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Research Article

Tree responses to edge effects and canopy openness in a tropical montane forest fragment in southern Costa Rica

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Abstract

Tropical forests frequently experience the opening and closing of canopy gaps as part of their natural dynamics. When fragmented, the forests are also exposed to edges, which (at least in the lowlands) cause increased mortality on the fragment's periphery and—depending on the fragment size—also on the forest interior. Here we explore if the presence of edges increase the rate at which the canopy opens in a montane forest and if and how that interaction affects the vegetation composition and structure. At Las Cruces Biological Station (SW Costa Rica), we surveyed four 150 m edge-to-interior transects to evaluate changes in vegetation structure (stem density and basal area for all plants with DBH > 5 cm) and species richness and composition as a function of both distance to the edge and canopy openness. Edge proximity did not increase canopy openness. Canopy openness, however, did affect stem density, species richness, and composition. Consequently, heterogeneity in forest structure, diversity, or composition could not be attributed to indirect edge effects. Forest edges, however, had a direct effect on species composition, but with a negligible effect on species diversity and forest structure. Overall, these results reveal that the structure, diversity, and composition of tree communities in this tropical premontane forest fragment are more strongly influenced by canopy openness than by the proximity of edges.

Key words: Fragmentation; Gap dynamics; Las Cruces Biological Station; Species composition; Species richness.

Resumen

Los bosques tropicales experimentan con frecuencia la apertura y cierre de claros como parte de su dinámica natural. Cuando se fragmentan, estos bosques también quedan expuestos a zonas de borde, las cuáles (al menos en las tierras bajas) aumentan la mortalidad de árboles en la periferia del fragmento y -dependiendo en el tamaño del mismo- a veces también en el interior del bosque. En este trabajo se investiga si la presencia de bordes, la formación natural de claros y la interacción entre ambos procesos afectan a las comunidades de árboles en un bosque tropical premontano. Para ello, muestreamos cuatro transectos de 150 m desde el borde hacia el interior del bosque en la Estación Biológica de Las Cruces (SO Costa Rica), y evaluamos cambios en la estructura de la vegetación (densidad de árboles y área basal para todos los árboles con un DAP > 5 cm), la riqueza y composición de especies en función de la distancia al borde del fragmento y la apertura del dosel. La proximidad al borde no tuvo ningún efecto sobre la apertura del dosel. La apertura del dosel, sin embargo, sí afectó a la densidad de árboles, la riqueza y la composición de especies. La variabilidad en la estructura, diversidad y composición del bosque no pudo, por tanto, ser atribuida a efectos de borde indirectos (i.e., mediados por su efecto sobre la formación de claros en la proximidad al borde). La proximidad al borde tuvo, sin embargo, un efecto directo sobre la composición de especies, si bien no afectó ni a la diversidad ni a la estructura del bosque. En conjunto, los resultados apuntan a que la estructura, la diversidad y la composición de las comunidades de árboles en este fragmento de bosque tropical premontano están más fuertemente influenciadas por la dinámica natural de formación de claros que por los efectos de borde.

Palabras clave: Fragmentación; Dinámica de claros; Estación Biológica de Las Cruces; Composición de especies; Riqueza de especies.

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Introduction

Tropical montane forests are inherently dynamic [1, 2], with as much as 1.4% of the area naturally occurring in canopy gaps [3]. Canopy gaps temporarily modify the physical conditions of the understory, increasing light and solar radiation, and allowing the proliferation of saplings and the transient establishment of pioneer plant species. Gap creation and regeneration are part of the natural dynamics of these forests, and under natural conditions there is a balance between these two processes, which ultimately sustains a high species diversity [4]. This balance, however, can be altered by human activities, and by forest fragmentation in particular.

Fragmentation can effectively reduce the remnants' size through edge effects. The vegetation at the edges may seal the fragment laterally with a thick growth of thin stems and with the lateral growth of tree crowns [5, 6]; but in the tropical lowlands, edges have also shown increased canopy tree mortality [7-12]. Edge-induced mortality of canopy trees would create additional gaps in the fragment's periphery, increasing canopy openness (a direct edge effect), and by increasing canopy openness, this could potentially and indirectly affect light penetration to the understory, which will alter the patterns of tree recruitment (indirect biological edge effects, *sensu* Murcia [13]). This will ultimately affect the vegetation's composition and structure in the fragment's periphery [6, 7, 14-20], extending to the forest interior in the case of small fragments (< 100 ha). Thus, canopy openness can be both part of a natural gap-dynamics cycle and, additionally, the direct manifestation of human edge effects. Canopy gaps created by natural disturbance disappear within years or a few decades through secondary succession. In contrast, breaches in the canopy due to forest fragmentation, tend to have a long-term nature imposing a permanent (or semi-permanent) source of disturbance that is likely to interfere with the natural rate of gap regeneration and ultimately cause a permanent (or very long-term) change in the forest structure and composition.

In tropical montane areas, rich soils and cooler temperatures encourage human settlement, and make them ideal for agriculture and cattle ranching. Thus, once the forest is cleared, it tends to stay that way for centuries. In fact, montane regions in the northern Andes have been fragmented since pre-Columbian times [21]. Yet, the effects of fragmentation on these forests are not well understood. Few studies on forest edges have been conducted in montane areas [e.g., 22-25] and, to our knowledge, none has tried to separate the effects of both forest edges and canopy openness on tree communities (but see the study by Restrepo and Vargas [26] on the effects of anthropogenic edges and treefall gaps on two understory shrubs in a

neotropical montane forest). In this study, we analyze forest structure and composition along the edge-interior gradient in a tropical montane fragment to determine whether there is an interaction between gaps and edges. Specifically, we address the following questions: (1) Do edges interact with gaps and further reduce canopy cover at the fragment's periphery? (2) What are the separate effects of distance to edge and canopy openness on structural (stem density and basal area) and biotic (species richness, species composition) response variables? (3) Do different species guilds (pioneers, shade tolerant) show differential responses to these effects? It is particularly important to address these questions in tropical montane forests, because they have been severely fragmented, and are likely to remain so. By analyzing the relative importance of edge effects and canopy openings on tree communities, this study aims to provide better insight into how to address the conservation of neotropical montane forests.



Fig. 1. Typical physiognomy of the type of abrupt forest-pasture edge in the Coto Brus landscape

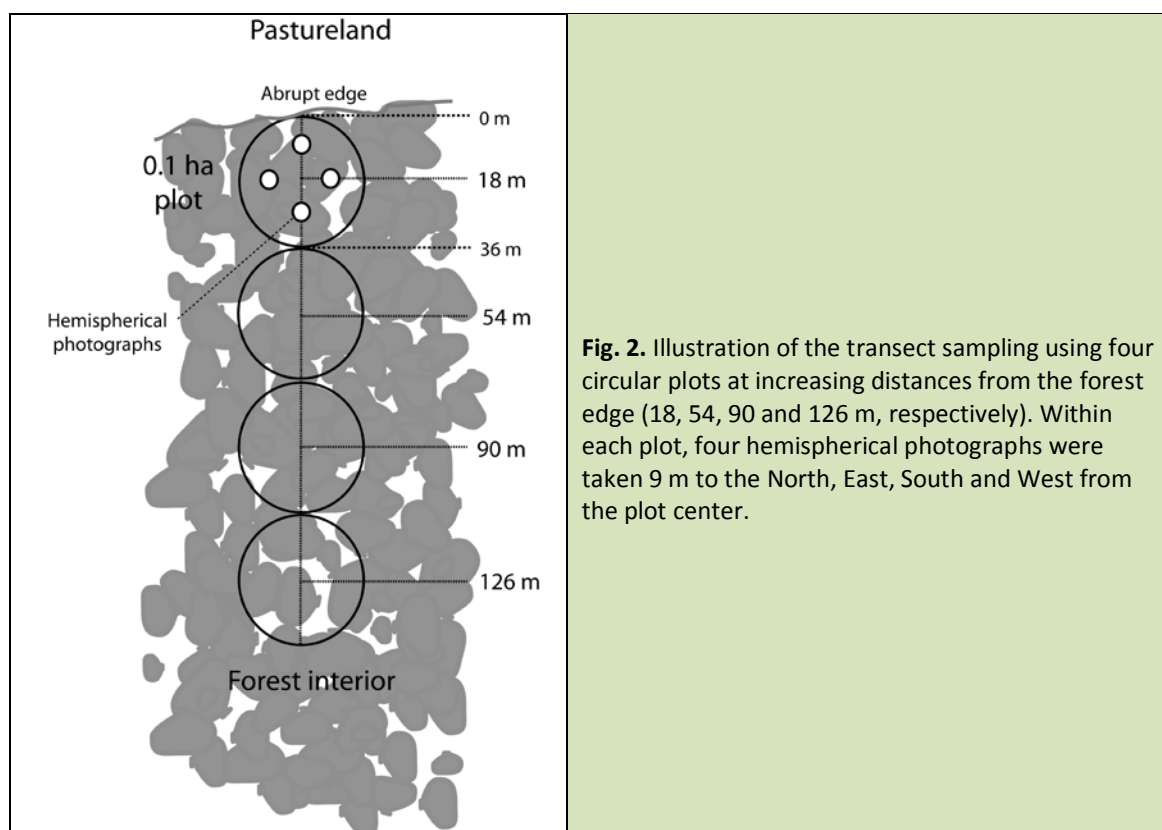
Methods

Study site

Our study was conducted at the Las Cruces Biological Station (LCBS) Forest Reserve (8°47'N, 82°57'W), in Coto Brus county, southern Costa Rica. The 266 ha Forest Reserve is the largest mid-elevation forest fragment in the region [27] and is home to more than 2,000 plant species, of which about 300 are trees. The reserve (henceforth called LCBS) covers an altitudinal gradient from 995 to 1,374 m. The region that surrounds the LCBS has a 20 °C average temperature (14-25°C) and a mean annual rainfall of 3,804 mm (2860-5617 mm) [28], and can be classified as Tropical Premontane Wet Forest in the Holdridge Life Zone System [29]. The annual rainfall regime is unimodal, with a long wet season (April to December) and a shorter dry season (January to March) (LCBS, unpublished data).

Much of the county's landscape was converted from forest to farms 40–50 years ago [27] leaving isolated fragments in a matrix of coffee farms and pastures. The forest has stayed fragmented since, with very abrupt edges maintained by fencing and an active management of the productive matrix (**Fig. 1**). At present, 73% of the 70,000 ha landscape surrounding the LCBS consists of degraded cattle pastures, small coffee plantations (0.5–5 ha) mixed with

bananas and family garden plots, and small forest fragments [30]. Although some fragments have some selective tree extraction, the LCBS one has been protected for the last 45 years from further disturbance. A more detailed description of the study area is provided elsewhere [27, 31].



Sampling

Trees were inventoried at four edge-to-interior transects, located perpendicular to the southern, eastern and western borders of the LCBS fragment. Transects were located on undisturbed mature forest, which comprises 200 ha of the fragment, and were separated 70-800 m from each other. The disposition of the transects controlled for differences in aspect and slope, and minimized lateral exposure to other edges.

Each transect started at the forest edge and entered 150 m into the forest. We considered this a reasonable distance, given that most studies on edge effects in tropical montane forests usually report a penetration no higher than 50 m into the forest [16, 25, 32]. Along each transect, four adjacent 1000 m² circular plots were set at increasing distances from the forest edge (0-36m, 36-72m, 72-108 m and 108-144 m) (**Fig. 2**). In each plot, all trees with diameter at breast height (DBH) \geq 5 cm were measured and identified. Two thirds of the trees were identified to species (68.4 %), while the rest were identified to genus (16.4 %) or family (12.4 %). A few morphospecies (2.8 %) could not be identified. To evaluate the vegetation's response to a potentially increased light availability, we classified species according to their light requirements for recruitment and germination as either pioneer or shade-tolerant species [33]. This classification was based on the main successional stage at which each species is typically found [34].

We estimated canopy openness in each plot from the average value of four hemispherical photographs. The photographs were taken 9 m to the north, east, south and west of the plot center (**Fig. 2**), with a Nikon 10.5 mm f/2.8G fish eye lens. Photographs were analyzed with Gap Light Analyzer 2.0 software [35]. We also estimated the slope in each plot using a 10 m pixel size digital elevation model.

Data analysis

Using linear regressions, we evaluated the independence of canopy openness from distance to the edge and slope (the two factors that could potentially affect this variable). In these analyses, canopy openness was treated as the dependent variable. To account for the effects of each distance to the edge and canopy openness on each of three vegetation response variables (stem density, basal area, and species richness), we used separate linear regression models for each combination of explanatory and dependent variables. Although total basal area can be the same at any distance from the forest edge, the relative proportion of small vs. large stems may change. To explore for changes in the size distribution of this variable at increasing distances from the edge, we divided the range of DBH into intervals. Based on the quantile distribution of DBH we defined the following intervals: small (5-10 cm), medium-sized (10-20 cm), and large (> 20 cm) trees. We used a two way ANOVA to specifically test the interaction between DBH range and distance to the edge (which was categorized as a factor for this specific analysis). We expected a consistent shift from smaller to larger trees among all transects with increased distance to the edge (this shift would be represented by the interaction between the two factors).

To check for compliance with the test's assumptions we examined the normal probability plot and the histogram of the residuals for each model. We included transects as a random factor within the models, to account for the spatial autocorrelation of plots clustered within fragments [36]. Distribution of basal area was highly skewed, so data were log-transformed. We repeated these analyses using only pioneer and shade-tolerant species.

Changes in species composition were investigated with the semi-parametric permutational multivariate analysis of variance (PERMANOVA) [37]. Because it is not yet possible to use linear mixed effect models for multivariate data, we included the transect as an explanatory fixed factor in the models. For this analysis, we used the Bray-Curtis dissimilarity distance and ran 10,000 permutations. PERMANOVA was also applied to data from each guild. All statistical analyses were performed using the R statistical software [38] and the 'vegan' R package [39].

Results

We measured a total of 1,306 individual trees belonging to 177 species or morphospecies, or 60% of the species represented in the LCBS fragment. Our samples did not show a significant effect of either distance to edge or slope on canopy openness (**Table 1**). Distance to edge was only significantly associated with species richness, and the direction of the effect was contrary to expectations (i.e., we observed a higher richness closer to the edge) (**Table 1**). In contrast, canopy openness had a significant and inverse effect on both stem density ($p = 0.002$, **Table 1**) and overall species richness ($p < 0.001$, **Table 1**). Neither variable affected basal area. The same analyses conducted in each guild revealed that these effects were more noticeable in the case of pioneer than in shade-tolerant species. Among pioneer species, increasing canopy openness led to decreased stem density ($p = 0.056$, results not shown) and species richness ($p = 0.082$, results not shown).

A two-way ANOVA revealed no consistent differences in the proportion of small, medium, and large trees among all transects with increased distance to the edge (interaction term between DBH range and distance to edge, $p = 0.438$). Therefore, distance to edge had no influence on the relative proportion of small vs. large stems. Similar results were found for pioneer ($p = 0.409$) and shade-tolerant species ($p = 0.403$).

When all species were considered, composition was mostly explained by the transect ($R^2 = 0.257$, $p = 0.006$), canopy openness ($R^2 = 0.147$, $p < 0.001$), and distance to edge ($R^2 = 0.099$, $p = 0.024$), in that order (**Appendix 1**). However, the relative importance of these variables varied among the two plant groups. Differences in pioneer species composition were attributable to differences among transects ($R^2 = 0.273$, $p = 0.002$, **Appendix 1**) and canopy openness ($R^2 = 0.112$, $p = 0.002$), but were not affected by distance to the edge. In contrast, differences in shade-tolerant species were explained almost equally by transect ($R^2 = 0.280$, $p = 0.017$, **Appendix 1**) and canopy openness ($R^2 = 0.211$, $p < 0.001$) and then, marginally, by distance to edge ($R^2 = 0.097$, $p = 0.056$).

Table 1. Results of linear regression models testing the effects of *distance to edge* and *slope* on *canopy openness*, and *distance to edge* and *canopy openness* on *stem density*, *basal area*, and *species richness*. Coeff. = Estimated coefficients; Df = Degrees of freedom; SS = Sum of squares; MS = Mean squares; F = F-Statistic; R^2 = Explained variance; p = p-value based on permutations. Bolded p -values are significant at 0.05.

	Coeff	Df	SS	MS	F	<i>p</i>
Canopy openness						
Distance to edge	0.002	1	0.12	0.12	0.003	0.960
Slope	-0.068	1	7.23	7.23	0.163	0.695
Residuals		10	443.25	44.32		
Stem density						
Distance to edge	-0.655	1	12910	12910	2.104	0.178
Canopy openness	-15.502	1	108280	108280	17.647	0.002
Residuals		10	61360	6136		
Basal area						
Distance to edge	0.683	1	16667	16667	0.122	0.734
Canopy openness	-14.612	1	96267	96267	0.705	0.421
Residuals		10	1365434	136543.4		
Species richness						
Distance to edge	-0.061	1	119.29	119.29	14.649	0.003
Canopy openness	-0.709	1	226.53	226.53	27.817	<0.001
Residuals		10	81.43	8.143		

Discussion

Our study shows that edges do not increase canopy openness at LCBS. Consequently, the observed changes in forest structure cannot be attributed to indirect edge effects, only to how open the canopy is, irrespective of its distance to the edge. Our results did show, however, that edges reduce species richness and affect species composition, but not through the hypothesized pathway (i.e., through the opening of gaps near the edges). We also found that pioneer and shade-tolerant species respond differently to the edge. This is, however, not an unexpected result.

Typically, forest edges are expected to increase tree mortality which, in turn, leads to reduced canopy cover at edges [11, 18, 20, 40-47]. This results in physical and biological changes along forest edges [8]. Most studies on edge effects have typically investigated changes in canopy cover, various structural variables, and diversity and species composition across the forest edge-to-interior gradient [e.g. 6, 14, 16, 17, 19]. Few studies, however, have considered the disturbance regime—which contributes to reduced canopy cover inside the forest—as a factor contributing to overall physical and biological changes that can interact with edge effects [2, 23, 48]. Our study specifically investigates the relative importance of both processes in a tropical premontane forest fragment.

Other studies that have explored edge effects on younger edges have found that the vegetation near the edge becomes denser with time [5-7], “sealing” the edge, and acting as a light and temperature buffer to the fragment. Schedlbauer et al. [6] argues that this thicker vegetation ultimately attenuates biotic edge effects in older fragments (> 20 yr old). This is likely to be the case in our study fragment, which has been protected by a fence for decades, resulting in the establishment of dense vegetation—at least as dense and with the same structural characteristics as in the forest interior—at the forest edge. Patterns observed here are likely to represent the long-term manifestation of edge effects.

Forest edges did have, however, some effects on species composition. The fact that some particular species were found predominantly near edges while others concentrated in the forest interior is probably due to direct and indirect responses to edge-related changes other than light availability. Proximity to edges can favor, for instance, seed predation for some species [25] or seed dispersal from adjacent fragments for other species [23]. These types of processes may thus be responsible for the detected differences in species composition along the forest edge-to-interior gradient. The asymmetrical response of pioneer and shade-tolerant species to edge conditions was an unexpected result, but easily explainable by our results. While shade-tolerant species may be less likely to occur near edges, pioneer species thrive whenever there is a canopy disturbance. Given that canopy openness does not significantly change with distance to edge, pioneers are as likely to occur near the edge as in the forest interior.

Implications for conservation

Although edge effects can be minimized—or even suppressed—in older fragments [17, 49, this study], the effects of fragmentation on montane forests cannot be disregarded. This study shows that, through their effect on the composition of shade-tolerant species in the fragment’s periphery, edges may be effectively reducing the habitat available for this particular plant group. In addition, there are other more pervasive effects of fragmentation on biodiversity that are related to sampling effects [8]. In montane systems, this sampling effect is

not random. Accessibility is a major factor that determines where fragments remain in montane systems, usually relegated to the steepest slopes [50]. Thus, the potential of fragmentation for acting as a selective filter is very high because it is likely to be biased against species that typically occur in flatter areas.

Finally, given the slow response of tree populations to isolation of the remnant fragments, it is likely that the full impact of these changes will not become apparent for many decades [51, 52]. This study shows the long-term response of a tropical montane forest fragment to edge effects, when the fragment remains protected from further human disturbance. Nevertheless, given the lack of information on similar fragments in the area or the general region, we cannot assert that edges are not increasing gaps in equivalent sites.

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Appendix 1. Summary of semi-parametric permutational analysis of variance (PERMANOVA) used to test the effects of *distance to edge* and *canopy openness* on the species composition of tree communities in premontane tropical forests of southern Costa Rica. *Transect* was included to account for variation attributable to site-specific characteristics. Df = Degrees of freedom; SS = Sum of squares; MS = Mean squares; F = F-Statistic; R^2 = Explained variance; p = p-value based on permutations. Bolded p-values are significant at 0.05.

	Df	SS	MS	F	R^2	p
All species						
Distance to edge	1	0.390	0.390	1.986	0.099	0.024
Canopy openness	1	0.580	0.580	2.951	0.147	< 0.001
Transect	3	1.015	0.338	1.723	0.257	0.006
Residuals	10	1.964	0.196		0.497	
Total	15	3.949				
Pioneers						
Distance to edge	1	0.277	0.277	1.238	0.068	0.191
Canopy openness	1	0.459	0.459	2.053	0.112	0.002
Transect	3	1.120	0.373	1.668	0.273	0.002
Residuals	10	2.239	0.223		0.547	
Total	15	4.096				
Shade tolerant						
Distance to edge	1	0.384	0.384	2.348	0.097	0.056
Canopy openness	1	0.834	0.834	5.134	0.211	< 0.001
Transect	3	1.110	0.370	2.264	0.280	0.017
Residuals	10	1.635	0.163		0.412	
Total	15	3.968				