Relationship between herbivory rates and insectivorous bird abundance in primary and secondary tropical forest

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Abstract: Secondary forests tend to have a greater abundance of highly palatable tree species than primary forests, and thus more herbivory, which could result in more insects available to foraging birds. We therefore predicted that secondary forests at Corcovado National Park, Costa Rica would have a greater amount of insect-caused herbivory, and, as a consequence, a greater abundance of insectivorous birds than would primary forest. We found that herbivory was significantly higher in secondary forest. Also, there were relatively more insectivorous birds, and fewer frugivorous ones, in secondary forest than primary forest. In general, our data suggest that there may be a relationship between levels of herbivory and insectivorous bird abundance.

Key Words: bird community structure, feeding guilds, mist-netting, trophic levels

Introduction

Examining interactions between multiple trophic levels is important in understanding the structure of communities. We examined whether differences in the conversion of primary productivity by herbivores could explain, at least in part, the differences in bird community composition between primary and secondary forest.

A past study at Corcovado National Park, Costa Rica, demonstrated that secondary forest had higher avian abundance and diversity than primary forest (Ginsburg et al. 1995). Another study (Coley 1983) showed that the early successional tree species of second-growth tropical forest often have more palatable leaves than the persistent canopy species of primary forests. Thus, we hypothesized that higher leaf palatability in secondary forests could lead to increased herbivorous insect densities, which could result in greater insectivorous bird abundance. Compared to primary forest, we predicted that 1) there would be more leaf biomass eaten by insects in secondary growth, and that 2) there would be more insectivorous birds abundance in the understory of secondary forest.

Methods

We sampled herbivory and bird abundance along Sendero Espaveles, ~1 km east of Sirena Station at Corcovado National Park. Secondary forest sites were sampled on the west side of Quebrada Dantes, with primary forest sites ~0.3 km east, near the large *Anacardia excelsium* trees.

For the herbivory estimates, we randomly laid out two 50 m transects in secondary forest, 10 m off of Sendero Espaveles, parallel to the trail. We sampled the seedlings of all woody species 0.15 – 1 m tall that crossed the transect line. For each seedling, we calculated leaf area of the youngest and oldest leaf using maximum length x maximum width. The mean of the two leaf areas was multiplied by total number of leaves on the plant to obtain total leaf area. Total herbivory per plant was calculated as total leaf area x average percent herbivory on the four youngest leaves (abscised leaves were not counted in our herbivory measurements). For primary forest, we used data collected on 4 February 1999 by the FSP herbivory comparative project, using the same methods as above.

The density of woody dicot seedlings was measured on four 25 m x 1 m transects in both the primary and secondary forest sites. Mean seedling density was multiplied by the average area of herbivory per plant to obtain the total amount of herbivory per unit area of forest.

On 5-9 February 1999, we operated four mist-nets in both the primary and secondary forest sites, sampling from 06:00-10:00 hrs each day. Nets were ~50 m apart, and were relocated ~50 m before the third sampling day to reduce the effects of net wariness. We identified each bird caught, but usually only measured the weight for the first individual of each species.

Results

The mean leaf area (m^2) lost to herbivory per m^2 forest was significantly higher in secondary forest than primary forest (Fig. 1., Kruskal-Wallis: $X^2 = 4.08$, df = 1, $P < 0.04$). All leaf damage measured appeared to be due to chewing by insects.

We caught 37 birds of 16 species in primary forest, and 40 birds of 24 species in secondary forest (Fig. 2A, Appendix A). The nine species that overlapped between primary and secondary forest were distributed throughout the five guilds (Appendix A). The Shannon diversity and evenness indices for birds caught in primary forest and secondary forest were similar (H = 2.40, J = 0.89; H = 2.85, J = 0.91, respectively).

The total mean biomass of insectivorous birds (all species combined) caught each morning was lower in the primary forest (62.9g ± 19.3 SE; n = 4 mornings) than in the secondary forest (113.3g ± 42.9 SE; n = 4 mornings) but the difference was not statistically significant (Kruskal-Wallis: $X^2 = 0.75$, df = 1, P = 0.39). However, both the relative and absolute abundance of insectivorous birds were greater in secondary forest (57.5% of captures, 23 individuals) than primary forest (27.8% of captures, 10 individuals, Fig. 2A, 2B). Consequently, the difference in feeding guild composition was highly significant between the two forest types (G-test: $X^2 = 50.0$, df = 4, $P < 0.0001$, Fig. 2A, 2B). Frugivores were most common in primary forest, while insectivores dominated the secondary forest (Fig. 2A, 2B).

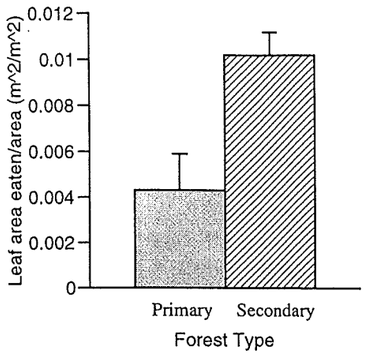

Fig. 1. Leaf area eaten from woody seedlings (0.15-1.0 m) per unit area of forest floor in primary (n=4 transects) and secondary (n=4 transects) forests at Corcovado National Park, Costa Rica (P<0.004).

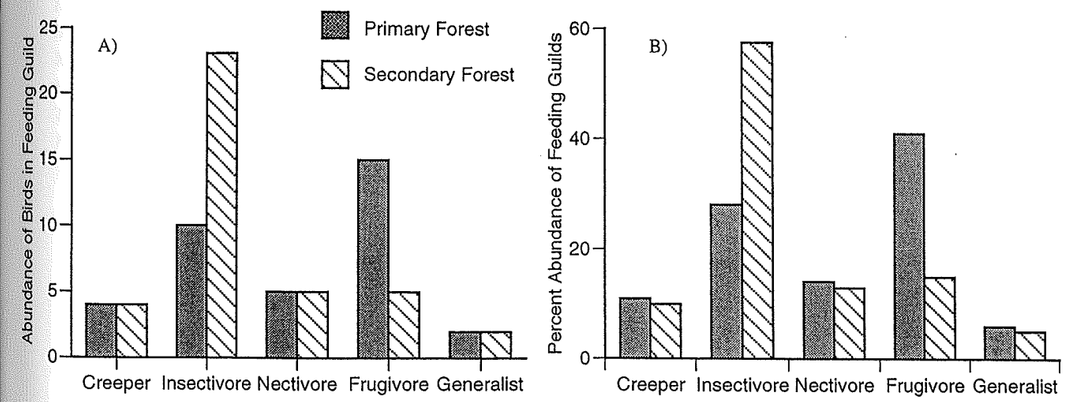

Fig. 2. A) Absolute abundance and B) percent abundance of bird feeding guilds for individuals caught in mist-nets in primary and secondary forests of Corcovado National Park, Costa Rica from 5-9 February 1999.

Discussion

The higher degree of insect herbivory in the secondary forest suggests a greater insect abundance in secondary than primary forest. Secondary forests also appeared to have a greater number and relative abundance of insectivorous birds, suggesting a positive relationship between levels of herbivory and insectivorous bird abundance.

The higher number of bird species found in secondary forests confirms the findings of Ginsberg et al. (1995) and could be due to greater patchiness in secondary forests. Greater patchiness probably leads to increased habitat and niche diversity, providing insectivorous birds with a wider variety of understory insects. This diversity of insects may allow multiple species of insectivorous birds to employ different foraging strategies, thereby allowing for specialized foraging niches and increased local species diversity. The greater proportion of frugivores in the primary forest may be explained by a greater diversity of fruit-bearing trees there as compared to secondary forest. In general, our results suggest that food resources may be an important factor in determining bird abundance and community composition.

Acknowledgments

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Appendix A – Bird species found in 2 forest types from Feb. 5-9, 1999 (06:00-10:00 hrs each day) in Corcovado National Park, Costa Rica. Guild types: c - woodcreeper, f – frugivore, g – generalist, i – insectivore, n – nectar-feeder.

Species	Common name	Guild	Primary	Secondary
Dendrocincla homochroa	Tawny-winged Woodcreeper	c	3	1
Xiphorhynchus lachrymosus	Black-striped Woodcreeper	c	0	1
Lepidocolaptes souleyetii	Streaked-headed Woodcreeper	c	0	1
Deconychura longicauda	Long-tailed Woodcreeper	c	1	0
Glyphorhynchys spirurus	Wedge-billed Woodcreeper	c	0	1
Pipra mentalis	Red-capped Manakin	f	1	1
Manacus aurantiacus	Orange-collared Manakin	f	0	1
unknown	Large Dove	f	1	0
Pipra coronata	Blue-crowned Manakin	f	9	2
Geotrygon montana	Ruddy Quail-Dove	f	0	1
Trogon rufus	Black-throated Trogon	g	0	1
Motmotus momota	Blue-crowned Motmot	g	1	0
Turdus assimilis	White-throated Robin	g	1	1
Platyrinchus coronatus	Golden-crowned Spadebill	i	3	8
Thamnophilus bridgesi	Black-hooded Antshrike	i	0	3
Hylophilus ochraceiceps	Tawny-crowned Greenlet	i	1	1
Habia atrimaxillaris	Black-cheeked Ant Tanager	i	1	0
Mionectes olivaceus	Ochre-bellied Flycatcher	i	4	1
Xenops minutus	Plain Xenops	i	0	2
Myrmeciza exsul	Chestnut-backed Antbird	i	1	1
Thyrothorus rufalbus	Riverside Wren	i	0	1
Attila spadiceus	Bright-rumped Attila	i	0	1
Lanio leucothorax	White-throated Shrike-Tanager	i	0	1
Formicarius analis	Black-faced Antthrush	i	2	0
Myiobius fasciatus	Black-tailed Flycatcher	i	0	1
Rhynochocyclus brevirostris	Eye-ringed Flatbill	i	3	0
Eucometis penicillata	Gray-headed Tanager	i	0	3
Thalurania colombica	Crowned Woodnymph	n	0	1
Phaethornis longuemareus	Long-Tailed Hermit	n	5	8
Totals			37	43