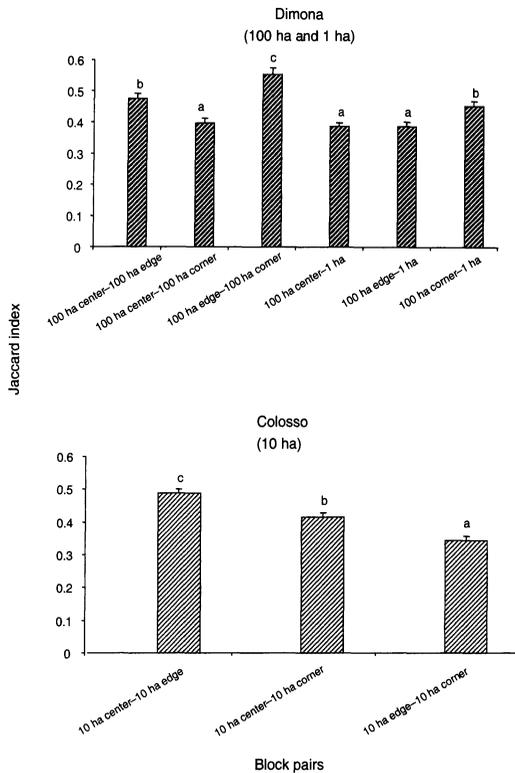


FIGURE 3. Block-pair comparisons ($\bar{x} \pm 1SE$) of species similarity (Jaccard index) at two localities between different positions within 100 ha and 1 ha fragments and between positions within a 10 ha forest fragment. Different letters indicate significant differences among study blocks.

particular fragments that were studied; however, the same pattern of lower species richness with increased edge exposure (corner) was observed in the 100 and 10 ha fragments. Thus, our results strongly suggest that the level of edge exposure affected species recruitment. The higher the number of edges in a given forest patch (1 ha block), the lower the number of seedling species recruited. This phenomenon was observed regardless of whether differences in seedling abundance were taken into account.

On the other hand, the poor recovery capacity of the seedling community suggested that seedling density in a given forest spot was the outcome of long-term regeneration processes that take more than six years to occur. Previous studies in Manaus, Brazil and Chajul, Mexico, have shown that following removal, initial seedling density did not recover after one or more years (Benítez-Malvido *et al.* 2001, Benítez-Malvido & Martínez-Ramos 2003). We do not know if the recovery rate would have

changed if understory vegetation in life-forms other than tree seedlings were present in the plots. At "Los Tuxtlas," Mexico, the experimental removal of palms, herbs, and ferns resulted in an increase of light-demanding tree seedling species and a decreased recruitment of shade-tolerant, large-seeded tree species (Martínez-Ramos, pers. obs.). In our study plots, however, the proportion of non-tree seedlings (28%; Benítez-Malvido, pers. obs.) was 2.2 times lower than that in "Los Tuxtlas" (61%; M. Martínez-Ramos, pers. obs.), which suggests a lower effect of vegetation removal on tree seedling recruitment. Differences in species recruitment within forest patches exposed to different numbers of edges may be explained by a complexity of ecological factors that reduce establishment and increase mortality of seedlings (Benítez-Malvido 1998).

BARRIERS TO SEEDLING RECRUITMENT IN FOREST FRAGMENT EDGES.—In tropical rain forests, propagule fluxes are important for the colonization of new habitats, the renewal of seedling banks, and the maintenance of understory plant diversity (Martínez-Ramos & Soto-Castro 1993). One of the consequences of habitat fragmentation for plant communities is that propagule sources decrease and their fluxes are interrupted. Forest fragmentation severely reduces seed output of reproductive trees (Lovejoy *et al.* 1983, Laurance *et al.* 1997, 1998a, b, 2000; Cunningham 2000, Cascante *et al.* 2002), whereas clear-cut areas act as barriers to dispersal vectors (primates, bats, birds, and insects). Therefore, isolated forest fragments may be cut off from colonization and recruitment of new species from nearby forest areas (Primack 1992, Chapman & Onderdonk 1998). Such recruitment limitation within fragments may be stronger at edges, particularly at corners, where higher mortality of trees (Lewis 1998, Laurance *et al.* 2000) may severely reduce local seed production.

A decline in seed fluxes leads to the occurrence of rare or non-abundant seedling species. Such species may be prone to local extinction due to random fluctuations in population sizes (Scariot 1999, Benítez-Malvido & Martínez-Ramos 2003), whereas other species, independent of their abundance, may be eliminated from the regenerative plant pool in fragments because of genetic deficiencies that reduce germination and seedling vigor (Young *et al.* 1996). Trees from continuous populations produce more viable seeds and vigorous offspring than isolated trees (Cascante *et al.* 2002).

The microclimate in small fragments and near

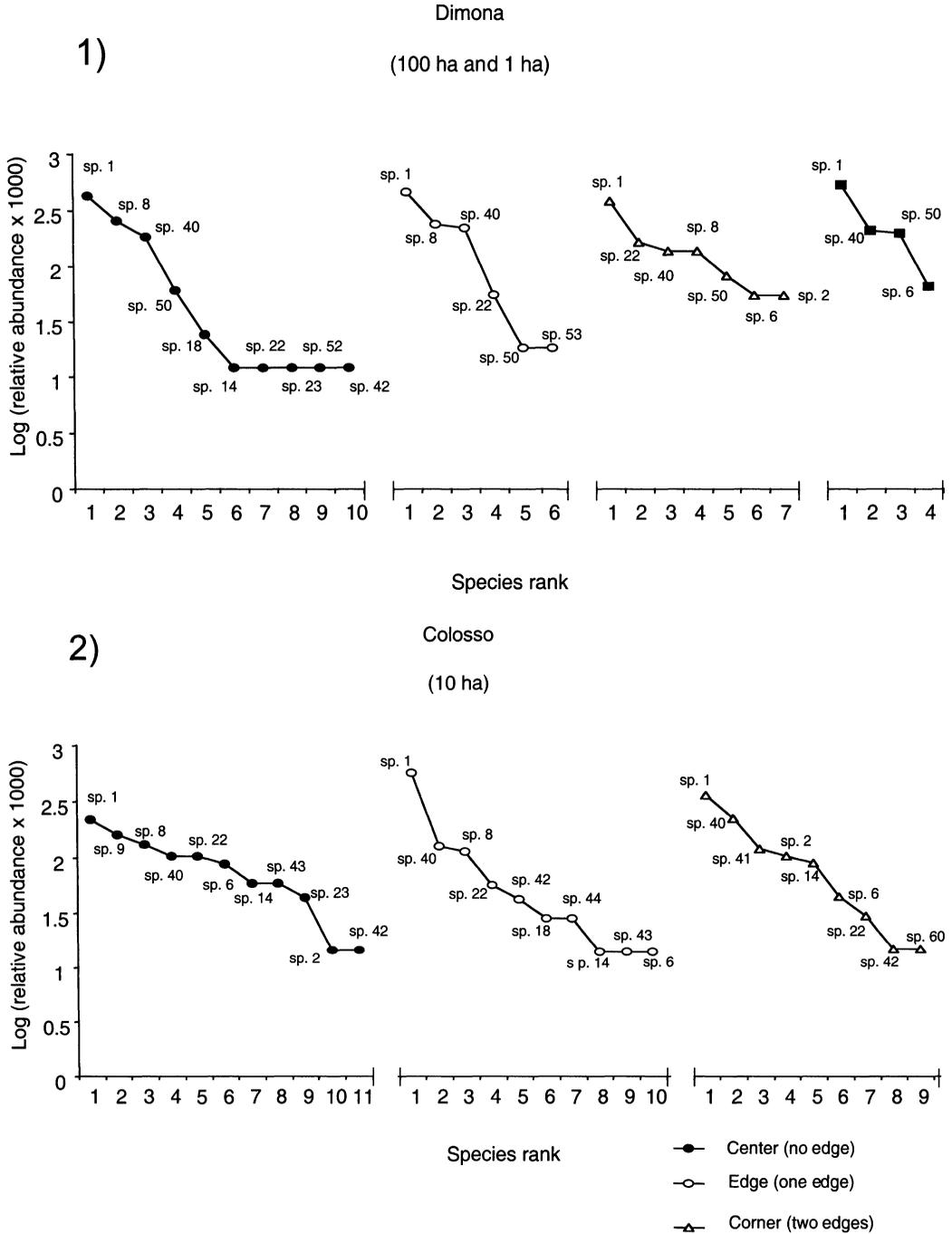


FIGURE 4. Rank/abundance plots for the tree seedling community recruited into different positions within 100 ha and 10 ha fragments and in a 1 ha fragment north of Manaus, Brazil. Number (1) is the seedling community at the Dimona site and (2) is the seedling community at the Colosso site. For each site, we plotted the relative abundance of each species on a logarithmic scale against the species' rank in order from the most abundant to the least abundant species.

forest edges is hotter and drier than in continuous forest and may not be suitable for the germination and establishment of certain seedling species (Bruna 1999, 2002). Increased litterfall and harsh external events such as fire may kill seeds and seedlings that colonize fragments (Janzen 1983, 1986, 1988; Bruna 1999, 2002; Cochrane *et al.* 1999; Sizer *et al.* 2000). Therefore, successful establishment of tree seedlings in fragments will depend on their ability to cope with the altered environment.

Soon after edge creation, many seedling species establishing in edges, corners, and very small fragments are likely to be pioneer, secondary, or exotic ruderal species (Chen *et al.* 1992, Benítez-Malvido 1998, 2001; Sizer & Tanner 1999). As time elapses and forest edges are "sealed" by dense secondary growth (Didham & Lawton 1999), however, fragments could become colonized by generalist species. For example, *P. hebetatum*, the most common species recruited in our experiment, is also the most common tree species in the BDFFP (E. Bruna and H. Vasconcelos, pers. comm.). As seedlings, *P. hebetatum* individuals could be found recruiting into canopy gaps as well as in the shaded understory (S. Laurance, pers. comm.), whereas as adult trees, individuals are generalists and can be found in any habitat within the study region (Ribeiro *et al.* 1999). Increased survival and abundance of certain seedling species will alter plant species composition in the fragments (Dirzo & Miranda 1990, Scariot 1999, Wright & Duber 2001), as shown in the present study where the same subset of species was common at all sites (Benítez-Malvido & Martínez-Ramos 2003).

FRAGMENT SIZE AND EDGE EFFECTS.—It is expected that larger forest areas will have more species than smaller ones because larger fragments have a larger number of different habitats for establishment. Furthermore, smaller fragments have proportionally more edge-altered habitat and less forest interior area. Our results showed that fragment centers had higher species richness than blocks exposed to one or multiple edges, but fragment size unexpectedly had no severe effects on seedling species richness when 100 and 10 ha fragments were compared, except for the smallest fragment (1 ha). Blocks within the 10 ha fragment showed no marked differences among positions in species richness as has been previously observed for the standing density of tree seedlings (Benítez-Malvido 1998, 2001). The lack of strong differences in species richness among positions within the 10 ha fragment suggests that edges completely affected

the fragment area. For a temperate forest in the western United States, Chen *et al.* (1992) suggested that there was no "interior forest" in fragments of 10 ha or smaller. Greater species richness in the 10 ha fragment than in the edge and corner blocks within the 100 ha fragment may have resulted from initial differences in species composition among reserves (Oliveira & Mori 1999) and management history that strongly affects the surrounding matrix and the magnitude of edge effects on the vegetation (Didham & Lawton 1999, Mesquita *et al.* 1999, Gascon & Bierregaard 2001).

The change in canopy structure along forest edges is one of the principal determinants of the extent and magnitude of edge effects in forest fragments (Didham & Lawton 1999). Fragment corners display a more damaged overstory and understory than do linear edges and fragment interiors (Benítez-Malvido, pers. obs.). Therefore, because edge effects are additive they can be particularly strong near fragment corners and in very small fragments (Malcolm 2001). Evidence of reduced seedling abundance, survival, species richness, and levels of herbivory suggests that small fragments and fragments corners are poor habitats for seedling establishment and for the insects that feed on them (Benítez-Malvido 2001). Seedling establishment in these habitats would be hindered even for the most resilient species. Therefore, the successful establishment of tree seedlings into fragment corners and small fragments (<1 ha) will depend on their ability to cope with severe environmental conditions (Kapos 1989, Camargo & Kapos 1995, Sizer *et al.* 2000).

The 100 ha fragment central block was the single area in which the individual-based species accumulation curves showed that seedling species richness was not completely recorded. For palm and tree seedlings, previous studies have shown that 100 ha fragments more closely resemble the continuous forest in understory plant community structure and floristic composition (Scariot 2001, Benítez-Malvido & Martínez-Ramos 2003); however, species richness in the 100 ha center was still lower than that recorded in continuous forest using the same experimental methods (Benítez-Malvido & Martínez-Ramos 2003). Very few species are recruiting seedlings into forest fragments, especially at the edges, corners, and in the 1 ha fragment. Reduced species richness, even for the core of the largest fragment, suggests that edge effects may occur over hundreds of meters (Laurance 2000). There is evidence that edge effects penetrated the core area of the 100 ha fragment, producing higher

rates of tree mortality and lower seedling density than in a non-isolated forest (Benítez-Malvido 2001, Rankin-de-Merona & Hutchings 2001). Large spatial scale (10^3 m; Laurance 2000) edge effects that reach forest interiors have been reported to influence forest structure (Laurance *et al.* 1997), facilitate the introduction of exotic invasive species (Peters 2001), and diminish seedling recruitment (Curran *et al.* 1999). Although the whole of the 100 ha fragment may be affected by the edge, these effects were less pronounced than for the 10 ha and 1 ha fragments.

Our results suggest that the degree of edge exposure determines tree seedling recruitment into forest fragments. Altered environmental conditions and modified biotic interactions in forest fragments may be exacerbated along edges, significantly affecting plant species recruitment (Benítez-Malvido 1998, Bruna 2002). Losses of seedling species may, in turn, affect recruitment to later life stages, compromising future forest regeneration and the maintenance of diversity (Benítez-Malvido 1998, Scarriot, 2001, Benítez-Malvido & Martínez-Ramos 2003). To entirely evaluate the effect of edge ex-

posure on seedling species recruitment and future forest regeneration, however, the identification of seedlings to species and the use of more than one sample per fragment size is required. In this way, we could have discriminated among native, secondary, and exotic species, provide stronger evidence of the generality and implications of these changes, and obtain more valuable ecological information. Nevertheless, regardless of the Latin names of the species, our study strongly indicates that the number of edges, and hence higher habitat disturbance, influences seedling species recruitment in forest fragments.

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