Forest structure and the effects of tree-falls on heterogeneity in four types of tropical forest in Costa Rica

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Abstract: Forests are dynamic systems in a perpetual state of regeneration from disturbance events. Disturbances in the form of tree-falls create texture and heterogeneity in forest structure by creating gaps. To study the relationship between forest structure and disturbance events, we sampled four types of primary forest in Costa Rica: dry deciduous forest, pre-montane cloud forest, seasonally wet forest, and tropical wet forest. Forests were generally distinguishable based on structural features, and plots within forests differed in some predictable ways depending on the presence or absence of recent tree-falls. While structural changes in forests are generally attributed to the presence of tree-fall gaps, our results suggest a reciprocal interaction between forest structure and gap formation.

Key words: charismatic megaflora, Corcovado, disturbance regime, La Selva, Monteverde, Palo Verde, principle components analysis

Introduction

Within Costa Rica there are many different described forest types including dry deciduous forest, pre-montane cloud forest, seasonally wet forest, and tropical wet forest (Hartshorn 1983). While these forests are geographically proximate, they represent very different forest types. These forests are demonstrably different in water and nutrient availability, seasonality of precipitation, elevation, temperature, species composition, herbivore communities, and soil type (Osterling et al. 1995). The forests could also differ in their disturbance regimes (Lieberman et al. 1989). We studied these four forest types to test if these differences correspond to variation in physical structure of the forests.

The tempo and scale of disturbance events may change forests in numerous ways, including species composition. Intermediate levels of disturbance are hypothesized to maximize species diversity (Connell 1978). Disturbance events such as tree-falls also add heterogeneity or texture to forest structure. We examined whether disturbance caused by tree-falls created increased forest heterogeneity via the processes of regeneration and succession. To determine the effects of tree-falls in these four forests types, we compared structural characteristics of the forests in areas with and without tree-falls. Our sampling was designed to determine what structural characteristics differ between the forests and if some variation within forests can be understood as a product of tree-fall disturbances.

Methods

We measured forest characteristics at four sites across Costa Rica: Palo Verde National Park (9 January 2004), Guanacaste; Monteverde Biological Reserve, Monteverde (15 January 2005); Corcovado National Park, Osa Peninsula (3 February 2004); and La Selva Biological Station, La Selva (13 February 2004). At each site, we walked a transect of primary forest, stopping every 50 m to measure forest characteristics in plots with 10 m radius. We noted all tree-falls along the transect and the presence of any tree-fall in plots. We examined six to ten plots at each forest site. All plots were centered at least

15 m away from existing paths and unnatural disturbances. We measured six variables: (1) From the center of each plot, we measured basal area using an English 4X forestry prism for forests with low stem density (Palo Verde and Corcovado) and 10X forestry prism for forests with high stem density (Monteverde and La Selva). (2) Using a laser hypsometer, we measured the height of the tallest tree within the 10 m radius of each plot. (3) We measured percent open canopy using a spherical densitometer, taking readings at the center of each plot, as well as one reading in each of four quadrants of the plot. (4) We estimated percent ground cover as all plant growth below chest height by visually assessing how much ground would appear covered if viewed from directly above. (5) To measure sapling density, we walked four 10 m transects in each plot, counting the number of sapling within reach of our standardized outstretched arms (~ 1 m height and 2 m width). (6) We measured the diameter at breast height (DBH) of all trees > 6 cm in diameter within the radius of the plot.

Height of tallest tree, basal area, percent ground cover, variance in sapling density, variance in percent open canopy, and variance in DBH, which were estimated from a single measurement per plot, were analyzed with an ANOVA model that included forest and tree-fall presence. Percent of open canopy, sapling density and DBH, which were estimated from variables composed of multiple measurements within each plot, were analyzed with a nested ANOVA that included forest, tree-fall presence, and plot within forest and tree-fall presence (plot was considered a random effect). We constructed a correlation matrix (based on 32 plot means) of all nine of the above variables. This correlation matrix was the basis for a principle component analysis (PCA).

RESULTS

Many variables differed among the four forests (Fig. 1), and some patterns within forests were related to tree-falls (Table 1). The incidence of tree-falls was 0.4 tree-falls / 10 m transect in Palo Verde and Monteverde, and 0.8 tree-falls / 10 m transect in Corcovado and La Selva.

Height of tallest tree

The height of the tallest tree varied among forests, with the tallest trees located in Corcovado and La Selva ($F_{3,24}$ = 15.72, P < 0.0001). Trees were taller in plots that had tree-falls ($F_{1,24}$ = 6.02, P = 0.0013). The interaction of forest and tree-fall presence was not significant ($F_{3,24}$ = 0.80, P = 0.51).

Basal area

The basal area at Monteverde was higher than all the other forests ($F_{3,24}$ = 27.66, P < 0.0001). In all forests, basal area was higher in the plots that had tree-falls ($F_{1,24}$ = 6.46, P = 0.02). The interaction of forest and tree-fall presence was not significant ($F_{3,24}$ = 2.05, P = 0.14).

Percent ground cover

The percent ground cover was highest in Monteverde and lowest in Palo Verde ($F_{3,24}$ = 31.65, P = 0.001) and did not differ among plots with and without tree-falls ($F_{1,24}$ = 0.02, P = 0.89). The interaction of forest and tree-fall presence was not significant ($F_{3,24}$ = 1.78, P = 0.18).

Sapling density

Sapling density was lowest in Palo Verde, highest in Monteverde, and intermediate in both Corcovado and La Selva ($F_{3,64}$ = 17.39, P < 0.0001). While plots within a forest differed ($F_{24,64}$ = 2.99, P = 0.0001), there was no pattern with respect to tree-falls ($F_{1,64}$ = 0.17, P = 0.68). There was also no interaction between forest and tree-fall presence ($F_{3,64}$ = 0.37, P = 0.77). The

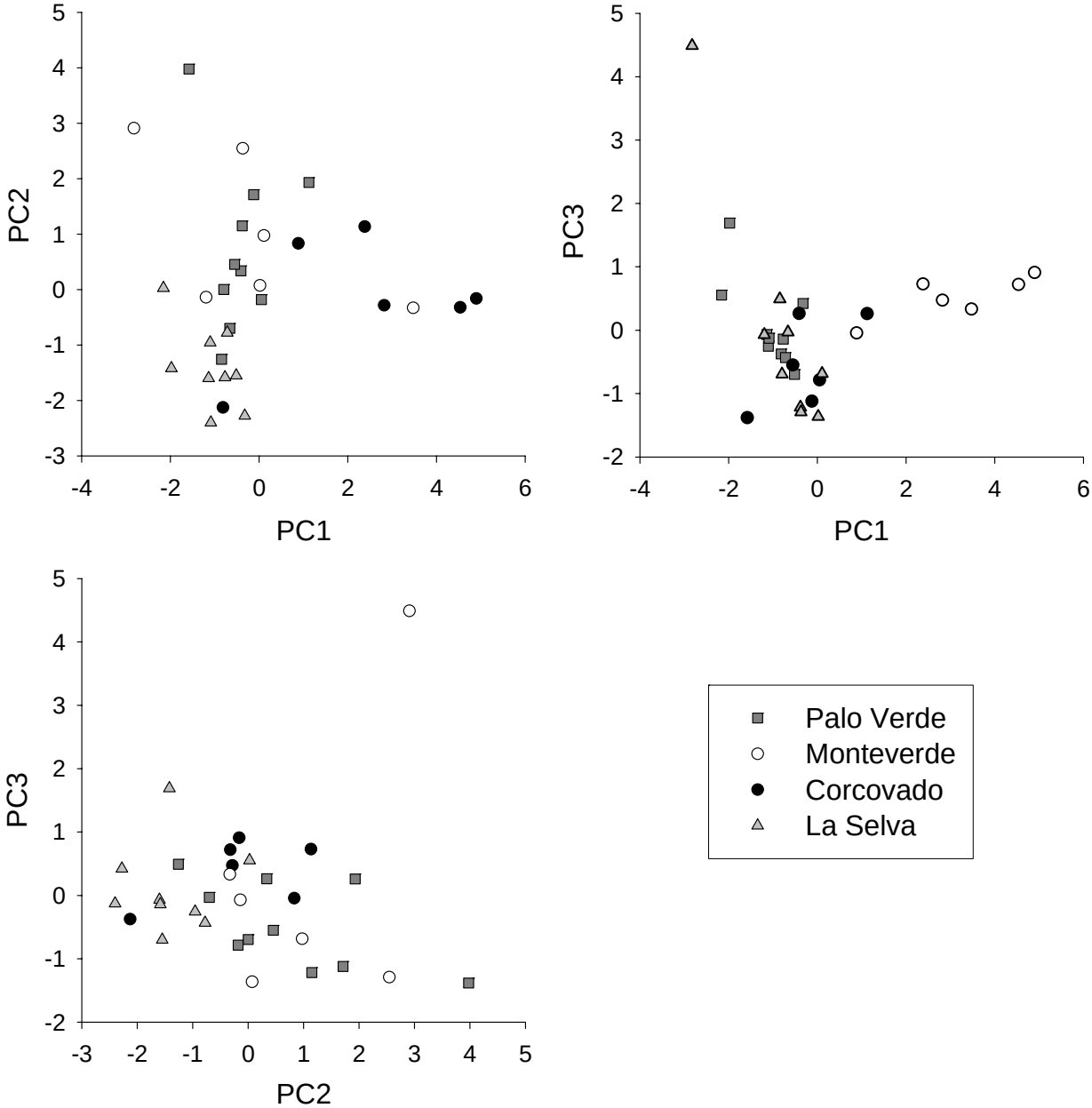

Figure 1. Replicate samples from each of four forests plotted with respect to first three axes of a principle components analysis Spatial separation of points from the same forest indicates differences in forest structure.

variance in sapling density followed the same pattern between forests ($F_{3,24}$ = 6.50, P = 0.002), with respect to tree-fall presence ($F_{1,24}$ = 0.31, P = 0.58), and with respect to the interaction of forest and tree-fall presence ($F_{3,24}$ = 0.11, P = 0.95).

DBH

The mean tree diameter did not differ among the forests ($F_{3,64}$ = 2.06, P = 0.12) or with respect to tree-fall presence ($F_{1,64}$ = 1.59, P = 0.21). However, in all of the forests except for Corcovado, the tree diameters were smaller in plots with tree-falls. There was a significant interaction of forest and tree-fall presence ($F_{3,64}$ = 1.09, P = 0.0003). The variance in tree diameter did not significantly differ among forests ($F_{3,24}$ = 1.82, P = 0.17), between plots with and without tree-falls ($F_{1,24}$ = 0.08, P = 0.78), or with the interaction of forest and tree-fall presence ($F_{3,24}$ = 1.27, P = 0.31).

Table 1. Measures of forest structure at four biogeographically distinct sites in Costa Rica. Means ± SE were calculated separately for plots with and without a still recognizable tree-fall. Final three columns are the factor loadings from a principle components analysis (see Fig. 1).

	Tree-fall	Palo Verde	Monteverde	Corcovado	La Selva	PC1 37.4%	PC2 63.7%	PC3 77.4%
Tallest tree (m)	yes	14.7	15.7 ± 0.3	28.3 ± 0.9	26.4 ± 3.3	-0.09	0.52	0.00
	no	9.5 ± 0.9	12.5 ± 1.8	22.9 ± 0.5	17.4 ± 1.7			
Basal area (ft^2 / acre)	yes	82	255.0 ± 45.0	51.3 ± 9.2	105.0 ± 10.4	0.40	0.11	0.17
	no	53.5 ± 3.6	165.0 ± 31.7	43.1 ± 10.3	92.0 ± 12.4			
% ground cover	yes	12	70 ± 20	52.5 ± 5.9	37.5 ± 7.8	0.38	0.29	0.21
	no	9.9 ± 1.4	85.0 ± 3.5	50.0 ± 15	24.4 ± 2.6			
Ave. sapling density	yes	3.8	27.3 ± 6.8	12.6 ± 2.8	8.3 ± 0.9	0.51	0.05	0.13
	no	9.1 ± 1.2	26.1 ± 4.8	11.4 ± 0.9	8.9 ± 0.8			
Var. sapling density	yes	4.9	121.8 ± 26.8	43.3 ± 32.1	14.2 ± 5.8	0.46	0.07	0.19
	no	12.1 ± 4.7	97.8 ± 48.1	24.9 ± 14.0	6.7 ± 2.4			
Ave. DBH	yes	22.2	16.6 ± 2.7	16.7 ± 1.5	21.3 ± 0.7	-0.17	0.53	-0.13
	no	14.8 ± 0.8	15.2 ± 0.5	25.1 ± 4.9	17.9 ± 1.1			
Var. DBH	yes	27.05	142.0 ± 110.1	265.1 ± 74.9	313.9 ± 78.6	-0.18	0.55	-0.09
	no	127.9 ± 30.7	140.7 ± 62.2	452.7 ± 354.6	192.5 ± 42.4			
Ave. % open canopy	yes	20.0	7.9 ± 2.7	7.1 ± 1.2	20.2 ± 9.1	-0.33	-0.16	0.55
	no	13.1 ± 1.2	6.4 ± 0.9	11.9 ± 3.1	8.9 ± 2.3			
Var. % open canopy	yes	56.1	4.7 ± 3.6	13.7 ± 5.5	242 ± 143.7	-0.22	0.14	0.74
	no	40.9 ± 14.7	10.8 ± 3.1	9.5 ± 0	22.9 ± 9.6			

Percent open canopy

The average percent open canopy did not vary among forests ($F_{3,64}$ = 1.09, P = 0.37) or between plots with and without tree ($F_{1,64}$ = 0.53, P = 0.47). The interaction of forest and tree-fall presence was not significant ($F_{3,64}$ = 1.04, P = 0.39). The variance in percent open canopy followed the same pattern between forests ($F_{3,24}$ = 0.91, P = 0.45), with respect to tree-fall presence ($F_{1,24}$ = 0.60, P = 0.45), and with respect to the interaction of forest and tree-fall presence ($F_{3,24}$ = 0.64, P = 0.60).

PCA

Using a 3-axis PCA, we explained 77.4 % of the variation in the four forests. Sapling density and variance in sapling density were strongly positively weighted into PC1. Tree diameter and variance in tree diameter were the largest components of PC2. Characteristics of open canopy measures accounted for the most variance in PC3 (Table 1). Using those three axes, the forests of Monteverde and Palo Verde were quite distinct from each other and from the other forests. La Selva and Corcovado are broadly overlapping (Fig 1).

DISCUSSION

Height of tallest tree

The smaller heights of the tallest trees in Monteverde and Palo Verde may be attributed to constraints imposed by altitude and moisture. The greater height of the tallest tree associated with the presence of tree falls is likely a product of older stands with taller trees being more susceptible to agents of gap formation, such as wind and epiphyte loads.

Basal area

The higher basal area at Monteverde was due to high stem density, not high tree diameter, (see DBH below). Higher basal area in plots with tree-falls was likely the result of high densities of younger trees filling in gaps.

Percent ground cover

The percent ground cover, highest in Monteverde and lowest in Palo Verde, is likely affected by seasonality and nutrient availability. Surprisingly, the lack of difference between plots with and without tree falls suggests that gap formation does not facilitate the growth of understory species.

Sapling density

Sapling density and variance in density, highest in Monteverde and lowest in Palo Verde, may be indicative of recruitment, and is likely the product of abiotic conditions combined with effects of herbivore communities, which differ among the four forests. Interestingly, sapling density did not differ in plots with tree falls, suggesting that recruitment does not necessarily increase in response to a gap. The lack of higher variance in plots with tree falls contradicts the hypothesis that gap formation increases heterogeneity.

DBH

Mean tree diameter was not a characteristic that differed across sites. While DBH may differ among forests of different ages, the four forests we sampled were primary growth. The average DBH may have been lower in plots with tree falls as a result of greater relative abundance of younger trees, though the number of larger trees might not necessarily be different. The reverse pattern in Corcovado remains to be explained. The lack of higher variance in plots with tree falls contradicts the hypothesis that gap formation increases heterogeneity.

Percent open canopy

The lack of difference between plots with and without tree falls suggests that gaps are

quickly filled, though the height to canopy cover may be lower where a gap was recently filled. The lack of higher variance in plots with tree falls again contradicts the hypothesis that gap formation increases heterogeneity.

PCA

Multivariate analyses seemed to reflect the separation of Monteverde and Palo Verde from La Selva and Corcovado with respect to water and nutrient availability, seasonality of precipitation, elevation, temperature, species compositions, herbivore communities, soil type, and other factors. Rates of tree-fall were also similar in La Selva and Corcovado, perhaps as a consequence or as a partial cause of similarities in forest structure.

We identified important structural differences and similarities between the four forests. The vegetation and ecosystem differences between these forests were understood prior to this study, but a systematic comparison of the forest structures was lacking. Within forests, gap formation does not appear to affect heterogeneity in forest structure as we predicted. However, tree-fall gaps have other effects on forest structure. Presumably, there is a feedback in that forest structure also affects susceptibility to gap formation.

Global climate change may affect disturbance regimes, which in turn influence tree-fall dynamics of forests. It is possible that global climate change will influence forest structure and the rate of disturbance events. It is difficult to predict how forest dynamics will be influenced, but this is an area of considerable ecological and social concern. Dealing with the effects of climate change requires deeper understanding of the nature and mechanisms by which it may alter forest structure.

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