Rain Forest Structure at Forest-Pasture Edges in Northeastern Costa Rica

Jessica L. Schedlbauer[1,2,3], **Bryan Finegan**[2], and **Kathleen L. Kavanagh**[1]

[1]Department of Forest Resources, University of Idaho, Moscow, Idaho 83844-1133, U.S.A.

[2]Departamento Recursos Naturales y Ambiente, Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Sede Central 7170, Turrialba, Costa Rica

ABSTRACT

Land-use change in the Sarapiquí region of Costa Rica has resulted in a fragmented forest landscape with abrupt edges between forest and pasture. Forest responses to edge effects vary widely and can significantly affect ecosystem integrity. Our objective was to examine forest structure at 20+ yr old forest-pasture edges in Sarapiquí. Three transects with 0.095-ha plots at seven distances from forest edges were established in each of six forest patches. Stem density, basal area, and aboveground biomass in trees and palms $\geq$ 10-cm diameter at breast height were measured in all plots. In addition, hemispherical photographs were taken to determine leaf area index, understory light availability, and percent canopy openness. Linear mixed-effects models showed significantly higher tree stem density at forest edges, relative to interiors, a pattern reflected by increased stem density, basal area, and aboveground biomass in small diameter trees ($\leq$ 20 cm) growing near edges. No differences in total tree basal area, aboveground biomass, or hemispherical photograph-derived parameters were detected across the forest edge to interior gradient. The recruitment of small diameter trees following edge creation has contributed to the development of dense vegetation at the forest edge and has aided in the maintenance of similar tree basal area and aboveground biomass between edge and interior environments. These data reflect on the robustness of forest edges in Sarapiquí, a characteristic that will likely minimize future detrimental edge effects and promote a number of high-value environmental services in these forests.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: edge effects; forest fragmentation; hemispherical photography; tropical wet forest.

GLOBAL PATTERNS OF LAND-USE CHANGE HAVE SIGNIFICANTLY ALTERED forested landscapes by increasing fragmentation, a process that has been concurrent with a rise in the abundance of forest edges on the landscape. Edge zones may have positive, negative, or neutral effects on abiotic and biotic factors within a forest due to the complexity of interacting factors at these boundaries (Murcia 1995, Ries *et al.* 2004). Further, edge effects may vary with time following edge creation as newly created abiotic and biotic gradients at forest edges give rise to further edge responses.

A common response at newly created edges is increased tree mortality (Williams-Linera 1990a, Chen *et al.* 1992, Ferreira & Laurance 1997, Laurance *et al.* 1998, Harper & Macdonald 2002), a change that may lead to further structural changes and influence plant and animal distributions, abundance, and diversity (Pearman 1997, Spies 1998, Beier *et al.* 2002). Newly created edges and new treefall gaps close to the forest edge increase understory light availability and give rise to enhanced seedling and sapling growth (Fetcher *et al.* 1983, Williams-Linera 1990b, Chen *et al.* 1992, Sizer & Tanner 1999). This widely reported response to forest fragmentation is often short-lived, and longer-term structural changes are more variable. A range of mid-term edge responses have been reported in forests up to approximately 20 yr after edge creation, including severe aboveground biomass (AGBM) loss (Ferreira & Laurance 1997; Laurance *et al.* 1997, 1998) and increased tree density and basal area at the forest edge (Williams-Linera 1990a, Williams-Linera *et al.* 1998). These responses vary by ecosystem,

climatic condition, and natural disturbance regime, so detailed regional studies of intermediate-aged forest edges will help to further clarify the mid-term effects of edges on forest structure.

Within the Sarapiquí region of Costa Rica, a unique political and social context overlies a history of deforestation, lending increased consequence to local ecological studies. Sarapiquí has experienced widespread land-use change since the 1950s, and steady conversion of land from forest to pasture or agricultural use has led to annual deforestation rates of 2.8–3.6 percent over the last two decades (Butterfield 1994, Sánchez-Azofeifa *et al.* 1999). Costa Rica has worked to reduce forest loss via the 1996 Forestry Law (no. 7575) that banned deforestation and placed monetary value on forests through payments for environmental services (PES). Sarapiquí is part of a regional biological corridor and is consequently a target area for PES (García 1996, Méndez 2003). Knowledge of forest edge effects in this highly fragmented landscape will help to define the quality of forest land benefiting from the PES program.

It has been suggested that forests in Sarapiquí develop edges sealed with vegetation as a response to increased light available for growth at forest edges (Forero & Finegan 2002). If this is the case, it is possible that some of the detrimental effects of forest fragmentation may be attenuated in these forests, thus helping to preserve ecosystem integrity. The goal of this study was to examine forest structure at 20+ yr old forest-pasture edges in Sarapiquí, and we developed predictions consistent with the hypothesis that these edges are dominated by dense vegetation. We expected to find forest edges with higher stem density, increased frequency of small diameter trees, and greater total basal area and AGBM relative to the forest interior. We also anticipated that dense forest cover

would result in edges with higher leaf area index (LAI) and lower understory light availability and canopy openness than in the forest interior.

METHODS

STUDY REGION.—This study was conducted in the Sarapiquí Canton, Heredia Province, Costa Rica, in an area classified as tropical wet forest by the Holdridge life zone system (Tosi 1969). Annual rainfall is *ca* 4000 mm and annual temperatures average 26°C with little monthly variation (Sanford *et al.* 1994). The forests of the Sarapiquí region are highly fragmented and the surrounding agricultural matrix comprises primarily pasture land and agricultural plantations (Butterfield 1994).

The upland forests of Sarapiquí are dominated by a single leguminous tree species, *Pentaclethra macroloba* (Willd.) Kuntze, that represents 32–35 percent of the total basal area in these forests (Clark & Clark 2000). The dominance of *P. macroloba* decreases with elevation and is not found at elevations > 250 m asl (Lieberman *et al.* 1996). These forests are also characterized by the presence of midstory palms, that account for 22–25 percent of all stems > 10-cm diameter at breast height (dbh, 1.37 m) at elevations ≤ 100 m (Lieberman *et al.* 1996). In addition to *P. macroloba*, the most abundant trees in these forests are *Tetragastris panamensis* (Engl.) Kuntze, *Carapa guianensis* Aubl., and *Licania affinis* Fritsch, and the dominant palms are *Welfia regia* Mast., *Iriartea deltoidea* Ruiz & Pav., *Socratea exorrhiza* (Mart.) H. Wendl., and *Euterpe precatoria* Mart.

SITE SELECTION.—Six forest sites on privately owned land with a forest-pasture border 20–30 yr old were selected for this study (Fig. 1). This age limit was chosen so that we could focus on the mid-term effects of edge creation that occur following the initial reassortment and restabilization of physical gradients at newly created edges (Matlack 1994). Individual landowners were interviewed to establish the year in which pastures were created and point data were collected with a GPS unit (GPS III, Garmin International, KS, U.S.A.) at each forest edge. To verify that forest edges were at least 20 yr old, analog aerial photographs acquired in 1983 (Instituto Geográfico Nacional, San José, Costa Rica) were visually compared to the GPS data overlaid on a Landsat TM image acquired in 2001.

We studied forest edges adjacent to pasture rather than those adjacent to other common land uses in the area (*e.g.*, tree plantations, agriculture) because the strength of edge effects is often greatest between land uses with abrupt changes in vegetation density and structure (Ries *et al.* 2004). It should be noted that some structural heterogeneity existed in pastures adjoining forest patches, as all had remnant trees and some also contained live fences. Study sites were located between 50 m and 200 m asl (Table 1) on gently rolling terrain. Sites 1 and 3 were located on acidic, highly weathered Ultisols derived from volcanic parent materials and all other sites were situated on Inceptisols derived from Quaternary alluvial deposits (ITCR 2004).

All study sites were located on land adjacent to other forested tracts; therefore the forest area sampled at each site (Table 1) repre-
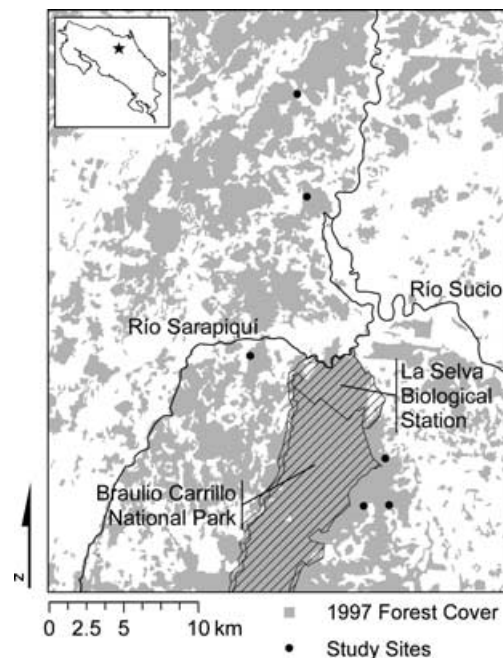

FIGURE 1.   Inlay of Costa Rica indicates the location of the Sarapiquí region with a star. The detailed map shows the location of all study sites as black dots. Grey shaded areas represent forest cover in 1997 and areas covered by hatching are national parks and protected areas (ITCR 2004).

sents only the forest land area belonging to an individual landowner. No attempt was made to quantify the extent of the forest area in which study sites were embedded because in some cases the adjoining forest was part of an extensive national park (Fig. 1). All sites were either unmanaged primary forest (sites 3 and 6) or had been selectively harvested for timber in the past under approved sustainable forest management plans (Table 1).

FIELD SAMPLING.—Within study sites, areas with streams running parallel or perpendicular to the forest edge were excluded as sampling sites to reduce variation introduced by riparian vegetation. A set of three transects perpendicular to the forest edge was randomly situated at each site. Within transects, plots were established at distances of 0, 25, 50, 100, 150, 200, and 300 m from the forest edge. The numbers used to describe the plots represent the plot boundary closest to the forest edge. Each plot consisted of three adjacent circular subplots laid out parallel to the forest edge. The radius of each circular subplot was 10 m, so the total plot area sampled at each distance was 942.5 m^2. In most cases, the distance between transects (*i.e.*, the distance from the end of one plot boundary to the beginning of the next plot boundary in the adjacent transect) was at least 100 m. However, short forest-pasture edges led us to reduce this distance to 22 m at site 2 and 50 m at site 6.

In each plot the dbh of all trees and palms ≥ 10-cm dbh was measured with a fabric diameter tape. Diameter measurements were made above stilt roots or buttresses when present, and when physical measurements were not possible tree diameters were estimated

TABLE 1. *Name, elevation, size of sampled forest area, site history characteristics (SH = selectively harvested for timber, UH = unharvested) followed by date of last harvest, and summary statistics for tree stem density, basal area, and aboveground biomass (AGBM) (mean ± 1 SE) in each study site. Summary statistics were calculated based on measurements of all trees ≥ 10-cm dbh.*

Site	Elevation (m asl)	Size (ha)	Site history	Stem density (stems/ha)	Basal area (m²/ha)	AGBM (Mg/ha)
1	58	375	SH, 1991	427 ± 14	21.5 ± 0.8	148.1 ± 6.2
2	62	120	SH, 2000	461 ± 26	25.4 ± 1.2	177.2 ± 9.0
3	116	196	UH	411 ± 22	25.4 ± 1.4	180.8 ± 10.9
4	66	111	SH, 1995	486 ± 25	27.6 ± 1.4	192.8 ± 10.1
5	176	139	SH, 2003	522 ± 28	23.4 ± 1.7	155.2 ± 12.3
6	200	80	UH	488 ± 33	24.2 ± 1.8	164.8 ± 13.7

visually. These measurements were used to calculate the stem density (number of stems/ha) and basal area for both trees and palms. These data were also used to estimate tree AGBM using Brown and Iverson's (1992) equation for wet tropical forests,

$$Y = 21.297 - 6.953(D) + 0.740(D^2),$$

where Y is biomass per tree in kg and D is dbh in cm. Biomass estimates derived from this equation represent the biomass of the bole as well as that of all leaves, twigs, branches, and bark. Estimates of palm AGBM were not made because accurate prediction equations do not exist for the palm species common in Sarapiquí. Tree data were divided into five diameter classes (10–15, 15.1–20, 20.1–30, 30.1–60, ≥ 60.1 cm dbh) to examine the contribution of each class to total tree stem density, basal area, and AGBM.

Hemispherical photographs were taken with a digital camera fitted with a fisheye lens (Coolpix 4500, Fisheye Converter FC-E8, Nikon Corporation, Tokyo, Japan) at each plot center. Photographs were taken with the top of the camera oriented toward north under uniformly overcast sky conditions at a height of 1 m above the forest floor. Camera aperture and shutter speed were allowed to vary with lighting conditions to obtain the most balanced image possible. Hemispherical photographs were analyzed by a single operator using HemiView Canopy Analysis Software (version 2.1, Delta-T Devices Ltd., Cambridge, UK).

Variables derived from image analysis included LAI, global site factor (GSF), and canopy openness. LAI is defined as half the total leaf area per unit ground area, but in this study we effectively measured plant area index (PAI) because hemispherical photographs include woody elements in the canopy (*e.g.*, tree boles, branches; Weiss *et al.* 2004). For the sake of consistency, we use the term LAI in lieu of PAI because most values of hemispherical photograph-derived LAI in the literature represent PAI. GSF is a term that combines direct and diffuse light in the understory and expresses it relative to total light availability above canopy. Weighting factors for direct and diffuse light in the understory were used in the calculation of GSF (Rich *et al.* 1993). Canopy openness was calculated as a percentage from the visible sky term generated from the analysis of each photograph.

DATA ANALYSIS.—The design of this study, in which three identical transects were nested within each study site, lent itself to the use of linear mixed-effects models (Pinheiro & Bates 2000). These models contain both fixed and random effects and, in circumstances like those in the present study, are analogous to a blocked design. Fixed effects are parameters associated with a population and the estimates of these parameters are of primary importance in mixed-effects models. In contrast, estimates of random effects are not centrally important to questions about a population, as they represent grouped covariates in the data. In this study, the fixed effect was 'distance to forest edge,' specified as a continuous variable, and the factors 'transect' nested within 'site' were specified as the random effects in all models.

The mixed-effects model configuration described above was used in analyses of the following variables: palm stem density and basal area, tree stem density, basal area, and AGBM for all diameter classes pooled and for each of the five diameter classes described above, LAI, GSF, and canopy openness. Data transformations suggested by Box–Cox tests (Box & Cox 1964) were used as needed to normalize data prior to analysis. Specifically, a square root transform was used for all palm data, as well as for all tree data from the 10–15, 20.1–30, and 30.1–60 cm dbh classes. A log transform was used to normalize tree basal area and AGBM data, and a reciprocal square transform was used for LAI data.

Analysis of variance (ANOVA) was used to examine each of these variables in relation to the fixed effect, distance to the forest edge. Significant differences detected along forest edge to interior gradients with ANOVA were not further evaluated with multiple comparisons because the fixed effect was analyzed as a continuous rather than a categorical variable. All data processing, model fitting, and analyses were performed using the open-source statistical language R (version 2.0.1, R Development Core Team 2004).

RESULTS

FOREST STRUCTURAL PARAMETERS.—Among trees, stem density was significantly higher (ANOVA, $F = 8.50$, df $= 104$, $P = 0.0044$) in plots close to the forest edge and ranged from a maximum of 549 ± 27 stems/ha (throughout the text, ± values represent 1 SE) at 0 m to a minimum of 415 ± 20 stems/ha at 300 m (Fig. 2A).
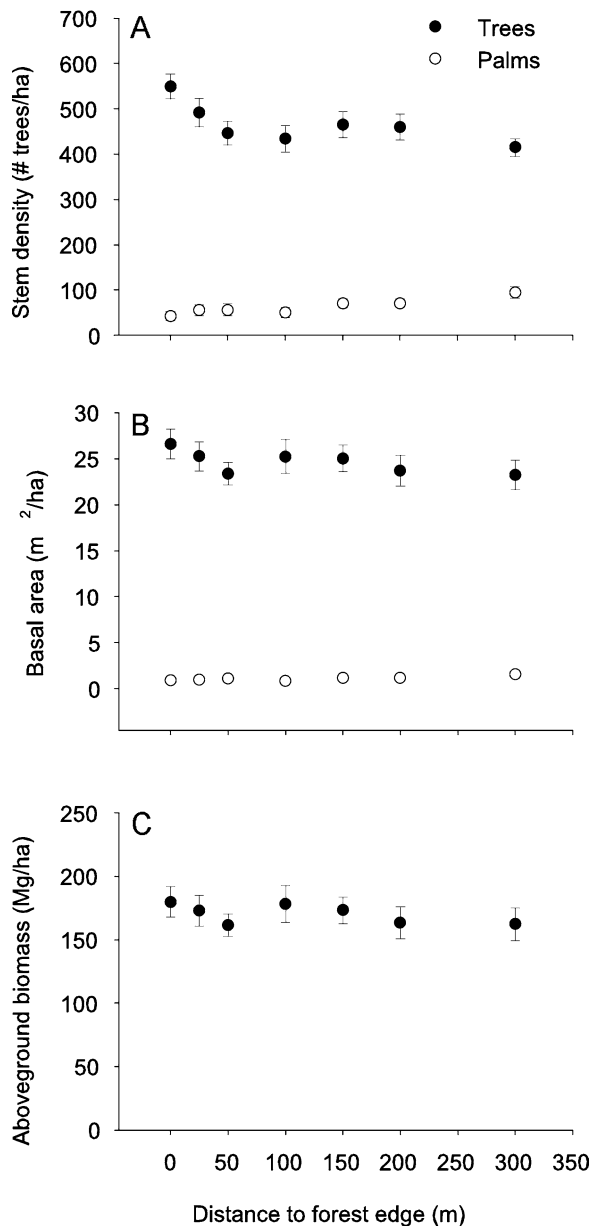
FIGURE 2.   Mean ± 1 SE of stem density (A), basal area (B), and aboveground biomass (C) (AGBM) for trees and palms, in relation to the distance of each plot to the forest edge. AGBM estimates for palms were not made because accurate prediction equations do not exist. Significant differences in tree and palm stem density ($P = 0.0044$, $P < 0.0001$, respectively) and palm basal area ($P < 0.0001$) were detected among distance classes.

FIGURE 3.   Mean ± 1 SE of stem density (A), basal area (B), and aboveground biomass (C) (AGBM) for trees in relation to the distance of each plot to the forest edge. Data are presented for five diameter classes, and significant differences along the forest edge to interior gradient were found for basal area ($P = 0.0318$) and AGBM ($P = 0.0252$) in the 10–15 cm diameter class and for stem density ($P = 0.0144$), basal area ($P = 0.0165$), and AGBM ($P = 0.0176$) in the 15.1–20 cm diameter class. Statistical analyses were not performed for the 60.1+ cm diameter class because of the small number of individuals in this category.

The opposite pattern was observed for palms, with significantly higher stem density ($F = 33.98$, df = 104, $P < 0.0001$) observed in forest interior plots, relative to edge plots (range: 42 ± 10 stems/ha at 0 m to 94 ± 13 stems/ha at 300 m; Fig. 2A). Palms also exhibited significantly greater basal area ($F = 25.52$, df = 104, $P < 0.0001$) in the forest interior than at the edge (range: 0.9 ± 0.2 m²/ha at 0 m to 1.6 ± 0.2 m²/ha at 300 m; Fig. 2B). Neither basal area
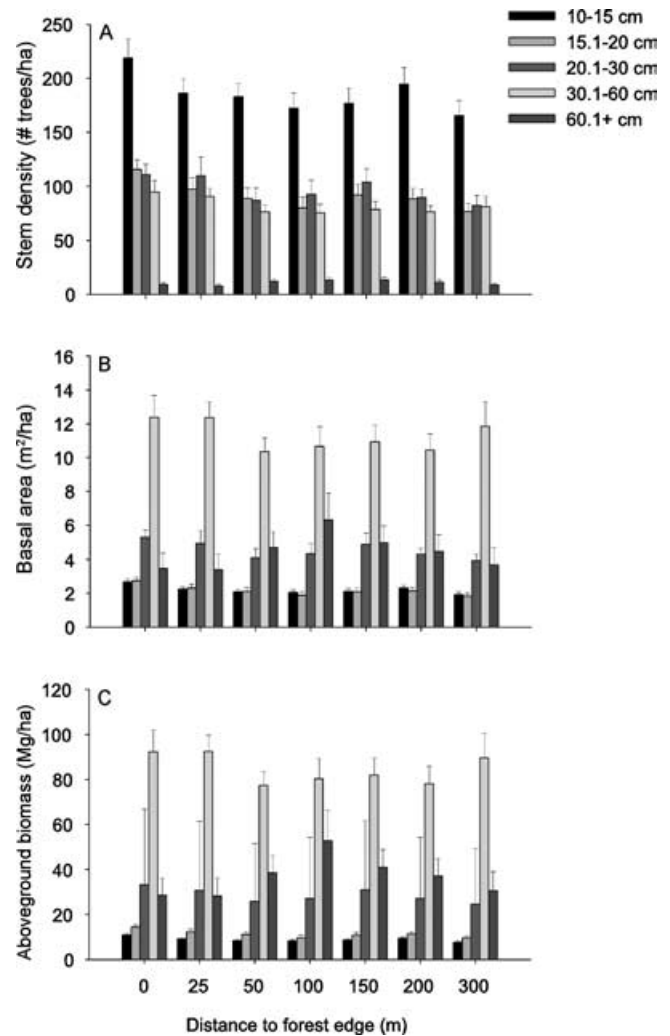
nor AGBM varied significantly for trees along the forest edge to interior gradient (Fig. 2B and C). Among trees, mean basal area was 24.6 ± 0.6 m²/ha, while mean AGBM was 170.3 ± 4.5 Mg/ha. For all stems ≥ 10-cm dbh, palms occupied between 7 and 18 percent of the total stem density and between 3 and 6 percent of the total basal area.

Tree data were divided into five diameter classes to explore the contribution of different diameter classes to total tree stem density, basal area, and AGBM. Within the class of stems from 10 to 15 cm dbh, a trend toward higher stem density at the forest edge was observed (Fig. 3A), but was marginally nonsignificant (ANOVA,

TABLE 2. *Mean ± 1 SE of leaf area index (LAI), global site factor (GSF), and canopy openness, as calculated from hemispherical photographs. No significant differences were observed along the forest edge to interior gradient.*

Distance class (m)	LAI (m²/m²)	GSF (%)	Canopy openness (%)
0	3.33 ± 0.21	9.2 ± 0.8	5.9 ± 0.5
25	3.50 ± 0.28	9.8 ± 0.9	6.0 ± 0.6
50	3.42 ± 0.21	9.7 ± 0.8	5.9 ± 0.5
100	3.25 ± 0.16	10.1 ± 0.6	6.2 ± 0.4
150	3.20 ± 0.15	8.4 ± 0.7	5.5 ± 0.5
200	3.91 ± 0.31	10.4 ± 0.6	6.0 ± 0.4
300	3.29 ± 0.15	8.9 ± 0.6	5.6 ± 0.4

$F = 3.66$, df = 104, $P = 0.058$). However, significantly greater basal area ($F = 4.73$, df = 104, $P = 0.032$) and AGBM ($F = 5.16$, df = 104, $P = 0.025$) were found for this diameter class in plots closest to the forest edge (Fig. 3B and C). Similarly, in the 15.1–20 cm dbh class, significantly greater stem density ($F = 6.19$, df = 104, $P = 0.014$), basal area ($F = 5.94$, df = 104, $P = 0.0165$), and AGBM ($F = 5.81$, df = 104, $P = 0.018$) were observed at forest edges (Fig. 3). No significant differences in these forest structural parameters were found in the remaining two diameter classes, 20.1–30 and 30.1–60 cm dbh (Fig. 3). Statistical analyses could not be performed for stems ≥ 60.1 cm dbh because these individuals were rare given the total land area sampled. Thirty-one percent of plots contained no trees in this diameter class and 46 percent of plots contained only one tree ≥ 60.1-cm dbh.

LEAF AREA INDEX AND UNDERSTORY LIGHT AVAILABILITY.—LAI did not differ along the forest edge to interior gradient (Table 2). Mean LAI across all sites and distance classes was 3.41 ± 0.08 m²/m². Similarly, GSF and canopy openness were invariant along the edge to interior gradient (Table 2).

DISCUSSION

FOREST STRUCTURAL PARAMETERS.—Consistent with our overarching hypothesis, forests in the Sarapiquí region of Costa Rica developed a dense wall of vegetation at forest edges in the 20+ yr following edge creation. Specifically, we observed elevated tree stem density at forest edges, and this pattern was reflected by higher stem density, basal area, and AGBM for trees in small diameter classes growing close to forest edges. This indicates that the germination and growth of small diameter trees following edge creation was instrumental in sealing forest edges with vegetation. The presence of dense vegetation at forest edges has likely stabilized these forests and contributed to the structural similarity between forest edge and interior environments observed for both tree basal area and AGBM. The decline in palm stem density and basal area detected at forest edges may be the result of human harvesting pressures, given the

gradual increase in both of these variables with increased distance from the edge.

Measures of tree stem density, basal area, and AGBM compare favorably with those made in undisturbed primary forests at the nearby La Selva Biological Station (10°26′ N, 83°59′ W, 35–137 m asl; see Fig. 1). Mean tree stem density, basal area, and AGBM data fell within the range of values reported at La Selva, though the La Selva study included palms in measures of these variables (Clark & Clark 2000). In relation to other studies of edge effects in the Neotropics, these results are most consistent with findings in Panamanian premontane wet forest and low-elevation tropical forest in Mexico (Williams-Linera 1990a, Williams-Linera et al. 1998), indicating that similar processes of edge development may exist across these ecosystems.

Shifts in species composition favoring early successional species at forest edges have been reported in Sarapiquí and related to an increase in small diameter trees at forest edges (Forero & Finegan 2002). A similar increase in early successional species at edges has also been reported in the experimentally fragmented forests of the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon (Laurance et al. 2006). However, the long-term implications for forest structural responses to edge effects are likely to differ between these two systems.

The observed increase in pioneer species abundance at edges in the BDFFP has been related to chronic wind disturbance and AGBM loss at edges (Kapos 1989, Ferreira & Laurance 1997, Laurance et al. 1997). These changes are expected to trigger additional biotic and abiotic edge effects, leading to the degradation of these forest fragments over time (Laurance et al. 2002). Although the present study does not focus on changes in edge structure with time, the presence of dense vegetation at the forest edge and the similarity of basal area and AGBM in edge and interior locations indicate that edges in Sarapiquí are not subject to chronic disturbances or significant AGBM loss. It is likely that many edge effects, including microclimatic changes and those influencing plant and animal distribution and abundance, will be attenuated in these forests due to the presence of dense vegetation at forest edges (Didham & Lawton 1999). Future investigation will be needed to further clarify the role of successional vegetation in stabilizing forest edges in Sarapiquí over the long term.

In general, drawing conclusions about long-term edge effects on forest structure is difficult in most ecosystems because old forest fragments are rare. Most studies addressing long-term edge effects have focused on gallery forests in the savanna ecosystems of Central America thought to have been established at the beginning of the Holocene (MacDougall & Kellman 1992, Meave & Kellman 1994, Kellman et al. 1996). Though isolated, these forest fragments have persisted through time and are maintained by dense vegetation at the forest edge (Kellman et al. 1996). This feature has been effective in stabilizing these extremely old forest fragments, suggesting that Sarapiquí's fragmented forests may also be protected by this shared attribute.

LEAF AREA INDEX AND UNDERSTORY LIGHT AVAILABILITY.—LAI, GSF, and canopy openness did not vary along the forest edge to

interior gradient. Although higher LAI was predicted at the forest edge relative to the interior, a lack of significant variation along this gradient reflects the findings discussed above. Increased understory light availability has been reported in other Neotropical forests with edges dominated by dense vegetation, but this increase was always confined to the immediate edge ($\sim$5–10 m from the edge) (Williams-Linera 1990a, MacDougall & Kellman 1992). In the present study, hemispherical photographs in edge plots were taken at a distance of 10 m from the edge, and may not accurately represent the understory light environment at points closer to the edge. Overall, our data indicate that understory light availability is not likely to differentially influence future seedling development and sapling recruitment at the edge relative to the forest interior.

Recent research indicates that LAI is typically underestimated by digital hemispherical photographs relative to film-derived estimates of LAI, in part because GSF and canopy openness are overestimated in digital photographs (Englund *et al.* 2000, Frazer *et al.* 2001). In addition, destructive sampling of canopy foliage for LAI determination has shown that digital hemispherical photography considerably underestimates LAI in the forests of Sarapiquí (P. Olivas, pers. comm.). Although the LAI values presented in this paper may not reflect true LAI, it should be recognized that as a relative measure LAI was invariant across the forest edge to interior gradient.

CONSERVATION IMPLICATIONS.—The study region lies within the boundaries of the San Juan–La Selva portion of the Mesoamerican Biological Corridor, a regional corridor designed to connect protected forests in Costa Rica's central mountains to those in southern Nicaragua. Corridor objectives include protecting habitat for the endangered Great Green Macaw (*Ara ambiguus*), as well as decreasing forest fragmentation, promoting biodiversity conservation, and contributing to sustainable resource use (Chassot & Monge 2002). Because the corridor has been a target area for Costa Rica's PES program (García 1996, Méndez 2003), a relatively high ecological value has been placed on forests of the region.

Forest edge structure is of central importance in attenuating abiotic and biotic edge effects in fragmented forest patches (Didham & Lawton 1999). As such, the structural integrity of forest edges in Sarapiquí will be beneficial in maintaining forest productivity as well as processes such as water and nutrient cycling (Landsberg & Gower 1997, Spies 1998). Further, many organisms dependent upon remaining forest patches for survival will benefit from the presence of robust edges, as forest structural parameters are often linked to the maintenance of biodiversity (Bawa & Seidler 1998, Brokaw & Lent 1999). Given the concentration of conservation efforts directed at the Sarapiquí region, data from the present study confirm that these forests are valuable and worthy of this high level of attention.

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