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ANTHROPOGENIC EDGES, TREEFALL GAPS, AND FRUIT–FRUGIVORE INTERACTIONS IN A NEOTROPICAL MONTANE FOREST

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Abstract. In a montane tropical forest in southwestern Colombia, we investigated how anthropogenic edges may alter bird-mediated seed dispersal from edge to forest interior as a function of edge age and presence of treefall gaps. We estimated fruit abundance and mist-netted birds at four distances from edge to forest interior (0–10, 30–40, 60–70, and 190–200 m) in three young ($<$12 yr) and three old ($>$40 yr) edges. Fruit-sampling plots (50-m^2 plots) at each of the four distances were classified into gap and intact forest.

Fruit abundance and frugivore capture rates varied from edge to forest interior, but such changes depended on edge age. At new edges, the total number of fruits was higher at the forest edge than at the forest interior, whereas bird captures showed the opposite trend. At old edges, the total number of fruits and bird capture rates did not vary among the four distances. In a first group of 12 plant and four bird species, the distribution of individuals in fruit (7 species) and captures (3 species) from edge to forest interior differed between old and new edges. In a second group of 18 plant and five bird species, which included those that were not amenable for a comparison between old and new edges and those that were not influenced by edge age, the distribution of individuals in fruit (12 species) and captures (3 species) was not uniform from forest edge to forest interior. Lastly, 124 plant and 19 bird species with $<$20 individuals in fruit and captures, respectively, were classified into very sparse and sparse species. We found that all but the sparse frugivores were more abundant at the forest edge than in the forest interior. Because very sparse and sparse plant species showed such a clear trend, we used seeds retrieved from mist-netted birds to assess potential seed movement of these species from edge to forest interior. Seeds of very sparse and sparse plant species were found both at forest ‘‘edge’’ (0–10 m) and at forest ‘‘interior’’ (the three other distances combined).

Our results suggest that birds are not responding to changes in fruit abundance (resource-base-driven mechanism). Instead, they indicate that frugivore capture rates reflect either a direct edge effect or a non-edge induced effect on birds. The apparent uncoupling of processes generating the observed patterns in fruit and frugivore abundance may affect seed dispersal in important ways. Furthermore, our results indicate that, as edges age, ‘‘edge effects’’ (i.e., maximum distance at which changes induced by edge creation are apparent within forest stands) change.

Key words: anthropogenic edges; edge age; edge effects; forest fragmentation; fruit–frugivore interactions; fruit removal; neotropical montane ecosystems; seed dispersal; treefall gaps; understory frugivorous birds; understory fruits.

INTRODUCTION

A general consequence of disturbance is the creation of boundaries or edges between the disturbed and undisturbed areas. Boundaries mediate fluxes of material and energy and influence the dynamics and structure of adjacent systems (Margalef 1968, Wiens et al. 1985, Correll 1991, Gosz 1991, Ryszkowski 1992). In this context, edges bounding forest fragments and disturbed areas may regulate the distribution of resources and movement of organisms between them (Crist et al. 1992, Johnson et al. 1992, Wiens 1992). For example, edges may affect seed dispersal and consequently, over time, the location and structure of edges. In many tropical ecosystems, a high proportion of plants produces fleshy fruits that are ingested by birds (Terborgh 1977, Gentry 1983, Stiles 1985). In such systems, edges may affect seed dispersal in particularly complex ways (Fig. 1).

The influence of edges on seed dispersal is likely to differ depending on disturbance size and time elapsed since disturbance. Edges bounding large-scale anthropogenic forest clearings may primarily affect plant colonization, whereas edges bounding small-scale disturbances, such as treefall gaps, may primarily affect plant recruitment (Harper 1994, Matlack 1994*a*, Nason et al.

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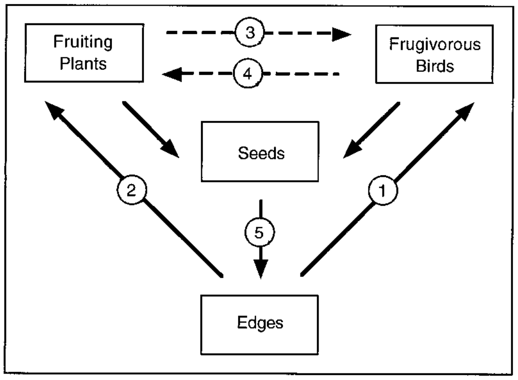

FIG. 1. Edges may influence animal-mediated seed dispersal directly through changes in microclimatic conditions and the distribution of suitable habitats for frugivorous birds (arrow 1) and plants (arrow 2) (Wiens et al. 1985, Blanchard 1992, Seizer 1992, Kuitunen and Mäakinen 1993, Kapos et al. 1997). Alternatively, edges may influence seed dispersal indirectly through changes in the resource base of frugivores (fruits, arrow 3) and fruiting plants (dispersers, arrow 4) (Snow 1965, Croat 1974, Stiles 1980, Greenberg 1981, Levey 1988*b*, Blake and Loiselle 1991, Rey 1995, Zurovchak 1997). Over time, seed dispersal, in turn, can affect the structure and location of edges (arrow 5).

1997, Thébaud and Strasberg 1997). Although some studies have examined how anthropogenic edges or treefall gaps influence the distribution of fruiting plants (Blake and Hoppes 1986, Levey 1988*b*, Blanchard 1992) and frugivores (Quintela 1986, Wong 1986, Levey 1988*b*), none to our knowledge has examined at a single site their combined effect on fruiting plants and frugivores or on the outcome of such interaction, namely seed dispersal. These studies can be particularly important for understanding how weeds and second-growth species colonize forest fragments, because, as Janzen (1983) suggests, seed dispersal of these pioneer plants might be favored by the interaction between anthropogenic edges and treefall gaps.

Time elapsed since disturbance may also influence the dynamics of seed dispersal across edges. Capture rates of frugivorous birds from edge to forest interior can vary on a monthly basis, suggesting that seed movement may vary in the same fashion (Restrepo and Gómez 1998). Less well documented, however, are the long-term effects of edges on seed dispersal. For example, vegetation structure varies from forest edge to forest interior depending on edge age (Williams-Linera 1990, Blanchard 1992, Matlack 1994*a*, *b*), suggesting that edges undergo succession and, consequently, that ‘‘edge effects’’ (sensu Harris 1984) vary over time. Establishing the long-term effects of edges on seed dispersal can contribute to our understanding of how edge location and structure may change over time (Fig. 1, arrow 5). Moreover, it can help in designing more realistic research and management schemes that have for objectives the evaluation of suitable habitat and design of reserves. So far, most of this work has relied on the notion that edge effects remain unchanged over time (e.g., Hansen et al. 1992, Skole and Tucker 1993), which clearly can be misleading.

In this paper, we present results of a study that investigated how edges influence the abundance of understory fruits and frugivorous birds. In particular, we examine (1) how edge age, in combination with distance from edge to forest interior and treefall gaps, influences the abundance of understory fruits (Fig. 1, arrow 2); (2) how capture rates of frugivorous birds change in response to changes in fruit abundance (Fig. 1, arrow 3); (3) how distance from forest edge in combination with treefall gaps affects removal of *Palicoura gibbosa* (Rubiaceae) fruits, the most common understory shrub at our study site (Fig. 1, arrow 5); and (4) how potential seed movement of ‘‘edge’’ species, inferred from seeds contained in bird droppings, differs between edge and forest interior (Fig. 1, arrow 5).

METHODS

Study area

This study was conducted at the Reserva Natural La Planada and Finca El Bosque (referred to hereafter as ‘‘La Planada’’), located in southwestern Colombia (78°00′ W and 1°10′ N). The forest of La Planada is a mosaic of mature forest, selectively logged forest, and second-growth surrounded by pastures. Mean annual rainfall and temperature are 4437 mm and 19°C, respectively (Reserva Natural La Planada, *unpublished data*). Rainfall is distributed in two wet seasons, interrupted by a mild (February–March) and a stronger (June–August) dry season (Restrepo and Gómez 1998). According to the available climatological data, La Planada is a transitional life zone between tropical premontane rain and wet forest (Holdridge 1967).

Soils at La Planada are derived partially from volcanic ash (Dystrandept) and are well-drained, moderately acid, with a sandy to clay loam texture (De Las Salas and Ballesteros 1986). Mean canopy height is 22 m and mean basal area (for dbh >4 cm) is 33.4 m^2/ha (De Las Salas and Ballesteros 1986). Of plants with dbh >2.5 cm, 121 species were recorded in a 0.1-ha plot (Gentry 1992). The most abundant species in this plot were *Quararibea* sp., *Elaegia* sp., *Hieronyma* sp., *Alchornea* sp., *Billia colombiana, Inga* sp., *Otoba* sp., *Ocotea* sp. (trees), *Faramea elegans, Prestoea* cf. *purpurea, Aiphanes* sp., *Geonoma weberbaueri, Palicourea gibbosa,* and *Miconia* sp. (treelets and shrubs; A. Gentry, *unpublished data*).

Sampling design

We chose six sites to evaluate how edges influenced fruit abundance and frugivore capture rates. These sites, hereafter referred to as edges, were active pastures contiguous with forest (except Pialapi; see Table 1). Three ‘‘old’’ edges (Celimo I, Celimo II, and Pialapi) were created around 1950, when colonists first

TABLE 1. Characteristics of the edges included in this study.

Edge	T†	O‡	A§	C‖	PS¶	G#	CU††	Use of forest
Celimo I	S	40° NE	1953	H	6.0	4.2	cattle ranching; pasture	sporadic extraction of palm hearts and poles; cattle grazing
Celimo II	S	19° NE	1953	M	7.6	7.6	cattle ranching; pasture	sporadic extraction of palm hearts and poles; cattle grazing
Pialapi	F	8° NE	1950	L	6.0	9.9	trail to Pialapi; second-growth	selective logging 40 yr ago
Acantayac	F	24° NE	1981	H	11.0	11.0	cattle ranching; pasture	sporadic extraction of palm hearts and poles; cattle ranching
Hermogenes	M	68° NE	1982	H	10.0	10.0	cattle ranching; pasture	sporadic extraction of palm hearts
Marcos	S	59° NE	1982	H	7.5	7.5	cattle ranching; pasture	sporadic extraction of palm hearts and poles; cattle grazing

† T, topography: S, steep; M, moderate; F, flat.
‡ O, orientation: position of edges regarding the cardinal points (in degrees).
§ A, age (year of creation of the clear-cut area).
‖ C, forest/edge contrast: H, high; M, moderate; L, low.
¶ PS, size of the clear-cut (ha).
# G, percentage of the sampling area covered by gaps.
†† CU, use of clear-cut.

arrived in the area and cleared the forest to establish pastures. Three ‘‘new’’ edges (Marcos, Hermogenes, and Acantayac) were created around 1982, when neighbors felled the forest in an effort to establish clear boundaries with the recently created reserve (Restrepo 1995).

At each edge, we delimited an area of 100 × 200 m (2 ha) with the long axis perpendicular to the forest edge (Restrepo 1995, Restrepo and Gómez 1998). In each area, we established four strips (100 × 10 m) running parallel to the edge and located at four distances from the edge to the forest interior: 0–10 (D1), 30–40 (D2), 60–70 (D3), and 190–200 (D4) m. To sample fruits and birds, we subdivided each of the four 100 × 10 m strips within each edge into five 20 × 10 m quadrats. Sampling took place over a 12-mo period (September 1992–August 1993, excluding December).

Fruit abundance

Each 20 × 10 m quadrat was further subdivided into four 10 × 5 m subquadrats. We chose two at random for monitoring fruit abundance, and assigned each subquadrat to either ‘‘gap’’ or ‘‘intact forest’’ habitat. A subquadrat was classified as ‘‘gap’’ if it was within a treefall gap (a canopy opening penetrating down to within 2 m of the ground; Brokaw 1982) or was located <5 m from a treefall gap edge. It was classified as ‘‘intact forest’’ if it was located ≥5 m from the nearest treefall gap edge at the time the study began. These two categories do not reflect the environmental continuum from the center of the treefall gap to the intact forest, nor do they take into account differences in gap size and shape (Brown 1993, Denslow and Hartshorn 1994). Nevertheless, they provide an operational way to classify the subquadrats according to habitat.

In each subquadrat, we identified and counted all individual plants ≤7 m tall bearing unripe or ripe fleshy fruits (Levey 1988*a*, *b*, Blake and Loiselle 1991). Most plant species included in this study complete their life cycle within this arbitrarily delineated ‘‘understory’’ stratum. For each plant in fruit, plus three canopy limbs bearing fruits and that had fallen naturally, we counted the total number of unripe and ripe fruits once every two weeks. We averaged these fortnightly counts to obtain a single value of fruit abundance for each month. Fruit abundance was expressed in three ways: (1) total number of fruits, unripe and ripe (TF); (2) total number of ripe fruits (RF); and (3) total number of individuals in fruit (plants bearing unripe and/or ripe fruits; TI). In all cases, fruit abundance represents the mean number of fruits or individuals in fruit per 50 m^2, the area of each 10 × 5 m subquadrat. We excluded the Araceae (anthuriums) from variables 1 and 2 because it was difficult to estimate fruit numbers for each infructescence. There were three important assumptions underlying our work. First, we assumed that fruit abundance as previously defined reflects fruit availability for the assemblage of understory frugivores. Second, we assumed that all species producing fleshy fruits are used by these birds to some degree, and not by terrestrial or arboreal mammals. Lastly, we assumed that unripe fruits provide a measure of future fruit abundance. Palms, for example, produced many fruits that ripened over a period of time longer than the length of this study.

To explore the response of individual species to edges, we focused on the total number of individuals bearing unripe and/or ripe fruits. We totaled the number of fruiting individuals for all subquadrats and months to obtain a single value for each edge age and distance.

Frugivorous birds

We chose at random three of the 20 × 10 m quadrats per distance per edge and placed at each quadrat a pair of mist nets (9 × 2.5 m with 32 mm mesh), with one net perpendicular to the other (Restrepo 1995, Restrepo and Gómez 1998). We operated 12 pairs of mist nets simultaneously from 0530 to 1300 for two consecutive days per month per distance per edge, trying to complete 14 h of mist-netting per pair of mist nets. Mist nets were checked every 1 to 1.5 h, and for each captured bird we recorded species and mist net position. All birds were individually marked with color bands. Recaptures on the same day were excluded from the analyses. Because the sampling unit was a pair of mist nets instead of the traditional single net, we define mist-net hours as the numbers of hours that a pair of nets was opened. In total, the mist-netting effort was equivalent to 11 892 mist-net hours. Frugivores were defined as species that commonly consumed fruit and/or seeds; most of them also consumed insects to some degree. The placement of species in this category was based on the analysis of fecal samples, our own observations, and published reports (Miller 1963, Stiles and Skutch 1989, Andrade 1993, Arango 1994).

Bird abundance is expressed throughout this paper as capture rates per 100 paired mist-net hours. The relationship between mist-net capture rates and bird abundance has been the subject of recent debate (Remsen and Good 1996 and references therein). We stress, however, that the combination of relative structural habitat homogeneity from edge to forest interior and our large mist-netting effort resulted in capture rate values that provide a good measure of bird activity for the purposes of this study.

Fruit removal

We conducted an experiment to evaluate the effect of distance from forest edge in combination with treefall gaps on removal of *Palicoura gibbosa* (Rubiaceae) fruits. *P. gibbosa* is among the five most abundant species in the understory of La Planada and produces abundant fruits (A. Gentry, *unpublished data*; C. Restrepo, *unpublished data*). The experiment was conducted at two edges (Hermogenes and Celimo I) that differed in their age, but that were close enough to allow frequent monitoring of fruits. We did not include edge age as a variable because we did not have true replicates. Thus, the interpretation of our results is limited to the effect of distance from forest edge and treefall gaps on fruit removal.

At each of four distances, we mapped treefall gaps and randomly chose four of them. We paired each treefall gap with an intact forest location and placed eight artificial shrubs per distance per edge, four in gaps and four in intact forest locations. Each shrub consisted of a 1.5 m tall bamboo stick to which we attached one artificial infructescence resembling those of *P. gibbosa.* The artificial infructescences consisted of a 15 cm long wooden rod from which four pairs of toothpicks extended. The rods and toothpicks were dyed bright yellow. At the end of each toothpick, we inserted a recently collected purple ripe fruit, totaling eight fruits per infructescence. On the morning of the first day of the experiment (0600), we inserted fresh fruits; 12 h later, we counted and replaced missing fruits. A missing fruit was recorded as being removed by frugivorous birds. All fruits were changed every 24 h to start a new run of the experiment. We ran the experiment at each edge for four consecutive days from 26 June to 3 July 1993.

Potential seed movement

We retrieved seeds from droppings of captured birds, identified, and counted them. After capture, birds were kept in cloth bags lined with filter paper for ~20 min. Bird droppings were preserved in alcohol and seeds were compared to a reference collection compiled during the study period. This method for evaluating potential seed movement has several biases. In particular, seeds recovered from bird droppings might represent a nonrandom sample of seeds ingested, because seed handling varies within and among species depending on seed size and other seed characteristics (Levey 1986, 1987). Nevertheless, this method provides information on seed movement that would be difficult to determine by other means (e.g., seed traps).

Data analysis

We analyzed fruit and frugivore abundance data with ANOVAs for mixed-factorial designs (Winer et al. 1991, Girden 1992). In the ANOVA tables, we specify the type of design, which included edge age, distance from the edge, habitat, and month as factors of interest. We averaged the subquadrat counts of fruit and individuals in fruit per habitat per month per distance per edge. This procedure improved the normality of the data sets, reduced their dimensionality, and eliminated problems associated with unbalanced data sets (there were 3.1 ± 1.5 ''gap'' subquadrats (mean ± 1 SD) and 6.9 ± 1.5 ''intact forest'' subquadrats per distance). We verified the assumption of compound symmetry for ANOVAs that included within-factors, and we report *P*-corrected values based on the liberal Huynh-Feldt method (Girden 1992). In addition, we plotted the residuals as a function of fitted Y values to detect any violation of assumptions for ANOVAs (Manly 1992).

We used a replicated goodness-of-fit test (Sokal and Rohlf 1981) to determine how the distribution of plant and bird species from edge to forest interior varied with edge age. For a large number of species, however, small sample sizes precluded the comparison between old and young edges; hence, we restricted our analyses to comparing plant and bird distributions among the four distances. Species were analyzed individually with a G (goodness-of-fit) test when sample sizes were large enough so that >80% of the expected cell frequencies were >5 (Siegel and Castellan 1988). Species that did not meet this criterion were grouped into two abundance categories, very sparse (1–5 individuals in fruit or captures) and sparse (6–20 individuals in fruit or captures) to establish how the distribution of individ-

TABLE 2. Results of three ANOVAs on number of fruits (TF), number of ripe fruits (RF), and number of individual plants bearing ripe and/or unripe fruit (TI) per 50 m^2.

Effect	df	TF		RF		TI	
		MS	*F*	MS	*F*	MS	*F*
Age (A)	1	0.03	0.01	0.78	0.19	95.88	1.08
Error [Edge (Age)]	4	4.27		4.18		88.47	
Distance (D)	3	6.55	5.20*	7.74	3.58*	64.93	1.82
D × A	3	3.17	2.51†	1.30	0.60	24.62	0.69
Error [D × Edge (Age)]	12	1.26		2.16		35.77	
Habitat (H)	1	5.49	4.76*	6.72	5.40*	27.73	1.09
H × D	3	5.43	4.71*	5.45	4.38*	48.21	1.89
H × A	1	0.68	0.59	1.29	1.04	10.65	0.42
H × D × A	3	0.48	0.41	1.59	1.28	0.35	0.01
Error [H (D) × Edge (Age)]	16	1.15		1.24		25.53	
Month (M)	10	1.42	22.89***	4.30	17.92***	39.88	50.54***
M × A	10	0.16	1.00	0.97	2.35*	1.69	1.36
Error [M × Edge (Age)]	40	0.16		0.41		1.24	
M × D	30	0.08	1.52†	0.22	1.00	1.42	1.46†
M × D × A	30	0.06	1.16	0.28	1.26	0.88	0.91
Error [M × D × Edge (Age)]	120	0.05		0.22		0.97	
M × H	10	0.16	2.50**	0.54	2.25*	0.72	0.91
M × H × D	30	0.04	0.71	0.11	0.48	1.07	1.36
M × H × A	10	0.07	1.06	0.34	1.42	0.17	0.21
M × H × D × A	30	0.06	0.98	0.22	0.93	0.76	0.96
Error [M × H (D) × Edge (Age)]	160	0.06		0.24		0.79	

Notes: The mixed-factorial design ANOVA is a split-split-plot with one repeated measure (month). Age represents the plot; distance and habitat represent the subplot and sub-subplot units, respectively; and edge represents the replicates. The *F* values for the effects of the repeated measures are corrected based on the Huynh-Feldt method. Log-transformed data are used for TF and RF.

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

uals in fruit and bird captures changed from edge to forest interior.

We used a rejection level at $\alpha = 0.10$ to interpret results from the ANOVAs, because our design could lead to increases in Type II errors (reduced power; Zolman 1993). This departure from ecological tradition was justified for two reasons. First, we were limited by the number of accessible replicates for the edge age effect, which is often the case when dealing with large-scale ecological phenomena (Scheiner 1993). Second, we were limited by the area encompassed by each edge (2 ha). For effective sampling, we assigned to each edge the four levels of the distance factor, and to each distance the two levels of the habitat factor. In mixed-factorial designs, the number of degrees of freedom is reduced in comparison to factorial designs, because of multiple nesting (Zolman 1993).

RESULTS

Fruit abundance

Distance from forest edge, edge age, habitat, and month influenced fruit abundance; however, results differed for the three variables used to express fruit abundance (Table 2). Although the total number of fruits (TF) differed significantly among the four distances, the significant distance × edge age interaction (Table 2, Fig. 2a) indicates that the changes depended on edge age. The total number of fruits (TF) was higher at D1 (0–10 m) in new edges than at the same distance in old edges and showed a sharp decline toward the forest interior. At old edges, TF varied little among the four distances (Fig. 2a). The interaction between distance and habitat (''gap'' and ''intact forest'') was significant for total number of fruits (TF) and total number of ripe fruits (RF; Table 2, Fig. 2b, c). The total number of fruits at forest edge (0–10 m, D1) was higher in ''gaps'' (mean ± 1 SE, 1776 ± 236 fruits/50 m^2) than in ''intact forest'' (608 ± 61 fruits/50 m^2). These differences were smaller or disappeared at the other distances. Ripe fruits (RF) exhibited the same trend.

The significant interaction between month and distance for total number of fruits (TF) and total number of individuals in fruit (TI) indicates that fruit abundance varies among distances, depending on month of the year (Table 2, Fig. 3a, b). Fruit abundance differed among D2 (30–40 m), D3 (60–70 m), and D4 (190–200 m) in some months, but overall remained lower than at the forest edge (0–10 m, D1). This suggests a steep gradient in fruit abundance over the entire year. The number of ripe fruits (RF) differed between young and old edges in some months (Table 2, Fig. 3c). Although fruit abundance was low and indistinguishable between young and old edges from September to January (strong wet season at La Planada), it started to diverge thereafter, most likely reflecting differences in the onset of fruiting and ripening times of fruits of the various plant species.

In the understory, 149 plant species fruited; 35 were exclusive to new edges and 14 to old edges (see Appendix). In this respect, new edges had more species

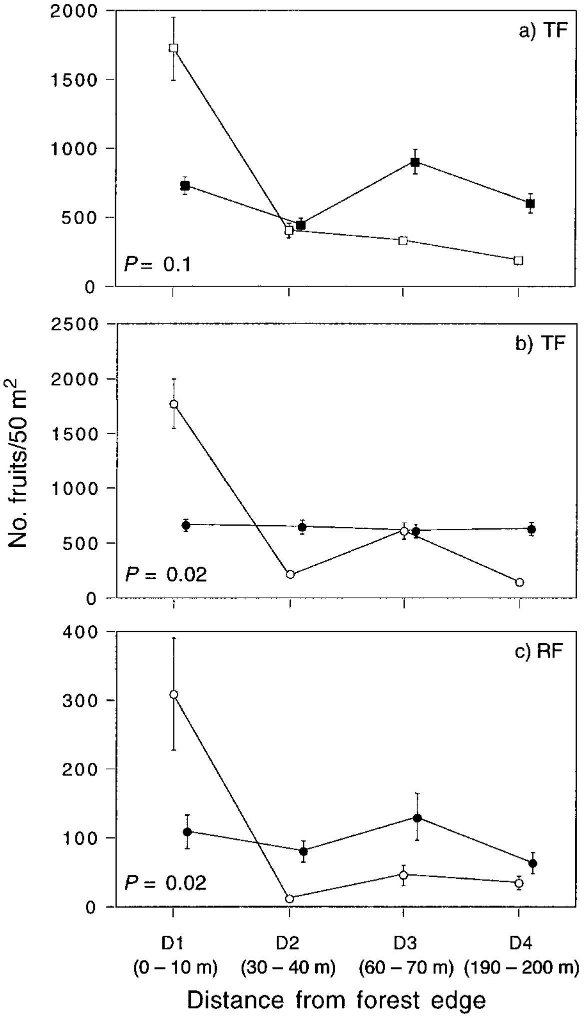

FIG. 2. Variation from edge to forest interior in (a) total number of fruits (TF) plotted separately for different edge ages, and in (b) total number of fruits (TF) and (c) number of ripe fruits (RF) plotted separately for different habitat types. Data are presented as mean ± 1 SE. In (a), open squares indicate new edges, and solid squares indicate old edges. For (b) and (c), open circles indicate gaps, and solid circles indicate intact forest.

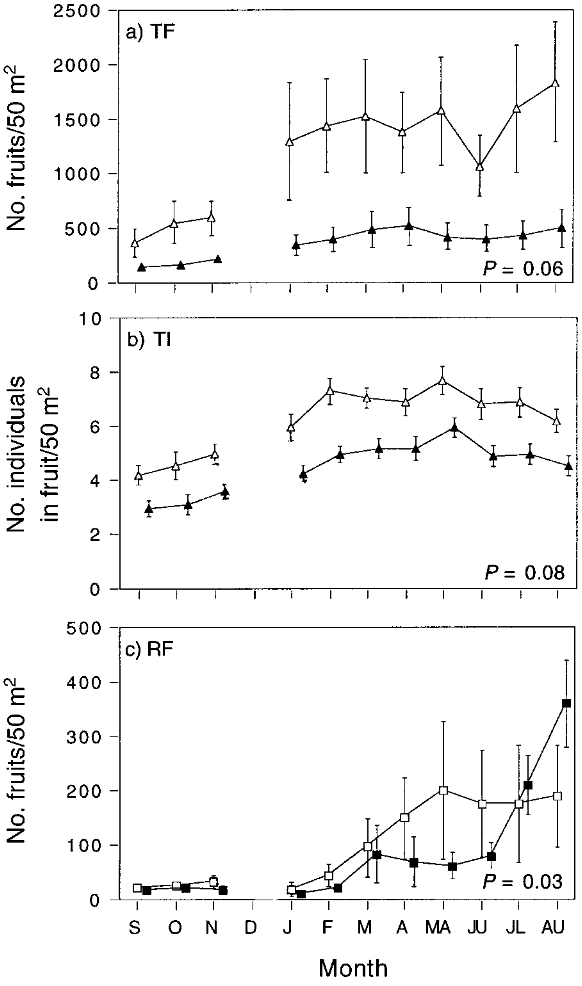

FIG. 3. Variation by month in (a) total number of fruits and (b) total number of individuals in fruit plotted separately for different distances from edge, and in (c) number of ripe fruits plotted separately for new and old edges. In (a) and (b), open triangles represent D1 (0–10 m from edge), and solid triangles represent D4 (190–200 m from edge). In (c), open squares are new edges, and solid squares are old edges.

than old edges (goodness-of-fit test, $G = 9.3$, $P < 0.01$). The distribution of individuals in fruit from edge to forest interior differed between old and new edges in seven species (G for heterogeneity, $P \leq 0.1$, Fig. 4). We pooled the data for old and new edges for the five species that did not show a significant distance × edge age interaction and for the 13 remaining abundant species (≥21 individuals in fruit) for which sample sizes precluded such analysis. We found that 12 out of 18 species showed a non-uniform distribution from edge to forest interior (Table 3). It is unlikely that chance alone can explain these results (binomial test, $P = 9.8 \times 10^{-9}$), given a 0.1 probability of obtaining a species with a non-uniform distribution. Clearly, the distribution of fruiting plants varied from edge to forest interior, but not necessarily because of the presence of edges, as suggested by five species that showed neither an increase nor a decrease from edge to forest interior (''other patterns'' in Table 3).

Most of the species (83%) found in our edges were represented by few individuals (<21 individuals in fruit). We grouped these species into two categories (very sparse and sparse species) and found that they were not uniformly distributed from edge to forest interior (Table 4). More importantly, all fruiting individuals of these species were found at the forest edge (0–10 m, D1).

Frugivorous birds

Capture rates of frugivores differed with distance, but this effect was modified by edge age (Table 5, Fig. 5a). Capture rates were higher at D4 (190–200 m) in

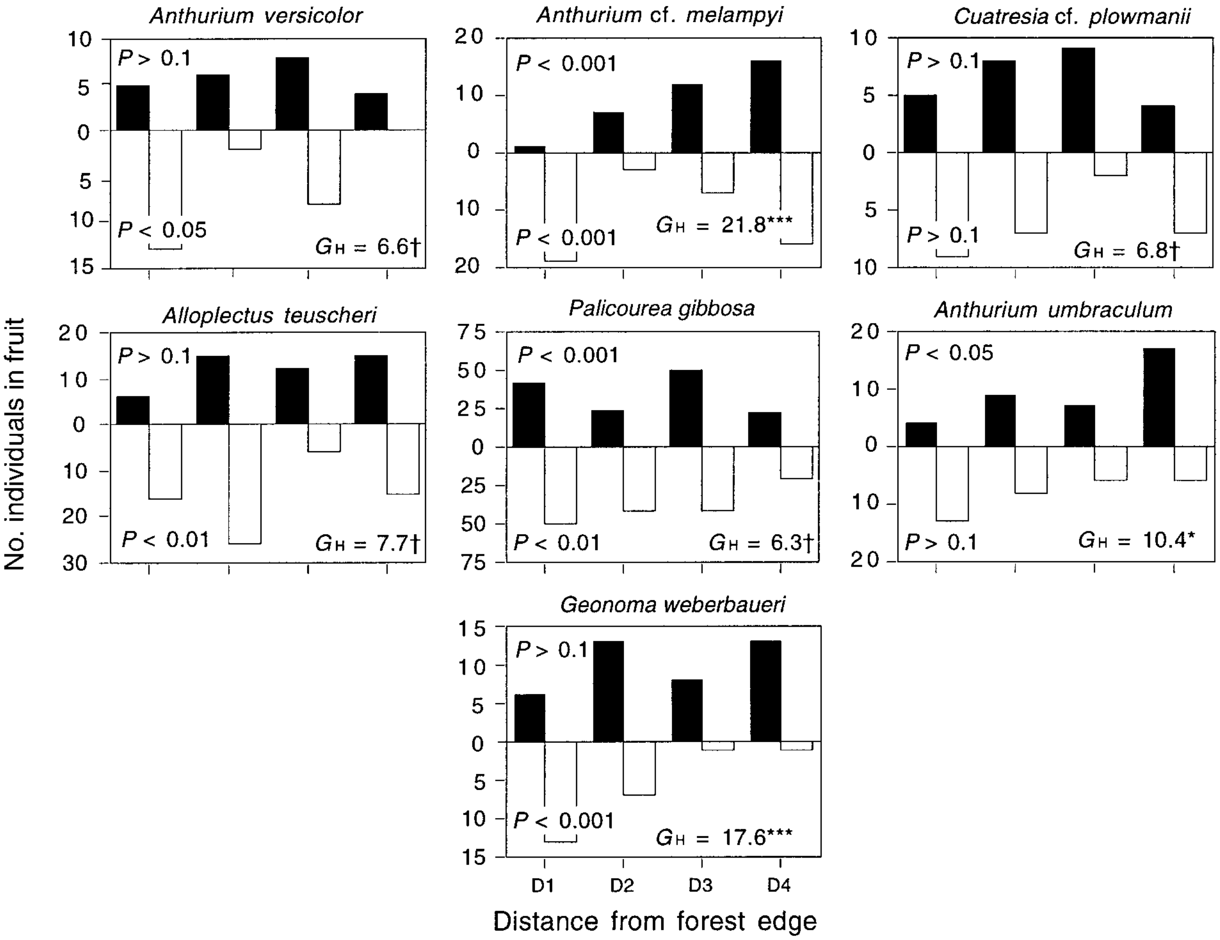

FIG. 4. Distribution of fruiting individuals from edge to forest interior as a function of edge age (new edges, open bars; old edges, solid bars) for plants in which G for heterogeneity (G_H) was significant. Significance levels are indicated by: † $P < 0.1$, * $P < 0.05$, ** $P < 0.001$, *** $P < 0.001$.

new edges (mean ± 1 SE, 9.5 ± 1.3 captures/100 mist-net hours) than at the same distance in old edges (4.5 ± 0.6 captures/100 mist-net hours). Capture rates at D1 (0–10 m), D2 (30–40 m), and D3 (60–70 m) were similar between new and old edges. A significant interaction between distance and month indicates that capture rates differed among distances, depending on month (Table 5, Fig. 5b). Although capture rates were indistinguishable between D1 (0–10 m) and D4 (190–200 m), the extremes of our distances, for most of the year, they diverged from November to February. During this time, capture rates were higher at the forest interior than at the edge. These results, opposite to those obtained for plants, suggest that the steepness of the gradient in the distribution of understory frugivorous birds varies over the year.

Among a total of 28 bird species, eight contributed 89% of the total captures ($n = 659$; see Restrepo and Gómez 1998: Appendix). We found that bird captures from edge to forest interior differed between young and new edges for three species (G for heterogeneity, $P \leq 0.1$; Fig. 6). For the single species for which the heterogeneity G was not significant, and for those in which sample sizes were too small to make a comparison between young and old edges, we pooled the data and compared the number of captures among the four distances. Three species showed a non-uniform distribution, either increasing or decreasing from the edge to the forest interior (goodness-of-fit test, $P \leq 0.1$; Table 6). Birds with very few captures were lumped into two categories for analysis. Very sparse species were found more often at the forest edge (0–10 m, D1), whereas sparse species were found more often at the forest interior (190–200 m, D4; goodness-of-fit test, $P < 0.001$ and $P < 0.05$, respectively; Table 4).

Fruit removal

Of 1536 fruits of *Palicourea gibbosa* that we placed in the artificial infructescences, only 83 were removed. We found that fruit removal differed among the four distances, but depended on whether the infructescences were in "gap" or "intact forest" (G for heterogeneity

TABLE 3. Distribution of abundant (≥ 21 individuals) understory plant species of La Planada in relation to distance from forest edge.

Plant species	No. individuals in fruit at each distance D1 (0–10)	D2 (30–40)	D3 (60–70)	D4 (190–200)	*G*
Uniform distribution					
Burmeistera carnosa	10	11	13	14	0.83
Anthurium membranaceum	32	30	27	24	1.31
Burmeistera sp. nov.	7	4	5	9	2.35
Columnea cinerea	10	5	4	5	3.34
Spheraedenia steyermarkii	7	2	6	6	3.37
Anthurium cf. *pulverulentum*	8	6	5	2	3.99
Non-uniform distribution					
a) Increase from edge to interior					
Dicranoypygium sp.	0	0	0	27	7.1†
Chamaedorea polychlada	5	7	15	18	10.8*
Solanum deflexiflorum	3	14	14	17	12.2**
b) Decrease from edge to interior					
Psammisia aff. *debilis*	20	9	4	8	12.9**
Besleria solanoides	39	16	14	4	35.5***
Clidemia sp. 1	54	59	27	10	48.7***
Psychotria aubletiana	45	14	12	5	40.3***
c) Other patterns					
Asplundia sp. 1	2	10	5	8	6.6†
Anthurium cf. *marmoratum*	10	9	17	5	7.2†
Faramea elegans	104	146	127	117	7.6†
Anthurium carchiense	3	15	5	12	11.7**
Anthurium umbricolum	9	7	22	7	12.2**

Notes: Distance ranges in the four categories (D1–D4) are in meters. Data are the number of individuals that produced fruit during one year. We used the residuals to further classify the species as increasing or decreasing from forest edge to forest interior, or as showing other patterns.

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

= 13.7, $P < 0.001$; Table 7). In gaps, the number of fruits removed did not differ from a uniform distribution, but the same was not true for intact forest, where the greatest number of fruits removed occurred at D2 (30–40 m).

Potential seed movement

We recovered 394 bird droppings containing seeds of 92 plant species. Only 51 of these species belong to plants found in our edges, which shows that seeds contained in bird droppings represent a relatively small subsample of the plant species found in an area (n = 149; Appendix). In order to evaluate seed movement between edge and forest interior, we focused on very sparse and sparse species (<20 individuals). First,

TABLE 4. Distribution of very sparse (1–5 individuals in fruit or captures) and sparse (6–20 individuals in fruit or captures) understory plant and bird species in relation to distance from forest edge (D1–D4, in meters).

Category	No. species	No. individuals/captures at each distance (m) D1 (0–10)	D2 (30–40)	D3 (60–70)	D4 (190–200)	*G*
Plant species						
Very sparse	74	77	25	35	34	34.2***
Sparse	50	167	144	138	120	7.9*
Bird species						
Very sparse	14	14	5	8	2	32.7***
Sparse	5	9	13	10	23	8.21*

* $P < 0.05$, *** $P < 0.001$.

TABLE 5. Results of an ANOVA on capture rates of frugivores (square-root transformation of number of captures per 100 mist-net hours). The mixed-factoral design ANOVA has one between- and two within-repeated-measure (distance and month) factors. Age represents the ‘‘between’’ factor, and edge represents the subjects or replicates. The *F* values for the effects of the repeated measures are corrected, based on the Huynh-Feldt method.

Effect	df	MS	*F*
Age (A)	1	6.3	1.77
Error [Edge (Age)]	4	3.7	
Distance (D)	3	10.1	4.85*
D × A	3	5.7	2.75†
Error [D × Edge (Age)]	12	2.1	
Month (M)	10	3.8	4.4***
M × A	10	0.7	0.79
Error [M × Edge (Age)]	40	0.9	
M × D	30	1.7	1.93**
M × D × A	30	1.0	1.1
Error [M × D × A × Edge (Age)]	120	0.9	

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

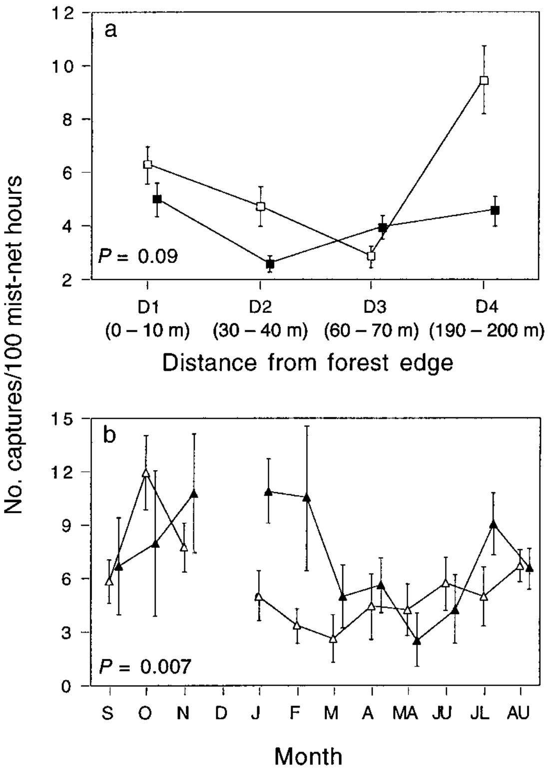

FIG. 5. Variation from edge to forest interior in capture rates of frugivorous birds as a function of edge age (a) and as a function of month of the year (b). Points are means ± 1 SE. In (a), open squares represent new edges, and solid squares represent old edges. In (b), D1 (0–10 m) is shown as open triangles, and D4 (190–200 m) is shown as solid triangles.

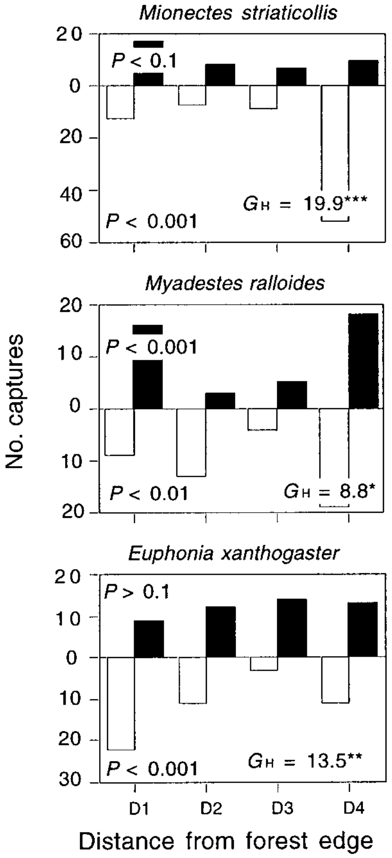

FIG. 6. Distribution of captures from edge to forest interior by edge age for frugivorous birds in which G for heterogeneity (G_H) was significant: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Filled bars show the distribution for old edges, and open bars show the distribution for new edges.

these species were found more often at the forest edge (0–10 m, D1) than at the other distances (Table 4). Second, droppings retrieved from birds captured at the forest interior and containing seeds of these species would suggest seed movement from edge to forest interior. Plant species were classified into four categories, according to the distribution of individuals in fruit and bird droppings containing their seeds (Table 8). If the number of individuals in fruit and the number of bird droppings containing the seeds of a given species were more common at the "edge" (D1, 0–10 m) than at the other three distances combined together, then the species was classified as "edge" for both categories. Conversely, if the number of individuals in fruit and the number of bird droppings were less common at the "edge" (D1, 0–10 m) than at the other three distances combined together, then the species was classified as "interior" for both categories. We found that the distribution of seeds contained in bird droppings was independent from the distribution of individuals in fruit (test of independence, $\chi^2 = 0.05$, df = 1, $P = 0.8$; Table 8). Even though very sparse and sparse species were found more often at the forest edge, their seeds reached the forest interior.

DISCUSSION

Edges can influence animal-mediated seed dispersal in several ways (Fig. 1). We found that fruit abundance decreased from edge to forest interior, but frugivore capture rates showed an opposite trend. This result suggests that birds are not responding to changes in fruit abundance (resource-base-driven mechanism; Fig. 1, arrow 3), but rather that frugivore capture rates reflect either a direct edge effect (Fig. 1, arrow 1) or a non-edge induced effect on birds. The apparent uncoupling of processes generating the observed patterns in fruit and frugivore abundance may affect seed dispersal in important ways.

Non-edge induced effects

If frugivore capture rates do not reflect changes in fruit abundance, then three hypotheses, not mutually exclusive, can explain the observed increase from edge to forest interior. First, edges may be influencing directly, but in opposite ways compared to plants, the behavior of frugivores through changes in microclimate and the distribution of suitable habitats (Wiens et al.

TABLE 6. Distribution of abundant (≥21 captures) frugivorous birds in relation to distance from forest edge (D1–D4, in meters). Data are number of captures.

Species	No. captures at each distance D1 (0–10)	D2 (30–40)	D3 (60–70)	D4 (190–200)	G
Uniform distribution					
Allocotopterus deliciosus	13	10	11	12	0.4
Pipreola riefferii	7	5	4	5	0.9
Non-uniform distribution					
a)Increase from edge to interior					
Atlapetes brunneinucha	3	4	11	10	7.5†
Masius chrysopterus	37	27	25	58	17.5***
b) Decrease from edge to interior					
Chlorospingus semifuscus	13	2	3	5	13.6**

Note: We used the residuals to further classify the species as increasing or decreasing from forest edge to forest interior, or as showing other patterns.

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

1985, Kuitunen and Mäkinen 1993). Second, edges may be influencing indirectly the behavior of frugivores through changes in the distribution of predators (Howe 1979). Lastly, species features, such as social behavior, may generate patterns in the distribution of birds from edge to forest interior that are independent from the creation of edges (Wiens 1992).

We have evidence that the latter can explain part of our results. Two species, *Mionectes striaticollis* and *Masius chrysopterus*, contributed 42% of all captures. The capture of the same individuals (*M. striaticollis*) and of a high proportion of males (*M. chrysopterus*) at D4 (190–200 m) in one of our young edges indicated an unusual dispersion pattern of bird captures, which we associated later with the presence of display arenas or leks in the vicinity of two pairs of mist nets (Restrepo and Gómez 1998). The long-term use of the same display area by lekking species (Höglund and Alatalo 1995) may indicate that the leks of *M. striaticollis* and *M. chrysopterus* existed prior to edge creation in 1982; i.e., locations of these leks are likely to be independent of edge locations. If this is true, then the social behavior of a species can generate changes in frugivore capture rates uncoupled from changes in fruit abundance. We propose that the uncoupling of processes generating the observed patterns in fruit and frugivore abundance can affect seed dispersal in two ways: favoring the movement of weeds and second-growth species to forest interior (points of attraction) and limiting the movement of interior species to forest edge. This might explain why seeds of very sparse and sparse species were found in the forest interior, even though fruiting individuals were found more often at the forest edge (Table 8).

A high proportion of understory plants and frugivores at our study sites showed non-uniform distributions from edge to forest interior (Tables 3 and 6). Some of these species clearly decreased or increased from edge to forest interior; others, however, did not. Our results parallel those obtained by other authors (e.g., Williams-Linera 1990, Noss 1991, Didham 1997) and may also be the result of effects unrelated to edges (Wiens 1992, Matlack 1994*b*). For example, the area covered by treefall gaps may not vary from edge to forest interior (Laurance 1997), suggesting that the rates of treefall gap formation do not always increase at the forest edge (Lovejoy et al. 1986, Kapos et al. 1997). If this is true, then the presence of treefall gaps at any distance from forest edges may provide the conditions for the establishment, growth, and reproduction of plant species (Brown 1993, Denslow and Hartshorn 1994). Thus, as with lekking behavior, treefall gaps can generate patterns in the distribution of organisms from edge to forest interior that are unrelated to the creation of edges. Such patterns, however, may also result when two or more variables affected differently by the creation of edges interact (Murcia 1995).

TABLE 7. Number of *Palicourea gibbosa* fruits removed from artificial infructescences from edge to forest interior, by habitat. The number of fruits removed from ''intact forest'' infructescences differed among the four distances ($P < 0.01$), but the same was not true for ''gap'' infructescences ($P < 0.9$).

Habitat	D1	D2	D3	D4
Gap	9	11	11	6
Intact forest	7	23	2	14

TABLE 8. Plant species classified in relation to the number of individuals in fruit and bird droppings containing their seeds in ''edge'' (D1, 0–10 m) and ''interior'' (D2, D3, and D4 combined) habitats.

Habitat from which fruiting individuals of species x were recorded	Habitat from which bird droppings containing seeds of species x were retrieved Edge	Interior
Edge	4	10
Interior	5	15

Edge-induced effects

Fruit abundance was highest at D1 (0–10 m), showing a sharp decline at the other three distances (Fig. 2a; see Blanchard 1992). Either plants produced more fruits, as has been shown by studies comparing disturbed vs. undisturbed areas (Martin 1985, Blake and Hoppes 1986, Fleming 1988, Levey 1988*a*, *b*, Blake and Loiselle 1991, Lugo and Frangi 1993, Walker and Neris 1993; but see Wong 1986), or fruit removal rates were low at D1, as the bird data suggest. The presence of a high number of very sparse and sparse species at D1 (Table 4) and a general trend showing a decline in the number of fruiting individuals from edge toward forest interior (Restrepo 1995) indicate that changes in fruit abundance may be driven directly by the creation of edges. For example, leaf area index may decrease from edge to forest interior (Blanchard 1992), suggesting that irradiance levels follow the same trend. In many agricultural and natural forest ecosystems, irradiance levels and fruit abundance are positively correlated (Auchter et al. 1926, May and Antcliff 1963, Halls 1973, Jackson and Palmer 1977, Piñero and Sarukhan 1982, Clark and Clark 1987, Ågren 1988, Mathai and Sastry 1988, Levey 1990). Thus, reduced fruit abundance from edge to forest interior can be attributed to lower irradiance levels as one moves from edge to forest interior (Blanchard 1992). At La Planada, however, the evidence for such a mechanism is weak at best. For example, measurements of leaf area index at old edges showed no correlation with the total number of fruits or the number of individuals in fruit (Restrepo 1995). Also, leaf area index did not change with distance from edge to forest interior, mirroring results from two other studies in tropical areas (Laurance 1997, Turton and Freiburger 1997).

Temperature, water availability, nutrients, and pollinators also affect fruit abundance (Gentry and Emmons 1987, Heideman 1989, George et al. 1990, Stephenson 1992, Tutin and Fernández 1993, Chaikiattiyos et al. 1994, Compton et al. 1994, Seghieri et al. 1995), and these variables can change from edge to forest interior (Chen et al. 1992, Matlack 1993, Turton and Freiburger 1997). For example, our observation of understory plant and vine leaves wilting and abscising at the forest edge, but not at the forest interior, during La Planada's dry season (C. Restrepo, *personal observation*) suggests that water availability for plants may be low at the edge (Seizer 1992, Murcia 1993, Kapos et al. 1997). Also, increased litterfall during the dry season and deposition of andesitic ash at the edges may alter soil fertility from edge to forest interior (Geiger 1965, Draiijers et al. 1988, Seizer 1992; C. Restrepo, *personal observation*). In nutrient-poor soils sites like those at La Planada (De Las Salas and Ballesteros 1986), the addition of nutrients may affect fruit production at edges.

Whatever the mechanisms driving changes in fruit abundance from edge to forest interior, the consequences for seed dispersal are varied. If fruit and frugivore abundance are uncoupled, as shown in this study, then seed dispersal can affect the structure and location of edges in time in at least three ways. First, increased fruit abundance at the edge may accelerate plant senescence (e.g., Noodén 1988, Watkinson 1992) and thus change vegetation structure. Second, low capture rates of the abundant frugivores at the edge may decrease fruit removal and, thus, the rates at which interior forest plants colonize, edges ‘‘advance,’’ or forest influences the adjacent disturbed area. Third, high capture rates of frugivores adapted to disturbed conditions (extremely and very sparse species in Restrepo and Gómez 1998) at the forest edge may increase fruit removal and, thus, the rate at which weeds and second-growth species advance into forest fragments.

Fruit removal

Low capture rates of frugivores at the forest edge suggest that fruit removal may be affected negatively at these locations (Fig. 1, arrow 5). *Palicourea gibbosa*, a forest understory shrub that thrives in treefall gaps and >10-yr-old second-growth forest, is dispersed mainly by *Myadestes ralloides, Masius chrysopterus,* and *Pipreola riefferi* (C. Restrepo and N. Gómez, *unpublished data*). We found that the number of *P. gibbosa* fruits removed from artificial infructescences was greatest at D2 (30–40 m) in intact forest, even though the greatest abundance of its main dispersers occurred at D4 (190–200 m; Table 7). Our fruit removal experiment thus provides little support for the idea that fruit removal may be affected negatively at the forest edge. Experiments like the one described here, however, may fail to reveal any real pattern, because frugivorous birds, like hummingbirds, may be good at remembering the location of plants that they used, and will use in the future, but may be bad at responding to ‘‘novel’’ food sources (Feinsinger et al. 1988).

Edge age

The observed changes in fruit abundance, frugivore capture rates, and the distribution of several plant and bird species from edge to forest interior as a function of edge age suggest that edges undergo succession. Because the results for frugivore capture rates and, in particular, for *Mionectes striaticollis* and *Masius chrysopterus*, are likely to be biased by the presence of their leks in one of the new edges (Hermogenes), they will not be discussed further in relation to edge age. Initial differences between young and new edges may result from overcrowding due to the increased need for shelter after disturbance and the release of resources (Bierregaard and Lovejoy 1988). As edges undergo succession, the depletion of resources may generate conditions similar to those that existed prior to edge creation (Williams-Linera 1990, Matlack 1994*b*, Kapos et al. 1997). In tropical montane ecosystems, for example, woody (Ericaceae, Marcgraviaceae, and Melastomataceae) and nonwoody (Araceae) epiphytic shrubs and scandent bamboos (*Chusquea*) may ''seal'' forest edges (Young 1993; C. Restrepo, *personal observation*), most likely affecting irradiance levels, temperature, and humidity conditions as edges age. In one locality in the northeastern United States, Cadenasso (1998) manipulated vegetation at the forest edge to evaluate how vegetation structure affected the movement of wind-dispersed seeds into forest fragments, and found that where the vegetation was manipulated, seeds penetrated the forest and moved farther than where it was left intact. This experiment further demonstrates that ''edge effects'' (sensu Harris 1984) change over time as edge succession proceeds.

Implications for conservation

We have avoided using the term ''edge effects'' throughout this paper, because our results challenge three ideas implicit in early definitions, namely, that the effect of edges on forest fragments remains unchanged over time, that patterns in the distribution of organisms from edge to forest interior are due to the creation of edges, and that edges are detrimental to forest fragments (e.g., Harris 1984, Lovejoy et al. 1986). Depth of ''edge effects'' (e.g., Laurance et al. 1997: Fig 32.1) may change depending on several edge features (reviewed by Murcia 1995). More importantly, however, depth of ''edge effects'' may change within year and with edge age (Restrepo and Gómez 1998). It is clear from this that the temporal component or the dynamics of edges should be taken into consideration when modeling and evaluating the availabiliy of ''edge'' and ''forest interior'' habitats in fragmented landscapes and designing natural reserves (e.g., Laurance 1990, Hansen et al. 1992, Skole and Tucker 1993). Otherwise, results of such studies clearly can be misleading. Patterns in the distribution of organisms from edge to forest interior may not necessarily reflect the influence of edges. Yet, the processes generating such patterns can interact with edges to either reduce or amplify edge effects into forest fragments. Although we do not know how important these processes are in different ecosystems, we suspect that they are pervasive in tropical forests, given the diversity of animal and plant behaviors that tend to create dispersion patterns that are aggregated in space and time. It has been held that edges are detrimental to forest fragments because nest predation and parasitism, plant herbivory, and seed predation increase at these sites (e.g., Gates and Gysel 1978, Brittingham and Temple 1983, Alverson et al. 1988; but see Sork 1983, Burkey 1993, Arango-Velez and Kattan 1997 for opposite results). Variation in capture rates of frugivores between edge and forest interior, depending on month, and the retrieval of seeds of very sparse plant species both at ''edge'' and ''forest interior'' suggest that seeds from forest interior might be dispersed to edges. Perch use by birds at various distances from forest edge to the center of clearings has shown that seed deposition decreases from edges to the center of clearings (McDonnell and Stiles 1983, McClanahan and Wolfe 1987). These observations suggest that, in fragmented landscapes, edges may not be detrimental. On the contrary, they may represent the key elements for the restoration of entire landscapes, especially if we understand how edges and seed dispersal interact.

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APPENDIX

Plant species fruiting in the understory of La Planada, Colombia, at study sites (September 1992–August 1993).

Family and species†	Edge age‡	Abundance§	Bird droppings‖
Acanthaceae			
Mendoncia orbicularis Turrill	N	VS	
Actinidiaceae			
Saurauia parviflora Tr. & Pl.	O	VS	+
Amaryllidaceae			
Bomarea pardina Herbert	O	VS	
Araceae			
Anthurium andinum Engl.	O, N	S	+
Anthurium carchiense Croat	O, N	A	
Anthurium cf. *chamberlainii* Masters	N	VS	
Anthurium cf. marmoratum Sodiro	O, N	A	
Anthurium cf. *melampyi* Croat	O, N	VA	+
Anthurium cf. *pulverulentum* Sodiro	O, N	A	
Anthurium lancea Sodiro	O, N	VS	
Anthurium longicaudatum Engl.	O, N	S	+
Anthurium membranaceum Sodiro	O, N	VA	+
Anthurium mindense Sodiro	O, N	S	
Anthurium ovatifolium Engl.	O, N	S	+
Anthurium sp. CR 556, CR 583	O, N	VS	+
Anthurium sp. nov. CR 639, CR 650	N	VS	
Anthurium terracolum Croat	O, N	S	
Anthurium trinerve Mig.	O, N	VS	
Anthurium umbraculum Sodiro	O, N	VA	+
Anthurium umbricolum Engl.	O, N	A	+
Anthurium versicolor Sodiro	O, N	VA	
Monstera sp.	O, N	VS	
Philodendron oligospermum Engl.	N	VS	
Stenospermatium longipetiolatum Engl.	N	VS	+
Stenospermatium longispadix Croat	N	VS	+
Stenospermatium sparrei Croat	N	VS	
Xanthosoma subandinum Schott	N	VS	
Araliaceae			
Schefflera aff. *lasiogyne* Harms	O, N	VS	
Schefflera cf. *violacea* Cuatr.	N	VS	
Schefflera lasiogyne Harms	O, N	VS	+
Arecaceae			
Aiphanes sp.	O, N	S	+
Chamaedorea polyclada Burret	O, N	A	
Chamaedorea sp. CR 466, CR 467	O, N	S	+
Genoma weberbaueri Dammer ex Burret	O, N	VA	+
Prestoea aff. *purpurea* Engel	O, N	S	
Boraginaceae			
Tournefortia gigantifolia Killip	O, N	VS	
Bromeliaceae			
Ronnbergia aff. *deleani* L. B. Smith	O, N	VS	
Campanulaceae			
Burmeistera aff. *longifolia* Gleason	O, N	S	
Burmeistera carnosa Gleason	O, N	A	
Burmeistera sp. nov. CR 543, CR 716	O, N	A	+
Burmeistera sp. OB 8863	O, N	S	+
Centropogon aff. *solanifolius* Benth	N	VS	
Clusiaceae			
Clusia venusta Little	O	VS	
Clusia sp. CR 796	O, N	VS	+
Cyclanthaceae			
Asplundia sp. 5 CR 757	N	VS	
Asplundia sp. 1 CR553, CR 680	O, N	A	
Asplundia stenophylla (Standley) Harlling	O, N	S	
Dicranopygium sp. CR 552, CR 771	N	A	+
Sphaeradenia sp. CR 789	O, N	S	
Sphaeradenia steyermarkii (Harling)	O, N	A	+

APPENDIX. Continued.

Family and species†	Edge age‡	Abundance§	Bird droppings‖
Ericaceae			
Cavendishia engleriana Hoer.	O, N	S	+
Cavendishia tarapotana (Benth.) Meisner	O, N	VS	+
Macleania bullata Yeo	O	S	+
Macleania stricta A. A. Smith	O, N	VS	
Psammisia aff. *debilis* Sleumer sp. nov. CR 666	O, N	A	
Psammisia cf. *dolichopoda* A. A. Smith	O, N	S	
Psammisia cf. *ulbrichiana* Hoerold.	O, N	S	
Psammisia ferruginea A. A. Smith	O, N	VS	
Psammisia montana Luteyn sp. nov. CR 620	N	VS	
Psammisia sodiroi Hoerold.	O, N	S	
Sphyrospermum cordifolium Bentham	O	VS	+
Euphorbiaceae			
Hyeronima sp. CR 706	O	VS	+
Gesneriaceae			
Alloplectus bolivianus (Britton) Wiehler	N	VS	
Alloplectus schultzei Mansf.	O	VS	
Alloplectus sp. CR 475, CR 761	O, N	S	
Alloplectus sp. 1 CR 790, CR 654	O, N	VS	
Alloplectus tenuis Benth.	O, N	S	
Alloplectus tetragonus (Hanst.) Hanst.	O, N	S	
Alloplectus teuscheri (Raymond) Wiehler	O, N	VA	
Besleria solanoides H. B. K.	O, N	VA	+
Besleria sp. CR 759	O, N	S	
Columnea byrnsina (W) L. P. Kvist & L. E. Skog	O, N	S	+
Columnea cf. *picta* Karsten	N	VS	
Columnea cinerea Kvist & L. E. Skog	O, N	A	+
Columnea eburnea (W) L. P. Kvist & L. E. Skog	O, N	VS	
Columnea eubracteata Mansfield	O, N	S	+
Columnea gigantifolia Kvist & L. E. Skog	O, N	S	+
Columnea minor (Hooker) Hanstein	O, N	S	
Drymonia sp. CR 559, CR 688	O, N	S	+
Drymonia turrialvae Hanstein	N	VS	
Drymonya warscewicziana Hanstein	O, N	S	
Gasteranthus aff. *oncogastrus* (Hanstein)	N	S	
Gasteranthus aff. *wendlandianus* (Hanstein) Wiehler	O, N	S	
Gasteranthus oncogastrus (Hanstein) Wiehler	N	S	
Kohleria villosa (Fritsch) Weihler	N	VS	
Unknown CR 582, CR 647	O, N	S	
Heliconiaceae			
Heliconia impudica Abalo & Morales	N	VS	
Lauraceae			
Unknown	O	VS	
Loranthaceae			
Aetanthus sp.	O	VS	
Struthanthus aequatoris Kuijt	O	VS	
Marcgraviaceae			
Marcgravia eichleriana Wittmack	O, N	VS	+
Marcgraviastrum subssesilis (Benth) Bedell	O, N	VS	
Melastomataceae			
Blakea cf. *quadriflora* Gleason	N	VS	
Blakea cf. *stipulacea* Wurdack	O, N	S	+
Blakea punctulata (Triana) Wurdack	O, N	VS	
Clidemia sp. 1 CR 776	O, N	VA	+
Clidemia sp. 2 CR 777	O, N	S	+
Miconia aff. *neurotricha* CR 782	O, N	S	
Miconia hymenanthera Triana	N	VS	
Miconia loreyoides Triana	O, N	VS	+
Miconia pseudoradula Cogn. & Gleason ex Gleason	O, N	VS	+
Miconia smaragdina Naudin	O, N	VS	+
Miconia sp. 5 CR 533, CR 745	O, N	VS	+
Miconia theazans (Bonpland) Cogniaux	O, N	VS	+
Ossaea micrantha (Swarz) Macfadyen ex Cogniaux	O, N	VS	+
Topobea pittieri Cogniaux	O, N	S	+
Topobea sp. CR 263	O, N	VS	
Unknown CR 676, CR 415, CR 433	O, N	VS	

APPENDIX. Continued.

Family and species†	Edge age‡	Abundance§	Bird droppings‖
Meliaceae			
Ruagea glabra Triana & Planchon	O, N	VS	
Unknown CR 751	N	VS	
Monimiaceae			
Siparuna sp. CR 694	O, N	S	
Moraceae			
Ficus cf. *apollinaris* Dugand	O	VS	
Ficus garcia-barrigae Dugand	O	VS	
Myrsinaceae			
Cybianthus sprucei (Hook.f.) Agos.	O	VS	
Cybianthus simplex (Hook.f.) Agost.	O, N	S	
Myrtaceae			
Eugenia anastomosus DC	O, N	VS	
Onagraceae			
Fuchsia macrostigma Bentham	O, N	VS	
Phytolacaceae			
Phytolacca rivinoides Kunth & Bouche	N	VS	
Piperaceae			
Piper gutierrezii T. & J.	N	VS	
Rubiaceae			
Faramea elegans	O, N	VA	+
Faramea killipii Standley	O, N	S	+
Hoffmania sp. CR 682	O	VS	+
Palicourea gibbosa Dwyer	O, N	VA	+
Palicourea sp. 1 CR 461, CR 695	O, N	S	+
Palicourea sp. 2 CR 430	O, N	VS	
Palicourea sp. 4 CR 592	N	VS	
Palicourea standleyana A. M. Taylor	N	S	
Psychotria allenii Standley	N	VS	
Psychotria aubletiana Steyermark	O, N	VA	+
Psychotria braulioi A. M. Taylor sp. nov. CR 749	N	VS	
Psychotria dukei Dwyer	N	S	
Psychotria hazenii Standley	O, N	S	+
Psychotria panamensis Standley	O, N	S	+
Psychotria solitudinum Standley	O, N	S	
Solanaceae			
Cestrum sp. CR 485, CR 535, CR 779	O, N	S	
Cuatrecasia cf. *riparia* (HBK.) A. Hunz.	O, N	S	
Deprea sp. CR 488	O, N	S	
Lycianthes sp. CR 486, CR 750, CR 762	O, N	S	
Solanum caripense Dunal	N	VS	
Solanum evolvulifolium Greenm.	O, N	S	
Solanum lepidotum Dunal	O, N	S	+
Solanum cf. *deflexifolium* Bitter	O, N	VS	
Solanum nudum Dunal	N	VS	
Solanum deflexifolium Bitter	O, N	A	
Solanum longevirgatum Bitter	N	VS	
Solanum cf. plowmanii A. Hunz	O, N	VA	
Thymelaeaceae			
Schoenobiblus daphnoides Mart. & Zucc. vel sp. aff.	N	VS	
Zingiberaceae			
Renealmia aff. *concinna* Standley sp. nov. CR 638	O, N	VS	
Unknown			
CR 665	N	VS	

† Collection numbers are included for some species.

‡ Abbreviations are 0, old; N, new.

§ VS, very sparse (1–5 individuals in fruit); S, sparse (6–20 individuals in fruit); A, abundant (21–50 individuals in fruit); VA, very abundant (≥51 individuals in fruit).

‖ Presence of seeds in bird droppings is indicated by + signs.