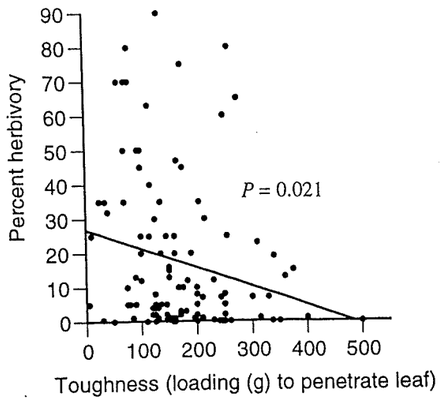

Fig. 5. Association between leaf toughness and tissue loss due to insect herbivores from the oldest leaf (n = 109) of woody juveniles in four neotropical forest sites in Costa Rica.

argument to explain the herbivory differences observed. More likely, since plants in the dry forest of Palo Verde drop their leaves annually, they have less time to increase their toughness or accumulate chemical defenses to deter herbivores.

The deciduous lifestyle of plants at Palo Verde thus appears to lead to higher herbivory levels than in wet forests. Juveniles apparently invest less in toughening their leaves, which will be dropped during the dry season, thus making the leaves more vulnerable to herbivory.

These results demonstrate how environmental conditions and seasonal patterns can influence the susceptibility of plants to herbivore attack.

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Comparison of avian diversity, abundance and composition in four Costa Rican forests

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Abstract. We compared four forests in Costa Rica to test the hypothesis that both avian diversity and abundance increase with increasing structural complexity of the environment. We found that Corcovado and La Selva, two wet lowland forests, had higher abundances, more taxonomic groups and higher indices of diversity than either Monteverde or Palo Verde. This may be attributed to the higher diversity of microhabitats and lower seasonality of lowland tropical rain forests compared to montane cloud forests and dry forests. Taxonomic composition of birds was similar between La Selva and Corcovado; these two sites also had the highest relative abundance of frugivores and omnivores. Finally, relative abundance of nectivores was highest at Monteverde. Although our sampling was not adequate to allow us to fully characterize the avian composition at each site, the results demonstrate that avian diversity and composition are affected by forest complexity.

Key Words: bird community structure, forest complexity, spatial heterogeneity

INTRODUCTION

It has been hypothesized that the high spatial heterogeneity of tropical forests provides more habitats and resources than temperate forests, enabling the tropics to support a greater biodiversity. Birds have very specific habitat requirements relating to the physical structure of the environment. Therefore, avian diversity may increase with forest structural complexity, not only between tropical and temperate zones but also within the tropics. Wet lowland forests presumably contain more microhabitats, a greater variety of food resources, and more nesting sites than tropical dry or montane forests (Stiles and Skutch 1989). Therefore, we predicted that the rainforests at Corcovado and La Selva would have higher avian diversity and abundance than the dry forest at Palo Verde, with the Monteverde cloud forest being intermediate.

METHODS

With help from our FSP colleagues, we surveyed bird diversity and abundance in January and February 1999 at four forested sites in Costa Rica: Palo Verde National Park, Monteverde Cloud Forest Preserve, Corcovado National Park (Estación Sirena), and La Selva Biological Station. At each site, we sampled along three different trails of similar elevation and took eight point count censuses 100 m apart along each trail. We waited for 1 min at each point to allow the birds to adjust to our presence, then counted all individuals observed or heard during a 10 min period. Birds were categorized into feeding guilds and taxonomic groups, and identified to species when possible. Diversity (richness and evenness) of taxonomic groups was calculated using the Shannon-Weiner diversity index.

Forest structure was characterized by forest type, canopy height, tree density, epiphyte abundance, and rainfall. These data were obtained from a previous Dartmouth FSP study (Barnhorst et al. 1995; see Appendix 1).

Site descriptions (Hartshorn 1983): Palo Verde is a tropical dry forest with a pronounced six month dry season and a high proportion of deciduous trees. Average annual rainfall is 1 - 1.5 m, and elevation is 100 - 200 m. Monteverde is a tropical montane cloud forest at mid-elevation (1500 - 1800 m), with intermediate rainfall throughout the year (2 - 3 m) and low seasonality. Corcovado is a tropical rain forest at low elevation (<100 m), with high rainfall (3 - 6 m) and a 3 month dry period. La Selva is also a lowland tropical rain forest with rainfall throughout the year and low seasonality. Annual rainfall is 3-4 m and elevation is ~70 m.

RESULTS

The two lowland rainforests, Corcovado and La Selva, had higher avian abundance, diversity, taxonomic richness and evenness than both the dry deciduous forest of Palo Verde and the montane cloud forest of Monteverde (Table 1). Palo Verde had the lowest bird abundance, while Monteverde had the fewest taxonomic groups represented in the point count samples and the lowest diversity and evenness.

Overall, La Selva and Corcovado had comparable bird abundances and taxonomic composition (Fig. 1). However, sub-oscines and columbiforms were more abundant at Corcovado than at La Selva. Also, both La Selva and Monteverde had high abundances of oscines compared to the other two sites. Trogons were recorded in the point counts only at Corcovado, while oropendolas were found only at La Selva. Toucans and parrots were most abundant in the lowland rainforest sites. Finally, hummingbirds were more abundant at Monteverde, while tinamous were recorded most frequently at Corcovado.

Table 1. Abundance, number of taxonomic groups, diversity and evenness of birds at four forest sites in Costa Rica.

Site:	Palo Verde	Monteverde	Corcovado	La Selva
Total # of birds	41	81	174	141
Total # of taxonomic groups	9	5	13	11
Diversity (H)	1.81	1.10	2.39	2.01
Evenness (J)	0.82	0.68	0.93	0.83

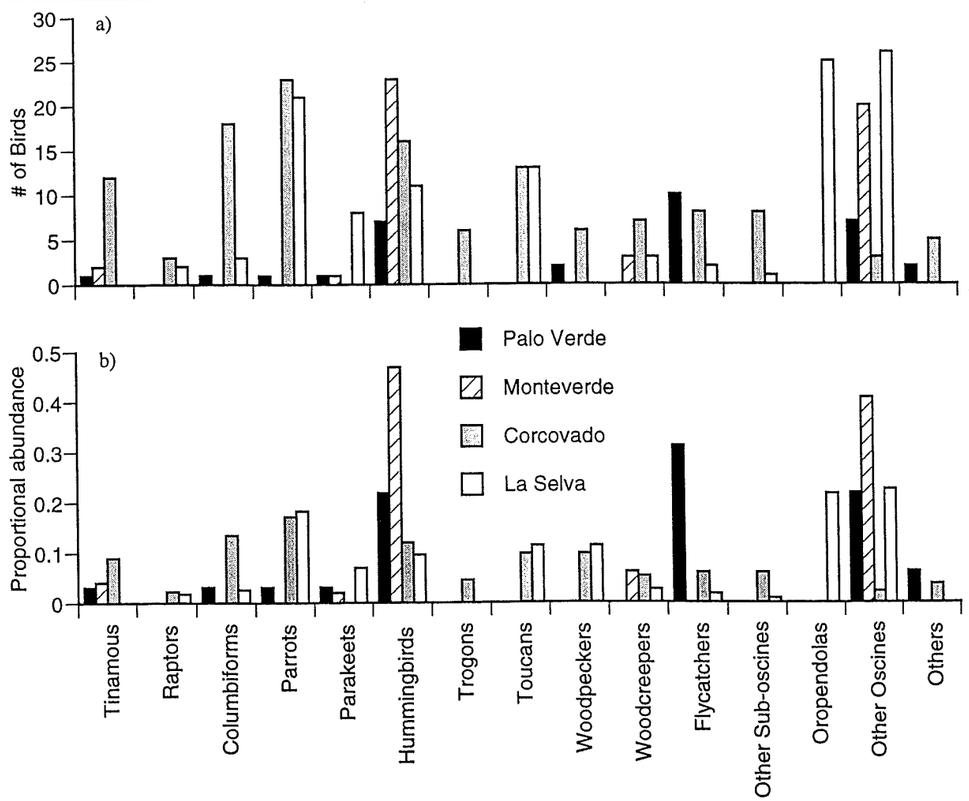

Fig. 1. Bird abundances, grouped by taxonomic affiliation, in four forest types in Costa Rica. a) Abundances (number of birds/ 24 points). b) Proportional abundance of each taxonomic group within each site. "Others" category includes one species of curassow and two of cuckoos.

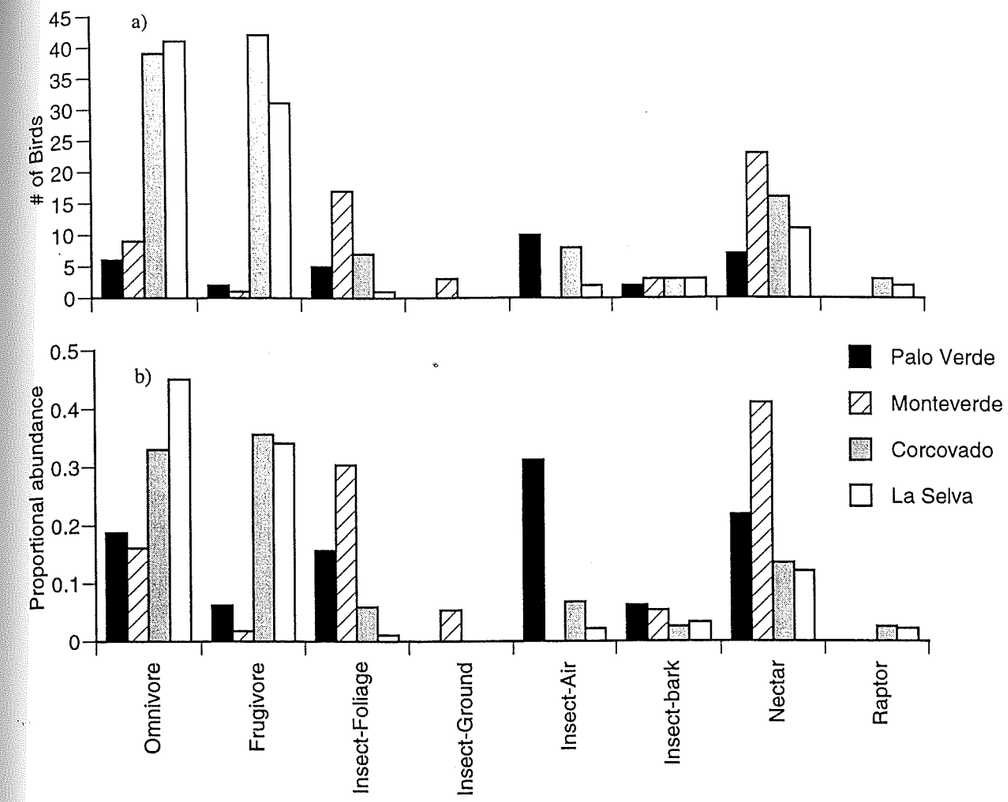

Fig. 2. Abundance of birds, grouped by feeding guilds, at four forest sites in Costa Rica. a) Abundances (number /24 points). b) proportional abundance of each feeding guild at each site.

When species were grouped by foraging guild, we found that omnivores and frugivores were most abundant in lowland rainforest, while aerially foraging insectivores (flycatchers) were most represented at Palo Verde (Fig. 2). Both nectar feeders (hummingbirds) and insectivores foraging among foliage were most abundant at Monteverde, while bark foraging insectivores were evenly distributed among three sites, but absent at Palo Verde (Fig. 2).

DISCUSSION

Lowland tropical rainforests appear to have greater structural complexity than Monteverde and Palo Verde, as evidenced by taller canopies and a greater number of epiphytes (Appendix 1). The greater structural diversity of these sites may provide more microhabitats for specialization in feeding and nesting niches, and thus may explain the higher bird diversity and abundance found at Corcovado and La Selva. Additionally, the comparable structural complexity and similar climatic conditions of the two lowland rainforests may explain the similar bird community composition at these sites.

Although it has been previously documented that among the sites sampled La Selva supports the highest diversity of birds in Costa Rica (Stiles and Skutch 1989), our results showed that Corcovado had the highest diversity. This may be due to varying sampling conditions because it was raining and overcast during our point counts at La Selva. Effects of rain may also account for the result that trogons and tinamous were not sighted at La Selva

where they are both known to exist (C. R. E. Dallison and FSP colleagues, pers. observ.).

There was a higher abundance of sub-oscines at Corcovado, perhaps because of its geographical proximity to South America, where birds of this sub-order are better represented. The reasons for the higher proportion and abundance of oscines at La Selva and Monteverde compared to the other sites are not clear. The high abundance of columbiforms at Corcovado may indicate a greater amount of available resources (seeds, fruits) there on which these birds feed.

The high relative abundance of nectar-feeders at Monteverde is probably related to the greater abundance of hummingbird-pollinated flowering plants in this forest. Also, the high abundance of insectivores feeding on foliage at Monteverde be due to high epiphytic densities at this site (Appendix 1), which provide abundant habitats for insects. Relative abundance of aerially foraging insectivores was highest at Palo Verde, where the more open forest and neighboring marsh may provide a more favorable habitat for flying insects and a greater ease of capture for insectivores. Tropical lowland forests had the highest relative abundance of frugivores, probably because consistently high rainfall throughout the year may result in high fruit densities at these sites. Finally, the higher diversity of food resources in lowland rainforests may account for the high relative abundance of omnivores found at La Selva and Corcovado.

Though the limited sampling (24 point counts on one day at each site) probably does not provide a representative picture of the actual bird compostion, we did find that bird communities are larger and more diverse in tropical lowland rainforests and that this is correlated with greater structural complexity of the forest at those sites. Moreover, certain taxonomic groups and foraging guilds appear to be restricted to particular forest types, depending on the type of habitat and resources they provide. Thus, the structural complexity of the habitats, coupled with the resources they provide, largely accounts for the differences in bird diversity and abundance among these tropical habitats.

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Appendix 1: Characterization of the forests studied († from Hartshorn 1983, * from Barnhorst et al. 1995)

Site	Forest type†	Mean Annual Rainfall (m)†	Mean Tree Density (No./100m^2)*	Mean Tree Height (m)*	Mean % Epiphyte*	Elevation (m)†
Palo Verde	Tropical dry forest	1-1.5	16	12.0	0	100-200
Monteverde	Montane cloud forest	2-3	24	15.5	50	1500-1800
Corcovado	Lowland rain forest	3-6	37	21.1	10	100
La Selva	Lowland rain forest	3-4	26	19.0	25	70