

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

Authors: Cayuela, Luis, Murcia, Carolina, Hawk, Anjanette A. ,  
Fernández-Vega, Javier, and Oviedo-Brenes, Federico

Source: Tropical Conservation Science, 2(4) : 425-436

Published By: SAGE Publishing

URL: <https://doi.org/10.1177/194008290900200404>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## Research Article

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

Luis Cayuela<sup>1,\*</sup>, Carolina Murcia<sup>2</sup>, Anjanette A. Hawk<sup>3</sup>, Javier Fernández-Vega<sup>4</sup>, Federico Oviedo-Brenes<sup>5</sup>

<sup>1</sup> EcoLab, Centro Andaluz de Medio Ambiente, Universidad de Granada – Junta de Andalucía, Av. del Mediterráneo s/n, E-18006, Granada, Spain. Phone: (+0034) 985241000 (ext. 31202); Fax: (+0034) 985137246.

<sup>2</sup> Organization for Tropical Studies, Apartado 0676-2050, San José, Costa Rica

<sup>3</sup> Southwestern Indian Polytechnic Institute, SIPI P.O. Box: 10146 9169 Coors Boulevard, N.W., Albuquerque, NM 87184, USA.

<sup>4</sup> School of Forestry and Environmental Studies, Yale University, 205 Prospect Street, New Haven, CT 06511, USA.

<sup>5</sup> Las Cruces Biological Station and Wilson Botanical Garden, P.O. Box: 73-8257 San Vito, Coto Brus, Costa Rica.

\* Corresponding author e-mail: [lcayuela@ugr.es](mailto:lcayuela@ugr.es)

### 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.

Received: 6 September 2009; Accepted: 28 October 2009; Published: 7 December 2009

**Copyright:** © Luis Cayuela, Carolina Murcia, Anjanette A. Hawk, Javier Fernández-Vega, Federico Oviedo-Brenes.. This is an open access paper. We use the Creative Commons Attribution 3.0 license <http://creativecommons.org/licenses/by/3.0/> - The license permits any user to download, print out, extract, archive, and distribute the article, so long as appropriate credit is given to the authors and source of the work. The license ensures that the published article will be as widely available as possible and that the article can be included in any scientific archive. Open Access authors retain the copyrights of their papers. Open access is a property of individual works, not necessarily journals or publishers.

**Cite this paper as:** Cayuela, L., Murcia, C., Hawk, A. A., Fernández-Vega, J. and Oviedo-Brenes, F. 2009. Tree responses to edge effects and canopy openness in a tropical montane forest fragment in southern Costa Rica. *Tropical Conservation Science* Vol. 2 (4):425-436. Available online: [www.tropicalconservationscience.org](http://www.tropicalconservationscience.org)

## 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

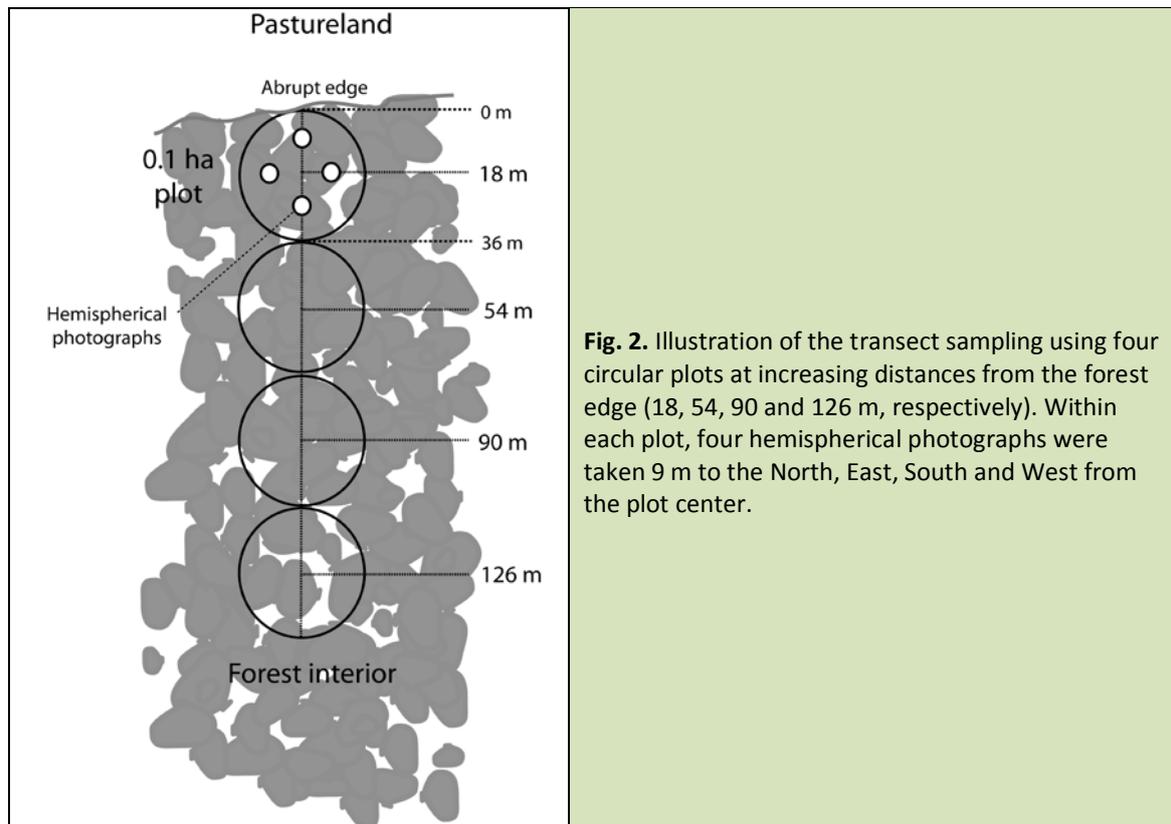
## Methods

### *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].



**Fig. 2.** Illustration of the transect sampling using four circular plots at increasing distances from the forest edge (18, 54, 90 and 126 m, respectively). Within each plot, four hemispherical photographs were taken 9 m to the North, East, South and West from the plot center.

### 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 m<sup>2</sup> 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.

	<b>Coeff</b>	<b>Df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b><i>p</i></b>
<b>Canopy openness</b>						
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		
<b>Stem density</b>						
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		
<b>Basal area</b>						
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		
<b>Species richness</b>						
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.

## Acknowledgements

We are particularly thankful to all the people who helped make our work possible and pleasant. Lucía Gálvez, José María Rey Benayas, Zak Zahawi, and two anonymous reviewers provided very useful comments on previous versions of this manuscript. Thanks also to Victor Milla for the technical support provided with the use of GIS. This study was conducted as part of the OTS Native American and Pacific Islanders Research (NAPIRE) Program. Participation of C. Murcia in this manuscript was possible thanks to an E. Bascom Scholarship from the Missouri Botanical Garden.

## References

- [1] Matelson, T. J., Nadkarni, N. M., and Solano, R. 1995. Tree damage and annual mortality in a montane forest in Monteverde, Costa Rica. *Biotropica* 27(4): 441-447.
- [2] Lima, R. A. F. De, and Moura, L. C. De. 2008. Gap disturbance regime and composition in the Atlantic montane rain forest: The influence of topography. *Plant Ecology* 197: 239-253.
- [3] Lawton, R. O., and Putz, F. E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69(3): 764-777.
- [4] Schnitzer, A. and Carson, W. P. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82(4): 913-919.
- [5] Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* 66: 185-194.
- [6] Schedlbauer, J. L., Finegan, B., and Kavanagh, K. L. 2007. Rain forest structure at forest-pasture edges in northeastern Costa Rica. *Biotropica* 39: 578-584.
- [7] Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78: 356-373.
- [8] Bierregaard, R. O. JR., Lovejoy, T. E., Kapos, V., Dos Santos, A.A., and Hutchings, R. W. 1992. The biological dynamics of tropical rainforest fragments. *BioScience* 42: 859-866.
- [9] Chen, J., Franklin, J. F., and Spies, T. A. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* 2: 387-396.
- [10] Ferreira, L. V., and Laurance, W. F. 1997. Effects of forest fragmentation on tree mortality and damage of selected trees in Central Amazonia. *Conservation Biology* 11(3): 797-801.
- [11] Laurance, W. F., Ferreira, L. V., Rankin-De-Merona, J. M., and Laurance, S.G. 1998. Rainforest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79: 2032-2040.
- [12] Harper, K. A., and MacDonald, S. E. 2002. Structure and composition of edges next to regenerating clearcuts in the mixed wood boreal forests. *Journal of Vegetation Science* 13: 535-546.

- [13] Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10(2): 58-62.
- [14] Fox, B. J., Taylor, J. E., Fox, M. D., and Williams, C. 1997. Vegetation changes across edges of rainforest remnants. *Biological Conservation* 82: 1-13.
- [15] Kapos, V., Wandelli, E., Camargo, J. L. and Gislene, G. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. In: *Tropical forest remnants: ecology, management and conservation of fragmented communities*. Laurance, W. F. and Bierregaard, R. O. Jr. (Eds), pp. 33-44. University of Chicago Press, Chicago.
- [16] Williams-Linera, G., Domínguez-Gastelú, V. and García-Zurita, M. E. 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Conservation Biology* 12: 1091-1102.
- [17] Didham, R. K., and Lawton, J. H. 1999. Edge structure determines the magnitude of change in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31: 17-30.
- [18] Harper, K. A., MacDonald, S. E., Burton, P. J., Chen, J., Brososke, K. D., Saunders, S. C., Euskirchen, E. S., Roberts, D., Jaith, M. S., and Per-Anders, E. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19: 768-782.
- [19] Baez, S., and Balslev, H. 2007. Edge effects on palm diversity in rain forest fragments in western Ecuador. *Biodiversity and Conservation* 16: 2201-2211.
- [20] Michalski, F., Nishi, I., and Peres, C. A. 2007. Disturbance-mediated drift in tree functional groups in Amazonian forest fragments. *Biotropica* 39: 691-701.
- [21] Etter, A., and Wyngaarden, W. Van. 2000. Patterns of landscape transformation in Colombia, with emphasis in the Andean region. *Ambio* 29: 432-439.
- [22] Restrepo, C., and Gómez, N. 1998. Responses of understory birds to anthropogenic edges in a neotropical montane forest. *Ecological Applications* 8: 170-183.
- [23] Restrepo, C., Gómez, N., and Heredia, S. 1999. Anthropogenic edges, treefall gaps, and fruit-frugivore interactions in a neotropical montane forest. *Ecology* 80(2): 668-685.
- [24] Tabarelli, M., Mantovani, W., and Peres, C. A. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* 91(2-3): 119-127.
- [25] López-Barrera, F., Newton, A., and Manson, R. 2005. Edge effects in a tropical montane forest mosaic: experimental tests on post-dispersal acorn removal. *Ecological Research* 20(1): 31-40.
- [26] Restrepo, C., and Vargas, A. 1999. Seeds and seedlings of two neotropical montane understory shrubs respond differently to anthropogenic edges and treefall gaps. *Oecologia* 119(3): 419-426.
- [27] Borgella, R. Jr., and Gavin, T. A. 2005. Avian community dynamics in a fragmented tropical landscape. *Ecological Applications* 15: 1062-1073.
- [28] Manger, W. F. 1992. *Colonization of the Southern Frontier of Costa Rica: A Historical-Cultural Landscape*. Master of Forest Science Thesis, Memphis State University.
- [29] Holdridge, L. R. 1967. *Lifeline ecology*. Tropical Science Center, San José, Costa Rica.
- [30] Daily, G. C., Ehrlich, P. R., and Sánchez-Azofeifa, G. A. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications* 11:1-13.
- [31] Borgella, R. Jr., Snow, A. A., and Gavin, T. A. 2001. Species richness and pollen loads of hummingbirds using forest fragments in southern Costa Rica. *Biotropica* 33(1): 90-109.

- [32] Hoopen, M. T. and Kappelle, M. 2006. Soil seed changes along a forest interior-edge-pasture gradient in a Costa Rican montane oak forest. In: *Ecology and Conservation of Neotropical Montane Oak Forests*. Ecological Studies vol. 185. M.Kappelle (Ed.), pp. 299-308. Springer-Verlag Berlin-Heidelberg.
- [33] Hill, J. L., and Curran, P. J. 2001. Species composition in fragmented forests: conservation implications of changing forest area. *Applied Geography* 21: 157–174.
- [34] Finegan, B. G. 1993. *Bases ecológicas para la producción forestal y agroforestal*. Curso de posgrado CATIE, Turrialba, Costa Rica.
- [35] Simon Fraser University and Institute of Ecosystem Studies. 1999. *Gap Data Analyzer 2.0*. Fraser University, British Columbia, and the Institute of Ecosystem Studies, New York.
- [36] Pinheiro, J. C. and Bates, D. M. 2000. *Mixed-effects models in S and S-PLUS*. Statistics and Computing, Springer, New York.
- [37] Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Australian Ecology* 26: 32-46.
- [38] R Development Core Team. 2008. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org>.
- [39] Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Stevens, M. H. H. and Wagner, H. 2008. *The vegan Package: Community Ecology Package*, version 1.13-1. URL: <http://vegan.r-forge.r-project.org/>.
- [40] Laurance, W. F., and Yensen, E. 1991. Edge effects in fragmented habitats. *Biological Conservation* 55: 77-92.
- [41] Oliveira-Filho, A. T., Mello, J. M., and Scolforo, J. R. S. 1997. Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987-1992). *Plant Ecology* 131: 45-66.
- [42] Viana, V. M., Tabanez, A. A., and Batista, J. 1997. Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. In: *Tropical forest remnants: ecology, management and conservation of fragmented communities*. Laurance, W. F. and Bierregaard, R. O. Jr. (Eds.), pp. 351-365. University of Chicago Press, Chicago.
- [43] Mesquita, R. C. G., Delamonica, P., and Laurance, W. F. 1999. Effects of matrix type on edge related tree mortality in Amazonian forest fragments. *Biological Conservation* 91: 129-134.
- [44] Laurance, W. F., Pérez-Salicrup, D. Delamonica, P., Fearnside, P. M., D'Angelo, S., Jerozolinski, A., Pohl, L., and Lovejoy, T. E. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82: 105-116.
- [45] Laurance, W. F., Nascimiento, H. E. M., Laurance, S. G., Andrade, A., Ribeiro, J. E. L. S., Giraldo, J. P., Lovejoy, T. E., Condit, R., Chave, J., Harms, K. E., and D'Angelo, S. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America* 103: 19010-19014.
- [46] Villela, D. M., Nascimiento, M. T., Aragão, L. E. O. C., and Gama, D. M. 2006. Effect of selective logging on forest structure and nutrient cycling in a seasonally dry Brazilian Atlantic forest. *Journal of Biogeography* 33: 506-516.
- [47] Faria, D., Mariano-Neto, E., Zanforlin Martini, A. M., Ortiz, J. V., Montingeli, R., Rosso, S., Paciencia, M. B., and Baumgarten, J. 2009. Forest structure in a mosaic of rainforest sites: the effect of fragmentation and recovery after clear cut. *Forest Ecology and Management* 257(11): 2226-2234.

- [48] Grau, H.R. 2002. Scale-dependent relationships between treefalls and species richness in a neotropical montane forest. *Ecology* 83(9): 2591-2601.
- [49] Gascon, C., Williamson, G. B., and Da Fonseca, G. A. B. 2000. Ecology – Receding forest edges and vanishing reserves. *Science* 288: 1356-1358.
- [50] Young, K. 1994. Roads and the environmental degradation of tropical montane forests. *Conservation Biology* 8(4): 972-976.
- [51] Hanski, I., and Ovaskainen, O. 2002. Extinction debt at extinction threshold. *Conservation Biology* 16: 666-673.
- [52] Helm, A., Hanski, I., and Pärtel, M. 2006. Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letter* 9: 72-77.

**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<sup>2</sup> = Explained variance; *p* = p-value based on permutations. Bolded p-values are significant at 0.05.

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