

FEMALE-DIRECTED DISPERSAL AND FACILITATION BETWEEN A TROPICAL MISTLETOE AND A DIOECIOUS HOST

TOMÁS A. CARLO^{1,4} AND JULIANN EVE AUKEMA^{2,3}

¹Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309-0334 USA

²International Institute of Tropical Forestry, USDA Forest Service, Río Piedras, Puerto Rico 00926-1119 USA

³Zoology Department, North Carolina State University, Raleigh, North Carolina 97695-7616 USA

Abstract. *Phoradendron hexastichum* is a bird-dispersed mistletoe that infects the dioecious tree *Cecropia schreberiana*. Because both species share frugivore seed dispersers, we hypothesized that female *Cecropia* would have a greater probability and intensity of mistletoe infection than males due to more frequent visitation by shared frugivores. Over 50% of female *Cecropia* were infected, in contrast with 25% of males. On average, female trees had twice as many mistletoes as male trees. Infection probability and intensity increased with basal area in females but not in males, suggesting that lifetime reinfection was also female biased. We found mistletoe frugivores visiting uninfected fruiting females twice as often as males. Although mistletoes were mostly consumed by the mistletoe specialist *Euphonia musica*, we did not record *Euphonia* visiting uninfected *Cecropia* trees. Uninfected *Cecropia* trees were frequently visited by generalist frugivores (such as *Spindalis portoricensis*) that used both mistletoes and *Cecropia* fruits. The *Cecropia*–frugivores–*Phoradendron* network of interactions seems to have led to the spatial linkage of the two plant species through directional dispersal, to plant–plant facilitation through shared frugivores, and to bird–bird facilitation in which generalist frugivores start new foci of infection that specialist frugivores can use.

Key words: *Cecropia schreberiana*; dioecious trees; directed dispersal; *Euphonia musica*; facilitation; frugivory; generalist consumers; mistletoes; *Phoradendron hexastichum*; Puerto Rico; seed dispersal.

INTRODUCTION

Seed dispersal processes are fundamental to building and sustaining species diversity in plant communities (Harper 1977, Tilman 1997, Webb and Peart 2001). Because frugivores disperse the seeds of many plant species, understanding spatial patterns of species assemblages in many plant communities requires an understanding of frugivore–plant interactions and their influences on plant distribution (Wang and Smith 2002). In frugivore-dispersed plants, indirect interactions such as competition and facilitation can be accentuated at the scale of plant neighborhoods when co-fruiting plant species share dispersal agents (Sargent 1990, van Ommeren and Whitham 2002, Carlo 2005, Saracco et al. 2005). Hence, neighborhood-scale intra- and interspecific associations of plant species can be important to a plant's fitness and may affect which species, and which genotypes within species obtain more dispersal services by frugivores. In turn, frugivores could strengthen beneficial plant associations and help in their replication in space and time through directional dispersal (*sensu* Wenny 2001), co-dispersal

(Clark et al. 2004), and interspecific facilitation in fruit removal (Tewksbury and Nabhan 2001, Saracco et al. 2005) and/or seed dispersal (Carlo 2005).

However, linking frugivore behavior and dispersal patterns to plant recruitment has proved difficult (Wang and Smith 2002). Wenny and Levey (1998) demonstrated how bird frugivores created a bimodal pattern of seed rain of *Ocotea endresiana* in a Costa Rican forest. One bird species (Three-wattled Bellbird, *Procnias tricarunculata*) seemed to benefit the plant's recruitment more than the others because it directed seeds to more suitable areas (gaps). Another study demonstrated how the behavior of a specialized frugivore (i.e., a fruit-eating animal that feeds almost exclusively on a plant species or genus), *Phainopepla nitens*, was responsible for spatial aggregation of the mistletoe *Phoradendron californicum* at two scales: among host trees and among neighborhoods of trees (Aukema 2003, 2004). Indeed, frugivore-dispersed mistletoes offer a rare opportunity to study relationships among frugivory, seed dispersal patterns, and plant populations because suitable recruitment areas can be readily identified (i.e., host trees). Hence, links between frugivore behavior and plant demography can be established more directly than for ordinary frugivore-dispersed plants (Reid 1991) in which dispersal and recruitment processes can be decoupled by a variety of factors (Schupp and Fuentes 1995).

Manuscript received 21 March 2005; revised 26 May 2005; accepted 31 May 2005. Corresponding Editor: C. Martínez del Rio.

⁴Present address: Biology Department, University of Washington, Seattle, Washington 98195-1800 USA.
E-mail: carlo@colorado.edu

In Puerto Rico, *Cecropia schreberiana* is a ubiquitous tree whose fruits are consumed year-round by many avian frugivores (Carlo et al. 2003; see also Cruz 1974). Because the tree is dioecious, female trees have fruits and males have only wind-dispersed, pollen-bearing flowers. There is no other apparent morphological or physiological difference between the sexes of this species. *Cecropia schreberiana* is frequently parasitized by one species of mistletoe, *Phoradendron hexastichum* (Viscaceae). The Antillean Euphonia (*Euphonia musica*) is the primary consumer of mistletoe species in Puerto Rico, but other frugivorous birds consume and disperse mistletoes as well (Wetmore 1916, Carlo et al. 2003). We hypothesized that female *Cecropia* would have a greater probability and intensity of mistletoe infection than male *Cecropia* due to the frequent visitation by frugivorous birds that use both *P. hexastichum* and *Cecropia* fruits where the two species coexist.

METHODS

Study site and mistletoe census

We conducted this study in Carite State Forest in the municipalities of Cayey and Patillas, Puerto Rico (18°6'10.6" N, 66°2'17.6" W). The vegetation of Carite is subtropical lower montane forest with an annual rainfall of 200–250 cm. From May through July 2004, we conducted a roadside census in which we mapped all trees of mistletoe host species. Common hosts for *P. hexastichum*, such as *C. schreberiana*, *Ocotea* spp., *Nectandra* spp., *Alchornea latifolia*, and *Myrcia splendens*, are common along roadsides and in secondary forests throughout the central mountain range of Puerto Rico (Marcano-Vega et al. 2002). The road also facilitated the census of mistletoes on trees and observations of foraging birds. Our transect ran for a length of 5 km from the north entrance of Carite State Forest on road PR-184 kilometer 27.4 (municipality of Cayey) through kilometer 18.4 on road PR-179 (municipality of Patillas), exiting the reserve in its southwest. At the intersection of PR-184 and PR-179, we chose to follow PR-179 by tossing a coin. We considered a tree as inside the transect if any part of it intersected the road (including the unpaved shoulder area). For each tree, we recorded species, location along the transect, and gender in the case of dioecious *Cecropia* trees. We also measured dbh and height, and tallied the number of all mistletoe species. In the cases of large mistletoes, it was difficult to distinguish individuals and we conservatively counted large “brooms” with multiple stems as a single individual. Mistletoe species were easily identified with the aid of binoculars and a spotting scope, using field marks such as venation pattern of leaves, fruit color, infructescence architecture, and growth form. We collected reference specimens from all species and deposited them at the University of

Puerto Rico Botanical Garden Herbarium (UPR, San Juan, Puerto Rico).

We used Multiple Ordinal Logistic Regression to examine the effects of *Cecropia* sex, height, dbh, and their interaction factors on the probability of infection of male and female trees. We also examined the relationships of sex, dbh, and height on the number of mistletoes per *Cecropia* tree using least-square regression models. For this we included all variables and interaction terms in a backward stepping procedure to select the best models, with probability of stepping set to 0.1.

Frugivores using P. hexastichum

We established four plots to study mistletoe frugivory by the bird community. Plots were 50-m transects along road PR-184 in areas of heavy *P. hexastichum* infection on *Cecropia*, but all plots also contained additional mistletoe species (growing on other hosts): *P. dipterum* (parasitic on the other mistletoes), *P. anceps*, *P. piperoides*, and *Dendrophthora flagelliformis*. Plots were at least 500 m from each other. We recorded the number of instances in which birds visited an infected host tree and fed on mistletoe fruits, including the time that birds spent feeding in *P. hexastichum*. We observed each plot on eight different days from 07:00 to 09:00 hours in the months of September and October of 2004, for a total of 64 hours of observation. Based on these observations, we calculated the proportion of visits in which each bird species was observed consuming *P. hexastichum* fruits per plot. We used Contingency Table analysis (four birds \times four sites) to test for differences in the frequency of use of *P. hexastichum* fruits by bird frugivore species.

Frugivore visitation to uninfected Cecropia trees

During July–October 2004, we conducted simultaneous focal observations of pairs of *Cecropia* trees (i.e., two observers watching a pair of trees at the same time) consisting of a flowering male and a fruiting female along roads PR-184 and PR-179, but within the limits of Carite State Forest. We selected 16 pairs of male and female *Cecropia* trees not infected with mistletoes and of similar dbh (paired $t = 0.62$, $df = 14$, $P = 0.28$) and height (paired $t = 1.13$, $df = 14$, $P = 0.54$) that were 25–100 m from each other. Females were chosen if they had at least one ripe fruit and males if they had at least one open inflorescence. We watched each tree for two hours in the morning, for a total of 64 hours of focal observation. We watched trees from a distance of 20–40 m to allow a view of the whole canopy. During that time, we recorded the number of visits from all bird species; time spent on the tree by each visitor; interactions among birds; and consumption of fruits, flowers, leaves, arthropods, or any other food item. When observing a pair of *Cecropia*, observers switched focal trees after the first hour of observation to evenly distribute sampling error associated

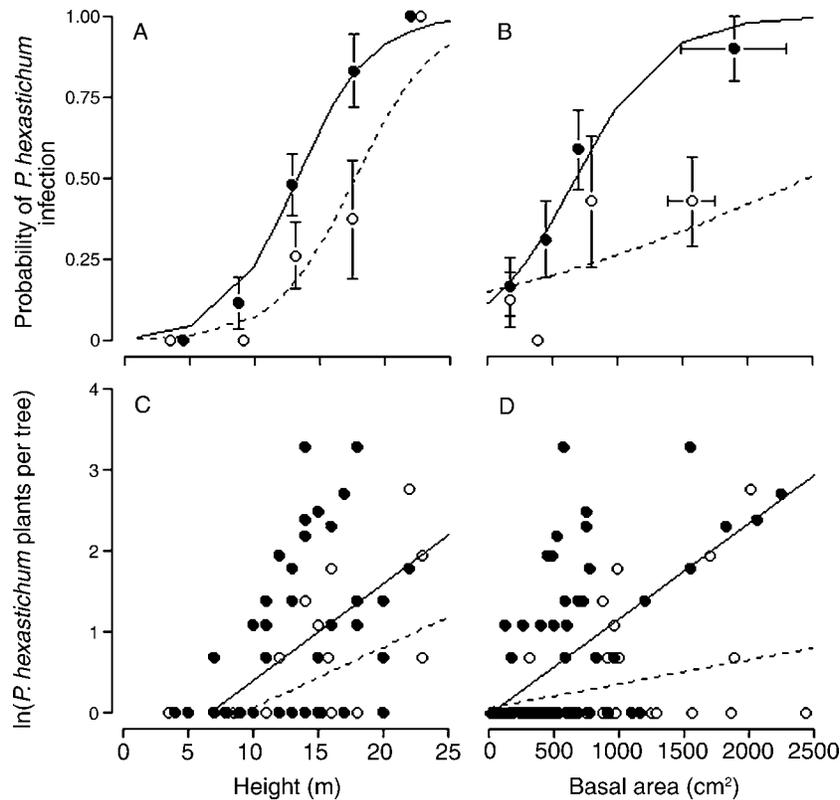


FIG. 1. Mistletoe infection probability (A–B) and intensity (C–D, log-transformed) were higher in female (solid circles, solid lines) than male (open circles, dashed lines) *Cecropia* trees, and increased with height (left) and basal area (right) of females, but only with height of males. Infection probabilities were analyzed using multiple logistic regression (see Appendix), but tree height and basal area have been divided into size classes here for visual clarity. Standard errors are shown for both x- and y-axes in (A) and (B). Logistic models for height (A): for females, $r^2 = 0.16$, $\chi^2 = 9.5$, $P = 0.002$; for males, $r^2 = 0.20$, $\chi^2 = 6.8$, $P = 0.009$. Logistic models for basal area (A–B): for females, $r^2 = 0.17$, $\chi^2 = 7.06$, $P = 0.007$; for males, $r^2 = 0.02$, $\chi^2 = 1.16$, $P = 0.28$. Least-square regression for height (C): for females, $r^2 = 0.19$, $F_{1,59} = 13.1$, $P < 0.001$; for males, $r^2 = 0.30$, $F_{1,42} = 15.4$, $P < 0.001$. Least-square regression for basal area (D): females $r^2 = 0.20$, $F_{1,59} = 13.6$, $P < 0.001$; males $r^2 = 0.08$, $F_{1,42} = 3.4$, $P = 0.072$. See the Appendix for the multiple regression model.

with observer. We recorded the dbh, height, and number of ripe fruits on trees. Using least-square regression models, we examined the effects of *Cecropia* gender, dbh, blocks (i.e., pairs of simultaneously observed male and female trees), height, and interaction factors on visitation rates of bird species that eat and disperse *P. hexastichum*, as well as visitation by the general bird community. We included all variables and interaction terms in a backward stepping procedure to select the best models, with probability of stepping set to 0.1.

RESULTS

Of the 105 *Cecropia* trees in our sample, 61 were female and 44 were male, which was not significantly different from a 1:1 sex ratio ($\chi^2 = 2.76$, $df = 1$, $P = 0.096$). Female *Cecropia schreberiana* trees had higher mistletoe loads and were more heavily infected than male trees (Fig. 1). On average, female *Cecropia* trees had twice as many *Phoradendron hexastichum* plants as did males ($t = 2.51$, $df = 103$, $P = 0.01$). Of the population of female *Cecropia*, 56% was infected with

P. hexastichum, whereas 25% of the male population was infected ($\chi^2 = 4.2$, $df = 1$, $P = 0.04$). Infection intensity increased with tree height for both males and females (Fig. 1A; see Appendix). However, although dbh and height of trees were positively correlated (Spearman's Rho = 0.69, $P < 0.001$, $r^2 = 0.29$), as tree dbh increased, infection increased for females but not for males (Fig. 1B; see Appendix). Similarly, the number of mistletoes per tree increased as a function of height in males and females, and as a function of dbh in females but not in males (Fig. 1B, C; Appendix). Neither dbh nor height differed significantly between sexes in our sample (for dbh, $t = 0.53$, $df = 104$, $P = 0.59$; for height, $t = 0.55$, $df = 104$, $P = 0.55$). Neither males nor females were spatially aggregated in our sample, but were overdispersed (for females, Nearest Neighbor Index = 7.7, $Z = 100.2$; for males, Nearest Neighbor Index = 12.8, $Z = 137.9$; CrimeStat II Software [Levine 2002]).

We recorded 182 bird foraging observations from eight bird species in our four observation sites. Of the

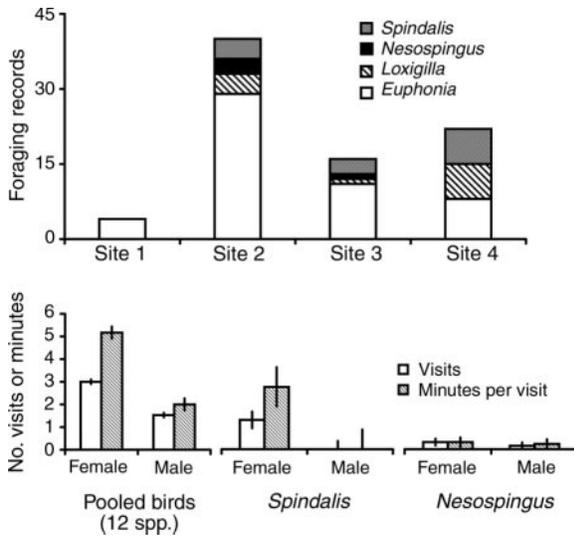


FIG. 2. Foraging records (number of observed visits, by species) show that *Euphonia musica* was the primary frugivore of *Phoradendron hexastichum* at four observation plots, with a high density of *P. hexastichum* in Carite forest, Puerto Rico (upper panel). Secondary frugivores, in decreasing order of importance, were: *Spindalis portoricensis*, *Loxigilla portoricensis*, and *Nesospingus speculiferus*. The frequency of frugivory records differed significantly among frugivores across sites (4×4 contingency table: $\chi^2 = 42.7$, $df = 3$, $N = 61$, $P < 0.001$). In observations of paired, unparasitized *Cecropia schreberiana* (lower panel), bird species visited more often and spent more time in fruiting female than in flowering male trees (mean \pm SE; $N = 16$ pairs; for paired visits, $F_{1,14} = 6.01$, $P = 0.029$; for time spent, $F_{1,14} = 6.97$, $P = 0.019$). *Spindalis portoricensis* and *Nesospingus speculiferus* were the only species observed both visiting uninfected *Cecropia* and consuming *P. hexastichum*.

eight bird species, only four consumed *P. hexastichum* fruits. *Euphonia musica* (hereafter *Euphonia*) was the main consumer of *P. hexastichum* (Fig. 2), with an average of 1.2 records per observation hour. Secondary consumers of *P. hexastichum* were Puerto Rican *Spindalis* (*Spindalis portoricensis*, hereafter *Spindalis*; see Plate 1), with 0.31 records/h; Puerto Rican Bullfinch (*Loxigilla portoricensis*, hereafter *Loxigilla*), with 0.25 records/h; and Puerto Rican Tanager (*Nesospingus speculiferus*, hereafter *Nesospingus*), with 0.12 records/h (Fig. 2). All four species were observed swallowing the mistletoe seeds after separating and dropping fruit husks through mandibulation (see also Carlo et al. 2003). Frequency of *P. hexastichum* frugivory was significantly different among bird frugivore species across sites (Fig. 2). However, the duration of frugivory visits to *P. hexastichum* plants ranged from 4.0 ± 0.82 min to 5.2 ± 2.12 min (mean \pm SE) and did not differ among bird species (one-way ANOVA, $F = 0.04$, $df = 3$, 59 , $P = 0.98$). *Euphonia*, the primary consumer of *P. hexastichum*, was recorded feeding almost exclusively on mistletoes (73 records in five mistletoe species), and the mistletoe-like epiphyte *Anthurium scandens* (11

records). In contrast, secondary bird consumers used a wider variety of fruiting plant species when available at observation sites. For example, *Spindalis* ate two *Phoradendron* species (13 records) and six other fruiting species (27 records). *Loxigilla* ate two *Phoradendron* species (12 records) and three other plant species (10 records). We observed *Nesospingus* feeding on four *Phoradendron* species (six records) and five other plant species (five records).

During the 64 hours of focal observation of uninfected pairs of male and female *Cecropia* trees, we recorded 68 visits from 12 bird species. The most common visitor was *Coereba flaveola* (20 records), followed by *Spindalis* (17 records). Nine bird species visited *Cecropia* males and 10 species visited females. Seven bird species visited female *Cecropia* to feed on fruits, whereas no bird that visited *Cecropia* males consumed inflorescences, although seven species foraged for arthropods on male trees. On average, birds visited fruiting female *Cecropia* trees twice as often as flowering males, and spent more than twice the visitation time in females as in males (Fig. 2). We observed *Spindalis* visiting only female *Cecropia* trees and feeding on fruit on all occasions (Fig. 2). On the other hand, *Nesospingus* consumed fruit from female trees, but also foraged for arthropods on both male and female trees, showing no significant difference in visitation between male and female trees (Fig. 2).

Our selected regression model for *Cecropia* visitation by the whole bird community explained over half of the variability and showed that gender and dbh were positively related to the number of bird visits (Appendix). Height was a predictor of visitation for female trees ($r^2 = 0.39$, $F = 8.43$, $df = 1,13$, $P = 0.012$), but not for males ($r^2 = 0.004$, $F = 0.058$, $df = 1,13$, $P = 0.812$), and therefore produced a significant interaction between height and gender (Appendix). On the other hand, one model better predicted *Spindalis* and *Nesospingus* visitation with only *Cecropia* gender as a variable (Appendix).

DISCUSSION

Infection by *Phoradendron hexastichum* on *Cecropia schreberiana* trees was female biased. On average, females were twice as infected and carried twice the mistletoe loads of male trees (Fig. 1). We also observed birds visiting more often and spending more time on *Cecropia* females than on males (Fig. 2), especially frugivorous species that were observed using the fruits of both *P. hexastichum* and *Cecropia* frequently (Fig. 2). These observations suggest that the female-biased infection pattern was caused by differences in the intensity of *P. hexastichum* seed rain between sexes, and that heightened parasitism can be an overlooked cost of a mutualism in some cases (but see van Ommeren and Whitham 2002). The spatial linkage of *Cecropia* and *P. hexastichum* fruits probably is produced by the action of birds such as *Spindalis portoricensis*, which



PLATE 1. Male Puerto Rican *Spindalis* (*Spindalis portoricensis*) feeding on the fruits of a female *Cecropia schreberiana*, a dioecious tree species. *Spindalis* visits female *Cecropia* trees more often than male trees to feed on fruit, but also feeds frequently on mistletoes that grow on *Cecropia* trees. *Spindalis* behavioral pattern matches the female-biased mistletoe infection pattern observed on *Cecropia* trees in Carite State Forest, Puerto Rico. Photo credit: T. Carlo.

are important and abundant consumers of *P. hexastichum* fruits (Fig. 2) and predictable visitors to fruiting *Cecropia* females, but not to males (Fig. 2). It is noteworthy that we did not observe *Euphonia musica* visiting uninfected *Cecropia* trees. The absence of this species in our observations suggests that nonspecialized frugivores that use both *Cecropia* and *P. hexastichum* are responsible for the majority of first-time infections in noninfected *Cecropia*.

Our findings show that indirect ecological interactions can shape the spatial demography and distribution of frugivore-dispersed plants, as well as the spatial linkage of plant species, through directional patterns of dispersal (Wenny 2001). The dioecious *Cecropia* trees can be understood as two types of suitable habitat patches, differing only in the presence of another fruit resource. The presence of fruit resources in female *Cecropia* "patches" attracts shared frugivores and links female *Cecropia* and *P. hexastichum* in space. Similar mechanisms of directional dispersal may explain the results of studies such as Vieira et al. (1994), Slocum (2001), and Clark et al. (2004), which report frugivore-dispersed plants serving as recruitment foci for other fleshy-fruited species, linking them spatially. However, the role of generalist frugivores in seed dispersal pro-

cesses (including directed dispersal) has been overlooked. Because generalist frugivores consume wider arrays of fruits and may move more frequently among plant species and habitat types than do specialists, they may be important in successional processes and the structuring of plant communities through their role in seed dispersal.

In Carite forest, the mistletoe specialist *Euphonia* spends most of its time foraging on *P. hexastichum* and much less time visiting other fruiting plants (Carlo et al. 2003), whereas *Spindalis* feeds on and prefers a wider variety of fruiting plant species (Carlo et al. 2003). Thus, two contrasting feeding behaviors in members of a frugivore community may generate separate, but complementary, seed-rain patterns that benefit a plant species such as *P. hexastichum*. The dependency of *Euphonia* on Viscaceae mistletoes is well documented (see Carlo et al. 2003) and should have the effect of reinforcing the intensity of *P. hexastichum* seed rain in places where mistletoes are already present. The positive feedback between mistletoe infection and seed rain, mediated by a specialist frugivore, has been documented at the scales of individual trees and neighborhoods (Aukema and Martínez del Río 2002, Aukema 2004). On the other hand, generalist frugivores

such as *Spindalis* and *Nesospingus speculiferus* appear more likely than *Euphonia* to spread mistletoes to uninfected trees and areas, thus creating additional heterogeneity in its pattern of distribution.

Birds may be more attracted to taller trees for perching (Martínez del Río et al. 1995, Aukema and Martínez del Río 2002) and for foraging (taller trees are usually larger, thus providing more foraging substrate area). It is not surprising that both infection probability and mistletoe loads were positively correlated with *Cecropia* height in both male and female trees. Although tree height and basal area were correlated in our sample, the relationship was noisy ($r^2 = 0.16$, $P < 0.001$), probably because *Cecropia* is a fast-growing species. Trees can reach a threshold of height relatively rapidly while basal area keeps increasing (height may also decrease over time, due to storm damage to its brittle branches). It is revealing then, that basal area is a strong predictor of infection probability and mistletoe loads for females, but not for males (Fig. 1). This difference can be interpreted as a higher cumulative probability of infection and reinfection of female trees as a function of higher visitation rates by mistletoe vectors over a lifetime. *Cecropia* fruits provide an additional positive feedback that males lack; hence, males show an infection relationship with height, but not with basal area (i.e., age).

For the frugivore-mediated interaction between *P. hexastichum* and *Cecropia* fruits to be driving our observed pattern of infection, fruiting times of both plant species must overlap frequently. *Cecropia* and *Phoradendron* spp. in Puerto Rico have extended fruiting periods and, at virtually any time of the year, fruiting individuals of either species can be found (Carlo et al. 2003, 2004). The fruiting season overlap among plants that share seed dispersal vectors can promote competitive and/or facilitative plant–plant seed-dispersal interactions, especially in insular communities where most plants rely on a few frugivore species for dispersal services (Carlo et al. 2003). For example, Saracco et al. (2005) found that frugivore visitation to *Schefflera morototoni* trees in Puerto Rico was increased by the presence of heterospecific neighbors with shared frugivores. Similarly, Carlo (2005) found in an experiment that the seed dispersal of *Solanum americanum* increased (i.e., seeds reached more locations) when neighbored by *Cestrum diurnum* than by conspecifics, because shared-frugivore diversity increased in inter-specific neighborhoods.

Cecropia fruits may facilitate seed dispersal of *P. hexastichum* in two ways. First, female *Cecropia* can increase fruit removal of mistletoes growing on them by attracting more shared frugivores. Second, *P. hexastichum* can obtain directional dispersal toward suitable establishment sites (i.e., *Cecropia* hosts). Directional dispersal may be particularly important, given that mistletoes are limited by host compatibility (Reid 1991, Norton and Carpenter 1998). It is unclear if *Cec-*

ropia obtains any dispersal benefit from being infected by mistletoe. Van Ommereen and Whitham (2002) argue that *Juniperus monosperma* benefited from infection with *Phoradendron juniperinum* because bird frugivores were more attracted to the mistletoe and because mistletoes had a more constant fruit supply among years than did junipers. Because *Cecropia* is probably one of the least dispersal-limited tropical plants (Cruz 1974, Charles-Dominique 1986, Carlo et al. 2003), it is unlikely to accrue any benefits from the presence of mistletoes. Like other mistletoe species, *P. hexastichum* probably weakens the limbs where it grows, making them more susceptible to wind damage. However, the lack of difference in dbh and height between males and females in our sample suggests that the negative effects of *P. hexastichum* on *Cecropia* growth are not severe.

The differential mistletoe infection of female over male *Cecropia* appears to have its origin in the activities of frugivorous seed dispersers that feed on both *Cecropia* and mistletoe fruits. The pattern is then accentuated by the behavior of the more specialized *Euphonia*. The *Cecropia*–frugivores–*Phoradendron* network of interactions seems to have led to (1) spatial linkage of two plant species through directional dispersal; (2) plant–plant facilitation through shared frugivores; and (3) bird–bird facilitation, in which generalist frugivores start new foci of infection that specialist frugivores can take advantage of. The sex bias of *P. hexastichum* infections on *Cecropia* is a good example of a facilitative interaction mediated by seed dispersers. In spite of the recent interest in positive interactions in communities, little attention has been paid to the potential role of seed dispersal facilitation in communities (Callaway and Walker 1997, Bruno et al. 2003, Lortie et al. 2004). Because mistletoes are restricted to specific recruitment locations (host species) that are easily identified and observed, the influence of frugivores on mistletoe distribution is relatively easy to assess (Reid 1991, Aukema and Martínez del Río 2002). Although our study is on a seemingly peculiar system, we suggest that closer examination will reveal similar patterns in other plant–frugivore networks.

ACKNOWLEDGMENTS

We would like to thank Keren Umpierre, Ángel García, Sindialí Acosta, and Emma for assistance with fieldwork. N. Wheelwright, S. Sargent, A. Cruz, C. Martínez del Río, and A. Lugo provided helpful comments on the manuscript. This work was supported by NSF grant DEB 04-07826 to T. A. Carlo, a David H. Smith Conservation Research Fellowship to J. E. Aukema, the Department of Ecology and Evolutionary Biology of the University of Colorado, the University of Puerto Rico, the Botanical Garden of the University of Puerto Rico, the International Institute of Tropical Forestry GIS and Remote Sensing Laboratory, E. Santiago-Valentín, and W. Gould.

LITERATURE CITED

Aukema, J. E. 2003. Vectors, viscins, and Viscaceae: mistletoes as parasites, mutualists, and resources. *Frontiers in Ecology and the Environment* 1:212–219.

- Aukema, J. E. 2004. Distribution and dispersal of desert mistletoe is scale-dependent, hierarchically nested. *Ecography* **27**:137–144.
- Aukema, J. E., and C. Martínez del Río. 2002. Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. *Ecology* **83**:3489–3496.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* **18**:119–125.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**:1958–1965.
- Carlo, T. A. 2005. Interspecific neighbors change seed-dispersal pattern of an avian-dispersed plant. *Ecology* **86**:2440–2449.
- Carlo, T. A., J. A. Collazo, and M. J. Groom. 2003. Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia* **134**:119–131.
- Carlo, T. A., J. A. Collazo, and M. J. Groom. 2004. Influences of fruit diversity and abundance on bird use of two shaded coffee plantations. *Biotropica* **36**:602–614.
- Charles-Dominique, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guyana. Pages 119–135 in F. T. Estrada A, editor. *Frugivory and seed dispersal*. Dr W. Junk, Boston, Massachusetts, USA.
- Clark, C. J., J. R. Poulsen, E. F. Connor, and V. T. Parker. 2004. Fruiting trees as dispersal foci in a semi-deciduous tropical forest. *Oecologia* **139**:66–75.
- Cruz, A. 1974. Feeding assemblages of Jamaican Birds. *Condor* **76**:103–107.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London, UK.
- Levine, N. 2002. CrimeStat II. A spatial statistics program for the analysis of crime incident locations. Ned Levine and Associates and the National Institute of Justice, Washington, D.C., USA.
- Lortie, C. J., R. W. Brooker, P. Choler, R. Michalet, F. L. Pugnaire, and R. Callaway. 2004. Rethinking plant community theory. *Oikos* **107**:433–438.
- Marcano-Vega, H., T. M. Aide, and D. Baez. 2002. Forest regeneration in abandoned coffee plantations and pastures in the Cordillera Central of Puerto Rico. *Plant Ecology* **161**:75–87.
- Martínez del Río, C., M. Hourdequin, A. Silva, and R. Medel. 1995. The influence of cactus size and previous infection on bird deposition of mistletoe seeds. *Australian Journal of Ecology* **20**:571–576.
- Norton, D. A., and M. A. Carpenter. 1998. Mistletoes as parasites: host specificity and speciation. *Trends in Ecology and Evolution* **13**:101–105.
- Reid, N. 1991. Coevolution of mistletoes and frugivorous birds. *Australian Journal of Ecology* **16**:457–469.
- Saracco, J. F., J. A. Collazo, M. J. Groom, and T. A. Carlo. 2005. Crop size and fruit neighborhood effects on visitation to fruiting trees. *Biotropica* **37**:80–86.
- Sargent, S. 1990. Neighborhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology* **71**:1289–1298.
- Schupp, E. W., and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* **2**:267–275.
- Slocum, M. G. 2001. How tree species differ as recruitment foci in a tropical pasture. *Ecology* **89**:2547–2559.
- Tewksbury, J. J., and G. P. Nabhan. 2001. Seed dispersal. Directed deterrence by capsaicin in chillies. *Nature* **412**:403–404.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**:81–92.
- van Ommeren, R. J., and T. G. Whitham. 2002. Changes in interactions between juniper and mistletoe mediated by shared avian frugivores: parasitism to potential mutualism. *Oecologia* **130**:281–288.
- Vieira, I. C. G., C. Uhl, and D. Nepstad. 1994. The role of the shrub *Cordia multispicata* Cham. as a succession facilitator in an abandoned pasture in Paragominas, Amazonia. *Vegetatio* **115**:91–99.
- Wang, B. C., and T. B. Smith. 2002. Closing the seed dispersal loop. *Trends in Ecology and Evolution* **17**:379–385.
- Webb, C. O., and D. R. Peart. 2001. High seed dispersal rates in faunally intact tropical rain forest: theoretical and conservation implications. *Ecology Letters* **4**:491–499.
- Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research* **3**:51–74.
- Wenny, D. G., and D. J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences (USA)* **95**:6204–6207.
- Wetmore, A. 1916. *Birds of Porto Rico*. USDA, Washington, D.C., USA.

APPENDIX

A table showing results of multiple regression models is available in ESA's Electronic Data Archive: *Ecological Archives* E086-176-A1.