EFFECTS OF ENVIRONMENTAL HETEROGENEITY AND GAP DYNAMICS ON ß-DIVERSITY IN A TROPICAL WET FOREST

STASIA A. BEMBENEK, DAVID S. CANNY, JAMES W. HOURDEQUIN, AND JUSTIN Z. RUBEN

Abstract. We evaluated differences in environmental heterogeneity and gap dynamics as possible mechanisms for higher ß-diversity in primary forests as compared to secondary forests in the lowland tropics. Soils were more heterogeneous in the primary forest than in either the secondary forest or a 50 yr. old clearing. Forest gaps were larger in primary forest, which should result in more distinct vegetative communities in gaps. *Cecropia* were more clumped in primary forest, supporting the hypothesis that pioneer species are restricted to disturbed areas in primary forest, but compose much of the intact canopy in secondary forest. Recovery of ß- diversity during forest regeneration may depend on a host of factors including the re-establishment of soil heterogeneity and the development of distinct gap communities.

INTRODUCTION

Although the unparalleled diversity of tropical systems has been the object of study for more than a century, the processes that maintain this diversity remain poorly understood. As more and more tropical wet forests are degraded or destroyed, the conservation of biodiversity will require a refined understanding of the effects of anthropogenic disturbance on these processes. The effects of land use practices on alpha, or within-plot, diversity, are probably better understood than the effects on ß-, or between-plot, diversity. Bansak and Blue (1993) found decreased ß-diversity in tree communities of secondary tropical wet and dry forests compared to primary forests of each type. This decrease in ß-diversity may result from several possible mechanisms: differences in dispersal characteristics between trees that inhabit primary and secondary forest; differences in the abundance and effectiveness of dispersers between primary and secondary forest; density-dependent processes such as pathogen-induced mortality and seed predation; decreased environmental heterogeneity resulting from clearing or cultivation; and differences in disturbance frequency, size and type between primary and secondary forests. We chose to investigate the hypotheses of environmental heterogeneity and disturbance-regimes.

Environmental heterogeneity may result in part from feedbacks between soil development and vegetative communities associated with particular soil characteristics. Anthropogenic disturbance, particularly grazing and cultivation, may reverse this process and result in decreased heterogeneity of the soil environment in secondary forests. If the distribution of trees is affected by environmental gradients, clearing of forests may result in decreased ß-diversity.

In contrast to large-scale clearing, intermediate types of disturbance such as treefall gaps may actually increase diversity (Connell 1978). Species assemblages in gaps are often very different from those found below an intact canopy (Brokaw 1985, Brady and Wray 1995). Large gaps (>300 m^2) differ from small gaps in terms of abiotic conditions and biotic interactions like root competition, and may allow establishment of a different group of species (Denslow and Hartshorn 1994). Because trees of the primary forest are larger and older, gaps may be larger and more frequent, resulting in increased biotic and abiotic heterogeneity.

The impact of disturbance on ß-diversity also depends on the life history traits of the species that dominate the forest. Many of the species that prevail in gaps in the primary forest are pioneer species that are also common throughout the secondary forest. Thus, in contrast to the primary forest, species composition in gaps in the secondary forest might not differ appreciably from non-gap areas, resulting in decreased ß-diversity.

METHODS

Research was conducted at Sirena Biological Station, Corcovado National Park, Costa Rica on 2-4 February 1996. We sampled three sites: the airstrip in front of the Sirena Field Station originally cleared for pasture in 1948, secondary forest 500 m from the field station on the Rio Pavo Trail cleared for pasture and/or cultivation in 1952 and returned to forest in 1977-80; and primary forest 10 m from the intersection of the Ollas and Espevales Trails (Phillips 1989).

Soil measurements were taken every 10 m along one 70 m transect in each of the three habitats. Transects were deliberately located within areas containing clay soils to eliminate differences in variance due to different parent materials. We measured organic horizon thickness and depth to the next horizon and collected two soil samples at each location; one for analyzing soil color and one for measuring soil moisture. Soil moisture was determined by weighing samples before and after air-drying for 36 h. Soil color was determined along a gradient within habitat from light red soils to dark brown soils. Each sample was indexed from lightest to darkest and similar colors were grouped within each habitat. The steps between color were comparable between habitats. Hartley's test for homogeneity was used to compare the variance in soil characteristics between the three habitats.

Cecropia distribution patterns were measured around 10 focal trees in both forest habitats. Focal trees were haphazardly selected from within ≈ 4 ha of habitat. We positioned a randomly directed 10 x 30 m transect around each focal tree and assigned each Cecropia within the transect to a distance class of 0 - 5 m, 5 - 10 m, or 10 - 15 m from the focal tree. A Chi-square test was used to compare distribution within these distance classes between primary and secondary forests.

We assessed gap size and frequency along 200 m transects in each forest habitat. Transects were initiated at arbitrary points and extended in random directions within ≈ 4 ha of each habitat Gap size was measured by visually estimating the area of canopy opening. We used a t-test to compare gap size between primary and secondary forest.

RESULTS

Soil color and organic horizon thickness both varied most in the primary forest and least in the airstrip (Hartley's F = 13.56, P < 0.01 and Hartley's F = 6.81, P < 0.10, respectively; Table 1). There were five soil colors and three distinct soil profiles in the primary forest, compared to three colors and two profiles in the secondary forest, and two colors and two profiles in the airstrip. Depth to the second (B or B2) mineral horizon and moisture content also varied most in the primary forest, but differences between the habitats were not statistically significant (Table 1).

Table 1. Differences in variance in soil color, depth to second mineral horizon, and relative moisture content associated with anthropogenic disturbance in Corcovado National Park, Costa Rica. F_{max} values indicate differences in plot variance between sites. All df = 2.

	Air-strip	2°	1°	Fmax	P[a]
Color	0.12	0.78	1.69	13.56	< 0.01
Depth	7.61	13.35	18.34	2.41	> 0.10
OHT	0.16	0.052	0.35	6.81	< 0.10
Relative Moisture Content	0.01	0.007	0.01	2.40	> 0.10

[a]Evaluates null hypothesis that variance is the same within all three sites.

We found four gaps in the secondary forest and six gaps in the primary forest. Gaps were significantly larger in the primary forest (Mean ± SE = 287 ± 70 vs. 20 ± 10 m in diameter; t = 2.88, df = 8, P < 0.02). *Cecropia* were more clumped in the primary forest than in the secondary forest. That is, there was a steeper decrease in density with distance from the focal tree in the primary forest than in the secondary forest (Fig. 1; X^2 = 7.55, df = 2, p < 0.025).

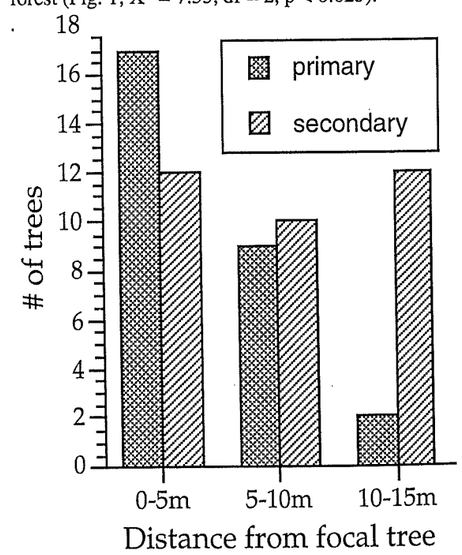

Fig. 1. Number of *Cecropia* trees as a function of distance from focal tree in primary and secondary forests.

Discussion

Soil heterogeneity: Results supported the prediction that upper horizon soils and soil profiles are more heterogeneous in primary forest than in secondary forest. The greater variation in soil color and organic layer depth in primary forest may indicate greater variation in the amount of aluminum and iron oxides and the organic content in soils. These factors may relate to overall soil nutrient status, which plays an important role in determining plant distribution patterns. Where there is more spatial variation in soil nutrient levels, there is likely to be greater opportunity for a wide range of species to establish. The similarity in variation of soil moisture between primary and secondary forests suggests that water limitation does not have an appreciable effect on ß- diversity.

Gap frequency and size: Gaps occurred in similar frequency between primary and secondary forest, but average gap size was greater in primary forest. Large gaps may create habitats where total incident light levels are ten times higher than in primary forest (Denslow et al. 1987). Bazazz et. al. (1980) found that as gap size increases, branching and advanced regeneration contribute relatively less to gap filling while immigration and seed bank regeneration contribute more. Thus large gaps create opportunities for increased species numbers that are not present in secondary forest where gaps are smaller and more likely to be filled by branching.

Cecropia distribution: *Cecropia* were more clumped in primary forest than in secondary forests, suggesting that with forest maturation Cecropia becomes increasingly limited to rare sites (gaps). Differences in dispersal seem an unlikely alternative explanation given that we observed toucans and other *Cecropia* dispersers in both secondary and primary forest (pers. obs.). Because many of the abundant trees in the secondary forest are pioneer species with life-histories similar to *Cecropia*, it appears that ß- diversity is lower in secondary forest partly because these pioneer species occur in both gaps and in the background forest.

Conclusion: ß- diversity is undoubtedly influenced by a host of factors, including soil heterogeneity, gap size, and life history characteristics of common tree species in the background forest. Even grazing for the relatively short period of 30 years at Corcovado may have been enough to homogenize soils and slow the establishment of edaphic associations in secondary forest. This suggests that the recovery of original patterns of diversity depend not only on the return of primary forest species, but also on the re-establishment of spatial processes that contribute to biotic and abiotic heterogeneity.

Future studies could examine within-forest variation in soil nutrients and correlate them to distribution patterns in the vegetative community. Research could also focus on the relative importance of seed dispersal and pollination in determining tree distribution in primary and secondary forest.

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