Impact of Forest Fragmentation on Understory Plant Species Richness in Amazonia

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Abstract: *Forest fragmentation in the tropics severely affects large trees, but its effect on other life stages and plant life forms is poorly understood. In Central Amazonia, 9 to 19 years after fragmentation, we recorded species richness and net seedling recruitment rate in forest fragments of 1, 10, and 100 ha and in continuous forest. In 1991 all seedlings 5–100 cm tall within permanent 1-m^2 plots in fragments and continuous forest were counted and grouped into tree, liana, palm, and herb life-form classes. In 1993 we manually removed all seedlings that were <1 m tall from the permanent plots. Six years and 5 months later (1999), all new seedlings recruited into the plots were counted, grouped into different life forms, and classified into distinct morphospecies. The species richness of recruited tree, liana, herb, and palm seedlings was lower in forest fragments than in continuous forest, with the 1-ha fragment having the poorest species richness. The total number of recruited individuals was 40% less than that previously present for all life forms, except lianas. Liana recruitment was 7% to 500% higher than the original abundance in the forest fragments and continuous forest. In general, species similarity was higher among fragments than between fragments and continuous forest, with the 1-ha fragment being less similar. Species rank/abundance curves showed that continuous forest species in all life forms tended to disappear in forest fragments, whereas common species in forest fragments were absent from continuous forest. Overall, our results suggest that the life-form composition and structure of the regenerative plant pool in fragments were shifting toward a species-poor seedling community. Losses of understory species diversity, but especially of tree seedlings, threaten the maintenance of rainforest biodiversity and compromise future forest regeneration.*

Impacto de la Fragmentación de la Selva sobre la Riqueza de Especies del Sotobosque en el Amazonas

Resumen: *La fragmentación de las selvas tropicales afecta severamente a a los árboles de gran porte, sin embargo, su efecto sobre otros estadíos y formas de vida de las plantas es poco conocido. En la Amazonia central, de 9 a 19 años después de la fragmentación, se registró la riqueza de especies y la tasa neta de reclutamiento de plántulas en fragmentos de selva de 1, 10, y 100 ha y en selva contínua. En 1991, todas las plántulas de 5–100 cm de altura dentro de cuadrantes permanentes de 1-m^2 en los fragmentos y en la selva contínua, fueron contadas y agrupadas en diferentes formas de vida: árboles, lianas, palmas y hierbas. En 1993 se removieron manualmente todas las plántulas <1 m de altura dentro de los cuadrantes. Seis años y cinco meses más tarde (1999) se contaron todas las plántulas reclutadas dentro de los cuadrantes, se agruparon en diferentes formas de vida v se clasificaron en morfoespecies distintivas. La riqueza de especies de plántulas reclutadas en todas las formas de vida fue menor en los fragmentos que en la selva contínua, con el fragmento de 1 ha presentando la menor riqueza de especies. El número total de individuos reclutados fue 40% menor que los previamente presentes para todas las formas de vida, excepto lianas. El reclutamiento de lianas fué de 7 a 500% mayor que la abundancia original en los fragmentos y en la selva contínua. En gen-*

eral la similitud de especies fué mayor entre fragmentos que entre fragmentos y selva contínua, con el fragmento de 1-ha siendo el menos similar. Las curvas de rango/abundancia de especies, mostraron que las especies de selva contínua en todas las formas de vida tendieron a desaparecer de los fragmentos, mientras que las especies comunes en los fragmentos estuvieron ausentes en la selva contínua. En general, nuestros resultados sugieren que la composición de formas de vida y la estructura del banco regenerativo en fragmentos tienden a convertirse en una comunidad de plántulas pobre en especies. La pérdida de diversidad de especies del sotobosque, pero especialmente de plántulas de árboles, amenaza el mantenimiento de la biodiversidad y pone en peligro la regeneración futura de la selva.

Introduction

Global biodiversity loss is closely related to the destruction and fragmentation of the tropical rainforests. Deforestation in the tropics often creates matrices of human-managed areas, secondary vegetation regrowth, and fragments of primary forest. Although plant species diversity is rapidly lost in forest areas cleared for agriculture and cattle ranching (Ehrlich 1988), the rate at which plant species diversity changes in the remaining fragmented forest is poorly known.

Recent research has shown that fragmentation produces severe changes in the demography and community attributes of trees present before disturbance (Turner et al. 1996; Laurance et al. 1997, 1998*a,* 1998*b,* 2000; Curran et al. 1999; Gascon et al. 2000). Mortality rates of canopy trees in forest fragments are higher than those in unfragmented forest (Laurance et al. 1997, 1998*a,* 1998*b*), and the abundance of pioneer species tends to increase near fragment edges (Laurance et al. 1998*a,* 1998*b*; Gascon et al. 2000). Because most tropical rainforests tree species have low population densities (Gentry 1990; Hubbell & Foster 1996), it is likely that high mortality rates will result in the loss of many rare species in forest fragments.

In the long term, species persistence in fragments depends on the availability of seeds, seedlings, and saplings. There is evidence that the density and species diversity of tree (woody) and palm seedlings is lower in forest fragments than in continuous forest. Also, edge creation affects the species composition of seedlings (Benitez-Malvido 1998; Scariot 1999; Sizer & Tanner 1999), producing an explosion of secondary species at the expense of mature forest species. These results come from static or short-term studies of seedlings that had become established before or soon after fragmentation, complicating direct assessments of fragmentation effects. In this study we show that the species diversity of tree, liana, palm, and herb seedlings in Central Amazonia, recruited 9 to 19 years after fragmentation, is significantly lower in fragments than that recorded in continuous forest. The results not only suggest that loss of plant species will occur, but also that a qualitative change in life-form and species composition in forest fragments is occurring.

Methods

Study Site

The study was conducted at the experimentally fragmented landscape of 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, and 100 ha) isolated between 1980 and 1990 (Bierreggard et al. 1992). Fragments are located within four cattle ranches. Average annual rainfall at the site is 1900–3500 mm (Laurance 2001). The mean annual temperature is 27° C; on rare occasions temperature 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 averaging 35 m in height, with occasional emergents up to 55 m (Lovejoy & Bierregaard 1990; Rankin-de Merona et al. 1990). The forest is characterized by a high density of small-diameter trees with a few trees of ≥60 cm dbh and by remarkably high species richness (1250–1300 tree species in 69 ha; de Oliveira & Mori 1999; Laurance 2001; W. Laurance, personal communication) coupled with low population densities of most species. The understory is dominated by stemless palms (Klein 1989), and there is an extremely low density of herbs and understory shrubs (Gentry & Emmons 1987). Lianas are sparsely distributed but appear to increase in abundance close to forest edges (Laurance et al. 2001).

Experimental Design

In 1991 we counted all seedlings 5–100 cm tall within permanent 1-m^2 plots in four fragments of various sizes: continuous forest (10,000 ha) and three fragments 100, 10, and 1 ha in area. We grouped seedlings into tree, liana, palm, and herb life-form classes. Fragments were clustered in two localities (cattle ranches): "Esteio," which included continuous forest (BDFFP reserve 1501, control area) and a 10-ha fragment (no. 1202), and "Dimona," which included a 100-ha fragment (no. 2303) and a 1-ha fragment (no. 2107) (cf. Lovejoy et al. 1986). Frag-

ments of 100 and 1 ha were partially or totally isolated in 1984, and the 10-ha fragment was isolated in 1980.

Seedling density in the fragments was sampled in 1-ha blocks, each of which contained 20 1-m^2 plots arranged in a stratified random manner, with four plots located along each of five 100-m-long parallel transects that were 20 m apart (Benitez-Malvido 1998; Benitez-Malvido et al. 1999). To consider the variation between fragment edge and interior, we placed 1-ha blocks within the 10- and 100-ha fragments at the center, edge, and corner of each fragment (Benitez-Malvido 1998). In the analysis, these plots (center, edge, and corner) were lumped to show the effect of fragment size rather than that of positions within the fragments, which are discussed elsewhere (Benitez-Malvido 1998, 2001, unpublished data). The number of 1-ha blocks per site were as follows: $n = 2$, continuous forest; $n = 3$, 100-ha fragments; $n = 3$, 10-ha fragments; and $n = 1$, 1-ha fragment. The fragments and continuous forest were separated by distances of 0.3–40 km (see map at http://www.inpa.gov.br/pdbff).

To assess plant recruitment after isolation, in May 1993 we manually removed all understory plants <1 m tall from the 1-m^2 plots. Six years and 5 months later (October 1999), all new seedlings recruited into the plots were counted, grouped into different life forms, and classified into distinct morphospecies. With the help of a local parataxonomist, we categorized seedlings into morphospecies based on stem, leaf, and root traits. Seedling vouchers were placed with the Department of Tropical Silviculture of the National Institute for Research in the Amazon. In continuous forest, seedling recruitment was measured in 33 out of 40 plots because some plots were lost to unknown causes. The fragments were surrounded by shrubby pasture when the experiment was initiated in 1991, but by 1999 this had become a 10- to15-m-tall regrowth forest dominated by *Cecropia* spp. and *Vismia* spp. trees.

Species Richness

We assessed differences in the species richness of recruited plants between different size fragments by constructing mean species-area accumulation curves after 100 randomizations of the order of sample quadrats by using the program EstimateS (Colwell 1997). Observed accumulation species-area curves underestimate species richness (Colwell & Coddington 1994). Therefore, in an attempt to discover true species richness, we used nonparametric methods provided by the EstimateS program, selecting three methods that have proved the best estimators of species richness of tree seedling communities in the tropical rainforest of Costa Rica (Chazdon et al. 1998). Incidence-based coverage estimators (ICE) chao-2, and jacknife-2 are based on the incidence (presence/absence) of species. Colwell and Coddington (1994, 1995) and Chazdon et al. (1998) fully describe these methods.

The nonparametric estimators (Chazdon et al. 1998) were expressed for 20 m^2 and calculated from accumulation curves obtained after 100 randomizations of sample quadrat order. In all cases we performed EstimateS, setting patchiness at 0. Patchiness 0 means that each plant was sorted at random to a sample within species, whereas the distribution of plants among species and the number of samples were maintained as in the observed community input matrix (Colwell & Coddington 1995). This procedure eliminates biases in the species-richness estimates caused by species patchiness (Colwell & Coddington 1994).

Species Similarity

To estimate the proportion of species shared between site pairs, we used the Jaccard index of similarity (JI) based on species presence/absence data. The JI is a measure of similarity in species composition between two communities (A and B), calculated as $C_J = j/(a + b - j)$, where j is the number of species common to both communities and a and b are the numbers of species occurring only in communities A and B, respectively. The index is designed to equal 1 in cases of complete similarity—that is, when two sets of species are identical—and 0 if the sites are dissimilar and have no species in common (Magurran 1988). We obtained average JI values after bootstrapping 100 times the data from 20 plots (minimum plot sample size) from the plot pool of each site.

Species Dominance

To determine whether species relative abundance is modified by fragmentation, we constructed rank/abundance plots for the seedling community in all life forms and for the tree-seedling community in fragments and continuous forest (Magurran 1988). For each site we plotted the relative abundance of each species on a logarithmic scale against the species' rank, ordered from the most abundant to the least abundant species (Magurran 1988).

Statistical Analysis

Because each fragment was not replicated, to assess seedling density differences among fragments and address pseudoreplication (Hurlbert 1984), we obtained a single density value per fragment. To do this, we randomly selected 20 plots (minimum plot sample size) from the plot pool of each fragment and expressed seedling density per 20 m^2. We analyzed differences in the density of seedlings among fragments in 1991 and 1999 with log-linear models for count variables (Crawley 1993) by using the GLIM statistical package (Green & Payne 1994). For Poisson data, the deviance will be approximately distributed as a chi-square (Crawley 1993). The proportion of plants in different life forms found in

1999 with respect to those found in 1991 (R:O) were analyzed with chi-square tests. Species similarity among different size fragments and continuous forest was analyzed by one-way analysis of variance of arcsine square-root JI values. The number of palm and herb individuals recruited into the plots was so low that we pooled data to permit statistical comparisons.

We performed Pearson's correlation tests to assess the relationship between seedling abundance and species richness, between species richness and similarity with distances among study sites, and between seedling density with fragment size and age. Mantel tests would have been useful to determine whether differences in species similarity were related to geographic distances among study sites (Sokal & Rohlf 1995), but our sample size (four fragments) was not large enough to permit such analysis. The use of each 1-ha study block ($n = 9$) as independent samples in the Mantel test was flawed in that the effects of distance among fragments on species similarity may have been confounded with effects attributable to positions (center, edge, and corner) within the 10- and 100-ha fragments. All statistical tests were performed for all pooled species and for each plant-life form. Significant differences were set at ≤0.05.

Results

Seedling Density

In 1991, total seedling density was higher in continuous forest than in isolated fragments for all pooled species ($\chi^2 = 13.52$, df = 3, $p = 0.01$) and for palms and herbs together ($\chi^2 = 16.87$, df = 3, $p = 0.0001$), whereas trees had higher density in continuous forest than in the 100- and 1-ha fragments ($\chi^2 = 9.32$, df = 3, $p = 0.05$), and liana density was higher in the 1-ha fragment than in continuous forest and the 10-ha fragment ($\chi^2 = 12.06$, df = 3, $p = 0.05$) (Table 1). Intersite density variation, however, was not related to fragment size or age ($p > 0.10$). This pattern changed for seedlings recruited after 1993. After more than 6 years, the initial abundance of seedlings or any other life form had not recovered in any of the sites, including continuous forest, except for lianas. Liana recruitment was 7% to 500% higher than in 1991 in the fragments and continuous forest (Table 1). On average, palms and herbs showed the lowest recovery, and trees recovered less than half of their initial density.

Species Richness

For all life forms, species/accumulation curves showed that species richness was far from being completely recorded in the continuous forest with our sampling effort (Fig. 1). In contrast, the fragments showed an asymptotic trend, particularly the 1-ha fragment. For all life

Table 1. Density of understory plants (<1 m tall) in 20 m² in continuous forest and forest fragments north of Manaus, Brazil, in 1991 and 1999.[a]

Site and life forms	1991	1999	R:O[b]
All plants			
continuous forest	293b	109a	0.37**
100-ha reserve	220a	84a	0.38**
10-ha reserve	246a	82a	0.33**
1-ha reserve	223a	97a	0.43**
mean R:O ± SE			0.38 ± 0.02
Trees			
continuous forest	240b	90a	0.38**
100-ha reserve	188a	59a	0.31**
10-ha reserve	220ab	73a	0.33**
1-ha reserve	188a	72a	0.38**
mean R:O ± SE			0.35 ± 0.02
Lianas			
continuous forest	2a	12ab	6.00**
100-ha reserve	8ab	20b	2.50**
10-ha reserve	4a	6a	1.5*
1-ha reserve	14b	15ab	1.07
mean R:O ± SE			2.77 ± 1.12
Palms and herbs			
continuous forest	49b	7a	0.14**
100-ha reserve	21a	8a	0.38**
10-ha reserve	25a	4a	0.16**
1-ha reserve	21a	6a	0.29**
mean R:O ± SE			0.24 ± 0.11

[a] *Sites with different letters are significantly different (p < 0.05).*
[b] *The R:O ratio is the ratio of plants found in 1999 (R) to those found in 1991 (O). With chi-square analysis, R:O values significantly different from 1.0 are * p < 0.05 and ** p < 0.001. Those not marked are not significant.*

forms, at an equal quadrat sample size of 20, species richness was considerably higher in continuous forest than in forest fragments. Except for lianas, the lowest species richness was recorded in the 1-ha fragment.

The nonparametric estimators magnified the differences in species richness between continuous forest and fragments. In most cases, species richness declined with fragment size (Fig. 2) and was independent of seedling abundance. The reduction in species richness from continuous forest to fragments was on the order of 2.6 to 9.1 times, depending on the life form and the species-richness estimator (Fig. 2). Differences in species richness were not related to distances among study sites. Depending on life form and species-richness estimator, correlation coefficients varied from 0.03 to 0.63 (df = 2, $p > 0.5$) for the relationship between species richness and abundance and from 0.00 to 0.33 (df = 4, $p > 0.5$) for the relationship between change in species richness and distance between study sites.

Species Similarity

Differences in species richness were linked with differences in species similarity among sites. In general, continuous forest and fragments had lower similarity than did forest fragments, and the species similarity of trees and lianas between
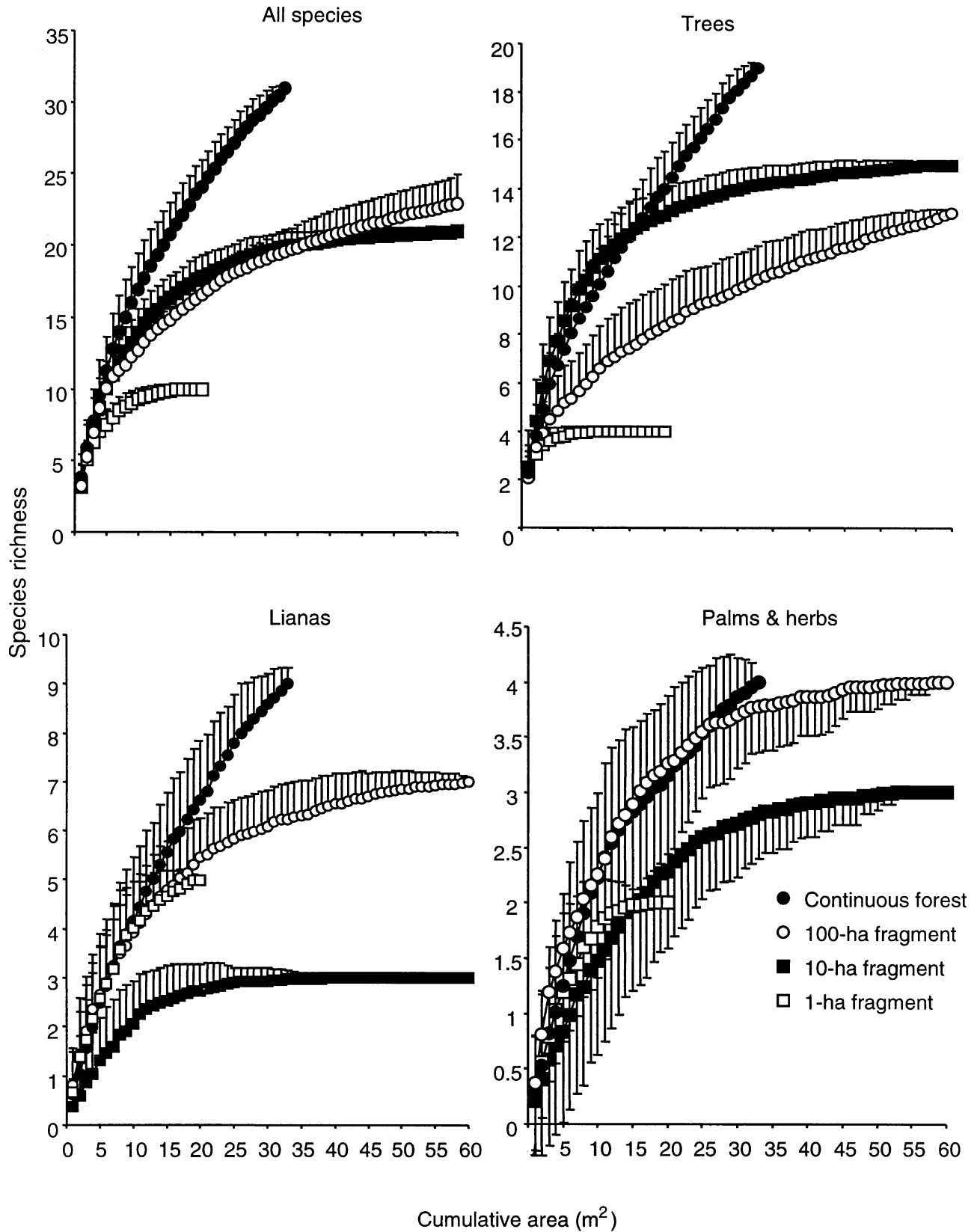
Figure 1. Species-area accumulation curves (mean ± 1 SD) for seedlings recruited into forest fragments and continuous forest near Manaus, Brazil.
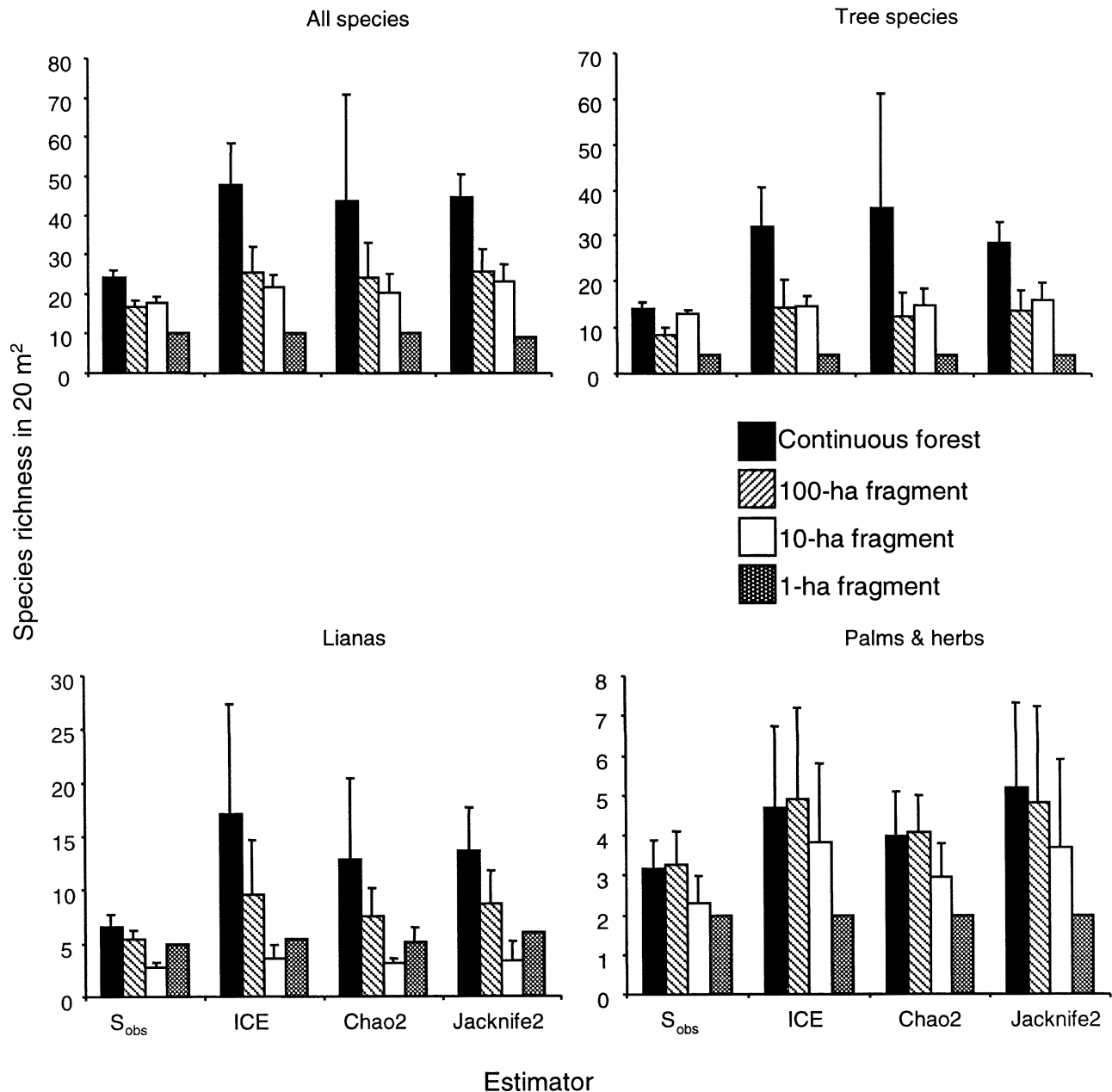
Figure 2. Species richness (mean ± 1 SD) per plant group recruited into continuous forest and forest fragments. The observed species richness (S_{obs}) is indicated, as are the three different nonparametric estimators, where incidence-based coverage estimator (ICE), Chao-2, and jacknife-2 estimators are based on incidence (presence/absence) of species.

continuous forest and forest fragments declined with fragment size (Fig. 3). In general, fragments that were closer did not have greater similarity than fragments that were farther apart (Fig. 4). On average, depending on life form, continuous forest and fragments shared 8–40% of species, whereas fragmented sites shared 20–65% of species.

Species Dominance

The seedling community in fragments and continuous forest followed a log-series model of a small number of abundant species and a large proportion of rare species.

The dominant seedling throughout the study sites was a tree species from the Burseraceae (Figs. 5a & 5b). The following patterns emerged in the rank-abundance plots: (1) the dominant seedling species (species 1) in continuous forest was also dominant in the forest fragments, regardless of fragment size; (2) for all life forms, rare species present in continuous forest tended to be absent as fragments became smaller; (3) even some species that were dominant in continuous forest were rare in forest fragments and tended to be absent in the 1-ha fragment; and (4) some dominant species in fragments were not registered in continuous forest (Figs. 5a & 5b).
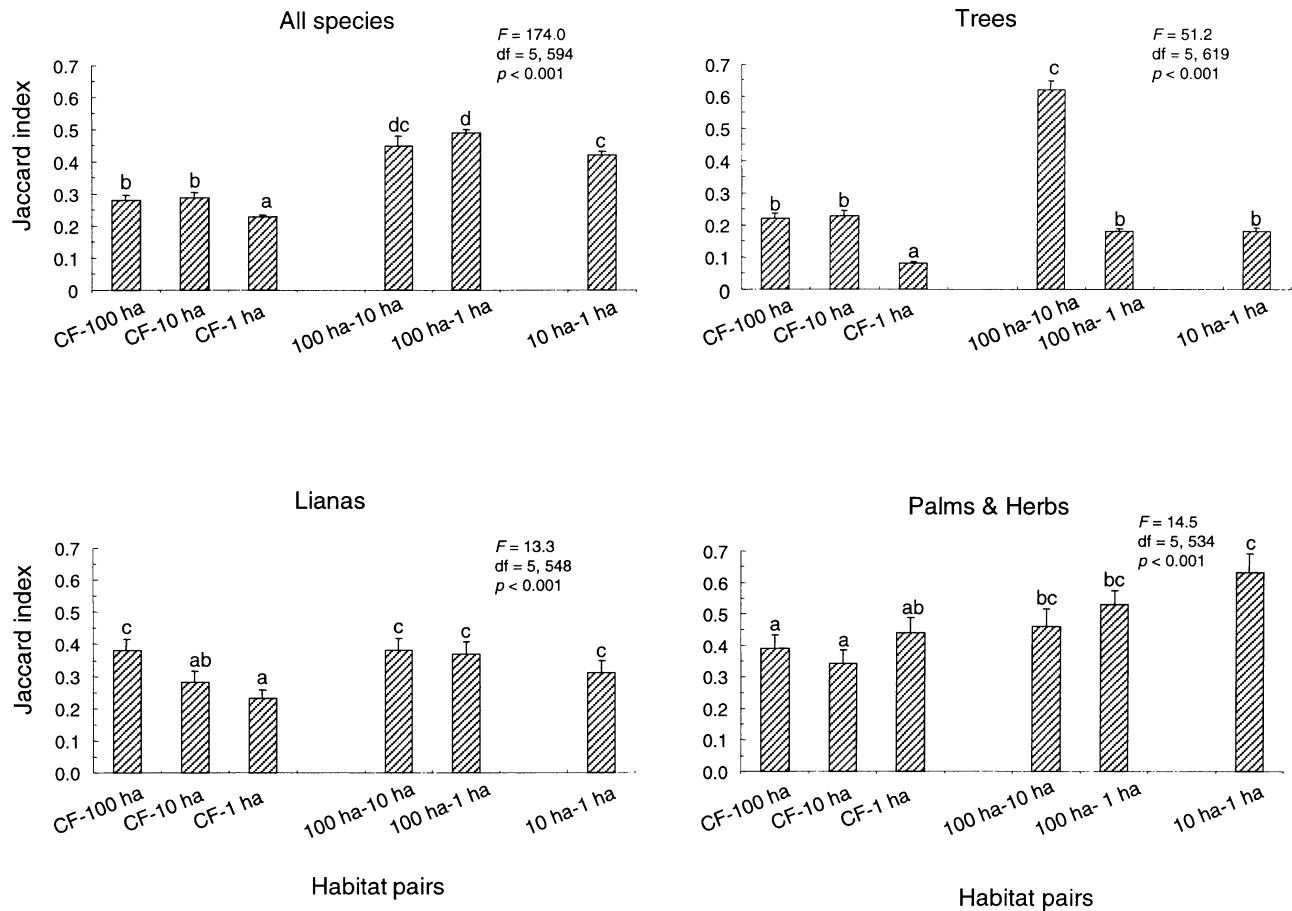
Figure 3. Site-pair comparisons (mean ± 1 SE) of species similarity (Jaccard index) between fragments and continuous forest (CF) and between fragments of different size (1, 10, and 100 ha). Different letters indicate significant differences among habitat pairs.

Discussion

Overall, our results suggest that a process of plant-species loss operates in the seedling community within forest fragments. Although we have no replicates for fragment sizes, the generality of the results is supported by the fact that significant reductions in species richness occurred from large to small fragments at two different localities or cattle ranches. At Esteio cattle ranch, species richness declined from continuous forest to the 10-ha fragment, whereas at Dimona cattle ranch, species richness declined from the 100-ha to the 1-ha fragment (Figs. 1 & 2). The poor recovery capacity of the understory vegetation, in life forms other than lianas, suggests that seedling density in a given forest spot was the outcome of long-term regeneration processes that take more than 6 years to develop. Underlying the process of species loss is a complexity of ecological factors and mechanisms that remain to be understood.

Seedling Ecology

Species composition in fragments shifted toward a plant community dominated by few species. Apparently only

those plant species that withstand drastic environmental changes and that are characteristic of disturbed areas, including lianas, were able to flourish within fragments. The fact that liana recruitment surpasses the original liana density in forest fragments suggests that these sites are undergoing a decaying process as lianas increase in abundance in forest subjected to disturbances (Putz 1983, 1984; Laurance et al. 2001; Pérez-Salicrup 2001). Lianas are known to favor forest disturbance and to increase in density and diversity along forest edges in the BDFFP study sites (Laurance 1998; Laurance et al. 2000, 2001). Although we have no data to explain why liana recruitment was enhanced in continuous forest, there are several possible non-exclusive causes. One possibility is that the disturbance produced within the 1-m^2 plots, when seedlings were removed at the beginning of the experiment, induced germination of buried liana seeds. A second possibility is the occurrence of gap disturbances during the study period (J. Benitez-Malvido, personal observation). Third, the presence of a high number of reproductive lianas in continuous mature forest may account for the high seedling liana recruitment. Laurance et al. (2001) noted that mature lianas increase toward
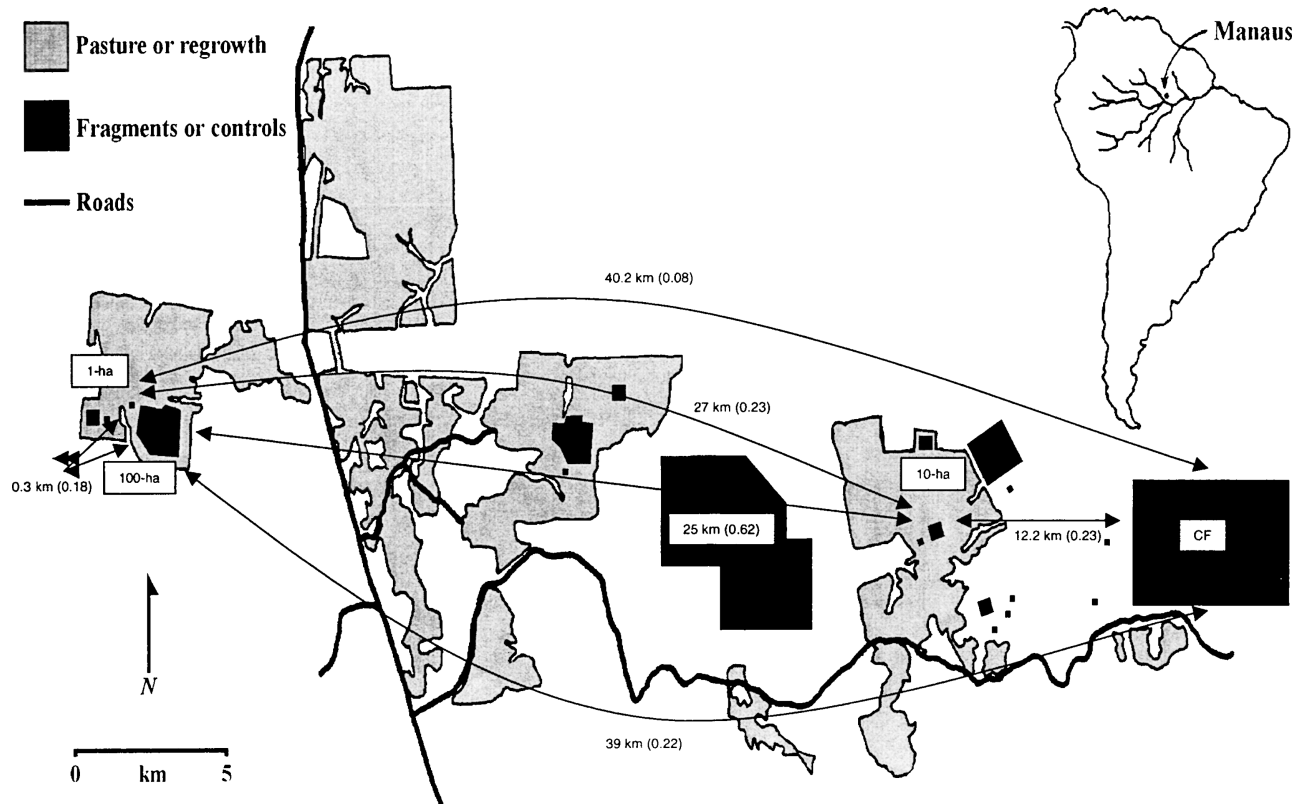
Figure 4. Map of the Biological Dynamics of Forest Fragments Project north of Manaus, Brazil. Black squares indicate the reserves used in this study; continuous forest areas are in white, and shaded areas are secondary forest and pastures. Distances among different fragments and between fragments and continuous forest are indicated beside the lines. For tree seedling species, Jaccard indexes of similarity between habitat pairs are in parentheses. Fragment sizes are in squares, and CF is continuous forest.

deep forest interiors (>1000 m from the forest edge) in the same study area.

In terms of abundance, seedling species in all life forms showed three types of responses to forest fragmentation. Some species decreased in abundance or vanished from fragments, some increased in abundance or appeared in fragments, whereas others were unaffected. Similar findings have been observed for palm species in the same study area, where some taxa were restricted to particular sites and fragment sizes (Scariot 1999). The shifts in abundance of different seedling species in fragments and continuous forest suggest that some species can withstand the environmental alterations produced by forest fragmentation, whereas others are susceptible and tend to disappear from fragments. It is likely that species that withstand fragmentation have certain ecological characteristics such as being generalist pollinators, having a high reproductive capacity independent of the environment, having successful germination in fragments and continuous forest (Bruna 1999), being stress-tolerant at the seedling stage, and being resistant to natural enemies (herbivores and pathogens) and physical damage. For example, we found that forest fragmentation at our study site had

species-specific effects (differential survival, growth, herbivory, and pathogen damage) on three seedling species (Sapotaceae) transplanted into fragments and continuous forest (Benitez-Malvido et al. 1999; Benitez-Malvido 2001; J.B.-M. and M.M.-R., unpublished data;). On the other hand, seedling species absent from continuous forest but abundant in forest fragments could be successional, exotic, or invasive plant species that replace oldgrowth forest species, as has been shown for the Arecaceae and other tree families (Annonaceae, Cecropiaceae, Clusiaceae, Euphorbiaceae, Malpighiaceae) at the same study sites (Laurance et al. 1998*a*; Scariot 1999).

Propagule Availability and Species Richness

The populations of several animal pollinators and seed dispersers have been reduced in size or have vanished from fragmented forests (Powell & Powell 1987; Klein 1989; Chapman & Onderdonk 1998). A reduction in the number of dispersal vectors, in addition to an increase in the mortality and poor reproductive capacity of plants, may reduce seed output and hence seedling recruitment and colonization into fragmented forests (Laurance et al.
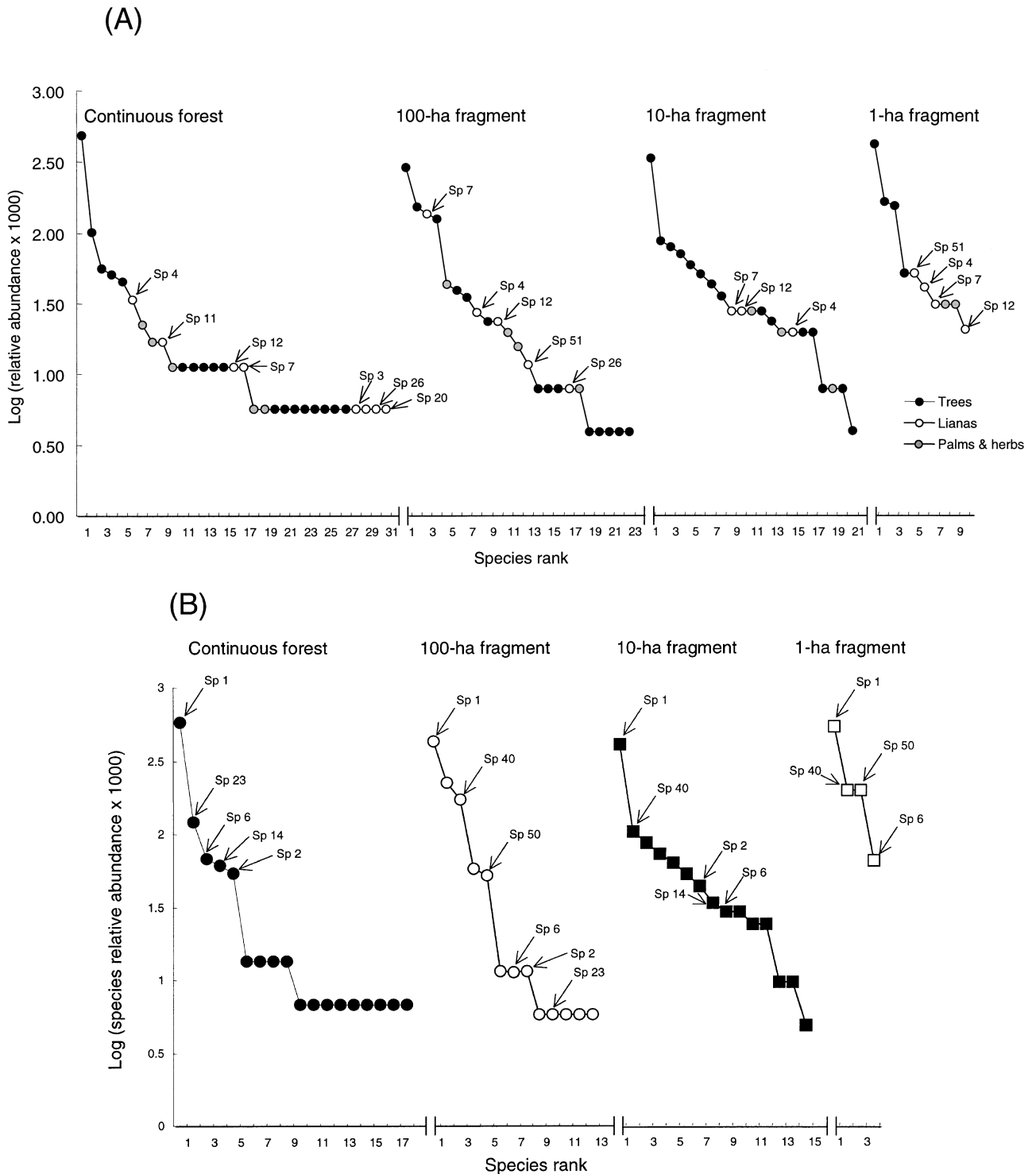
Figure 5. Rank/abundance plots for the seedling community recruited into fragments and continuous forest, north of Manaus, Brazil: (a) the seedling community in all life forms and (b) the tree seedling community. For each site we plotted the relative abundance of each species on a logarithmic scale against the species' rank, from the most abundant to the least abundant species.

1997, 2000; Chapman & Onderdonk 1998; Curran et al. 1999). For example, primates are important primary seed-dispersal agents for trees (Rylands & Keuroghlian 1988; Julliot 1994, 1996; Chapman 1995; W. Spironello,

unpublished data). Declines in primate populations may influence the seedling recruitment of many plant species. At Kibale National Park, Uganda, forest fragments in which primate populations had been reduced had lower

seedling density and fewer species than an intact continuous forest (Chapman & Onderdonk 1998).

In a given isolated forest fragment, species reproducing locally would be the most common in the seed rain, whereas rare species that arrive from seed sources outside the isolated fragment would tend to disappear. At Los Tuxtlas, Mexico, nearly 50% of seedling richness results from external patch dispersal sources (Martínez-Ramos & Soto-Castro 1993). Therefore, as fragments become smaller as a result of the process of "receding edges" (Gascon et al. 2000), fewer species are likely to occur in the seed rain and hence in the seed and seedling banks. Tropical tree species need large forest areas to maintain viable populations (Alvarez-Buylla et al. 1996).

Seedling Survival and Species Richness

The species richness of seedlings in fragments could decline in two other ways. First, if survival probability is similar for common and rare seed and seedling species, we would expect species richness to decline within the fragment if mortality rates increase for both types of species (e.g., increased predation, reduced germination, increased physical damage) (Santos & Tellería 1997; Bruna 1999). Second, if survivorship tends to be reduced only for rare species, due to genetic deficiencies for example (Alvarez-Buylla et al. 1996; Young et al. 1996), we would expect the species richness of rare species to decline most. Also, rare species in fragments are prone to local extinction by density-independent mortality factors such as drought (Cochrane et al. 1999; Curran et al. 1999) and physical damage (increased canopy debris).

Distance Effects

It has been documented that tropical rainforest undergoes high spatial turnover rates in species composition (Gentry 1988; Campbell 1994). The dramatic shifts in species composition among fragments and continuous forest could be a consequence of such turnover rather than of fragmentation effects. Recent studies in western Amazonia, however, have shown that a few common species dominates the tree community at local (1 ha), landscape (10^4 km^2), and regional (>10^6 km^2) scales, forming predictable oligarchies over immense tracts of forest (Pittman et al. 2001). The same pattern was observed in our study system: the most abundant seedling species (species 1, Burseraceae) was the same for all sites. Excluding this dominant species, the species similarity between fragments changed with fragment size in spite of the distance among sites. For example, the similarity (JI) of seedling tree species between continuous forest and the 100-ha fragment was almost four times higher than between that of continuous forest and the 1-ha fragment, despite the fact that both fragments were about the same distance from continuous forest (Fig. 4). Also, the JI

value between 1- and 100-ha fragments, which were 300 m apart, was more than three times lower than the JI value between 10- and 100-ha fragments, which were 25 km apart. Scariot (1999) found similar results with palm seedlings: species similarity between fragments of comparable size was greater than between fragments of extremely different size. He also found, however, that some palm species were restricted to particular sites in the BDFFP study area. Also in Scariot's study, the continuous forest sites and 1-ha fragments exhibited the lowest similarity, as was the case in our study on seedlings of different life forms. All these observations support the idea that fragmentation tends to change the species composition of seedlings. However, our lack of a larger sample size does not enable us to segregate the effects of fragmentation from those related to the spatial arrangement of the sites.

Conclusion

The lack of replication for any fragment size limits our results to the particular sites studied. However, we found a relevant decline in the species diversity of recruited seedlings in fragmented forest. Because forest fragmentation reduces understory plant diversity, it compromises future forest regeneration. The strong reduction in the species diversity of tree seedlings is of particular concern because trees are the major component of the diversity, structure, and function of tropical rain forests (Denslow 1987). The relentless loss of tree species diversity in the understory may be an imperceptible phenomenon in the short term, but it may have dramatic future consequences for the diversity of tropical rain forests.

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