ON THE RELATIONSHIP AMONG BIRDS AND *TREMA MICRANTHA* IN MONTANE FORESTS OF HISPANIOLA

Relación entre varias especies de aves y *Trema micrantha* en bosques montanos de La Española

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ABSTRACT

Avian frugivores are of great interest to ecologists because they play an important role in ecosystem functioning, and can serve as important components in habitat restoration. In the Neotropics, observational studies have demonstrated the importance of a variety of fruit trees to numerous bird species, but undoubtedly other tree species exist that are a key resource for birds. I explored the relationship between *Trema micrantha* (L.) Blume, which produces superabundant fruit nearly continuously, and its disperser assemblage in Hispaniolan pine forest and montane broadleaf forest in the Sierra de Bahoruco, Dominican Republic. In 174 hours of observation at sixteen trees I recorded 513 visits by nineteen species of birds. Birds did not visit *Trema* in numbers reflecting their relative abundance in each habitat. The most frequent consumer of *Trema* fruit was the migratory Cape May Warbler, *Setophaga tigrina* (Gmelin, 1789), but other frequent visitors included the Black-throated Blue Warbler, *S. caerulescens* (Gmelin, 1789), and the endemic Palmchat, *Dulus dominicus* (Linnaeus, 1766), and Hispaniolan Highland-Tanager, *Xenoligea montana* (Chapman, 1917). I recorded 85 aggressive interactions among nine species of birds in *Trema* trees, with female Cape May Warblers involved in most of these. There was no evidence that *Trema* was dependent on any one species of bird for dispersal of its seeds, and despite the large proportion of visits by the Cape May Warbler, I found no evidence that any species of bird was dependent upon fruit from *Trema*. Rather, because male Cape May Warblers dominate females and defend nectar sources in these habitats, I suggest that for female Cape May Warblers, these scattered *Trema* trees represent a known, reliable, and accessible source of food which they can defend. *Trema* trees will benefit these bird species as a food resource, but may also function as a target for many other birds moving across the landscape, thereby facilitating the dispersal of a wider variety of seeds and the restoration of deforested sites.

Keywords: Dominican Republic, endemic, foraging behavior, frugivory, Neotropical migratory birds, *Setophaga tigrina*, Sierra de Bahoruco, *Xenoligea montana*.

RESUMEN

Las aves frugívoras son de gran interés para los ecólogos porque juegan un papel importante en el funcionamiento del ecosistema y pueden servir como componentes importantes en la restauración del hábitat. En los neotrópicos, las observaciones han demostrado la importancia de una variedad de árboles frutales para muchas especies de aves, pero indudablemente existen otras especies de árboles que son un recurso clave para las mismas. Se estudió la relación entre *Trema micrantha* (L.) Blume, que produce frutos superabundantes casi continuamente, y el conjunto de aves dispersoras en el bosque de pinos de la Española y el bosque montano de hoja ancha en la Sierra de Bahoruco, República Dominicana. En 174 horas de observación en dieciséis árboles, se registraron 513 visitas de diecinueve especies de aves. Se encontró que las cantidades de aves que visitaban la planta no reflejaban su abundancia relativa en cada hábitat.

El consumidor más frecuente de la fruta de *Trema* fue la migratoria Cigüita Tigrina, *Setophaga tigrina* (Gmelin, 1789), pero otros visitantes frecuentes incluyeron Cigüita Azul de Garganta Negra, *S. caerulescens* (Gmelin, 1789) y los endémicos Cigua Palmera, *Dulus dominicus* (Linnaeus, 1766) y Cigüita Aliblanca, *Xenoligea montana* (Chapman, 1917). Se registraron 85 interacciones agresivas entre nueve especies de aves en árboles de *Trema*, con hembras de *S. tigrina* involucradas en la mayoría de estos. No hubo prueba de que esta planta dependiera de una sola especie de ave para la dispersión de sus semillas. A pesar de la gran proporción de visitas de *S. tigrina*, no se encontró ninguna evidencia de que alguna especie de ave dependiera de la fruta de *Trema*. Por el contrario, debido a que los machos de *S. tigrina* dominan a las hembras y defienden las fuentes de néctar en estos hábitats, sugiero que para las hembras de *S. tigrina* estos árboles dispersos representan una fuente de alimento conocida, confiable y accesible que pueden defender. Los árboles de *Trema* estarían beneficiando a estas especies de aves como recurso alimenticio, pero también podrían funcionar como un objetivo para muchas otras aves que se mueven a través del paisaje, facilitando así la dispersión de una variedad más amplia de semillas y la restauración de sitios deforestados.

Palabras clave: República Dominicana, endémico, comportamiento de alimentación, frugívoro, aves migratorias neotropicales, *Setophaga tigrina*, Sierra de Bahoruco, *Xenoligea montana*.

INTRODUCTION

In an era of human population growth, habitat conversion, over-consumption of resources, and widespread introductions of exotic species, the loss of key plant or animal species whose structural or functional attributes might impact or even shape an entire ecological community or ecosystem can be critically important. For example, in some ecosystems, particular tree species are considered key organisms and their presence or absence can have broad consequences for associated biota, ecosystem function, and stability (Ellison *et al*., 2005). These trees may serve as critical nurse plants, or as sources of shade and food for animals (e.g. Belsky *et al*., 1989; Dean *et al*., 1999; Ellison *et al*., 2005).

Fruit trees are of particular importance to birds, as 14% of all terrestrial bird species are classified as frugivorous (Kissling *et al*., 2009), where a frugivore is defined as an animal whose diet is composed of >50% fleshy fruits (e.g. Fleming *et al*., 1987). On a global scale and across all orders, the species richness of frugivorous birds is highest in the Neotropics (Kissling *et al*., 2009). Avian frugivores are of great interest to ecologists because they play an important role in plant reproduction and ecosystem functioning by providing a critical means of seed dispersal (Karr, 1976; Fleming *et al*., 1987; Herrera, 2002), and maintaining plant genetic diversity at a landscape level (Wang and Smith, 2002). They can also serve as important components of reforestation and habitat restoration schemes, not only because they can provide an important food resource, but also because the presence of scattered fruit trees can be keystone structures, a target for birds, and a focal point for natural restoration of deforested sites (Manning *et al*., 2006; Cottee-Jones *et al*., 2016; Prevedello *et al*., 2018).

In the Neotropics, including the Caribbean Basin, observational studies have demonstrated the importance of a variety of key fruit trees to numerous bird species. These studies have highlighted the importance of *Cecropia* (Cecropiaceae; Oniki *et al*., 1994), *Bursera simaruba* L., (Burseraceae; Trainer and Will, 1984; Scott and Martin, 1984), *Inga* (Fabaceae; Wunderle and Latta, 1998), *Ficus* (Moraceae; Scott and Martin, 1984), *Guarea glabra* Vahl (Meliaceae; Howe and De Steven, 1979), and *Trichilia cuneata* Radlk (Meliaceae; Leck, 1969). But undoubtedly other tree species that are a key resource for avian communities exist, and knowledge of these species and the bird species that may rely on their fruit would be beneficial for conservation and management planning purposes.

Trema micrantha is a fast growing, small to medium-sized tree found from Southern Florida and Mexico to Northern Argentina (Vázquez-Yanes, 1998). Traditionally placed in the family Ulmaceae, some recent revisions have placed *Trema* in the Cannabaceae (Sytsma *et al*., 2002; Yang *et al*., 2013; Judd *et al*., 2016). The species typically occurs in tropical moist forests but also ranges to moist semi-deciduous forests at higher elevations. *Trema* has been shown to very quickly take advantage of natural gaps in the canopy as a pioneer species (Brokaw, 1987; Vázquez-Yanes, 1998), but will also occur in anthropogenically disturbed sites such as along the edges of roads built through forests in the tropics. Birds foraging on *Trema micrantha* have been noted previously through broad surveys of frugivory (i.e. Snow, 1981; Wheelwright *et al*., 1984), with Snow (1981) suggesting that *Trema* is consumed by unspecialized, opportunist frugivores, but very few studies have focused particularly on frugivory of *Trema* (Galetti and Pizo, 1996).

OBJECTIVE

-To explore the relationship between *Trema micrantha* and its disperser assemblage by determining: (1) the avian species foraging on *Trema micrantha*; (2) the relative importance of permanent residents and over-wintering migratory birds in the consumption and dissemination of *Trema* seeds; (3) variation in numbers of birds visiting *Trema* throughout the day; (4) whether *Trema* specialists are present and whether the disperser community reflects the avian frugivore community in two distinct habitats containing *Trema*; and (5) aggression around *Trema* as a key resource for birds.

MATERIALS AND METHODS

I studied winter-resident birds and their relationship with *Trema micrantha* on 27-28 October, 7-8 November, and 14-16 December 1997 at two study sites in the Sierra de Bahoruco National Park, Dominican Republic.

Pine site. One study site was located in native pine savanna at 1100 m elevation (18° 07’ N, 71° 35’ W). Pine forest in the Sierra de Bahoruco is dominated by the endemic Hispaniolan pine (*Pinus occidentalis* Swartz, 1788); the only other common tree is the endemic palm *Coccothrinax scoparia* Becc., 1908. At our study site, disturbance resulting from road cuts and open pits associated with test mines for the extraction of bauxite promoted the growth of scattered *Trema micrantha*. A well-developed shrub layer is also present, and common broadleaf species include *Cestrum brevifolium* Urb., *Chamaescrista glandulosa* L., *Coreopsis buchii* Urb. *Hypericum hypericoides* L., *Lyonia truncata* Urb., *L. microcarpa* Urb. and Ekman, *Myrica picardae* Krug and Urb., and *Senecio picardae* Krug and Urb., as well as the succulent *Agave antillarum* Descourt (Fisher-Meerow and Judd, 1989). The ground is covered by a thick layer of grasses. Pine forest in the Sierra de Bahoruco typically has a fairly open canopy with a canopy cover of ~50%, a sparse intermediate layer of pine, and a dense mixed-broadleaf and pine understory (Latta and Sondreal, 1999). Studies at the pine site occurred 27-28 October and 14-16 December 1997.

Montane broadleaf forest site. A second study site, known locally as Las Abejas (18° 09’ N, 71° 37’ W), is a moist, broadleaf forest located in a ravine at 1150 m ~10 km northwest of our pine forest site. In the Sierra de Bahoruco, high-elevation moist broadleaf sites are very diverse hardwood forests that are humid and heavily shaded with a canopy cover of ~100% and a well-developed subcanopy and understory (Latta *et al*., 2003). The most distinctive feature of these sites is the abundance of lianas and epiphytes, including orchids, ferns, and bromeliads.

The most abundant tree species include members of the genera *Cupania*, *Dendropanax*, *Guarea*, *Mecranium*, *Miconia*, *Myrcia*, *Piper*, *Psychotria*, and *Trema* (Fisher-Meerow and Judd, 1989). At this site, *Trema micrantha* is a common and prominent small tree associated with natural and anthropogenic disturbances (tree fall gaps and abandoned slash and burn agricultural sites). Studies at Las Abejas occurred on 7-8 November 1997.

Field observations. Data were collected on birds visiting *Trema* trees in 28 observation sessions of 1.5-8.0 hr each. Twelve trees were observed at the pine forest site, while four additional trees were observed at the montane broadleaf forest site. Focal trees were selected based on size (with larger trees preferred) and availability at study sites utilized for co-occurring field studies. During each session, bird presence was recorded at 5 min intervals resulting in 12 point observations/hr. In addition, bird behavior was noted as foraging on *Trema* fruit, other foraging behavior, or resting. Aggressive interactions between birds were noted throughout the observation session with the species and sex of the dominant and subordinate individuals recorded.

Statistical analyses. I used Excel 2003 and on-line worksheets provided by McDonald (2009) to perform various statistical tests described by Sokal and Rohlf (1995). I accepted a probability of type I error of 0.05 or less as significant. I did not analyze variation in bird behavior among trees but pooled data to increase sample sizes. I use descriptive statistics to summarize bird activity in each habitat and in both habitats combined. Some analyses are based on presence/absence of species or proportions of birds observed.

Birds were grouped by diet on the basis of principal food items consumed in optimal habitats (Wunderle and Latta, 1996; Latta *et al*., 2003; SCL, unpubl. data). Groups included frugivores, insectivores, nectarivores, granivores, and omnivores. For some analyses, birds known to consume any amount of fruit were then reclassified as frugivores. Groups based on residency status included permanent residents present throughout the year, and Neotropical (latitudinal) migrants which breed north of the tropics. Birds are presented in phylogenetic order (AOU, 1998) with scientific names following AOU (1998) and common names following Latta *et al*. (2006).

To compare bird occurrences at *Trema* trees to overall abundance, I used abundance estimates for birds derived from point counts and previously published in Latta *et al*. (2003). Point count data in Latta *et al*. (2003) for pine forest habitat included points from this *Trema* study site. Point count data in Latta *et al*. (2003) for montane broadleaf habitat were collected from sites very similar to the Las Abejas site (SCL, pers. observ.), and were located ~10 km east of Las Abejas in the Sierra de Bahoruco. I then used Spearman's rank correlation coefficient, which converts the measurement variable to ranks, to quantify the association between the number of individuals of each species of bird recorded in *Trema* trees, and their abundance as recorded in point counts in pine forest or montane broadleaf forest habitats. For these tests I included in our analyses only species known to forage on fruit as part of their diet, and expanded the list to include additional species from the point counts so as to fully cover the range of abundances of all of the frugivorous species observed in *Trema*.

I used a *G*-test of independence to test for significant heterogeneity in the proportion of individuals observed foraging in different 2-hr time blocks. Counts were treated as a nominal variable and then summarized by the proportion of all observations in each of five time blocks with the expected count calculated as an equal proportion (20%) in each block (McDonald, 2009). A chi-square test of goodness-of-fit was used to compare the observed counts of aggression by males and females with the expected counts calculated based on published estimates of males (52.9% of Cape May Warblers) and females (47.1%) in pine forest habitat (Latta and Faaborg, 2002).

RESULTS

In 174 hours of observation (2 070 point observations) at 16 trees I recorded 513 visits by 19 species of birds (Table I). Most observations (168 hours at 12 trees) occurred at the pine forest site, while an additional 6 hours of observations were made at 4 trees at the montane broadleaf forest site. With data pooled across both sites, the Cape May Warbler (*Setophaga tigrina*; 69.2% of observations) was the most frequent visitor to the *Trema* trees, followed by the Palmchat (*Dulus dominicus*; 9.0%) and the Black-throated Blue Warbler (*S. caerulescens*; 7.0%). When habitats were considered separately, while the same three species were the most frequent visitors to *Trema* in the pine forest habitat, results from the montane broadleaf forest differed. At this site, the most frequent visitor was the endemic Hispaniolan Highland-Tanager (*Xenoligea montana*; 55.6%) followed by Cape May Warbler (30.6%) and Black-throated Blue Warbler (13.9%).

Over-wintering Neotropical migratory birds were a significant proportion of the species and individuals recorded in *Trema* (Table I). As noted, the Cape May (69.2% of observations) and Black-throated Blue (7.0%) warblers were significant consumers of fruit, with all of the observed Black-throated Blues being females. Other migrants observed in *Trema* did not consume fruit, but included the insectivorous Prairie Warbler (*S. discolor* Vieillot, 1809), Palm Warbler (*S. palmarum* Gmelin, 1789), Ovenbird (*Seiurus auracapillus* L., 1766) and Common Yellowthroat (*Geothlypis trichas* L., 1766).

Most visits (93.4%) to *Trema* trees were by frugivores or species with fruit as a portion of their diet (Table I). Beyond Neotropical migrants, of particular note were the several endemic species found to forage on *Trema*. Other than the Hispaniolan Highland-Tanager, I also observed Palmchat (*Dulus dominicus*), Black-crowned Palm-Tanager (*Phaenicophilus palmarum* L., 1766), and Hispaniolan Spindalis (*Spindalis dominicensis* Bryant, 1866). Numerous insectivores also visited and actively foraged in *Trema* (Table I), including four Neotropical migrants and four additional endemics. The only species observed in *Trema* but never foraging was the endemic granivore, Hispaniolan Crossbill (*Loxia megaplaga* Riley, 1916).

Birds showed significant variation in numbers visiting *Trema* trees throughout the day (G_4=12.96, p=0.011; Fig. 1). Visitation rates were high in the morning time blocks and late in the afternoon, but were relatively low during the mid-day time blocks.

Birds did not visit *Trema* trees in numbers reflecting their relative abundance in each habitat (Table II). Using Spearman rank correlation, I found low correlations between the number of individuals of each species of bird recorded in *Trema* trees, and their abundance as recorded in point counts in pine forest (Spearman's rho = -0.11, 13 d.f., p = 0.70), or montane broadleaf forest (Spearman's rho = -0.06, 16 d.f., p = 0.80) habitats.

Finally, I recorded 85 aggressive interactions among 9 species of birds (Table III). The Cape May Warbler was involved in 84 (98.8%) of these, and was the aggressor in 83 (97.6%) interactions. Most interactions (52; 61.2%) were intraspecific, but the Cape May Warbler also interacted aggressively with the Black-throated Blue Warbler (16.5% of events) and the Palm Warbler (10.6% of events). Of 83 interactions where the Cape May Warbler was the aggressor, 61 (73.5%) were by a female individual, 11 (13.2%) involved a male, and in 11 cases (13.2%) the sex was not identified. Females were significantly more often the aggressor than expected based on sex ratios occurring in pine forest habitat (X^2=40.62, df=1, p<0.001).

Table I. Birds present in *Trema micrantha* trees in pine forest and montane broadleaf in the Sierra de Bahoruco National Park, including residency status, principal diet, occurance of frugivory in the diet, and observations (Obs) of frugivory of *Trema*.

Species	Residency[1]	Dietary Group[2]	Frugivory	Total Obs	Pine Forest % of Obs	Mt Broadleaf % of Obs	Sites Combined % of Obs
Hispaniolan Emerald (*Chlorostilbon swainsonii*)	ER	N		1	0.2		0.2
Narrow-billed Tody (*Todus angustirostris*)	ER	I		4	0.8		0.8
Greater Antillean Elaenia (*Elaenia fallax*)	PR	O	F	2	0.4		0.4
Hispaniolan Pewee (*Contopus hispaniolensis*)	ER	I		2	0.4		0.4
Palmchat (*Dulus dominicus*)	ER	F	F	46	9.6		9.0
Cape May Warbler (*Setophaga tigrina*)	M	O	F	355	72.1	30.6	69.2
Black-throated Blue Warbler (*Setophaga caerulescens*)	M	O	F	36	6.5	13.9	7.0
Prairie Warbler (*Setophaga discolor*)	M	I		5	1.0		1.0
Palm Warbler (*Stetophaga palmarum*)	M	I		9	1.9		1.8
Ovenbird (*Seiurus aurocapillus*)	M	I		1	0.2		0.2
Common Yellowthroat (*Geothlypis trichas*)	M	I		8	1.7		1.6
Green-tailed Ground-Tanager (*Microligea palustris*)	ER	I		3	0.6		0.6
Hispaniolan Highland-Tanager (*Xenoligea montana*)	ER	O	F	20		55.6	3.9
Black-crowned Palm-Tanager (*Phaenicophilus palmarum*)	ER	O	F	6	1.3		1.2
Hispaniolan Spindalis (*Spindalis dominicensis*)	ER	F	F	5	1.0		1.0
Yellow-faced Grassquit (*Tiaris olivaceus*)	PR	O	F	6	1.3		1.2
Black-faced Grassquit (*Tiaris bicolor*)	PR	O	F	2	0.4		0.4
Greater Antillean Bullfinch (*Melopyrrha violacea*)	PR	O	F	1	0.2		0.2
Hispaniolan Crossbill (*Loxia megaplaga*)	ER	G		1	0.2		0.2

[1] Avian species, including permanent residents (PR), endemic residents (ER), and overwintering migrants (M).

[2] Dietary group, including (N) nectarivores, (I) insectivores, (F) frugivores, (G) granivores, and (O) omnivores.

Table II. Comparison of bird occurrences at *Trema* trees to overall abundance as determined by avian abundance estimates derived from point counts in pine forest and montane broadleaf forest. Species included are birds recorded at *Trema* or in point counts, and known to include fruit as part of their diet.

	Pine Forest			Montane Broadleaf		
Species	Point Count Abundance	Point Count Abundance Rank	*Trema* Occurrence Rank	Point Count Abundance	Point Count Abundance Rank	*Trema* Occurrence Rank
Plain Pigeon (*Patagioenas inornata*)	30.0	1.0	11.0	9.5	9	10.5
White-winged Dove (*Zenaida asiatica*)				2.2	16.5	10.5
Common Ground-Dove (*Columbina passerina*)	2.8	12.0	11.0			
Hispaniolan Parakeet (*Psittacara chloropterus*)	4.4	10.0	11.0	6.7	11	10.5
Olive-throated Parakeet (*Eupsittula nana*)	2.2	13.5	11.0			
Hispaniolan Parrot (*Amazona ventralis*)	24.4	2.0	11.0	16.7	7	10.5
Hispaniolan Trogon (*Priotelus roseigaster*)				3.3	15	10.5
Greater Antillean Elaenia (*Elaenia fallax*)	16.1	4.0	11.0	34.8	4	10.5
Stolid Flycatcher (*Myiarchus stolidus*)	7.2	7.5	11.0			
Rufous-throated Solitaire (*Myadestes genibarbis*)				4.4	14	10.5
Bicknell’s Thrush (*Catharus bicknelli*)				6.7	11	10.5
Palmchat (*Dulus dominicus*)		18.0	2.0	2.2	16.5	10.5
Cape May Warbler (*Setophaga tigrina*)	15.0	5.0	1.0		18	2
Black-throated Blue Warbler (*Setophaga caerulescens*)	7.2	7.5	3.0	38.9	3	3
Hispaniolan Highland-Tanager (*Xenoligea montana*)				27.8	5	1
Black-crowned Palm-Tanager (*Phaenicophilus palmarum*)	18.9	3.0	4.5	51.3	2	10.5
Western Chat-Tanager (*Calyptophilus tertius*)				4.8	13	10.5
Hispaniolan Spindalis (*Spindalis dominicensis*)	5.5	9.0	11.0	57.5	1	10.5
Antillean Euphonia (*Euphonia musica*)	3.9	11.0	11.0	12.9	8	10.5
Yellow-faced Grassquit (*Tiaris olivaceus*)	1.7	15.0	4.5			
Black-faced Grassquit (*Tiaris bicolor*)				22.2	6	10.5
Greater Antillean Bullfinch (*Melopyrrha violacea*)				6.7	11	10.5
Hispaniolan Crossbill (*Loxia megaplaga*)	2.2	13.5	11			

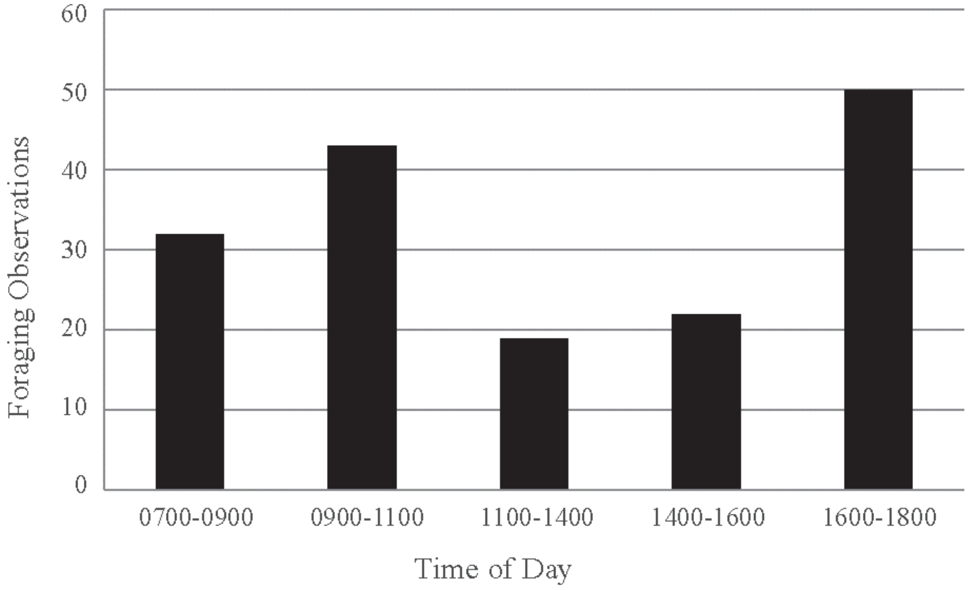

Figure 1. Number of foraging observations occurring in 2-hr time-blocks at *Trema* trees in pine forest, the Sierra de Bahoruco National Park, Dominican Republic. No observations were made from 1200-1300.

Table III. Number of aggressive intraspecific and interspecific interactions in *Trema* trees in pine forest and montane broadleaf forest in the Sierra de Bahoruco National Park, Dominican Republic.

Dominant	Subordinate Individual[1]								
Aggressor	CMWA	HIPE	BTBW	PRAW	PAWA	COYE	BANA	BCPT	HISP
CMWA	51	1	14	2	9	2	2		2
HIPE									
BTBW	1								
PRAW									
PAWA									
COYE									
BANA									
BCPT								1	
HISP									

[1] Species codes (scientific names of each appear in Table I): CMWA (Cape May Warbler), HIPE (Hispaniolan Pewee), BTBW (Black-throated Blue Warbler), PRAW (Prairie Warbler), PAWA (Palm Warbler), COYE (Common Yellowthroat), BANA (Bananaquit), BCPT (Black-crowned Palm-Tanager), HISP (Hispaniolan Spindalis).

DISCUSSION

I recorded visitations by a large number of avian species to *Trema micrantha* trees in Hispaniolan pine forest and montane broadleaf forests, with the majority of visits by the over-wintering Neotropical migrant Cape May Warbler and the restricted-range endemic Hispaniolan Highland-Tanager, both of which fed on *Trema* fruit. Non-frugivorous birds were also recorded visiting *Trema* trees, and these were mostly insectivores. Species such as the endemic Narrow-billed Tody (*Todus angustirostris* Lafresnaye, 1851), and the migratory Palm Warbler, Prairie Warbler, and Common Yellowthroat, may have been foraging on any of a variety of insects because *Trema* are pollinated by a diversity of small insects (Vázquez-Yanes, 1998), while other insects (e.g. Drosophila) have been associated with *Trema* fruits (Leck, 1969) and may serve as avian prey.

The importance of *Trema micrantha* to some over-wintering Neotropical migratory birds was suggested by Galetti and Pizo (1996) who noted that over-wintering migrants are particularly common in second-growth habitats in the tropics. In their study site, Red-eyed Vireo (*Vireo olivaceus* L., 1766), was an abundant winter resident and frequently consumed fruit. Over-wintering migratory birds from North America frequently occur in lists of species visiting other fruiting trees such as *Bursera* (Trainer and Will, 1984), and also account for the majority of the visits (70%) and the seeds removed (60%) at *Guarea glabra* trees in Brazil (Howe and De Steven, 1979). These migrants included Great Crested Flycatcher (*Myiarchus crinitus* L., 1758), Swainson's Thrush (*Catharus ustulatus* Nuttall, 1840), Red-eyed Vireo, and Tennessee Warbler (*Vermivora peregrina* Wilson, 1811). Howe and DeSteven (1979) hypothesized that the fruiting season of this tree species was "adaptively synchronized" with the northbound migration of these frugivorous migrants.

There was no evidence that *Trema* was dependent on any one species of bird for dispersal of its superabundant seeds. The most common consumers of *Trema* differed between habitats, and numerous species were observed eating *Trema* fruit. Thus, the present study supports the argument that a superabundant fruit promotes widespread use by a variety of species. *Trema* fruit may be considered superabundant both in terms of numbers of small fruit produced simultaneously throughout the tree, as well as in the production of fruit through a very long fruiting season. The superabundance of *Trema* fruit may be an adaptive characteristic of early-successional plants in tropical areas (Gómez-Pompa and Vázquez-Yanes, 1974). This reproductive strategy, where *Trema micrantha* inflorescences and infructescences can be found simultaneously in almost any month (SCL, pers. observ.; Gómez-Pompa and Vázquez-Yanes, 1974), is presumably characteristic of pioneer species in disturbed habitats where it would be advantageous if the greater part of the energy budget were dedicated to reproduction rather than to investment in growth in the size of the plant so as to take full advantage of ephemeral habitat disturbance (Gómez-Pompa and Vázquez-Yanes, 1974).

While *Trema micrantha* fruit may be superabundant, the nutritive quality of the fruit would be important in insuring that they are eaten and dispersed by birds. The nutritive content of *Trema micrantha* has not been analyzed, but the nutritional content of the closely related *T. orientalis* L. was found to be typical of many other fruits eaten by specialized frugivores (Snow, 1981). Combined with the large number of fruits and their long fruiting season, the nutritive quality appears to be sufficient in maintaining *Trema's* attraction for birds and the services of avian dispersal agents throughout the long fruiting season in these habitats.

I found no evidence that any one species of bird was dependent upon fruit from *Trema*. Although one might suggest because of the large numbers of individuals that the Cape May Warbler was dependent on *Trema* at the pine forest site, in previous work Latta and Faaborg (2002) used foraging observations and studies of this warbler across a variety of habitats to demonstrate that the Cape May actually relies on a much wider variety of food items and sources. Cape May Warblers are frequently considered nectarivores (Baltz and Latta, 1998), and Latta and Faaborg (2002) found that in pine habitat nectar sources such as *Agave* blossoms and *Coccothrinax* palm flowers were preferred food. These sources of nectar are relatively plentiful and consistently available, and even tend to increase in abundance in late winter when other food sources often diminish.

I noted a considerable number of aggressive events. While many tropical frugivores tend to arrive and leave fruiting trees in small groups (Diamond and Terborgh, 1967; Leck, 1969), aggression generally limited numbers of birds at *Trema* trees. Oniki *et al*. (1994) noted that there was little fighting among birds visiting *Cecropia* trees in Brazil. Similarly, Howe and De Steven (1979) noted that aggressive encounters between visitors to *Guarea glabra* trees in Panama were rare, even though several birds were often in the same small tree. They hypothesized that the low level of aggressive interaction was the result of the "superabundance of fruit" suggesting that competition in this situation was negligible. In contrast, Leck (1969) also recorded fairly large numbers of aggressive encounters, with intraspecific aggression more frequent that interspecific aggression, but few cases resulted in the supplanted individual leaving the tree or even ceasing foraging.

Almost all of the aggression that I observed was attributed to the Cape May Warbler. Aggressive competition and territoriality have been previously described for Cape May Warblers (Greenberg *et al*., 1994; Baltz and Latta, 1998), with male individuals dominant and significantly more aggressive than females (Latta *et al*., 2001). Previously published data on aggressive interactions around honeydew as a food source support a hypothesis that there are intersexual dominance hierarchies operating among Cape May Warblers. Latta *et al*. (2001) showed that honeydew sources in Hispaniolan dry forest habitat were most actively defended by male Cape May Warblers who dominated females, and males preferentially defended nectar sources in pine forest habitat (Latta and Faaborg, 2002). Because in the present study females were significantly more often the aggressor than expected based on sex ratios occurring in pine forest habitat, I suggest that rather than female dominance among Cape May Warblers, males are more likely defending more valuable nectar sources in pine habitat, leaving the *Trema* trees to females. For female Cape May Warblers, these scattered *Trema* trees represent a known, reliable, and accessible source of food which these highly territorial birds can defend.

Beyond intraspecific dominance, these aggression data also emphasize the role of interspecific aggressive interactions, and support the hypothesis that interspecific territoriality may be a regular feature of some species of over-wintering migrants such as the Cape May Warbler (Greenberg *et al*., 1994). These data support the idea that interspecific defense focuses on keystone resources (Terborgh, 1986) and patchy, defensible resources such as nectar, fruit, or honeydew (Greenberg *et al*., 1993; Greenberg *et al*., 1994; Latta *et al*., 2001) that may be especially important for maintaining migratory bird populations in particular habitats.

Finally, it should be noted relative to the critically important conservation and restoration of tropical habitats, that *Trema micrantha* should be considered as a promising tree for restoration in deforested landscapes. Vázquez-Yanes (1998) suggested that *Trema* belongs to a group of pioneer species that evolved to occupy canopy openings resulting from the occurrence of natural disturbances in the tropical moist forest ecosystems. The present study suggests that *Trema* also favors anthropogenically disturbed sites and thus is particularly valuable to a variety of bird species. The presence of *Trema* trees will not only benefit these birds as a food resource, but also serve as a focal point for restoration of deforested sites as keystone structures and a target for birds moving across the landscape thereby facilitating the dispersal of a wider variety of seeds (Manning *et al*., 2006; Cottee-Jones *et al*., 2016; Prevedello *et al*., 2018).

ACKNOWLEDGMENTS

Field assistance was provided by Christopher Brown, Bolivar Cabrera, Danilo Mejía, and Mia Sondreal. Funding was provided by the University of Missouri Research Board and National Fish and Wildlife Foundation. S. C. Latta was supported by a STAR Graduate Fellowship from the U.S. Environmental Protection Agency. Valuable comments and editorial suggestions were offered by Carlos Suriel and two anonymous reviewers. Permission to work in the Sierra de Bahoruco was provided by the Dirección Nacional de Parques and the Departamento de Vida Silvestre.

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[Recibido: 08 de enero, 2018. Aceptado para publicación: 20 de abril, 2018]