

ABSTRACT

SARACCO, JAMES FREDERICK. Fruit Neighborhoods and Interactions between Birds and Plants in Puerto Rico. (Under the direction of Jaime A. Collazo and Martha J. Groom.)

Many species of plants that produce fleshy fruits depend on birds for seed dispersal, and many of the birds that disperse seeds rely on fruits for a substantial proportion of their diets. From an ecological and evolutionary standpoint, it is important to understand why frugivorous birds feed in the particular plants they do. Intrinsic plant characteristics (e.g., crop size) influence the foraging patterns of birds; however, these factors cannot be fully understood outside the context of the communities within which birds and plants find themselves. Here I report on spatial patterns of bird use of fruiting plants in central Puerto Rico and its relationship to plant distributions and fruit abundance.

From Feb.-Jun. 1998 I quantified frugivorous bird visitation to fruiting trees of *Schefflera morototoni* in a secondary forest-shade coffee plantation mosaic. Visitation rate was positively related to crop size and negatively related to conspecific fruit abundance within 30 m of focal plants. The presence or abundance of heterospecific bird-consumed fruits had mixed relationships with visitation: four species were positively related to visitation; one was negatively related. The fruit neighborhood explained most variation in visitation to focal trees, suggesting that such variables might help explain the high variability seen in other fruiting plant frugivore systems.

In order to evaluate spatial dependency in tree distributions, fruiting, and frugivory over a range of tree species and spatial scales, I mapped bird-consumed fruiting plants on a 4.05 ha study grid in secondary wet forest and monitored fruiting and frugivory from Aug.-Nov. 1999. I focused analyses on four tree species: *Dendropanax arboreus*, *Guarea guidonia*, *Miconia serrulata*, and *Schefflera morototoni*. All of these were intraspecifically aggregated at scales < 80 m, but differed markedly in degree of crowding experienced by individuals. *G. guidonia* was the most, and *M. serrulata* the least crowded. Distributions of visited trees and autocorrelation in the number of frugivory observations at trees suggested that individuals of some species (e.g., *S. morototoni*) facilitated visitation to one another at small spatial scales (< ~30 m). Frugivory was positively correlated with fruit abundance on trees for all species; spatial variation in fruit abundance appeared to have reduced, and in some cases outweighed (e.g., *M. serrulata*), facilitative benefits of visited neighbors. Evidence of facilitation was especially weak for *G. guidonia* and may have reflected its particularly high density in the study area.

Consideration of interspecific tree distributions showed *S. morototoni* to be aggregated with *M. serrulata* at scales > 69 m, and *G. guidonia* to be aggregated with *D. arboreus* at scales < 5 m. All other pairs were randomly or regularly distributed with respect to one another. Spatial patterns of fruiting and frugivory of *M. serrulata* appeared linked to the distribution of fruiting *S. morototoni*. Spatial patterns of frugivory also overlapped for other species and generally suggested facilitation at larger scales. Interspecific interactions were probably strongest at larger scales because of shifts in the

relative abundances of conspecifics and heterospecifics at those scales. These findings highlight the potentially large size of plant neighborhoods with respect to use by avian frugivores and the dependence of neighborhood effects on local plant densities and crop sizes.

From the perspective of birds, spatial patterns of frugivory suggested birds closely tracked fruit abundance. I observed few agonistic interactions between birds and found little evidence of their negatively influencing one another's use of fruiting trees. Similarity in spatial patterns of frugivory between bird species, and positive cross-correlation in frugivory of different species at patch boundaries, suggested birds may have assisted one another (via calling) in locating new foraging patches. This could explain mixed-species flock formation.

**FRUIT NEIGHBORHOODS AND INTERACTIONS BETWEEN BIRDS AND
PLANTS IN PUERTO RICO**

by

JAMES FREDERICK SARACCO

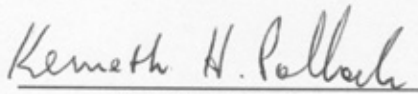
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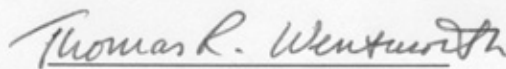
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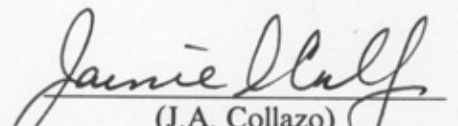
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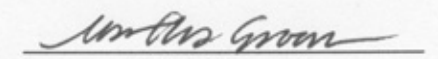
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This work is dedicated to my parents, who always supported me, and encouraged me to pursue my interests.

BIOGRAPHY

James Frederick Saracco was born on July 7, 1969 in Pittsburgh, Pennsylvania. His early interests in nature led him to spend many days afield in pursuit of fish and game on the rivers and rolling hills of western Pennsylvania. He graduated from Thomas Jefferson High School in 1987. Although not especially inclined towards academic pursuits in high school, Jim showed a particular interest in biology. Following a brief stint as an accounting major in college, his scientific interests were rekindled while fulfilling a general science requirement in biology. This eventually led him to receive his BS in Biology from Indiana University of Pennsylvania in 1992. Following college, he worked as an intern, and then biologist, for the Institute for Bird Populations in Point Reyes Station, California. This work led him to work at field sites throughout the east and west coasts of the USA. He also worked at a variety of other field and random jobs (e.g., bicycle messenger) before ending up at North Carolina State University in 1995. After a summer working on breeding birds in North Carolina bottomland hardwood forests, Jim took a short field course in Costa Rica. This experience whet his appetite for tropical field biology, and the lure of the tropics soon led him to pursue his dissertation field work on frugivorous birds and fruiting plants in Puerto Rico. Jim married fellow graduate student Lisa Etherington in June 2000, nearly five years after she first foolishly agreed to go birdwatching with him.

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INTRODUCTION

Many species of plants produce fleshy or arillate fruits adapted for seed dispersal by birds, and many of the birds that disperse seeds rely on fruits for a substantial proportion of their diets (Howe and Smallwood 1982, Wheelwright 1988). A large body of work investigating the evolutionary ecology of these mutualistic interactions has accumulated since early theoretical papers by Snow (1971) and McKey (1975), yet few generalities have emerged. Consider for example, the problem of explaining why birds feed in the particular plants that they do. Because bird-dispersed fruits from a wide variety of plant taxa and geographic regions are remarkably similar in size, shape, color, etc. (the “bird-fruit syndrome;” van der Pijl 1972), it was expected that field studies would show birds to exert strong selection pressure on plant traits. Despite great effort, no consistent patterns have emerged concerning bird selection for aspects of fruit quality (e.g., size, nutritive quality), although fruit quantity (i.e., crop size) does seem to be selected for in many cases (e.g., Moore and Willson 1982, Denslow 1987, Jordano 1987, Herrera 1988, Willson and Comet 1993, Willson and Whelan 1993; but see Manasse and Howe 1983, Sallabanks 1993). The apparent lack of frugivore selectivity for fruit traits has led many researchers to question the widely held notion that fruiting plant-frugivore interactions were tightly coevolved. Take for example the following passage from Wheelwright (1988):

The emerging view is that most interactions between fruiting plants and their avian seed dispersers – whether in the tropics or the temperate zone – are loose, asymmetric, variable in time and space, inefficient and non-obligate. The average fruit everywhere is small, often dull-colored, not particularly nutritious, and likely to have its seeds land in the wrong place. Birds are opportunistic foragers, concerned more with their own reproductive interests than those of the plants that provide them food.

So, where does this leave us? The fact that there does appear to be a “bird-fruit syndrome,” as well as the fact that some birds show adaptations for the efficient handling and processing of fruit, suggests that these traits were important in the evolutionary history of these interactions. Yet, the coevolution paradigm, although still a plausible theory, remains essentially untestable (Wheelwright 1991). The interesting questions related to explaining variation in fruit removal rates, and thus to understanding many of the current selective pressures faced by fruiting plants, should accordingly focus on factors extrinsic to the parent plant.

The numbers and types of other fruits available to frugivores within some area surrounding parent plants (i.e., the fruit neighborhood) may help explain some of the high variation in visitation and fruit removal rates among plants. Several studies have shown the density or presence of conspecific fruits or fruiting plants near individuals to negatively affect fruit removal (Moore and Willson 1982, Manasse and Howe 1983, Denslow 1987; but see Sargent 1990). Few studies have explored effects of

heterospecific fruits on fruit removal (Herrera 1984). Although the problem of studying neighborhood effects is inherently spatial in nature, few studies have considered multiple spatial scales in the study of these interactions.

In this dissertation I address questions related to how conspecific and heterospecific fruiting plants affect one another's ability to attract visitation by frugivorous birds within forested habitats in central Puerto Rico. I also consider interactions between frugivorous birds and their potential influence on spatial patterns of frugivory. In Chapter 1, I describe visitation rates of frugivores at focal trees of *Schefflera morototoni* as a function of crop size and the abundance or presence of conspecific and heterospecific fruits within 30 m of focal trees. In Chapter 2, I approach the study of spatial patterns of fruiting and frugivory from a different perspective. Rather than pre-defining areas within which plants are assumed to affect one another equally, I allow spatial patterns in the distributions of trees, fruiting trees, and visited trees to define themselves. This was done using a complete map of bird-dispersed trees within a 225 m × 180 m study area and monitoring of fruiting phenology and frugivory during a single fruiting season. Chapter 3 expands upon Chapter 2 by examining neighborhood vs. crop size effects in explaining spatial patterns in frugivory. This chapter also examines interactions between tree species explicitly. In Chapter 4, I take the bird's perspective. Specifically, I compare spatial patterns in frugivory for the three most commonly observed frugivorous bird species and relate these patterns to patterns of fruit abundance and interactions between bird species.

Results of this work suggest that the context within which fruiting plants find themselves may be generally important in explaining the typically high levels of variation in visitation and fruit removal rates seen among plants in natural communities. Because of the likely wide- ranging foraging behavior of frugivorous birds, the zone of influence of fruit neighborhoods surrounding plants can involve large numbers of individual plants and cover large spatial extents. Nevertheless, I found that avian foraging patterns within these larger areas can be extremely patchy. This patchiness in avian frugivore foraging suggests that dissemination of seeds is probably also patchy. Future studies aimed at linking spatial patterns of seed removal to patterns of seed dissemination and plant recruitment will greatly aid our understanding of plant mutualisms with seed dispersers and competitive and facilitative interactions among plants (Schupp and Fuentes 1995).

LITERATURE CITED

- Denslow, J. S. 1987. Fruit removal from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. *Canadian Journal of Botany* 65:1229-1235.
- Foster, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58:73-85.
- Herrera, C. M. 1984. Seed dispersal and fitness determinants in wild rose: combined effects of hawthorn, birds, mice, and browsing ungulates. *Oecologia* 63:386-393.
- Herrera, C. M. 1988. Fruiting ecology of *Osyris quadripartita*: individual variation and evolutionary potential. *Ecology* 69:233-249.

- Howe, H. F. and J. Smallwood. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13:201-228.
- Janzen, D. H. 1977. Promising directions of study in tropical animal-plant interactions. *Ann. Missouri Bot. Gard.* 64:706-736.
- Jordano, P. 1987. Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology* 68:1711-1723.
- Levey, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58:251-269.
- Loiselle, B. A., and J. G. Blake. 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a neotropical lowland wet forest. *Vegetatio* 107/108:177-189.
- Manasse, R. S. and H. F. Howe. 1983. Competition for dispersal agents among tropical trees: influences of neighbors. *Oecologia* 59:185-190.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pp. 159-191 *In*: *Coevolution of animals and plants* (L. D. Gilbert and P. Raven, Eds.). University of Texas Press, Austin, Texas.
- Moore, L. A., and M. F. Willson. 1982. The effect of microhabitat, spatial distribution, and display size on dispersal of *Lindera benzoin* by avian frugivores. *Canadian Journal of Botany* 60:557-560.
- Sallabanks, R. 1993. On fruit-frugivore relationships: variety is the spice of life. *Oikos* 68:567-570.

- 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.
- Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113:194-202.
- van der Pijl, L. 1972. Principles of dispersal in higher plants. 2nd Ed. Springer-Verlag, New York.
- Wheelwright, N. T. 1988. Fruit-eating birds and bird-dispersed plants in the tropics and temperate zone. *Trends Ecol. Evol.* 3:270-274.
- Wheelwright, N. T. 1991. Frugivory and seed dispersal: '¡La coevolución ha muerto – viva la coevolución!' *Trends Ecol. Evol.* 6:312-313.
- White, D. W. and F. G. Stiles. 1983. The adaptive significance of nutritional differences in North American bird-dispersed fruits. *Bulletin of the Ecological Society of America* 64:166-167.
- Willson, M. F. and T. C. Comet. 1993. Food choices by Northwestern Crows: experiments with captive, free-ranging, and hand-raised birds. *Condor* 95:596-615.
- Willson, M. F. and C. J. Whelan. 1993. Variation in dispersal phenology in a bird-dispersed shrub, *Cornus drummondii*. *Ecological Monographs* 63:151-172.

CHAPTER 1

FRUIT NEIGHBORHOODS AND VISITATION TO A BIRD-DISPERSED TREE

Abstract. A major goal of evolutionary ecologists studying fruiting plant-frugivore interactions has been to identify factors important in explaining variation in fruit removal among conspecific plants. Most previous studies attempting to explain this variation have focused on factors intrinsic to plants (i.e., attributes of fruit quality and/or crop size). Extrinsic factors, such as the amount and types of fruits surrounding parent plants (i.e., the “fruit neighborhood”) and interference interactions among consumers may be at least as important in affecting fruit removal among plants, but are seldom considered.

In this study, I report on visitation rate and fruit consumption by avian frugivores at fruiting trees of *Schefflera morototoni* at a study site in north-central Puerto Rico from February-June 1998 (the peak period of fruit production for this species in this year). From observations collected at 24 focal trees, I assessed the potential role that interactions among frugivores may have on *S. morototoni* fruit consumption. I also quantified avian frugivore use of other fruiting plant species in the study area in order to identify plants that may be important in influencing interactions between *S. morototoni* trees and their dispersers. I then explored the roles of crop size, and characteristics of the local fruit neighborhood (within 30 m of focal trees) in affecting visitation rates to focal trees.

Most foraging observations at *S. morototoni* trees and most visits to focal trees were made by a single frugivore species, *Spindalis portoricensis*. The typical visit was short in duration (< 2 min) and resulted in few fruits being consumed (2-4). I found no difference in the number of fruits consumed per visit between *S. portoricensis* and the

other frugivore species. Few interference interactions were observed at focal trees, and visitation rate and the number of displacements were not significantly correlated with the number of fruits consumed per visit. Positive correlation coefficients suggested that, if anything, the number of fruits removed per visit was higher at trees with more displacements and higher visitation rates. Variation in visitation rate to focal trees was high and followed a seasonal trend. Most of the variation in focal tree visitation rate, including essentially all of the variation described by the temporal trend, could be explained by crop size and fruit neighborhood variables. Visitation was positively related to crop size and negatively related to conspecific fruit abundance, suggesting that trees competed intraspecifically for dispersers. A number of other fruit species were also consumed by the *S. morototoni* disperser coterie and heterospecific neighborhood variables were also important in explaining variation in visitation. The presence or abundance of four fruit species appeared to enhance visitation to focal trees, while one species was negatively related to visitation. These results suggest that the local fruiting environments in which plants find themselves may be important in diluting any strong selection pressure on parentally controlled fruiting traits. The fact that most fruiting plant-frugivore systems involve many species of both fruiting plants and consumers suggests that local interactions among plants with respect to their use by fruit consumers are probably widely important in determining the dynamics of these systems.

INTRODUCTION

Plants that effectively disperse seeds may benefit from increased colonization ability and escape from predation or competition (Howe and Smallwood 1982). The demographic importance of dispersal for plants is perhaps best evidenced by the widespread evolution of dispersal structures, despite their obvious energetic cost (Willson and Travaset 2000). One such class of adaptations, nutritious fleshy pericarps or arils (i.e., fruits), has enabled many plants to exploit animal dispersal agents. Indeed, many fruiting trees, particularly in the tropics, attract large numbers of feeding animals of a variety of taxa (e.g., Willis 1966, Terborg and Diamond 1970, Fleming 1979, Fleming and Williams 1990, Dowsett-Lemaire 1996). However, utilization of fruiting trees by frugivores can be highly variable in space in time (e.g., Sallabanks and Courtney 1993, Herrera 1998, Ortiz-Pulido and Rico-Gray 2000), and not all frugivores disperse seeds effectively (Schupp 1993, Jordano and Schupp 2000).

Identifying factors that influence spatial and temporal patterns of fruiting plant visitation and fruit consumption by seed-dispersing frugivores is a critical first step in linking frugivore behavior and plant demography (Schupp 1993). Most studies attempting to make this link have focused on how traits under the direct control of parent plants (i.e., attributes of fruit quality and/or crop size) affects variation in fruit removal rates among plants. In some cases, under controlled conditions, avian dispersers do clearly distinguish among fruits that vary in aspects of fruit quality, such as color, nutrients, or accessibility (Moermond and Denslow 1983, Johnson et al. 1985, Stiles

1993, Siitari et al. 1999). However, even under such controlled conditions, there can be high variability. Altering conditions on even very small spatial scales, for example by manipulating the distance between fruits of different types, can affect preference patterns (Levey et al. 1984). From these findings it is not surprising that field studies often fail to support the notion that animals exert strong selection pressure on aspects of fruit quality (Herrera 1986, Whelan and Wilson 1994). In contrast, field studies of crop size effects typically show positive relationships between crop size and fruit removal (e.g., Davidar and Morton 1986, Denslow 1987, French et al. 1992, Alcántara et al. 1997, Jordano and Schupp 2000). However, frugivore responses to crop size can also be highly variable over space and time (e.g., Sallabanks and Conway 1993, Ortiz-Pulido and Rico-Gray 2000). The failure to establish consistently strong relationships between parentally-controlled factors (both qualitative and quantitative) and fruit removal suggests that external variables are important in diluting any strong selection pressure on parental traits, yet these variables are seldom considered.

Among the most likely external variables to influence rates of fruit removal are the kinds and amounts of other fruits available to dispersers within some area surrounding parent plants (Herrera 1986). Tropical fruiting plants are typically patchily distributed (e.g., Levey 1988, Loiselle and Blake 1993, Chapter 2), and so interactions among neighboring plants that rely on the same disperser coterie are probably common. Most studies that have explored the role of neighborhood fruit abundance in affecting fruit removal have limited consideration to conspecific neighbors. In accordance with the positive relationships often found between crop size and fruit removal, these studies have

suggested that plants compete for dispersers (e.g. Moore and Willson 1982, Manasse and Howe 1983, Denslow 1987; but see Sargent 1990, French et al. 1992); however, in many systems frugivores are confronted with a variety of fruits from which to choose. Thus, interspecific interactions among plants that rely on the same coterie of dispersers may also be common. Some studies have reported competitive interactions among plant species. For example, Herrera (1984a) showed that individuals of the erect or climbing shrub, *Rosa canina*, experienced higher fruit removal rates when growing alone than when growing on *Crataegus monogyna*, a fruiting tree species preferred by frugivores in the area. At the population level, *R. canina* had higher relative removal rates when growing in isolation, than when coexisting with *C. monogyna*. However, in many cases one could expect interspecific interactions to be facilitative. For example, fruit-eating birds may rely on many types of fruits to fulfill nutritional needs (Izhaki and Safriel 1989) or avoid over-consumption of particular toxic secondary compounds (Cipollini and Levey 1997). Whelan et al. (1998) suggested that many bird-consumed fruits may be complementary, such that a mixed-fruit diet may confer greater fitness benefits than consumption of one fruit species. For these reasons, areas with a number of fruiting plants of different species in close proximity might be particularly attractive to foraging frugivores.

In addition to local fruit neighborhood effects on bird visitation and fruit removal (i.e., plant-plant interactions), interactions among individual frugivores may also affect dispersal success (Martin 1985). For example, interference interactions occurring as a result of birds defending feeding territories (e.g. Pratt 1994) or intra- or interspecific

social hierarchies (e.g. Daily and Ehrlich 1994) could reduce visitation or foraging rates of subordinate birds, although such interactions may be avoided by spatial (e.g., Diamond and Terborg 1967) or temporal (e.g., Kantak 1981, Daily and Ehrlich 1994, Athreya 1997) partitioning of the fruit resource. In any case, use of a fruiting tree by an individual frugivore may influence use of the fruiting tree by another.

In this study, I describe patterns of frugivory by birds on the bird-dispersed tree, *Schefflera morototoni*, in north-central Puerto Rico. For the various avian fruit consumers, I considered among-plant variation in two quantitative components of dispersal success: (1) visitation rate, and (2) the number of fruits consumed per visit (Schupp 1993). I also considered the time spent in plants per visit by dispersers, which is also related to the number of seeds dispersed, although its relationship to dispersal is less direct. I summarized displacement interactions among birds at trees and addressed hypotheses concerning how such interactions might affect fruit removal. Specifically, I hypothesized that the number of fruits consumed per visit would be lower at trees where visitation and displacement rates were highest as a result of birds departing trees before the completion of foraging bouts (Daily and Ehrlich 1994). I also collected data on the relative use of other fruiting plant species by frugivores to identify plants important in influencing the interaction between *S. morototoni* and its disperser coterie. Of the dispersal success measures I considered, visitation rate typically correlates most strongly with the number of seeds dispersed (Schupp 1993, Jordano and Schupp 2000). I considered variation in this measure of dispersal success in more detail. Specifically, I used multiple regression models to explore the role of crop size, conspecific fruit

abundance, and the presence or abundance of heterospecific fruits within local neighborhoods in affecting visitation rates to focal trees.

METHODS

Study area

The study was conducted at a lower montane site of approximately 80 ha in north-central Puerto Rico (18°14'N, 66°31'W; approx. elev. range 625-710 m). The habitat was a mosaic of moist secondary subtropical forest (Ewel and Whitmore 1973) and shaded coffee plantation. Common trees included typical coffee shade species such as *Inga vera*, *Inga laurina*, *Andira inermis*, and *Guarea guidonia*, pioneers such as *Schefflera morototoni*, *Cecropia schreberiana*, and *Miconia* spp., and other trees common to montane secondary forests such as *Alchornia latifolia*, Lauraceae spp., *Casearia* spp., and *Cordia sulcata*. Common fruit-eating bird species were Puerto Rican Stripe-headed Tanager (*Spindalis portoricensis*), Puerto Rican Tanager (*Nesospingus speculiferus*), Antillean Euphonia (*Euphonia musica*), Puerto Rican Bullfinch (*Loxigilla portoricensis*), Black-whiskered Vireo (*Vireo altiloquus*), Pearly-eyed Thrasher, (*Margarops fuscatus*), Red-legged Thrush (*Turdus plumbeus*), Scaly-naped Pigeon (*Columba squamosa*), and Puerto Rican Woodpecker (*Melanerpes portoricensis*).

Focal plant species

Schefflera morototoni is widely distributed throughout much of the humid neotropics (Liogier 1995). It is a pioneer species (*sensu* Swaine and Whitmore 1988), typical of disturbed forests and gaps (Crow 1980, Denslow 1980). In Puerto Rico, it occurs in montane forests at middle elevations, particularly on steep slopes, and less commonly at lower elevations in the northern coastal limestone hills (Little and Woodbury 1976). It was common, but patchily distributed on the study area. Adults were often large canopy or emergent trees, averaging 30.0 cm dbh (n=225) and 16 m in height.

S. morototoni produces large crops of 2-seeded berry-like drupes (4-6 mm long, 6-10 mm broad) borne on 20-60 cm compound panicles (Liogier 1995). *S. morototoni* fruit pulp is relatively rich in lipids and proteins, and in this respect it is similar to other “high quality” fruits typical in the diets of specialized frugivores (Snow 1971). However, its small size makes it attractive to a wide range of generalist frugivores as well (Martin 1982). Crop sizes observed during the study averaged about 68,000 fruits; the largest tree contained an estimated 1,000,000 fruits (estimation method described below in “*Crop size and neighborhood measurements*”). It was by far the most abundant fruit in the study area (Carlo 1999). Mature fruits have been reported in almost every month in Puerto Rico, with peak production between November and June (Nieves 1979). During the study period, ripe fruit were available primarily between February and June at Cialitos, seeming to peak in abundance during March and April (*personal observation*).

I have observed all major frugivores in the area consuming *S. morototoni* fruits, at least occasionally. All regular consumers of *S. morototoni* fruits swallow seeds as well as pulp, and all, except perhaps for *Columba squamosa* (Moermond and Denslow 1985), probably serve as effective dispersers. Seeds that appeared to be viable were recovered from fecal samples of *Spindalis portoricensis*, *Nesospingus speculariferus*, and *Vireo altiloquus* (Carlo 1999).

Plot-level foraging observations

In order to assess bird use of *Schefflera morototoni* trees and to identify other fruiting plants frequently consumed by the *S. morototoni* consumer coterie, foraging observations were conducted within a central 8.28 ha grid on the study area between 2 February-18 May 1998. These data are a subset of those reported in Carlo (1999). On 6-7 days each month a single observer traversed the plot for approximately five hrs, beginning about 1 hr after sunrise. From a random starting point, movement through the plot was guided by visual and auditory cues of selected focal fruit-eating bird species. Focal bird species were *Spindalis portoricensis*, *Nesospingus speculariferus*, *Euphonia musica*, *Loxigilla portoricensis*, *Vireo altiloquus*, *Margarops fuscatus*, and *Turdus plumbeus*. Although effort was concentrated on these species, incidental frugivory observations by other bird species were also recorded. Birds were followed until their first feeding attempt was completed and classified in terms of the food item consumed. The plant species and number of fruits consumed (whenever it could be determined) were

also recorded. I did not make sequential observations on the same individual bird in an effort to avoid statistical problems associated with serially autocorrelated data, (Petit et al. 1990, Sallie et al. 1990).

Focal tree observations

I selected 24 *Schefflera morototoni* focal plants from 12 February-3 May 1998. Because few individuals had ripe fruit very early and late in the fruiting season, I searched haphazardly for trees with ripe fruit at these times. If multiple individuals were found, I chose from among these randomly. During the middle period of higher fruit abundance, I selected trees by beginning the search from a random starting point and then choosing the first tree found with ripe fruit. Again, if I found more than one individual with ripe fruit within similar proximity to the random point, I chose from among these randomly. Finally, selection of trees was constrained in that (1) the entire canopy had to be visible from a nearby vantage point and (2) the tree had to be located > 70 m from another focal tree (to increase the likelihood of statistical independence).

Each focal plant was observed for four hours (usually on a single day) between 06:30-13:00 AST. All visiting birds were noted and identified to species (and age/sex, when possible) with the aid of binoculars. I recorded whether or not fruit was consumed (when known) as well as the number of fruits consumed (whenever it could be determined) during each visit. I also noted aggressive interactions, defecation or regurgitation of seeds, and the consumption of other food items in the tree (e.g., foliage,

insects). In many cases I recorded the time spent in focal trees by visitors (to the nearest second) using a stopwatch.

Crop size and neighborhood measurements

On observation days, the number of ripe and unripe fruits on focal trees was visually estimated from the ground using binoculars. I accomplished this by counting fruits on portions of infructescences and extrapolating for the remainder of the tree. I considered fruits that were grayish-purple in color and rounded in shape to be ripe. Thinner green fruits were seldom observed to be eaten by birds. Because *Schefflera morototoni* produce very large crops of small fruits, estimates were aided by previous complete counts of fruits on infructescences that had fallen to the ground. Prior to analyses, estimates of ripe fruit abundance were categorized using an index that essentially followed a log₂-scale (0 = no ripe, 1 = 1-16 ripe, 2 = 17-32 ripe, 3 = 33-64 ripe, ... , 16 = 262,145-524,288, 17 = >524,288).

For each focal plant I measured the distance and direction to all other plants bearing fruit within 30 m (2827 m² area ~ the largest area that could consistently be mapped by a single observer within about 1 wk of the observation day). The dbh of all fruiting trees and their estimated height was also recorded. I estimated the numbers of ripe and unripe fruits in a manner similar to that described above for focal trees, with the exception that crop size was counted directly for plants with small crops and canopies entirely visible from the ground. Prior to analyses, I summed the estimated fruit

abundance across individuals for each species (or for less frequently encountered species, I grouped plants at the genus level), and assigned a score from the fruit abundance index described above for focal trees.

Data analysis

I report medians and 25th-75th percentiles for data summaries, as raw data were often either highly skewed or few. For all hypothesis tests, I used $\alpha = 0.05$ to determine significance. I used standard product-moment (using log- or square root transformed data to meet normality, linearity, and homoscedasticity assumptions) or Spearman's rank correlations (when transformations were not successful) when testing for relationships between two random variables. I used t-tests (when variances equal) or Wilcoxon tests (whenever assumption of equal variances was not met) when testing for differences among groups.

Temporal variation in visitation to focal trees and its correlates

I used polynomial regressions to examine the temporal trend in focal tree visitation (REG procedure; SAS Institute 1990). I examined two response variables: (1) the number of visits by *Spindalis portoricensis* (the most frequent visitor to *S. morototoni* trees) and (2) the number of visits by all species. Both were square root (+ 0.5) transformed in order to meet normality, linearity, and homoscedasticity assumptions

(Chatterjee et al. 2000). For the quantification of frugivore visitation, I defined a visit as a bird entering the focal tree and either directly observed consuming fruit or observed occupying a part of the tree with ripe fruit, but in a position that was obscured from view. I do not include visits by birds alighting briefly or otherwise known not to have consumed fruit. Explanatory variables were day of year (DATE) and its quadratic term (DATE²). Plots of standardized residuals vs. DATE and DATE², as well as Durbin-Watson tests for autocorrelated errors suggested that there were no remaining temporal patterns in the data after model fitting (Chatterjee et al. 2000).

I used multiple regression models to assess the contribution of crop size and neighborhood variables in explaining variation in visitation to focal trees (REG procedure, SAS Institute 1990). As for the examination of seasonal trend, I examined both *S. portoricensis* visitation and visitation by all frugivores. Explanatory variables considered in multiple regression models are listed in Table 1. I limited consideration of heterospecific fruit neighborhood variables to those species (or genera) that occurred in ≥ 5 neighborhoods, had ripe fruit, and were commonly consumed by birds (see *Results: Plot-level frugivory*). With the exception of *Inga vera*, which was present in all but two neighborhoods, the fruit abundance index of all heterospecific fruiting plant taxa exhibited strongly right-skewed distributions; transformations failed to reduce this skewness in most cases. Thus, most taxa were uncommon, and one or a few neighborhoods were often highly influential, determining apparent relationships with visitation. Because of this, I treated all heterospecific taxa except for *Inga vera* categorically, with single indicator variables denoting presence or absence. Explanatory

variables were standardized to mean zero and unit variance to facilitate interpretation of their relative importance.

For each response variable I evaluated all possible crop size-neighborhood regression equations (not including interactions and higher-order terms). Examination of eigenvalues of the correlation matrix, and variance inflation factors (VIFs) of the full model suggested multicollinearity was not a problem for these data. Based on the adjusted R^2 , there was a clear “best” model in each case; the addition of explanatory variables to this model failed to yield slopes significantly different from zero. Plots of predicted values against residuals, explanatory variables against residuals, and index plots of Cook’s Distances were examined for fitted models to check for violations of assumptions and outliers (Chatterjee et al. 2000). No gross violations of model assumptions were evident. Because focal trees were sampled sequentially throughout the season, I also examined plots of residuals from the selected models vs. day of year. These plots, as well as Durbin-Watson tests for autocorrelated errors suggested that there were no remaining temporal patterns in the data after model fitting. In addition, I used partial regressions to determine the proportion of the variation in visitation that was uniquely described by the temporal trend models and crop size-neighborhood models.

Finally, it should be noted that with respect to the regression analyses, the approach was largely exploratory in nature. A large number of analyses were performed prior to arriving at the results presented here (including ones that considered alternative summaries of neighborhood variables). Thus, the probability of Type I Errors in hypothesis tests was inflated to some unknown degree (Philippi 1993). The reader should

not interpret P -values from multiple regressions as inferring patterns at the level of the entire population of trees, but merely as measures of how well the models fit this particular data set. Despite inferential limitations, I feel that the good fit of my models to these data is compelling; I hope it will stimulate further research into what I feel is an important area of inquiry.

RESULTS

Bird use of Schefflera trees

Fourteen bird species were noted eating *Schefflera morototoni* fruits during the study (Table 2). Not all of these species were recorded from both focal tree and plot-level observations (10 species for each method); however, in each case it was clear that *Spindalis portoricensis* was the dominant consumer of *S. morototoni* fruits. *S. portoricensis* accounted for 86% of focal tree visits and visited all focal trees but one (which was not visited by any birds in the four hrs it was observed). Similarly, from the plot-level data, *S. portoricensis* accounted for more than two-thirds of all *S. morototoni* frugivory observations and was the only bird species observed consuming *S. morototoni* fruits on most days. The number of species visiting focal trees ranged from zero to six (median = 2) and was strongly correlated with the number focal tree visits ($r = 0.72$, $P = 0.0001$, $N = 24$).

In addition to the ten species observed consuming fruits at focal trees, a number of other species visited but were not observed to consume fruits. Some of these, including Bananaquit (*Coereba flaveola*), Northern Parula (*Parula americana*), Cape May Warbler (*Dendroica tigrina*), Black-throated Blue Warbler (*Dendroica caerulescens*), and Black-cowled Oriole (*Icterus dominicensis*), visited infructescences but consumed arthropods or other small food items rather than fruit. *D. tigrina* was observed consuming *S. morototoni* fruits during plot-level foraging observations. Thus, this species, and perhaps others on this list, at least occasionally consumed *S. morototoni* fruits. Other species visited focal trees but were not observed feeding at infructescences. These included: Puerto Rican Emerald (*Chlorostilbon maugaeus*), Green Mango (*Anthracothorax viridis*), Puerto Rican Tody (*Todus mexicanus*), Black-and-white Warbler (*Mniotilta varia*), Antillean Euphonia (*Euphonia musica*), Puerto Rican Bullfinch (*Loxigilla portoricensis*), and Black-faced Grassquit (*Tiaris bicolor*). Here again, the plot-level observations showed that at least *E. musica* and *L. portoricensis* occasionally consume *S. morototoni* fruits, although these species clearly play, at best, a relatively minor role in this dispersal system.

Most birds visiting *S. morototoni* trees consumed only a few fruits per visit (median = 3 fruits, quartiles = 1, 4). I found nearly identical fruit consumption for *S. portoricensis* and other fruit consumers ($t = 0.83$, $df = 168$, $P = 0.93$; Fig. 1). Similarly, most visits to focal trees were short in duration (median = 95 s, quartiles = 60, 158). I did, however, find a significant difference in visit length between *S. portoricensis* and the other *S. morototoni* consumers ($\chi^2 = 7.72$, $df = 1$, $P < 0.01$; Fig. 2). In addition, outliers

in Fig. 2 show that at least some *S. portoricensis* (males or pairs) did spend much longer than average periods of time in focal trees. It should be noted that because of small sample sizes, I lumped all non- *S. portoricensis* species for these comparisons, which may have obscured very real differences among species in fruit consumption and time spent in plants. Indeed, my only two fruit consumption observations for *Columba squamosa* suggest that this species may typically consume large quantities of fruit in a single visit (Fig. 1). Furthermore, two *C. squamosa* in one *S. morotoni* focal tree that were not detected entering the tree were probably in the plant for at least 13 minutes before being noted departing, based on the elapsed time since the beginning of the observation period.

Aggressive interactions at focal trees

Limiting consideration to bird species listed in Table 2 (i.e., likely *Schefflera morotoni* fruit consumers), displacement interactions at focal trees were uncommon (63 birds displaced in 658 total visits recorded at focal trees), usually occurring between conspecifics or with a larger species displacing a smaller one (Table 3). As expected from the high proportion of all visits made by *Spindalis portoricensis*, most interference interactions were between individuals of this species (76%). Almost all of these were between males (88% of interactions for which sex was determined for both participants). In many cases, the aggressor consumed no fruits and appeared to visit the tree solely to interrupt the foraging bout of the displaced bird (25 of 36 complete observations).

Limiting further consideration to *S. portoricensis*, I found little evidence of correlation between the mean number of fruits removed per visit and the number of displacements at focal trees ($r_s = 0.30$, $P = 0.23$, $N = 12$ trees). There was a marginally significant relationship between the number of visits to focal trees and the number of fruits consumed per visit ($r_s = 0.43$, $P = 0.08$, $N = 12$ trees). Contrary to my expectations, the correlation coefficients were positive in both cases, suggesting that not only did a higher likelihood of displacement not adversely affect fruit consumption, but that this higher likelihood of displacement may have resulted from birds spending longer periods of time foraging in frequently visited trees.

Plot-level frugivory

Most observations of frugivory were on *Schefflera morototoni* fruits, and most of these were by *Spindalis portoricensis* (Fig. 3). However, other avian fruit consumers also often fed at *S. morototoni* trees; it was third in importance (tied with *Cecropia schreberiana*), behind mistletoes, *Phoradendron* spp., and the tree, *Guarea guidonia*. There was a great deal of overlap in plant species used between *S. portoricensis* and the other fruit consumers, however there were also notable exceptions of species that were consumed by only either *S. portoricensis* or the other frugivores. For example, I only observed *Cordia sulcata* being consumed by *S. portoricensis*, while I never saw *G. guidonia* being eaten by *S. portoricensis*.

Seasonal trend in focal tree visitation and its correlates

Visitation rates at focal trees ranged from zero to 71 visits per four hrs (for all bird species) and were highest early and late in the season (Fig. 4). The quadratic equation describing this temporal trend was significant for both *Spindalis portoricensis* visitation ($R^2 = 0.47$, $F = 9.37$, $df = 2, 21$, $P = 0.001$) and total visitation ($R^2 = 0.39$, $F = 6.82$, $df = 2, 21$, $P < 0.01$).

A large percentage of the variation in visitation to focal trees by *S. portoricensis* and by all species combined could be explained by the crop size and neighborhood variables. As would be expected from the large proportion of all visits made by *S. portoricensis*, the selected regression model in each case included the same set of explanatory variables (all variables listed in Table 1 were included in models except for GUGU and PLSR). This model explained 82% of the variation in *S. portoricensis* visitation and 79% of the variation in visitation by all frugivore species (Table 4). There was a strong positive relationship between FTFI and visitation and strong negative relationship with CFI and visitation. All five of the heterospecific neighborhood variables included in models had slopes significantly different than zero. Four of these (MELA, COSU, CESC, INVE) had positive relationships with visitation, while PHOR was negatively related to visitation.

Nearly all of the variation in focal tree visitation described by the date variables (temporal trend) was accounted for by the crop size and neighborhood variables (Table 5). For both response variables, less than 1% of the variation in visitation was uniquely

explained by DATE and DATE², while more than one-third of the variation in visitation was uniquely explained by the crop size and neighborhood variables.

DISCUSSION

Bird use of Schefflera morototoni trees and interactions among frugivores

Although I found a large number of species visiting *Schefflera morototoni* trees, most visits were by a single specialist frugivore, *Spindalis portoricensis*. Furthermore, foraging observations suggested that *S. morototoni* was the single most important food item in the diet of *S. portoricensis* during the study (37% of *S. portoricensis* observations). Studies in other neotropical forests have also found *S. morototoni* to be an important dietary component of other specialized frugivores (in Trinidad: Snow 1962a, b, Snow 1970; in Panama: Martin 1982). It is also of note that in addition to the frugivores, a number of other bird species fed at infructescences, but on insects or other small food items rather than fruit. These species may play an important indirect role in this dispersal system by reducing fruit damage by invertebrate frugivores (Herrera 1984b), however this hypothesis remains to be tested.

Similar to patterns reported for other systems, most frugivores made short visits (< 2 min), and consumed few fruits per visit (2-4). There was little indication that the number of fruits removed per visit differed between *S. portoricensis* and the other avian frugivores. Some larger frugivores, e.g. *Columba squamosa*, may consume large

numbers of fruits per visit; however, the importance of this species in this system is probably minimal (at least at this site) as it was only rarely observed foraging in *S. morotoni* trees. Although visits by *S. portoricensis* were significantly longer than visits by other species, the typical visit length in both cases was short, suggesting that birds probably dispersed seeds away from parent trees. At least some *S. portoricensis* spent much longer than average periods of time in some focal trees (6-20 min), however even these extreme values are probably shorter than the period of time seeds are retained in the gut (see Travaset 1998 for review). Nonetheless, if some individual frugivores visit particular trees frequently, then some seeds may not be dispersed from underneath parent crowns. Although I lacked the data that would have allowed me to critically evaluate this possibility, behavioral observations suggested that some *S. portoricensis* utilizing focal trees may have been defending feeding or breeding territories, and thus may have spent long periods of time in or around these trees. For example, birds that were in focal trees for extended time periods spent most of this time sitting, preening, or singing, rather than feeding. In addition, *S. portoricensis* aggressors in most displacement interactions did not consume fruits, but rather appeared to visit focal trees with the sole intention of displacing the subordinate bird.

I found displacements at focal trees to be rare, with little evidence that interference interactions had a substantial impact on fruit consumption. This finding is in agreement with numerous other studies that have reported agonistic interactions between birds at tropical fruiting trees to be rare (e.g., Willis 1966, Leck 1972, Cruz 1974, 1981, Kantak 1981, Breitwisch 1983, Athreya 1997). In contrast, social interactions could be

important in affecting visitation and fruit removal. For example, visitation to *S. morototoni* trees by *S. portoricensis* often occurred in pairs, and male birds were observed feeding fruits to females on several occasions. In addition to interactions between mates, birds calling from fruiting trees could alert other birds to the fruit source (Olupot et al.1998; Chapter 4). Although I did not observe large feeding aggregations in this study, I have observed such aggregations at *S. morototoni* at other locations in the central mountains of Puerto Rico, particularly where *Nesospingus speculiferus* is abundant (e.g., on the LTP study area of Chapters 2-4). *Nesospingus* is the “core” species of interspecific flocks (Recher and Recher 1966), and calling individuals attract the attention of not just other conspecifics, but of many other species as well (*personal observation*). How social interactions might influence visitation and fruit removal from individual trees requires further evaluation.

Seasonal variation in visitation and its correlates

In contrast to the relatively constant number of fruits removed per visit observed at *S. morototoni* trees, visitation rates were highly variable. This finding is in agreement with Schupp (1993) and Jordano and Schupp (2000) who report that visitation rate typically correlates more strongly with the number of seeds dispersed by a bird species than does the number of seeds removed per visit. The high variability in visitation rate I found followed a seasonal trend and was highest early and late in the season. This seasonal trend was described almost entirely by crop size and neighborhood variables. I

found strong positive effects of focal tree ripe fruit abundance and strong negative effects of neighborhood conspecific ripe fruit abundance, suggesting that plants competed for dispersers. This finding is not surprising, and the idea that plants compete for dispersers is not new. In fact, the importance of competition among plants has been emphasized since it was noted by seminal papers on the evolutionary ecology of fruiting plant-vertebrate frugivore interactions that fruit crops of animal-dispersed plants typically remained undepleted (McKey 1975, Howe and Estabrook 1977). A large number of studies have since shown the number of fruits or percentage of fruit crop removed from individuals to be positively related to crop size or negatively related to the density or presence of conspecific fruits or fruiting plants nearby (e.g., Moore and Willson 1982, Manasse and Howe 1983, Davidar and Morton 1986, Denslow 1987). My findings, with respect to visitation, are in accordance with these studies; however, I believe the effects of conspecifics on one another will vary depending on average crop size and the spatial scale considered. For example, the strong competitive conspecific effects I found may have resulted, at least in part, from the exceptionally large crop sizes typical of this species. In species with smaller crops, conspecific neighbors may be needed to attract sufficient numbers of frugivores to disperse seeds (Rathcke 1983; Sargent 1990). Similarly, the importance of intraspecific competition for a given species will also be expected to vary between fruiting periods having different fruiting intensity (Ortiz-Pulido and Rico-Gray 2000).

In addition to intraspecific competition, I also found evidence of strong interspecific interactions among fruiting plants. Similar types of interspecific interactions

have been reported for other plant-animal interactions (e.g., for pollination: Feinsinger et al. 1986; for herbivory: Hambäck et al. 2000, White and Whitham 2000), however studies of such interactions in fruiting plant-frugivore systems are rare (Herrera 1984a). I found that Mistletoes of the genus *Phoradendron* appeared to compete with focal trees. Both *S. morotoni* and *Phoradendron* spp. likely provide similarly high rewards to frugivores in terms of high proportions of lipids and proteins (Herrera 1981, Stiles 1993). The notion that each of these provides high quality fruits is supported by the fact that each relies primarily on a single specialized frugivore for dispersal [*S. morotoni* on *S. portoricensis*, and *Phoradendron* spp. on *Euphonia musica* (Carlo 1999)]. *S. portoricensis* also showed strong preference for *Phoradendron* spp. at Cialitos during the course of the study (Carlo 1999). Thus, because both *S. morotoni* and *Phoradendron* spp. probably provide similar reward and are both preferred by the principal disperser, *S. portoricensis*, it is not surprising that the direction of the interaction was competitive in both cases. It is, perhaps, surprising that the effect size was greater for *Phoradendron* spp. than for conspecifics. Howe and Estabrook (1977) suggested that plants should compete interspecifically, although to a lesser extent, than intraspecifically. It is unclear as to why this may not have been the case here, although it may be that if the two fruits are antagonistic in terms of secondary compounds, then a particular bird may consume only one or the other fruit type within short time periods. If this is the case, then birds might consume the same fruit type from multiple plants, but only one fruit type within a particular fruit neighborhood.

The four fruiting plant species that showed positive relationships with visitation suggest that facilitative interactions may be more common among neighboring plants than competition. Similarly, Oniki et al. (1994) found that birds that visited *Cecropia* trees to feed on fruits in Brazilian Atlantic Forest often visited nearby legume trees, as well. In some cases these birds were observed foraging in the legume trees, although in this case, feeding was directed towards insects, rather than fruits. These findings are in accord with studies that have shown, via the analysis of fecal samples, widespread dietary mixing by frugivorous birds on short time scales (Loiselle 1990, White and Stiles 1990, Blake and Loiselle 1992). The reason for such dietary mixing is unclear; however, frugivorous birds probably require such mixed diets to balance nutritional needs or reduce overconsumption of particular toxic secondary compounds (Izhaki and Safriel 1989, Cipollini and Levey 1997). Although I lack information regarding the nutritional content or secondary compounds contained in fruits at this site, each of the four species produces very sweet-tasting fruits (*personal observation*), and as such may provide nutritional complements to the high lipid, high protein *S. morototoni* fruits. Published data has shown *Cecropia peltata* (formerly conspecific with *C. schreberiana*) to produce sugar-rich fruits in Costa Rica (Herbst 1986). In addition, *Inga vera* provides abundant nectar and flowers that are consumed by frugivores on the site as well, and thus *S. morototoni* consumers may have also been responding to these other food resources.

Finally, it should be noted that although visitation and, presumably fruit removal, may be enhanced in the presence of particular heterospecific fruits, and I refer to such interactions as “facilitative” in nature, the fitness consequences of such patterns remains

unclear. For example, Loiselle (1990) showed that competition among seedlings of different species may be important in determining the survival of species that are typically deposited in feces together. Linking spatial patterns of seed removal, deposition, and survival for assemblages of interacting plants will be required before the true nature of these types of interactions can be fully understood.

Implications and future directions

The high variability seemingly inherent in most fruiting plant-frugivore systems has led many researchers to view the notion of tight coevolution among frugivores and fruiting plants as a reasonable, yet essentially untestable concept (Wheelwright 1991). In the longest yet reported study of any such system, Herrera (1998) found little correlation between fruit and frugivore abundance over twelve years of study. In addition, the diet of the most abundant seed dispersers seemed to vary independently of the abundance of fruits. Based on these findings, Levey and Benkman (1999) suggest that tight coupling between fruit and frugivores in such systems may be overwhelmed by the influence of abiotic variables. My findings suggest that, at least in this system, which was dominated by one highly frugivorous bird species, biotic interactions among neighboring plants may be at least as important in decoupling tight interactions between particular bird-plant species pairs. Although I did not find strong evidence of interactions among frugivores affecting patterns of frugivory in this study, the importance of such interactions in situations where dense feeding aggregations occur more commonly should not be

discounted. In such situations “spillover” from preferred to less preferred plant species may be common (Pratt 1984, Mitchell 1990, Daily and Ehrlich 1994). Clearly, a number of sources of external variation will be important in affecting fruit removal from parent plants in any given fruiting plant frugivore system. The identification of these external sources of variation (both abiotic and biotic), as well as the disentangling of these various factors from characteristics under the direct control of parent plants, presents a considerable challenge to evolutionary ecologists studying fruiting plant-frugivore systems. Although understanding these sources of variation will be further complicated by the fact that their relative influences will be dependent on the spatial and temporal scales at which they are measured, the alternative of resigning oneself to attributing the high variation observed to the “noise” of a system comprised of many asymmetric pairwise relationships, is unlikely to yield new insights into these systems.

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LITERATURE CITED

- Alcántara, J. M., P. J. Rey, F. Valera, A. M. Sánchez-Lafuente, and J. E. Guitiérrez. 1997. Habitat alteration and plant intra-specific competition for seed dispersers. An example with *Olea europaea* var. *sylvestris*. *Oikos* 79:291-300.
- Athreya, V. R. 1997. Temporal patterns of visitation among avian frugivores at fruiting strangler figs in a tropical evergreen forest in the Western Ghats, Southern India. *Current Science* 72:405-408.
- Blake, J. G. and B. A. Loiselle. 1992. Fruits in the diets of neotropical migrant birds in Costa Rica. *Biotropica* 24:200-210.
- Breitwisch, R. 1983. Frugivores at a fruiting *Ficus* vine in a southern Cameroon tropical wet forest. *Biotropica* 15:125-128.
- Carlo, T. A. 1999. Fruit preference and seed dispersal capabilities of fruit-eating birds in north central Puerto Rico. M.S. Thesis. North Carolina State University, Raleigh, NC.
- Chatterjee, S., A. S. Hadi, and B. Price. 2000. *Regression analysis by example*. 3rd Edition. John Wiley and Sons, Inc., New York.
- Cipollini, M. L. and D. J. Levey. 1997. Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *American Naturalist* 150:346-372.
- Crow, T. R. 1980. A rainforest chronicle: a 30-year record of change in structure and composition at El Verde, Puerto Rico. *Biotropica* 12 (Suppl.):42-55.

- Cruz, A. 1974. Feeding assemblages of Jamaican birds. *Condor* 76:103-107.
- Cruz, A. 1981. Bird activity and seed dispersal of a montane forest tree (*Dunalia arborescens*) in Jamaica. *Biotropica* (Suppl) 13:34-44.
- Daily, G. C., and P. R. Ehrlich. 1994. Influence of social status on individual foraging and community structure in a bird guild. *Oecologia* 100:153-165.
- Davidar, P. and E. S. Morton. 1986. The relationship between crop sizes and fruit removal rates by birds. *Ecology* 67:262-265.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* (Suppl) 12:42-45.
- Denslow, J. S. 1987. Fruit removal from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. *Canadian Journal of Botany* 65:1229-1235.
- Diamond, J. M. and J. Terborg. 1967. Observations on bird distribution and feeding assemblages along the Rio Callaria, Department of Loreto, Peru. *Wilson Bulletin* 79:273-282.
- Dowsett-Lemaire, F. 1996. Avian frugivore assemblages at three small-fruited tree species in the forests of northern Congo. *Ostrich* 67:88-89.
- Ewel, J. J. and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. U.S. Forest Service Research Paper ITF-18. Institute of Tropical Forestry, Río Piedras, Puerto Rico. 72 pp.
- Feinsinger, P., K. G. Murray, S. Kinsman, and W. H. Busby. 1986. Floral neighborhood and pollination success in four hummingbird-pollinated cloud forest plant species. *Ecology* 67:449-464.

- Fleming, T. H. 1979. Do tropical frugivores compete for food? *American Zoologist* 19:1157-1172.
- Fleming, T. H. and C. F. Williams. 1990. Phenology, seed dispersal, and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest. *Journal of Tropical Ecology* 6:163-178.
- French, K., D.J. O'Dowd, and A. Lill. 1992. Fruit removal of *Coprosma quadrifida* (Rubiaceae) by birds in south-eastern Australia. *Australian Journal of Ecology* 17:35-42.
- Hambäck, P. A., J. Ågren, and Lars Ericson. 2000. Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. *Ecology* 81:1784-1794.
- Herbst, L. H. 1986. The role of nitrogen from fruit pulp in the nutrition of a frugivorous bat *Carollia perspicillata*. *Biotropica* 18:39-44.
- Herrera, C. M. 1981. Are tropical fruits more rewarding to dispersers than temperate ones? *American Naturalist* 118:896-907.
- Herrera, C. M. 1984a. Seed dispersal and fitness determinants in wild rose: combined effects of hawthorn, birds, mice, and browsing ungulates. *Oecologia* 63:386-393.
- Herrera, C. M. 1984b. Avian interference of insect frugivory: an exploration into the plant-bird-fruit pest evolutionary triad. *Oikos* 42:203-210.
- Herrera, C. M. 1986. Vertebrate-dispersed plants: why they don't behave the way they should. Pp. 5-18 in *Frugivory and Seed Dispersal: Ecology and Evolutionary Aspects* (T. H. Fleming and A. Estrada, Eds.) Kluwer Academic Publishers, Belgium.

- Herrera, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* 68:511-538.
- Howe, H. F., and G. F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. *American Naturalist* 111:817-832.
- Howe, H. F. and J. Smallwood. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13:201-228.
- Izhaki, I. and U. N. Safriel. 1989. Why are there so few exclusively frugivorous birds? – experiments on fruit digestibility. *Oikos* 54:23-32.
- Johnson, R. A., M. F. Willson, J. N. Thompson, and R. I. Bertin. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology* 66:819-827.
- Jordano, P. and E. W. Schupp. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70:591-615.
- Kantak, G. E. 1981. Temporal feeding patterns of some tropical frugivores. *Condor* 83:185-187.
- Leck, C. F. 1972. Seasonal changes in feeding pressures of fruit- and nectar-eating birds in Panamá. *Condor* 74:54-60.
- Levey, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58:251-269.
- Levey, D. J. and C. W. Benkman. 1999. Fruit-seed disperser interactions: timely insights from a long-term perspective. *TREE* 14:41-43.

- Levey, D. J., T. C. Moermond, and J. S. Denslow. 1984. Fruit choice in neotropical birds: the effect of distance between fruits on preference patterns. *Ecology* 65:844-850.
- Liogier, H. A. 1995. Descriptive flora of Puerto Rico and adjacent islands. Vol. IV: Melastomataceae to Lentibulariaceae. Universidad de Puerto Rico, Río Piedras, Puerto Rico.
- Little, E. L. and R. O. Woodbury. 1976. Trees of the Caribbean National Forest, Puerto Rico. USDA Forest Service, Research Paper ITF-20. Institute of Tropical Forestry, Rio Piedras, PR. 27 pp.
- Loiselle, B. A. 1990. Seeds in droppings of tropical fruit-eating birds: importance of considering seed composition. *Oecologia* 82:494-500.
- Loiselle, B. A., and J. G. Blake. 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a neotropical lowland wet forest. *Vegetatio* 107/108:177-189.
- Manasse, R. S. and H. F. Howe. 1983. Competition for dispersal agents among tropical trees: influences of neighbors. *Oecologia* 59:185-190.
- Martin, T. E. 1982. Frugivory and North American migrants in a neotropical second-growth woodland. Ph.D. dissertation, University of Illinois, Champaign, IL, USA.
- Martin, T. E. 1985. Resource selection by tropical frugivorous birds: integrating multiple interactions. *Oecologia* 66:563-573.

- McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pp. 159-191 *In*:
Coevolution of animals and plants (L. D. Gilbert and P. Raven, Eds.). University of
Texas Press, Austin, Texas.
- Mitchell, W. A. 1990. An optimal control theory of diet selection: the effects of resource
depletion and exploitative competition. *Oikos* 58:16-24.
- Moermond, T. C. and J. S. Denslow. 1983. Fruit choice in neotropical birds: effects of
fruit type and accessibility on selectivity. *Journal of Animal Ecology* 52:407-420.
- Moermond, T. C. and J. S. Denslow. 1985. Neotropical avian frugivores: patterns of
behavior, morphology, and nutrition, with consequences for fruit selection. Pp. 865-
897 *in* Neotropical Ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S.
Ridgley, and N. G. Smith, eds.). American Ornithologists' Union Monographs, No.
36, Allen Press, Washington, D. C.
- Moore, L. A. and M. F. Willson. 1982. The effect of microhabitat, spatial distribution,
and display size on dispersal of *Lindera benzoin* by avian frugivores. *Canadian
Journal of Botany* 60:557-560.
- Nieves, L. O. 1979. Ecological life history study of *Didymopanax morototoni*. M. S.
Thesis. University of Puerto Rico, Rio Piedras, PR. 85 pp.
- Olupot, W., P. M. Waser, and C. A. Chapman. 1998. Fruit finding by mangabeys
(*Lophocebus albigena*): are monitoring of fig trees and use of sympatric frugivore
calls possible strategies? *International Journal of Primatology* 19:339-353.

- Oniki, Y., T. A. de Melo Júnior, E. T. Scopel, and E. O. Willis. 1994. Bird use of *Cecropia* (Cecropiaceae) and nearby trees in Espírito Santo state, Brazil. *Ornitologia Neotropical* 5:109-114.
- Ortiz-Pulido, R. and V. Rico-Gray. 2000. The effect of spatio-temporal variation in understanding the fruit crop size hypothesis. *Oikos* 91:523-527.
- Petit, L. J., D. R. Petit, and K. G. Smith. 1990. Precision, confidence, and sample size in the quantification of avian behavior. Pp. 193-198 *in* Avian foraging: theory, methodology, and applications (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., eds.). *Studies in Avian Biology* No. 13, Cooper Ornithological Society, San Diego, CA.
- Philippi, T. E. 1993. Multiple regression: herbivory. Pages 183-210 *in* S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Chapman and Hall, New York, New York, USA.
- Pratt, T. K. 1984. Examples of tropical frugivores defending fruit-bearing plants. *Condor* 86:123-129.
- Ratheke, B. 1983. Competition and facilitation among plants for pollination. Pp. 305-329 *in* *Pollination biology* (L. Real, ed.). Academic Press, New York.
- Recher, H. F. and J. T. Recher. 1966. A contribution to the knowledge of the avifauna of the Sierra de Luquillo, Puerto Rico. *Caribbean Journal of Science* 6:151-161.
- Sallabanks, R. 1993. On fruit-frugivore relationships: variety is the spice of life. *Oikos* 68:567-570.

- Sallie, J. H., J. Verner, and G. W. Bell. 1990. Sequential versus initial observations in studies of avian foraging. Pp. 166-173 *in* Avian foraging: theory, methodology, and applications (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., eds.). Studies in Avian Biology No. 13, Cooper Ornithological Society, San Diego, CA.
- Sargent, S. 1990. Neighborhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology* 71:1289-1298.
- SAS Institute. 1990. SAS/STAT user's guide, Version 6. Fourth Edition. Volume 2, SAS Institute, Cary, North Carolina, USA.
- Schupp, E. W. 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. Pages 15-29 *in* T. H. Fleming and A. Estrada, editors. Frugivory and seed dispersal: ecology and evolutionary aspects. Kluwer Academic, Dordrecht, The Netherlands.
- Siitari, H., J. Honkavaara, and J. Viitala. 1999. Ultraviolet reflection of berries attracts foraging birds. A laboratory study with redwings (*Turdus iliacus*) and bilberries (*Vaccinium myrtillus*). *Proc. R. Soc. Lond. B* 266:2125-2129.
- Snow, B. K. 1970. A field study of the Bearded Bellbird in Trinidad. *Ibis* 112:299-329.
- Snow, D. W. 1962a. A field study of the Black-and-white Manakin, *Manacus manacus*, in Trinidad. *Zoologica* 47:65-104.
- Snow, D. W. 1962b. A field study of the Golden-headed Manakin, *Pipra eythrocephala*, in Trinidad. *Zoologica* 47:183-198.
- Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113:194-202.

- Stiles, E. W. 1993. The influence of pulp lipids on fruit preference by birds. Pages 227-235 in *Frugivory and Seed Dispersal: Ecology and Evolutionary Aspects* (T. H. Fleming and A. Estrada, Eds.) Kluwer Academic Publishers, Belgium.
- Swaine, M. D. and T. C. Whitmore. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81-86.
- Terborg, J., and J. M. Diamond. 1970. Niche overlap in feeding assemblages of New Guinea birds. *Wilson Bulletin* 82:29-52.
- Travaset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics*. 1/2:151-190.
- 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.
- Whelan, C. J., and M. F. Willson. 1994. Fruit choice in migrating North American Birds: field and aviary experiments. *Oikos* 71:137-151.
- Wheelwright, N. T. 1991. Frugivory and seed dispersal: '¡la coevolución ha muerto – viva la coevolución!'. *Trends in Ecology and Evolution* 6:312-313.
- White, D. W., and E. W. Stiles. 1990. Co-occurrences of foods in the stomachs and feces of fruit-eating birds. *Condor* 92:291-303.
- White, J. A., and T. G. Whitham. 2000. Associational susceptibility of cottonwood to a box elder herbivore. *Ecology* 81:1795-1803.
- Willis, E. O. 1966. Competitive exclusion and birds at fruiting trees in western Columbia. *Auk* 83:479-480.

Willson, M. F., and A. Traveset. 2000. The Ecology of seed dispersal. Pp. 85-110 *in* Seeds: the ecology of regeneration in plant communities (M. Fenner, ed.). CABI Publishing, Oxon, UK.

FIGURE LEGENDS

Fig. 1. Box plots for fruit consumption at *Schefflera morototoni* trees by *Spindalis portoricensis* (SPPO; N=142) and all other species (N=28) at the Cialitos plot in north-central Puerto Rico. Horizontal lines show medians, boxes span first and third quartiles, whiskers span the 10-90% range, and dots depict extreme values. Most birds consumed few (2-4) fruits per visit, and there was little apparent difference in fruit consumption between *S. portoricensis* and other consumers. The two extreme values on the "OTHER" plot were *Columba squamosa* (COSQ); these were the only two observations I had for this species.

Fig. 2. Box plots of time spent per visit at *Schefflera morototoni* trees by *Spindalis portoricensis* (SPPO; N=175) and all other species (N=10) from observations at focal trees at the Cialitos study area in north-central Puerto Rico from Feb-May 1998. Horizontal lines show medians, boxes span first and third quartiles, whiskers span the 10-90% range, and dots depict extreme values. Most birds were in plants for short periods of time (< 2 min) and probably dispersed seeds away from focal trees. It should be noted, however, that there were a number of *S. portoricensis* outliers. Some of these were birds that spent long periods of time "loafing", preening, singing, and occasionally displaying to or chasing off other birds.

Fig. 3. Frugivory by *Spindalis portoricensis* (SPPO) and all other frugivores from 2 Feb-18 May 1998 at the Cialitos study area in north-central Puerto Rico. Consumption of an additional 14 plant species was recorded, but only infrequently (< 5 observations). Abbreviations for species codes are: *Schefflera morototoni* (SCMO), *Cecropia schreberiana* (CESC), *Cordia sulcata* (COSU), *Ficus* spp. (FICU), *Phoradendron* spp. (PHOR), *Inga vera* (INVE), *Miconia* spp. (MISP), *Musa* sp. (MUSP), *Guarea guidonia* (GUGU), *Clusia rosea* (CLRO), *Alchornia latifolia* (ALLA).

Fig. 4. Number of visits by *Spindalis portoricensis* (SPPO; closed circles) and by all species (open circles) plotted against Julian date for the 24 focal trees censused on the Cialitos study area in north-central Puerto Rico from 12 Feb-3 May 1998. There was a seasonal trend with visitation tending to be higher early and late in the season.

Table 1. Explanatory variables used in multiple regression models considering variation in visitation rate among the 24 focal trees censused in north-central Puerto Rico from Feb-May 1998. All neighborhood variables were measured within 30 m radius circles centered on focal trees.

<u>Focal Plant Characteristics</u>	
FTFI	Focal tree ripe fruit abundance index [†]
<u>Conspecific Neighborhood</u>	
CFI	Conspecific ripe fruit abundance index
<u>Heterospecific Neighborhood</u>	
CESC	Presence/absence (P/A) of <i>Cecropia schreberiana</i> with ripe fruit
COSU	P/A of <i>Cordia sulcata</i> with ripe fruit
GUGU	P/A of <i>Guarea guidonia</i> with ripe fruit
INVE	Ripe fruit abundance index for <i>Inga vera</i>
MISP	P/A of <i>Miconia</i> spp. with ripe fruit
PHOR	P/A of <i>Phoradendron</i> spp. with ripe fruit
PLSR	Species richness of bird-consumed plants with ripe fruit

[†] See Methods: Crop size and neighborhood measurements for details of fruit abundance index calculation.

Table 2. Avian frugivore use of *Schefflera morototoni* from Feb-May 1998 at the Cialitos study area in north-central Puerto Rico. Most focal tree visits were made by *Spindalis portoricensis*, which was observed feeding at all but one focal tree (which was not visited by any bird). Similarly, from foraging observations conducted at the plot-level, *S. portoricensis* accounted for most frugivory observations at *S. morototoni* trees and was the only species recorded consuming *S. morototoni* fruits on most observation days.

Bird species	Focal tree visitation ($N=24$ trees) [†]		<i>Schefflera</i> foraging observations ($N=26$ days)	
	No. visits (%)	No. trees visited (%)	No. obs. (%)	No. days observed (%)
<i>Spindalis portoricensis</i>	382 (86.2)	23 (95.8)	45 (68.2)	18 (69.2)
<i>Vireo altiloquus</i>	25 (5.6)	10 (41.7)	3 (4.5)	3 (11.5)
<i>Turdus plumbeus</i>	9 (2.0)	2 (8.3)	0 (0.0)	0 (0.0)
<i>Nesospingus speculiferus</i>	8 (1.8)	5 (20.8)	4 (6.1)	2 (7.7)
<i>Melanerpes portoricensis</i>	7 (1.6)	3 (12.5)	0 (0.0)	0 (0.0)
<i>Columba squamosa</i>	4 (0.9)	2 (8.3)	5 (7.6)	3 (11.5)
<i>Myarchis antillarum</i>	3 (0.7)	3 (12.5)	0 (0.0)	0 (0.0)
<i>Contopis portoricensis</i>	2 (0.5)	1 (4.2)	0 (0.0)	0 (0.0)
<i>Margarops fuscatus</i>	2 (0.5)	2 (8.3)	1 (1.5)	1 (3.8)
<i>Tyrannus caudifasciatus</i>	1 (0.2)	1 (4.2)	1 (1.5)	1 (3.8)
<i>Tyrannus dominicensis</i>	* (0.0)	* *	4 (6.1)	3 (11.5)
<i>Loxigilla portoricensis</i>	* (0.0)	* *	1 (1.5)	1 (3.8)
<i>Euphonia musica</i>	* (0.0)	* *	1 (1.5)	1 (3.8)
<i>Dendroica tigrina</i>	* (0.0)	* *	1 (1.5)	1 (3.8)
Total	443	14	66	

Note: Visits only counted if birds either directly observed consuming fruit or in a portion of the tree containing ripe fruit, but not directly observed feeding.

† * = Species observed visiting focal trees but did not consume fruit.

Table 3. Aggressive interactions recorded at the 24 *Schefflera morototoni* focal trees censused in north-central Puerto Rico from Feb-May 1998. Almost all displacements were between *Spindalis portoricensis*. Species are listed from smallest to largest by weight (weights taken from my unpublished banding data).

Aggressor	Supplanted Species							
	DETI	VIAL	MYPO	SPPO	NESP	TYDO	MEPO	TUPL
<i>Dendroica tigrina</i> (DETI)	3							
<i>Vireo altiloquous</i> (VIAL)		1						
<i>Myarchis portoricensis</i> (MYPO)		2	1					
<i>Spindalis portoricensis</i> (SPPO)		2		48			1	
<i>Nesospingus speculiferus</i> (NESP)					2			
<i>Tyrannus dominicensis</i> (TYDO)						2		
<i>Melanerpes portoricensis</i> (MEPO)								
<i>Turdus plumbeus</i> (TUPL)								1

Table 4. Results of selected multiple regressions modeling visitation to 24 focal trees at the Cialitos study area in north-central Puerto Rico as a function of crop size and neighborhood variables (see Table 1 for definitions of explanatory variables). Focal tree fruit abundance (FTFI) was strongly positively related to visitation, while the amount of conspecific fruits in the neighborhood (CFI) was negatively related to visitation, suggesting competition for dispersers. The presence of neighbors of various heterospecific taxa had mixed relationships with focal tree visitation.

Variable	<i>Spindalis</i> visitation				Total visitation			
	Estimate	SE	<i>t</i> -test	<i>P</i> -value	Estimate	SE	<i>t</i> -test	<i>P</i> -value
FTFI	0.70	0.26	2.66	< 0.05	0.87	0.31	2.78	< 0.05
CFI	-0.97	0.25	-3.88	< 0.01	-1.06	0.30	-3.59	< 0.01
MISP	1.00	0.28	3.55	< 0.01	1.12	0.33	3.35	< 0.01
COSU	0.73	0.24	3.06	< 0.01	0.71	0.28	2.49	< 0.05
PHOR	-1.42	0.26	-5.47	< 0.0001	-1.44	0.31	-4.64	< 0.001
CESC	0.82	0.24	3.46	< 0.01	0.76	0.28	2.71	< 0.05
INVE	1.04	0.24	4.27	< 0.001	1.23	0.29	4.24	< 0.001
<i>N</i> = 24, Model $R^2 = 0.82$, <i>P</i> < 0.0001					<i>N</i> = 24, Model $R = 0.79$, <i>P</i> < 0.0001			

Table 5. Partial regressions comparing models describing variation in visitation to focal trees at the Cialitos study area in north-central Puerto Rico from Feb-May 1998 as a function of date (temporal trend) and as a function of crop size and neighborhood variables. Nearly all of the temporal trend in visitation was accounted for by the crop-size and neighborhood variables.

Source of variation	% variation explained	
	<i>Spindalis portoricensis</i> visitation	Total visitation
Crop size-neighborhood	36.0	39.8
Temporal trend	0.9	0.5
Temporal trend/crop size-neighborhood	46.2	38.8
Unexplained	16.9	20.9

Fig. 1

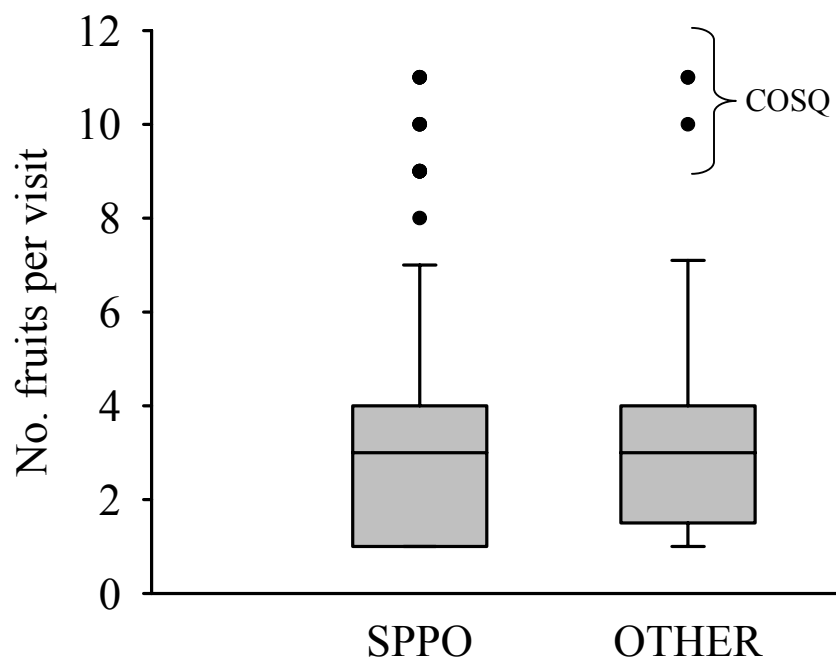


Fig. 2

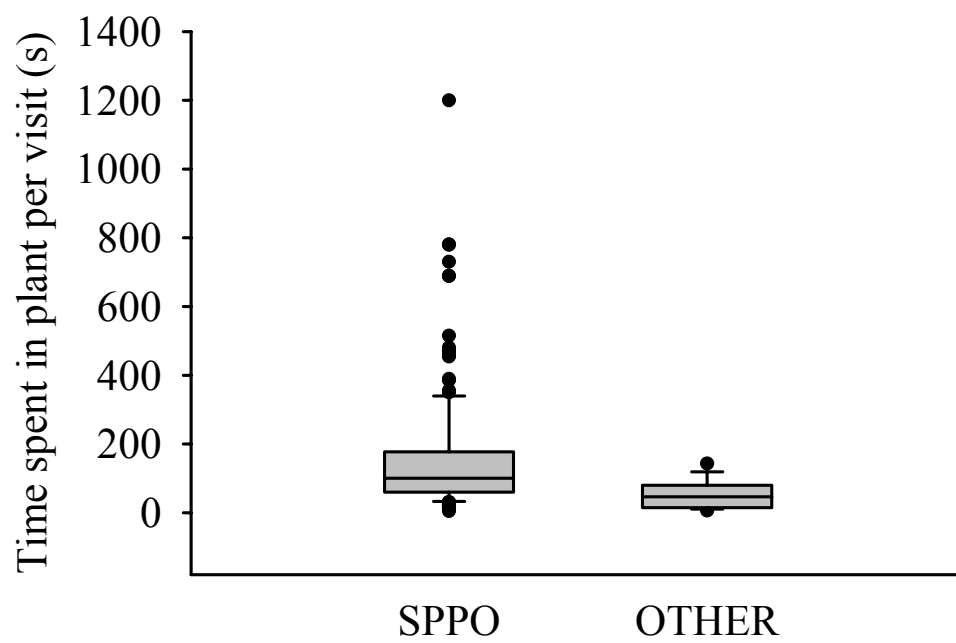


Fig. 3

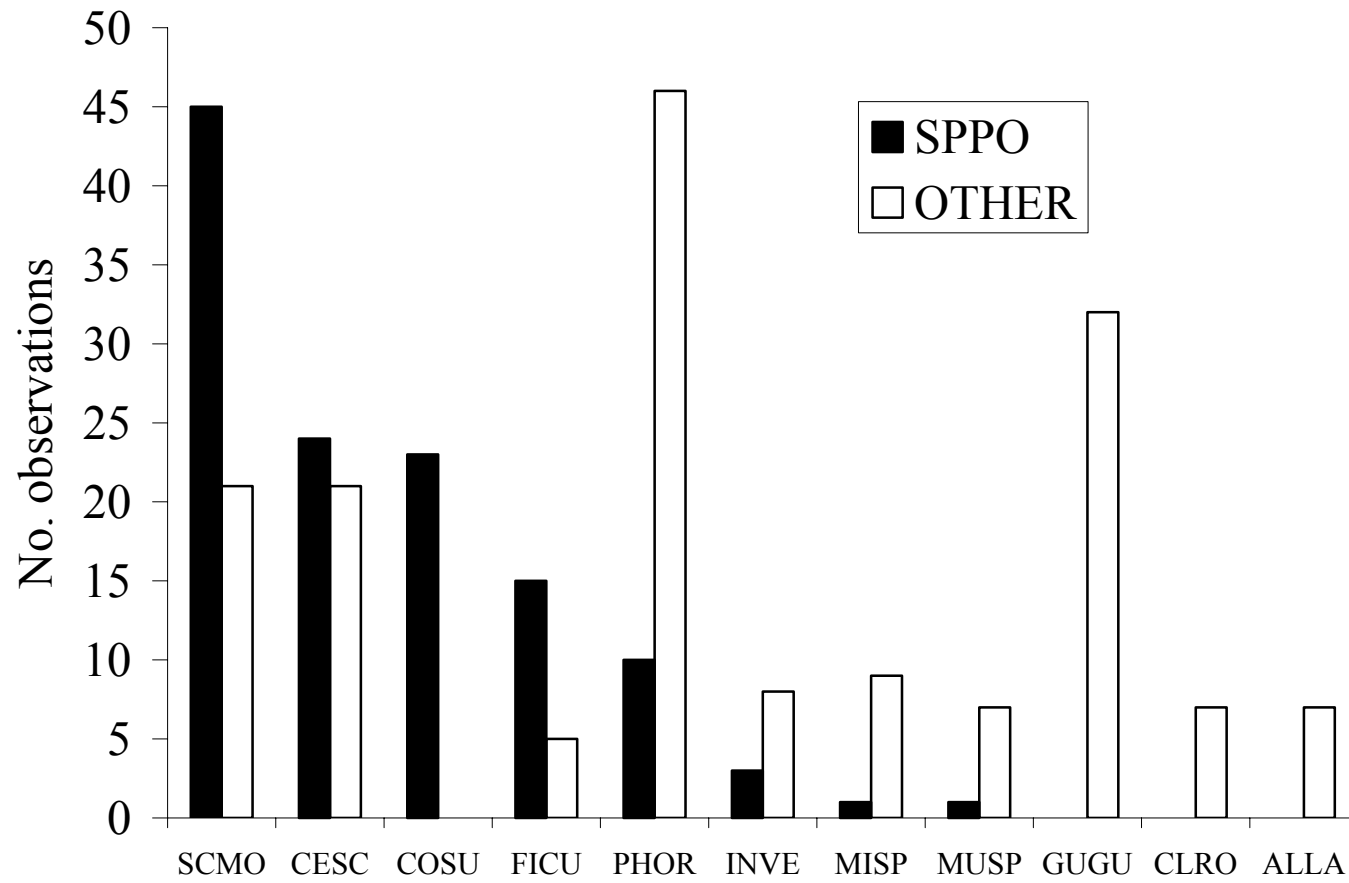
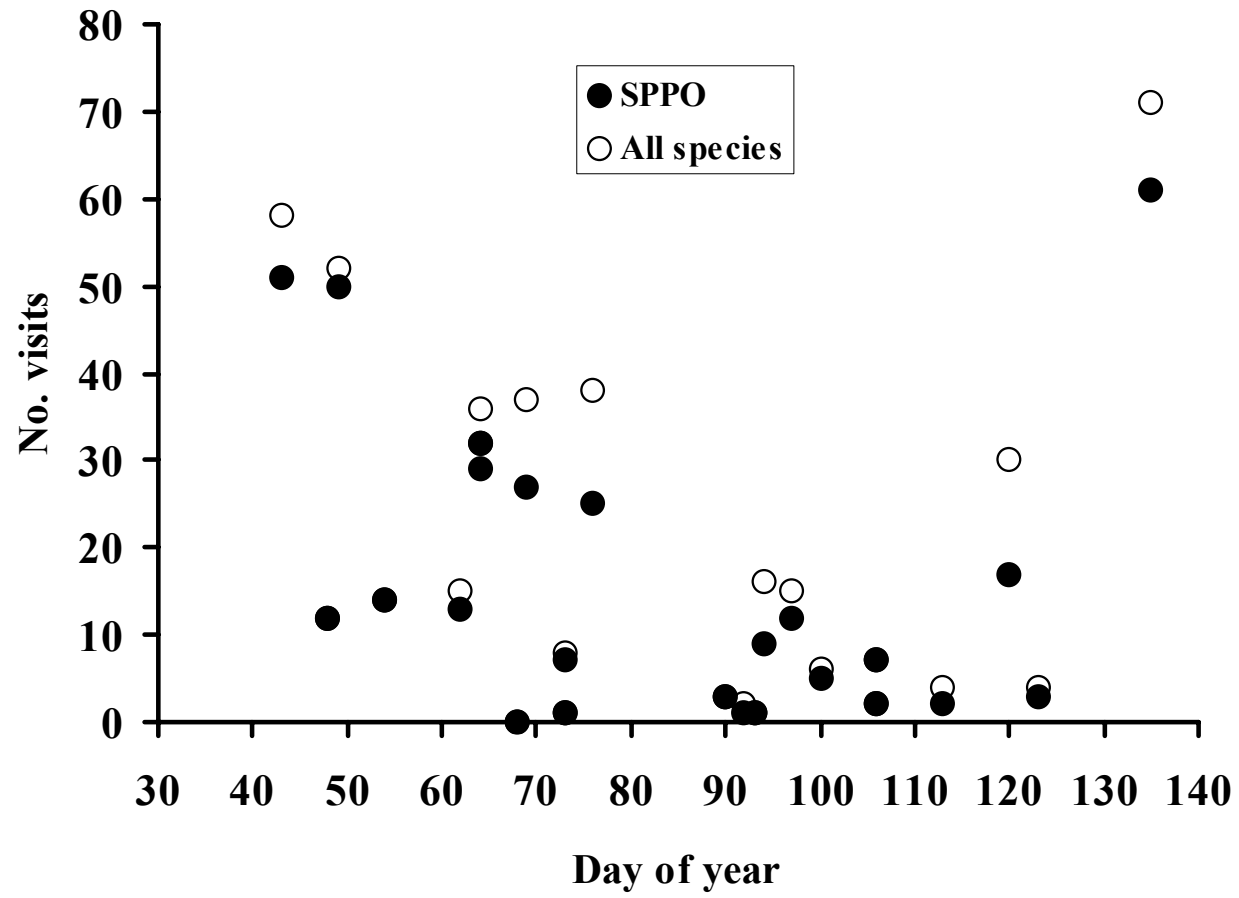


Fig. 4



CHAPTER 2

LOCAL SCALES OF SPATIAL PATTERN IN THE DISTRIBUTIONS OF FRUITING
BIRD-DISPERSED TREES AND USE BY AVIAN FRUGIVORES

Abstract. Identifying spatial pattern in plant populations is a fundamental objective of plant ecology. These underlying patterns can be used to better understand not only interactions among plants, but also interactions with the animals that consume them. In this paper, I used second-order spatial point pattern analyses to identify scales of aggregation or over-dispersion in the distributions of four bird-dispersed tree species (*Schefflera morototoni*, *Dendropanax arboreus*, *Miconia serrulata*, and *Guarea guidonia*) on a 4.05 ha grid in secondary wet forest in the Cordillera Central of Puerto Rico. In order to link these underlying patterns with interactions with seed-dispersing frugivorous birds, I monitored the fruiting phenology of all individual trees and collected foraging observations, noting the individual plants in which birds foraged during a single fruiting season (Aug.-Nov. 1999). For each tree species, I tested the null hypotheses that (1) fruiting trees were distributed randomly with respect to the population of adult trees, and (2) trees visited by frugivores were randomly distributed with respect to the distribution of fruiting trees. Two tree species fruited and were utilized by frugivores during two of the four months (*D. arboreus* and *M. serrulata*). The remaining two species fruited and were utilized by frugivores during the entire study period, and for these I examined spatial patterns during shorter time intervals [monthly (*S. morototoni*) or bimonthly (*G. guidonia*)].

All tree species were significantly aggregated at scales < 80 m; however, the mean crowding experienced by individual trees and the sizes of deviations from random distributions differed markedly among the four species, particularly at spatial scales $> \sim 20$ m. The four species differed somewhat with respect to the regions of the study area

they occupied. *S. morototoni* was aggregated with respect to *M. serrulata* at scales > 69 m, while *G. guidonia* was aggregated with respect to *D. arboreus* at scales < 5 m. All other pairs were either randomly distributed or regularly spaced with respect to one another. I found no significant spatial patterning in fruiting or frugivory in excess of what would have been expected if plants fruited or were visited randomly with the possible exception some statistically marginally-significant cases. Fruiting and visitation patterns for *S. morototoni* and *M. serrulata* suggested these two species were strongly linked with respect to interactions with frugivores – *M. serrulata* apparently competed with *S. morototoni* on small spatial scales ($< \sim 60$ m) while benefiting from high *S. morototoni* abundance at larger scales ($> \sim 60$ m). Finally, examination of spatial patterns of fruiting and visitation across shorter time scales for *S. morototoni* and *G. guidonia* did reveal significant patterns that were masked by my consideration of all months combined. Fruiting of *S. morototoni* was significantly over-dispersed on small scales (< 20 m), while visitation was significantly aggregated at small and intermediate scales (< 60 m). In contrast, fruiting of *G. guidonia* tended to be aggregated (although not significantly so), while also tending to be aggregated with respect to visitation. Because the mean crowding of visited trees was very similar for the two species, I postulate that differences in the direction of the fruiting spatial pattern may have reflected differences in crowding of adult trees. These findings highlight the potentially large size of plant neighborhoods with respect to interactions with avian seed dispersers, and suggest that knowledge of tree distributions is a critical first step for understanding interactions with frugivores.

INTRODUCTION

A fundamental objective of plant ecology is the description of spatial pattern in plant populations (Dale 1999). The identification of spatial pattern at various scales is a critical step in the formulation and testing of hypotheses related to the multitude of processes responsible for generating these patterns. For example, it has been observed that tropical tree species are typically clumped in distribution (Armesto et al. 1986, Hubbell et al. 1990); however, on very small scales, trees may be over-dispersed (i.e., regularly spaced) due to density dependent predation on, or competition among, seeds and seedlings beneath parent trees (Janzen 1970, Connell 1971, Wills et al. 1997). Patchiness often becomes evident only at larger (but still local) scales where patchily distributed resources (Good 1931; e.g., nutrients, light; Nicotra et al. 1999) or clumped seed dissemination (Hubbell et al. 1999, Jordano and Schupp 2000, Wenny 2000) may largely determine plant distributions.

The identification of pattern in the spatial distributions of trees at various scales also provides a general framework from which to view current ecological interactions and understand selection pressures faced by plants (Stoll and Weiner 2000). For example, at some spatial scales conspecific adult plants may compete for mutualistic pollinators or seed dispersers (Levin and Anderson 1970, Moore and Willson 1982, Manasse and Howe 1983, Davidar and Morton 1986, Denslow 1987, Chapter 1); at other (smaller) scales, plants may facilitate visitation to one another via their increased ability of attracting these mutualist consumers when in close proximity to one another (Rathcke 1983, Feinsinger et

al. 1986, Sargent 1990; see Wiens 1989 for general discussion of scale considerations). Although it is clear that interactions such as these occur, they take on evolutionary significance for plant populations only if the scale of the interaction (i.e., the ecological neighborhood: Addicott et al. 1987, Stoll and Weiner 2000) coincides with scales at which plants are patchily distributed. Thus, it is important to be able to link scales of population patchiness to scales of important ecological interactions.

Finally, trees are limited in their ability to mediate interactions with consumers because of their fixed spatial locations; however, they may alter their effective spatial proximity to neighbors (with respect to these interactions) by modifying their phenology. Indeed, variation among individuals in flowering and fruiting phenology may in some cases be high (e.g., Rathcke and Lacey 1985, Newstrom et al. 1994), and could result in an additional level of spatial patterning in plant populations above that of the distribution of plants themselves. Such patterning could occur via a number of mechanisms (e.g., patchy abiotic conditions such as gaps (Levey 1990), effects of consumers on phenology (Levey 1987), or direct communication among plants (Agrawal 2000), and must be taken into consideration in any study of the spatial components of ecological interactions between plants and consumers.

In this paper I consider the spatial distributions of four bird-dispersed plant species on a 4.05 ha study area in secondary montane forest in north-central Puerto Rico and identify scales of spatial interactions among plants with respect to fruiting and frugivory. The four species were *Schefflera morototoni*, *Guarea guidonia*, *Dendropanax arboreus*, and *Miconia serrulata*. For each tree species I tested the null hypothesis that

individuals were distributed as completely spatially random (hereafter CSR) against the alternative hypotheses of aggregation or inhibition (regular spacing). In order to facilitate interpretation of similarities or differences among species in spatial patterns of fruiting and use by frugivores, I also tested the null hypothesis that pairs of each of the four species were distributed independently of one another against the alternative hypotheses of aggregation (attraction) or regular spacing. I then asked whether there were any patterns of aggregation or inhibition with respect to fruiting or use by frugivores in excess of what would be expected based on the distributions of adult trees and fruiting trees. For species that were used by frugivores throughout the study period, I also considered temporal variation in spatial patterns of fruiting and frugivory.

METHODS

Study area

The study was conducted from August to November 1999 in the Cordillera Central of Puerto Rico within Los Tres Picachos State Forest (LTP). LTP is comprised of approximately 12,000 ha ranging from 300 to 1,205 m elevation. Most of the forest lies within Holdridge's (1974) Subtropical Wet Forest Life Zone, with an average annual rainfall of 2,000-4,000 mm and average temperature of 18-24°C (Birdsey and Weaver 1982). The highest elevations of LTP are characterized by elfin forest (>1,090 m; Ewel and Whitmore 1973). Below this elevation (850-1,090 m), particularly on steep slopes,

are sierra palm (*Prestoea montana*) stands, and between 700-850 m elevation are stands dominated by the tabonuco tree (*Dacryodes excelsa*). Overlapping the tabonuco forest zone, and at lower elevations, are mixed secondary forests, whose species composition reflects both current ecological processes and human land use history (primarily coffee and fruit production). It is in a stand of this type that the study was conducted.

I established a 225 m x 180 m rectangular plot (4.05 ha) in secondary forest at approximately 620 m elevation (18°13'N, 66°32'W). The plot was laid out in 15 m x 15 m grid cells by 3-5 people using compasses and measuring tape. Plant species composition was similar to that of forests in the surrounding region. Thus, I feel it was representative of mid-elevation montane secondary forests in this area. Most of the plot was on a gentle slope, although it rose steeply in one corner and was bisected by a stream on one side. A steep bank was present on either side of the stream. Dominant canopy species included *Inga vera* and *Ocotea leucoxyton* and two focal species *Guarea guidonia*, and *Schefflera morototoni*. Two other focal species, *Dendropanax arboreus* and *Miconia serrulata*, as well as other *Miconia* spp., *Piper glabrescens*, and plants in the family Rubiaceae dominated the subcanopy and understory. A number of cultivated species such as coffee (*Coffea arabica*), oranges (*Citrus sinensis*), and bananas (*Musa* sp.) were also common in the understory and subcanopy.

Focal species

The four focal species, along with a fifth species, *Cecropia schreberiana*, comprised the most commonly consumed species by avian frugivores during the study period (see Chapter 4 for summary of bird observations by plant species). I do not consider *C. schreberiana* here because it was uncommon on the study area (25 females) and showed little variation in fruiting or visitation; nearly all individuals fruited, and most were visited by frugivores.

Guarea guidonia and *Schefflera morototoni* are canopy trees. *Dendropanax arboreus* is an understory or subcanopy tree; *Miconia serrulata* is large shrub or small tree. All are widely distributed in the neotropics (Little and Wadsworth 1964). *M. serrulata* and *S. morototoni* are pioneers, commonly found in disturbed forests, gaps, and edges (Crow 1980, Denslow 1980). *D. arboreus* is found in a variety of forest types in wet districts at middle and upper elevations (Birdsey and Weaver 1982, Liogier 1995). *G. guidonia* is common in abandoned coffee plantations and montane secondary forests at middle elevations in Puerto Rico (Ewel and Whitmore 1973, Birdsey and Weaver 1982, Zimmerman et al. 1995).

Fruits of the four species differed markedly. *S. morototoni* produces 2-seeded berry-like drupes (4-6 mm long, 6-10 mm broad) borne on 20-60 cm compound terminal panicles (Liogier 1995). Although variable in color, *S. morototoni* fruits are generally grayish-purple when ripe. *D. arboreus* produces terminal infructescences containing dark purple fruits 6-8 mm in diameter (Liogier 1995). *G. guidonia* produces axillary racemes

containing capsules 1.5-1.9 cm in diameter that open to display four red arillate seeds. *M. serrulata* fruits, which are borne on terminal racemes, are white to deep purple (when ripe) subglobose or ovoid berries approximately 1 cm diameter and containing hundreds of small seeds (Liogier 1995). Crop sizes varied from hundreds to tens of thousands for *D. arboreus*, *G. guidonia*, and *M. serrulata*, to tens to hundreds of thousands of fruits for *S. morototoni*.

Avian frugivore coterries for the four tree species also differed markedly during the study period. *S. morototoni* was primarily consumed by the tanagers, *Spindalis portoricensis* (53% of foraging observations recorded for this species) and *Nesospingus speculiferus* (18% of observations). *D. arboreus* and *M. serrulata* were primarily consumed by *N. speculiferus* (65% and 46% of observations, respectively); *M. serrulata* was also heavily utilized by the neotropical migrant, *Dendroica caerulescens* (32% of observations). Half of all observations on *G. guidonia* fruit were of the breeding resident *Vireo altiloquus*. Fourteen percent of foraging observations on *G. guidonia* were by the Puerto Rican Bullfinch, *Loxigilla portoricensis*. Although this species generally did not disperse seeds of *G. guidonia*, all trees visited by *L. portoricensis* were also visited by more effective dispersers. Further details on frugivory on the study area during this time can be found in Chapter 4.

Plant mapping and phenological monitoring

All individuals of focal species in the plot were mapped in reference to grid points. Each tree was tagged with a unique number, its diameter-at-breast-height (dbh) was recorded, and its fruiting phenology was monitored monthly from July-Nov 1999. For analyses, I included only individuals with dbh > that of the smallest individual that fruited during the study period.

Bird observations

Foraging observations were conducted on six days in August, September, and November 1999, and on three days in October, during which time exceptionally rainy weather precluded further sampling. Four observers surveyed the plot in the following manner. First, we divided the plot into twelve 75 m x 45 m blocks (i.e., one block = fifteen 15 m x 15 m cells). Each observer was randomly assigned (without replacement) three blocks per day, such that all blocks were observed on all observation days (4 observers \times 3 blocks). Each block was observed for two hours, with approximately $\frac{1}{2}$ hr separating consecutive observation periods. Thus, on each day observations were conducted over six hours covering three observation periods (early, middle, and late). We began the first observation period within $\frac{1}{2}$ hr of sunrise and usually completed the last within seven hrs of the starting time. The random assignment of blocks was constrained such that each block was observed at least once by each observer and twice

during each daily time period (once during each time period in October), to avoid observer and temporal biases, respectively. At the beginning of each two-hr observation period, observers slowly proceeded from a randomly assigned starting cell and systematically traversed the block looking and listening for bird activity. Once located, birds were followed with the aid of binoculars, and the plant number(s) in which frugivory events occurred were noted.

DATA ANALYSES

In addressing each of my hypotheses, I used methods developed for the analysis of the second-order properties of spatial point patterns. The second-order properties of a spatial point process (a spatial point *pattern* being a partial realization of a spatial point *process*) describe the variation in the dependence among points (or “events”) through space (Diggle 1983). These methods will undoubtedly be familiar to many readers; however, I explain them in some detail below for two reasons. First, although second-order point pattern analyses have been used by ecologists to test null hypotheses of CSR before, seldom has the size of departures from CSR been related back to the more familiar ideas of concentration, crowding, and the ecological neighborhood (but see Orensanz et al. 1998). Because I feel that a connection between departures from randomness and “effect size” is critical for the evaluation of the relative importance of various ecological interactions, I define second order statistics to facilitate making this link. Second, I make use of two types of bivariate second-order analyses that rely on

different tests specific to the null hypotheses they address. I make a clear distinction between the two in order to justify the particular test statistics and Monte Carlo methods used for assessing significance.

All analyses were performed using the Splancs library of functions (Rowlingson and Diggle 1993; <http://www.lancs.ac.uk/Software/Splancs>) written for S-PLUS software (Mathsoft 2000).

Univariate point pattern analyses: tree spatial distributions

In order to evaluate the second order properties of focal tree spatial distributions, I used Ripley's K -function (Ripley 1976, 1977),

$$K(t) = \lambda^{-1} E[\text{number of further events} \leq \text{distance } t \text{ of an arbitrary event}], \quad (1)$$

where λ is the intensity of the point process, defined as the expected number of events per unit area, and $E[\cdot]$ is the expectation of (\cdot) . Under the null hypothesis of CSR (i.e., for a homogeneous Poisson process), $K(t) = \pi t^2$; under regularity $K(t) < \pi t^2$; and under aggregation $K(t) > \pi t^2$. For any given spatial point pattern (i.e., partial realization of a spatial point process), $K(t)$ can be estimated by (corrected for edge effects; Ripley 1976):

$$\hat{K}(t) = \hat{\lambda}^{-1} \frac{\sum_{i=1}^n \sum_{j=1}^n w_{ij} I(t_{ij})}{n} \quad (2)$$

where $\hat{\lambda}$ is the estimated intensity, defined as $n/|A|$ (n is the number of trees in region A , with area $|A|$), $t_{i,j}$ is the distance between the i th and j th trees, $I_t(t_{i,j})$ is an indicator function equal to 1 if $t_{i,j} \leq t$, and 0 otherwise, and $w_{i,j}$ is the proportion of a circle with center i and passing through j that lies within A (the edge correction). Put simply, $\hat{K}(t)$ as an estimate of the crowding (sensu Lloyd 1967, Orensanz et al. 1998) experienced by the average tree, scaled by the intensity of the pattern (i.e., the overall density). Because this statistic combines elements of both quadrat counts and distance measurement, it yields a sensitive assessment of spatial pattern, giving weight to both local and global characteristics. In addition, because $K(t)$ is estimated from a complete map, it can be evaluated for any arbitrary t , up to about half the length of the shortest plot side (90 m in my case; Peterson and Squiers 1995), the limitation on t_{\max} stemming from the $w_{i,j}$ s becoming unbounded as t increases. I report results in terms of the commonly used transformation of $\hat{K}(t)$,

$$\hat{L}(t) = t - [\hat{K}(t)/\pi]^{1/2}, \quad (3)$$

which is easier to interpret because its expected value under CSR is zero (Ripley 1977, Diggle 1983). This transformation also has the statistically desirable property of

stabilizing the variance. Positive values of $\hat{L}(t)$ indicate regular departures from random; negative values indicate aggregation. I assessed the significance of $\hat{L}(t)$ from 99% confidence envelopes constructed from 99 realizations of a homogeneous Poisson process (my null hypothesis of CSR) conditioned on the original number of trees (Diggle 1983). Upper and lower envelope boundaries were delineated by the maximum and minimum values of $\hat{L}(t)$ s computed from the 99 simulations. The distances at which departures from envelope boundaries occurred indicated the scale of the spatial pattern.

As noted above, $\hat{K}(t)$ is the estimated crowding experienced by the average individual scaled by the overall density of plants. It can easily be converted to an unscaled measure of crowding (the ‘mean crowding’ of Lloyd 1967, Orensanz et al. 1998):

$$\bar{C}(t) = \hat{K}(t)\lambda .$$

Using this transformation I was able to compare differences in crowding experienced by the different tree species in units that have biological meaning (i.e., number of plants). I also calculated departures from randomness for the four species in these units by subtracting an estimate of the expected crowding, $E[\bar{C}(t)] = \hat{\lambda} \pi t^2$, from the calculated crowding.

Bivariate point pattern analyses I: patterns of attraction or inhibition between tree species

In order to test the null hypothesis that tree species were distributed independently of one another I used the bivariate analog of the K -function,

$$K_{ij}(t) = \lambda_j^{-1} E[\text{number of type } j \text{ events} \leq \text{distance } t \text{ of an arbitrary type } i \text{ event}], \quad (4)$$

where λ_j is the intensity of type j events. It can easily be seen that equation (4) is just a special case of (1) defined above; i.e., when $i = j$ equations (1) and (4) are equivalent. Thus, $K_{11}(t)$ and $K_{22}(t)$ can be estimated using equation (2). $K_{12}(t)$ [or, equivalently $K_{21}(t)$] can be estimated as:

$$\hat{K}_{12}(t) = \frac{\sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij} I(t_{ij})}{\hat{\lambda}_1 \hat{\lambda}_2 |A|} \quad (5)$$

where n_1 is the number of type 1 events, n_2 is the number of type 2 events, $\hat{\lambda}_1$ is the intensity of type 1 events, and $\hat{\lambda}_2$ is the intensity of type 2 events. Under the null hypothesis, the two event types are located independently of one another; i.e., the event types belong to two populations (which may each be distributed in any stationary, isotropic, and orderly manner). As for the univariate case, I present results as the

transformation $\hat{L}_{12}(t)$ [calculated as in equation (3), but replacing $\hat{K}(t)$ with $\hat{K}_{12}(t)$], where positive values of $\hat{L}_{12}(t)$ denote regular departures from random (inhibition) and negative values denote attraction. Significance of departures from independence was inferred from 99% confidence envelopes computed in a manner analogous to what was done for my assessment of univariate point patterns; however, here I compared the observed $\hat{L}_{12}(t)$ to minimum and maximum $\hat{L}_{12}(t)$ values obtained from 99 simulated toroidal shifts (Diggle 1983, Lotwick and Silverman 1982). This method obtains new patterns by perturbing all locations of one species (but not the other) by a random amount $(\Delta x, \Delta y)$, thus preserving the observed patterns of each species separately.

Bivariate point pattern analyses II:

In order to investigate patterns of spatial aggregation or inhibition in fruiting or use by avian frugivores, I drew on methods used by epidemiologists for the detection of disease clusters (Diggle and Chetwynd 1991). Specifically, I used tests of what is commonly referred to as “random labeling”. Under random labeling, a single underlying point process determines point locations, and point types are determined by a second random mechanism that operates independently of the point process (Diggle 1983). Specifically, my null hypotheses were:

H_{01} : There is no spatial patterning in fruiting in excess of that due to the locations of adult trees.

H_{02} : There is no spatial patterning in visited trees in excess of that due to the locations of fruiting trees.

For H_{01} , the “population” (i.e., the underlying pattern, n) was the total number of adult trees of a species in the study area (occasionally a few observations were missing, but assuming no spatial bias in missing values, results remain unaffected; missing observations accounted for a very small percentage of the total number of trees); the population of adult trees was then divided into the two sets of points comprised of n_1 fruiting trees and n_2 non-fruiting trees. For H_{02} , the population was the number of fruiting trees, which was then divided into the two sets of points comprised of n_1 visited fruiting trees and n_2 unvisited fruiting trees.

Because under the null hypothesis point types are determined randomly, it follows that $K_{11}(t) = K_{22}(t) = K_{12}(t)$ for all t . Note that this finding does not make any assumptions about the underlying point process, which in ecological (as in epidemiological) studies is typically patchy (i.e., an inhomogeneous point process). Because the underlying point process is patchy, the expected value of $K_{12}(t)$ does not equal πt^2 (as it did under independence), and the expected value of $L_{12}(t)$ does not equal zero. Thus, the intuitive appeal of $\hat{L}_{12}(t)$ as a test statistic is diminished (although it has been used for tests of random labeling in other ecological studies; e.g., see Kenkel 1988, Szwagrzyk and Czerwczak 1993, Peterson and Squiers 1995). Clearly, a more meaningful test statistic would be preferable.

Diggle and Chetwynd (1991) suggest $D(t) = K_{11}(t) - K_{22}(t)$ as a more meaningful statistic for assessing random labeling hypotheses. Because $K_{11}(t) = K_{22}(t) = K_{12}(t)$ under random labeling, the expected value of $D(t)$ is zero; $D(t) > 0$ indicates significant clustering of type 1 events (labels); $D(t) < 0$ indicates regular spacing of type 1 events. Furthermore, $D(t)$ has a straightforward interpretation: $\lambda_1 D(t)$ equals the expected number of excess labeled points $\leq t$ for a typical labeled point in the absence of spatial clustering. I evaluated the random labeling hypotheses using an estimate of $D(t)$:

$$\hat{D}(t) = \hat{K}_{11}(t) - \hat{K}_{22}(t),$$

where $\hat{K}_{11}(t)$ and $\hat{K}_{22}(t)$ were calculated using the univariate K -function estimator defined in equation (2). Positive values of $\hat{D}(t)$ indicated aggregated patterns of fruiting or frugivory; negative values indicated regular spacing of fruiting and frugivory. Significance of departures from random were assessed by simulating n_1 random labelings of the original n points 99 times and then calculating minimum and maximum $\hat{D}(t)$'s to define 99% confidence envelopes in a manner analogous to what was done for the univariate assessments of $\hat{L}(t)$ above. Here again, the scale at which departures of the observed $\hat{D}(t)$ from envelope boundaries occurred indicated the scales of the pattern.

I interpreted scales of departures from random as representing the ecological neighborhood (*sensu* Addicott et al. 1987; or, equivalently the 'ecological effective distance', Antonovics and Levin 1980) with respect interactions among plants. I assessed

the mean crowding (Lloyd 1967, Orensanz et al. 1998) of fruiting trees and frugivory [$\bar{C}_{11}(t)$] at these scales and the degree to which aggregation or regularity occurred in excess of what would be expected from randomly labeled patterns (Diggle and Chetwynd 1991).

RESULTS

Univariate tree spatial distributions

The four tree species showed very different large-scale patterns of distribution across the study area (Fig. 1). *Guarea guidonia* (Fig. 1D) was abundant and uniformly distributed. The remaining species were less abundant and heterogeneously distributed. *Dendropanax arboreus* (Fig. 1B) was mostly restricted to the upper (southwestern) half of the study area, while *Schefflera morototoni* (Fig. 1A) and *Miconia serrulata* (Fig. 1C) were primarily found in the lower (northeastern) half. *S. morototoni* was more common on the left (southeastern) side of the plot, while *M. serrulata* was more common on the right (northwest).

Tests of CSR showed three of the four species, *S. morototoni*, *D. arboreus*, and *M. serrulata* (Fig. 2A-C), to be significantly aggregated at all scales (0-90 m). *G. guidonia* was significantly aggregated at all but the largest scales (> 78 m; Fig. 2D).

All species showed similar levels of crowding at very small spatial scales ($< \sim 11$ m); at intermediate scales (~ 15 -40 m) *S. morototoni* and *G. guidonia* began to diverge from the other two in having much higher levels of crowding (Fig 3A). At the largest

spatial scale (90 m), all four were markedly different, and the rank order of crowding reflected differences in overall density. The difference in mean crowding between the most (*G. guidonia*) and least (*M. serrulata*) crowded species at this scale was more than 200 individuals*individual⁻¹.

The species also differed in the degree to which their spatial distributions deviated from CSR at the various scales considered (Fig. 3B). *G. guidonia*, the most abundant species, was also the most evenly distributed, and showed the smallest departure from CSR at all scales. Individuals of *S. morototoni* were the most crowded of the four species, and the degree to which its distribution deviated from CSR continued to increase over all scales considered (although there was some indication that it was leveling off at about 90 m). The remaining species showed maximum deviation from CSR at scales of between 60 and 70 m.

Bivariate tree spatial distributions

Patterns of spatial association and avoidance among tree species can be inferred both from referral to Fig. 1, as well as from results of the formal analysis presented in Fig. 4. *Schefflera morototoni* showed a significant positive association with *M. serrulata* (Fig. 4B) at large scales (> 69 m). *S. morototoni* showed no pattern of association with *G. guidonia* (Fig. 4C), while tending to be regularly spaced with respect to *D. arboreus* at all scales, although not significantly so (Fig. 4A). *M. serrulata* tended to be regularly spaced with respect to both *G. guidonia* (Fig. 4F) and *D. arboreus* (Fig. 4D), although

only significantly so at small scales for *G. guidonia* (~ 5 m) and at small to intermediate scales for *D. arboreus* (~12-50 m). Finally, *D. arboreus* tended to be clumped with respect to *G. guidonia* at all scales, yet this pattern of attraction was only significant at small scales (< 5 m) (Fig. 4E).

Spatial patterns of fruiting and frugivory

I found weak evidence of spatial patterning in fruiting in the direction of regularity for *S. morototoni* and *D. arboreus*, albeit at very different scales (Fig. 5A, B). $\hat{D}(t)$ for *S. morototoni* approached the envelope boundary only at small scales (7-15 m; Fig. 5A), while $\hat{D}(t)$ for *D. arboreus* approached its envelope boundary at the largest scale considered of 90 m (Fig. 5B). For *S. morototoni*, about 0.5 fewer individuals fruited than would be expected within a circle of about 12 m surrounding fruiting trees. Although this may seem like an inconsequential amount, it represents a reduction of fruiting from random of about 25%. For *D. arboreus*, about 9 fewer fruiting individuals were found within a circle of 90 m radius than would be expected if fruiting were random. Again, for an area of this size (2.5 ha), this may also sound like a small amount, however it amounts to about a 19% reduction from the 48 fruiting individuals that would be expected within this distance of other fruiting plants under the null hypothesis of random fruiting. The other two species showed little evidence of spatial pattern (Fig. 5C, D, although $\hat{D}(t)$ for *G. guidonia* did approach the envelope boundary in the direction of regularity at 7 m, probably as a result of spatial patterning in tree size, unpubl. data).

I found no significant departures from random for frugivory (Fig. 6); however, $\hat{D}(t)$ did approach the confidence envelope boundary in the direction of regularity for *M. serrulata* at a scale of about 58 m (Fig. 6C). There were 4.3 fewer other visited *M. serrulata* within this distance of the average visited *M. serrulata* than would be expected if visitation to other trees occurred randomly. Under random labeling, I would have expected 11.5 other visited individuals within 58 m of visited plants; the actual number of 7.3 thus represented 38% fewer than what would have been expected under random labeling.

Temporal variation in spatial patterns of frugivory

Fruiting of *D. arboreus* and *M. serrulata* was primarily restricted to two of the four months studied – *D. arboreus* had ripe fruit in August and September, while *M. serrulata* had ripe fruit primarily in October and November. Almost all visitation to *D. arboreus* was observed during August, and only one additional plant was visited in September. Thus, I did not consider this species further. Although the number of plants visited was more equitably distributed across the two principal fruiting months for *M. serrulata* (13 plants visited in October, 12 in November, 18 of which were unique to one of the two months), I do not consider this species further either because of both its small sample size and limited fruiting period.

The two remaining species, *S. morotoni* and *G. guidonia*, although utilized most heavily during Aug.-Sept., were visited in larger numbers than *D. arboreus* and *M.*

serrulata throughout the study period. In order to explore spatial patterns in fruiting and frugivory on finer time scales for these two species, I divided the study period into monthly intervals for *S. morototoni* and bimonthly intervals for *G. guidonia* and reanalyzed the data. I considered bimonthly, rather than monthly, intervals for *G. guidonia* for two reasons. First, relatively few individuals were visited in the second half of the study period (12 trees, only four of which were visited in November). Second, there was a distinct change in the frugivore assemblage for *G. guidonia* between Aug.-Sept. and Oct.-Nov., as its principal consumer, *Vireo altiloquus*, migrated from the area during this time.

I found little monthly variation in the spatial pattern of *S. morototoni* fruiting (Fig. 7A-D), and the monthly patterns correspond closely to the $\hat{D}(t)$ plot for all months combined (see Fig. 5A). This was not surprising, as there was little monthly turnover in fruiting plants: < 4% of the total fruiting individuals were unique to any one month, and most (81%) fruited in at least 3 of the four months. Significant departures of fruiting from random were found at scales of 9-23 m in August, and at 9-19 m in September. Although $\hat{D}(t)$ plots for fruiting were similar in shape in October and November, no significant departures from random were found.

In contrast, turnover was much higher for visited plants, which was reflected in a lack of correspondence between the $\hat{D}(t)$ plot for overall frugivory (i.e., all months combined) and monthly $\hat{D}(t)$ plots. As noted above, I found no spatial patterns in visitation for all months combined (see Fig. 6A), yet when considered separately, I found

significant clustering of visited trees in each month (Fig. 7 E-H). The scales at which significant clustering occurred increased between August, where it was only found at very small scales (16 m), and Sept.-Oct., where significant clustering was found at a variety of scales ranging from 14 to 65 m. Significant clustering was only found at a scale of 14 m during November.

$\hat{D}(t)$ plots for both fruiting and frugivory of *G. guidonia* in Aug.-Sept. (Fig. 8A, C) were very similar in shape to the $\hat{D}(t)$ plots for all months combined (Figs 5D, 6D). The nearly significant regularity in fruiting at very small scales (< 7 m) for all months combined noted above, was also evident in the Aug.-Sept. $\hat{D}(t)$ plot for fruiting. The number of visited trees was significantly aggregated in Aug.-Sept. at a scale of 37 m, a scale at which fruiting also tended to be clustered, although not significantly so. For the remaining two month period, there was no indication of any spatial patterning in fruiting or frugivory (Fig. 8B, D).

I evaluated spatial patterns of fruiting and frugivory for *G. guidonia* in Aug.-Sept. and *S. morototoni* in Sept. at distance $t = 37$ m in more detail in an effort to better understand differences in the direction of fruiting patterns for the two species. Visited trees of both species were significantly aggregated and had very similar levels of crowding: $\bar{C}(t) = 5.7$ individuals*individual⁻¹ for *G. guidonia* and $\bar{C}(t) = 5.4$ individuals*individual⁻¹ for *S. morototoni*. If fruiting of each species had been random, I would have expected an average of 11.4 fruiting conspecific neighbors for fruiting *G. guidonia* trees and 21.7 fruiting conspecific neighbors for fruiting *S. morototoni* at this

scale. I found, however, that fruiting *G. guidonia* were more crowded, with an average of 12.4 fruiting neighbors, and fruiting *S. morotoni* were less crowded, with an average of 17.3 fruiting neighbors.

DISCUSSION

Tree distributions

All four tree species were significantly clumped at all spatial scales less than about 78 m, at which point only *Guarea guidonia* was distributed in a manner indistinguishable from random. This was surprising in a couple of respects. First, the lack of regularity at very small scales suggested density-dependent mortality was not important in affecting tree recruitment beneath parents (Janzen 1970). Anecdotally, I have found evidence of high seed mortality beneath adult plants of many species in this area, and in general there are few saplings beneath parents. Nevertheless, high mortality beneath parents may be insufficient to limit patterns of tree recruitment. Second, Armesto et al. (1986) postulated that forests subject to frequent large-scale disturbances such as landslides and hurricanes should show random tree distributions, yet spatial randomness in trees on the study plot was also rare (further supported by analyses of an additional 11 species not presented here) despite several recent impacts from hurricanes and strong storms (notably Hurricane Georges in Sept. 1998).

Although each of the four species showed similar strong patterns of aggregation at almost all scales, they varied considerably with respect to the average degree of crowding experienced by individuals. This was especially true at larger scales ($> \sim 40$ m), where the rank order of crowding generally matched the rank order of abundance in the study area. The most crowded species, *G. guidonia*, was the most evenly distributed of the four, having the smallest deviation from CSR at all scales. Because *G. guidonia* is a common shade tree in traditional coffee plantations (Ewel and Whitmore 1973, Birdsey and Weaver 1982, Zimmerman et al. 1995), this pattern probably reflected the historical importance of coffee production in this area to some extent (abandoned ca. 50-60 yrs. previous). The second most crowded species, *Schefflera morototoni*, experienced the greatest deviation from random at all scales. It was the only species whose departure from random increased monotonically at all scales (suggesting it was tracking an ecological gradient); all other species showed diminishing deviation from random at the largest spatial scales ($> \sim 70$ m). These differences in crowding among species may have had important consequences with respect to spatial patterns in fruiting and use by frugivores.

Spatial patterns of fruiting and frugivory

When considered over the entire study period, there were no significant spatial patterns in fruiting for *S. morototoni* or *G. guidonia*. Spatial patterns were, however, evident across shorter time windows. There was a tendency for over-dispersion in the

fruiting of *S. morototoni* on small spatial scales (e.g., during Sept.; $< \sim 40$ m), while fruiting of *G. guidonia* (during Aug.-Sept.) was aggregated at these scales. This difference in the direction of departure from random fruiting may have reflected selection pressures on plants to maximize visitation and fruit consumption rates of dispersers. For example, given the relatively small percentage of *G. guidonia* individuals that fruited (20% during Aug.-Sept.), patchy fruiting was probably favorable as a means of attracting dispersers (*sensu* Rathcke 1983). In contrast, random fruiting in *S. morototoni* would have resulted in far more fruiting individuals at small spatial scales than was observed for fruiting *G. guidonia* (e.g., 21.7 v. 12.4 individuals*individual⁻¹ at a scale of 37 m). Because the two species experienced nearly identical crowding of visited trees at this scale (5.4 individuals*individual⁻¹ for *S. morototoni* v. 5.7 individuals*individual⁻¹ for *G. guidonia*), additional fruiting individuals of *S. morototoni* would have been unlikely to be visited because of satiation of seed dispersers; regularly spaced fruiting was probably a better strategy for this species.

Two species pairs showed patterns of attraction on at least some scales with respect to the distributions of adult trees. Taking the case of *M. serrulata* and *S. morototoni* first, the spatial patterning of fruiting trees was very similar for the two species, tending to be regularly spaced at small scales (< 60 m) and clumped at larger scales. *M. serrulata* adults were significantly clumped with respect to *S. morototoni* at 80m, and interestingly, it was also at this scale that the number of visited *M. serrulata* individuals crossed over from tending to be regularly distributed to being clumped. In addition, the nearly significant regularity of visited *M. serrulata* trees at smaller scales

corresponded closely to the scale of patchiness of adult *M. serrulata* trees and patchiness of visited *S. morototoni* during the two principal months of *M. serrulata* fruiting.

The combination of these findings strongly suggests that visitation to *M. serrulata* was closely linked to the distribution of *S. morototoni*. At small scales, where the distribution of *M. serrulata* and visitation to *S. morototoni* were most aggregated, *M. serrulata* visitation was over-dispersed, suggesting most individuals may have suffered from competition with *S. morototoni*. Nevertheless, individuals near visited *S. morototoni* probably benefited from their proximity to these visited individuals. This is the first field evidence I am aware of that supports previous aviary studies that have shown the proximity between fruits of different types to influence patterns of selection by frugivores (Levey et al. 1984). For example, relatively less preferred *M. serrulata* trees may have been visited most often when in close proximity to (presumably) more preferred visited *S. morototoni* trees (Chapter 3). Similar patterns could have, however, also occurred due to “spillover” from more to less preferred plants due to the presence of avian competitors (Pratt 1984, Mitchell 1990, Daily and Ehrlich 1994, White and Whitham 2000). Indeed, many foraging observations were recorded during the passing of mixed species foraging flocks where such spillover between neighboring fruiting plants clearly occurred. At larger scales, where *M. serrulata* was less aggregated, and *S. morototoni* was more aggregated, visitation to *M. serrulata* tended to be clumped. The relative shift in abundance may have been responsible for the apparent shift in the nature of the interaction between the two species at these larger scales, where the average *M. serrulata* probably benefited from bird use of *S. morototoni*. The apparent shift in *S.*

morototoni from being a competitor to a facilitator of visitation will be considered more explicitly in Chapter 3.

In contrast to *S. morototoni* and *M. serrulata*, *D. arboreus* and *G. guidonia* were aggregated with respect to one another at small scales. There were no striking patterns with respect to fruiting or frugivory on these two species. These two species did not overlap strongly in frugivore coterries (Chapter 3), and so in this case the link between spatial distributions and interactions with frugivores was weak. The fact that I did not find significant spatial patterning in fruiting or frugivory at the small scales at which these two were significantly aggregated with respect to one another probably reflects the relatively even distribution of *G. guidonia* across the study area.

Conclusions

The majority of tropical woody plant species rely on animal consumption for seed dispersal (as many as 90% or more in local forests; Jordano 2000). I have shown here that the ecological neighborhood, with respect to interactions between plants that share the same dispersers, may extend over large areas and involve hundreds of individual plants. This is in sharp contrast with results that find interactions among plants for shared abiotic resources may be restricted to very small spatial scales and involve only a few individuals (e.g., individual saplings on BCI forest plot, Panama compete with a mean of only 6.3 saplings during entire ontogeny; Hubbell et al. 1999). Clearly, there is much to be gained from linking patterns in the physical distributions of adult plants to patterns of fruiting

and visitation by mutualist frugivores. Such linkages will undoubtedly lead to new insights with respect to understanding the scales at which birds and plants respond to one another and may help to explain the high variability in frugivore responses to fruiting plants (Herrera 1998). Additional study with respect to interactions among fruiting plant species will also undoubtedly aid in our understanding this variability.

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LITERATURE CITED

- Addicott, J. F., J. M. Aho, M. F. Antolin, M. F. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49:340-346.
- Antonovics, J., and D. A. Levin. 1980. The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics* 11:411-452.

- Armesto, J. J., J. D. Mitchell, and C. Villagran. 1986. A comparison of spatial patterns of trees in some tropical and temperate forests. *Biotropica* 18:1-11.
- Birdsey, R. A. and P. L. Weaver. 1982. The forest resources of Puerto Rico. USDA Forest Service Resource Bulletin SO-85, 59 pp.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298-310 in P. J. den Boer and G. R. Gradwell, eds. Dynamics of populations. Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations. Oosterbeek, 1970. Centre for Agricultural Publishing and Documentation, Wageningen.
- Crow, T. R. 1980. A rainforest chronicle: a 30-year record of change in structure and composition at El Verde, Puerto Rico. *Biotropica* 12 (Suppl.):42-55.
- Daily, G. C., and P. R. Ehrlich. 1994. Influence of social status on individual foraging and community structure in a bird guild. *Oecologia* 100:153-165.
- Dale, M. R. T. 1999. Spatial Pattern Analysis in Plant Ecology. Cambridge University Press, New York.
- Davidar, P. and E. S. Morton. 1986. The relationship between crop sizes and fruit removal rates by birds. *Ecology* 67:262-265.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* (Suppl) 12:42-45.
- Denslow, J. S. 1987. Fruit removal from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. *Canadian Journal of Botany* 65:1229-1235.

- Diggle, P. J. 1983. *Statistical analysis of spatial point patterns*. Academic Press, New York.
- Diggle, P. J., and A. G. Chetwynd. 1991. Second-order analysis of spatial clustering for inhomogeneous populations. *Biometrics* 47:1155-1163.
- Ewel, J. J. and J. L. Whitmore. 1973. *The ecological life zones of Puerto Rico and the U.S. Virgin Islands*. U.S. Forest Service Research Paper ITF-18. Institute of Tropical Forestry, Río Piedras, Puerto Rico. 72 pp.
- Feinsinger, P., K. G. Murray, S. Kinsman, and W. H. Busby. 1986. Floral neighborhood and pollination success in four hummingbird-pollinated cloud forest plant species. *Ecology* 67:449-464.
- Good, R. E. 1931. A theory of plant geography. *New Phytologist* 30:149-203.
- Herrera, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* 68:511-538.
- Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* 105:367-368.
- Hubbell, S. P., R. Condit, and R. B. Foster. 1990. Presence and absence of density dependence in a neotropical tree community. *Philos. Trans. R. Soc. London B* 330:269-281.
- Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554-557.

- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forest. *American Naturalist* 104:501-528.
- Jordano, P. 2000. Fruits and Frugivory. Pp. 125-165 *in* Seeds: the ecology of regeneration in plant communities (M. Fenner, Ed.). 2nd Ed. CABI Publishing, New York.
- Jordano, P. and E. W. Schupp. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70:591-615.
- Kenkel, N. C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69:1017-1024.
- Levey, D. J., T. C. Moermond, and J. S. Denslow. 1984. Fruit choice in neotropical birds: the effect of distance between fruits on preference patterns. *Ecology* 65:844-850.
- Levin, D. A. and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. *American Naturalist* 104:455-467.
- Liogier, H. A. 1995. Descriptive flora of Puerto Rico and adjacent islands. Vol. IV: Melastomataceae to Lentibulariaceae. Universidad de Puerto Rico, Río Piedras, Puerto Rico.
- Little, E. L., Jr. and F. H. Wadsworth. 1964. Common trees of Puerto Rico and the Virgin Islands. USDA Handbook 249. Washington, D.C. 548 pp.
- Lloyd, M. 1967. 'Mean crowding'. *Journal of Animal Ecology* 36:1-30.

- Lotwick, H. W. and B. W. Silverman. 1983. Methods for analysing spatial processes of several types of points. *Journal of the Royal Statistical Society-B* 44:406-413.
- Manasse, R. S. and H. F. Howe. 1983. Competition for dispersal agents among tropical trees: influences of neighbors. *Oecologia* 59:185-190.
- Mitchell, W. A. 1990. An optimal control theory of diet selection: the effects of resource depletion and exploitative competition. *Oikos* 58:16-24.
- Moermond, T. C. and J. S. Denslow. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Pp. 865-897 *in* *Neotropical Ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.), American Ornithologists Union.
- Moore, L. A. and M. F. Willson. 1982. The effect of microhabitat, spatial distribution, and display size on dispersal of *Lindera benzoin* by avian frugivores. *Canadian Journal of Botany* 60:557-560.
- Newstrom, L. E., G. W. Frankie, and H. G. Baker. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* 26:141-159.
- Nicotra, A. B., R. L. Chazdon, and S. V. B. Iriarte. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80: 1908-1926.
- Orensanz, J. M., A. M. Parma, and M. A. Hall. 1998. The analysis of concentration and crowding in shellfish research. Pp. 143-157 *in* *Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management* (G. S. Jamieson and A. Campbell, Eds.). *Can. Spec. Publ. Fish. Aquat. Sci.*

- Peterson, C. J. and E. R. Squiers. 1995. An unexpected change in spatial pattern across 10 years in an aspen-white pine forest. *Journal of Ecology* 83:847-855.
- Pratt, T. K. 1984. Examples of tropical frugivores defending fruit-bearing plants. *Condor* 86:123-129.
- Rathcke, B. 1983. Competition and facilitation among plants for pollination. Pp. 305-329 *in* *Pollination biology* (L. Real, ed.). Academic Press, New York.
- Rathcke, B. and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16:179-214.
- Ripley, B. D. 1976. The second-order analysis of stationary point processes. *Journal of Applied Probability* 13:255-266.
- Ripley, B. D. 1977. Modelling spatial patterns. *Journal of the Royal Statistical Society B* 39:172-212.
- Rowlingson, B. S. and P. J. Diggle. 1993. Splancs: spatial point pattern analysis code in S-plus. *Computers and Geosciences* 19:627-655.
- Sargent, S. 1990. Neighborhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology* 71:1289-1298.
- Stoll, P. and J. Weiner. 2000. A neighborhood view of interactions among individual plants. Pp. 11-27 *in* *The geometry of ecological interactions:simplifying spatial complexity* (U. Dieckmann, R. Law, and J.A.J. Metz, Eds.). Cambridge University Press, Cambridge, UK.
- Szwagrzyk, J. and M. Czerwczak. 1993. Spatial patterns of trees in natural forests of east-central Europe. *Journal of Vegetation Science* 4: 469-476.

- van Schaik, C. P., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353-377.
- Wenny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs* 70:331-351.
- White, J. A. and T. G. Whitham. 2000. Associational susceptibility of cottonwood to a box elder herbivore. *Ecology* 81:1795-1803.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Wills, C., R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences USA* 94:1252-1257.
- Zimmerman, J. K., T. M. Aide, M. Rosario, M. Serrano, and L. Herrera. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management* 77:65-76.

FIGURE LEGENDS

Fig. 1. Locations of the four bird-dispersed tree species on the 4.05 ha LTP study area, Puerto Rico.

Fig. 2. $\hat{L}(t)$ plots for the four tree species on the LTP study area, Puerto Rico. Solid lines are the observed $\hat{L}(t)$'s. Dashed lines delineate 99% confidence envelopes based on 99 simulations of a homogeneous Poisson process (i.e., CSR distributions). $\hat{L}(t)$ values falling outside the lower envelope indicate scales of significant aggregation.

Fig. 3. (A) Mean crowding, $\bar{C}(t)$, within circular plots of radii t ranging from 0-90 m for individuals of the four tree species on the LTP study area, Puerto Rico, and (B) deviation of the observed mean crowding from the expected mean crowding under the null hypothesis of CSR.

Figure 4. Bivariate $\hat{L}(t)$ plots for pairs of tree species on the LTP study area. Solid lines are $\hat{L}(t)$'s estimated from the data. Dashed lines delineate 99% confidence envelopes based on $\hat{L}(t)$'s estimated from simulated toroidal shifts. Positive values of $\hat{L}(t)$ indicate departure from random in the direction of regularity, negative values indicate aggregation.

Fig. 5. $\hat{D}(t)$ plots for tests of the null hypothesis that fruiting occurs randomly with respect to spatial location for the four tree species on the LTP study area, Puerto Rico. Data were collected from Aug.-Nov. 1999. Solid lines are the observed $\hat{D}(t)$'s. Dashed lines delineate 99% confidence envelopes based on random labelings of the underlying point pattern. $\hat{D}(t)$ values falling outside the lower envelope suggest significant regularity (inhibition) in fruiting. The distance at which departures from envelope boundaries occur indicates the scale of the pattern. Sample sizes, n_1 and n_2 are the number of fruiting and non-fruiting individuals, respectively.

Fig. 6. $\hat{D}(t)$ plots for tests of the null hypothesis that visited fruiting plants of the four species occurred randomly with respect to spatial location, given the underlying distribution of fruiting plants. Data were collected from Aug.-Nov. 1999 on the LTP study area in Puerto Rico. Solid lines are the observed $\hat{D}(t)$'s. Dashed lines delineate 99% confidence envelopes based on 99 random labelings of the underlying point pattern. $\hat{D}(t)$ values falling outside the bounds of the lower envelope are significantly regular, suggesting competition. The distance at which departures from envelope boundaries occur indicates the scale of the pattern. Sample sizes, n_1 and n_2 are the number of fruiting and non-fruiting individuals, respectively.

Fig. 7. $\hat{D}(t)$ plots for fruiting and frugivory of *Schefflera morototoni* by month from Aug.-Nov. 1999. Solid lines are the observed $\hat{D}(t)$'s. Dashed lines delineate 99% confidence envelopes based on random labelings of the underlying point pattern. $\hat{D}(t)$ values falling outside the bounds of the lower envelope are significantly regular, suggesting competition. The distance at which departures from envelope boundaries occur indicates the scale of the pattern. Sample sizes, n_1 and n_2 , are the numbers of fruiting and non-fruiting individuals (A-D) or the number of visited and non-visited individuals (E-H).

Fig. 8. $\hat{D}(t)$ plots for fruiting and frugivory of *Guarea guidonia* on the LTP study area, Puerto Rico for the two month periods Aug.-Sept. and Oct.-Nov. 1999. Solid lines are the observed $\hat{D}(t)$'s. Dashed lines delineate 99% confidence envelopes based on random labelings of the underlying point pattern. $\hat{D}(t)$ values falling outside the bounds of the lower envelope are significantly regular, suggesting competition. The distance at which departures from envelope boundaries occur indicates the scale of the pattern. Sample sizes, n_1 and n_2 , are the numbers of fruiting and non-fruiting individuals (A-D) and the number of visited and non-visited individuals (E-H).

Fig. 1

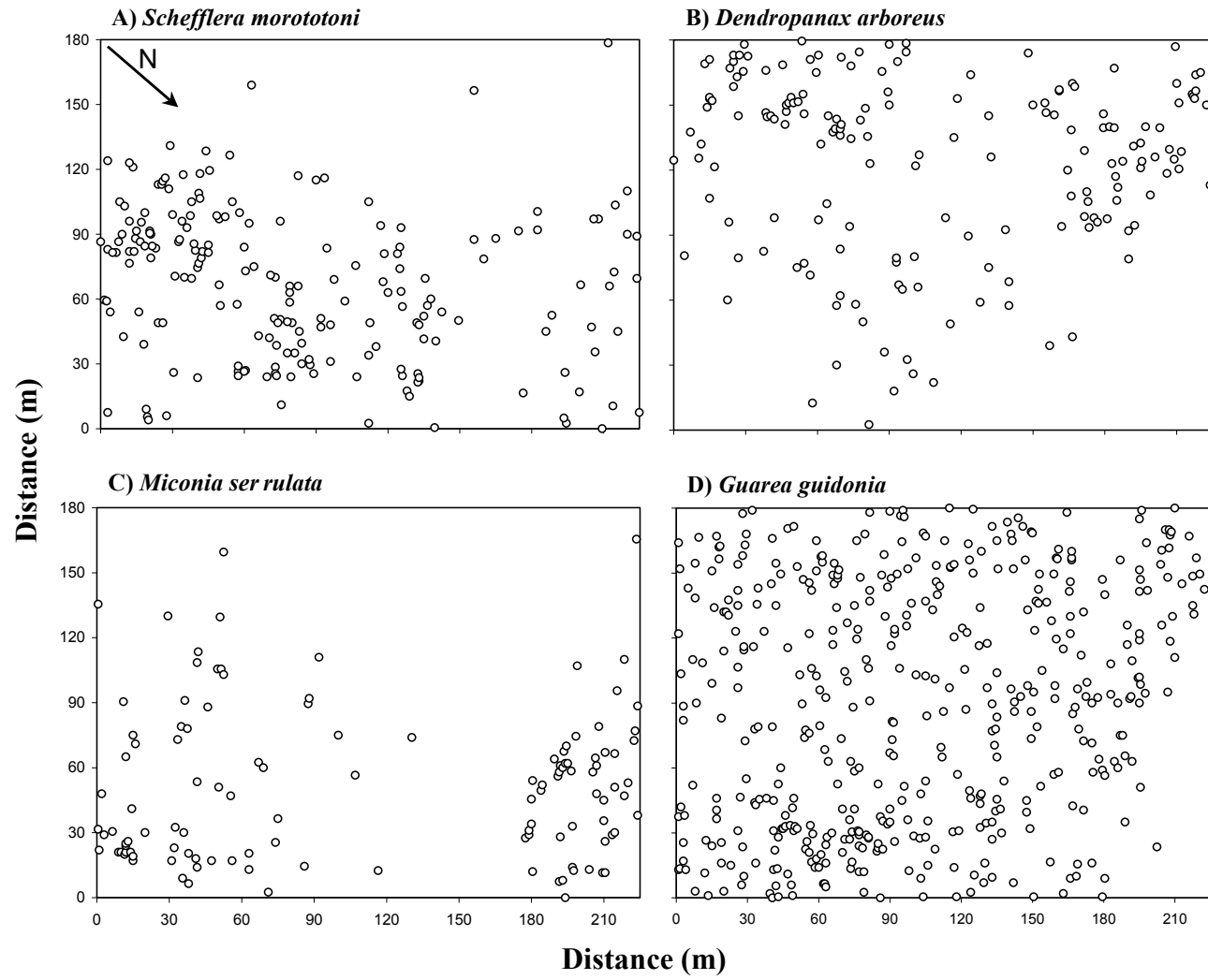


Fig. 2

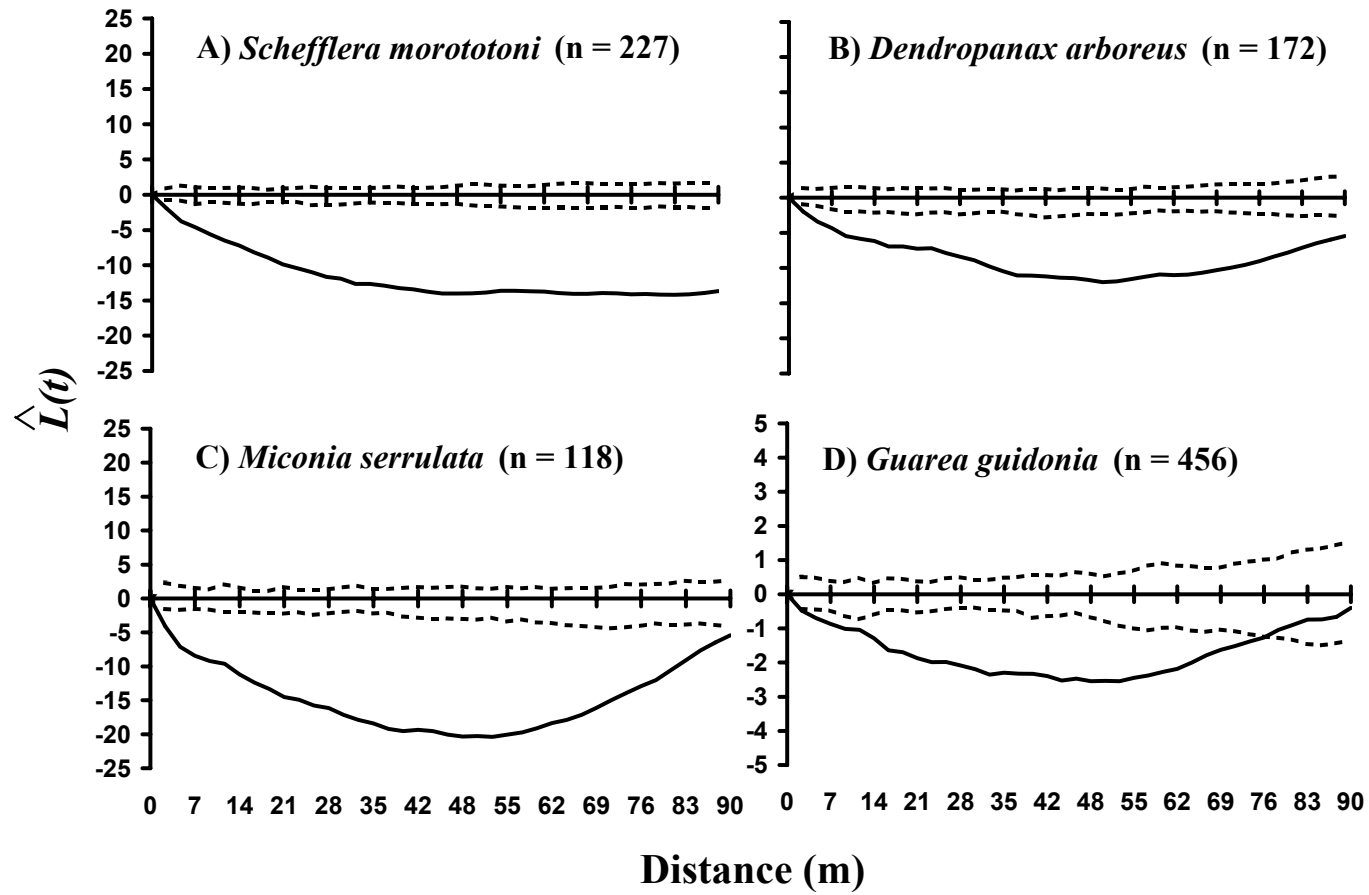


Fig. 3

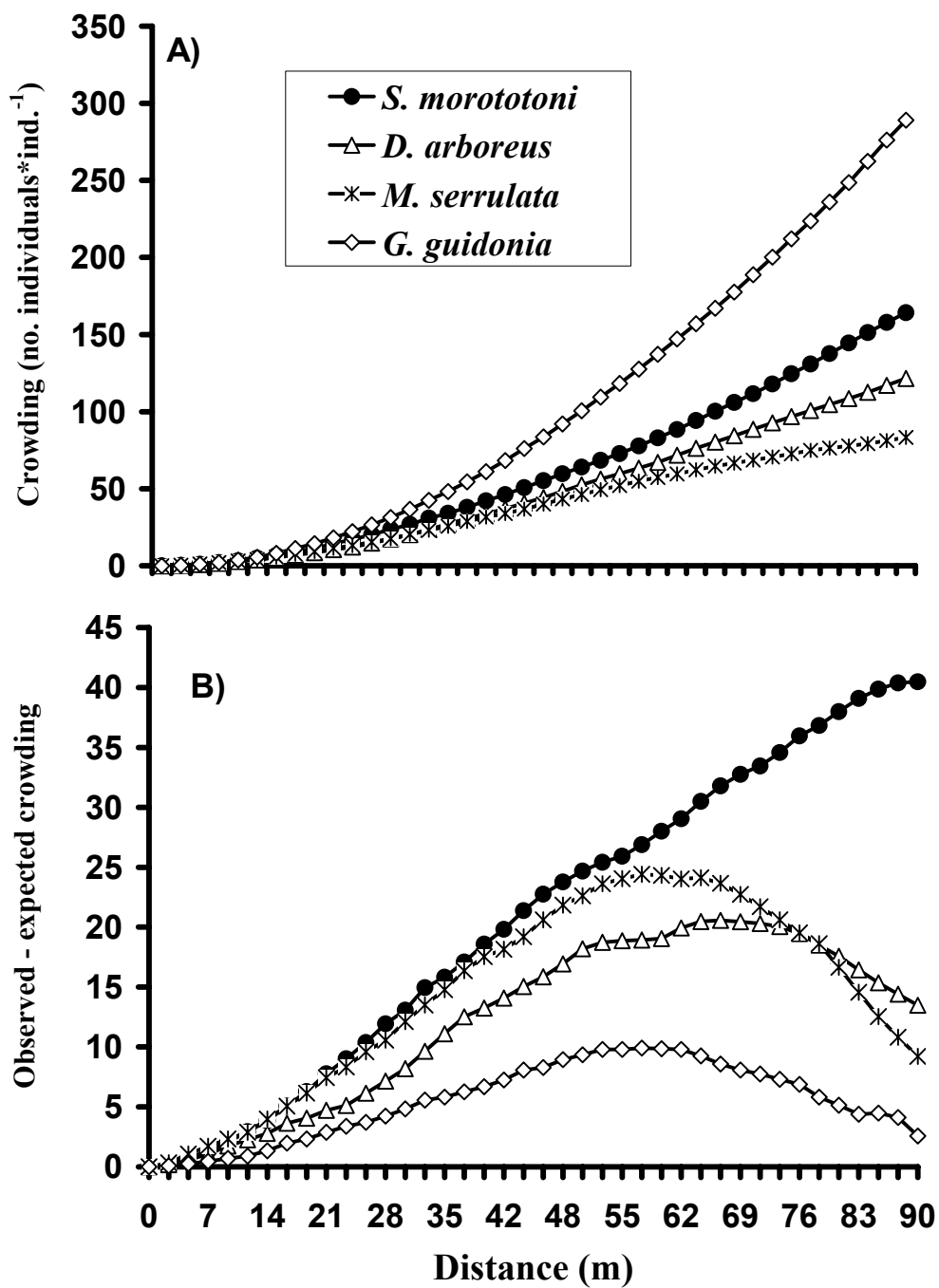


Fig. 4

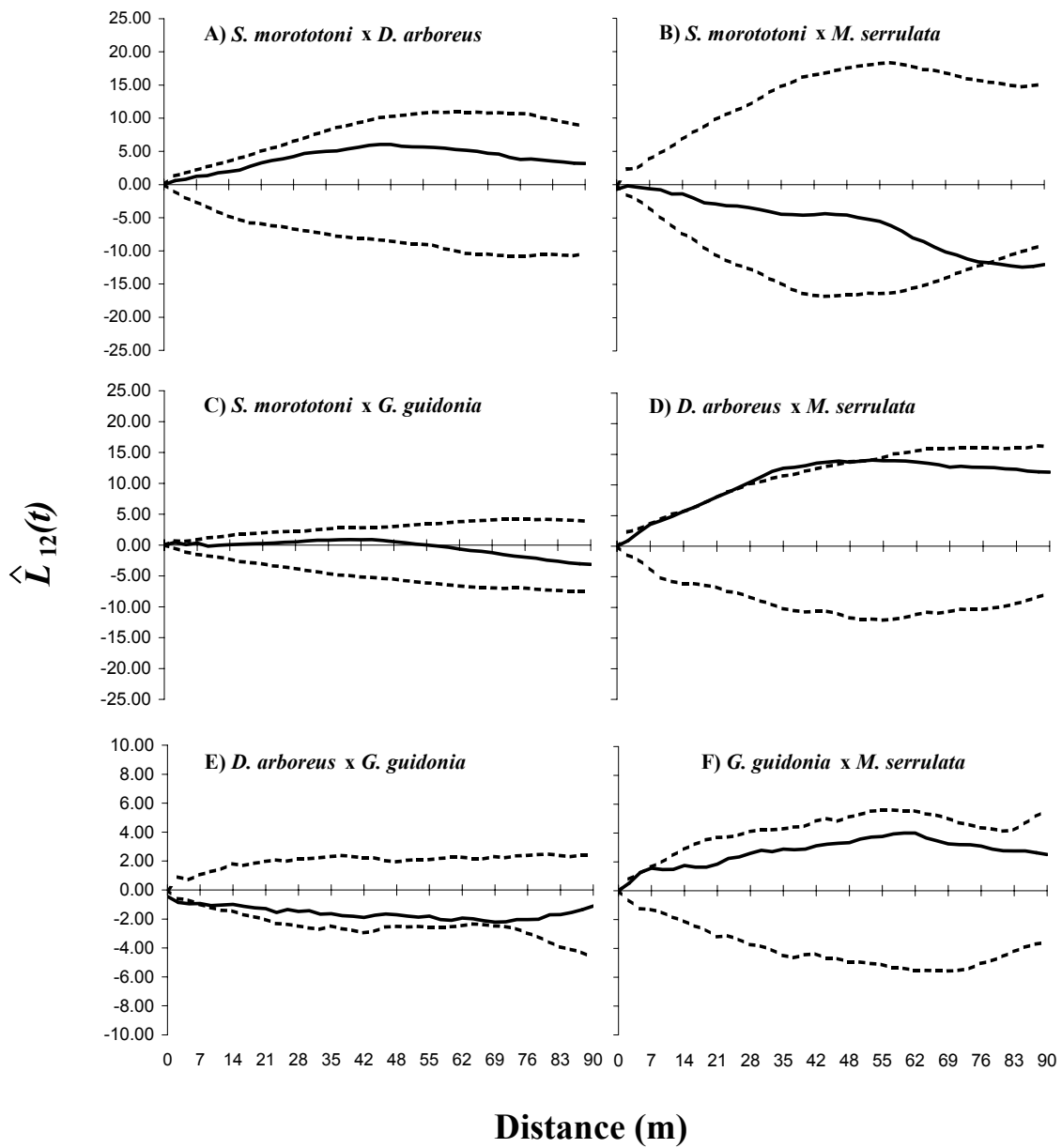


Fig. 5

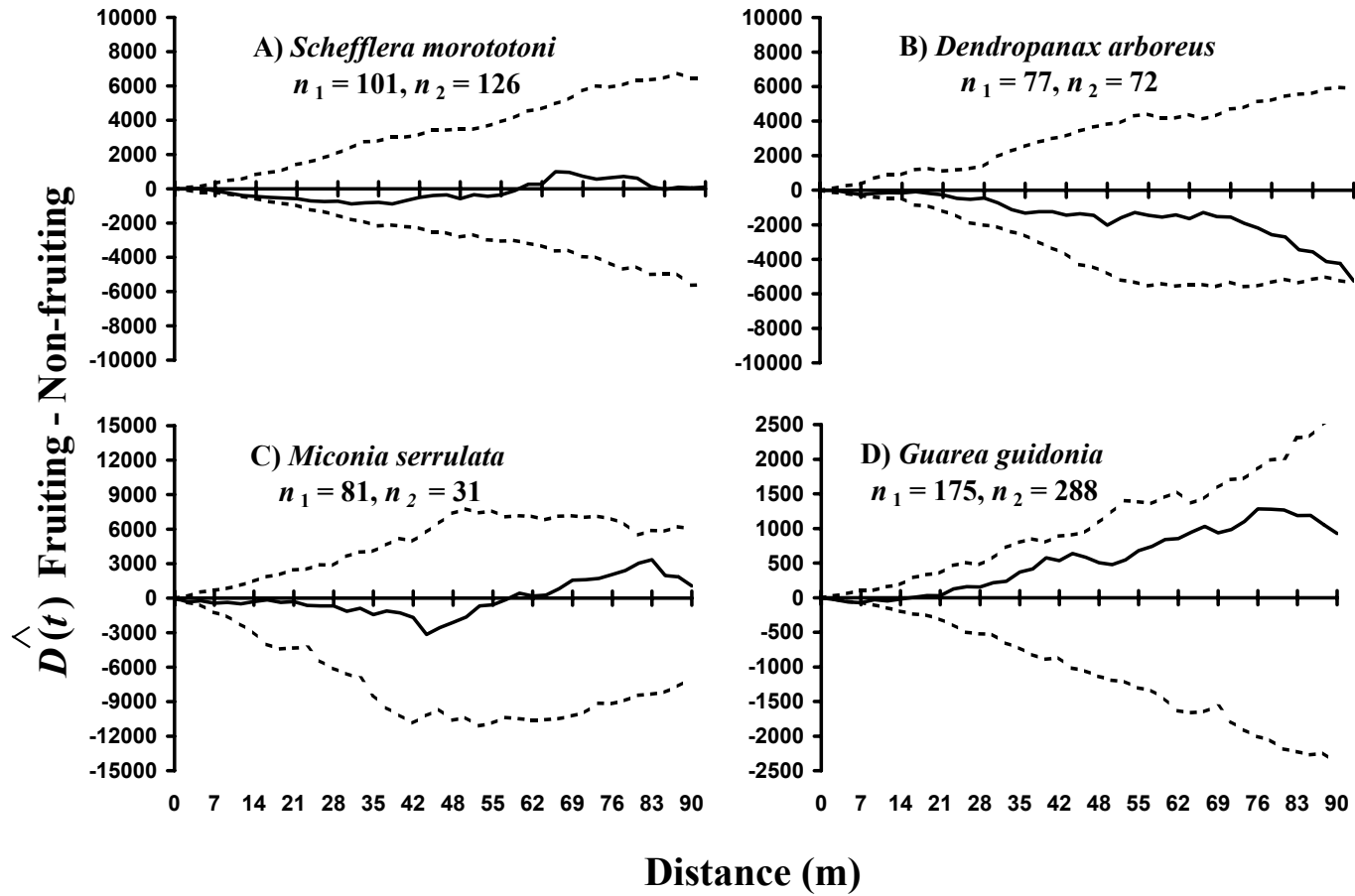


Fig. 6

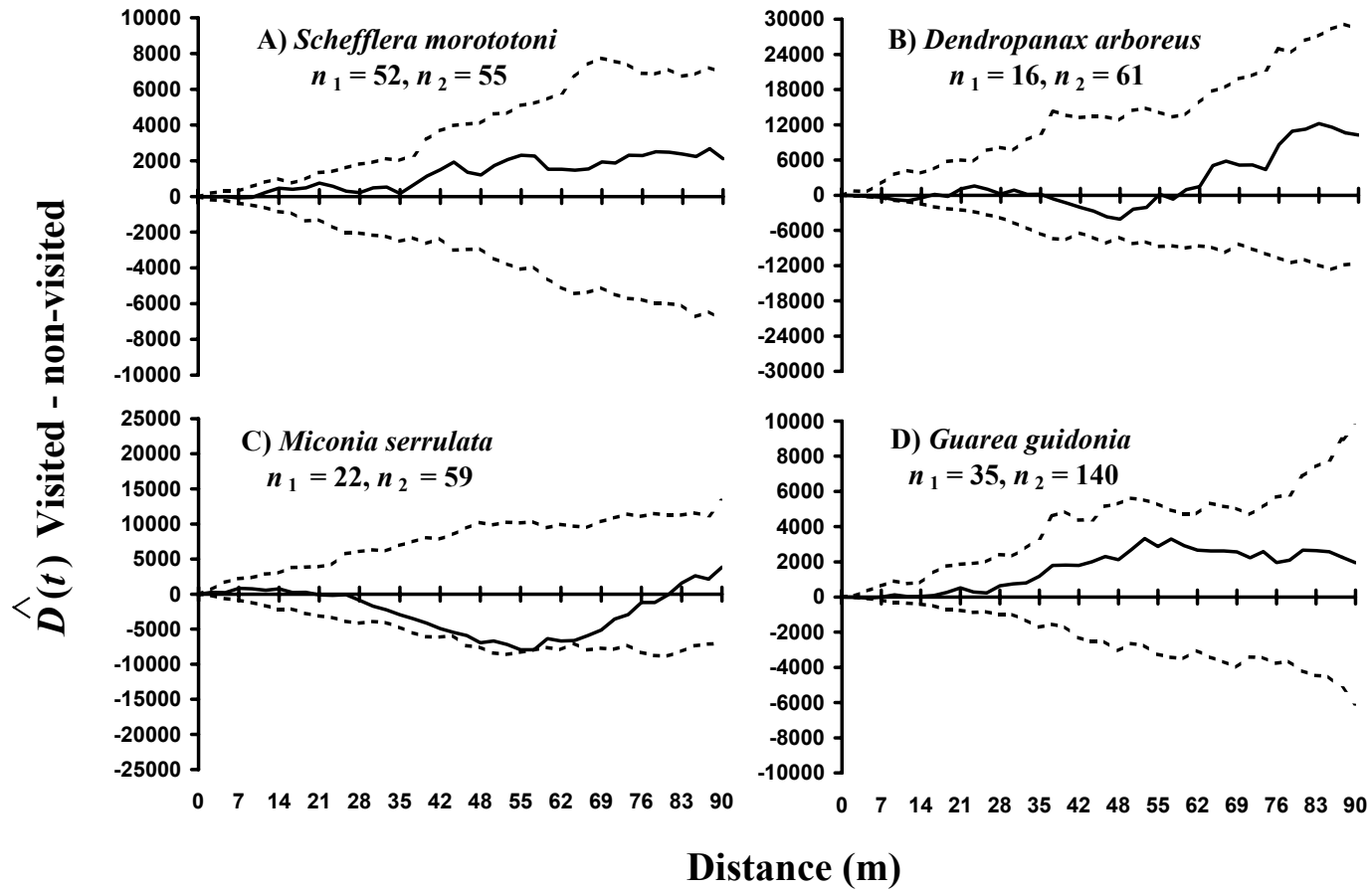


Fig. 7

Schefflera morototoni

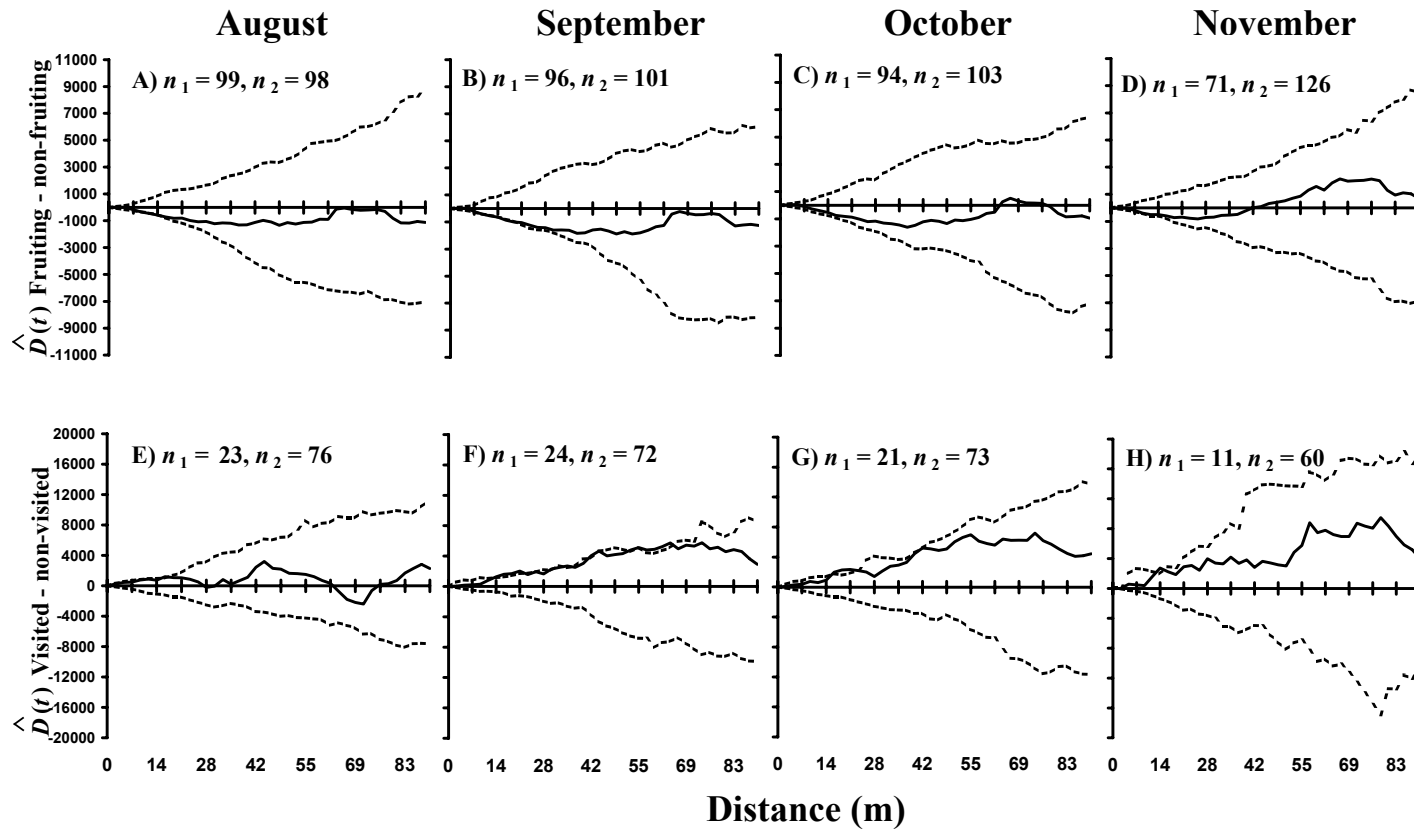
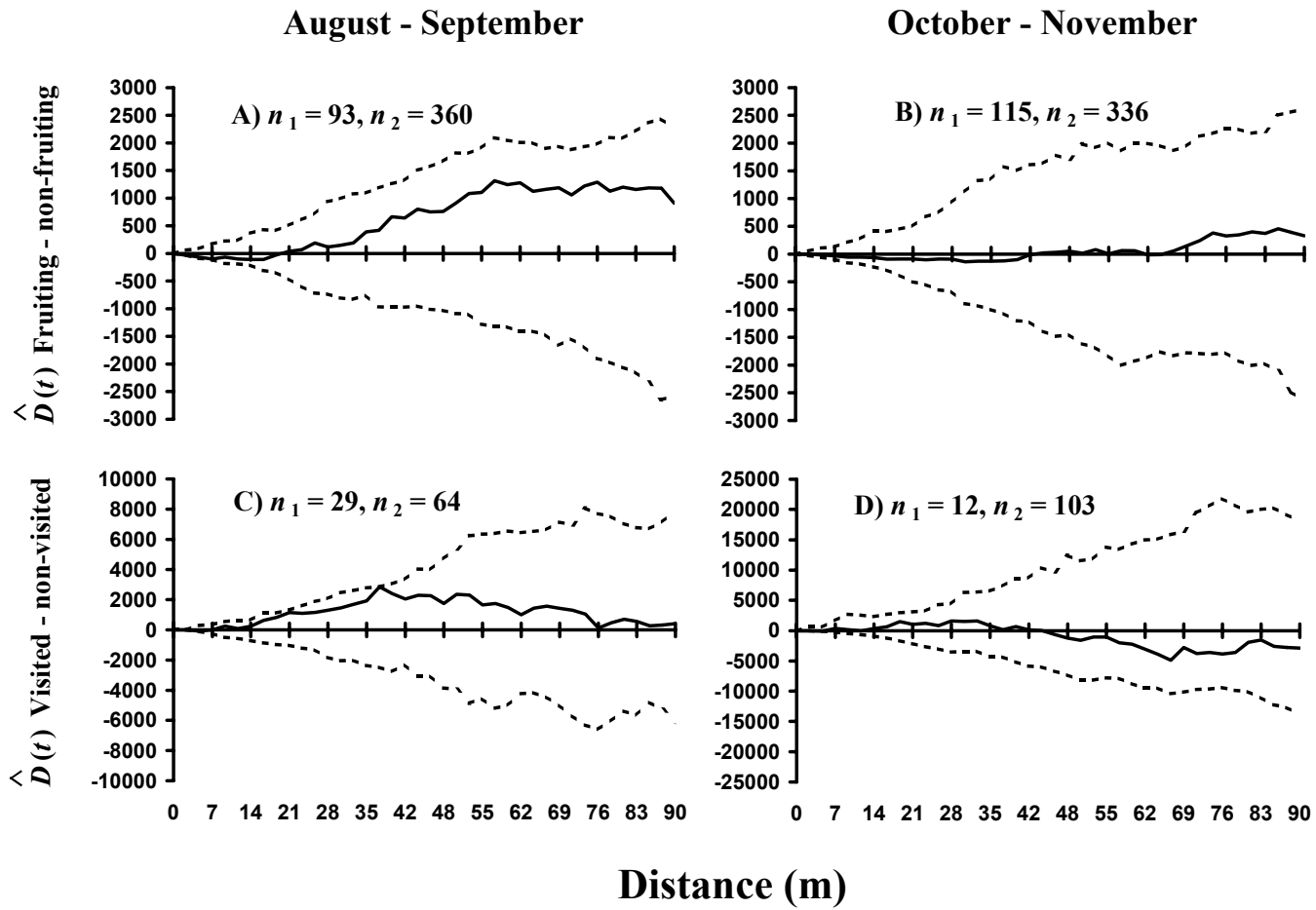


Fig. 8

Guarea guidonia



CHAPTER 3

INTRA- AND INTER-SPECIFIC NEIGHBORHOOD INTERACTIONS AMONG
FRUITING TREES THAT SHARE SEED DISPERSERS

Abstract. Because of their fixed spatial locations, interactions among plants are inherently local in nature; i.e., they occur within definable neighborhoods. Nevertheless, neighborhood size with respect to use by mutualistic animal consumers (pollinators and seed dispersers) can be large, and the nature and strength of interactions among individuals may change across the neighborhood space. In addition, influences of neighbors on one another also depend on within-plant factors, such as crop size. Here I describe patterns of spatial autocorrelation in fruit abundance at, and visitation to, fruiting trees of four species. In order to evaluate frugivore responses to fruit abundance at individual plants and the relative influence of fruit abundance (i.e., within-plant) and neighborhood influences, I examined spatial cross-correlation between visitation and fruit abundance and autocorrelation in preference for individual trees (i.e., visitation adjusted for fruit abundance). I also explored potential interspecific interactions among plants by examining spatial overlap in visitation and preference between tree species.

In general, I found intraspecific interactions among plants on small spatial scales to be facilitative in nature (i.e., plants near one another shared similar levels of visitation). Nevertheless, facilitative effects were to some extent obscured by variation in fruit abundance among plants. Visitation levels were strongly correlated with fruit abundance at individual plants for all focal species, and plants with the largest crops, or that had ripe fruit for extended periods of time, had reduced dependence on neighbors. I also found evidence of strong interactions between trees of different species. In general, these interactions were also facilitative in nature. Interspecific facilitation was most strongly manifested at larger scales, probably as a result of changes in the relative crowding of

conspecific and heterospecific fruiting plants at those scales. These findings suggest that forests with high small scale diversity (i.e., within-neighborhood) of fruiting plants may be optimal for preserving bird-plant interactions by providing conditions conducive to bird foraging and seed dispersal.

INTRODUCTION

Ecological studies that fail to account for complexities introduced into systems by spatial heterogeneity often prove inadequate for explaining dynamics of populations and communities (Dieckmann et al. 2000). The role of space is particularly important in the study of sessile organisms, such as plants, which cannot uproot themselves to seek more favorable conditions whenever the need arises (Stoll and Weiner 2000). Because of their fixed spatial locations, interactions among plants are inherently local in nature; i.e., they occur within some definable neighborhood (Addicott 1987).

The size of a plant's neighborhood will vary through time and depend on the type of resource being shared. Interactions for abiotic resources generally occur on small scales and are primarily limited to the extent to which plant canopies and root systems overlap (e.g., see Hutchings and de Kroon 1994). In contrast, a plant's neighborhood with respect to shared animal resources (e.g., mutualistic pollinators or seed dispersers) can be much larger, consisting of an area containing all home ranges of the animals that overlap with the plant's location (Chapter 2). Because interactions among neighbors with respect to their use of mobile biotic resources such as pollinators or seed dispersers can occur over very large spatial scales (and involve hundreds of individuals; Chapter 2), it is unreasonable to assume that all individuals within the neighborhood affect one another equally. Instead, the direction (facilitative or competitive) and strength of interactions among plants will depend on their spatial proximities to one another; i.e., interactions will vary across the neighborhood space. In addition, a variety of factors may mediate this

spatial dependence, e.g., the degree to which pollinator or frugivore coterie overlap, the degree of crowding of flowering or fruiting plants, crop sizes of individual plants, reproductive phenology, the size or diversity of pollinator or disperser pools, etc.

If one considers neighborhood interactions from the perspective of the individual, neighborhood effects on some aspect of the individual's performance will depend on both characteristics of the individual and characteristics of neighbors (Stoll and Weiner 2000; e.g., Feinsinger et al. 1986, Tremmel and Bazzaz 1993, Pacala and Silander 1997, Chapter 1). Identifying the degree to which individual (i.e., within-plant) vs. neighborhood characteristics affect plant performance across the scale of the neighborhood is critical for understanding the strength of selection pressures felt by individual plants; however, seldom are such studies undertaken. Furthermore, individual plants of different species overlap to varying extents with respect to their reliance on the same resources. Thus, it is also important to consider spatial relationships among heterospecific plants, particularly in cases where their distributions overlap substantially.

In this paper, I consider the specific case of fruiting plant interactions with respect to their use of avian frugivore seed dispersers. Although successful seed dispersal of plants depends on both seed removal and the deposition of seeds in sites favorable for germination (Schupp 1993), I consider only the former here. Most studies that have attempted to explain variation in visitation or fruit (seed) removal among individual conspecific plants have focused on parentally controlled factors (e.g., fruit color, size, nutrient content, crop size, etc.), of which only crop size consistently proves to be important (e.g., Davidar and Morton 1986, Denslow 1987, Alcántara et al. 1997, Jordano

and Schupp 2000, Chapter 1). Even when relationships between parentally controlled factors and visitation or fruit removal rate have been found, these factors often fail to explain large percentages of the variation in the data (e.g., see Ortiz-Pulido and Rico-Gray 2000). Neighborhood characteristics may be important in explaining variation in visitation and fruit removal among plants, yet they are rarely considered. When neighborhood characteristics have been considered, it has either been at a single scale (in one case two scales) or without reference to a particular spatial scale (e.g., Moore and Willson 1982, Manasse and Howe 1983, Herrera 1984, Herrera 1986, Denslow 1987, Sargent 1990, French et al. 1992, Chapter 1). As might be expected, results of these studies have varied, making it difficult to generalize regarding the expected nature and strength of such interactions.

My broad objective here was to describe spatial structure of fruit abundance at, and avian frugivore visitation to, individual trees of four bird-dispersed species in a Puerto Rican forest during a single fruiting season. The four focal tree species were: *Schefflera morototoni*, *Guarea guidonia*, *Dendropanax arboreus*, and *Miconia serrulata* (nomenclature follows Liogier and Martorell 2000). In order to better understand the dependence of intraspecific interactions on fruiting patterns of individuals, I examined (1) spatial structure of cross-correlation between fruit abundance and the number of frugivory events recorded at individual trees and (2) spatial autocorrelation in frugivore preference for individual trees. Preference herein refers to use of trees adjusted for fruit abundance, a metric that reflected some degree of selectivity on the part of birds. I discuss variation in intraspecific interactions with respect to variation in crowding and the

typical crop size of tree species. In order to identify the nature and scales of interspecific interactions among trees, I examined the spatial structure of cross-correlations for all pair-wise combinations of four focal tree species. For each pair, I examined the numbers of frugivory events recorded at individuals of different species, preference, and the cross-correlation between visitation and preference. Examination of these cross-correlations allowed me to identify asymmetries in interactions between tree species. Finally, I discuss differences in interspecific interactions among pairs of the four focal species in relation to patterns of overlap in the spatial distributions of adult trees, disperser coterries, and phenology of fruiting and use by frugivores.

METHODS

Study area

The study was conducted in the Cordillera Central of Puerto Rico within Los Tres Picachos State Forest (LTP). LTP is comprised of approximately 12,000 ha ranging from 300 to 1,205 m elevation. Most of the forest lies within Holdridge's (1974) Subtropical Wet Forest Life Zone, with an average annual rainfall of 2,000-4,000 mm and average temperature of 18-24°C (Birdsey and Weaver 1982). A brief description of dominant plant associations and details of the vertebrate fauna of LTP forest can be found in Miranda-Castro et al. (2000). The present study was conducted within a 225 m x 180 m rectangular plot within secondary forest at approximately 620 m elevation (18°13'N,

66°32'W). Most of the plot was on a gentle slope, although it rose steeply in one corner and was bisected by a stream on one side. A steep bank was present on either side of the stream. Dominant canopy species included *Inga vera*, *Ocotea leucoxylon*, and two focal species, *Guarea guidonia*, and *Schefflera morototoni*. *Dendropanax arboreus* was a common subcanopy and understory tree. *Miconia* spp. (especially *M. serrulata*), *Piper glabrescens*, and plants in the family Rubiaceae dominated the understory. A number of cultivated species such as coffee (*Coffea arabica*), oranges (*Citrus sinensis*), and bananas (*Musa* sp.) were also common in the understory and subcanopy.

Focal species: summary of previously reported results

The following summary is based on results of second order spatial point pattern analyses that are reported in Chapter 2. Readers seeking additional details with respect to these particular results or with respect to the natural history of these plants are referred to this paper. All spatial relationships were considered across scales of 0-90 m. All data were collected during a single fruiting season (Aug-Nov 1999); field methods are described below in “*Plant mapping and phenological monitoring*” and “*Bird observations*.” The numbers of (1) adult-sized trees (defined as all those with dbh \geq that of smallest fruiting individual during the study), (2) adult-sized trees that fruited during the study period, and (3) fruiting trees observed to be visited by avian frugivores are presented in Table 1. Based on our foraging observations, fruits of the four focal species, along with a fifth (*Cecropia schreberiana*), were the most frequently consumed by avian

frugivores during the study period (Saracco 2001, Chapter 4). I do not consider *C. schreberiana* here as it was uncommon in the study area, and most individuals fruited and were visited by frugivores, resulting in little spatial patterning and few points of contrast with respect to the other four focal species.

Spatial distributions of trees. Adult-sized individuals of each focal species were significantly aggregated on the study area at spatial scales < 80 m. Of the four species, *Schefferla morotoni* was the most patchily distributed, showing the greatest departure from random at all scales considered (0-90 m). Consideration of bivariate spatial patterns showed two pairs of species to be significantly aggregated with respect to one another on at least some scales: *D. arboreus*-*G. guidonia* were aggregated on small scales (< 50 m); *S. morotoni*-*M. serrulata* tended to be aggregated on somewhat larger scales (> 75 m). *M. serrulata* was significantly over-dispersed with respect to both *D. arboreus* and *G. guidonia* on at least some scales.

Spatial distributions of fruiting trees. When considered over the entire study period, I found no strong (i.e., statistically significant) evidence of spatial patterning in fruiting in excess of what would have been expected, given the clumped spatial distribution of adult trees. When considered over shorter (monthly) time windows, however, fruiting *S. morotoni* were significantly aggregated at scales of 9-23 m.

Spatial distributions of visited plants. Visited trees of *M. serrulata* tended to be regularly spaced at a scale of about 58 m. When considered over the entire study period, the distributions of visited *S. morotoni* and *G. guidonia* showed little evidence of spatial patterning; however, when considered over shorter time intervals (monthly or

bimonthly) there was significant clustering of visited *S. morototoni* trees at spatial scales ranging from 14-65 m and significant clustering of visited *G. guidonia* at a scale of about 37 m. There was no spatial patterning evident in the distribution of visited *D. arboreus* trees.

Plant mapping and phenological monitoring

All individuals of the four focal species were mapped in reference to grid points, which were spaced at 15 m intervals. Each tree was tagged with a unique number, its dbh was recorded, and its flowering and fruiting phenology was monitored monthly by one of four observers from July to November 1999. For each tree, I noted the presence or absence of flowers; I did not distinguish between buds, closed and open flowers. For the fruiting phenology, I assigned a fruit abundance index (FAI) for total, unripe, and ripe fruit abundance according to the following scale: 0 = no fruits, 1 = 1-10 fruits, 2 = 11-100 fruits, 3 = 101-1000 fruits, 4 = 1001-10000 fruits, 5 = 10001-100000 fruits, and 6 = >100000 fruits. Fruit ripeness was determined based on previous experience with fruits of the various species, and all observers were trained and periodically checked to reduce observer bias.

Bird observations

Foraging observations were conducted on six days in August, September, and November 1999, and on three days in October, during which time exceptionally rainy weather precluded further sampling. Four observers surveyed the plot in the following manner. First, we divided the plot into twelve 75 m x 45 m blocks (i.e., one block = fifteen grid cells). Each observer was randomly assigned (without replacement) three blocks per day, such that all blocks were observed on all observation days (4 observers x 3 blocks). Each block was observed for two hrs; approximately ½ hr separated consecutive observation periods. Thus, on each day observations were conducted over six hours covering three observation periods (early, middle, and late). We began the first observation period within ½ hr of sunrise and usually completed the last within 7 hrs of the starting time. Random assignment of blocks was constrained such that each block was observed at least once by each observer and twice during each daily time period (once during each time period in October), to avoid observer and temporal biases, respectively. At the beginning of each two-hr observation period, observers slowly proceeded from a randomly assigned starting cell and systematically traversed the block looking and listening for bird activity. Once located, birds were followed with the aid binoculars, and the plant (in the case of trees and shrubs) or cell (in the case of epiphytes, mistletoes, and vines) numbers in which frugivory events occurred were noted. I define a “frugivory event,” or equivalently “visit,” to be any observation of a bird eating fruit or in a part of a fruiting plant known to have ripe fruit but not directly observed feeding.

Whenever possible, for each plant we recorded the quantity of fruit eaten (number of fruits or bites), the estimated height where the frugivory event occurred, other food items eaten (e.g., arthropod, flowers), social interactions (e.g., flocking, displacements), and the next plant visited. Whenever multiple birds were encountered at the same time, we usually recorded only whether or not fruit was eaten (and the plant or cell number) in attempt to observe as many birds as possible.

DATA ANALYSES

Overlap in frugivore coterries, fruiting, and frugivory phenology

In order to better understand spatial patterns of interactions among plant species, I calculated Morisita's (1959) index of overlap for each focal species pair with respect to use by avian frugivores. I calculated the index in two ways. First, I considered the number of observations by all bird species observed to consume fruits of the two plant species. Second, because I was interested in mutualistic frugivory observations, I also calculated overlap using only species likely to disperse seeds of the two species. This amounted to deletion of Bananaquit (*Coereba flaveola*) observations for all plant species and deletion of Puerto Rican Bullfinch observations on *Guarea guidonia*. Both bird species fed on pulp or arils without ingesting seeds and rarely carried seeds away from parent trees. Of the four focal tree species considered, only *Schefflera morototoni* was consumed by Scaly-naped Pigeons (*Columba squamosa*), which may destroy seeds of

some species (Moermond and Denslow 1985). I included observations of *C. squamosa* here because I lacked data on seed viability after passing through pigeon guts. Furthermore, their inclusion had no qualitative effect on results as they accounted for only 1% of all observations to *S. morototoni* trees.

I also considered temporal overlap in fruiting and use of each focal species by frugivores by calculating Pearson's correlation coefficients between FAI's summed across all individuals for each species pair (over 5 months: July-November), and the summed numbers of foraging observations for each species pair (over 4 months: Aug-Nov).

Spatial structures of fruit abundance, frugivory, and preference

For examination of fruit abundance autocorrelation, I calculated fruit abundance of each individual as the summed FAI over the five months July-November 1999. For examinations of cross-correlation of fruit abundance with other variables, I used the summed FAI over the months August-July to be consistent with frugivory observations, which were only collected during those months. I included only individual plants with $\text{dbh} \geq$ that of the smallest plant that fruited during the study period.

For spatial analyses of avian frugivore visitation, I summed the number of foraging observations at individual trees across the four months August-November 1999 (adjusted for monthly effort; i.e., all months divided by 2 except for October, which was sampled with half the effort of the other two periods). I excluded Bananaquits (*Coereba*

flaveola) from summations because it rarely if ever dispersed seeds of any species. I included observations of Puerto Rican Bullfinches (*Loxigilla portoricensis*) because they probably dispersed seeds of *Miconia serrulata* and *Dendropanax arboreus*. Bullfinches typically did not disperse seeds of the principal species it consumed, *Guarea guidonia*; however, total number of observations on *G. guidonia* individuals was highly correlated with the summed number of observations excluding bullfinches ($r = 0.99$, $N = 164$, $P < 0.0001$), and their inclusion did not have any qualitative effect on results. For all visitation analyses I included only individuals that fruited during the study period.

For spatial analyses of preference for individual trees of a species I used Johnson's Rank Preference Index (Johnson 1980). I ranked fruit abundance and the number of frugivory observations using data recorded between August and November. If I assume that my measure of fruit abundance was biologically meaningful (from the perspective of the birds), then considering preference gives a more accurate assessment of the nature of interactions among neighbors. Furthermore, comparing spatial patterns in preference to those found for visitation allowed us to evaluate the ability of neighbors to overcome neighbor effects by the within-plant factor, fruit abundance. I used Johnson's Rank Preference Index because it consistently produced less skewed data distributions than other preference measures and typically was strongly correlated with both the summed fruit abundance index and visitation. In addition, this index is robust to the inclusion or exclusion of rarely-visited trees (Krebs 1999). Because plants with the highest negative Johnson's Rank Preference score are the most preferred, I reversed the sign of these values for examination of cross-correlation with the number of frugivory

observations (a positive value) in order to make interpretation of correlograms more intuitive.

I used all-directional Moran's I correlograms to examine patterns of spatial autocorrelation (Moran 1950, Legendre and Fortin 1989). I considered ten lag intervals of 15 m width and a maximum distance of 150 m. Lag classes are reported as the maximum distance for each class. For spatially patchy structures, the scale at which the correlogram crosses the x -intercept is indicative of patch size (Sokal 1979). Significance was assessed by randomly permuting the original data with respect to geographic locations and re-calculating Moran's I 1,000 times. I used one-tailed tests and a progressive Bonferroni correction for multiple testing (Legendre and Legendre 1998).

I computed autocorrelograms for fruit abundance using both raw data (summed FAI across months) and residuals from a linear regression model of FAI as a function of dbh. For all species, the relationship between the summed FAI and dbh was positive and significant at the $\alpha = 0.05$ level; however, normality and homoscedasticity assumptions were violated in each case because of large numbers of non-fruiting individuals; transformations and alternative generalized linear models (e.g. Poisson regression) failed to alleviate this problem. Although there was spatial trend, as well as small-scale autocorrelation in most cases, the addition of spatial coordinates to regression models typically increased model R^2 's by relatively small amounts. Furthermore, because I was also interested in cross-correlation among variables (see below), I wanted to explore the possibility that the spatial trend in variables might be explained by other variables showing the same spatial trend.

In order to assess the degree to which spatial structures of two variables x and y overlap, I computed cross-correlograms using the bivariate analog of Moran's I (Wartenberg 1985, Reich et al. 1994):

$$I(d) = \frac{\frac{n_x + n_y}{2} \sum_i \sum_j w_{ij} (x_i - \bar{x})(y_j - \bar{y})}{W \sqrt{\sum_i (x_i - \bar{x})^2} \sqrt{\sum_j (y_j - \bar{y})^2}},$$

where, n_x, n_y = sample sizes of x and y , respectively;

$w_{ij} = 1$ when the pair (x_i, y_j) is within distance class d , zero otherwise;

W is the sum of w_{ij} (i.e., the number of pairs in distance class d).

Moran's I for fruit abundance \times visitation cross-correlograms was computed for lag = 0 and for each of the ten lag classes considered for autocorrelograms. Moran's I at lag zero is equivalent to a Pearson's correlation coefficient. Significance of fruit abundance \times visitation cross-correlation statistics was assessed by comparing them to a distribution of Moran's I values obtained from 1,000 random permutations of observed values of the number of frugivory observations with respect to the geographic locations. For interspecific cross-correlograms I calculated Moran's I for only the ten lag classes considered for autocorrelograms. I could not compute cross-correlation at lag = 0 for these comparisons because trees of the different species had unique spatial locations (i.e., no individuals of the two species shared the same location).

As was the case for the fruit abundance \times visitation cross-correlograms, significance of Moran's I for interspecific cross-correlograms was assessed via randomization; however, for tests of visitation \times visitation and preference \times preference cross-correlation, I permuted visitation values with respect to geographic coordinates for one species while holding the other constant and then repeating for the second species. Thus, I essentially tested two alternative null hypotheses of each species fruiting randomly with respect to the other. For testing the significance of visitation \times preference cross-correlation I only randomly permuted the preference values, because the only hypothesis of interest was whether preference of one species depended on patterns of visitation to the other. Because interspecific cross-correlation values depended on both the spatial distribution of tree locations of each species and on the distribution of values associated with these locations, a larger number of permutations was required (in some cases) to obtain consistent results. Thus, for these significance tests I increased the number of permutations to 10,000. For all cross-correlograms I employed one-tailed tests and progressive Bonferroni correction for multiple testing (Legendre and Legendre 1998). All correlograms, cross-correlograms, and permutation tests were computed using functions written for Matlab software (<http://www.mathworks.com/products/matlab/>).

RESULTS

Frugivore coterie overlap

Pairs of the four focal tree species varied considerably in degree of frugivore coterie overlap (Table 2). Morisita's index was similar regardless of whether all frugivores or just seed dispersers was considered. *G. guidonia* had the most unique frugivore coterie of the four focal species with an average seed disperser overlap of only 0.22. The remaining three species had average overlap values that were more similar to one another, ranging from 0.41 and 0.56.

Phenology and overlap of fruiting and frugivory

Fruiting phenology varied considerably among the four species during the study period (Fig. 1A). In general, there were very few fruits of any of the four species in July (corresponding to a seasonal period of general fruit scarcity in this region of Puerto Rico; Carlo 1999). *S. morototoni*, *M. serrulata*, and *G. guidonia* followed roughly parallel paths of fruiting (Fig. 1A, Table 3), with the summed FAI for each species peaking in October (although *S. morototoni* abundance was similar for both September and October). Fruit abundance was negatively correlated between *D. arboreus* and *M. serrulata*, the former being most abundant in August, and the latter in November.

The phenological pattern of frugivory, as measured by the number of observations per unit effort, roughly tracked patterns of fruit abundance for all focal species except *G.*

guidonia (Fig. 1B). *G. guidonia* increased in ripe fruit abundance between August and September, while the number of frugivory observations recorded declined during this time. This pattern undoubtedly resulted from the migration of *Vireo altiloquus*, the principal consumer of *G. guidonia*, off the island during this time. Temporal patterns of frugivory were negatively correlated between *M. serrulata* and the other three species, which were all positively correlated with one another (Table 3).

Spatial autocorrelation in fruiting and frugivory

In general, I found only low levels of spatial autocorrelation in the summed FAI for the four species; however Moran's *I* coefficients were significant in many cases (Fig. 2). In all cases, autocorrelation tended to be positive at short distance classes and negative at larger distances. Fruiting patch size was larger for *S. morototoni* and *G. guidonia* (60-90 m) than for *M. serrulata* and *D. arboreus* (30-45 m). Removal of trend in summed FAI associated with tree size (dbh) accounted for small-scale spatial autocorrelation only for *S. morototoni* (Fig. 2A).

I found significant positive autocorrelation in the number of foraging observations for *S. morototoni* at 15 and 30 m and at 30 m for *D. arboreus* (Fig. 3). Autocorrelation coefficients were not significantly different from zero for either of the other two species. Shapes of visitation autocorrelograms for both *S. morototoni* and *D. arboreus* suggested large-scale spatial trend in visitation across the study area. Visitation patch size (i.e., the

scale at which frugivores perceived patches) was similar for *D. arboreus* and *G. guidonia*, with correlograms crossing the x -axis between 45 and 60 m.

Spatial cross-correlation between frugivory and fruit abundance

Statistically significant positive cross-correlation between fruiting and frugivory was found at lag = 0 for all species (Fig. 4). In addition, the summed FAI and number of frugivory observations were significantly negatively cross-correlated at 15-30 m and positively cross-correlated at 90-105 m for *S. morototoni* (Fig. 4A). *G. guidonia* summed FAI and number of frugivory observations were significantly negatively cross-correlated at 45 m (Fig. 4D).

Spatial autocorrelation in foraging tree preference

Preference for fruiting trees of *S. morototoni* (i.e., use in excess of what would be expected based on summed FAI) and the number of foraging observations on this species showed identical scales of spatial pattern; however, autocorrelation was stronger for preference than for the number of observations (Figs. 3A, 5A). Preference for both *D. arboreus* and *M. serrulata* trees was positively autocorrelated only at the smallest scale of 15 m (Fig. 5B, C). As was the case for the number of frugivory observations, preference for trees of *G. guidonia* showed no evidence of autocorrelation at any scale (Figs 3D, 5D).

Spatial cross-correlation in frugivory and preference between species

Statistically significant cross-correlations between the numbers of frugivory observations of different tree species mostly occurred at intermediate and larger spatial scales (Fig. 6). One exception was found at the shortest lag class (0-15 m) for the *D. arboreus*-*M. serrulata* pair, where the number of *M. serrulata* observations was found to be non-random with respect to the number of observations at *D. arboreus* (Fig. 6D).

The scale of cross-correlation between *S. morototoni* preference and *D. arboreus* preference was identical to the scale of autocorrelation of *S. morototoni* preference (75-90 m; Figs. 5A, 7A). Significant positive cross-correlation was found for this species pair at all spatial scales up to 60 m; significant negative cross-correlation was found at scales of 120-135 m. The only other significant cross-correlation was for the *S. morototoni*-*G. guidonia* pair, which were significantly negatively cross-correlated at a scale of 135 m (Fig. 7C). Relatively high positive values of Moran's *I* cross-correlation coefficients were found for the *D. arboreus*-*M. serrulata* pair; however, my ability to detect significant differences for this pair was hindered for the smaller lag classes due to relatively few pairs of trees (i.e., low power due to regular spacing of trees of these two species at these scales).

Consideration of cross-correlations between preference and visitation provided further insights into which plant species may have been influenced by which, and at what scales (Fig. 8). Strong positive cross-correlation between *S. morototoni* visitation and

both *M. serrulata* and *D. arboreus* preference was found at the shortest lag interval (0-15 m; Fig. 8A, B). *S. morotoni* preference was significantly positively cross-correlated with visitation to each of these two species at slightly larger lag intervals. The strongest observed positive cross-correlation was between *D. arboreus* preference and *M. serrulata* visitation at short lag distances (< 30 m, significantly so at <15 m; Fig. 8D). *G. guidonia* preference was also positively cross-correlated with *D. arboreus* visitation at scales < 45 m; however, correlation coefficients were smaller in this case.

DISCUSSION

Intraspecific interactions among trees

Based on the number of foraging observations at trees, I found evidence of facilitative interactions among conspecifics (i.e., trees close to one another experienced similar levels of visitation) for two focal tree species at small spatial scales: *Schefflera morotoni* and *Dendropanax arboreus*. Facilitative interactions at small scales are not surprising, given that larger patches would be expected to attract more frugivores (Rathcke 1983). Nevertheless, autocorrelation in visitation for *D. arboreus* was not positive or significant at the shortest lag distance, suggesting that non-spatially structured variables were more important in explaining variation in visitation among individuals of this species at this scale (i.e., facilitative effects were masked). Furthermore, visitation was significantly correlated with fruit abundance for each tree species, suggesting that

trees were able to reduce spatial dependence on neighbors by producing larger crops, ripening fruit for an extended period, or both. The potential for individuals to decrease their dependence on neighbors was particularly evident for *S. morototoni*, for which I found significant negative cross-correlation between visitation and fruit abundance at small scales (< 30 m). This is likely the result of the particularly large fruit crops and extended fruiting periods of some individuals of this species (> 100,000 fruits for several months). Although particularly large fruit crops could potentially satiate fruit consumers in a local area, such situations were uncommon during this study, as evidenced by the facilitative effects of neighbors not diminishing markedly until a scale > 30 m.

The strong and significant correlation between fruit abundance and visitation for each species suggested that the summed FAI, although coarse-grained, was a meaningful measure of fruit abundance from the perspective of avian frugivores. Furthermore, because the relationship between fruit abundance and visitation was significant, consideration of spatial patterns of preference allows for a more refined assessment of the strength of neighbor interactions. Comparison of visitation and preference correlograms allowed me to assess the degree to which such interactions may have been obscured by the parentally controlled trait, fruit abundance. Because effects of crop size were removed, I expected stronger evidence of facilitation at small scales for preference than for the visitation. Indeed, this was the case for *S. morototoni*. In addition, examination of preference revealed evidence of facilitation for *M. serrulata* at the shortest lag interval (0-15 m), and a shift in autocorrelation from positive and significant from the second shortest to shortest lag intervals for *D. arboreus*. Each of these findings emphasizes the

point that spatial variation among plants with respect to crop size can obscure (and outweigh) facilitative effects of neighbors. For example, *M. serrulata* individual (fruit abundance) and neighbor (proximity) effects appear to have canceled each other out at the shortest spatial scale, with the net effect of the interaction being neutral (*sensu* Berkowitz et al. 1995). Because plants with the highest preference have visitation levels that are disproportionately high relative to their fruit abundance levels, plants with relatively small crop sizes (or that fruit for only brief periods) have the potential to benefit the most from being near preferred neighbors.

Finally, *Guarea guidonia* showed little evidence of spatial autocorrelation in either visitation or preference. This lack of spatial patterning was somewhat surprising given the tendency for visited trees to be significantly aggregated at small scales (at least when considered during Sept.-Oct., when most visitation occurred). I believe that this apparent inconsistency was an artifact of the relatively high abundance and even distribution of *G. guidonia* across the study area. The implication of this assertion is that any facilitative effects of fruiting neighbors may be diminished in large, mono-dominant stands of trees.

Interspecific interactions

Consideration of interspecific spatial correlations in visitation also revealed evidence of facilitation among individuals. Positive spatial correlations in visitation between species, however, generally occurred at larger spatial scales. This finding was

not surprising given that the distributions of adults of all focal species were highly aggregated and intraspecific crowding was much greater than interspecific crowding on small scales (Chapter 2). For example, the average *S. morototoni* adult had more than twice the number of conspecific neighbors within 30 m than neighbors of any other focal species. At larger spatial scales, there were relatively larger numbers of heterospecific neighbors, and interspecific interactions may have been more important. For example, evidence for facilitation in visitation among *S. morototoni* individuals was strongest at small spatial scales (< 30 m). At larger scales, *S. morototoni* visitation was strongly positively cross-correlated with visitation of the two other species with which its frugivore coterie overlapped strongly (*D. arboreus* and *M. serrulata*). Both positive cross-correlations, however, occurred within the patch size (as perceived by frugivores) of *S. morototoni* (75-90 m), suggesting that they were not spurious and probably served to define *S. morototoni* patch boundaries.

Positive interrelations among tree species such as these could arise via a number of mechanisms. For example, frugivorous birds may require mixed diets to balance nutritional needs or reduce over-consumption of particular toxic secondary compounds (Foster 1977, White and Stiles 1983, Cipollini and Levey 1997). A number of studies have supported this idea by reporting high dietary mixing in frugivorous birds on short time scales (Loiselle 1990, White and Stiles 1990, Blake and Loiselle 1992) or providing evidence of complementarity among fruits (Whelan et al. 1998). I did observe individual birds eating fruits of different plant species within very short time windows (< 1 min);

however, I am unable to speculate as to the relative importance of such behavior because we rarely tracked individual birds for any length of time.

Positive interspecific interactions probably also resulted from birds selecting new foraging areas based on their proximity to foraging patches whose profitability had deteriorated over time because of changes in the relative abundances of the various fruit species (i.e., resource switching). Evidence for such a mechanism comes from consideration of cross-correlations in visitation and preference for the *S. morototoni*-*M. serrulata* and *M. serrulata*-*D. arboreus* pairs. These three species all overlapped strongly with respect to their frugivore coteries; however, *M. serrulata* ripened fruit later in the season, and the number of visits to this species increased as visitation to the other two species diminished. Significant spatial correlation between *S. morototoni* and *M. serrulata* visitation occurred where distributions of the two tended to be clumped; for the *M. serrulata*-*D. arboreus* pair, significant spatial correlations occurred where the two were relatively less over-dispersed with respect to one another (Chapter 2). The staggered phenology of these species may reflect a larger (temporal) scale strategy to avoid competition (e.g., see Snow 1965) or to maximize the degree of facilitation.

Examination of preference \times preference and preference \times visitation cross-correlograms lends further insight as to the possible nature and mechanisms of interactions among focal species (again, assuming the preference measure accurately portrays selectivity in birds), as well as asymmetries in species pairs during the study period. For example, consider the three species discussed above, which all overlapped heavily with respect to their frugivore coteries. *S. morototoni* and *D. arboreus* had ripe

fruit earlier and were utilized earlier in the season than was *M. serrulata*. This was the only pair that showed significant spatial patterning in preference. Preference for *D. arboreus* on small scales was strongly tied to locations of *S. morototoni* visitation. These two species overlapped little with respect to their spatial distributions at this scale, suggesting that preferred *D. arboreus* were on the periphery of the spatial patchiness of adult trees of this species. This contention may explain the strong correlation between *M. serrulata* visitation and *D. arboreus* preference at this scale, and indicates that *M. serrulata* and *D. arboreus* visitation may have been linked primarily through frugivore interactions with *S. morototoni*. This example is in accord with the idea that spatial patterns, to some degree, represented resource switching during the season; however, it must be emphasized that my ability to draw inference regarding interspecific interactions is limited due to both the correlative nature of the data, and the methodological limitation of having to examine interactions in a pair-wise fashion. Nevertheless, given the large spatial scales at which these interactions appear to be manifested, experimental approaches may not be logistically feasible.

Evolutionary implications of interspecific interactions

If patterns of seed removal translate to patterns of seed dispersal, then one might expect the distributions of trees that facilitate visitation to one another to be closely linked. Based on the data presented here, this may sometimes be the case (e.g., the *M. serrulata*-*S. morototoni* pair). Such interactions, if stable through space and time, should

lead to the evolutionary histories of the interacting species becoming especially intertwined. It can easily be envisioned how complementarity of animal-dispersed fruits could evolve under such a scenario (Tilman 1982, Whelan et al. 1998). Nevertheless, strong overlap in spatial patterns of visitation (and presumably fruit removal) among species does not seem to generally imply that their spatial distributions will be tightly linked (e.g., the *D. arboreus*-*S. morototoni* pair). Such situations could arise from differences in tolerance for abiotic conditions (e.g., *D. arboreus* tended to occur on steeper slopes than *S. morototoni*), competition among seeds that get deposited together (Loiselle 1990), staggered fruiting phenology (as indicated above), or correlation with spatial patterns of use of other plant species (e.g., the *D. arboreus*-*M. serrulata* pair). In addition, human alterations of habitats and large-scale disturbances (e.g., hurricanes) may also lead to the spatial proximities of trees of different species becoming more segregated than they might be otherwise, resulting in a weakening of interspecific plant interactions and a disentangling of selection pressures.

Conclusions

Based on the correlative evidence presented here, it seems that positive (i.e., facilitative) relationships among fruiting plants may be common; however, they may be missed if not viewed from the appropriate scale. Scales at which interspecific interactions are strongest may be especially large. Nevertheless, the fact that interspecific facilitative relationships (based on visitation data) were not found in the present study

until larger spatial scales is in part a reflection of the spatial distributions of the plants. Trees of most focal tree species were highly aggregated with respect to conspecifics, but randomly distributed (or over-dispersed) with respect to trees of other tree species at small spatial scales (< 30 m). At larger scales the various species were more evenly distributed with respect to one another, yielding conditions more conducive to strong interspecific interactions. Examination of preference, on the other hand, showed that facilitative interactions probably did in fact occur at small spatial scales, but were obscured by spatial variation in fruit abundance among individuals. If we assume that my preference measure accurately portrays true patterns of selectivity in the birds, then these findings have important implications for the conservation and management of forests. For example, managing forests for high small scale (i.e., within-neighborhood) diversity of fruiting trees may yield conditions that are most favorable as bird habitat and effective seed removal for plants. The fact that the mechanism of neighborhood enhancement of visitation may, to some extent, represent resource switching suggests that the optimal assemblage of plants in any neighborhood (both from the perspective of birds and plants) will be one that provides fruit for extended periods of the year.

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LITERATURE CITED

- Addicott, J. F., J. M. Aho, M. F. Antolin, M. F. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49:340-346.
- Alcántara, J. M., P. J. Rey, F. Valera, A. M. Sánchez-Lafuente, and J. E. Guitiérrez. 1997. Habitat alteration and plant intra-specific competition for seed dispersers. An example with *Olea europaea* var. *sylvestris*. *Oikos* 79:291-300.
- Birdsey, R. A. and P. L. Weaver. 1982. The forest resources of Puerto Rico. USDA Forest Service Resource Bulletin SO-85, 59 pp.
- Blake, J. G. and B. A. Loiselle. 1992. Fruits in the diets of neotropical migrant birds in Costa Rica. *Biotropica* 24:200-210.
- Cipollini, M. L. and D. J. Levey. 1997. Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *American Naturalist* 150:346-372.
- Davidar, P. and E. S. Morton. 1986. The relationship between crop sizes and fruit removal rates by birds. *Ecology* 67:262-265.
- Denslow, J. S. 1987. Fruit removal from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. *Canadian Journal of Botany* 65:1229-1235.
- Dieckmann, U., R. Law, and J.A.J. Metz. 2000. The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, Cambridge, UK.

- Feinsinger, P., K. G. Murray, S. Kinsman, and W. H. Busby. 1986. Floral neighborhood and pollination success in four hummingbird-pollinated cloud forest plant species. *Ecology* 67:449-464.
- French, K., D.J. O'Dowd, and A. Lill. 1992. Fruit removal of *Coprosma quadrifida* (Rubiaceae) by birds in south-eastern Australia. *Australian Journal of Ecology* 17:35-42.
- Herrera, C. M. 1984. Seed dispersal and fitness determinants in wild rose: combined effects of hawthorn, birds, mice, and browsing ungulates. *Oecologia* 63:386-393.
- Herrera, C. M. 1986. Vertebrate-dispersed plants: why they don't behave the way they should. Pp. 5-18 in *Frugivory and Seed Dispersal: Ecology and Evolutionary Aspects* (T. H. Fleming and A. Estrada, Eds.) Kluwer Academic Publishers, Belgium.
- Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* 105:367-368.
- Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554-557.
- Hutchings, M.J. and H. de Kroon. 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. *Advances in Ecological Research* 25:160-223.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forest. *American Naturalist* 104:501-528.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.

- Jordano, P. 2000. Fruits and Frugivory. Pp. 125-165 in *Seeds: the ecology of regeneration in plant communities* (M. Fenner, Ed.). 2nd Ed. CABI Publishing, New York.
- Jordano, P. and E. W. Schupp. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70:591-615.
- Krebs, C.J. 1999. *Ecological methodology*. Benjamin/Cummings, Menlo Park, CA, USA.
- Legendre, P. and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80:107-138.
- Legendre, P. and L. Legendre. 1998. *Numerical Ecology*. 2nd Ed. Elsevier Science B. V., Amsterdam, The Netherlands.
- Levey, D. J. 1987. Facultative ripening in *Hamelia patens* (Rubiaceae): effects of fruit removal and rotting. *Oecologia* 74:203-208.
- Levey, D. J. 1990. Habitat-dependent fruiting behaviour of an understory tree, *Miconia centrodesma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology* 6:409-420.
- Levin, D. A. and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. *American Naturalist* 104:455-467.
- Liogier, H. A. and L. F. Martorell. 2000. *Flora of Puerto Rico and adjacent islands: a systematic synopsis*. 2nd Ed. Editorial de la Universidad de Puerto Rico, San Juan, PR.

- Loiselle, B. A. 1990. Seeds in droppings of tropical fruit-eating birds: importance of considering seed composition. *Oecologia* 82:494-500.
- Manasse, R. S. and H. F. Howe. 1983. Competition for dispersal agents among tropical trees: influences of neighbors. *Oecologia* 59:185-190.
- Miranda-Castro, L., A. R. Puente-Rolón, and S. Vega-Castillo. 2000. First list of the vertebrates of Los Tres Picachos State Forest, Puerto Rico, with data on relative abundance and altitudinal distribution. *Caribbean Journal of Science* 36:117-126.
- Moermond, T. C. and J. S. Denslow. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Pp. 865-897 in *Neotropical Ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.), American Ornithologists Union.
- Moore, L. A. and M. F. Willson. 1982. The effect of microhabitat, spatial distribution, and display size on dispersal of *Lindera benzoin* by avian frugivores. *Canadian Journal of Botany* 60:557-560.
- Moran, P. A. P. 1950. Notes on continuous stochastic phenomena. *Biometrika* 37:17-23.
- Morisita, M. 1959. Measuring of interspecific association and similarity between communities. *Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol.)* 3:65-80.
- Ortiz-Pulido, R. and V. Rico-Gray. 2000. The effect of spatio-temporal variation in understanding the fruit crop size hypothesis. *Oikos* 91:523-527.

- Pacala, S.W. and J.A. Silander Jr. 1990. Field tests of neighborhood population dynamic models of two annual weed species. *Ecological Monographs* 60:113-134.
- Rathcke, B. 1983. Competition and facilitation among plants for pollination. Pp. 305-329 *in* *Pollination biology* (L. Real, ed.). Academic Press, New York.
- Reich, R. M., R. L. Czaplewski, and W. A. Bechtold. 1994. Spatial cross-correlation of undisturbed, natural shortleaf pine stands in northern Georgia. *Environmental and Ecological Statistics* 1:201-217.
- Schupp, E. W. 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. Pages 15-29 *in* T. H. Fleming and A. Estrada, editors. *Frugivory and seed dispersal: ecology and evolutionary aspects*. Kluwer Academic, Dordrecht, The Netherlands.
- Snow, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. *Oikos* 15:274-281.
- Sokal, R.R. 1979. Ecological parameters inferred from spatial correlograms. Pp. 167-196 *in* *Contemporary quantitative ecology and related eometrics* (G.P. Patil and M. Rosenzweig, eds.). International Co-operative Publishing House, Fairland, MD, USA.
- Stoll, P. and J. Weiner. 2000. A neighborhood view of interactions among individual plants. Pp. 11-27 *in* *The geometry of ecological interactions: simplifying spatial complexity* (U. Dieckmann, R. Law, and J.A. J. Metz, eds.). Cambridge University Press, Cambridge, UK.

- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.
- Tremmel, D.C. and F.A. Bazzaz. 1993. How neighbor canopy architecture affects target plant performance. *Ecology* 74:2114-2124.
- Wartenberg, D. 1985. Multivariate spatial correlation: a method for exploratory geographical analysis. *Geographic Analysis* 17:263-283.
- 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.
- White, D. W., and E. W. Stiles. 1990. Co-occurrences of foods in the stomachs and feces of fruit-eating birds. *Condor* 92:291-303.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.

FIGURE LEGENDS

Fig. 1. (a) Monthly fruit abundance index (FAI summed across all individuals) and (b) number of frugivory observations (per unit effort [1 unit effort = 72 person-hrs of observation]) for four tree species on the LTP study area Jul-Nov 1999. Frugivory observations were not conducted during July, a period of relatively low overall fruit abundance. Species codes are SCMO = *Schefflera morototoni*, DEAR = *Dendropanax arboreus*, MISE = *Miconia serrulata*, and GUGU = *Guarea guidonia*.

Fig. 2. Moran's *I* autocorrelograms showing spatial structure of fruit abundance (summed FAI across months) among individual trees for four tree species on the LTP study area July-November 1999. Lag distances indicate the maximum distance of consideration for that lag interval. Positive values of Moran's *I* represent positive autocorrelation; negative values represent negative autocorrelation. Significance is indicated by black symbols and was assessed using one-tailed randomization tests ($\alpha=0.05$) and a progressive Bonferroni correction. Species codes are SCMO = *Schefflera morototoni*, DEAR = *Dendropanax arboreus*, MISE = *Miconia serrulata*, and GUGU = *Guarea guidonia*.

Fig. 3. Moran's *I* autocorrelograms showing spatial structure in visitation to individual fruiting trees (no. of observations * 72 person-hrs of observation⁻¹) for the four focal tree species on the LTP study area August-November 1999. Positive values of Moran's *I* represent positive autocorrelation; negative values represent negative autocorrelation. Significance is indicated by black symbols and was assessed using one-tailed randomization tests (alpha=0.05) and a progressive Bonferroni correction. I used one-tailed tests and a progressive Bonferroni correction. Species codes are SCMO = *Schefflera morototoni*, DEAR = *Dendropanax arboreus*, MISE = *Miconia serrulata*, and GUGU = *Guarea guidonia*.

Fig. 4. Moran's *I* cross-correlograms showing spatial correlation between fruit abundance (summed FAI across months) and the number of frugivory observations at individual trees. Species codes are SCMO = *Schefflera morototoni*, DEAR = *Dendropanax arboreus*, MISE = *Miconia serrulata*, and GUGU = *Guarea guidonia*. Positive values of Moran's *I* represent positive cross-correlation; negative values represent negative cross-correlation. Significance is indicated by black symbols and was assessed using one-tailed randomization tests (alpha=0.05) and a progressive Bonferroni correction.

Fig. 5. Moran's I autocorrelograms showing spatial structure of Johnson's Rank Preference Index calculated for individual plants within a tree species. Data were collected on the LTP study area July-November 1999. Lag distances indicate the maximum distance of consideration for that lag interval. Positive values of Moran's I represent positive autocorrelation; negative values represent negative autocorrelation. Significance is indicated by black symbols and was assessed using one-tailed randomization tests ($\alpha=0.05$) and a progressive Bonferroni correction. Species codes are SCMO = *Schefflera morototoni*, DEAR = *Dendropanax arboreus*, MISE = *Miconia serrulata*, and GUGU = *Guarea guidonia*.

Fig. 6. Moran's I cross-correlograms showing spatial correlation between the number of frugivory events recorded at individuals of different species on the Tres Picachos study area August-November 1999. Species codes are SCMO = *Schefflera morototoni*, DEAR = *Dendropanax arboreus*, MISE = *Miconia serrulata*, and GUGU = *Guarea guidonia*. Significance was assessed using one-tailed randomization tests ($\alpha=0.05$) and a progressive Bonferroni correction. Black symbols indicate cross-correlations that were significant for both species of the pair. Gray symbols indicate situations where visitation to one of the species did not significantly overlap with the other. In these situations I have indicated the species whose visitation spatial structure significantly overlapped with that of the other species.

Fig. 7. Moran's *I* cross-correlograms showing spatial scales of correlation between Johnson's Rank Preference Index values for individual trees for each pair of tree species. Species codes are SCMO = *Schefflera morototoni*, DEAR = *Dendropanax arboreus*, MISE = *Miconia serrulata*, and GUGU = *Guarea guidonia*. Positive values of Moran's *I* represent positive cross-correlation; negative values represent negative cross-correlation. Significance is indicated by black symbols and was assessed using one-tailed randomization tests ($\alpha=0.05$) and a progressive Bonferroni correction.

Fig. 8. Moran's *I* cross-correlograms showing spatial overlap between preference of one species and visitation to another. Species codes are SCMO = *Schefflera morototoni*, DEAR = *Dendropanax arboreus*, MISE = *Miconia serrulata*, and GUGU = *Guarea guidonia*. Positive values of Moran's *I* represent positive cross-correlation; negative values represent negative cross-correlation. For each Moran's *I* coefficient, I tested the null hypothesis that preference was random with respect to visitation of the other species. Significance is indicated by black symbols and was assessed using one-tailed randomization tests ($\alpha=0.05$) and a progressive Bonferroni correction.

Table. 1. Summary of the number of adult-sized trees, the number of fruiting trees, and the number of visited trees of each of the four focal species on the 4.05 ha LTP study area.

Species	<i>N</i>	No. Fruiting (% of <i>N</i>)	No. Visited (% of fruiting)
<i>Schefflera morototoni</i>	227	101 (44)	52 (51)
<i>Guarea guidonia</i>	456	175 (38)	35 (20)
<i>Dendropanax arboreus</i>	172	77 (52)	16 (21)
<i>Miconia serrulata</i>	118	81 (72)	22 (27)

Table 2. Morisita's Index of overlap for the four focal tree species on the Tres Picachos study area August-November 1999. Overlap values above the diagonal include all frugivore species. Values below the diagonal include only seed dispersers.

SPECIES	<i>Schefflera morototoni</i>	<i>Guarea guidonia</i>	<i>Dendropanax arboreus</i>	<i>Miconia serrulata</i>
<i>Schefflera morototoni</i>	-	0.205	0.565	0.485
<i>Guarea guidonia</i>	0.189	-	0.325	0.186
<i>Dendropanax arboreus</i>	0.565	0.296	-	0.823
<i>Miconia serrulata</i>	0.475	0.175	0.807	-

Table 3. Pearson's correlation coefficients for temporal patterns of fruit abundance for the five months July-November 1999 (above diagonal) and frugivory for the four months August-November 1999 (below diagonal) on the LTP study area, Puerto Rico.

SPECIES	<i>Schefflera morototoni</i>	<i>Guarea guidonia</i>	<i>Dendropanax arboreus</i>	<i>Miconia serrulata</i>
<i>Schefflera morototoni</i>	-	0.955	0.326	0.570
<i>Guarea guidonia</i>	0.594	-	0.036	0.765
<i>Dendropanax arboreus</i>	0.579	1.000	-	-0.487
<i>Miconia serrulata</i>	-0.602	-0.824	-0.811	-

Fig. 1

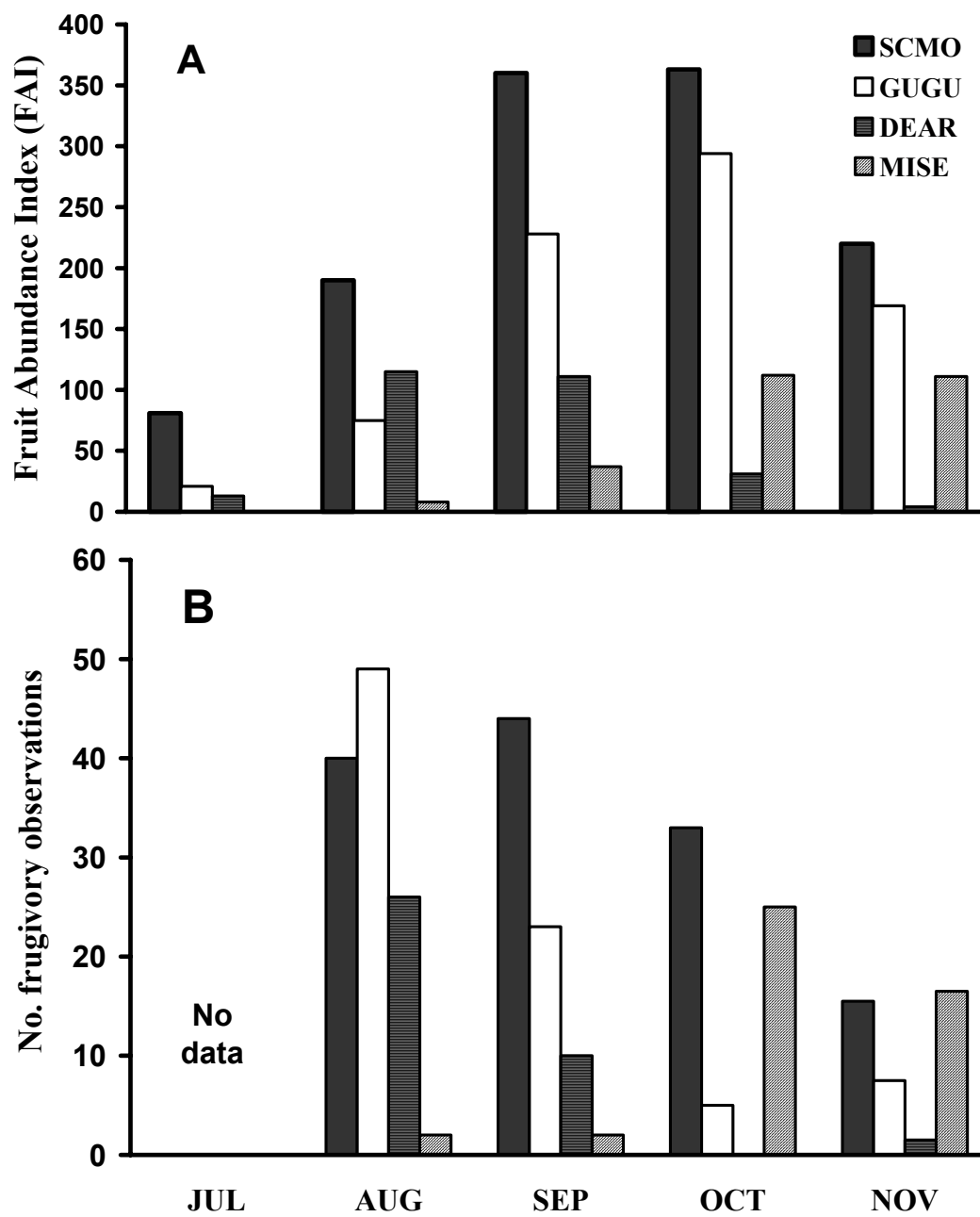


Fig. 2

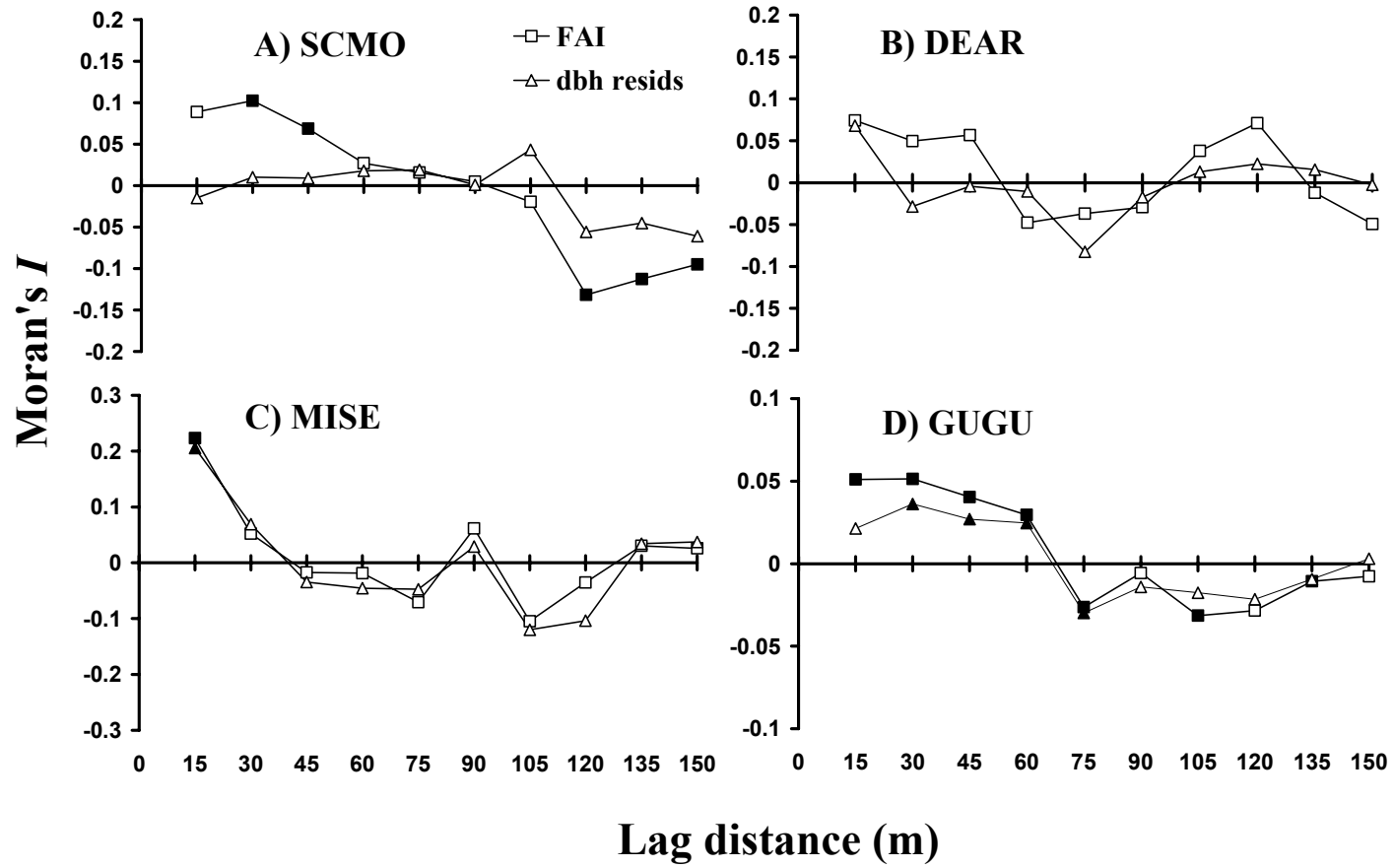


Fig. 3

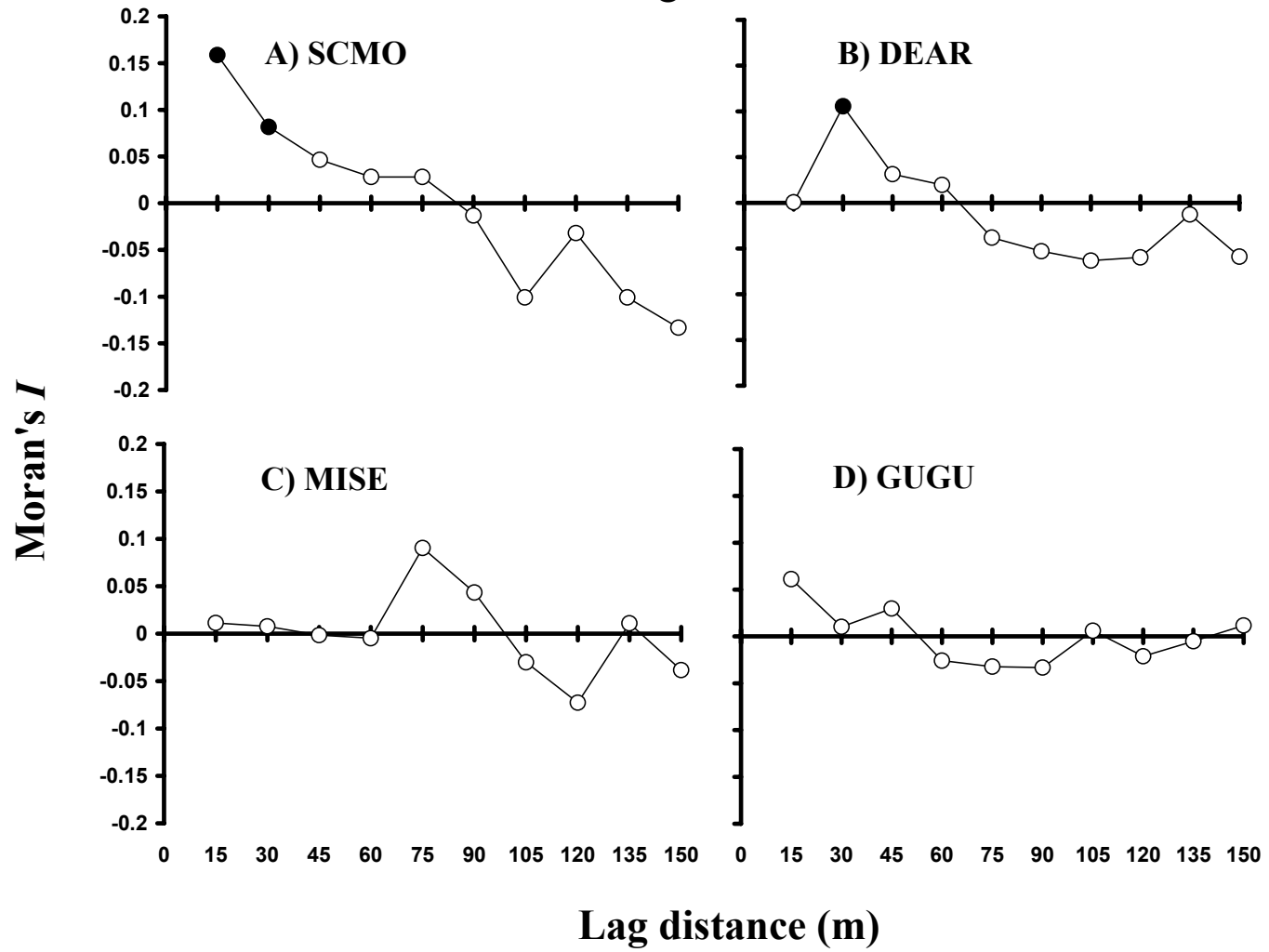


Fig. 4

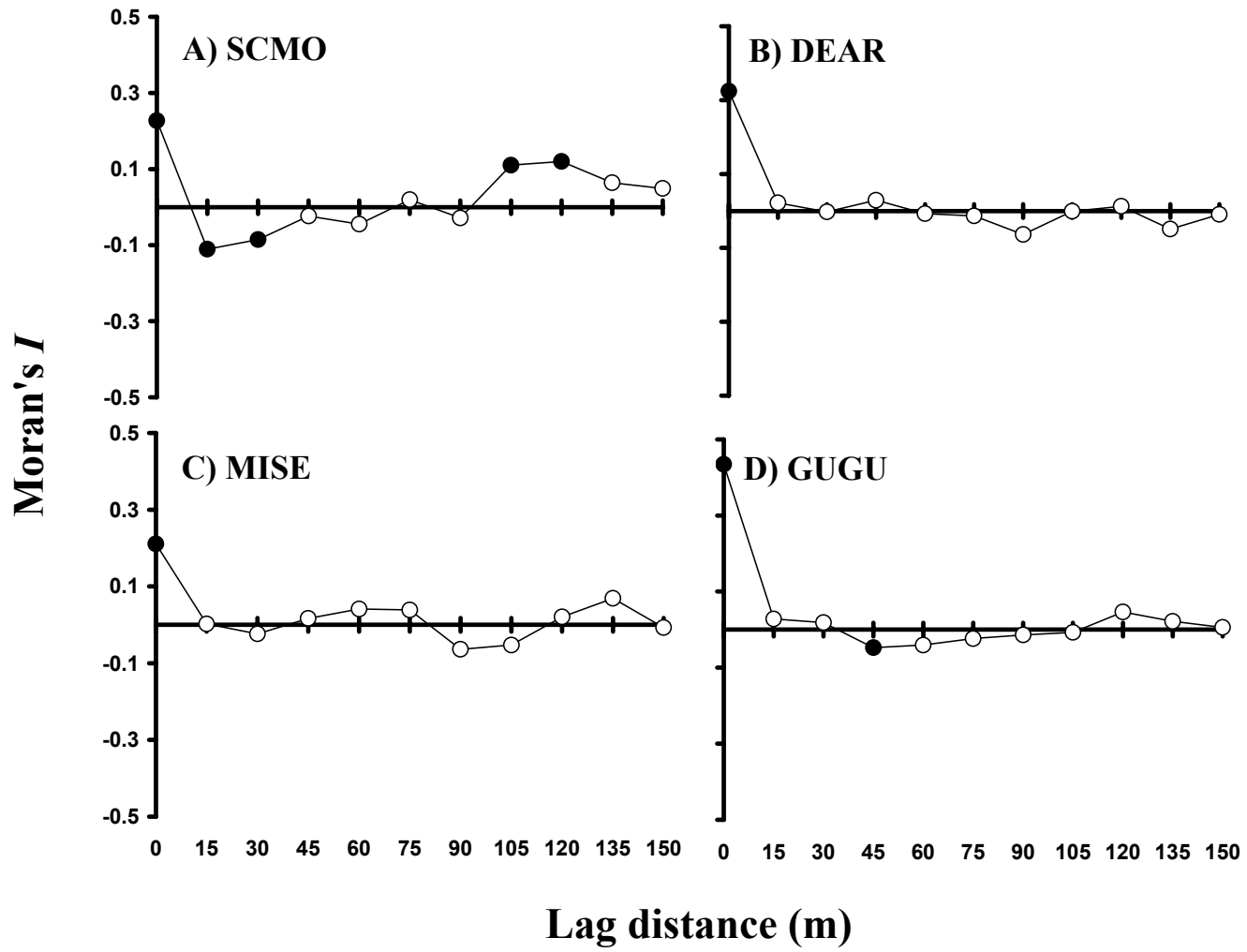


Fig. 5

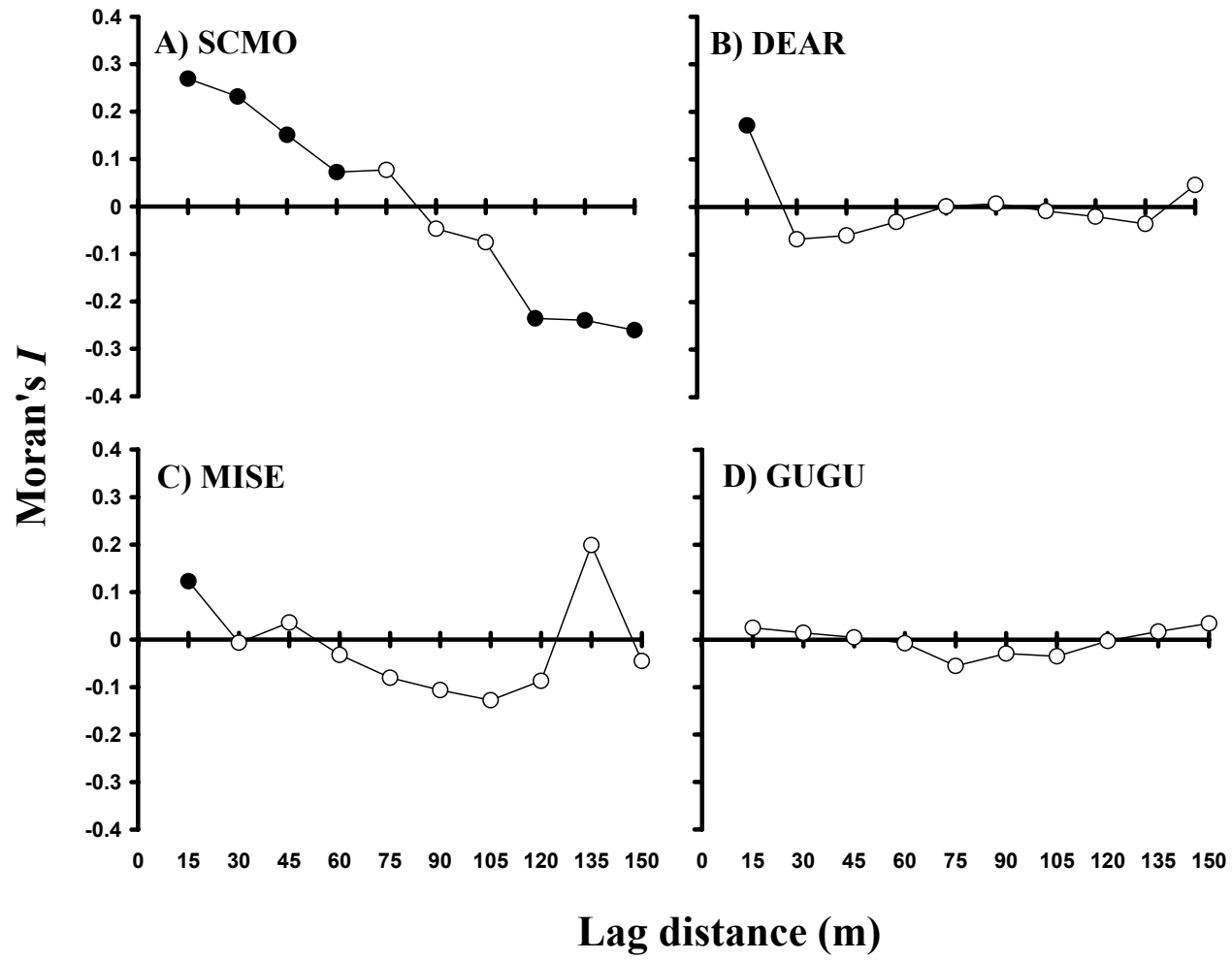


Fig. 6

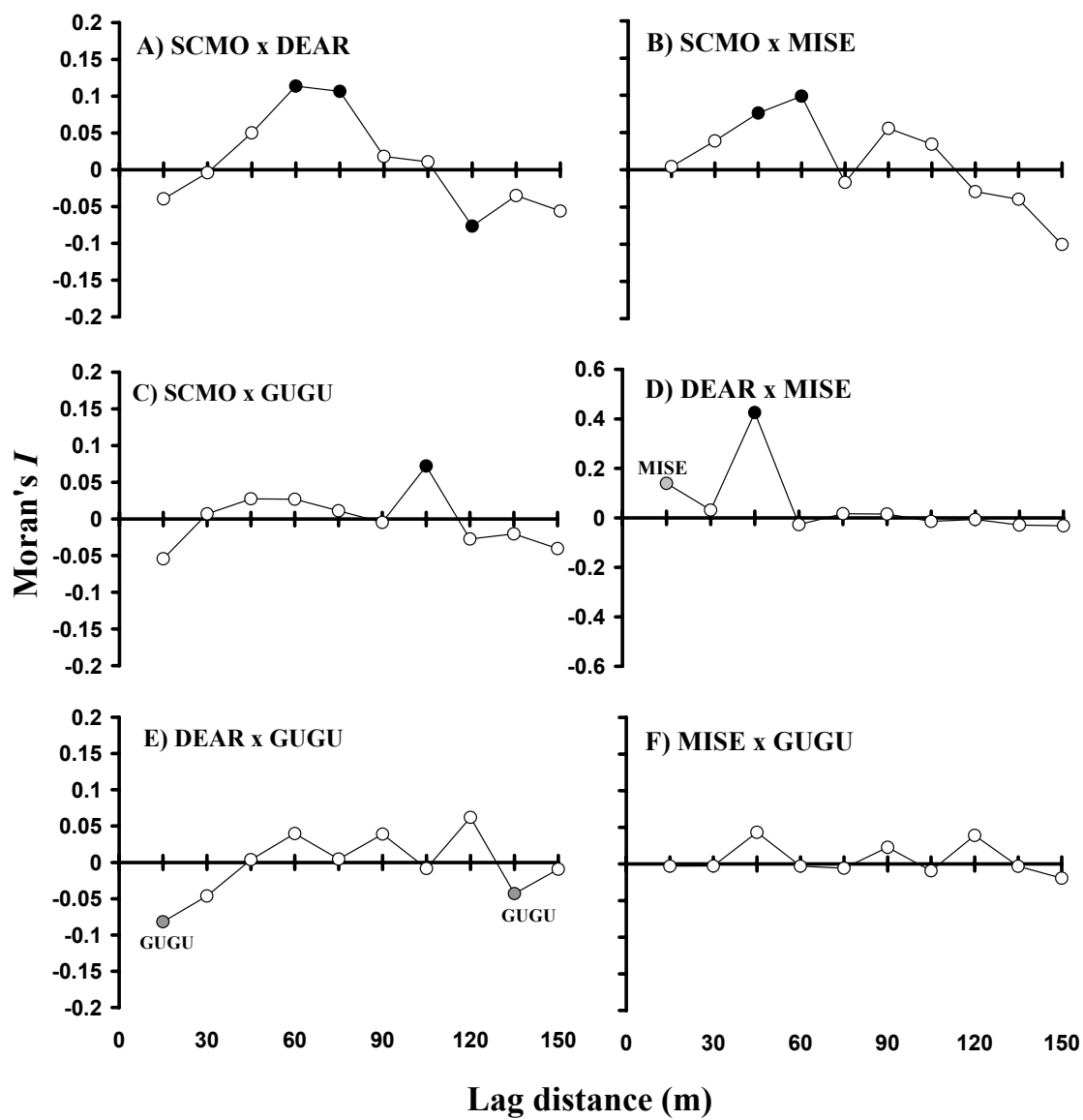


Fig. 7

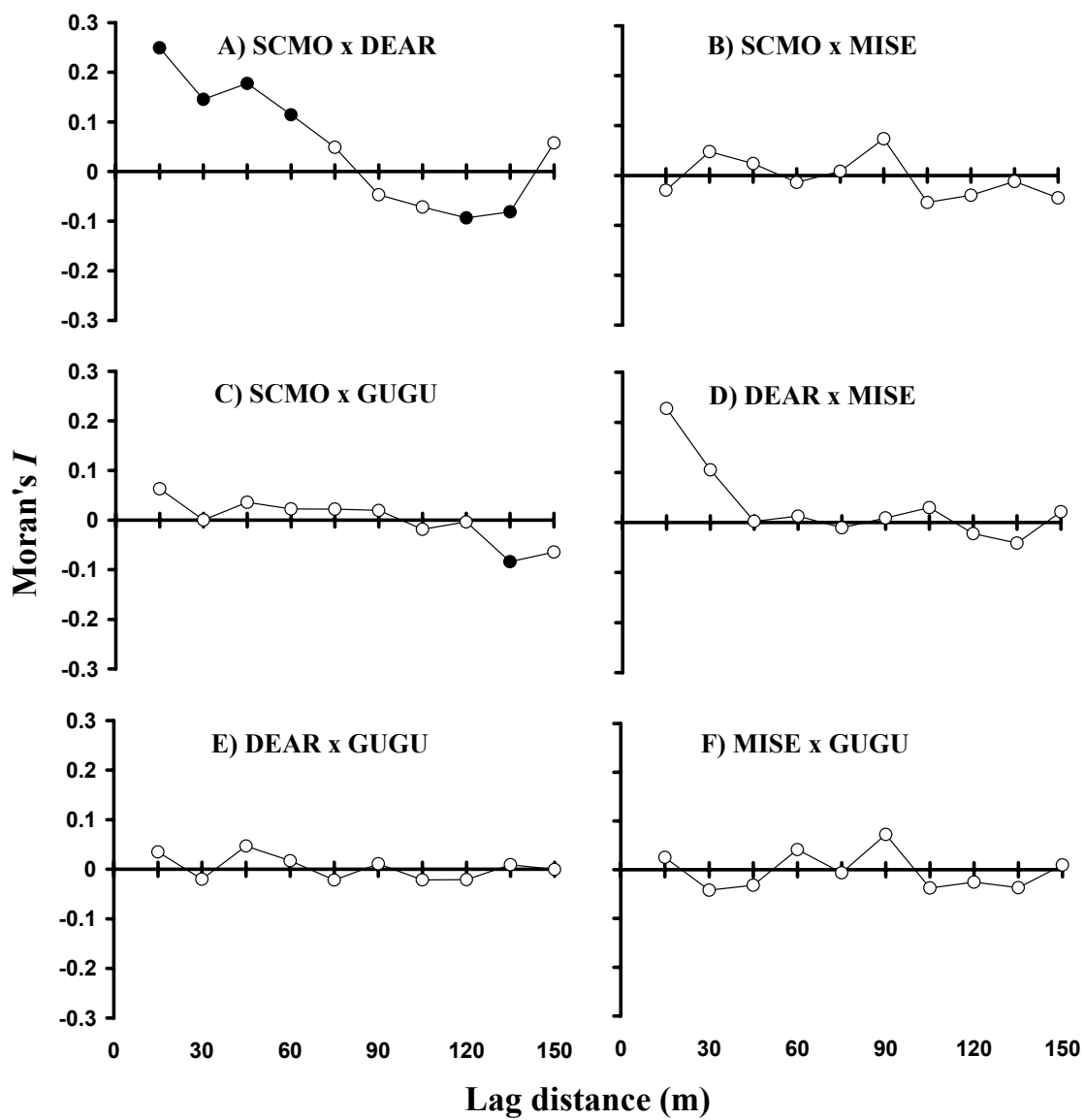
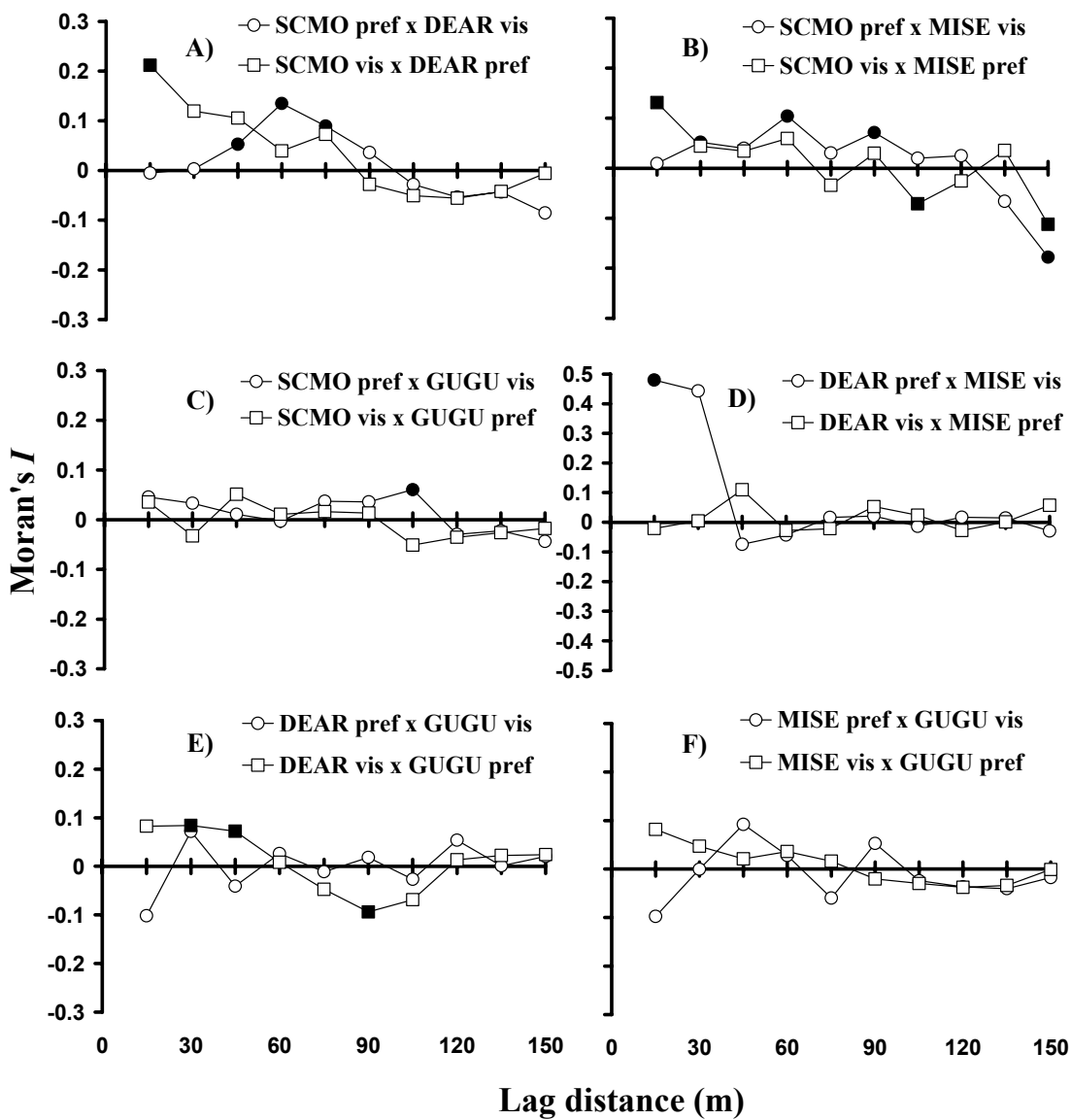


Fig. 8



CHAPTER 4

FORAGING PATCHINESS OF FRUGIVOROUS BIRDS: CORRELATIONS WITH
FRUIT ABUNDANCE AND SPATIAL OVERLAP BETWEEN BIRD SPECIES

Abstract. Little is known about the scales of foraging patchiness of frugivorous birds or its correlates. Here I summarize fruiting plant-frugivore interactions from observations collected on a 4.05 ha plot in the Cordillera Central of Puerto Rico during a single fruiting season. Three bird species accounted for more than 58% of all frugivory observations: *Spindalis portoricensis*, *Nesospingus speculiferus*, and *Vireo altiloquus*. For these I examined spatial structure in foraging intensity (no. observations * 15 m × 15 m block⁻¹) using Moran's *I* autocorrelograms. Two of the bird species relied heavily on single species of fruiting plants: *S. portoricensis* on *Schefflera morototoni*, and *V. altiloquus* on *Guarea guidonia*. For each of these plant species, I examined spatial autocorrelation in fruit abundance, and cross-correlation between their fruit abundances and the foraging intensities of their respective consumers. I also examined spatial cross-correlation in the foraging intensities of each pair of bird species.

Foraging intensities of all three frugivore species was significantly positively autocorrelated at small spatial scales (24-33 m). Correlogram shapes were similar for foraging intensity and fruit abundance for the bird species that relied heavily on a particular species of fruit, and strong correlation between fruit abundance and foraging intensities suggested birds effectively tracked resource abundance. Foraging intensity correlograms were similar for the three frugivore species, particularly for *S. portoricensis* and *N. speculiferus*, whose fruit diets overlapped heavily. Interestingly, the foraging intensities of these two species also significantly overlapped at the scale of the foraging patch boundary of each species. *N. speculiferus* is a noisy and conspicuous nuclear species of mixed-species foraging flocks, and its diet overlaps heavily with that of *S.*

portoricensis. I speculate that the positive cross-correlation in foraging intensities of these two species at larger spatial scales may represent individuals of *S. portoricensis* responding to *N. specularis* calls, suggesting that *S. portoricensis* uses *N. specularis* to find new foraging areas. Thus, birds may in part, be able to effectively track widely scattered and ephemeral fruit patches by cuing in on and exploiting new patches discovered by other birds.

INTRODUCTION

Tropical fruiting trees are well known for attracting large numbers of feeding animals, most notably birds (e.g., Willis 1966, Terborg and Diamond 1970, Dowsett-Lemaire 1996). Avian frugivores comprise a particularly important and conspicuous foraging guild in West Indian forest bird communities, where they often make up more than twice the percentage of total avian biomass and number of species than is found in mainland tropical forests (Waide 1996). Despite the importance of avian frugivores in Caribbean forests, little is known about the spatial scales of their movements or patchiness in their foraging behavior.

A number of factors could influence spatial patterns of foraging of frugivorous birds, the most obvious of which being the spatial distribution of fruits (Levey 1988, Loiselle and Blake 1993). Intra- and interspecific interactions among birds may also influence spatial patterns of frugivory. For example, interference interactions between dominant and subordinate birds could reduce use of some fruiting plants by subordinates, forcing them to utilize other plants (Pratt 1984, Daily and Ehrlich 1994). Alternatively, birds could alert one another as to the location of fruit sources by calling (e.g., Olupot et al. 1998). This situation may be especially likely for birds that participate in ephemeral mixed-species flocks that form following calls of noisy nuclear species (Moynihan 1962).

Some insight into the scales of movement of avian frugivores and patchiness of their foraging locations can be gained by examining spatial structure of autocorrelation in the number of foraging events recorded within fixed areas (herein referred to as “foraging

intensity;” see Legendre and Fortin 1989). Furthermore, examination of overlap in the spatial structures of foraging intensities and potential explanatory variables can aid in the development of hypotheses concerning controlling factors (Reich et al. 1994).

In this paper, I summarize foraging observations of frugivorous birds collected during a single fruiting season on a 4.05 ha forested study area in Puerto Rico. For the three most frequently observed bird species, I examined fruit diet overlap and spatial autocorrelation in foraging intensity. Two of these bird species relied particularly heavily on a single plant species, and for these I examined the degree to which spatial structures of fruit abundance and foraging intensity overlapped. Finally, many of the foraging observations recorded during this study were of birds that were participating in mixed-species flocks, and I expected that the foraging intensities of the three species would, accordingly, overlap to some extent. Thus, I also examined spatial cross-correlation between the foraging intensities of the three bird species.

METHODS

Study area

The study was conducted in the Cordillera Central of Puerto Rico within Los Tres Picachos State Forest (LTP). LTP is comprised of approximately 12,000 ha ranging from 300 to 1,205 m elevation. Most of the forest lies within Holdridge’s (1947) Subtropical Wet Forest Life Zone, with an average annual rainfall of 2,000-4,000 mm and average

temperature of 18-24°C (Birdsey and Weaver 1982). A brief description of dominant plant associations and details of the vertebrate fauna of LTP forest can be found in Miranda-Castro et al. (2000). The present study was conducted within a 225 m x 180 m rectangular plot within secondary forest at approximately 620 m elevation (18°13'N, 66°32'W). Most of the plot was on a gentle slope, although it rose steeply in one corner and was bisected by a stream on one side. A steep bank was present on either side of the stream. Dominant canopy species included *Inga vera*, *Ocotea leucoxylon*, *Guarea guidonia*, and *Schefflera morototoni*. *Dendropanax arboreus* was a common subcanopy tree. A variety of *Miconia* spp., *Piper glabrescens*, and plants in the family Rubiaceae were abundant in the understory. A number of cultivated species such as coffee (*Coffea arabica*), oranges (*Citrus sinensis*), and bananas (*Musa* sp.) were also common in the understory and subcanopy, reflecting the historical land use of this area (plantation abandoned ca. 50-60 yrs ago).

Plant mapping and phenological monitoring

All (bird-consumed) fruiting trees and shrubs in the plot were identified to species and mapped in reference to grid points. Grid points were spaced at 15 m intervals. Plant species nomenclature follows Liogier and Martorell (2000). Each tree was tagged with a unique number, its dbh was recorded, and its flowering and fruiting phenology was monitored monthly from July to November 1999. For each tree, I assigned a fruit abundance index (FAI) for total, unripe, and ripe fruit abundance according to the

following scale: 0 = no fruits, 1 = 1-10 fruits, 2 = 11-100 fruits, 3 = 101-1000 fruits, 4 = 1001-10000 fruits, 5 = 10001-100000 fruits, and 6 = >100000 fruits. Fruit ripeness was determined based on previous experience with fruits of the various species, and all observers were trained and checked to reduce observer bias. In addition to trees and shrubs, I monitored the phenology of epiphytes, mistletoes (*Phoradendron* spp.), and vines that produced bird-consumed fruits by assigning a FAI score for all individuals within each 15 m × 15 m cell where it occurred.

Bird observations

Four observers conducted foraging observations on six days in August, September, and November 1999, and on three days in October, during which time exceptionally rainy weather precluded further sampling. For the purpose of providing equal and intensive coverage for the entire study plot, I divided it into twelve 75 m × 45 m blocks (i.e., one block = fifteen grid cells). Each observer was randomly assigned (without replacement) three blocks per day, such that all blocks were observed on all observation days (4 observers × 3 blocks). Each block was observed for two hrs; approximately ½ hr separated consecutive observation periods. Thus, on each day observations were conducted over six hours covering three observation periods (early, middle, and late). The first observation period was begun within ½ hr of sunrise; the last was usually completed within 7 hrs of the starting time. The random assignment of blocks was constrained such that each block was observed at least once by each observer

and twice during each daily time period (once during each time period in October), to avoid observer and temporal biases, respectively. At the beginning of each 2-hr observation period, observers slowly proceeded from a randomly assigned starting cell and systematically traversed the block looking and listening for bird activity. Once located, birds were followed with the aid of binoculars, and the plant (in the case of trees and shrubs) or cell (in the case of epiphytes, mistletoes, and vines) numbers in which frugivory events occurred were noted. Whenever possible, for each plant we recorded the quantity of fruit eaten (number of fruits or bites), the estimated height where the frugivory event occurred, other food items eaten (e.g., arthropod, flowers), social interactions (e.g., flocking, displacements), and the next plant visited. Whenever multiple birds were encountered at the same time, we usually recorded only whether or not fruit was eaten (and the plant or cell number) in an attempt to observe as many birds as possible.

Data analyses

In order to evaluate the importance of different fruiting trees and fruit diet overlap for the various bird species, I summed the number of foraging observations for each bird-plant pair over the study period. I also quantified fruit diet overlap for the most frequently observed bird species using Morisita's Index (Morisita 1959).

For spatial analyses, I considered two response variables: (1) the summed number of foraging observations ("foraging intensity," adjusted for monthly effort; i.e., values for

all months were divided by 2 except for October, which was sampled with half the effort of the other two periods) and (2) the summed FAI (“fruit abundance”) across all individual trees of each species of interest across the study period. The sampling units over which these variables were summed (“grain size” of Wiens 1989) were the 180 15 m × 15 m blocks that comprised the study grid. This grain size represented a compromise between being small enough to have sufficient samples for powerful tests of autocorrelation, yet large enough to avoid very large numbers of zeros. This grain size also allowed for a sampling interval small enough to offer sufficient resolution for detecting very local scale spatial patterns.

I used all-directional Moran’s *I* correlograms to examine patterns of spatial autocorrelation in each response variable (Legendre and Fortin 1989). I considered fifteen lag intervals of 9 m width and a maximum distance of 150 m (lag classes are reported in terms of the maximum distance for each class). The first lag class began at a distance of 15 m, and distances between sampling units were measured as the distance between centroids. For spatially patchy structures, the scale at which the correlogram crosses the *x*-intercept is indicative of patch size (Sokal 1979). Distances between successive peaks represent inter-patch distances. Significance was assessed by randomly permuting the original data with respect to geographic locations and re-calculating Moran’s *I* 1,000 times. I used one-tailed tests ($\alpha = 0.05$) and a progressive Bonferroni correction for multiple testing (Legendre and Legendre 1998).

For examining spatial cross-correlation between the number of foraging observations by a bird species and fruit abundance and between the number of foraging

observations recorded for different bird species, I used the bivariate analog of Moran's I (defined in chapter 3; Wartenberg 1985, Reich et al. 1994). I computed this cross-correlation statistic for lag = 0 and for each of the ten lag classes considered for autocorrelograms. Moran's I at lag zero is equivalent to a Pearson's correlation coefficient. Significance of fruit abundance \times visitation cross-correlation statistics was assessed by comparing to a distribution of Moran's I values obtained from 1,000 random permutations of observed values of one of the response variables with respect to the geographic locations while holding the other constant. I used one-tailed tests ($\alpha = 0.05$) and a progressive Bonferroni correction for multiple testing (Legendre and Legendre 1998). All correlograms, cross-correlograms, and permutation tests were computed using functions written for Matlab software (<http://www.mathworks.com/products/matlab/>).

RESULTS

Overview

A summary of the number of frugivory observations for each bird and plant species recorded during the study is provided in Table 1. Three bird species accounted for 58% of all frugivory observations: Puerto Rican Tanager (*Nesospingus portoricensis*), Puerto Rican Stripe-headed Tanager (*Spindalis portoricensis*), and Black-whiskered Vireo (*Vireo altiloquus*). For the remainder of the paper I limit consideration to these three fruit-eating bird species.

The three bird species differed somewhat in their fruit diets (Table 1). *S. portoricensis* and *V. altiloquus* were relatively specialized, relying heavily on a single fruiting tree species. *S. portoricensis* mostly consumed *Schefflera morototoni*, while *V. altiloquus* mostly consumed *Guarea guidonia*. Although *N. speculiferus* foraged more evenly among plant species, its fruit diet was most similar to that of *S. portoricensis*. *S. morototoni* was the most frequently consumed plant for both of these bird species. Fruit diet overlap was highest for the *N. speculiferus* × *S. portoricensis* pair, with a Morisita's Index value of 0.67, compared to a value of 0.25 for the *N. speculiferus* × *V. altiloquus* pair. *S. portoricensis* and *V. altiloquus* had the least degree of overlap, with a Morisita's Index value of 0.17.

Spatial patterns

I found no evidence of autocorrelation in foraging intensity for any of the three focal bird species at the shortest lag distance (Fig. 1). This finding does not necessarily mean there was no spatial patterning in frugivory at this scale, only that the size of my sampling unit (“grain size”) may have been too large (relative to the sampling interval) to detect such patterns (Legendre and Legendre 1998). Correlogram shape was very similar for *N. portoricensis* and *S. portoricensis* with strong positive autocorrelation at the second lag distance of 33 m and a characteristic patch size of 51-60 m (Fig. 1A, B). A second patch peak was found at a scale of 60-69 m for both of these species, although autocorrelation at this scale was only significant for *N. speculiferus*. As was the case for

the other two species, *V. altiloquus* foraging was significantly positively autocorrelated at the second lag class, although patch size for this species was slightly smaller than for the other two, occurring between 33-42 m (Fig. 1C). Correlogram shape for this species was rather flat at scales beyond that of the characteristic patch size.

Fruit abundance was strongly positively autocorrelated for the two tree species that were heavily utilized by one of the three focal bird species, and fruit abundance patch size was larger than the patch size for foraging intensity (Fig. 2). *S. morototoni* fruit abundance was significantly autocorrelated at scales < 60 m and had a characteristic patch size of 61-78 (Fig. 2A). *G. guidonia* was significantly autocorrelated at < 51 m with a patch size of 51-60 m (Fig. 2B).

The number of *Spindalis portoricensis* frugivory observations was significantly positively correlated with fruit abundance of its most frequently consumed fruiting plant species, *S. morototoni* (Fig. 3A). There was no spatial overlap between these two species beyond the scale of the 15 m × 15 m block. *V. altiloquus* frugivory was significantly positively correlated with *G. guidonia* fruit abundance; however, in this case the two were also significantly cross-correlated at the 15 m lag class. Reference back to Figs 1 and 2 further emphasizes the close correspondence between fruit abundance and frugivory for these species. For example, there was a second peak in *S. portoricensis* foraging corresponding to the second peak within the larger patch size for *S. morototoni* fruit abundance.

The number of foraging observations was positively correlated for each pair of bird species, significantly so for the *N. speculiferus* - *S. portoricensis* and *S. portoricensis*

- *V. altiloquus* pairs (Fig. 4). Interestingly, *N. speculiferus* and *S. portoricensis* were also significantly positively cross-correlated at distance 51-60 m, a scale that was intermediate between patch peaks of autocorrelation in foraging intensities for each species (Figs. 1, 4A); the two were significantly negatively cross-correlated at a scale of 105 m. There was no strong pattern for the *N. speculiferus*-*V. altiloquus* pair; however, the cross-correlation coefficient for the foraging intensities of these two was positive at distance 33-42 m, and nearly significant ($P = 0.03$ before Bonferroni correction).

DISCUSSION

I found foraging intensities and fruit abundance of the two species that relied heavily on a single species of fruit to be strongly correlated. This finding was not surprising and agreed with a number of other studies that have reported close correspondence between frugivorous bird habitat use and the distribution of fruits at local scales (e.g., Levey 1988, Loiselle and Blake 1993, Rey 1995). The correlation between foraging intensity and fruit abundance of the principal fruit species was particularly strong for the *Vireo altiloquus*-*Guarea guidonia* pair and supports the contention of Carlo (1999) that *G. guidonia* fruits are highly preferred by *V. altiloquus* in Puerto Rico. Frugivory by this species was higher, not only in cells with the greatest *G. guidonia* fruit abundance, but also in adjacent 15×15 m cells.

Shapes of foraging intensity correlograms of *S. portoricensis* and *N. speculiferus* were nearly identical. Such a pattern could have arisen due to the similarity with which

both species responded to the fruit resources. This explanation is supported by the relatively high dietary overlap of these two species. I believe that the similarity in foraging patchiness of these two species also resulted to some extent from birds responding positively to one another, rather than directly to a particular resource. Support for this notion comes from comparison of cross-correlogram shape to that of the autocorrelograms of each species. *S. portoricensis* and *N. speculiferus* were significantly positively cross-correlated at a scale that matched patch boundaries of foraging for each species. My interpretation of this pattern is that birds foraging near patch edges encountered low resource abundance and thus experienced low foraging efficiency. Calls of other species may have been used by birds in such situations to quickly locate new more profitable patches (Olupot et al. 1998). Thus, this scale of significant cross-correlation may represent the scale at which birds respond to other birds to join flocks. This scale of movement is well within the range of those reported for foraging bouts of other small tropical frugivores (e.g., Lambert 1989, Westcott and Graham 2000). In this particular system, *Nesospingus speculiferus* is the nuclear species (*sensu* Moynihan 1962) of such flocks (Recher and Recher 1966, Willis 1973, Pérez-Rivera 1994) and their loud calls attract the attention of both conspecifics and many other species, including *S. portoricensis* (*personal observation*). It is also of interest that there was a peak in *N. portoricensis* and *V. altiloquus* foraging cross-correlation (although not statistically significant) at the scale of the *V. altiloquus* patch boundary, and my flocking interpretation may extend to this case as well. Indeed, *V. altiloquus* are also common members of such flocks.

A variety of empirical and theoretical studies support the notion that birds benefit from joining flocks by finding new resource patches (e.g., Krebs et al. 1972, Krebs 1973, Giraldeau 1984). Such benefits of group foraging may be particularly important for birds that rely on fruits for a substantial proportion of their diets. For example, fruit abundance, relative to the abundance of many other resources utilized by small forest birds (e.g., insects), is highly variable in space and time (van Schaik et al. 1993). Birds that are able to cue in on calls of other species to detect productive foraging patches from great distances would be especially well-equipped to feed on such variable resources (Olupot et al. 1998). Although variable in space and time, once located, fruiting patches may yield superabundant resources (at least for a while) and so costs of group foraging (e.g., see Hutto 1988) may be especially low for birds that exploit fruits (Willis 1966). Support for this idea for Puerto Rican forests comes both from Cruz's (1980) impression that foraging niches of birds overlap broadly when feeding on fruits, and my own observations that show aggressive interactions between frugivores at fruiting trees to be uncommon (Chapter 1). Indeed, group foraging may be especially favored in such situations due to the additional benefit of increased protection from predators (Bertram 1978).

Conclusions

The fact that I found strong correlations between fruit abundance and foraging intensity suggests that frugivorous birds are able to efficiently track fruit abundance on local scales. Although not a novel or surprising finding, it does beg the question of how

birds are able to track these resources so effectively. Effectively addressing this question has important implications for understanding not just the foraging ecology of birds, but also the population ecology of the plants whose seeds they disperse. Nevertheless, this question has been seldom addressed.

Using spatial correlation analyses I was able to show evidence that birds may take advantage of the searching abilities of one another to monitor fruit abundance over large spatial scales. These ideas would be relatively simple to test experimentally (e.g., via call playbacks; Olupot et al. 1996). In addition, studies aimed at examining how the strength and scales of spatial correlation in foraging between bird species relates to changing fruit abundance would also provide important insights into these systems. Does dependence on other bird species increase in times of fruit scarcity? For example, Fleming (1979) proposed that seasonal fruit shortages in tropical forests could yield competitive interactions among birds; however, birds may in fact be particularly reliant on one another under such conditions to find fruit. Under such situations they may act as facilitators, rather than competitors.

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LITERATURE CITED

- Bertram, B. C. R. 1978. Living in groups: predators and prey. Pp. 64-96 *in* Behavioral Ecology (J. R. Krebs and N. B. Davies, eds.). Blackwell, Oxford, UK.
- Carlo, T. A. 1999. Fruit preference and seed dispersal capabilities of fruit-eating birds in north central Puerto Rico. M.S. Thesis. North Carolina State University, Raleigh, NC.
- Cruz, A. 1980. Avian feeding assemblages in Puerto Rico. *Caribbean Journal of Science* 15:21-27.
- Daily, G. C., and P. R. Ehrlich. 1994. Influence of social status on individual foraging and community structure in a bird guild. *Oecologia* 100:153-165.
- Dowsett-Lemaire, F. 1996. Avian frugivore assemblages at three small-fruited tree species in the forests of northern Congo. *Ostrich* 67:88-89.
- Fleming, T. H. 1979. Do tropical frugivores compete for food? *American Zoologist* 19:1157-1172.
- Giraldeau, L.-A. Group foraging: the skill pool effect and frequency-dependent learning. *American Naturalist* 124:72-79.
- Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* 105:367-368.
- Hutto, R. L. 1988. Foraging behavior patterns suggest a possible cost associated with participation in mixed-species bird flocks. *Oikos* 51:79-83.

- Krebs, J. R. 1973. Social learning and the significance of mixed-species flocks of chickadees. *Canadian Journal of Zoology* 51:1275-1288.
- Krebs, J. R., M. H. MacRoberts, and J. M. Cullen. 1972. Flocking and feeding in the Great Tit, *Parus major* – an experimental study. *Ibis* 114:507-530.
- Lambert, F. R. 1989. Daily ranging behaviour of three tropical forest frugivores. *Forktail* 4:107-116.
- Legendre, P. and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80:107-138.
- Legendre, P. and L. Legendre. 1998. *Numerical Ecology*. 2nd Ed. Elsevier Science B. V., Amsterdam, The Netherlands.
- Levey, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58:251-269.
- Loiselle, B. A., and J. G. Blake. 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a neotropical lowland wet forest. *Vegetatio* 107/108:177-189.
- Morisita, M. 1959. Measuring of interspecific association and similarity between communities. *Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol.)* 3:65-80.
- Moynihan, M. 1962. The organization and probable evolution of some mixed-species foraging flocks of neotropical birds. *Smithsonian Misc. Coll. No.* 143.
- Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. *Ibis* 109:33-98.

- Olupot, W., P. M. Waser, and C. A. Chapman. 1998. Fruit finding by mangabeys (*Lophocebus albigena*): are monitoring of fig trees and use of sympatric frugivore calls possible strategies? *International Journal of Primatology* 19:339-353.
- Pérez-Rivera, R. A. 1994. Feeding ecology of the Puerto Rican Bullfinch (*Loxigilla portoricensis*) in the Carite and Guánica Forests. *Caribbean Journal of Science* 30:242-249.
- Pratt, T. K. 1984. Examples of tropical frugivores defending fruit-bearing plants. *Condor* 86:123-129.
- Recher, H. F. and J. T. Recher. 1966. A contribution to the knowledge of the avifauna of the Sierra de Luquillo, Puerto Rico. *Caribbean Journal of Science* 6:151-161.
- Reich, R. M., R. L. Czaplewski, and W. A. Bechtold. 1994. Spatial cross-correlation of undisturbed, natural shortleaf pine stands in northern Georgia. *Environmental and Ecological Statistics* 1:201-217.
- Rey, P. J. 1995. Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. *Ecology* 76:1625-1635.
- Sokal, R.R. 1979. Ecological parameters inferred from spatial correlograms. Pp. 167-196 *in* Contemporary quantitative ecology and related ecometrics (G.P. Patil and M. Rosenzweig, eds.). International Co-operative Publishing House, Fairland, MD, USA.
- Terborg, J., and J. M. Diamond. 1970. Niche overlap in feeding assemblages of New Guinea birds. *Wilson Bulletin* 82:29-52.

- van Schaik, C. P., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353-377.
- Waide, R. B. 1996. Birds. Pp. 364-398 *in* The food web of a tropical rain forest. University of Chicago Press, Chicago, IL, USA.
- Wartenberg, D. 1985. Multivariate spatial correlation: a method for exploratory geographical analysis. *Geographic Analysis* 17:263-283.
- Westcott, D. A., and D. L. Graham. 2000. Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia* 122:249-257.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Willis, E. O. 1966. Competitive exclusion and birds at fruiting trees in western Columbia. *Auk* 83:479-480.
- Willis, E. O. 1973. Local distribution of mixed flocks in Puerto Rico. *Wilson Bulletin* 85:75-77.

FIGURE LEGENDS

Figure 1. Spatial autocorrelation in foraging intensity (no. observations * 15 m × 15 m block⁻¹) of three Puerto Rican frugivorous birds on the LTP study area, Aug.-Nov. 1999. Lag distances indicate the maximum distance considered for that lag interval. Significance is indicated by filled symbols and was assessed with one-tailed randomization tests ($\alpha = 0.05$) and a progressive Bonferroni correction for multiple testing.

Figure 2. Spatial autocorrelation in fruit abundance (summed FAI across months*15 m × 15 m block⁻¹) for two tree species on the LTP study area, Aug.-Nov. 1999. Lag distances indicate the maximum distance considered for that lag interval. Significance is indicated by filled symbols and was assessed with one-tailed randomization tests ($\alpha = 0.05$) and a progressive Bonferroni correction for multiple testing.

Figure 3. Spatial cross-correlation between foraging intensity and fruit abundance for bird species that relied heavily on single species of fruiting plant. Observations were collected on the LTP study area, Aug.-Nov. 1999. Lag distances indicate the maximum distance considered for that lag interval. Significance is indicated by filled symbols and was assessed with one-tailed randomization tests ($\alpha = 0.05$) and a progressive Bonferroni correction for multiple testing.

Figure 4. Spatial cross correlation between foraging intensities of bird species. Observations were collected on the LTP study area, Aug.-Nov. 1999. Lag distances indicate the maximum distance considered for that lag interval. Significance is indicated by filled symbols and was assessed with one-tailed randomization tests ($\alpha = 0.05$) and a progressive Bonferroni correction for multiple testing.

Table 1. Number of frugivory observations by bird and plant species recorded at trees on the Tres Picachos study area August-November 1999. Plant species (top-to-bottom) and bird species (left-to-right) are listed in order of importance with respect to the total number of observations.

		Bird Species														Total		
		<i>Nesospingus speculiferus</i>	<i>Spindalis portoricensis</i>	<i>Melanerpes portoricensis</i>	<i>Vireo altiloquus</i>	<i>Coereba flaveola</i>	<i>Margarops fuscatus</i>	<i>Loxia portoricensis</i>	<i>Dendroica caerulescens</i>	<i>Columba caerulescens</i>	<i>Euphonia squamosa</i>	<i>Contopus portoricensis</i>	<i>Turdus plumbeus</i>	<i>Icterus dominicensis</i>	<i>Vireo latimeri</i>		<i>Myiarchus antillarum</i>	<i>Parula americana</i>
Plant Species	<i>Schefflera morototoni</i>	44	123	13	25	0	15	4	1	3	0	4	0	0	0	0	0	232
	<i>Cecropia schreberiana</i>	51	35	3	50	49	10	0	2	12	1	2	0	0	0	1	1	217
	<i>Guarea guidonia</i>	14	0	82	16	0	19	24	5	0	0	1	0	3	0	0	0	164
	<i>Dendropanax arboreus</i>	42	10	5	2	0	12	2	0	0	0	1	0	0	0	0	0	75
	<i>Miconia serrulata</i>	32	9	1	0	3	1	0	22	0	0	0	1	0	0	0	0	69
	<i>Urera baccifera</i>	0	3	0	0	40	0	2	14	0	0	0	0	0	0	0	0	59
	<i>Phoradendron sp.</i>	1	1	0	0	0	0	4	0	0	14	0	3	0	0	0	0	23
	<i>Cissus sycyoides</i>	9	6	3	0	0	2	0	0	1	0	0	0	0	1	0	0	22
	<i>Ficus trigonata</i>	4	11	3	0	0	0	3	0	0	0	0	0	0	0	0	0	21
	<i>Psychotria berteriana</i>	6	5	5	0	0	0	5	0	0	0	0	0	0	0	0	0	21
	<i>Magnolia portoricensis</i>	2	5	0	0	0	1	4	0	0	0	0	0	0	0	0	0	12
	<i>Anthurium scandens</i>	4	1	0	0	0	0	0	0	0	4	0	1	0	0	0	0	10
	<i>Inga laurina</i>	5	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	8
	<i>Miconia affinis</i>	6	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	8
	<i>Vitex divaricata</i>	1	5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	7
	<i>Alchornea latifolia</i>	0	2	1	0	0	0	0	0	3	0	0	0	0	0	0	0	6
	<i>Cayaponia racemosa</i>	0	0	0	0	0	1	5	0	0	0	0	0	0	0	0	0	6
	<i>Eugenia biflora</i>	1	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	6
	<i>Casearia sylvestris</i>	0	1	0	0	0	0	3	0	0	0	0	0	1	0	0	0	5
	<i>Inga vera</i>	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5
	<i>Cordia sulcata</i>	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
	<i>Miconia racemosa</i>	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3
	<i>Psychotria brachiata</i>	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	3
	<i>Byrsonima coriacea</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Cinnamomum elongatum</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Cissus sycyoides</i>	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
	<i>Miconia subcorymbosa</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Piper glabrescens</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Andira inermis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Cissus erosus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	<i>Casearia arborea</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
<i>Miconia prasina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Ocotea leucoxydon</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Syzygium jambos</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Unknown vine	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Total	233	231	118	93	92	63	59	51	19	19	8	5	4	4	1	1	1003	

Fig. 1

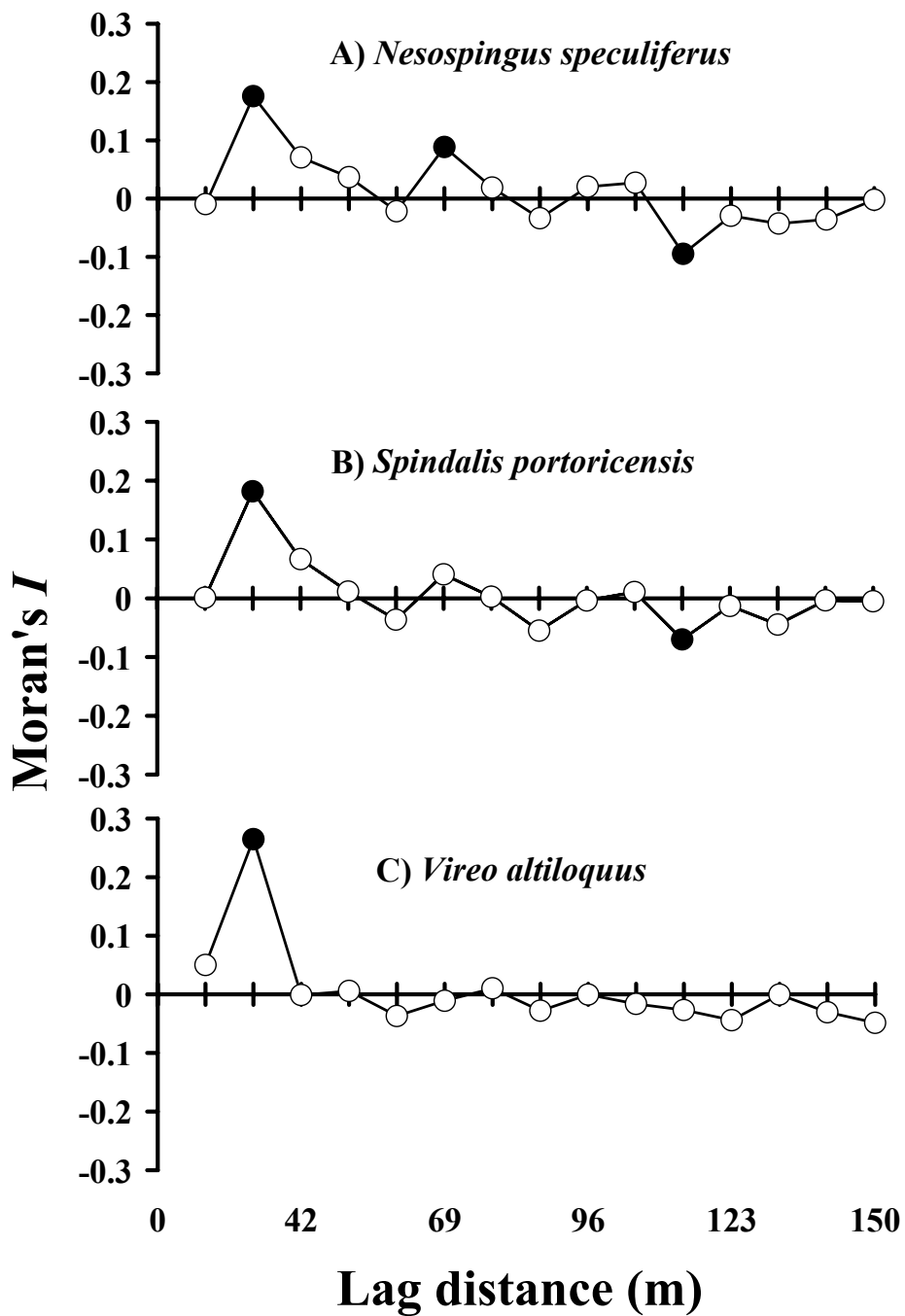


Fig. 2

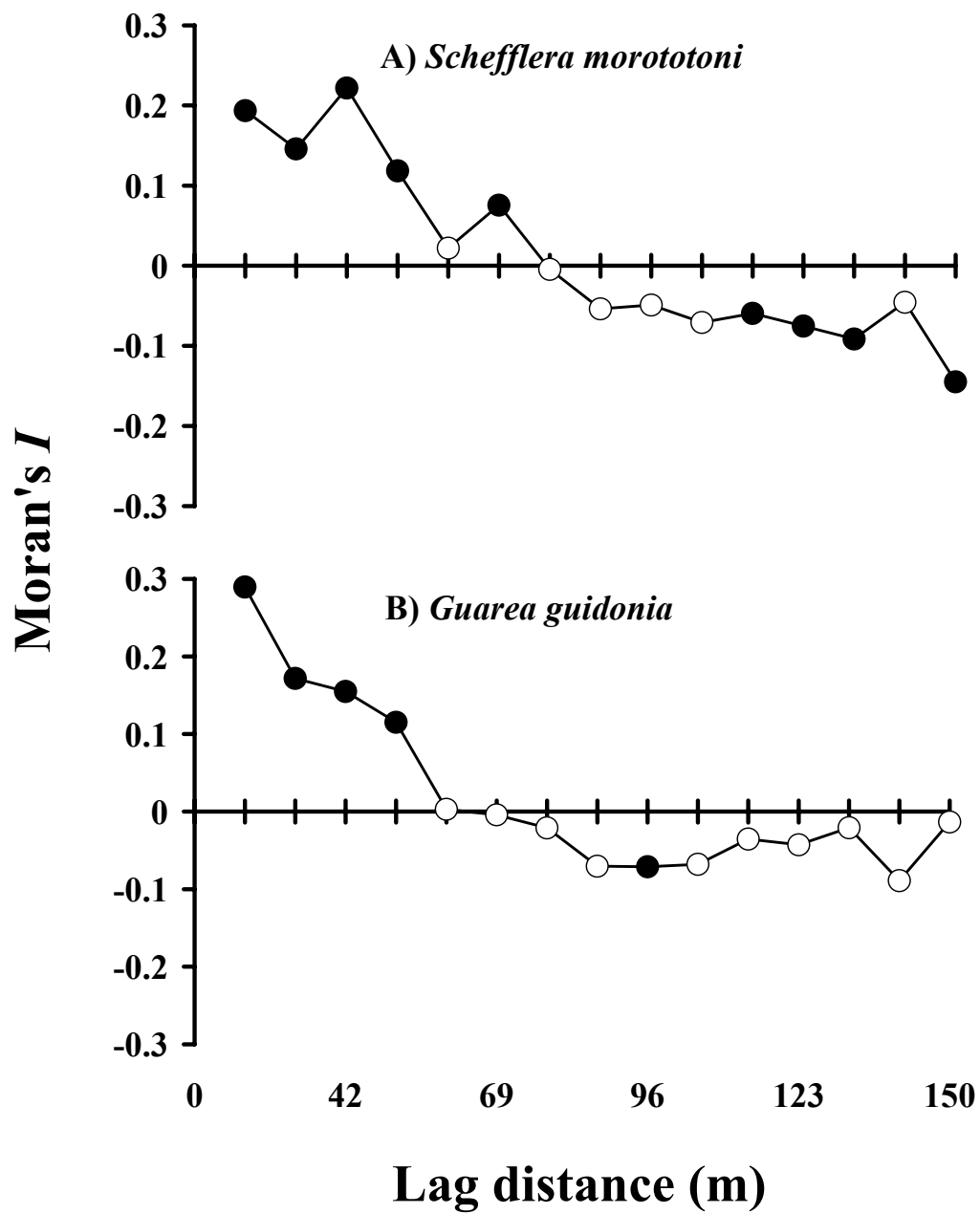


Fig. 3

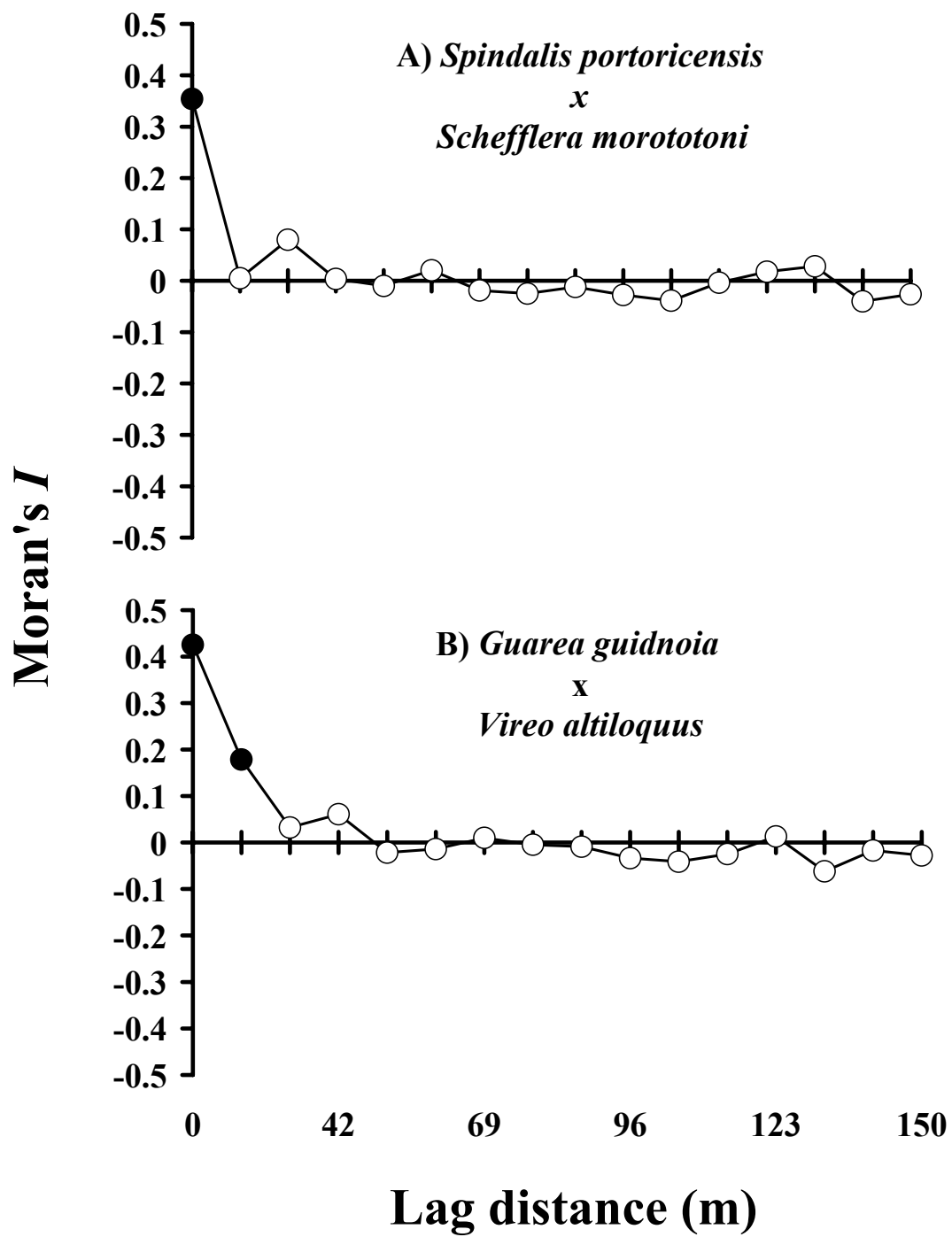


Fig. 4

