

## INTERSPECIFIC NEIGHBORS CHANGE SEED DISPERSAL PATTERN OF AN AVIAN-DISPERSED PLANT

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**Abstract.** Ecologists increasingly recognize that plant–plant facilitation can influence plant community structure. However, seed dispersal facilitation among plant neighbors that share seed dispersal agents has received little study. Seed dispersal facilitation among neighboring plants can be defined as an increase in the number, distances, and/or places reached by a plant’s seeds that is due to the presence of co-fruiting-plant neighbors with which it shares frugivore seed dispersers. I experimentally tested the potential for seed dispersal facilitation and competition among co-fruiting-plant neighbors using *Solanum americanum* and *Cestrum diurnum*, two plant species that co-occur in open habitats of Puerto Rico and whose seeds are dispersed by the same bird species. I constructed *S. americanum* neighborhoods with and without *C. diurnum* (i.e., mixed and non-mixed) while controlling plant ripe-fruit crop and surrounding fruiting landscape in six replicate fields. I quantified seed dispersal using a grid of seed-collecting trays bearing bird perches placed at four distance classes from experimental plant neighborhoods. I found no difference in the quantity or rate of fruit removal between mixed and non-mixed neighborhoods. However, there were significantly more bird droppings with seeds collected from mixed neighborhoods than from monospecific *S. americanum* neighborhoods. Although the quantity of seed dispersal was no different among treatments, *S. americanum* seeds were distributed into more “packaging units” and reached more sampling trays when neighbored by *C. diurnum*. This was explained by the higher number of frugivores that visited mixed neighborhoods compared to *Solanum*-only neighborhoods, and by an associated increase in agonistic interactions in mixed neighborhoods. Therefore, the seed dispersal pattern of *S. americanum* was facilitated by the presence of fruiting *C. diurnum* neighbors. This study provides the first experimental evidence that seed dispersal kernels of endozoochorous plants are context dependent and not entirely a property of individual plant or disperser species.

**Key words:** *Cestrum diurnum*; dispersal kernel; facilitation; frugivory; indirect interactions; *Mimus polyglottus*; Puerto Rico; seed dispersal; *Solanum americanum*; *Tyrannus dominicensis*.

### INTRODUCTION

Seed dispersal processes are fundamental to maintain populations and species diversity in plant communities (Tilman 1997, Nathan and Muller-Landau 2000, Condit et al. 2002) and mutualistic fruit-eating animals provide seed dispersal for many plant species (Van der Pijl 1972). Indeed, in many plant communities, endozoochory is the dominant form of species’ dispersal (Frankie et al. 1974, Gentry 1982); in some communities >90% of woody plant species have been reported to be animal dispersed (Terborgh et al. 2002). Thus, to understand the ecology of many plant species and communities, it is necessary to have a mechanistic understanding of frugivore–plant interactions and their relationship to plant population dynamics and diversity (Wang and Smith 2002).

Indirect interactions such as competition and facilitation could take place at local scales (e.g., plant neighborhoods) among plants that share frugivore seed

dispersers in a parallel way to pollinators that create both competition (Free 1968, Levin and Anderson 1970, Waser 1978) and facilitation (Schemske 1981, Feinsinger et al. 1986, Johnson et al. 2003) among co-flowering plants. However, competition and facilitation among plant neighbors in plant–pollinator and plant–frugivore systems differ in several important ways (Wheelwright and Orians 1982). For example, pollinators visiting multiple plant species in a floral neighborhood may cause plant–plant competition by clogging stigmas with foreign pollen (Free 1968), but there is not an analogous problem for frugivores feeding on multiple species in a fruiting neighborhood. Because frugivores affect the location of plant propagules through dispersal, they have the potential to create patterns of species associations of their food plants (Clark et al. 2004), something pollinators cannot do directly. On the other hand, the plant fitness consequences of a plant–pollinator interaction (i.e., fruit set) are easier to estimate than in plant–frugivore interactions because of methodological difficulties and the multiplicity of factors affecting post-dispersal stages of plant recruitment (Jordano and Herrera 1995, Wang and Smith 2002).

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Few frugivory studies have addressed plant neighborhood interactions, and those that have done so used only surrogate measures of seed dispersal such as fruit removal or frugivore visitation. For example, Manasse and Howe (1983) found a negative correlation between the number of neighboring fruiting conspecifics and fruit removal rates on *Virola surinamensis* in Panama, while Sargent (1990) found the opposite for *Viburnum dentatum* in eastern North America. French et al. (1992) found no influence of neighbors on fruit removal rates for *Coprosma quadrifida* in Australia. Last, Saracco et al. (2005) in Puerto Rico found that certain fruiting-plant species neighbors of *Schefflera morototoni* facilitated frugivore visitation, while other species hampered it. Other than these studies, and in spite of its potential relevance in seed limitation and recruitment limitation processes (Muller-Landau et al. 2002), seed dispersal interactions among neighboring plants that share frugivores has received little conceptual or empirical attention.

Frugivores can impact co-fruiting-plant species in various ways that could cause differences in the seed dispersal success of plant individuals. Differences in seed dispersal success of plants could be caused by a low availability of frugivores relative to the number of plants demanding services (i.e., frugivore limitation) and/or to the foraging behavior and movement patterns in relation to local habitat characteristics (Aldrich and Hamrick 1998). Intraspecific competition may occur due to frugivore limitation or when frugivores respond to crop size variation in a density-dependent fashion (Howe and Estabrook 1977, Davidar and Morton 1986, Sallabanks 1993), or to differences in plant height (Aukema and Martinez del Rio 2002). Similarly, hierarchical use of fruiting-plant species by frugivores could promote interspecific competition that reduces seed dispersal success for less preferred species when preferred species are present (Carlo et al. 2003). On the other hand, interspecific facilitation could be caused by a “magnet” effect of preferred or more rewarding plant species over less preferred species (Thomson 1978, Johnson et al. 2003), by nutritional complementarity (Whelan et al. 1998), or it could arise as an artifact of staggered phenology patterns of plants, which can allow frugivores to shift use of fruiting-plant species in situ (Wheelwright 1985). Species-diverse plant neighborhoods could then offer fruit resources for longer time periods, reducing temporal stochasticity in the local fruit supply and better retaining frugivores in the locality (Burns 2003, 2004).

Frugivore-mediated seed dispersal facilitation can be detected as a qualitative and/or quantitative increase (sensu Schupp 1993) in a plant’s seed dispersal pattern that is due to the indirect effects of other fruiting plants with which it shares frugivores. Facilitation would result in increased seed dispersal success that could be measured by changes in the dispersal *kernel* of plants: the density distribution of dispersed seeds across dis-

tances and/or locations (Nathan and Muller-Landau 2000). However, it is important to consider that a fine line may separate competition from facilitation because whether or not the interaction is beneficial or detrimental can be subject to temporal and spatial variation in ecological context or scale of measurement (Bruno et al. 2003).

Here, I tested the hypothesis that seed dispersal patterns of plants are affected by neighboring fruiting plants when frugivore seed dispersers are shared. I conducted field experiments using *Solanum americanum* (hereafter *Solanum*) and *Cestrum diurnum* (hereafter *Cestrum*), two plant species commonly found in association with one another in cattle pastures and other open and disturbed habitats in Puerto Rico. I tested the specific hypothesis that fruiting *C. diurnum* neighbors changed the dispersal of *S. americanum* plants in either a positive (facilitation) or negative (competition) way by changing the quantity or quality components of the *Solanum* seed rain (sensu Schupp 1993).

#### METHODS

I conducted this study from January through April 2004 in six experimental fields on grounds of the University of Puerto Rico Experimental Station in Rio Piedras. The fields were open pastures with scattered trees. Field ranged from 4500 m<sup>2</sup> to 7500 m<sup>2</sup> in size and were somewhat delimited by rows and groups of trees (see Appendix). The location of the six fields was selected so each one contained at least one unique pair of territorial *Mimus polyglottus* (hereafter *Mimus*) and *Tyrannus dominicensis* (hereafter *Tyrannus*) and was not <150 m from another field (see Appendix). *Mimus* and *Tyrannus* are omnivorous birds that most frequently feed on invertebrates, but also feed heavily on fruit resources opportunistically (see Plate 1). These two bird species were the main consumers of *Solanum* and *Cestrum* fruits in the study site, accounting for 97.6% ( $N = 698$  observations) of consumption during a fruit-removal experiment conducted in 2003 at the study site (T. A. Carlo, unpublished data). Movements and territories of *Mimus* and *Tyrannus* were determined by visually tracking the flights of color-banded individuals during September–December 2003 (T. A. Carlo, unpublished data). This ensured that each field represented similar but independent replicate environments where different bird individuals performed most of the fruit removal and seed dispersal.

I performed experiments using potted *Solanum* and *Cestrum* plants with ~200 individuals of each species. Fruits of both species are round berries that turn dark purple or black when ripe. On average, *Solanum* fruits are smaller than *Cestrum* fruits (*Cestrum*, mass  $0.27 \pm 0.08$  g, length  $8.23 \pm 1.44$  mm,  $N = 34$ ; *Solanum*, mass  $0.18 \pm 0.08$  g, length  $6.24 \pm 0.61$  mm,  $N = 34$  [mean  $\pm$  SE]), but *Solanum* had more seeds per fruit than *Cestrum* (*Solanum*,  $38.4 \pm 12.9$ ; *Cestrum*,  $8.8 \pm 2.2$ ). To reduce unwanted variation in fruit traits among in-



PLATE 1. Northern Mockingbird (*Mimus polyglottus*) feeding on the fruits of the black nightshade *Solanum americanum* in Rio Piedras, Puerto Rico. Photo credit: T. Carlos.

dividuals, I grew all *Solanum* plants from seeds from a single maternal plant. I transplanted mature *Cestrum* plants to pots from a single wild population in Arecibo, Puerto Rico. I kept plants in 26-L plastic pots in a standard mixture of topsoil (50%), peat moss (25%), and sand (25%). All plants received equal amounts of light, water, and fertilizer (Osmocote 14-14-14, Marysville, Ohio, USA).

To test for effects of *Cestrum* neighbors on the seed dispersal of *Solanum*, I used the following design. Experimental neighborhood treatments were S, SS, and SC, each replicated six times (one replicate per field). S treatments were composed of two *Solanum* plants, each bearing 150 ripe fruits; SS treatments were composed of four *Solanum* plants, each bearing 150 fruits; SC were composed of two *Solanum* and two *Cestrum* plants, each bearing 150 ripe fruits. Hence, the experiment tested the seed dispersal pattern of *Solanum* in mixed neighborhoods (SC) against *Solanum* growing with more *Solanum* controlling for crop size and against *Solanum* at half the fruit density. The S neighborhoods were controls for the exact number of *Solanum* fruits/seeds found in the mixed treatment while the SS acted as a control for the larger number of fruits in mixed neighborhoods. The response variables were

the number and location of fecal samples containing seeds from *Solanum* and/or *Cestrum* collected at 34 trays bearing perches 3 m tall (Appendix), the frequency of frugivore visitation, the number of fruits taken per visit, agonistic interactions per hour, and the number of visiting frugivores. The plastic trays under bird perches measured 30 × 60 cm with a depth of 5 cm, and were arranged in four concentric circles representing four distance classes centered at the plant neighborhood (Appendix). The number of trays at each distance class was roughly proportional to the perimeter of the circle: 1 at 1 m, 4 at 10 m, 10 at 30 m, and 19 at 60 m.

I performed the full set of treatment trials (S, SS, SC) in one field at a time to reduce the chances of contamination from seeds from other neighborhoods. I also surveyed the whole study site and surroundings and eradicated all *Solanum* (none found) and *Cestrum* plants (two plants removed) from the area. One trial consisted of one neighborhood treatment placed at the center of the tray grid of the experimental field. Trials lasted a minimum of one day and ended when the entire fruit crop had been removed from the neighborhood, which never lasted more than three days. I chose the order of neighborhood trials at random and performed

the trials in a field consecutively in a time span of two weeks. Hence, for statistical analyses I treated the full set of trials within a field as block set and use paired tests for analyses.

The day prior to each trial, I selected plants from the greenhouse population according to treatments and bearing at least 150 ripe fruits. Next, I set the ripe fruit crop of each focal plant to 150 by pruning the excess fruits (ripe and unripe) and set the height of plants to 1–1.5 m by pruning or bending and fastening tall branches with string. I tagged 40 fruits in each plant that were distributed in 7 infrutescences (5–7 fruits per infrutescence). At dusk I placed the plants in the center of the field (tray grid) and covered the 34 trays of the seed trap grid with new newspaper. The next day I conducted focal observations of the neighborhood for one hour between 0700 and 1000, and one hour between 1500 and 1700. I observed the neighborhood from a location outside the tray grid, equipped with binoculars and a spotting scope. I recorded bird species visitation, individuals, number, and species of fruits consumed per visit, agonistic interactions, and the duration of each visit. Because many birds were not color banded (although in some cases, plumage differences allowed individual recognition), I noted the number of different birds feeding at the neighborhoods by assigning each bird a temporary identification number and then noted the maximum number of birds feeding at any one time. At 1000, 1300, and 1700, I checked the tagged infrutescences and recorded the number of surviving fruits. After 1800 hrs, I counted the number of fecal samples on trays, examining each dropping and recording the presence or absence of *Solanum* and/or *Cestrum* seeds. In three of the six experimental fields, I collected all fecal samples from all treatments by placing each one in a small paper bag to later count the seeds. I cleaned trays during the seed counts and continued the experiment the next day using the same protocol until all fruits were removed from the neighborhood.

In addition, I conducted trials with a third plant species, *Rivina humilis* (Phytolaccaceae), that served to check for potential contamination with seeds from unknown *Solanum* and *Cestrum* sources other than experimental neighborhoods. *Rivina* is also consumed and dispersed by *Tyrannus* and *Mimus* (T. A. Carlo, unpublished data), and I had a potted population for uses in related research. If the *Solanum* and/or *Cestrum* seeds reached sampling trays during a *Rivina* trial, I could determine that contamination from foreign seed sources was taking place in the field. I performed *Rivina* trials in the same manner as *Solanum* and *Cestrum* trials in a randomly determined position within the succession of treatment trials. During the six check-tests using *Rivina* neighborhoods, I found no seed samples from either *Solanum* or *Cestrum*. Neither did I find *Cestrum* seed samples during any *Solanum*-only trials. In cases where trials lasted more than one day, the

numbers of seeds reaching trays decreased with each additional day of trial as the crop of neighborhoods was depleted. Hence, these observations provide confidence that *Solanum* and *Cestrum* seeds found at trays were from experimental plant sources and not from foreign plants unaccounted in the experiment.

#### Statistical analyses

For each experimental unit (i.e., neighborhood treatment per field), I calculated the average number of fruits consumed by each bird species per visit, the maximum number of different birds visiting each neighborhood, the average number of agonistic interactions (bird chases averaged across all observation periods), the number of fecal samples with seeds of *Solanum* and/or *Cestrum* (hereafter seed samples), the number of *Solanum* seed samples per plant (the number of fecal samples with *Solanum* seeds found at trays divided by the number of *Solanum* plants in the neighborhood of origin), and the number of different trays reached by *Solanum* seeds per plant (the number of different trays reached by *Solanum* seeds divided by the number of *Solanum* plants in the neighborhood of origin). I divided the number of *Solanum* seed samples by the number of *Solanum* plants in the neighborhood of origin as a way to compare the relative dispersal “fitness” of individual *Solanum* plants in the three neighborhood types.

Because I measured multiple interrelated response variables on the same set of treatments, I used MANOVA followed by post hoc univariate ANOVAs and/or *t* tests depending upon the question (Scheiner 1993). As recommended by Scheiner (1993), I included all of the responses to be compared a posteriori in univariate form. I used Pillai’s trace statistic, which is the most robust of MANOVA test statistics (particularly when response variables are correlated; see Scheiner 1993). I fitted all of the responses by treatment and field factors (i.e., treatment responses were paired by field) in MANOVA, ANOVAs, and *t* tests. To compare fruit-removal rates among treatments, I used survival analysis (Kaplan-Meier). For this analysis, I averaged, across replicates of each neighborhood, the time interval (i.e., daylight hours: 4, 8, 12, . . . 36) at which removal was detected for each of the 40-tagged fruits. I then performed survival analysis comparing neighborhood treatments. To compare the number of seed samples of neighborhood treatments per distance class I used a 3 × 4 contingency table (three treatments and four distance classes). For this I used the average seed samples per distance class of each treatment (averaged across fields). Last, I used chi-square goodness-of-fit to test the null hypothesis that bird species made proportional use (i.e., no preference) of *Solanum* and *Cestrum* fruits when feeding in SC neighborhoods. Because *Solanum* fruits are, on average, two-thirds the mass of *Cestrum* fruits, I weighted their relative mass to calculate the

TABLE 1. Bird frugivores visited *Solanum*–*Cestrum* (SC) plant neighborhoods more often than *Solanum* neighborhoods with *Mimus* birds removing most fruits (and preferring *Solanum americanum*; *Tyrannus* preferred *Cestrum diurnum*) and leading most agonistic intra- and interspecific interactions.

Category	Bird species		
	<i>Mimus polyglottus</i>	<i>Tyrannus dominicensis</i>	<i>Turdus plumbeus</i>
Visits per neighborhood treatment (mean ± SE)			
S	3.67 <sup>a</sup> ± 0.99	6.0 <sup>a</sup> ± 1.48	0
SS	9.17 <sup>ab</sup> ± 1.89	9.67 <sup>ab</sup> ± 3.27	0
SC	12.00 <sup>b</sup> ± 1.50	14.33 <sup>b</sup> ± 3.02	1.00 ± 1.00
Observed total fruit removal per neighborhood treatment			
S	158	50	0
SS	312	97	0
<i>Solanum</i> in SC	305** (234)	45* (55.8)	34 (35)
<i>Cestrum</i> in SC	85** (156)	48* (37.2)	17 (16)
Observed number of agonistic interactions			
Chasing <i>Mimus</i>	15	1	0
Chasing <i>Turdus</i>	3	0	0
Chasing <i>Tyrannus</i>	81	6	0

Notes: Expected observations for  $\chi^2$  test are in parentheses (SC only) and are based on fruit mass (1 *Solanum* fruit = 0.67 *Cestrum*). \*  $P < 0.05$ ; \*\*  $P < 0.001$  for  $\chi^2$  statistic,  $df = 1$ . Fruit availability was as follows: S neighborhoods had two *Solanum* plants with 150 fruits each; SS had four *Solanum* plants, with 150 fruits each; SC had two *Solanum* and two *Cestrum* plants with 150 fruits each. Superscript letters indicate treatment means that differ significantly at  $P < 0.05$  from other visitation means (within bird species) based on Tukey-Kramer hsd post hoc test.

expected values in the test. For example, to calculate the expected number of *Solanum* fruits taken by a bird species, I divided the average mass of *Cestrum* fruits by the sum of *Cestrum* and *Solanum* average fruit mass [i.e.,  $0.27/(0.27 + 0.18)$ ] and then multiplied it by the

total number of fruits taken (*Solanum* + *Cestrum*) at SC neighborhoods. The expected number of *Cestrum* fruits taken was then  $0.18/(0.27 + 0.18)$  multiplied by total consumption. I conducted all statistical analyses with JMPIN software (version 4.0.2; SAS Institute 2000).

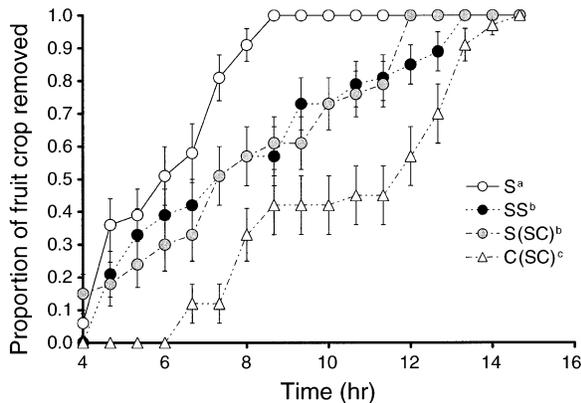


FIG. 1. Survival curves (Kaplan-Meier) using fruit-removal times (mean ± SE) of experimental plants in three neighborhood treatments. Removal times of 40 tagged fruits were averaged across six replicates per treatment: S indicates neighborhoods bearing 300 *Solanum americanum* ripe fruits (two plants bearing 150 fruits each); SS indicates neighborhoods bearing 600 *Solanum* ripe fruits (four plants bearing 150 fruits each); and S(SC) indicates *Solanum* fruits and C(SC) indicates *Cestrum diurnum* fruits in mixed neighborhoods (two *Solanum* plants bearing 150 fruits each and two *Cestrum* plants bearing 150 fruits each). Superscript letters indicate curves that are significantly different from each other in pairwise comparisons (Bonferroni corrected).

RESULTS

During 40 hours of focal observation, I recorded the removal of 1151 fruits: 1001 *Solanum*, and 150 *Cestrum* (Table 1), in 335 bird visits to experimental neighborhoods. The rate at which proportions of fruits disappeared from tagged infrutescences per neighborhood was fastest for S neighborhoods, lowest for *Cestrum* fruits in SC neighborhoods, and there was no difference for *Solanum* fruits between SC and SS neighborhoods (Fig. 1). I observed three bird species visiting neighborhoods and consuming fruit: *Mimus*, *Tyrannus*, and *Turdus plumbeus* (hereafter *Turdus*). *Tyrannus* visited more frequently, followed closely by *Mimus*, while *Turdus* visits were rare (Table 1). However, *Mimus* birds consumed more fruits per visit than *Tyrannus* and overall accounted for the removal of the largest number of *Solanum* and/or *Cestrum* fruits from experimental neighborhoods (Table 1), but with no difference among treatments (Fig. 2A). Visits in which birds were observed eating both *Solanum* and *Cestrum* fruits were not common, ranging from 0 to 15% of all visits to mixed neighborhoods. Therefore, although individual birds ate fruits of both plant species, within a single visit there was a significant tendency for birds to use

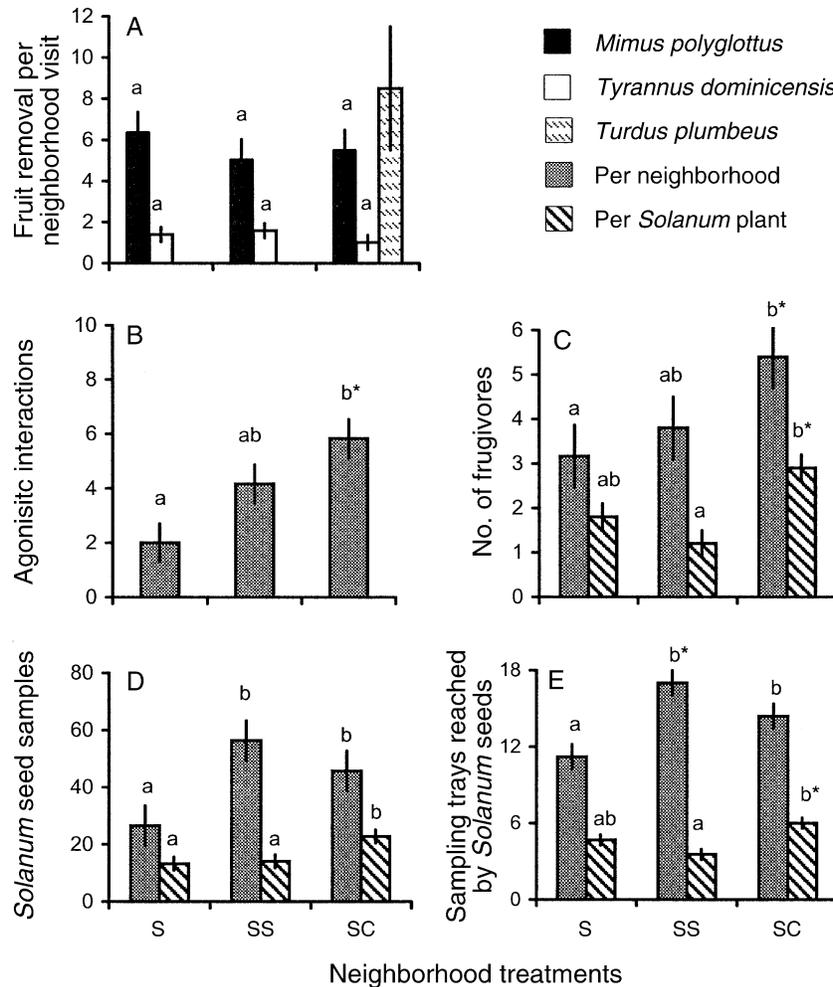


FIG. 2. One-way ANOVA comparisons of nine response variables measured on three fruiting-plant neighborhood treatments (six replicates per treatment); values are mean  $\pm$  SE. Treatments are: S, neighborhoods with two *Solanum* plants bearing 150 ripe fruits each; SS, neighborhoods with four *Solanum* plants bearing 250 ripe fruits each; and SC, neighborhoods bearing 300 ripe *Solanum* fruits (two plants bearing 150 fruits each) and 300 ripe *Cestrum* fruits (two plants bearing 150 fruits each). Letters represent the significance of Tukey-Kramer hsd mean comparisons of the three treatments, while asterisks indicate significance ( $\alpha \leq 0.05$ ) of *t* tests between SC and SS treatments (B, C, D), and between SC and S (E). Seed samples are the number of fecal samples containing *Solanum* and/or *Cestrum* seeds. *Solanum* seed samples are the number of fecal samples containing just *Solanum* seeds.

only one of the two plant species (Fig. 3). *Mimus* consumed more *Solanum* fruits and *Tyrannus* used more *Cestrum* fruits than expected by availability at SC neighborhoods (Table 1). Inter- and intraspecific agonistic interactions were frequent and occurred in 34% of visits. One pair of territorial *Mimus* was responsible for most aggressions within each experimental field. Most agonistic interactions involved a *Mimus* chasing a *Tyrannus* or another *Mimus*; rarely did *Tyrannus* lead attacks (Table 1).

On trays I collected a total of 1903 bird droppings, of which 1036 had *Solanum* and/or *Cestrum* seeds. The distribution of seed samples among treatments was as follows: SC neighborhoods produced 444 seed samples, of which 274 had *Solanum*, 170 had *Cestrum*, and

95 were mixed (both *Solanum* and *Cestrum* seeds); SS produced 338 seed samples; and S produced 159 seed samples. The percentage of fecal samples having both *Solanum* and *Cestrum* seeds (i.e., fecal samples with mixed seeds) from SC neighborhoods ranged from 18% to 61% per field. Contingency table analysis showed that the proportion of seed samples arriving at each distance class was significantly different among treatments (Fig. 4). When performing the analysis by weighting the number of *Solanum* seed samples by the number of *Solanum* plants in neighborhoods, there was no difference between S and SS neighborhoods, while *Solanum* seeds at SC neighborhoods were less than half as likely to be deposited within 1 m of the parent (Fig. 4B).

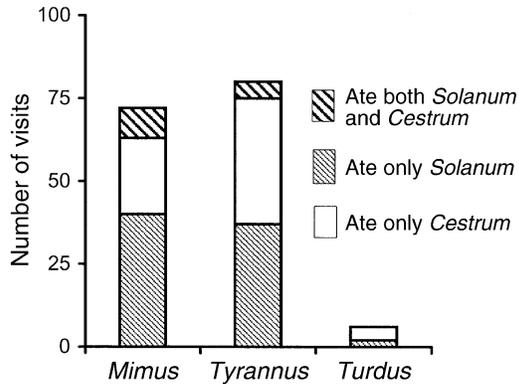


FIG. 3. When feeding in *Solanum*–*Cestrum* mixed fruiting-plant neighborhoods (i.e., SC neighborhoods), all bird species tended to concentrate use in only one plant species per visit. I used chi-square goodness-of-fit to test the null hypothesis of no difference in the proportion of visits in which a bird species ate either one or two plant species: for *Mimus*,  $\chi^2 = 21.2$ ,  $df = 2$ ,  $P < 0.001$ ; for *Tyrannus*,  $\chi^2 = 34.4$ ,  $df = 2$ ,  $P < 0.001$ ; for *Turdus*,  $\chi^2 = 3$ ,  $df = 1$ ,  $P < 0.10$ .

Neighborhood types differed significantly from each other in bird visitation (Table 1) and seed dispersal measures (Fig. 2C–E) as shown by MANOVA contrasts (Table 2). Similarly, SC neighborhoods had more agonistic interactions taking place (Fig. 2B) and higher numbers of visiting individuals (Fig. 2C) than SS and S neighborhoods. The average number of seed samples containing seeds from either species was highest for SC neighborhoods (Fig. 2D). When comparing *Solanum* seed density per dropping, all neighborhood treatments differed significantly from each other ( $F_{2,2} = 15.1$ ,  $P < 0.0001$ , with post hoc Tukey-Kramer hsd) with S seed density being the lowest ( $5.7 \pm 3.4$  [mean  $\pm$  SE]), SC intermediate ( $18.3 \pm 2.5$ ), and SS highest ( $26.5 \pm 1.9$ ). *Solanum* seeds at SC neighborhoods also reached a higher number of sampling locations per individual (Fig. 2E). Twice as many seed samples were collected from SS than from S neighborhoods, which translated into no difference in seed samples per individual plant (Fig. 2D) or number of trays reached per individual plant (Fig. 2E).

#### DISCUSSION

The results of this experiment show that seed dispersal patterns of endozoochorous plants that share frugivores can change depending on their neighborhood context. Here, the presence of *Cestrum* plants in *Solanum* neighborhoods increased the number of visiting frugivore individuals, resulting in a greater diffusion of seeds per *Solanum* plant (Fig. 2C, E). The facilitative effects of *Cestrum* neighbors on *Solanum* seed dispersal correspond to increased “quality” rather than “quantity” components of the dispersal process (Schupp 1993, Loiselle and Blake 1999) given that fruits from all experimental neighborhoods were effectively re-

moved and dispersed. Indirect neighborhood effects of *Cestrum* on *Solanum* were qualitative because they changed the seed dispersal pattern of individuals (i.e., number of sampling locations reached), not the net amount of seeds that were dispersed.

Qualitative differences in dispersal patterns of seeds are important for at least two reasons. First, the density at which seeds are deposited can be inversely related to predation risk and competition (Janzen 1970, Packer and Clay 2003, Peters 2003). Therefore, having fewer seeds “packed” into more dispersal units and reaching additional locations should benefit plant recruitment processes. Second, the observation that the seed dispersal kernels of endozoochorous plants can change through interactions of frugivores with local patterns of plant composition (Fig. 4B) has theoretical implications. To date, theoretical work regarding plant population dynamics, species coexistence, and spatial structuring of plant populations usually assumes a fixed-dispersal kernel (Pacala and Levin 1998, Bolker and Pacala 1999, Chesson 2000, Hubbell 2001). Therefore, it is necessary to investigate (1) how context-dependent kernel variation affects population, community, and spatial dynamics of plants; and (2) the variables that could influence and maybe predict such variation (e.g., skewed plant–frugivore ratios, frugivore limitation, plant–frugivore

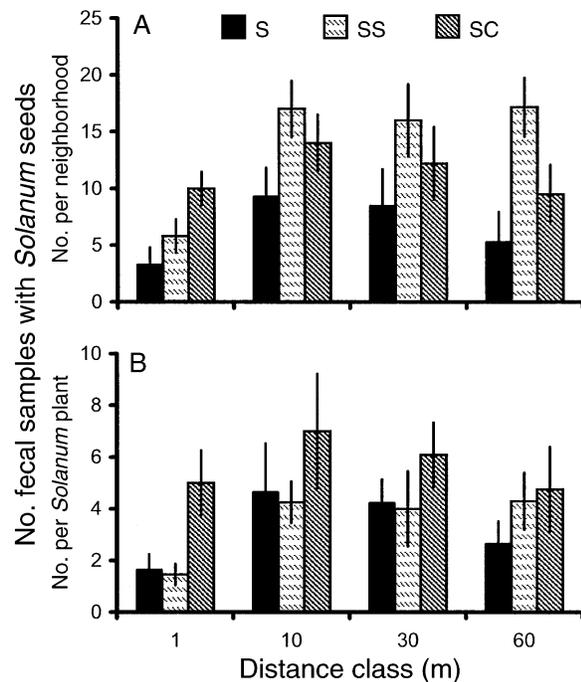


FIG. 4. Number of bird droppings (mean  $\pm$  SE) containing seeds collected at each of four distance classes from three fruiting-plant neighborhood types S, SS, and SC. Means are paired within each of six replicate experimental fields. Contingency table analysis (three treatments  $\times$  four distances) is significant (per neighborhood,  $\chi^2 = 2$ ,  $df = 6$ ,  $P = 0.001$ ). See Fig. 2 for an explanation of treatment abbreviations.

TABLE 2. Results of MANOVA and contrasts of three neighborhood types and seven response variables.

A) MANOVA						
Source	Pillai's trace	Approx. <i>F</i>	df		<i>P</i>	
			Numerator	Denominator		
Whole model	3.25	4.01	42	27	0.03	
Neighborhood	1.76	7.21	12	12	<0.001	
Field	2.76	1.85	30	45	0.03	

B) Multivariate contrasts of neighborhood types						
Contrast	Value	Exact <i>F</i>	df		<i>P</i>	
			Num.	Den.		
<i>Solanum</i> – <i>Cestrum</i> (SC) vs. <i>Solanum</i> – <i>Solanum</i> (SS)	4.83	4.03	6	5	0.032	
<i>Solanum</i> – <i>Cestrum</i> (SC) vs. <i>Solanum</i> (S)	36.7	30.6	6	5	<0.001	
<i>Solanum</i> – <i>Solanum</i> (SS) vs. <i>Solanum</i> (S)	24.9	20.8	6	5	0.001	

Notes: The response variables were: fruit removal by *Mimus*, fruit removal by *Tyrannus*, agonistic interactions, diversity of frugivores, *Solanum* seed samples per individual, total seed samples per neighborhood, and number of trays reached by *Solanum* seeds per individual (each shown as a one-way ANOVA in Fig. 2).

“connectivity” [sensu Jordano et al. 2003], and/or spatial structure of populations).

The wider dispersal pattern of *Solanum* in neighborhoods with *Cestrum* compared to *Solanum* in monospecific neighborhoods could have been due to changes in the behavior of frugivores in response to differences in neighborhood composition. However, frugivores were constant in their response to experimental neighborhoods as units. For example, *Mimus* consumed the majority of fruits in all neighborhood types and was the primary aggressor in attacks on other feeding birds. Hence, I found no evidence of changes in bird behavior depending upon neighborhood treatments (e.g., birds eating more fruits per visit; Fig. 2B). The other important factor affecting both fruit-removal and seed dispersal measures were the experimental fields (i.e., significant block effects). Some fields had more frugivores than others and it affected the rates of fruit removal and the amounts of seed samples. But in spite of local differences in frugivore abundance, SC neighborhoods increased local frugivore attraction in all experimental fields (Table 1, Fig. 2C).

*Solanum* fruits disappeared at a similar rate whether they had *Cestrum* or *Solanum* neighbors (Fig. 1), with the expected difference of neighborhood crop size inversely related to the slope of the removal rate (i.e., S twice as fast as SS). But the lack of difference in *Solanum* removal rates (Fig. 1) in SC and SS neighborhoods shows the opposite effects of compensation and competition between *Solanum* and *Cestrum* in SC neighborhoods. Because the mass of *Cestrum* fruits was 1.5 times that of *Solanum* fruits and there were equal numbers of fruits initially, without compensation in bird visitors to SC neighborhoods, removal per unit time should have been significantly slower for *Solanum* in SC than in SS neighborhoods. There are several explanations for the change in seed dispersal pattern of *Solanum* in SC neighborhoods. First, the *Solanum*–*Cestrum* fruit combination could have increased fru-

givre visitation by maximizing fruit preferences of birds. In other words, in spite of frugivores being generalists and capable of eating both plant species, frugivores may prefer one plant species or the other. This is consistent with my data in which *Mimus* birds ate more *Solanum* fruits and *Tyrannus* ate more *Cestrum* fruits than expected under a null hypothesis of proportional use (Table 1). Still, this represents a species-level approach that could conceal differences at the level of individuals (Jung 1992).

Another possibility is that the interspecific fruit combination increased an otherwise lower threshold of consumption imposed by nutrient content or secondary metabolites present in fruits that could interfere with protein assimilation (Izhaki et al. 2002). In this case, birds visiting SC neighborhoods may have increased fruit consumption per unit time. This explanation is not consistent with the fruit-removal data because consumption rates per bird visit did not change among neighborhood treatments as would be expected (Fig. 2A) and consumption of both fruit types was rare within the same neighborhood visit (Fig. 3). Last, the increased frugivore response to SC neighborhoods and the associated increase in seed dispersal may have been due to the higher fruit mass present at SC neighborhoods (due to *Cestrum*'s higher fruit mass) and not to the effects of interspecific neighbors per se. Unfortunately, in this case, differences in fruit mass are confounded with any other intrinsic differences in fruit quality (e.g., nutrients, seed:pulp ratio, secondary metabolites) between *Solanum* and *Cestrum* that could underlie frugivore responses. In fact, any advantages or disadvantages of having an interspecific fruiting neighbor instead of a conspecific lie in these differences.

The magnitude of the change in seed dispersal pattern found here could be greater in natural scenarios where frugivores are limited. In my experimental setting, all fruits were removed and dispersed (i.e., no fruit-removal limitation was found at experimental fruit

densities). In many natural scenarios, however, the inverse situation is often found: many fruits fail to be removed (Wheelwright 1985). Environments are easily saturated with fruit from several species at any one time (Carlo et al. 2003, Burns 2004, Saracco et al. 2004), and frugivores often cannot exhaust available fruit resources in species-rich plant communities. For example, during February–April 2003 in a 20-ha study plot with natural populations of *Solanum* and *Cestrum* in Puerto Rico, I estimated that there were 36.2 plants bearing ripe fruit for each individual bird, and that 73% of *Solanum* and 59.7% of *Cestrum* individuals received very little or no removal of fruits. Therefore, care must be taken in generalizing my experimental results, even to the same species in nature.

Frugivore-mediated seed dispersal facilitation among neighboring plants can be important because it provides an additional mechanism that could promote both the fitness of individuals and the coexistence of different species by reducing competitive exclusion (Lortie et al. 2004). This contributes to current conceptual advances seeking to incorporate positive species interactions into community theory (Callaway 1997, Bruno et al. 2003, Lortie et al. 2004). However, it remains an open question whether positive seed dispersal neighborhood interactions could have an impact on plant demographics and community structure because recruitment patterns may not reflect dispersal patterns (Jordano and Herrera 1995, Wang and Smith 2002). Future work should further investigate the strength of seed dispersal facilitation and/or competition in plant communities and its relationship to seed dispersal limitation at the level of plant individuals and species. Qualitative changes in the seed dispersal kernels of endozoochorous plants driven by interspecific neighborhood interactions could have profound causal consequences on the assemblage, diversity, and resilience of plant communities where plant–frugivore mutualisms are common.

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#### LITERATURE CITED

- Aldrich, P. R., and J. L. Hamrick. 1998. Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. *Science* **281**:103–105.
- 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.
- Bolker, B. M., and S. W. Pacala. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *American Naturalist* **153**:575–602.
- 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.
- Burns, K. C. 2003. Broad-scale reciprocity in an avian seed dispersal mutualism. *Global Ecology and Biogeography* **12**:421–426.
- Burns, K. C. 2004. Scale and macroecological patterns in seed dispersal mutualisms. *Global Ecology and Biogeography* **13**:289–293.
- Callaway, R. M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* **112**:143–149.
- 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.
- Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology* **58**:211–237.
- 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.
- Condit, R., et al. 2002. Beta-diversity in tropical forest trees. *Science* **295**:666–669.
- Davidar, P., and E. S. Morton. 1986. The relationship between fruit crop sizes and fruit removal rates by birds. *Ecology* **67**:262–265.
- Feinsinger, P., K. G. Murray, S. Kinsman, and W. H. Busby. 1986. Floral neighborhood and pollination success in four hummingbird pollinated cloud-forest species. *Ecology* **67**:449–464.
- Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in lowlands of Costa Rica. *Journal of Ecology* **62**:881–919.
- Free, J. B. 1968. Dandelion as a competitor to fruit trees for bee visits. *Journal of Applied Ecology* **5**:169–178.
- French, K., D. J. Odowd, and A. Lill. 1992. Fruit Removal of *Coprosma quadrifida* (Rubiaceae) by birds in south-eastern Australia. *Australian Journal of Ecology* **17**:35–42.
- Gentry, A. H. 1982. Patterns of Neotropical plant species diversity. *Evolutionary Ecology* **15**:1–84.
- Howe, H. F., and G. F. Estabrook. 1977. Intraspecific competition for avian dispersers in tropical trees. *American Naturalist* **111**:817–832.
- Hubbell, S. P. 2001. A unified theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Izhaki, I., E. Tsahar, I. Paluy, and J. Friedman. 2002. Within population variation and interrelationships between morphology, nutritional content, and secondary compounds of *Rhamnus alaternus* fruits. *New Phytologist* **156**:217–223.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**:501–528.
- Johnson, S. D., C. I. Peter, L. E. Nilsson, and J. Agren. 2003. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* **84**:2919–2927.
- Jordano, P., J. Bascompte, and J. M. Olesen. 2003. Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters* **6**:69–81.
- Jordano, P., and C. M. Herrera. 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience* **2**:230–237.
- Jung, R. E. 1992. Individual variation in fruit choice by American Robins (*Turdus migratorius*). *Auk* **109**:98–111.
- Levin, D. A., and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. *American Naturalist* **104**:455–467.

- Loiselle, B. A., and J. G. Blake. 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. *Ecology* **80**:330–336.
- 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.
- Manasse, R. S., and H. F. Howe. 1983. Competition for dispersal agents among tropical trees: influences of neighbors. *Ecology* **59**:185–190.
- Muller-Landau, H., J. P. Wright, O. Calderon, S. P. Hubbell, and R. B. Foster. 2002. Assessing recruitment limitation: concepts, methods, and case-studies from a tropical forest. Pages 35–54 in D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed dispersal and frugivory: ecology, evolution, and conservation. CABI International, Oxfordshire, UK.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* **15**:278–285.
- Pacala, S. W., and S. Levin. 1998. Biologically generated spatial pattern and the coexistence of competing species. Pages 204–232 in D. Tilman and P. Kareiva, editors. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, New Jersey, USA.
- Packer, A., and K. Clay. 2003. Soil pathogens and *Prunus serotina* seedling and sapling growth near conspecific trees. *Ecology* **84**:108–119.
- Peters, H. A. 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters* **8**:757–765.
- Sallabanks, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* **74**:1326–1336.
- Saracco, J. F., J. A. Collazo, and M. J. Groom. 2004. How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia* **139**:235–245.
- 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.
- SAS Institute. 2000. JMPIN. Version 4.0.2. SAS Institute, Cary, North Carolina, USA.
- Scheiner, S. M. 1993. MANOVA: multiple response variables and multispecies interactions. Pages 94–112 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
- Schemske, D. W. 1981. Floral convergence and pollinator sharing in two bee-pollinated tropical herbs. *Ecology* **62**:946–954.
- Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* **108**:15–29.
- Terborgh, J., N. Pitman, M. R. Silman, H. Schlichter, and P. Nunez. 2002. Maintenance of tree diversity in tropical forests. Pages 1–18 in D. Levey, W. R. Silva, and M. Galetti, editors. Seed dispersal and frugivory: ecology, evolution and conservation. CABI International, Oxfordshire, UK.
- Thomson, J. D. 1978. Effect of stand composition on insect visitation in two-species mixtures of *Hieracium*. *American Midland Naturalist* **100**:431–440.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**:81–92.
- Van der Pijl, L. 1972. Principles of dispersal in higher plants. Springer-Verlag, New York, New York, USA.
- Wang, B. C., and T. B. Smith. 2002. Closing the seed dispersal loop. *Trends in Ecology and Evolution* **17**:379–385.
- Waser, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* **59**:934–944.
- Wheelwright, N. T. 1985. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. *Oikos* **44**:465–477.
- Wheelwright, N. T., and G. H. Orians. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist* **119**:402–413.
- Whelan, C. J., K. A. Schmidt, B. B. Steele, W. J. Quinn, and S. Dilger. 1998. Are bird-consumed fruits complementary resources? *Oikos* **83**:195–205.

## APPENDIX

A figure of the setup of the six experimental plots at the UPR Experimental Station showing location of plant neighborhoods and the 34 seed-collecting trays bearing bird perches, placed at four distance categories from center, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-128-A1.