TROPICAL BIRD COMMUNITY STRUCTURE IN FLOWERING AND FRUITING TREES

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Abstract: Bird species may use flowering and fruiting trees differently in time and space, as a consequence of either niche-partitioning or a dominance hierarchy. At La Selva Biological Reserve, Costa Rica, we observed birds foraging on flowering and fruiting trees to evaluate whether the spatial or temporal distribution of birds on these trees was nonrandom. We found that some species are distributed nonrandomly in space, but temporal distribution was random. The nonrandom distribution did not seem to be a result of an established dominance hierarchy; rather, structure probably results from niche partitioning.

Key Words: Quararibea cordata, Ficus pertusa, *bird community structure, niche partitioning, dominance hierarchy*

INTRODUCTION

Many tropical bird species are attracted to fruiting and flowering trees, which are ephemeral sources of concentrated resources. At La Selva Biological Reserve, Costa Rica, we observed an introduced, cauliflorous Bombacaceae tree, *Quararibea cordata* that supported an abundance and richness of colorful bird species that fed on its nectar (even though the tree was only 10 m tall). We hypothesized that with the high concentration of birds and resources in a small area, species would segregate spatially or temporally. Alternatively, species could be distributed randomly in space and time.

Nonrandom distribution of bird species in space or time could be due to either niche partitioning or a dominance hierarchy. According to the niche partitioning hypothesis, bird species will use a common resource in different ways, and a species' use will not be affected by the presence of other species. In contrast, the dominance hierarchy hypothesis suggests that dominant birds will displace subdominant species to lower quality areas in the tree. These trends may apply on the temporal scale as well. Thus, by comparing how subdominant species behave in the presence and absence of dominant species, we can distinguish whether a dominance hierarchy influences foraging locations.

METHODS

We conducted our study 12 - 14 February at the OTS biological station, La Selva, Costa Rica. We searched extensively for flowering trees, but found only two trees (*Quararibea cordata* and *Erythrina* sp.) with birds visiting flowers. We also observed a fruiting tree, *Ficus pertusa*. We visited each of the three trees eight times daily. For each observation period, we recorded the time, what species were present, and the location of individuals in the tree at that moment in time. Vertical location was categorized as low, middle, or high and horizontal location was categorized as either interior or peripheral.

We evaluated our data for evidence of structure, and for evidence of mechanisms that could produce structure. To compare the mean abundance of birds and the mean species richness between trees, we ran t-tests. We performed a chi-square test of vertical position (low, middle, or high) by bird species, and another chi-square test of horizontal position (interior or periphery) by bird species. To evaluate temporal structure, we performed a chi-square test of the relative abundance of each bird species by the time of day. We evaluated whether the dominance hierarchy hypothesis explains structural arrangement in the trees, we used a chi-squared test to evaluate whether subdominant birds distribute differently in the presence of high or low abundances of dominant birds. We used JMP 5.0.1 for all analyses.

RESULTS

In 46 observations, we recorded 448 birds of 30 species in the three trees (Appendix A). We observed 17 species at *Q. cordata*, 14 species at *F. pertusa*, and five species at *Erythrina*. There was little overlap between the species represented on the three trees; one species overlapped between *Q. cordata* and *F. pertusa* and four species overlapped between *Q. cordata* and *Erythrina*. The number of birds on *Erythrina* was too low to evaluate structure, so we limited our comparisons to *Q. cordata* and *F. pertusa*. *Q. cordata* had more birds per observation (13.2 ± 1.8, mean ± SE) than *F. pertusa* (6.0 ± 2.3; $t_{1,33}$ = 2.47, P = 0.02), and more species per observation (5.1 ± 0.46) than *F. pertusa* (2.8 ± 0.60; $t_{1,33}$ = 3.10, P = 0.004).

We found non-random vertical spatial structure of bird species on both *Q. cordata* (χ^2 =43.99, df = 10, P = <0.0001), and *F. pertusa* (χ^2 = 10.03, df = 2, P = 0.01). On *Q. cordata*, Montezuma Oropendolas and Northern Orioles were higher in the tree, Green Honeycreepers were lower in the tree, and White-necked Jacobins and Rufous-tailed Hummingbirds favored the middle relative to other birds (Table 1). In *F. pertusa*, Olive-backed Euphonia preferred the middle, while Silver-throated Tanagers were higher in the tree (Table 1). The distribution of birds did not differ between the interior and periphery in either *Q. cordata* (χ^2 = 7.81, df = 5, P = 0.16) or *F. pertusa* (χ^2 = .54, df = 1, P = 0.46). Birds were also randomly distributed in time in both *Q. cordata* (χ^2 = 10.83, df = 10, P = 0.30) and in *F. pertusa* (χ^2 = 0.50, df = 2, P = 0.78).

We observed only four agonistic interactions between species. Montezuma Oropendolas were involved in two of these interactions; the other two interactions were between hummingbird species. We tested the dominance hierarchy hypothesis using the Montezuma Oropendolas as a dominant species, and Green Honeycreepers as the subdominant species because they were the most common species observed, and were smaller than the oropendolas.

There was a marginally significant shift in spatial arrangement of Green Honeycreepers, depending on the higher or lower abundance of Montezuma Oropendolas. Montezuma Oropendolas tended to be high in the tree. When there was a higher abundance of Montezuma

Oropendola on *Q. cordata*, Green Honeycreepers were concentrated in the top and bottom of the tree; in the absence of oropendola, a greater percentage of honeycreepers were found in the middle of the tree ($\chi^2 = 5.16$, df = 2, P = 0.06).

Table 1. Observations of vertical locations of birds in flowering (*Q. cordata*) and fruiting (*F. pertusa*) trees at La Selva, Costa Rica. Expected values for each strata are given in parantheses, and are based on the overall distribution of all bird species in each tree. A chi-squared test showed that the arrangement of birds in both trees was non-random, with certain species tending to be found in certain strata.

Quararibea cordata

Bird Species	Number	Low	Middle	High	Chi-square
Green Honeycreeper	81	28 (18.1)	23 (28.0)	30 (34.9)	7.0
Montezuma Oropendola	69	7 (15.4)	18 (23.9)	44 (29.7)	12.9
White-necked Jacobin	41	12 (9.1)	20 (14.2)	9 (17.7)	7.5
Northern Oriole	28	1 (6.2)	10 (9.7)	17 (12.1)	6.4
Shining Honeycreeper	23	9 (5.1)	9 (8.0)	5 (10.0)	5.5
Rufous-tailed Hummingbird	18	1 (4.0)	10 (6.2)	7 (7.8)	4.6
Totals	*260*	*58*	*90*	*112*	*44.0* *P<0.001*

Ficus pertusa

Bird Species	Number	Low	Middle	High	Chi-square
Olive-backed Euphonia	37	7 (4.8)	23 (20.6)	7 (11.6)	3.2
Silver-throated Tanager	17	0 (2.2)	7 (9.4)	10 (5.4)	6.9
Totals	*54*	*7*	*30*	*17*	*10.0* *P=0.003*

DISCUSSION

Birds were arranged non-randomly in our two sample trees, possibly due to niche partitioning. We found no evidence of a dominance hierarchy. Green Honeycreepers did not move into the space occupied by Montezuma Oropendola when the Montezuma Oropendolas were less abundant. Furthermore, we observed few agonistic interactions between species which would support a dominance hierarchy, and none of the species we observed are described as aggressive (Stiles & Skutch 1989).

The structure we observed appears to result from niche partitioning. On *Q. cordata*, birds that flew into the tree from above the canopy (Montezuma Oropendola and Northern Oriole) tended to forage high in the tree, whereas birds that flew to the tree from below the canopy (honeycreepers and hummingbirds) tended to forage in the low or middle section.

However, if niche partitioning alone is the mechanism driving structure, we would expect honeycreepers to remain in the same place in the tree regardless of the abundance of oropendolas. Because Green Honeycreepers changed positions in the absence of Montezuma Oropendolas (in the opposite direction predicted by the dominance hierarchy hypothesis), the relationship between Montezuma Oropendolas and Green Honeycreepers is more complicated than predicted by the niche portioning hypothesis, and it may be influenced by other bird species which we could not include in our test. This result suggests that structure in trees is caused by more than niche partitioning alone. More data from more bird species is needed to rigorously evaluate the mechanisms driving structure.

It is also possible that there is structure on scales we did not measure. Birds may partition flowers based on flower position on the branch, branch size, orientation of the branch, etc. Structure on other scales could also result from a dominance hierarchy.

Additionally, *Q. cordata* is an introduced species, but birds showed highly significant structure in their spatial arrangement. Future studies could evaluate if and how structure differs between similar introduced and native species.

LITERATURE CITED

Stiles, Gary F. and Skutch, A.F. 1989. A guide to the birds of Costa Rica. Ithaca: Comstock.

Appendix 1. Bird species observed feeding on nectar or fruit on three trees, Feb 12-14, 2006, at La Selva, Costa Rica. *Quararibea cordata* and *Erythrina* spp. provided nectar for birds, and *Ficus pertusa* provided fruit. Birds are arranged taxonomically.

Common name	Taxon	Tree(s) on which birds were found
Unidentified Parakeet	Family Psittacidae	*Erythrina*
Red-footed Plumeleteer	*Chalybura urochrysia*	*Q. cordata*
White-necked Jacobin	*Florisuga mellivora*	*Q. cordata*
Rufous-tailed Hummingbird	*Amazilia tzacatl*	*Q. cordata*
Chestnut-colored Woodpecker	*Celeus castaneus*	*Q. cordata*
Black-cheeked Woodpecker	*Melanerpes pucherani*	*Q. cordata*
White-ruffed Manakin	*Corapipo leucorrhoa*	*F. pertusa*
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	*F. pertusa*
Mistletoe Tyrannulet	*Zimmerius vilissimus*	*F. pertusa*
Pale-vented Robin	*Turdus obsoletus*	*F. pertusa*
White-throated Robin	*Turdus assimilis*	*F. pertusa*
Bananaquit	*Coereba flaveola*	*Q. cordata*
Black-cowled Oriole	*Icterus dominicensis*	*Q. cordata*
Northern Oriole	*Icterus galbula galbula*	*Q. cordata*
Montezuma Oropendola	*Psarocolius montezuma*	*Q. cordata*, *Erythrina*
Chestnut-headed Oropendola	*Psarocolius wagleri*	*Q. cordata*, *Erythrina*
Scarlet-rumped Cacique	*Cacicus uropygialis*	*Q. cordata*, *Erythrina*
Olive-backed Euphonia	*Euphonia gouldi*	*F. pertusa*
Shining Honeycreeper	*Cyanerpes lucidus*	*Q. cordata*
Red-legged Honeycreeper	*Cyanerpes cyaneus*	*Q. cordata*
Emerald Tanager	*Tangara florida*	*F. pertusa*
Silver-throated Tanager	*Tangara icterocephala*	*F. pertusa*
Green Honeycreeper	*Chlorophanes spiza*	*Q. cordata*, *F. pertusa*
Bay-headed Tanager	*Tangara gyrola*	*F. pertusa*
Golden-hooded Tanager	*Tangara larvata*	*Q. cordata*, *F. pertusa*
Scarlet-rumped Tanager	*Ramphocelus passerinii*	*Q. cordata*, *F. pertusa*
Buff-throated Saltator	*Saltator maximus*	*F. pertusa*
Black-faced Grosbeak	*Caryothraustes poliogaster*	*F. pertusa*