

FIG. 3. Mean (\pm S.E.) %proportion of leaf tissue lost to three herbivore groups at five sites in Costa Rica by herbivory agent.

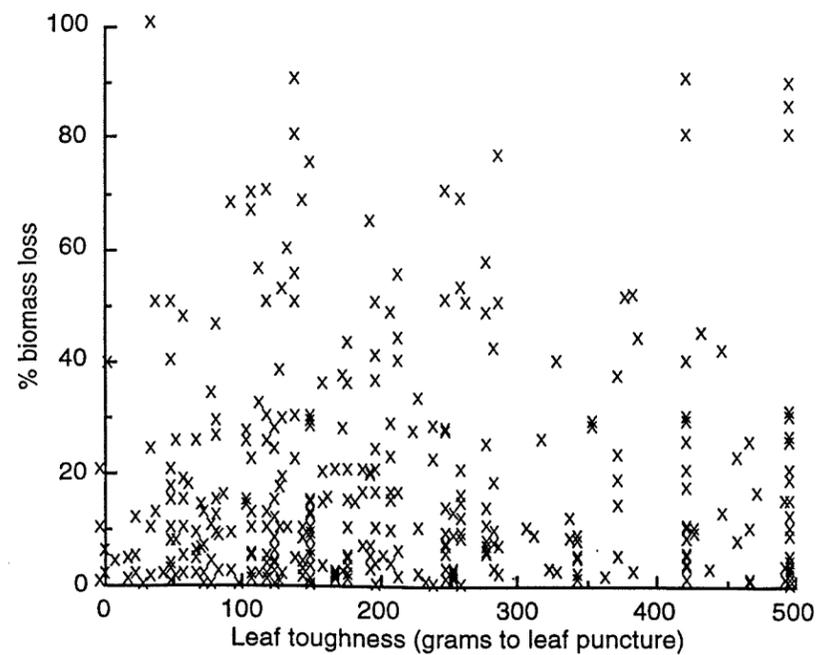


Fig. 4. Leaf tissue lost to herbivory is unrelated to the toughness of leaves at five Costa Rican forest sites. Each dot represents the mean %biomass lost and toughness of a single morphotype; n=162 morphotypes.

UNDERSTORY BIRD DISTRIBUTION AND SEED DISPERSAL IN EARLY SUCCESSIONAL AND PRIMARY FOREST SITES AT LA SELVA

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Abstract. Birds are an important seed dispersal agent for many plants. To attract foraging birds to patches of ripe seeds, plants encase seeds in nutrient rich fruit pulp. The characteristics of fruiting plants in a particular place may therefore affect the abundance and diversity of local bird populations. Since early successional sites have higher abundance and diversity of fruits than primary forests, we hypothesized that there would be a higher abundance of birds and a higher number of bird species in a successional forest. Our findings indicate trends toward increased bird abundance and richness in the successional forest. We found a greater proportion of insectivorous birds in the primary forest and a greater proportion of omnivorous birds in the early successional plants, but no differences in the relative proportions of nectivorous and frugivorous birds. However, there was a higher percentage of omnivores with seeds in their feces in the successional plot compared to the primary forest, suggesting that omnivores consume more fruit in the fruit-abundant early successional forest. The percentage of foreign seeds contained in bird fecal samples was higher in the successional forest, suggesting that seed input to early successional stands may come from surrounding habitats.

Key words: avian-assisted seed dispersal, mist netting

INTRODUCTION

Birds play an important role in tropical ecosystems as dispersal agents for plants. In wet lowland forests of Costa Rica, more than half of the trees species, especially in the understory, have fruits adapted for seed dispersal by bird (Stiles and Skutch 1989). More specifically, studies have shown that 49% of tree species of La Selva, Costa Rica, have fruits dispersed primarily or exclusively by birds (Stiles 1983). Birds therefore may play an integral role in maintaining the spatial heterogeneity and diversity of the forest by moving seeds among habitats.

Past studies in Costa Rica have shown that bird species diversity changes with food availability and habitat type (Field et al. 1993). At La Selva, Berry et al. (1994) found higher levels of bird diversity and resource availability in early successional plots than in 35-year old secondary forest. In this study, our objective was to: (1) compare the abundance and diversity of bird species between early successional plots (0-5 yr. old) and primary forest, and (2) to study the potential movement of seeds into these habitats by examining the seeds contained in the feces of frugivorous birds and comparing them to available seeds found in fruits within these habitats.

We predicted that species richness and abundance would be greater in the early successional plots than primary forest. Since early successional forest plots are more dense and diverse, consisting of both pioneer species and vegetation colonizing from surrounding

forests, we expected the habitat to be able to support a more abundant and diverse bird population. Because of higher fruit resources in the early successional forest (Berry et al. 1994), we expected there to be a greater proportion of frugivorous birds in the early successional stands and a greater proportion of insectivorous birds in the primary forest. Of the omnivorous birds that potentially eat both fruit and insects, we expected to find more seed-containing bird feces in the successional plots than in the primary forest. Since birds may be coming from other sites to feed in the early successional plots, our final prediction was that birds in the early successional plots would disperse a higher proportion of foreign seed species than birds in the primary forest.

METHODS

We conducted our study 14-17 February 1997 at the La Selva Biological Station, Costa Rica. We sampled the understory bird communities of two habitat types: early successional forest and primary forest. The early successional forest habitat was located in the experimental successional plots along the Senderos Oriental and Holdrige, an area where one plot is cleared every year and allowed to grow for five years before the next clearing. The primary forest habitat was located approximately 2 km away in undisturbed forest along the Sendero Suroeste.

We sampled the understory bird populations, using 12 m x 2.5 m mist nets in the successional plot

on 14-15 February and in the primary forest on 16-17 February. In the successional plot, seven nets were open from 07:00-11:00. In the primary forest, on 16-17 February, eight nets were open from 07:15-10:45 and 07:00-10:00, respectively. Comparisons of overall bird abundance and species richness were standardized for sampling effort.

Each captured bird was identified to species and classified into feeding guild, using information in Stiles and Skutch 1989. The following measurements were taken: weight, bill length, and wing length. We clipped a small portion of the right tail feather of each bird to enable us to recognize birds previously captured. The birds were placed in a fabric bag for 20 min. to collect fecal samples, and then released. Using a dissecting microscope, we counted the total number of seeds per seed morphotype found in each sample.

Four 100 m transects along the trail at each site were sampled for understory fruits. Additionally, during the course of the study, every fruit encountered within each habitat was collected to provide a reference collection of the understory fruits available to birds at the two sites. We compared the seeds found in the bird feces with those collected from plants within the plots to determine the number of defecated foreign seeds and the proportion of foreign seeds to native seeds within and between each forest type. We also determined the seed number per species and per omnivorous bird at each site and compared these values between the two sites.

RESULTS

We captured more birds per net hour in the early successional plot (0.63) than in the primary forest plot (0.25) (t-test, $t=2.89$, $df=2$, $P=0.10$; Table 1). We also found a trend with greater number of species per net hour in the early successional plot (0.29) than in the primary forest plot (0.15) (t-test, $t=1.73$, $df=2$, $P=0.23$; Table 1).

The percent of frugivorous and nectivorous birds did not differ substantially between early successional and primary forest plots. However, there appeared to be a lower percent insectivorous and higher percent omnivorous birds in the early successional than in the primary forest (Table 1).

We collected 17 fecal samples from the 35 birds captured in the early successional plot and four samples from the 13 birds captured in the primary forest. We found 11 different seed morphotypes in the samples from the successional plot habitat, and seven from the primary forest. Of the seed-containing fecal samples (from both frugivorous and omnivorous

birds) from the successional site, 26.7% of the seeds found were not found in that plot, while the one seed-containing fecal sample from the primary forest contained seeds of fruits found in that plot. Of the omnivorous fecal samples, seven of 11 (64%) in the early successional plot contained seeds, while zero of three (0%) omnivorous fecal samples in the primary forest plot contained seeds. In particular, fecal samples from Ochre-bellied Flycatchers caught in the primary forest contained no seeds while three of the four fecal samples taken from the same species in the successional habitat contained seeds.

DISCUSSION

Although the differences were not statistically significant, the trends suggest that there is a greater number of individual birds and a greater richness of species in the early successional habitat than in the primary forest. In fact, both the mean number of individuals and the mean number of species per net hour were twice as great in the successional habitat than in the primary forest. These differences between sites support our prediction that since successional habitats consist of a more heterogeneous canopy and understory structure and contain a greater diversity and abundance of fruit and nectar sources (Blake and Loiselle 1991), a greater diversity and abundance of birds will be able to successfully exploit early successional habitats. Although our results show strong trends, low sample sizes and high variance may have precluded our ability to detect statistically significant differences.

The greater percentage of omnivores in the early successional forest may account for the lack of the predicted difference in the percentage of frugivorous birds between the two habitats. In addition to frugivores, omnivores may also act as seed dispersers. The presence of seeds in feces of Ochre-bellied Flycatchers in the successional habitat and the absence of seeds in feces of the same species in the primary forests suggests that omnivores in successional habitats are capitalizing on the greater diversity and abundance of fruits, while those found in primary forests seem to be foraging solely on insects. The greater percentage of insectivorous birds in the primary forest suggest that there may be a greater abundance of insects in the primary forest which results in more insectivores utilizing this habitat than the successional plots.

In the successional plots, the presence of more foreign seeds in bird feces suggests that birds may be important dispersers of seeds both into the plots and

within plots. While it is apparent that birds play a key role in the dispersal of seeds, further studies may reveal to what extent the introduction of foreign seeds leads to the successful colonization of new plant species in successional habitats. Continuing studies of both the diversity and abundance of bird species between primary forests and successional habitats and the dispersal of seeds by birds will allow us a better understanding of how deforestation in the tropics affects bird populations and how birds play an integral part in the regeneration of disturbed habitats.

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Table 1: Number of each bird species by foraging guilds captured in early successional and in primary forest at La Selva, Costa Rica.

Bird species, common name	Successional	Primary
Frugivorous species	11.8%	15.4%
<i>Manacus candei</i> , White-collared Manakin	4	2
<i>Pipra mentalis</i> , Red-capped Manakin		
Insectivorous species	11.8%	30.8%
<i>Glyphorhynchus spirurus</i> , Wedge-billed Woodcreeper		2
<i>Phaenostictus mcleannani</i> , Ocellated Antbird		1
<i>Ramphocaenus melanurus</i> , Long-billed Gnatwren	1	
<i>Seiurus aurocapillus</i> , Ovenbird	1	
<i>Terenotriccus erythrurus</i> , Ruddy-tailed Flycatcher		1
<i>Xenops minutus</i> , Plain Xenops	2	
Nectivorous species	17.6%	23.0%
<i>Chalybura urochrysis</i> , Red-footed Plumeleteer	2	
<i>Phaethornis longuemareus</i> , Little Hermit	1	1
<i>Phaethornis superciliosus</i> , Long-tailed Hermit	1	1
<i>Thallurania colombica</i> , Crowned Woodnymph		1
<i>Threnetes ruckeri</i> , Band-tailed Barbthroat	1	
Omnivorous species	58.8%	30.8%
<i>Arremon aurantirostris</i> , Orange-billed Sparrow	1	
<i>Cyanocopsa cyanoides</i> , Blue-backed Grosbeak	2	
<i>Myonectes oleagineus</i> , Ochre-bellied Flycatcher	5	4
<i>Hylocichla mustelina</i> , Wood Thrush	1	
<i>Ramphocelus passerinii</i> , Scarlet-rumped Tanager	3	
<i>Saltator maximus</i> , Buff-throated Saltator	5	
<i>Tolmomyias sulfurescens</i> , Yellow-olive Flycatcher	1	
<i>Turdus grayi</i> , Clay-colored Robin	1	
Total number of species per net hour	0.29	0.15
Total number individual birds per net hour	0.63	0.25