Premnoplex brunnescens (2, Spotted Barbtail)

3. Tyrannidae

Rhynchocyclus brevirostris (Eye-Ringed Flatbill)

Mionectes olivaceus (2, Olive Striped Flycatcher)

Oscines

4. Emberizidae—Parulinae

Basileuterus culicivorus (2, Golden Crowned Warbler)

Oporornis formosus (Kentucky Warbler)

Basileuterus tristriatus (2, Three Striped Warbler)

5. Emberizidae—Thraupinae

Chlorospinqus ophthalmicus (2, Common Bush-Tanager)

6. Troglodytidae

Henicorhina leucophrys (Gray Breasted Wood-Wren)

7. Turdinae

Myadestes melanops (Black-Faced Solitaire)

Appendix C

Orders and families of birds netted at Corcovado

I. Trochilidiformes

Glaucis aenea (Bronzy Hermit)

Threnetes ruckeri (2, Band-tailed Barbthroat)

Phaethornis superciliosus (12, Long Tailed Hermit)

Hylocharis eliciae (Blue-Throated Goldentail)

Amazilia decora (Beryl-Crowned Hummingbird)

II. Coraciiformes

1. Alcedinidae

Chloroceryle americana (2, Green Kingfisher)

III. Passiformes

Suboscines

1. Furnaridae

Xenopus minutus (Plain Xenops)

2. Dendrocolaptidae

Dendrocincla anabatina (2, Tawny Winged Woodcreeper)

3. Formicaridae

Thamnophilus bridgesi (Black Hooded Antshrike)

Myrmotherula schishcolor (2, Slaty Antwren)

Myrmeciza exsul (2, Chestnut-Backed Antbird)

4. Tyrannidae

Mionectes oleagineus (5, Ochre Bellied Flycatcher)

Myiobius sulphureipygius (2, Sulphur-rumbed Flycatcher)

5. Pipridae

Pipra coronata (6, Blue-Crowned Manakin)

Pipra mentalis (2, Red-Capped Manakin)

Oscines

6. Emberizidae

Oporornis formosus (Kentucky Warbler)

Phaeothlypis fulvicauda (2, Buff-Rumped Warbler)

Euphonia imitans (Spot-Crowned Euphonia)

Eucometis penicillata (2, Gray-Headed Tanager)

Lanio leucothorax (White-Throated Shrike-Tanager)

Arremon aurantiirostris (3, Orange-Billed Sparrow)

FRUIT MORPHOLOGY AND SEED DISPERSAL IN THREE COSTA RICAN FORESTS

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Abstract. This study compared three Costa Rican forests during the dry season: Palo Verde, Monteverde, and Corcovado. Fruit morphology, fruit abundance, and dispersal syndrome data were obtained from trees found on 50m x 20m plots. Fruit morphology varied between sites but appeared to fall into distinct classes that share a common type of dispersal agent. The organisms observed feeding on the different fruit types supported our classification of these fruits into dispersal syndromes. Dispersal syndromes were found to be significantly different between sites ($G=16.03$, $p<0.005$); overall fruit abundance appeared to vary between sites as well. (SAW)

Introduction (JJB)

There are several advantages to long-distance seed dispersal: (i) reducing seed and seedling mortality from pathogens, predators, and competition which are often associated with the parent tree, (ii) enabling seeds to reach a suitable habitat, and for some species (iii) increased germination success due to treatment by a dispersal vector (e.g., passage through a gut). Dispersal syndromes are strategies used by a plant to facilitate seed dispersal. Dispersal syndromes include abiotic mechanisms, such as water or wind, and biotic mechanisms, such as birds, bats, and other vertebrates. During our stay in Costa Rica, dispersal syndromes were studied in three forests: Corcovado, a lowland seasonal wet forest; Monteverde, a premontane cloud forest; and Palo Verde, a seasonal dry forest. Abundance (total biomass) of fruit was recorded at each site and a number of questions were posed: (i) do fruit characteristics seem to fall into distinct dispersal syndromes, (ii) are these syndromes supported or upheld by the organisms observed feeding on these fruits, (iii) are different syndromes represented at different sites, and (iiii) is there a difference in overall abundance of fruit at each site.

Methods (JJS)

We collected fruits for classification into dispersal syndromes both by exhaustive sampling in a 50m x 20m plot and by a general sample of the area along the trail to and from the plot. Each fruit was dissected into husk, pulp, seed coat and seed, noting the color, texture and smell of each layer. Fruits were placed into dispersal syndromes based on morphological characteristics set out by other authors. Each syndrome predicted a dispersal agent, and these predictions were compared with observations of feeding events.

To compare abundance of dispersal syndromes in different tropical forests in Costa Rica, we sampled fruiting plants at three sites: Monteverde, Palo Verde and Corcovado. The numbers of species with wind/explosive dispersed, bird dispersed, and other vertebrate dispersed seeds were compared to test for differences within and between sites. Estimates of fruit bio-

Table 1. Dispersal syndromes of fruiting plants in Palo Verde, Monteverde, Corcovado.

ID	Dispersal Syndrome
Bursera simarouba	bat?
mangifer	bat
Rutaceae	mammal
Bauhinia	explosive
Pithecalobium	mammal?
Guazuma	bat?
Pithecalobum cluce	explosive
Bursera?	bats?
Canavalia	explosive
Luehea	wind
Cochlospermum	wind
Calycophyllum	?
Acrocomia	mammal
Legume	wind?
Jaquinia	bird
Pseudobombax	wind?
Bamboo?	wind?
Melastomaceae	small bird/bat
?	bird
Palmaceae	bird/bat
?	vertebrate
?	bird
?	bird
Melastomaceae	bird
Lauraceae, *Persea*?	bird/bat
Slonea?	bird
Cucurbitaceae?	bat?
?	bird
Ocotea? (Lauraceae)	bird (bat?)
Ficus	vertebrate
Piper sp. 1	bat
Virola	bird
Piper sp. 2	bat
Chrysophila	vertebrate
Aroid	bird
Herrania	primate
Palm	bird/vertebrate
Stemmadenia	bird
Aperba	bird/vertebrate
Sapium	bird
?	bird
Ochroma	wind
Basiloxlong	wind
Larapa	bird
Cecropia	bat
Passiflora	private/bird
Caoethalsia	wind
?	wind
?	wind
?	wind

mass for all trees within our plots were obtained. To estimate biomass, we first made a visual estimate of the number of fruits in each tree. This was then multiplied by the weight of a fruit, giving fruit biomass per tree. Diameter at breast height and growth habit were also noted for all trees for future comparison.

Results (EWG)

Fruit morphology seemed to fall into distinct syndromes, a result of sharing a common type of disperser. These syndromes are tabulated for the 48 fruiting plant species found in Palo Verde, Monteverde, and Corcovado (Table 1). Individuals for which we were uncertain of the species or dispersal syndrome are labeled with a question mark. Field observations gathered during walks around the sites are listed to provide specific examples of the dispersal syndromes of some fruiting species (Table 2).

Data on each of the plants in our plots were tabulated, including their approximate total fruit mass (Table 3). These masses are summed to give the total fruit mass per plot at each site: Palo Verde (2.8kg), Monteverde (69.4kg), Corcovado (13.3kg).

Each site is listed with frequencies of dispersal syndromes (Table 4a). Fruits which most likely had two or more dispersers are categorized in the General Vertebrate column. For the purpose of analysis, we placed each fruit into one of three dispersal classes (bird, wind/explosive, and vertebrate). A significant difference existed between the sites (Table 4b; $G=16.03$, $p<0.005$).

Table 2. Field observations of dispersers of fruiting plants at the different sites.

Site	Animal	Plant Species	Dispersal or Predation
Corcovado	Chestnut-Mandibled Toucan	Spiny palm	Dispersal
Palo Verde	Magpie jay	*Jaquina*	Dispersal
Monteverde	Spider monkey	Fig	Dispersal
La Selva	Agouti	*Dipteryx*	Predation
La Selva	Small squirrel	*Dipteryx*	Dispersal
Monteverde	Quetzal	*Guatteria*	Dispersal

Discussion (ALG)

When comparing fruit from all three sites, we found syndromes of morphological characteristics which appeared to be associated with a particular dispersal mechanism or organism. We saw few dispersal events, but those observed were consistent with these syndromes. However, we found that some fruits had characteristics overlapping two syndromes, such as some of the bird/bat dispersal fruits.

The distribution of these different mechanisms varied among sites. In Corcovado, there were similar numbers of plants using wind, birds, and other vertebrates as dispersal agents, while at Monteverde, the plants depended mainly on birds or other vertebrates as dispersers. This could result from the wet Monteverde environment—airborne seeds would travel a short distance and dehiscent fruits would have difficulty drying out. At Palo Verde, with a long dry season and high winds, most plants sampled had explosive or wind dispersal. Palo Verde's low, thin canopy also makes wind dispersal effective.

Fruit abundance in the Corcovado and Monteverde plots were reasonably similar, with Monteverde's being slightly higher; note, however, that >50% of the observed biomass in the Monteverde plots was from a single tree. Possibly as a consequence of the long dry season, Palo Verde plots had the lowest fruit abundance and crop sizes were generally small.

Possible errors in this study could have been introduced by bias in our sampling toward areas or trees with large or colorful fruits and away from areas where the fruit was high in the canopy or difficult to see.

Table 4a. Dispersal syndrome frequencies at the different sites.

	Wind	Explosive	Primate	Bird	Bat	General Vertebrate	?
P. Verde	4	3	0	1	3	2	3
Montev.	0	0	0	8	1	6	0
Corcovado	6	0	1	6	3	4	1

Table 4b. Table 4a data grouped for analysis. $G=16.03$, $p<.005$

	Birds	Other Vertebrates	Wind/Explosive
Palo Verde	1	5	7
Monteverde	8	7	0
Corcovado	6	8	6

Table 3. Characteristics of fruiting plants and an estimate of total fruit biomass by site.				
Fruiting tree	DBH	# of fruits	Ind. fruit mass (g)	Total mass(g)
Palo Verde				
Bamboo	–	120	0.008g	1
x11				10
x15				15
x6				6
x6				6
x20				20
x7				7
?		70	0.2	14
Legume	8cm	300	1.2	360
Calycophyllum		immeasurable		
Pseudobombax	103cm	10	25.3	253
Luehea	12cm	30	15.3	460
Luehea	75cm	20	15.3	306
Bursera		300-400	3.6	1260
Acrocomia	–	20	1.6	32
Calycophyllum		–.	–	–
Jaquina		15	3.6	54
			Total Mass/Plot	2.798 kg
Monteverde				
?	2cm	250	0.14	35
?	1cm	5	3.0	15
Palmaceae	60	6400	2.3g	14,720
?	75	104	4.0	40000
?	1	15	0.3	4.5
Melastomaceae	25	106	0.014	14,000
?	2	150	0.14	21
?	4	100	0.14	14
?	2	150	0.24	36
?	2	20	25	50
Melastomaceae	10	700	0.72	504
?	2	8	0.4	3.2
			Total Mass/Plot	69.402kg
Corcovado				
?	30	20	500	10000
Piper	2-3cm	31	1.2	37.2
Virola	60	800	3	2400
Piper	many	55	1.2	66
Piper	many	16	.5	8
Piper	many	8	.5	4
Piper	many	6	.5	3
Piper	many	2	.5	1
Chrysophila	10	350	2.3	805
			Total Mass/Plot	13.3kg

Location on leaf	Natural control	Stapled control	Treatment
Base	0	1	11
Middle	2	3	10
Tip	35	23	19

Table 1. Number of parrotfish bites on various *Thalassia* leaves.

DISCUSSION (KAI)

In order to test for the effect of epiphytes on leaf herbivory we created *Thalassia* blades of equal epiphytic load by stapling the tips of blades together. The effect of the staples was tested by comparing herbivory on a stapled control blade (with normal epiphytic load) and a manipulated control (regular blade stapled three times). It may have been better to make the manipulated control out of three cut sections of grass stapled together, but we did not feel this was critical. We found that the presence of staples did not effect herbivory.

When we compared the position of bites (number of bites at the tip, middle, and base) on the experiment blades to the number of bites on the corresponding stapled controls, we found a highly significant difference. This suggests that the fish are feeding on the entire surface of the blade with uniform epiphytic load, whereas they concentrate their feeding only at the epiphyte-rich tips of unmanipulated blades. This indicates that herbivorous fish are not constrained in their behavior to feed at the tips of a leaf; they appear to choose areas of high epiphytic load wherever they are. We also found that fish do not graze significantly more on any portion of a blade when epiphyte distribution is uniform; herbivory is randomly distributed on all portions of the blade.

The older portions of *Thalassia* blades are at a severe disadvantage due to colonization by epiphytes. Epiphytes have two negative effects, first they decrease photosynthetic activity by shading leaves. Second, as illustrated in this paper, they cause tissue loss by increasing fish herbivory.