hummingbird (*Amazilia tzacatl*) is the most common pollinator of *H. patens* (Bulova 1990) at La Selva, and its territorial behavior may produce spatial patterns in mite distribution that correspond to territory sizes. Trees that differ in hummingbird visitation rates (e.g., those that fall in the center of territories vs. between territories) could be hypothesized to differ in mite abundance. Alternatively, variation in mite abundance among clumps of trees could be due to differences in flowering patterns that influence the resource base for mites.

The high variation in mite populations between inflorescences could result from either frequent or infrequent movement within a tree. If mites are able to travel within trees, they may aggregate in areas of high resource density and leave an inflorescence when its resources decline. If mites do not travel between inflorescences without hummingbirds, inflorescence differences (e.g. visitation rates, age, or resource quantity) could affect the mite populations within them. Initial colonization of inflorescences could be affected by hummingbird preference for certain flowers. For example, hummingbirds may preferentially visit certain tree heights; Gabel et al. (1996 - 97) found mites to be more abundant near the top of trees. Aggregations of inflorescences and nectar differences between flowers may also influence hummingbird visitation patterns, with consequences for mite populations.

Contrary to our expectation that older inflorescences would accumulate larger mite populations, mite abundance was independent of inflorescence. Homogeneity between young and old inflorescences is best explained by frequent emigration and immigration of mites between inflorescences within a tree. A tendency for population accumulation in older inflorescences could also be offset by higher emigration or lower immigration on hummingbirds.

According to Colwell (1995) mites travel daily to new flowers within an inflorescence. This high mobility within inflorescences is reflected by our results, since mite population varied little at this level.

The attributes of this system that seem to affect the distribution of mites may similarly affect other systems of hummingbird mites. Mite demographics on the scale of trees or tree clumps seem to vary according to hummingbird behaviors such as territoriality, flower preferences, and specialization on certain plant species. If host trees allocate resources unequally between inflorescences, or have aggregated inflorescences, there could be consequences for mite distribution patterns that depend on the mobility of mites and how they respond to small-scale differences in habitat. Understanding these dynamic factors could allow reasonable predictions of mite demographic patterns in this and other systems.

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Variation in forest structure across four Costa Rican forest types

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Abstract: Tropical forests are known for their high rainfall, but the amount and timing of rainfall can vary greatly among regions. Changes in precipitation patterns could dramatically affect forest structure, which includes canopy and understory height, basal area and densities of juvenile, suppressed and adult trees. We hypothesized that basal area (product of stem size and stem number) would be less variable across sites than either stem size or stem number. We also predicted that understory trees and saplings would vary in abundance across forest types. Measurements of forest structure at four forest sites in Costa Rica showed that the driest forest tended to have the tallest trees and fewest saplings, and that the wettest forest had the shortest and stoutest trees. The physical structure of forests was surprisingly similar across regions, even though species composition, productivity and many other attributes vary markedly among the same forests.

Key Words: canopy, basal area, sapling, suppressed

Introduction

Tropical forests are known to be highly variable in species composition across gradients of rainfall, soil quality and climate. However, changes in species composition do not necessarily produce changes in the physical structure of forests, and there are relatively few studies that have compared Neotropical forest structure across regions (Clark and Clark 2000). In this study, we evaluated which measures of forest structure were most variable among forests within different regions of Costa Rica. We hypothesized that basal area, as the product of both tree size and density, would be less variable among sites than either tree height or tree density. We further hypothesized, following Gentry (1988), that understory diversity would increase along a moisture gradient, and that the density of understory saplings and small trees would be highly variable among sites. These hypotheses were tested by examining the forest structure of five forest types in Costa Rica that differ markedly in species composition: deciduous dry forest (Palo Verde), evergreen dry forest (Palo Verde), montane cloud forest (Monteverde), seasonal lowland rainforest (La Selva) and aseasonal lowland rainforest (Corcovado).

Methods

At each of the five sites, we laid out two parallel transects in the direction of a randomly chosen compass bearing, starting at a haphazard point along a chosen trail. Trails used were the Guayacan trail (Palo Verde), El Portrero (Monteverde), Espavales trail (Corcovado) and Camino Circular Cercano (La Selva). Censuses were taken at 8 plots, 4 along each transect (at Palo Verde, 4 were in dry forest and four were in evergreen forest). Each 10 x 10 m plot was spaced ~10 m apart. Areas near light gaps larger than 100 m^2 in size were avoided by pacing 10 m beyond the gap. When a transect entered unsuitable habitat (e.g., a deep ravine, very large light gap or secondary forest), a parallel transect was laid out 25 m from the original one.

Within each plot, we recorded the mean basal area, number of saplings, number of suppressed trees, number of canopy trees and the height of one suppressed and one canopy tree. Basal area was assessed using a prism (factor x 2.514 m^2/ha) in a 360° radius

1.5 m off the ground. Saplings were defined as woody stems 1 - 4 m tall and were counted in a 5 x 10 m subplot. Suppressed trees were defined as trees greater than 4 m tall with >50% of their crown shaded by other trees. Large trees with the majority of their crown unobstructed were classified as canopy trees. Multi-trunked palms and trees were counted as one tree if the trunks were within 1 m of each other, and as two trees if the trunks were >1 m. In one case, a multi-trunked fig tree, 5 m^2 in diameter, was counted as 5 distinct trees for purposes of calculating basal area. In all cases, only trees with their bases located in a plot were counted. Using an inclinometer, we measured the height of one suppressed and one canopy tree per plot (selected as those closest to one arbitrarily predetermined corner of the plot). Two of the tree height measurements (one each at Corcovado and Monteverde) were excluded due to impossible height estimates (76 and 300 m respectively).

Data were compared among sites using one-way ANOVA tests.

Results

Mean canopy height differed among forests ($F_{4,24} = 2.68$, $P = 0.06$), with the dry forest at Palo Verde tending to have taller trees than the Monteverde cloud forest (Fig. 1). The Monteverde cloud forest also had the highest basal area ($F_{4,24} = 15.03$, $P < 0.001$; Fig. 2). The height of understory trees did not differ among forests.

The average number of canopy trees per plot was consistent among forests, except for the Palo Verde wet forest, which had significantly fewer canopy trees ($F_{4,24} = 4.39$, $P = 0.01$; Fig. 3). The number of suppressed adult trees and the total number of adult trees (suppressed + canopy) did not differ among forests.

The Palo Verde dry forest tended to have fewer saplings per plot than the other forests ($F_{4,24} = 8.12$, $P = 0.07$; Fig. 4), but sapling density was consistent among the wetter forests.

Discussion

Forest structures that appeared different to our eye were remarkably similar when measured with the variables we tested. Contrary to expectations, no physical characteristic of forest structure was highly variable among five forest types. Basal area was greatest at Monteverde, but there was little variation between other sites (Fig. 2). Similarly, canopy tree density was lowest in the wet forest of Palo Verde, but other sites were similar (Fig. 3). The only measurement that suggested a gradient across forest types was mean height of canopy trees, but only Monteverde and Palo Verde were significantly different (Fig. 1). The physical structure of forests is surprisingly insensitive to regional variation in rainfall, climate and soil. However, results also indicate that forests structure cannot be adequately represented by any single measurement.

Adult tree density, suppressed tree density and height of suppressed trees apparently vary more within forests than among forests, since none of these measurements differed significantly between the sampled forests. It seems that these characteristics only change at the extremes of landscape gradients (e.g., forest ecotones) or along abiotic gradients not well represented in our study sites or by our sampling method.

Interestingly, our data did not indicate meaningful variation in biomass across sites (using coarse estimates of tree volume from measurements of height and basal area). Other studies have revealed significant variation in biomass across forest types (Clark and Clark 2000). The average tree heights and basal areas did vary, however, and these different morphologies might represent growth strategies across landscape and climate gradients. The abundance of short, stout trees in Monteverde could be explained by higher epiphyte loads, slope gradients or wind stress at that site.

The physical structure of forests does not necessarily vary among forests that differ

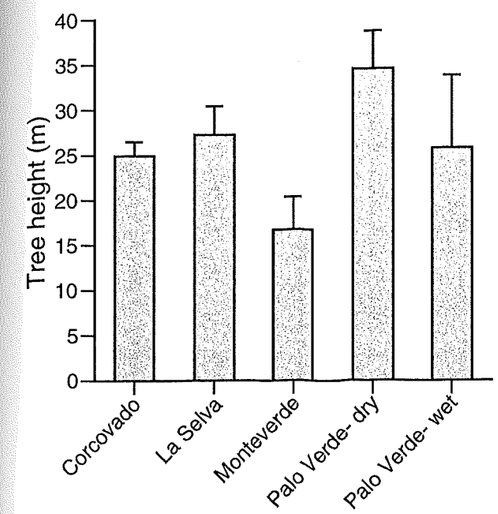

FIG. 1. Average height of canopy trees in five forest types in Costa rica. N = 4 in Palo Verde sites and n = 8 in all other sites. Error bars indicate standard error.

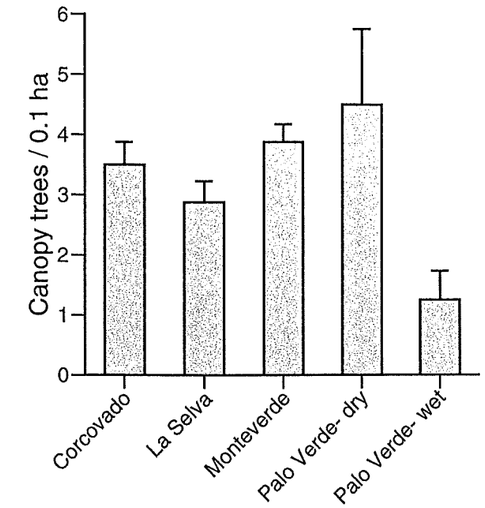

FIG. 3. Number of canopy trees per 0.1 ha in five forest types in Costa Rica. N = 4 in Palo Verde sites and n = 8 in all other sites. Error bars indicate standard error.

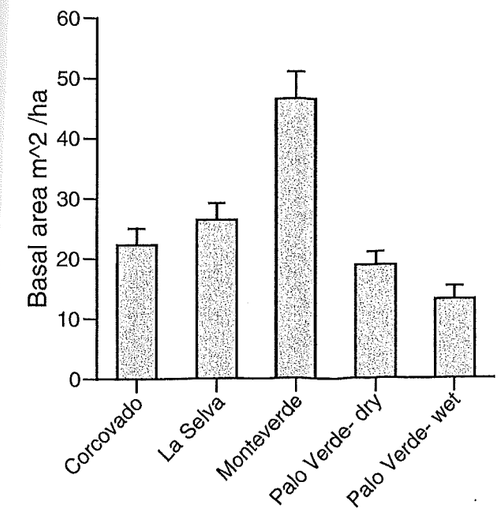

FIG. 2. Average basal area in five forest type in Costa Rica. N = 4 in Palo Verde sites and n = 8 in all other sites. Error bars are standard error.

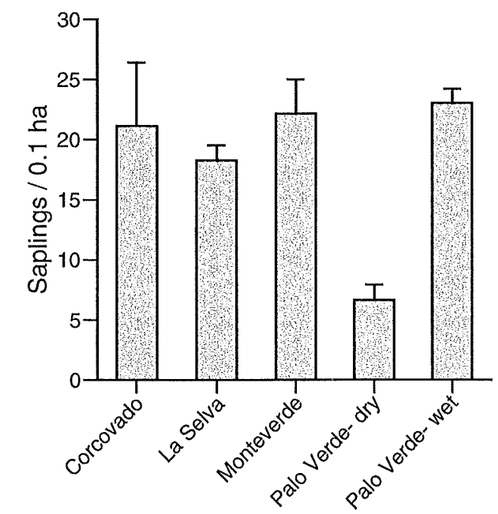

FIG. 4. Saplings per 0.1 ha in five forest types in Costa Rica. N = 4 in Palo Verde sites and n = 8 in all other sites. Error bars are standard error.

in species composition and visual appearance. Future studies might evaluate forest structure along moisture, nutrient and topographical gradients. Estimates of basal area and sapling density could be refined by measuring the basal area of individual trees and distinguishing the contribution of different life forms to density estimates (e.g., saplings vs. palms). Nonetheless, the lack of variation in forest structure among sites indicates that, while

forests differ in some respects across the landscape, there are fundamental similarities in physical structure.

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