DISCUSSION

Trees in the four sites sampled showed different growth strategies. In Palo Verde, where canopy cover was lowest, trees allocated relatively more resources toward enlarging trunk diameter than toward increasing in height. At Monteverde, Corcovado, and La Selva, where sunlight is a limiting factor, there is presumably vary strong selection to attain canopy-height as quickly as possible. Alternatively, the change in the ratio of trunk diameter to tree height between Palo Verde and the other sites could be explained by damage to saplings (broken stems) due to falling debris such as tree limbs and palm fronds, but if this were true we would have expected less height per diameter at Corcovado and La Selva where the canopy is taller and falling debris is known to result in frequent stem damage (D. B. Clark, pers. comm.).

As expected, we found significant variation in leaf morphology characteristics across the four sites. The need to keep water loss to a minimum in arid environments explains the higher leaf toughness and pubescence at Palo Verde than in the other sites. Gap-colonizers had larger, but less tough leaves than understory species. This is consistent with a strategy of photosynthetic surface area at the expense of the phenolics and fibers that influences leaf toughness (Coley, 1983). The greater presence of compound leaves in Palo Verde and in gaps at Corcovado and La Selva is most likely the result of a greater proportion of legumes in this area. The success of legumes in this kind of environment could be because nitrogen fixation (typical of legumes) is energetically costly and is most likely to be cost effective in areas of high light intensity and high photosynthetic potential. Serrated leaf edges are thought to increase early season photosynthesis by the expanding leaves of deciduous trees in areas with a seasonal dry season (Baker-Brosh and Peet 1996). However, we did not find more leaves with toothed margins in Palo Verde . Drip tips are thought to remove water from the leaf surface quickly and serve to reduce nutrient leaching as well as colonization by epiphylls. Consistent with this, we found more leaves with drip tips at sites with high annual rainfall than at sites with low annual rainfall.

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A COMPARATIVE STUDY OF VARIATION AMONG FORESTS IN BIRD FORAGING BEHAVIOR

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Abstract. One hypothesis to explain higher diversity in the tropics is that tropical forests are more structurally complex, yielding more opportunities for specialization. Since birds often have specific habitat requirements, we examined avian foraging behavior across four Costa Rican sites. If the spatial complexity theory holds, birds in more diverse habitats should exhibit a wider range of foraging behaviors. We found that more foraging niches were filled in the two most complex sites than in our two low complexity sites. Using Simpson's Diversity Index as a measure of evenness for the observed behaviors, we found that with increasing bird species diversity, the evenness of heights utilized by foraging birds increased suggesting that the birds evolve to fill the available niches. Foraging maneuvers were less evenly distributed as species diversity increased, perhaps because bird species are clumped into the most successful foraging guilds.

Keywords: Corcovado, La Selva, Monteverde, Palo Verde, species diversity

INTRODUCTION

Biological diversity is much higher in the tropics than at higher latitudes. This could be because tropical habitats are more spatially heterogeneous, thus offering more opportunities for specialized foraging tactics. This may be especially true for birds because they frequently have very specific morphological and behavioral adaptations that seem linked to the physical structure of their environment.

We employed surveys of bird foraging behavior to compare patterns of resource use by bird communities within four forests in Costa Rica that differed in the richness of their bird communities (Palo Verde - tropical dry forest, Monteverde - montane wet forest, Corcovado - tropical premontane wet forest, and La Selva - tropical lowland rain forest). At all sites we quantified the foraging behavior of all individual birds that we encountered and could observe during standardized sampling regimens. Under the foraging divergence hypothesis, birds in more diverse communities should exhibit a wider range of foraging maneuvers, and distribute their foraging more evenly across substrates, and forest canopy levels. Alternatively, foraging tactics of birds in diverse communities may be more similar as a result of increased use of a few resources that are of high abundance.

METHODS

We observed birds at each of the sites between 7:00 and 10:30. Palo Verde was sampled on 14 January, Monteverde on 20 January, Corcovado on 3 February, and La Selva on 16 February, 1998. Weather was sunny on all days. We worked in 3 pairs, with one person in each pair counting and observing while the other recorded (responsibilities were rotated to minimize observer bias). Each pair hiked along a different trail or through a different section of forest : at Palo Verde, the Pizote Trail, the airstrip, the road leading from the OTS station to the ranger station, and 2 trails behind the OTS station; at Monteverde, the trail by the waterfall, the South Rio trail, and part of the Chomogo trail; at Corcovado, the Naranjo and Pavo trails; and at La Selva Primary forest, forest edge, and the successional plots.) At La Selva only 3 people were able to collect data so we worked independently instead of in pairs.

For each bird seen, we observed it until we recorded its' first foraging action or until we lost sight of the bird. Foraging maneuvers were classified as glean (while standing, bird picks stationary prey from substrate), snatch (bird flies and picks stationary prey from substrate), hover (bird flies, hovers, and picks stationary prey from substrate), hawk (bird flies and captures flying prey), or probe (bird probes into or pries up substrate). We also recorded the food type (if it could be seen), the foraging substrate, and the height above ground at which the maneuver

occurred. Foraging substrates were categorized as leaves, vines, flowers, epiphytes, branches, boles, leaf litter, and fallen dead wood, or air. Height above ground was categorized as ground (0m), shrub (0.1- 2m), sapling (2- 10 m), lower canopy (10- 20 m), or upper canopy (>20 m).

Chi-square statistics were used to test for differences in use of maneuvers , substrates, and heights across sites. To assess evenness of foraging behaviors at each site, we calculated Simpson's Diversity Indices for maneuver, substrate and height.

RESULTS

The foraging patterns of bird communities differed markedly among sites. There were significant changes in the proportion of foraging maneuvers, substrate use, and foraging heights across sites (X^2 = 90.93, 92.65, and 39.10 respectively, df = 12, all $P < 0.005$; Tables 1 - 3).

We calculated Simpson's Diversity Indices for each site as measures of evenness among the different possible categories for each of these foraging variables (5 categories of foraging maneuver, 6 categories of substrate, and 5 categories of forest height). With increasing richness of the bird community, foraging maneuvers became less evenly distributed, foraging heights became more evenly distributed, and foraging substrates were similarly distributed (Fig. 1). A similar analysis, indicated no relationships (positive or negative) between measures of foraging events and avian functional diversity (Goodwin et al., 1997).

There were 33 possible combinations of foraging maneuver and foraging substrate (Tables 4 - 7): ~50% (17 of 33) or the possible combinations were employed by birds during the study. The number of observed combinations was smallest at Palo Verde and largest at Corcovado (Table 8). The number of combinations was only 10 at Monteverde compared to 16 at Corcovado even though similar numbers of foraging bouts were observed at both sites. The number of foraging combinations was only 14 at La Selva even though the number of recorded foraging events was greater than at any other site.

DISCUSSION

As expected, foraging behavior varied across sites . Our hypothesis that higher bird diversity is associated with a broader range of foraging strategies was supported by the high number of foraging maneuver x foraging substrate combinations observed at Corcovado and La Selva, where bird species richness is highest. Corcovado and La Selva are more structurally complex then either Palo Verde or Monteverde (Broughton et al., 1994). It seems that high structural complexity allows for more possible foraging niches for birds. Additional data would allow more rigorous comparisons of foraging behaviors as classified within the maneuver x substrate matrix (Tables 4 - 8). Analysis of abundance- rank relationships (as employed for community analyses of species abundance) might provide a framework for developing statistical null models against which to compare variation among sites.

Surprisingly, the evenness of foraging maneuvers appears to decline with increasing species richness (Fig. 1). This suggests that the increase in species richness arises from more bird species performing 1 or 2 foraging maneuvers. As predicted by the foraging divergence hypothesis, bird foraging did become more equitably distributed among canopy heights in forests with the highest species richness. This must be partly a consequence of the taller forests at Corcovado and La Selva, which offer more forest habitat in the upper canopy.

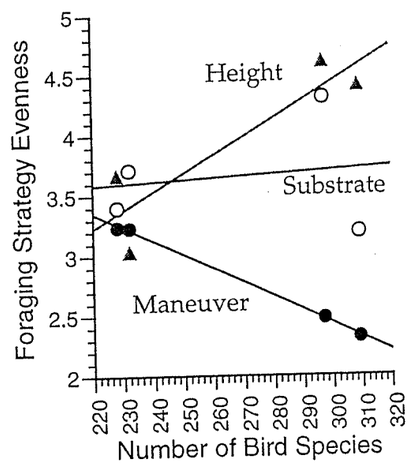

FIG. 1. Evenness of foraging strategies as a function of species richness in four forests in Costa Rica. Species richness was estimated from 20 years of accumulated Dartmouth observations as 228, 232, 309, and 297 for Palo Verde, Monteverde, Corcovado, and La Selva, respectively.

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TABLE 1. Percentages of each maneuver and total number of maneuvers seen across 4 sites.

	% of all maneuvers					Total number of maneuvers
Site	glean	snatch	hover	hawk	probe	
Palo Verde	33	0	23	38	5	39
Monteverde	44	23	23	10	2	62
Corcovado	57	4	9	3	26	68
La Selva	60	6	4	5	25	81

TABLE 2. Percentages of use of each substrate and total uses of foraging substrates across 4 sites.

	% of all substrates						Total number of substrates
Site	leaves + vines	flowers	branches	boles	litter + dead wood	air	
Palo Verde	3	5	28	0	26	38	39
Monteverde	21	18	42	8	2	10	62
Corcovado	49	22	9	9	9	3	68
La Selva	35	10	23	9	19	5	81

TABLE 3. Percentages of use of each height and total uses of foraging heights across 4 sites.

	% of all heights					Total number of heights
Site	ground	shrub	sapling	lower canopy	upper canopy	
Palo Verde	27	8	30	32	3	37
Monteverde	2	19	34	42	3	62
Corcovado	9	21	19	32	19	68
La Selva	19	25	14	27	16	81

TABLE 4. Number of foraging maneuvers by foraging substrate at Palo Verde. X's indicated impossible combinations.

Foraging substrate	Foraging maneuver				
	glean	snatch	hover	hawk	probe
leaves	1			X	
vines				X	
flowers			2	X	
epiphytes				X	
branches	2		7	X	2
boles				X	
leaf litter	10			X	
dead wood				X	
air	X	X	X	15	X

TABLE 5. Number of foraging maneuvers by foraging substrate at Monteverde. X's indicated impossible combinations.

Foraging substrate	Foraging maneuver				
	glean	snatch	hover	hawk	probe
leaves	7	6		X	
vines				X	
flowers			11	X	
epiphytes				X	
branches	16	7	3	X	
boles	4	1		X	
leaf litter				X	1
dead wood				X	
air	X	X	X	6	X

TABLE 6. Number of foraging maneuvers by foraging substrate at Corcovado. X's indicated impossible combinations.

Foraging substrate	Foraging maneuver				
	glean	snatch	hover	hawk	probe
leaves	24	2	5	X	
vines	2			X	
flowers	3		1	X	11
epiphytes				X	
branches	5			X	1
boles	1	1		X	4
leaf litter	2			X	2
dead wood	2			X	
air	X	X	X	2	X

TABLE 7. Number of foraging maneuvers by foraging substrate at La Selva. X's indicated impossible combinations.

Foraging substrate	Foraging maneuver				
	glean	snatch	hover	hawk	probe
leaves	21	2	3	X	
vines	2			X	
flowers	1			X	7
epiphytes				X	
branches	14	3		X	2
boles				X	7
leaf litter	10			X	4
dead wood	1			X	
air	X	X	X	4	X

TABLE 8. Number of foraging maneuver x foraging substrate combinations observed at each site

Site	Total number of foraging events	Observed number of maneuver x substrate combinations
Palo Verde	39	7
Monteverde	62	10
Corcovado	68	16
La Selva	81	14