RAIN FOREST FRAGMENTATION AND THE STRUCTURE
OF AMAZONIAN LIANA COMMUNITIES

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Abstract. In tropical forests, lianas (woody vines) are important structural parasites of trees. We assessed the effects of forest fragmentation, treefall disturbance, soils, and stand attributes on liana communities in central Amazonian rain forests. Over 27 500 liana stems ($\geq$2 cm diameter at breast height [dbh]) were recorded in 27 1-ha plots in continuous forest and 42 plots in 10 forest fragments ranging from 1 to 100 ha in area. For each plot, an index of forest disturbance was determined from a 20-yr study of tree-community dynamics, and 19 soil-texture and chemistry parameters were derived from soil surface samples (top 20 cm).

Liana abundance was 187–701 stems/ha, and liana aboveground dry biomass varied from 3.7 to 12.3 Mg/ha. Liana abundance increased significantly near forest edges and was significantly positively associated with forest disturbance and significantly negatively associated with tree biomass. Liana biomass was similarly associated with disturbance and tree biomass but also increased significantly along soil-fertility gradients. Plots near forest edges had a significantly higher proportion of small (2–3 cm dbh) lianas and relatively fewer large ($\geq$4 cm dbh) lianas than did sites in forest interiors.

Liana communities were further assessed by comparing their species richness, composition, climbing guilds, and frequency of tree infestation in three 10-ha fragments. Within each fragment, data were collected in 24 small (400-m^2) plots, with half of the plots near edges and half in interiors. Significantly more trees were infested on fragment edges than in interiors. All three major guilds (branch-twiners, mainstem-twiners, tendril-twiners) were significantly more abundant on edges. Species diversity of lianas (as measured by Fisher's diversity index) also was significantly higher on edges, and this was not simply an artifact of increased liana abundance on edges.

We conclude that many aspects of liana community structure are affected by habitat fragmentation, and we suggest that lianas can have important impacts on forest dynamics and functioning in fragmented rain forests. By creating physical stresses on trees and competing for light and nutrients, heavy liana infestations appear partly responsible for the dramatically elevated rates of tree mortality and damage observed near fragment edges.

Key words: Amazon; biomass; edge effects; forest dynamics; habitat fragmentation; liana communities; tree infestation; tropical rainforest; tree mortality; vines.

INTRODUCTION

Lianas (woody vines) are a conspicuous feature of tropical rain forests and important structural parasites of trees. Occasionally growing to >40 cm in diameter and several hundred meters in length, lianas exploit trees for physical support in order to reach the forest canopy. By creating structural stresses on trees and competing for light, moisture, and soil nutrients, lianas can reduce tree growth (Putz 1984, Whigham 1984, Pérez-Salicrup 1998) and reproduction (Stevens 1987), and increase rates of tree felling and limb breakage (Lowe and Walker 1977, Putz 1980, 1984).

Lianas are diverse and abundant in many tropical forests. On Barro Colorado Island, Panama, 45% of all plant species >10 m tall are lianas (Croat 1978). In both neotropical and southeast Asian forests, 40–60% of all large ($\geq$10 cm diameter) trees typically bear at least one liana (Putz 1983, Putz and Chai 1987, Campbell and Newbery 1993, Pérez-Salicrup 1998). Although they comprise less than one tenth of aboveground biomass, lianas produce up to 40% of all leaves in the forest (Ogawa et al. 1965, Klinge and Rodriguez 1974, Kato et al. 1978, Putz 1983, Avalos and Mulkey 1999). Many lianas propagate vegetatively as well as by seed (Putz 1984), enhancing their ability to proliferate under favorable conditions.

Most liana species are light loving and respond pos-

itively to forest disturbance (Webb 1958, Putz 1984). Treefall gaps provide both increased light and abundant small trees and liana stems that provide crucial supports for climbing lianas. As they colonize gaps, lianas often inhibit the regeneration of small trees via shading and mechanical damage (Nicholson 1958, Dawkins 1961, Fox 1968, Putz 1984). Liana infestations also promote formation of large treefall gaps by entangling the crowns of adjoining trees; in peninsular Malaysia, liana-laden trees dragged down nearly twice as many neighbors when felled as did similarly sized trees that were liana-free (7.2 vs. 3.9; Appanah and Putz 1984). Lianas tend to proliferate in logged forests (Pinard and Putz 1994) and are loathed by foresters because they suppress tree growth, deform boles, and increase tree mortality (Putz 1991).

Lianas have been shown to increase in fragmented forests in tropical Queensland (Laurance 1991, 1997) and southeastern Brazil (Oliveira-Filho et al. 1997, Tabanez et al. 1997, Viana et al. 1997), apparently in response to increased treefalls and lateral light penetration near forest edges. In the Amazon, rates of tree mortality and damage rise sharply in fragmented forests (Lovejoy et al. 1986, Ferreira and Laurance 1997, Laurance et al. 1998b), causing many ecological changes and a substantial loss of living tree biomass (Laurance et al. 1997, 1998a). Quantitative models incorporating these data suggest that biomass losses in fragmented tropical forests could be a globally significant source of greenhouse gases, releasing up to 150 million Mg of C emissions annually (Laurance et al. 1998d). To date, however, the role of lianas in fragmented Amazonian forests is unknown, and there have been very few ecological studies of Amazonian lianas (e.g., Rollet 1969, Putz 1983).

Here we present a large-scale integrative study of liana communities in fragmented and continuous Amazonian forests. Our study combines extensive liana surveys at landscape and local scales, with a major data set on forest soils and a 20-yr investigation of forest dynamics and disturbance. We focus on four questions: (1) Do the abundance and biomass of lianas increase in fragmented forests? (2) Does fragmentation affect liana species richness, composition, size distributions, or climbing guilds? (3) Do soils, forest disturbances, and stand features influence liana communities? (4) How do lianas affect the dynamics and biomass of fragmented forests?

METHODS

Study area

The study area is located in the central Amazon, 80 km north of Manaus, Brazil (2°30′ S, 60° W), at 50–100 m elevation (Lovejoy et al. 1986). Rain forests in the area are not seasonally inundated. Rainfall ranges from 1900–3500 mm annually with a pronounced dry season from June to October. The forest canopy is 30–37 m tall, with emergents to 55 m. Species richness of trees is very high and can exceed 280 species (≥10 cm dbh) per hectare (de Oliveira and Mori 1999).

The study area is surrounded by large expanses (> 200 km) of continuous forest to the west, north, and east. In the early 1980s, 11 1-, 10-, and 100-ha fragments (Fig. 1) were isolated by distances of 70–1000 m from surrounding forest by clearing the intervening vegetation to establish pastures in three large (~5000 ha) cattle ranches. Fragments were fenced to prevent encroachment by cattle. Nine reserves ranging from 1 to 1000 ha in area were delineated in nearby continuous forest to serve as experimental controls. Regrowth forests have regenerated in some cleared areas and are dominated by *Cecropia* spp. or *Vismia* spp.

The dominant soils in the study area are xanthic ferralsols (using the Food and Agricultural Organization/ United National Educational Scientific and Cultural Organization system; Beinroth 1975). Ferralsols are widespread in the Amazon basin, heavily weathered, and usually have a low base saturation. They often are well aggregated, porous, and friable, with variable clay contents. Clay particles in ferralsols can form very durable aggregations, giving the soil poor water-holding characteristics, even with high clay contents (Richter and Babbar 1991). Xanthic ferralsols in the Manaus area are derived from Tertiary deposits and are typically acidic and very poor in nutrients such as P, Ca, and K (Chauvel et al. 1987).

Network of permanent plots

Since 1980, a long-term study of tree-community dynamics, biomass, and composition has been conducted in fragmented and continuous forests in the study area. Over 62 000 trees (≥10 cm dbh) are being monitored at regular (typically 4–6 yr) intervals within 69 permanent, square, 1-ha plots spanning an extensive (~1000 km^2) experimental landscape (Fig. 1). Forty-two of the plots are located within five 1-ha fragments (5 plots), three 10-ha fragments (18 plots), and two 100-ha fragments (19 plots). The remaining 27 control plots are arrayed in nine reserves that roughly mimic the spatial arrangement of fragment plots, but in continuous forest. Plots within fragments and continuous forest are stratified so that edge and interior areas were both sampled. Because fragmentation effects on forest dynamics in these recently isolated forests (<20 yr) are strongly influenced by the distance of plots to forest edge (cf. Lovejoy et al. 1986, Ferreira and Laurance 1997, Laurance et al. 1997, 1998a, b, c, d), the present study focuses on edge distance as a key landscape variable. The effects of additional soil and habitat variables on lianas are also assessed.

Liana abundance and biomass

From 1997 to 1999, liana abundance, biomass, and size distributions were estimated within all 69 1-ha plots. Liana abundance was estimated by counting all
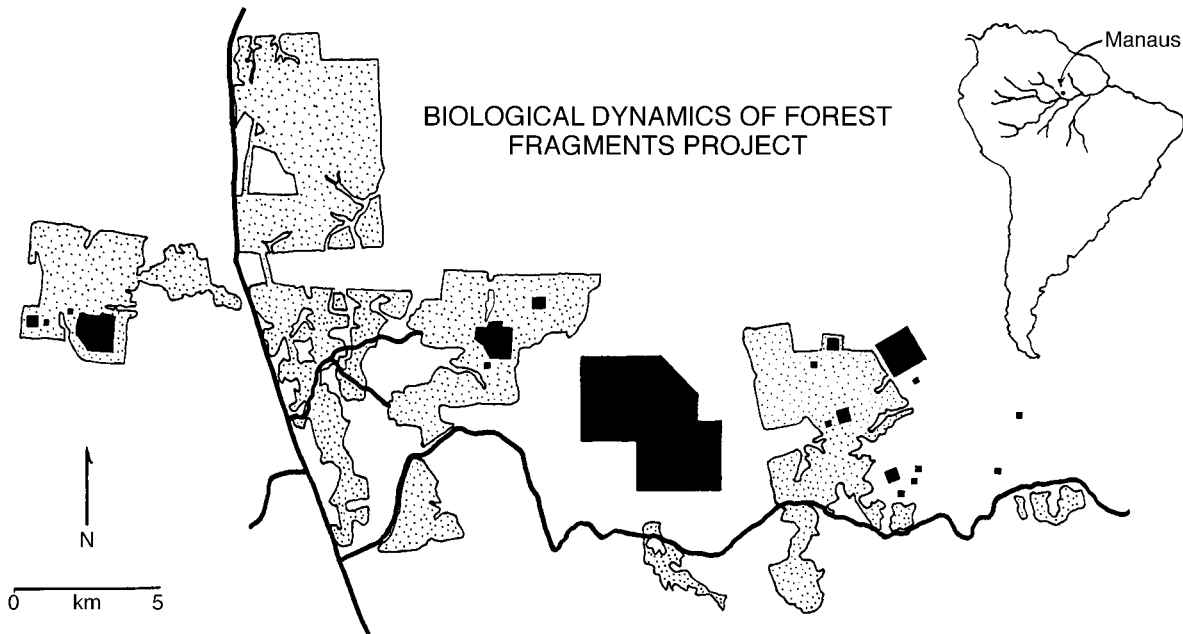
Fɪɢ. 1. Location of the study area in central Amazonia. Unshaded areas indicate primary rainforest, while stippled areas show cattle pastures or regrowth forest. Dark wavy lines are access roads. Darkly shaded blocks indicate experimental forest fragments and control sites in continuous forest.

liana stems ($\geq$ 2 cm dbh) within each plot, following the method of Putz (1983, 1984). It was not feasible to excavate each stem to determine whether it was linked to nearby stems (vegetatively propagated) or a distinctive individual (genet). The diameter of each stem at 1.3 m height was measured with a dbh-tape to the nearest 0.1 cm, then converted to an estimate of aboveground dry biomass using an allometric formula developed in an Amazonian rain forest in Venezuela (Putz 1983):

$$\text{Log biomass (kg)} = 0.12 + 0.91\log([\text{dbh}]^2). \quad (1)$$

Forest disturbance

An index of past forest disturbance was derived by calculating the mean annual rate of change in aboveground tree biomass in each plot, based on long-term (14–20 yr) data on tree-community dynamics (Laurance et al. 1997, 1998a, b). In mature forest, this index provides a more realistic indication of forest disturbance than tree-mortality rates, because it places greater emphasis on deaths of large trees.

All plots were initially censused between January 1980 and January 1987, then recensused 3–5 times, with the most recent recensus completed in June 1999 (mean = 4.0 censuses/plot). Estimates of aboveground dry biomass (AGBM) for each plot were derived by carefully measuring (to the nearest 1 mm) the diameters of all trees $\geq$10 cm dbh. Buttressed trees were measured just above the buttresses. Measurements of dbh

were converted to biomass estimates with an allometric model derived by destructively sampling 319 trees in nearby rain forests (Santos 1996). Total AGBM estimates for each plot were adjusted upward by 12% to account for trees of <10 cm dbh (Jordan and Uhl 1978). For each plot, AGBM values for all censuses were regressed against time (months since January 1980) in order to estimate the mean rate of biomass change (Laurance et al. 1997). Plots near forest edges (<100 m from edge) often lost considerable biomass (mean 3–14 Mg·ha^{-1}·yr^{-1}), especially if several large trees died, whereas plots in forest interiors were usually more stable (Laurance et al. 1997).

Soil parameters

Within 40 of the 1-ha plots, we measured 19 soil parameters. These 40 plots spanned the width and breadth of the study area (including eight of 11 fragments and seven of nine reserves in continuous forest), and varied greatly in distance to forest edge (53–3000 m). Field and laboratory methods used for soil analyses are detailed elsewhere (Laurance et al. 1999, Fearnside and Leal-Filho, *in press*), and briefly summarized here. Each 1-ha plot was divided into 25 quadrats of 20 × 20 m each. Within each plot, 9–13 quadrats were selected for sampling, using an alternating pattern to provide good coverage of the plot. In each quadrat, 15 samples were collected at haphazard locations with a soil auger (2 cm diameter, 20 cm deep cores), then bulked and subsampled. Composite samples for each quadrat were oven-dried, cleaned by removing stones

and charcoal fragments, then passed through 20 mm and 2 mm sieves. In all cases, values for soil parameters were derived separately for each quadrat, then combined to yield a mean value for each 1-ha plot.

Textural analyses were conducted to separate samples into clay (particles <0.002 mm diameter), silt (0.002–0.05 mm), and sand (0.05–2 mm) fractions, using the pipette method. Water-holding capacity, a measure of the amount of water the soil can hold in a form extractable by plant roots, was estimated as the difference between the field capacity (moisture content retained in soil under a suction of 0.33 atmospheres) and the wilting point (moisture content retained at 15 atmospheres), using a pressure membrane apparatus. As is standard practice, samples were dried, sieved, and rewetted before determining water-holding capacity, making the results only an index of water available to plants in the field.

A pH meter was used to measure soil pH in water. Total N was determined by Kjeldahl digestion (Parkinson and Allen 1975) and total organic C by dry combustion. Total P was determined by digestion in HNO_3, $HClO_4$, and HF (Lim and Jackson 1982), and reaction with ammonium molybdinate. We measured PO_4^{3-} in an autoanalyzer using the molybdenum blue method (Jorgenson 1977). K^+ was determined by atomic emission spectroscopy at the Brazilian Center for Nuclear Energy and Agriculture (CENA), Piracicaba, São Paulo, Brazil, while Ca^{2+}, Mg^{2+}, Al^{3+}, and H^+ in soil were measured by atomic absorption spectrophotometry at CENA after digestion in $HClO_4$, HNO_3, and H_2SO_4 (Jorgenson 1977). Organic (Walkley-Black) carbon to total nitrogen (C:N) ratios were calculated to provide an index of N availability; if C:N > 15, there is very little N available for plant growth (Fearnside and Leal-Filho, *in press*).

Cation measures were derived without Na^+, which is generally a minor constituent of exchangeable bases. These measures included cation exchange capacity (CEC), which is the sum of K^+, Ca^{2+}, Mg^{2+}, Al^{3+}, and H^+; total exchangeable bases (TEB), the sum of K^+, Ca^{2+}, and Mg^{2+}; and aluminum saturation, which is $((Al^{3+} + H^+)/CEC) \times 100$. Samples were digested in 0.0025 mol/L HCl and 0.005 mol/L H_2SO_4, and extracts for cation determination were buffered to pH 7.0, the standard practice in Brazil (Servício Nacional de Levantamento e Conservação de Solos–Empresa Brasileira de Pesquisa Agropecuária 1979). We also measured DpH (the difference between soil pH in KCl and in water), which indicates the charge status of the soil and is a useful indicator of organic matter concentration (Fearnside and Leal-Filho, *in press*).

Landscape-scale comparisons

Six variables were tested as predictors of liana abundance and biomass in the same 40 1-ha plots used for soil analysis. These variables were chosen to reflect key features of tree stands, treefall disturbance, vul-

nerability to edge effects, and soils that could potentially influence liana communities: (1) the number of trees (≥10 cm dbh) per plot; (2) aboveground biomass of trees in each plot; (3) the index of forest disturbance; (4) log distance to the nearest forest edge; and (5) two ordination axes that described major gradients in soil fertility and texture. The soil ordination was performed using Principal Components Analysis (PCA) on the PC-ORD package (McCune and Mefford 1995). Soil parameters were equally weighted before analysis with the standardization by maximum method (Noy-Meir et al. 1975).

The efficacy of the six predictors was assessed using best-subsets and multiple linear regressions (Sokal and Rohlf 1995). None of the predictors were strongly intercorrelated ($R^2 < 27\%$). Performance of the final regression model was assessed by comparing the standardized residuals to the fitted values and to each significant predictor (Crawley 1993).

Local-scale comparisons

In addition to landscape-scale data, detailed information on local liana communities was collected July–August 1997 by D. Pérez-Salicrup in three 10-ha fragments in the study area. The fragments (BDFFP numbers 1202, 2206, and 3209) were located on three different cattle ranches and separated by distances of 11–28 km. Liana data were collected in a total of 72 small (20 × 20 m) plots, with 12 plots near fragment edges (plot margin 10–30 m from the nearest edge) and 12 in the interior (>100 m from the nearest edge) of each fragment. To minimize effects of edge aspect, the edge plots were divided equally among 3–4 different edges of each fragment. Precise positions of all plots were determined using random *x–y* coordinates. Because the samples were intended to assess fine-scale variation within these particular fragments, concerns about pseudoreplication (Hurlbert 1984) are irrelevant, but the reader should be aware that the results may not be typical of other Amazonian fragments.

The following data were collected in each plot for lianas of ≥2 cm dbh: (1) number of liana stems; (2) number of liana taxa; (3) number of living trees (≥10 cm dbh); (4) frequency of infestation (percentage of trees with at least one liana); (5) median number of lianas per infested tree (medians were used because liana counts per tree could not be normalized by data transformations); and (6) number of lianas in each of three climbing guilds. Liana taxa were identified in the field to species level or, for some genera and families, to morphospecies level, usually on the basis of sterile features. Vouchers for each taxon were later compared to specimens in the INPA Herbarium, and the vouchers are permanently lodged there. Because liana abundance varied considerably among plots, we calculated liana diversity using Fisher's log series α, an index of species diversity that is insensitive to sample size (Magurran 1988).

Liana climbing guilds followed the schemes of Putz (1984) and Hegarty (1991), as follows: (1) Tendril-twiners have modified leaves, leaflets, inflorescences, or stipules that twine around supports. Such species often favor smaller (<7 cm diameter) supports. (2) Mainstem-twiners use the main stem axis to coil around the host, and tend to favor intermediate-sized supports (<16 cm diameter). (3) Branch-twiners use leaf-bearing branches to twine around the host, and generally use the largest supports (>12 cm diameter).

An ordination analysis was used to identify major gradients in liana species composition. Nonmetric multidimensional scaling (NMS) was used, with Sorensen's distance metric (Ludwig and Reynolds 1988), on the PC-ORD package. Uncommon species (detected at <10 plots), which can seriously distort ordinations (McCune and Mefford 1995), were deleted prior to analysis. Species used in the analysis were weighted equally with the standardization by maximum method. A two-way multivariate analysis of variance (MANOVA) was used to compare edge vs. interior, site (fragment), and interaction effects for all ordination axes simultaneously (Sokal and Rohlf 1995).

For all other liana community parameters, two-way ANOVAs were used to compare edge vs. interior, site (fragment), and interaction effects, followed where appropriate by Tukey's HSD tests to contrast sample means. To minimize heteroscedasticity and improve normality of samples, abundance and species-richness data were log-transformed, while infestation data and guild proportions were arcsine-square root transformed (Sokal and Rohlf 1995). Bartlett's tests were used to test for heteroscedasticity.

In comparing the three 10-ha fragments, both the ANOVA and MANOVA analyses were designed to assess site (fragment), edge vs. interior, and interaction effects separately. This approach was clearly justified because there were considerable differences in liana communities among fragments, which might otherwise confound direct comparisons of fragment edges and interiors. However, because there were very few significant interaction effects, and because the site effects are not of general interest, only the edge vs. interior contrasts are reported here.

RESULTS

Landscape-scale comparisons

Liana abundance and biomass.—A total of 27 590 lianas were measured in the 69 1-ha plots. Liana abundance (Fig. 2) was significantly higher near forest edges (<100 m from edge) than further (145–3000 m) from edges ($t = 2.20$, df $= 67$, $P = 0.032$; t test). There was, however, no simple, monotonic relationship between distance from edge and liana abundance ($r_s = -0.079$, $n = 69$, $P = 0.52$; Spearman rank correlation), because several plots in deep forest interiors (>1000 m from edge) also had many lianas.
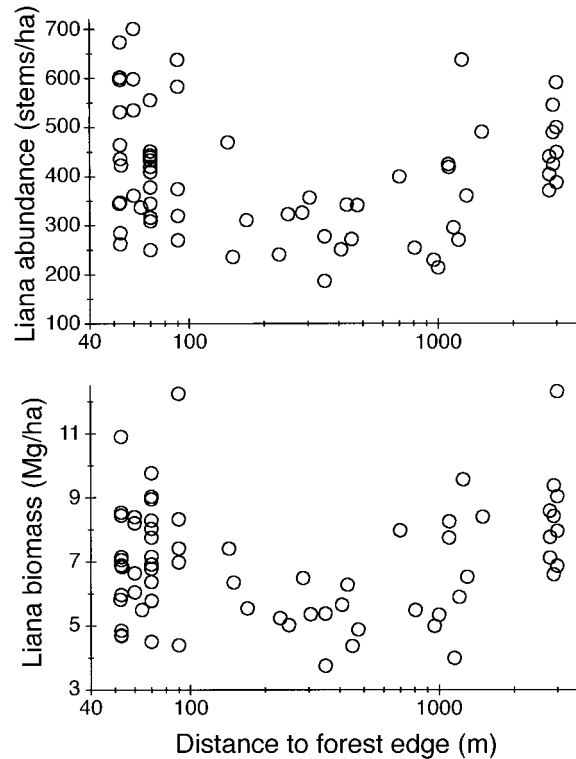

FIG. 2. Relationship between liana abundance (above) and aboveground dry biomass of lianas (below) as a function of distance of plots from the nearest forest edge.

Liana biomass (Fig. 2) also was high in many edge plots but, unlike liana abundance, did not differ significantly between forest edges and interiors ($t = 1.05$, df $= 67$, $P = 0.30$; t test). Several forest-interior plots also had high biomass, and as a result the correlation between distance to edge and biomass was nonsignificant ($r_s = 0.070$, $n = 69$, $P = 0.57$; Spearman rank correlation).

Liana size distributions.—Lianas ranged from 2–43 cm dbh, but most (97.1%) were <10 cm in diameter. Size distributions of lianas differed between forest edges and interiors (Fig. 3). Plots near edges had more small (2–3 cm dbh) lianas and relatively fewer medium and large (≥ 4 cm dbh) lianas, than did those in forest interiors (>100 m from edge). This difference was highly significant ($X^2 = 113.0$, df $= 9$, $P < 0.0001$; chi-square test for independence).

Ordination of soil variables.—The ordination analysis revealed two major soil gradients in the study area (Table 1). Axis 1, which captured 48% of the variation in the data set, described a continuum between relatively fertile sites with high clay content (having high total C, N, CEC, and exchangeable bases), and less fertile sites with high sand content (having high aluminum saturation). Axis 2, which captured 18% of the total variation, described a gradient between less acidic sites with more total P, and more acidic sites with some-
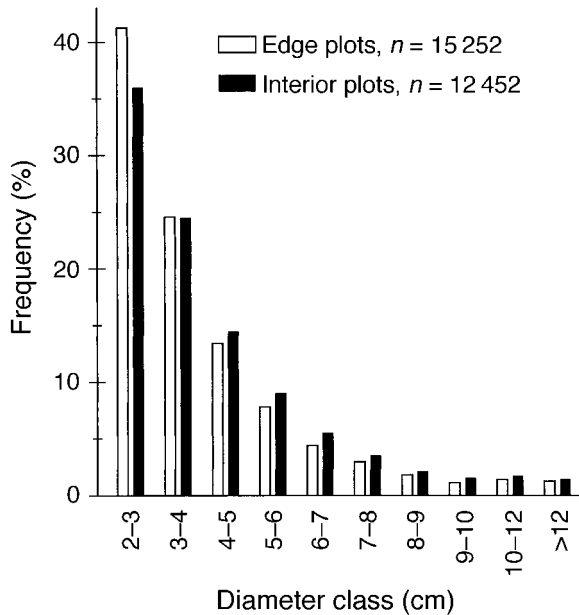
FIG. 3. Size distributions of lianas in forest edge and interior plots (edge plots are <100 m from the nearest edge; interior plots are >100 m from edge).

TABLE 1. Pearson correlations between 19 soil variables and three ordination axes produced by principal components analysis.

Variable	Axis 1	Axis 2	Axis 3
Percentages of soil texture components			
Clay	0.969§	−0.025	−0.047
Silt	0.631§	−0.239	−0.555§
Sand	−0.953§	0.076	0.167
Water-holding capacity	0.424	−0.430	−0.421
Carbon			
Organic C (%)	0.789§	0.183	0.255
C:N ratio	−0.321	0.471	0.303
Acidity			
pH in water	0.030	−0.920§	0.275
Primary nutrients			
Total N (%)	0.960†	−0.133	0.051
Total P (%)	0.456	−0.809§	−0.053
PO_4^{-3}†	−0.013	−0.235	0.684§
K^{2+}†	0.685§	−0.537§	0.308
Secondary nutrients			
Ca^{2+}†	0.673§	0.580§	0.018
Mg^{2+}†	0.899§	0.097	0.254
Other ions			
Al^{3+}†	0.617§	0.675§	−0.100
H^+†	0.729§	−0.212	−0.220
Cation measures			
Cation exchange capacity	0.799§	0.464	−0.114
Aluminum saturation	−0.797§	−0.032	−0.351
Total exchangeable bases	0.927§	0.208	0.205
DpH‡	0.025§	−0.068	−0.150
Variation explained by ordination axis (%)	47.7	18.3	8.6

† Expressed in μmoles of charge/kg of fine earth.
‡ Difference between soil pH in KCl and in water.
§ Correlations significant with a Bonferroni-corrected alpha value ($P < 0.002$). This was used to reduce the likelihood of spurious correlations.

what higher Al^{3+} and Ca^{2+}. Axis 3 captured <9% of the total variation, and is not considered further.

Multiple regressions.—We assessed the effects of soils, disturbance, tree stands, and distance to edge on liana distributions using multiple regressions. For liana abundance there were three significant predictors, yielding a highly significant multiple regression which explained 56% of the variation in liana abundance ($F_{3,36} = 14.98$, $P < 0.0001$). The first predictor was tree biomass, which was negatively associated with liana abundance (Fig. 4), followed by the index of forest disturbance (positive slope) and distance to forest edge (negative slope).

For liana biomass there were four predictors, producing a highly significant multiple regression ($F_{4,35} = 11.89$, $P < 0.0001$) which explained 58% of the total variation. The first predictor was soil PCA axis 2 (negative slope), followed by tree biomass (negative slope), forest disturbance (positive slope), and soil PCA axis 1 (positive slope). Thus, in addition to tree biomass and disturbance, gradients in soil fertility appeared to influence liana biomass, with higher biomass associated with less acidic soils with higher P, clay, and exchangeable bases.

Forest-interior plots.—Contrary to our expectations, some forest-interior plots had many lianas (Fig. 2). To further assess the factors responsible, we tested effects of five predictors (tree density, tree biomass, forest-disturbance index, and soil PCA axes 1 and 2) on liana abundance and biomass in 18 forest-interior plots (>100 m from edge). For liana abundance, there were three predictors, forest disturbance (slope positive),

soil axis 2 (slope negative), and tree biomass (slope negative), yielding a highly significant multiple regression ($F_{2,15} = 8.78$, $R^2 = 65\%$, $P = 0.0016$). For liana biomass, there were two predictors, soil axis 2 (slope negative) and forest disturbance (slope positive), again producing a highly significant multiple regression ($F_{2,15} = 13.06$, $R^2 = 64\%$, $P = 0.0005$). These
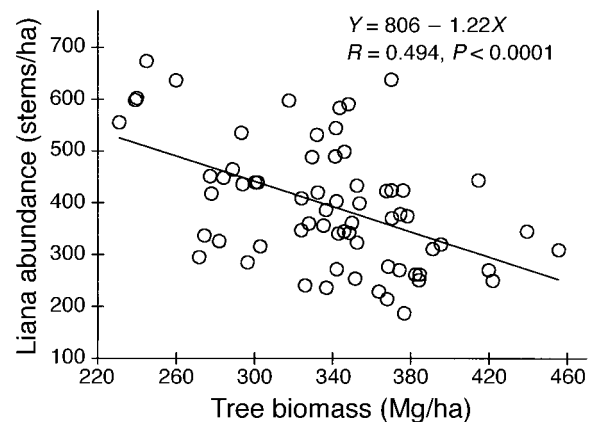

FIG. 4. Relationship between aboveground dry biomass of rain forest trees and liana abundance in permanent 1-ha plots.

TABLE 2. Results of ANOVAs comparing attributes of Amazonian liana communities between edges and interiors of three 10-ha rain forest fragments.

Attribute	$F_{1,66}$	P	Tukey's tests (P)
Liana abundance and diversity			
Abundance	9.84	0.003	Edge > Interior (<0.01)
Species richness	14.82	<0.001	Edge > Interior (<0.01)
Species diversity†	6.17	0.016	Edge > Interior (<0.05)
Tree infestations			
Percent of trees infested	8.61	0.005	Edge > Interior (<0.01)
Median no. lianas/infested tree	0.32	0.573	…
Abundances of lianas in three climbing guilds			
Branch twiners	3.91	0.052	Edge > Interior (0.053)
Mainstem twiners	5.32	0.024	Edge > Interior (<0.05)
Tendril twiners	4.39	0.040	Edge > Interior (<0.05)
Proportions of lianas in three climbing guilds			
Branch twiners	3.30	0.074	Interior > Edge (0.08)
Mainstem twiners	2.01	0.161	…
Tendril twiners	1.91	0.172	…

Note: Data on liana abundance and species richness were $\log_{10}$-transformed, while infestation data and guild proportions were arcsine-transformed.

† Using Fisher's α, a robust index of species diversity that is insensitive to sample size.

results are generally concordant with the regressions involving all 40 plots; forest-interior plots with high liana abundance and biomass were more disturbed and occurred on better (higher P and less acidic) soils, while liana abundance also was negatively associated with tree biomass.

Number of nearby edges.—To determine whether liana abundance was influenced by the number of nearby forest edges (<100 m away), we compared plots with one nearby edge ($n = 21$), two nearby edges (i.e., on the corner of a fragment; $n = 9$), and four nearby edges (i.e., in a 1-ha fragment; $n = 5$). Although plots with four edges had somewhat higher liana abundances (526 ± 134 stems/ha; mean ± 1 SD) than did those with only one (431 ± 129) or two (377 ± 91) edges, there
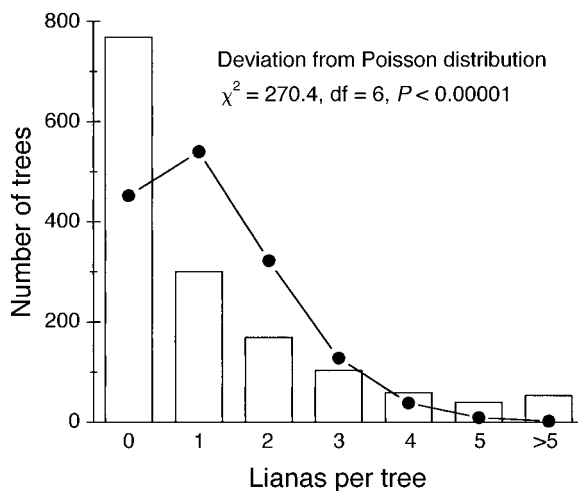

FIG. 5. Numbers of lianas borne by rain forest trees in central Amazonia (bars), compared to expected (random) values from the Poisson distribution (circles and lines).

was no significant difference overall ($F_{2,34} = 2.40$, $P = 0.11$; one-way ANOVA). Results were similar when distance to edge was included as a covariate.

Edge aspect.—Our study area receives prevailing easterly winds that might increase forest disturbance and microclimatic changes on east-facing forest edges. We therefore compared liana abundance in plots near edges with eastern aspects ($n = 12$) versus all other aspects ($n = 18$), but liana abundance did not vary significantly ($t = 0.92$, df = 8, $P = 0.36$; t test) between eastern (387 ± 105 stems/ha) and non-eastern (429 ± 131) aspects.

Local-scale comparisons

Liana abundance and tree infestation.—We found 1023 lianas (≥2 cm dbh) in the 72 small (400-m²) plots in the three 10-ha fragments (Table 2). When compared to a Poisson distribution (Fig. 5), there were significantly more trees than expected with no lianas, and many more trees than expected with heavy infestations (4–17 lianas). Thus, lianas were strongly aggregated, with some trees bearing very heavy infestations.

Lianas were significantly ($P < 0.01$) more abundant on fragment edges (413 ± 211 stems/ha) than interiors (298 ± 222; Table 2). Lianas also infested a significantly higher ($P < 0.01$) proportion of trees (≥10 cm dbh) near edges (40.5 ± 9.7%) than in interiors (34.2 ± 10.3%), although there was no significant difference in the median number of lianas per infested tree (Table 2).

Liana guilds.—Of the 1023 lianas, over half (59.6%) were branch-twiners, followed by mainstem-twiners (21.7%) and tendril-twiners (18.2%). A small number of lianas (0.5%) ascended via modified spines, and are not considered further.

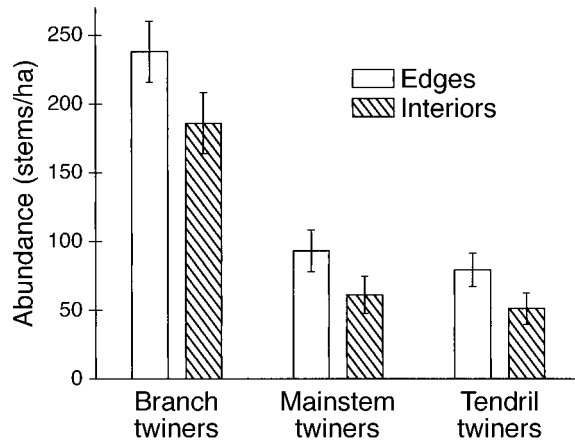All three major climbing guilds became significantly

FIG. 6. Mean abundances of major liana climbing guilds on edges and interiors of three 10-ha forest fragments (error bars indicate ± 1 SE).

($P < 0.05$) more abundant on fragment edges (Table 2). Branch-twiners increased by 28% on average, while mainstem-twiners rose by 52% and tendril-twiners by 55% (Fig. 6). The proportions of each guild also varied somewhat, with branch-twining lianas becoming relatively less abundant ($P < 0.08$) on edges than in interiors (Table 2).

Liana species diversity.—A total of 83 liana species or morphospecies were identified in the three fragments (total area sampled = 2.88 ha). About a quarter of the taxa (22 species) can be considered rare (mean density of ~≤1 stem/ha). Liana species richness was significantly ($P < 0.01$) higher on fragment edges than interiors (Table 2). The high species richness on edges resulted in part from elevated liana abundance in these areas; there was a strong, positive relationship between liana richness and the number of lianas per plot (R^2 = 77.2%, df = 70, $P < 0.0001$). However, the edge plots also had significantly higher Fisher's α values (18.06 ± 12.89) than did the interior plots (12.80 ± 8.36), suggesting that liana species diversity at edges was elevated irrespective of variation in liana abundance (Table 2).

Liana species composition.—The nonmetric multi-dimensional scaling (NMS) analysis was based on the 29 most prevalent liana species or morphospecies (detected at ≥10 plots). The analysis revealed three major gradients in species composition, with the axes capturing 19.3%, 18.7%, and 10.1% of the total variation in the data set, respectively. A comparison of the ordination scores, using a two-way MANOVA, revealed that floristic composition did not differ significantly between fragment edges and interiors ($F_{3,64}$ = 0.36, P = 0.78).

We also compared abundances of the most common liana taxa (≥10 individuals overall) between fragment edges and interiors, using a series of two-way ANOVAs with a stringent, Bonferroni-corrected alpha value (P < 0.007) to reduce the likelihood of experiment-wise errors. Of 34 common taxa, three increased significantly in abundance on edges (*Cheioclinium cognatum* [Celastraceae]; Bignoniaceae 1 and 4), while none declined on edges.

DISCUSSION

Our findings suggest that rain-forest fragmentation alters many aspects of liana community structure. Lianas in fragments were more abundant and diverse, and infested a higher proportion of trees than in forest interiors. Liana communities near forest edges contained many small lianas, and relatively few large lianas. All three major climbing guilds of lianas (branch-twiners, mainstem-twiners, tendril-twiners) increased significantly near edges. These patterns are quite similar to those found in 20–40-yr-old regrowth forests in Panama, which also had elevated liana abundance and diversity, but not biomass, relative to mature forests (DeWalt et al. 2000). For lianas, forest fragments and regrowth may be similar ecologically in that each has an abundance of treefall gaps and small trees (Laurance et al. 1997), which provide many trellises and increased light for actively climbing lianas.

On a broad landscape scale, there was considerable variation in liana abundance and biomass. As revealed by our multiple regression models, the abundance and biomass of lianas were affected somewhat differently by fragmentation, soils, and forest disturbance, despite the fact that liana abundance and biomass were quite strongly and positively correlated (R^2 = 53%).

Landscape-scale variation in liana abundance and biomass

On a landscape scale, the relationship between liana abundance and distance to forest edge was significant, but weaker than expected. While lianas were often abundant near edges, several plots in deep forest interiors also had high abundances (Fig. 2). We had hypothesized that edge distance would be a key correlate of liana abundance because tree mortality (Ferreira and Laurance 1997, Laurance et al. 1998b) and lateral light penetration (Kapos et al. 1997, Didham and Lawton 1999) increase sharply in Amazonian forest fragments, especially within 60–100 m of edges. Although edge distance was one of three significant predictors of liana abundance, tree biomass and the index of forest disturbance were more important.

The strong negative association between liana abundance and tree biomass (Fig. 3) could arise for three reasons. First, sites with high tree biomass may have been infrequently disturbed in the past. Such stable conditions would allow trees to grow larger and would provide few opportunities for lianas to proliferate. Second, lianas may actively depress tree biomass, by increasing mortality and damage (Putz 1980, 1984) and suppressing growth (Lowe and Walker 1977, Putz 1984, Whigham 1984, Viana et al. 1997). Finally, li-

anas and trees could be negatively correlated if they responded in opposite ways to soils or other edaphic factors. This latter proposition seems least likely, because in the very poor, heavily weathered soils of our study area, both lianas and trees respond positively (increased biomass) to soil fertility (cf. Laurance et al. 1999 for data on soil–tree biomass relationships). The first two propositions, however, are very plausible: forest disturbances beget liana infestations, which in turn may beget further disturbances. This view is supported by the fact that the index of forest disturbance also was a significant predictor of liana abundance, and is consistent with several earlier studies (e.g., Putz 1984, Hegarty and Caballé 1991, Oliveira-Filho et al. 1997).

Distance to forest edge had no significant effect on liana biomass, but this result was less surprising. A preponderance of large (>10 cm diameter) lianas appears to be an indicator of primary forest or areas subjected to few disturbances (Emmons and Gentry 1983, Peixoto and Gentry 1990, Hegarty and Caballé 1991). Areas prone to frequent perturbations apparently have many small, actively climbing lianas, as demonstrated by our comparison of liana size distributions on forest edges and interiors (Fig. 3).

Of the factors tested, liana biomass appeared most strongly influenced by soil fertility. The gradient describing variation in total P and pH was most important, which is consistent with the suggestion that in tropical lowland soils, P availability is often critically limiting to plant growth (Sollins 1998). Liana biomass also increased along a gradient from sandy to clay soils, with the latter having lower aluminum saturation and higher N, organic matter, cation exchange capacity, and exchangeable bases. The notion that soil factors are important to lianas accords with Gentry (1991), who found that Amazonian sites on very poor white-sand soils had lower liana densities (and thus lower biomass) than did nearby sites with less extreme soils. Proctor et al. (1983) and Putz and Chai (1987) also suggested that liana densities are higher on richer soils.

The above results were generally supported when we analyzed only plots in forest interiors (>100 m from edge). Although caution is needed because of the limited sample size ($n = 18$ plots), the regression models suggest forest-interior plots with many lianas were more disturbed and had relatively high soil fertility (higher P and lower acidity) and lower tree biomass. In intact forests of the central Amazon, periodic disturbances are caused by windstorms (Nelson et al. 1994, Foster and Terborgh 1998), small floods (Mori and Becker 1991), lightning strikes (Magnusson et al. 1996), and pathogen outbreaks. Such disturbances, along with natural heterogeneity in soils, apparently generate considerable variability in the local abundance of lianas.

Amazonian liana communities

It is important to emphasize that in our study area, the abundance and biomass of lianas are modest. In our forest-interior plots, aboveground biomass of lianas was lower, and comprised a smaller percentage of total forest biomass, than in other tropical rain forests in Brazil (Klinge and Rodriguez 1974), Venezuela (Putz 1983), Bolivia (Pérez-Salicrup 1998), Thailand (Ogawa et al. 1965), Malaysia (Kato et al. 1978), and Ghana (Greenland and Kowai 1960). This is consistent with the observation that, in intact forests of our study area, mortality rates of trees are naturally quite low (1.2 ± 0.4%/yr; W. F. Laurance, *unpublished data*). Putz (1983) has argued that on a geographic scale, differences in disturbance regimes affecting tree mortality may be the most important factor determining the abundance of lianas. The very acidic, heavily weathered soils prevalent in the central Amazon (Laurance et al. 1999, Fearnside and Leal-Filho, *in press*) could also depress liana abundance. Thus, the observed effects of lianas in this study are likely to be less than in regions with greater disturbance (e.g., cyclonic and hurricane forests; Webb 1958) or more fertile soils. In such areas, liana infestations in fragmented forests may become even more severe.

Liana diversity in our study area appears moderate. On Barro Colorado Island, Panama, Putz (1984) found 65 liana species (≥ 2 cm dbh) in 1.0 ha of plots, while using nearly identical methods we identified 83 species or morphospecies in 2.88 ha of plots spanning a larger geographic area (random subsamples of our plots totaling 1.0 ha averaged 69.6 species). This moderate richness of lianas is in stark contrast to tree diversity in our study area (averaging ∼280 species of ≥ 10 cm dbh per hectare), which is several times higher than on Barro Colorado Island and among the highest in the world (de Oliveira and Mori 1999).

Although fragmentation caused diverse changes in liana communities, there were only limited shifts in guild and species composition. All three major climbing guilds increased in abundance near edges, but the proportions of each guild did not change greatly (although there were somewhat fewer branch-twining lianas [$P < 0.08$], which use the largest supports). We had particularly expected tendril-twining species, which use the smallest trellises (Putz 1984, Hegarty 1991), to increase proportionally on edges. In addition, none of the ordination axes describing gradients in liana composition differed significantly between edges and interiors, and only three species increased on edges while none declined (without the stringent Bonferroni-corrected P values, seven species increased on edges [$P < 0.05$] and none declined). The fact that no species declined on edges is perhaps not surprising; although some liana species that attain large diameters are shade tolerant (Gentry 1991), many primary-forest plants benefit from increased light availability (Clark 1994, Sizer and Tanner 1999), such as occurs near edges. It is also possible that the forest edges in our study area are still in a dynamic state of transition. Our fragments were only 13–17-yr-old during the study, and some

authors have argued that rain-forest edges may require 20–80 yr to fully equilibrate in structure and floristic composition (Oliveira-Filho et al. 1997). If this view is valid, then the age of forest edges could also have a significant effect on liana communities.

Implications for fragmented forests

Proliferating lianas can have diverse impacts on fragmented forests. Forest fragments are especially prone to windstorms (Laurance 1991, 1997, Laurance et al. 1998b) and fire (Laurance 1998, Nepstad et al. 1999), and liana-infested trees are much more prone to damage from wind and fire than are liana-free trees (Putz 1991). Heavy liana infestations can inhibit successional processes near forest edges and reduce tree biomass and density (Tabanez et al. 1997, Viana et al. 1997). In a positive feedback loop, lianas respond positively to forest disturbance and then appear to promote and exacerbate subsequent disturbances.

Lianas may also help drive floristic changes in fragments. Because they are generally long lived and slow growing, old-growth tree species are often prone to liana infestations (Laurance et al. 2000). Pioneer trees such as *Cecropia* spp. and *Trema* spp. are, however, less vulnerable to lianas because of their rapid growth, monopodal form, large leaves, and flexible trunks, and also sometimes because of the activity of ants (Putz 1984). In our study area, the abundance of *Cecropia sciadophylla,* an ubiquitous pioneer, has increased 33-fold since our fragments were initially isolated (W. F. Laurance, *unpublished data*), and its ability to limit liana infestations could be one important factor in its success.

Biomass losses from fragmented forests appear to be an important source of greenhouse gas emissions, released upon decay of organic material (Laurance et al. 1997, 1998d). Lianas increase in fragments at the expense of trees but compensate for only a small fraction of the biomass lost from deaths of trees. In our study area, forest plots within 100 m of edges lost a mean of 36.1 Mg/ha of dry tree biomass (Laurance et al. 1998a), but gained only 0.46 Mg/ha of liana biomass (in part because lianas usually have much lower wood densities than primary-forest trees; Putz 1983). Thus, proliferating lianas compensated for <1.3% of the biomass lost from elevated tree mortality. Some evidence suggests that liana growth may accelerate in response to anthropogenic increases in atmospheric CO_2 (Phillips and Gentry 1994). If so, proliferating lianas could exacerbate biomass declines and other ecological changes in forests, especially in fragmented landscapes.

In regions where only small forest remnants survive, intensive management may be needed to control liana populations and facilitate forest recovery (e.g., Tabanez et al. 1997, Viana et al. 1997). Lianas are major contributors to forest productivity (Putz 1983) and provide food and resources for many animals (Emmons and Gentry 1983, Gentry 1991), but their abundance in fragmented forests can become unnaturally high, seriously affecting forest structure and functioning. In many tropical regions, lianas will play a key role in the ecology and dynamics of fragmented forests.

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APPENDIX

A list of liana taxa used in the analysis is available in ESA's Electronic Data Archive: *Ecological Archives* E082-002.