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How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest

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Abstract Frugivores often track ripe fruit abundance closely across local areas despite the ephemeral and typically patchy distributions of this resource. We use spatial auto- and cross-correlation analyses to quantify spatial patterns of fruit abundance and avian frugivory across a 4-month period within a forested 4.05-ha study grid in Puerto Rico. Analyses focused on two tanager species, *Spindalis portoricensis* and *Nesospingus speculiferus*, and their principal food plants. Three broad questions are addressed: (1) at what spatial scales is fruit abundance and frugivory patchy; (2) at what spatial scales do frugivores respond to fruit abundance; and (3) to what extent do spatial patterns of frugivory overlap between bird species? Fruit patch size, species composition, and heterogeneity was variable among months, despite fruit patch locations remaining relatively consistent between months. Positive correlations between frugivory and fruit abundance suggested tanagers successfully tracked fruit abundance. Frugivory was, however, more localized than fruit abundance. Scales of spatial overlap in frugivory and monthly variation in the foraging locations of the two tanager species suggested that interspecific facilitation may have been important in determining bird foraging

locations. In particular, *S. portoricensis*, a specialist frugivore, may have relied on the loud calls of the gregarious generalist, *N. speculiferus*, to find new foraging areas. Such a mechanism could help explain the formation of mixed species feeding flocks and highlights the potential importance of facilitation between species that share resources.

Keywords Facilitation · Frugivory · Puerto Rico · Spatial correlograms · Tanagers

Introduction

Tropical fruiting trees are well known for attracting large numbers of feeding animals, most notably birds (Dowsett-Lemaire 1996; Terborgh and Diamond 1970; Willis 1966). These food resources are often abundant, but patchily distributed in space and time (Levey 1988; van Schaik et al. 1993). The patchiness of ripe fruit abundance suggests these resources may be difficult to locate by frugivores; however, a number of studies have shown frugivores to track ripe fruit abundance at a variety of spatial scales (e.g., Levey 1988; Loiselle and Blake 1993).

Birds probably rely on a variety of cues to find fruits. The large fruit crops (Howe and Estabrook 1977) or conspicuously-colored fruit displays (Willson and Whelan 1990) of some plants may be detected from great distances. These visual signals are probably of limited use in dense forests where visibility is low. In such situations, birds may need to more actively seek out and monitor fruiting plants. However, the energetic cost of active searching may be reduced by also tracking the behavior of other frugivores. This type of indirect resource monitoring might allow birds to efficiently locate new patches over broad spatial scales because frugivore behavior may be assessed through sight (Krebs et al. 1972) or sound (Olupot et al. 1998). Although birds may assist one another in finding fruits, the use of particular patches by socially subordinate birds could be constrained

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by interference from dominant individuals (Daily and Ehrlich 1994; Pratt 1984).

In this paper, we use spatial auto- and cross-correlograms to investigate spatial patterns of fruit abundance and avian frugivory on a forested 4.05-ha study grid in Puerto Rico. We address three broad questions: (1) at what spatial scales is fruit abundance and frugivory patchy; (2) at what spatial scales does frugivory correspond to fruit abundance; and (3) to what extent do spatial patterns of frugivory overlap between bird species? We focus analyses on two tanager species, *Spindalis portoricensis* and *Nesospingus speculiferus*, and their principal food

plants during a 4-month fruiting season. In addition, we assess the temporal (monthly) consistency of spatial patterns and fruit patch and frugivory locations in order to better evaluate the degree to which bird foraging reflects direct responses to resources versus indirect responses to resources via social (competitive or facilitative) interactions.

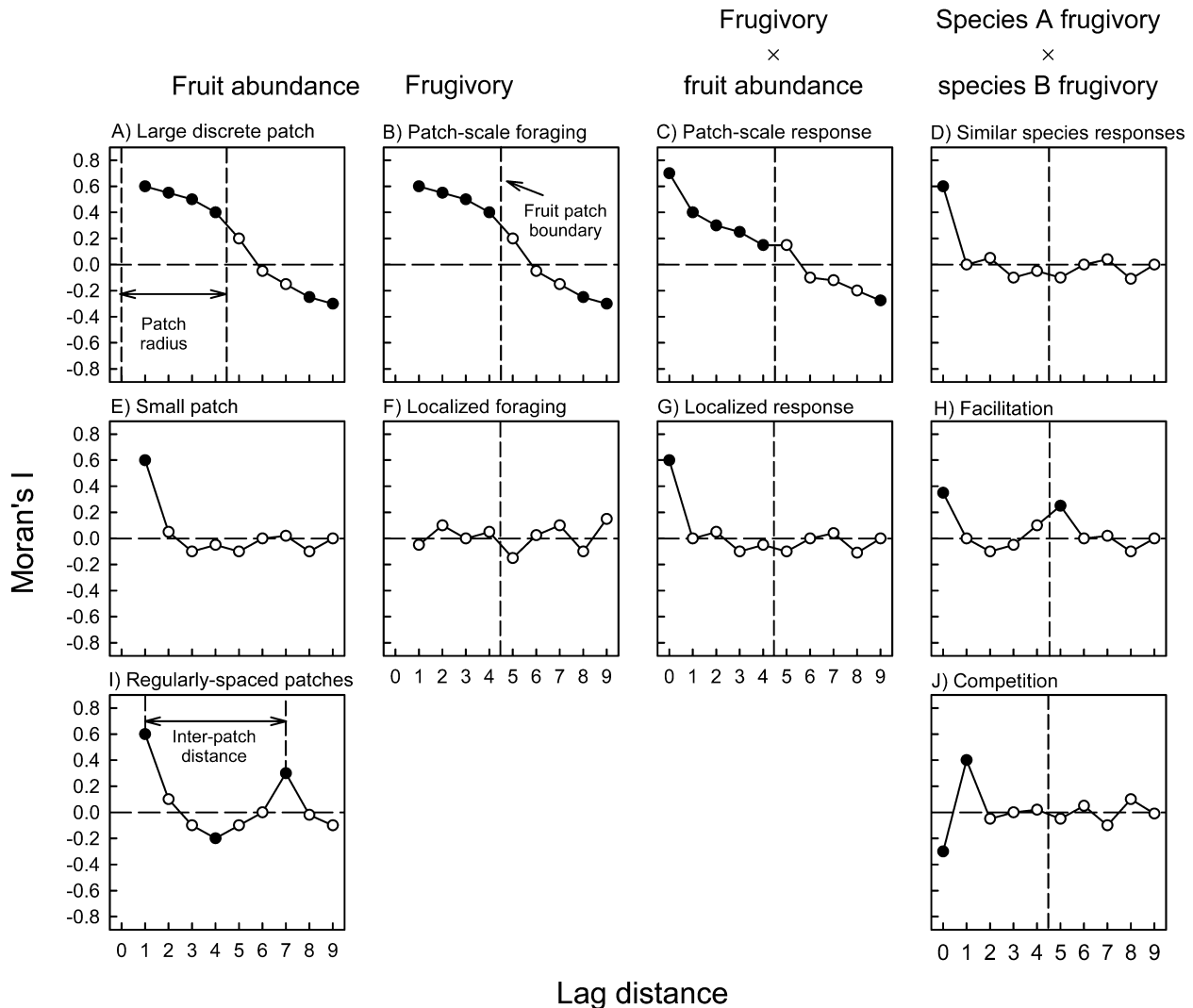


Fig. 1 Hypothetical correlograms describing spatial patterns of fruit abundance (A, E, I) and frugivory (B, F), spatial overlap between frugivory and fruit abundance (C, G), and spatial overlap between frugivory of two frugivore species, *Spindalis portoricensis* and *Nesospingus speculiferus*, (D, H, J). “Significant” Moran’s *I* values are indicated by filled circles. Fruit patches might be large and discrete (A), small with irregular edges (E), or small and regularly-spaced (I). Note that for spatially patchy structures, patch size (radius) can be quantified as the distance between the last significant and positive and next non-significant Moran’s *I* value (as indicated in A). Similarly, the distance between centers of regularly spaced patches can be quantified as the distance between

autocorrelogram peaks (as indicated in I). B–D, F–H, and J assume a fruit patch structure similar to A (patch boundaries indicated by dashed lines). A frugivore species might track fruit abundance on a scale that closely matches that at which it is patchy (B, C) or, alternatively, on a very local scale (i.e., at a scale smaller than lag distance = 1; F, G). Two frugivore species with high diet overlap will likely respond to fruit resources similarly (and could be attracted to one another; D). Interspecific facilitation (H) or competition (J) may also be evident in cross-correlograms describing spatial overlap between frugivore species. See text “Spatial correlograms: hypotheses and predictions” for further details

Spatial correlograms: hypotheses and predictions

As a guide to interpreting our results, we propose a series of hypothetical spatial auto- and cross-correlograms (Fig. 1). For all correlograms, we use Moran's I (Moran 1950) or its bivariate analog, I_{XY} (Reich et al. 1994; Wartenberg 1985), as our measures of auto- or cross-correlation, respectively. Although the interpretation of ecological structure from autocorrelograms has been examined in detail elsewhere (e.g., Sokal 1979; Legendre and Fortin 1989), there are few examples of the use of spatial cross-correlograms in ecology. When considered together, auto- and cross-correlograms can provide unique insights into the nature and scale(s) of ecological processes (Fauchald et al. 2000; Ellingson and Andersen 2002). Here, we briefly describe spatial correlograms as they relate to the specific process of frugivory.

First, we consider spatial patterns of fruit abundance, as they provide a template for understanding spatial patterns of frugivory. We expected fruit to be patchily distributed on our study area. In other words, we expected fruit abundance to be significantly and positively autocorrelated on small spatial scales and negatively autocorrelated (or at least non-significant) at larger spatial scales (Fig. 1A,E,I). The steepness and degree of autocorrelogram decline is indicative of fruit patch size and discreteness. Patches that are large and well-defined decline gradually from significant and positive to significant and negative within the scale of the autocorrelogram (Fig. 1A). Small patches that are not as characteristically discrete would have correlograms that decline sharply, but not to low negative or significant values (Fig. 1E). Patches that tend to be regularly-spaced will be evidenced as multiple autocorrelogram peaks (Fig. 1I).

If a frugivore species tracks fruit abundance closely, the shapes of autocorrelograms describing spatial patterns in its foraging intensity (hereafter "frugivory") and the abundance of its fruit resource should closely match (Fig. 1B). Furthermore, we would expect significant positive cross-correlation between frugivory and fruit abundance at distance class = 0 (i.e., at the level of the sampling unit, where Moran's I = Pearson's r), and a frugivory × fruit abundance cross-correlogram that is similar in shape to the respective autocorrelograms (Fig. 1C). If, on the other hand, frugivores respond to fruit abundance on scales smaller than fruit patches, positive autocorrelation in frugivory might be restricted to a smaller subset of lag classes within fruit patches. In the most extreme such example (i.e., in cases where frugivores respond at scales smaller than the first distance class), positive autocorrelation in frugivory might not be evident at any scale within fruit patches (Fig. 1F), despite exhibiting positive cross-correlation between frugivory and fruit abundance at the level of the sampling unit [Fig. 1G; note: the statistical explanation for such a pattern is that the sampling unit, or "grain size" (sensu Wiens 1989) is too large relative to the sampling interval to detect small scale spatial patterns (Legendre and Legendre 1998)].

It should be noted that positive autocorrelation in frugivory within fruit patches could also result from intraspecific social interactions. For example, interference between birds could cause them to forage over a wider area than they might otherwise (Daily and Ehrlich 1994; Pratt 1984). Or, alternatively, positive (facilitative) interactions between conspecifics could cause similar levels of foraging intensity in nearby areas. Clearly, it is difficult to distinguish among the various alternatives (direct tracking of the resource, interference, or facilitation) that describe why a particular frugivore species forages where it does. Nevertheless, the general hypothesis that social interactions are more important than the distribution of fruits in determining foraging locations would be supported if the frugivory autocorrelogram differed markedly in shape from the fruit abundance autocorrelogram.

In contrast to intraspecific interactions, the role of interspecific interactions in determining foraging locations can be more easily determined from spatial correlograms. Two frugivore species that respond to resources similarly or respond positively to one another will have foraging intensities that are positively correlated within sampling units (i.e., cross-correlation at lag distance = 0) (Fig. 1D). The relative roles of fruit abundance and inter-specific attraction (i.e., facilitation) can be ascertained, in part, from the relative strengths of correlation between frugivory of the two species and correlations between each frugivore species and fruit abundance. In addition, positive cross-correlation between species at scales corresponding to patch boundaries or inter-patch regions would lend further support to the hypothesis of inter-specific attraction (Fig. 1H). We would expect individuals of the two species to respond to the calls or behavior of one another at such scales because differences in fruit abundance and, presumably, foraging efficiency are great between areas separated by those distances. In contrast, species that compete strongly might be expected to have foraging intensities that are negatively correlated within sampling units due to spatial partitioning of resources (Fig. 1J). However, because of high diet overlap we would still expect their foraging intensities to overlap at some scale within fruit patch boundaries (equivalent to the distance birds usually space themselves).

These hypothetical correlograms should be used as a general guide for interpreting our results. We will discuss the relative merits of particular hypotheses based on various combinations of correlogram shapes and how they differed across the four months of the study.

Materials and methods

Study area

The study was conducted in the Cordillera Central of Puerto Rico on a 225 × 180 m plot (4.05 ha) within Los Tres Picachos State Forest (LTP). LTP is comprised of approximately 12,000 ha ranging from 300 to 1,205 m in elevation. Most of LTP lies within the Holdridge Subtropical Wet Forest Life Zone (Holdridge 1947). Annual rainfall averages 2,000–4,000 mm, and average temperatures are 18–24°C

(Birdsey and Weaver 1982). Miranda-Castro et al. (2000) describe dominant plant associations and a list of the vertebrate fauna of LTP.

Our study plot was located in secondary forest at approximately 620 m elevation (18°13'N, 66°32'W). Most of the plot was on a gentle slope, although steep banks were present in one corner and along a stream that bisected the plot. Dominant canopy trees included (nomenclature follows Liogier and Martorell 2000): *Inga vera*, *Ocotea leucoxydon*, *Guarea guidonia*, and *Schefflera morototoni*. *Dendropanax arboreus* was a common subcanopy tree. *Miconia* spp., *Piper glabrescens*, and plants in the family Rubiaceae were abundant in the understory. Cultivated species such as coffee (*Coffea arabica*), oranges (*Citrus sinensis*), and bananas (*Musa* sp.) were also present and reflect historical land use in the area (plantation abandoned ca 50–60 years ago). These cultivated species were found in small irregularly-spaced clumps and ripened few fruits during the study. As such, they probably were unlikely to affect strongly frugivore search behavior or use of other fruit resources.

Focal bird species

The two tanager species were among the most conspicuous frugivorous bird species in the study area; they made up about half of all foraging observations (see below for details of sampling methods). The two species differ with respect to their dietary dependence on fruit. *Spindalis portoricensis* is a specialist frugivore whose diet consists almost entirely of plant material, while *Nesospingus speculiferus* is omnivorous with a diet consisting of about equal parts plant and animal (primarily insect) material (Whetmore 1916). The two species also differ in the degree to which they forage socially. *N. speculiferus* is intraspecifically gregarious, and is often the nucleus species (sensu Winterbottom 1943) of mixed-species flocks (Pérez-Rivera 1994; Recher and Recher 1966; Willis 1973). In contrast, *S. portoricensis*, although an occasional participant in mixed-species flocks, more often forages solitarily or in pairs (J.F.S., personal observation).

Plant mapping and phenological monitoring

All bird-consumed fruiting trees and shrubs in the plot were identified to species and mapped in reference to 15×15-m grid cells. Each tree was tagged with a unique number, and its fruiting phenology was monitored monthly from August to November 1999. The phenological status of trees was scored using a ripe fruit abundance index (FAI). The FAI followed a logarithmic scale: 0= no fruits, 1=1–10 fruits, 2=11–100 fruits, 3=101–1,000 fruits, 4=1,001–10,000 fruits, 5=10,001–100,000 fruits, and 6=>100,000 fruits. Most fruits that were commonly consumed by tanagers during the study had small berry-like fruits that were eaten whole. Thus, we believe the FAI served as an adequate measure of the relative value of a most plants to frugivores. A notable exception, however, was *Cecropia schreberiana*, whose fruits consist of large spikes (5–10 cm long × 1 cm wide; Liogier 1985) containing thousands of small seeds embedded in fleshy pulp. Because *C. schreberiana* fruits are particularly large and eaten piecemeal, they were under-represented by our FAI to some extent. Ripeness of fruits of all species was determined based on previous experience observing the condition of fruits taken by birds. The number of fruits on plants with large crops was estimated by counting fruits on a small proportion of the plant (using binoculars) and extrapolating for the remainder of the tree. In order to minimize observer bias in counts and the determination of fruit ripeness, all observers were trained, and periodically checked, by haphazardly selecting plants, conducting independent counts, and comparing results.

Bird observations

Foraging observations were conducted on 21 days (3 or 6 days per month). The entire study area was covered over 3-day sampling intervals. We attempted to complete two sampling intervals (i.e., 6 days of sampling) per month, and this goal was accomplished in August, September, and November 1999. Only one sampling interval was completed in October due to exceptional rainfall levels in that month. In each month, all observation days were completed within a 7–9 day time window that was approximately equally spaced between months.

On each sampling day, four observers traversed separate “blocks” simultaneously to ensure equal and intensive spatial coverage of the plot. Each block consisted of a 75×45 m subdivision of the plot (i.e., one block = fifteen grid cells). Blocks were each observed for 2 h, and each observer sampled three blocks per day. Thus, a sampling day consisted of 6 h of observation over three time intervals (early, middle, and late; each separated by approximately 1/2 h. Sampling days commenced within 1/2 h of sunrise and were usually completed within 7 h. Sampling was occasionally suspended for brief periods due to rainfall. Block-observer assignment was random (without replacement) with the constraint that each block be observed at least once by each observer and twice during each daily time interval (once during each time interval in October). This protocol minimized any effects of observer and temporal sampling biases.

At the beginning of each 2-h observation period, observers slowly proceeded from randomly assigned starting cells and systematically traversed the block looking and listening for bird activity. Once located, birds were identified to species with the aid of binoculars. We recorded the plant and cell of all observed frugivory events. We define a “frugivory event” as any visit by a bird to a plant in which the bird was either directly observed to eat fruit or was noted entering a part of the plant with ripe fruit and remaining for a length of time consistent with fruit consumption. We attempted to follow individual birds to multiple plants; however, whenever multiple individuals were found foraging simultaneously, we instead opted to obtain observations on as many individuals as possible. This sampling strategy resulted in relatively few instances of multiple frugivory events being recorded for individual birds [7% (31/472) of tanager frugivory events]; exclusion of these records in spatial analyses had no qualitative effect on results. Although observers may have influenced frugivore behavior to some extent, we feel that such effects were probably minimal because blocks were small (75×45 m) and required only minimal levels of observer movement (mostly along cut trails) for their complete coverage. Our impression is that tanagers did not respond strongly to observer approach.

Data analysis

We summed the number of foraging observations for each bird-plant pair and month. From these summaries we quantified monthly and seasonal (total) fruit diet overlap using Morisita's Index (Morisita 1959). For spatial analyses, we considered three response variables: (1) the FAI summed across individuals of commonly consumed plant species (i.e., fruit abundance); (2) the number of *S. portoricensis* frugivory events; and (3) the number of *N. speculiferus* frugivory events. Each response variable was calculated for each 15×15-m grid cell ($n=180$) across monthly and seasonal time intervals. We interpret frugivory response variables as indices of the “foraging intensities” of each of the two tanager species.

We constructed all-directional spatial autocorrelograms (Moran 1950; Legendre and Legendre 1998) to examine patterns of spatial autocorrelation in each response variable (question 1 of “Introduction”) and cross-correlograms (Reich et al. 1994; Wartenberg 1985) to examine spatial overlap between response variables (questions 2 and 3 of “Introduction”). For autocorrelograms, We considered nine lag intervals of 9 m width and a maximum distance of 96 m (lag classes are reported as upper boundaries for each class). Cross-correlograms were constructed using lag = 0 (where Moran's I =

Pearson's r) and the same nine lag classes used for autocorrelograms. Euclidean distances between centroids of cells were used to measure spatial proximities. The significance of auto- and cross-correlation statistics was assessed from a reference distribution of Moran's I values obtained from 1,000 random permutations of the original data with respect to geographic locations (only one response variable permuted for cross-correlograms). We used two-tailed significance tests ($\alpha=0.05$) and applied a progressive Bonferroni correction for multiple testing (Legendre and Legendre 1998). We also indicate instances where Moran's I was "significant" before the progressive Bonferroni adjustment, although caution should be exercised when interpreting these uncorrected P -values.

Finally, we used Pearson's correlation coefficients to test for relationships between values of response variables in successive months. The significance of correlation coefficients was assessed using the randomization test described above for spatial analyses; however, in this case tests were one-tailed (we expected positive correlation). All correlograms and permutation tests were computed using functions written by J.F.S. for MATLAB software v 6.1 (The Mathworks, Natick, Mass., USA).

Results

We recorded 236 frugivory events for *Nesospingus speculiferus* and 230 for *Spindalis portoricensis* in 514 person-hours of observation. Fruits of 26 plant species were observed to be consumed by tanagers during the study. Four of these plant species accounted for most (75%) tanager frugivory events: *Schefflera morototoni*, *Cecropia schreberiana*, *Dendropanax arboreus*, and *Miconia serrulata* (Table 1). *S. portoricensis* relied heavily on *S. morototoni*, while fruit consumption by *N. speculiferus* was more evenly distributed among plant species.

Plot-level temporal variation

Fruit abundance

The abundance and species composition of tanager-consumed fruits varied over the study period (Fig. 2). Ripe fruit was most abundant during September and October, primarily as a result of high *S. morototoni* fruit

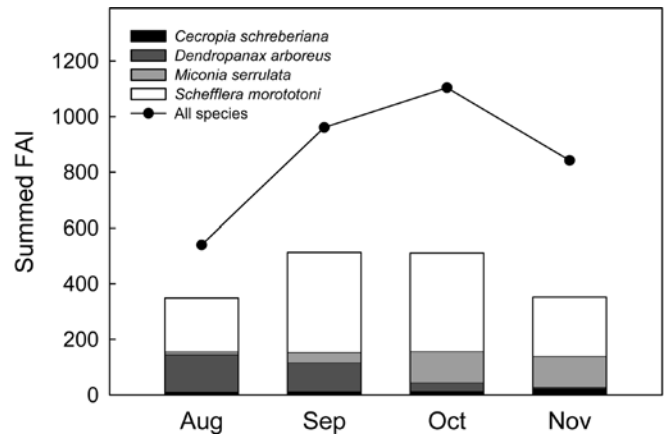


Fig. 2 Temporal variation in fruit abundance and species composition of fruit species commonly consumed by tanagers on the LTP study area, August to November 1999

abundance. Of the remaining three most commonly consumed plant species, *C. schreberiana* fruits were most abundant during November; *D. arboreus* declined and *M. serrulata* increased over the 4-month study period. *C. schreberiana* was sparsely distributed over the study grid and never had large numbers of fruits ripe at the same time.

Fruit diets

The species composition of tanager fruit diets also varied over the study period and largely reflected changes in the relative abundances of fruit species. Fruit diet overlap between the two tanager species was relatively low early in the season (Morisita's Index = 0.63 and 0.58 for August and September, respectively) and high late in the season (Morisita's Index = 0.85 and 0.86 for October and November). In all months, however, the bulk of the fruit diets of both tanager species was comprised of the four fruit species identified as being most important when considered across all months (ranging from 65–89% of *N.*

Table 1 Number (% in parentheses) of frugivory events recorded by plant species for the two tanager species, *Spindalis portoricensis* and *Nesospingus speculiferus*, on the LTP study grid. We include only species that accounted for >3% of all observations for at least

one of the species. Observations were recorded between August and November 1999. Plant species are ordered according to the number of events recorded for *N. speculiferus* and *S. portoricensis*, respectively

Plant species	Bird species	
	<i>Nesospingus speculiferus</i>	<i>Spindalis portoricensis</i>
<i>Schefflera morototoni</i>	45 (19)	124 (54)
<i>Cecropia schreberiana</i>	52 (22)	35 (15)
<i>Dendropanax arboreus</i>	42 (18)	11 (5)
<i>Miconia serrulata</i>	33 (14)	9 (4)
<i>Guarea guidonia</i>	14 (6)	0 (0)
<i>Cissus sycyoides</i>	9 (4)	9 (4)
<i>Ficus trigonata</i>	4 (2)	10 (4)
Other	37 (16)	32 (14)

speculiferus frugivory events and 62–82% of *S. portoricensis* frugivory events).

Within-plot spatial patterns and temporal consistency

Spatial autocorrelation in fruit abundance

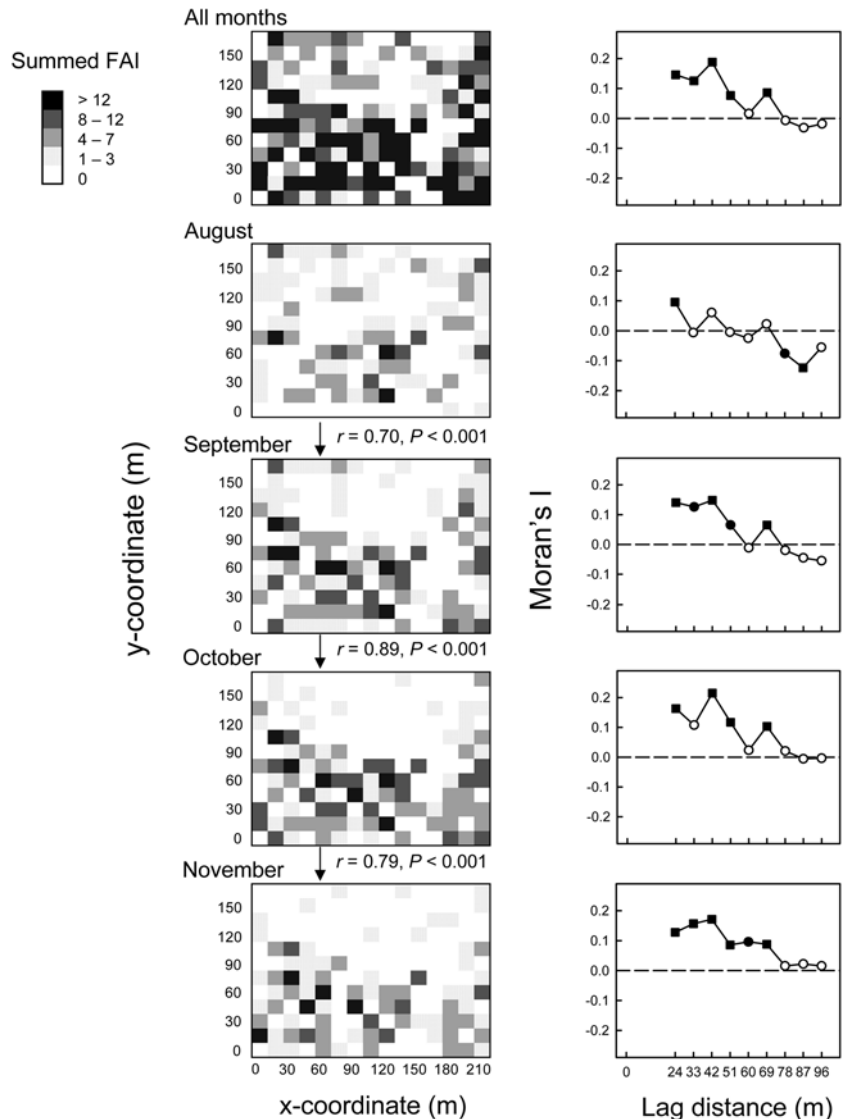
For comparison, we computed ripe fruit abundance response variables using (1) all fruit species observed to be eaten by tanagers (except *Guarea guidonia*, which was very abundant, but never consumed by *S. portoricensis* and mostly consumed by *N. speculiferus* in only one month) and (2) only the four most commonly consumed fruit species. Both methods yielded very similar autocorrelograms (although significance levels differed in some cases). We only report results using the four principal food plants because that response was always more strongly correlated with frugivory of the two tanager species.

Ripe fruit was patchily distributed during the study, as suggested by significant and positive autocorrelation in fruit abundance at small spatial scales (Fig. 3). Despite changes in the species composition and abundance of fruits during the study, the locations of fruit patches were fairly consistent from month-to-month (between month correlations ranged from $r=0.70-0.89$; $P<0.01$). The size of fruit patches did, however, change during the study. Fruit patches tended to be small in August (characteristic patch size = 15–24 m radius) and larger in later months (characteristic patch sizes = 60–78 m). In addition, multiple significant peaks in autocorrelograms in September to November suggested a nested patch structure that was not as evident in August.

Spatial autocorrelation in frugivory

When considered across all months, spatial patterns in the foraging intensities of both tanager species were similar (Figs. 4, 5). Foraging was only observed in about one-third

Fig. 3 Spatial patterns of fruit abundance for the four most commonly consumed plant species on the LTP study area, August to November 1999 for all months combined and for each month separately. *Left panels* are gray-scale maps showing the distribution of fruits (summed FAI within 15×15-m cells). Correlation coefficients between maps of adjacent months indicate temporal correlation in fruit abundance at the level of 15×15-m cells; *P*-values for these correlation coefficients were obtained from a one-tailed randomization test. *Right panels* show fruit abundance auto-correlograms. Lag distances indicate upper boundaries of lag intervals. Significance of Moran's *I* (denoted by *filled symbols*) was assessed with a two-tailed randomization test ($\alpha=0.05$). *Filled circles* were significant at an alpha-level that was not corrected for multiple testing. *Filled squares* were significant after progressive Bonferroni correction



of all cells for both species (57 cells for *N. speculiferus* and 58 cells for *S. portoricensis*). Spatial autocorrelograms for both species showed pronounced peaks at 24–33 m and 60–69 m (although the second peak was not significant for *S. portoricensis*). When considered on monthly intervals, however, frugivory autocorrelograms for the two tanager species were typically quite different (Figs. 4, 5). In addition, there was little evidence of spatial pattern for most species-month combinations. Significance at the progressive Bonferroni level was attained in only four instances. *S. portoricensis* foraging was significantly and positively autocorrelated at 24–33 m in August and October (Fig. 5), a scale at which fruit abundance was not significantly autocorrelated (Fig. 3). In contrast, *N. speculiferus* foraging was significantly and positively autocorrelated at 33–42 m and 60–69 m in September (Fig. 4), scales that did match those of significant positive autocorrelation in fruit abundance (Fig. 3).

The two species also differed in the degree to which their foraging locations were consistent between months.

S. portoricensis tended to forage in the same locations (between month correlations ranged from $r=0.33-0.63$; Fig. 5), while *N. speculiferus* foraging intensities were never strongly correlated between months (ranging from $r=-0.02$ to $+0.20$; Fig. 4).

Fruit abundance × *foraging intensity* cross-correlation

When considered over the entire study period, foraging intensities of both tanager species were significantly and positively correlated with fruit abundance within 15 × 15-m cells (i.e., at lag = 0; Fig. 6). In addition, the foraging intensity of each tanager species was significantly and positively cross-correlated with fruit abundance in three of four months. In most cases, there was little evidence that fruit abundance within 15 × 15-m cells influenced (or was correlated with) foraging intensities in neighboring cells. *N. speculiferus* frugivory, however, tended to be lower in cells nearby those with high fruit abundance, as evidenced

Fig. 4 Spatial patterns of frugivory for *Nesospingus speculiferus* (NESP) on the LTP study area, August to November 1999 for all months combined and for each month separately. See Fig. 3 for detail

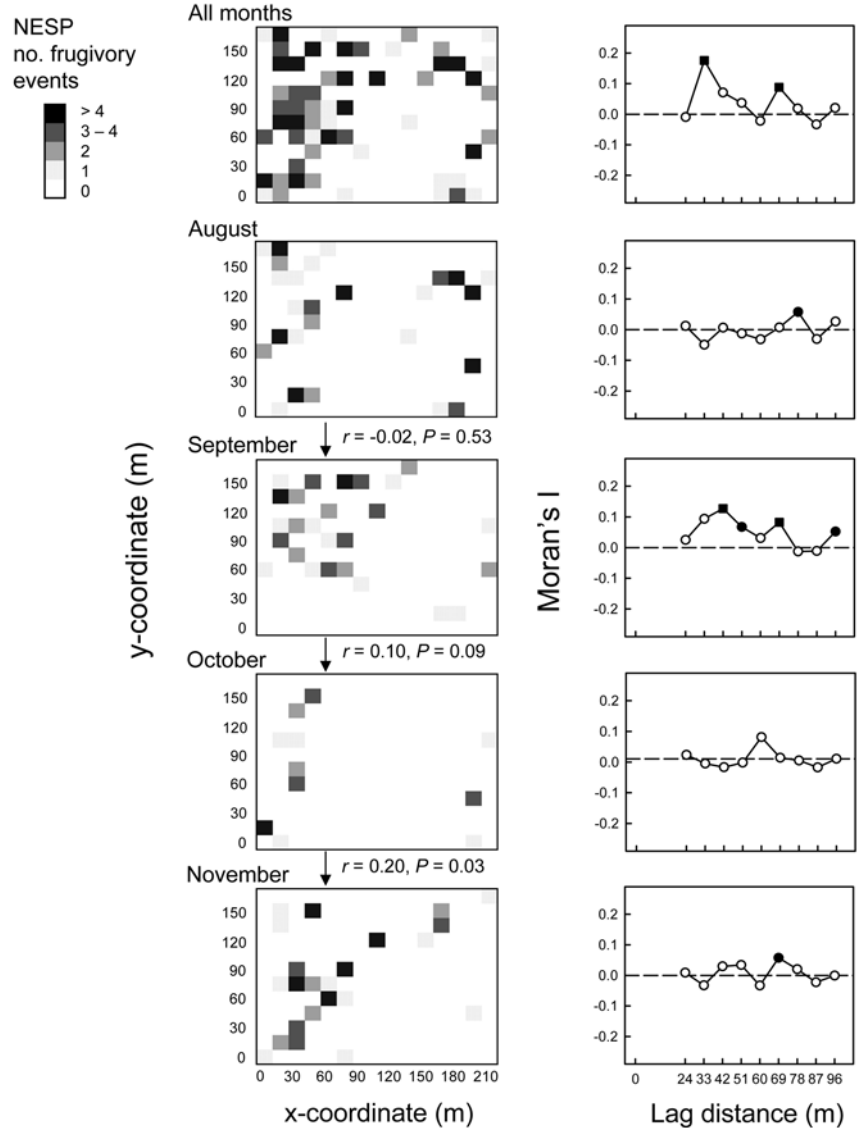
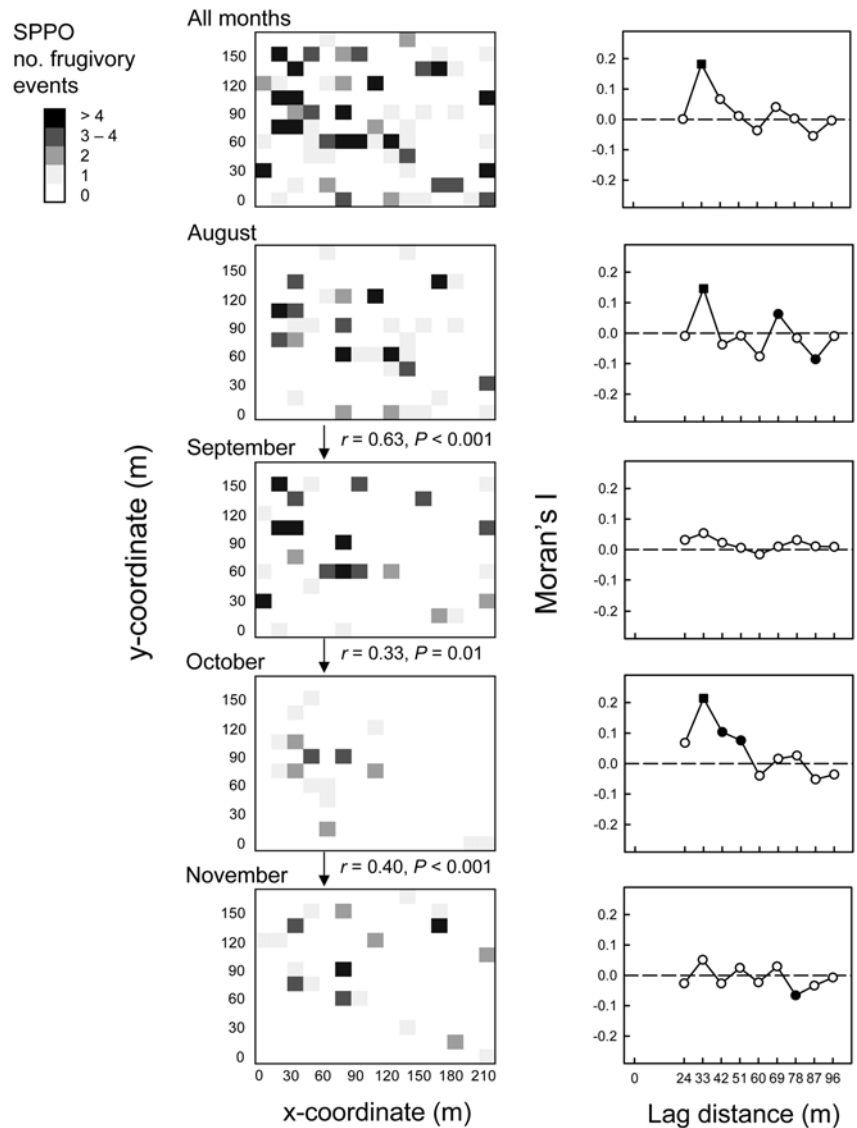


Fig. 5 Spatial patterns of frugivory for *Spindalis portoricensis* (SPPO) on the LTP study area, August to November 1999 for all months combined and for each month separately. See Fig. 3 for detail



by uncorrected significant negative cross-correlation between foraging intensity and fruit abundance at 24–33 m and 42–51 m during August and at 15–24 m for all months combined (Fig. 6).

Spatial overlap between bird species

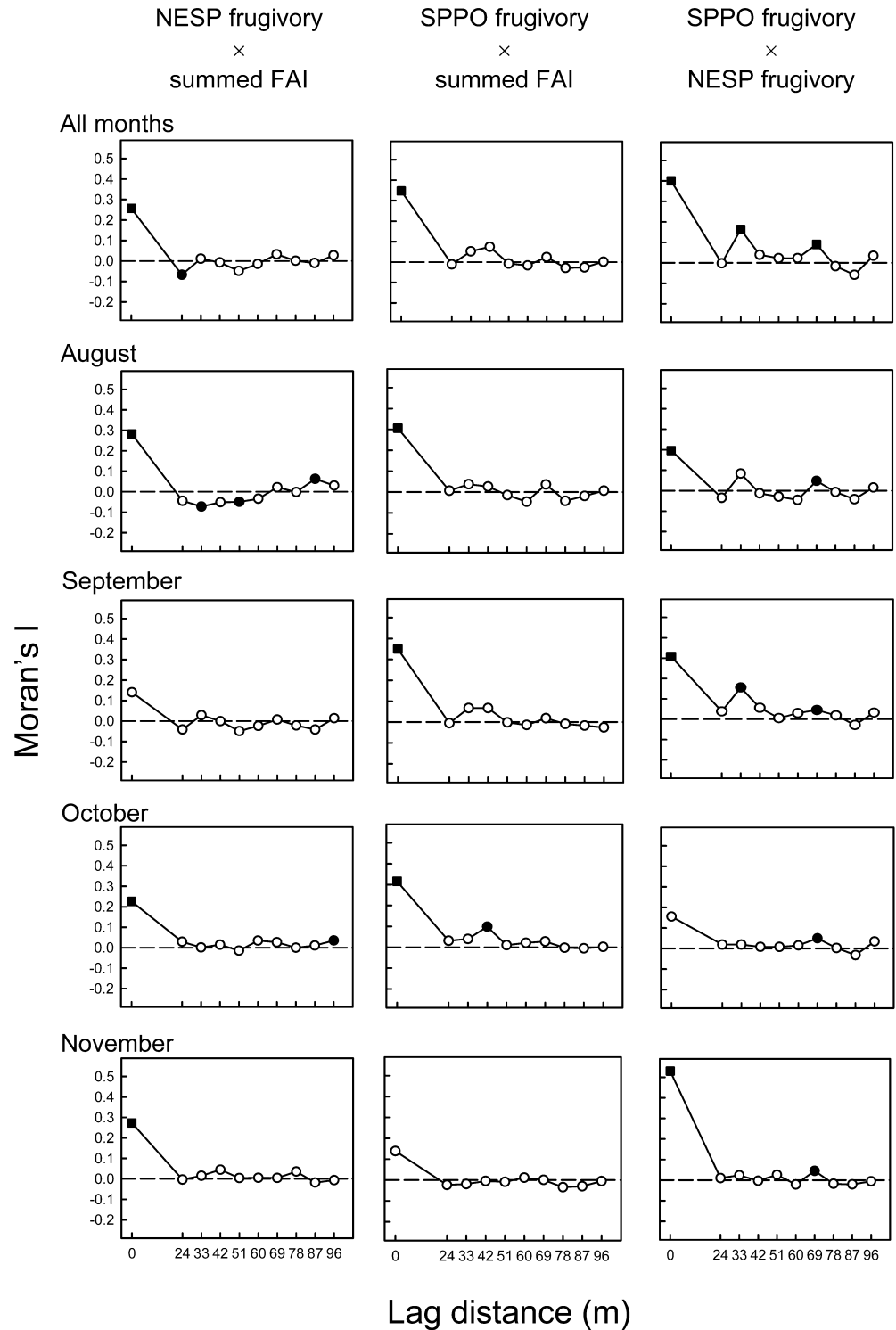
The foraging intensities of the two tanager species overlapped at several scales (Fig. 6); the pattern of overlap, when considered across all months, was consistent with hypotheses of both direct tracking of resources and interspecific facilitation (i.e., autocorrelograms of individual species foraging intensities and fruit abundance closely matched; see Figs. 3, 4, 5). Cross-correlation was strongest within 15×15-m cells, but was also significant at 24–33 m and 60–69 m (Fig. 6). As for autocorrelograms, however, monthly patterns were variable. Patterns of spatial overlap in frugivory in August and September were similar to the pattern found for all months combined, while

foraging of the two species was not strongly associated on small spatial scales in October, and was strongly correlated at the level of individual cells in November. There was at least some evidence (uncorrected $P < 0.05$) of positive cross-correlation in all months at 60–69 m, reflecting the larger scale separation of foraging areas used by the two species. For example, *N. speculariferus* tended to forage on the left side of the plot, while *S. portoricensis* tended to forage more in the center and lower right (Figs. 4, 5).

Discussion

The abundance and species composition of fruits commonly consumed by tanagers changed over the course of the 4-month study period. Nevertheless, the spatial distribution of fruit patches was fairly consistent through time. The strong association between the foraging intensities of the two tanager species and ripe fruit abundance within 15×15-m cells in most months sug-

Fig. 6 Spatial cross-correlations between frugivory and the abundance of commonly-consumed fruits (*first two columns*) and between frugivory of the two tanager species (*third column*). Lag distances indicate upper boundaries of lag intervals. Significance of Moran's *I* (denoted by *filled symbols*) was assessed using a two-tailed randomization test ($\alpha=0.05$). *Filled circles* were significant at the uncorrected alpha-level. *Filled squares* were significant after application of progressive Bonferroni correction



gested birds successfully tracked patterns of fruit abundance within these patches. Studies in other systems have reported similar correspondence between frugivorous bird habitat use and the abundance of commonly-consumed fruits (Levey 1988; Loiselle and Blake 1993; Rey 1995). Nevertheless, frugivory was much more localized than fruit abundance, and we did not observe frugivory events in many cells that had high fruit abundance. In addition,

tanager foraging intensities were never significantly and positively autocorrelated at the smallest scale (15–24 m), despite fruit abundance always being significantly and positively autocorrelated at that scale.

The lack of autocorrelation in frugivory at the smallest lag class could have resulted from birds using non-spatial criteria (e.g., crop sizes or fruit characteristics of individual plants, the presence of nearby cover, or the presence of

competitors or predators) to make foraging decisions at that scale (Martin 1985). Indeed, we did observe evidence of displacements of foraging birds fairly frequently, particularly between individuals of *S. portoricensis* (displacements were observed in at least 14% of *S. portoricensis* frugivory events; J.F.S., unpublished data). In addition, we observed significant autocorrelation in *S. portoricensis* frugivory at 24–33 m in August and October, a scale at which fruit abundance was not strongly autocorrelated in those months (a finding that could support intraspecific competition or facilitation). Alternatively, lack of autocorrelation in frugivory at the smallest spatial scale could simply reflect a disparity between the spatial scale of our sampling design and the scale of foraging decisions (as discussed for Fig. 1F in “Spatial correlograms: hypotheses and predictions”). In any case, it was clear that frugivory of both tanager species was very localized, regardless of whether we summed observations over monthly or seasonal time intervals.

We found little evidence of negative interactions between tanager species (i.e., there was no evidence of negative cross-correlation between foraging intensities of the two species). On the contrary, foraging intensities of the two tanager species were significantly and positively correlated at the level of 15×15-m cells in three of four months and for all months combined. It is possible that this correlation reflects similar independent responses to resources; however, the magnitude of correlation coefficients seemed to vary independently of fruit diet overlap. In addition, positive cross-correlation at scales larger than individual cells supported the hypothesis of interspecific facilitation. For example, the peak in cross-correlation between foraging intensities at 24–33 m during September (although not significant after progressive Bonferroni correction) occurred at a scale where there was no significant autocorrelation in frugivory for either individual species. A similar pattern was found at 60–69 m. These scales of cross-correlation suggest scales at which individuals of the two species may have responded to one another in moving to new foraging areas.

Auto- and cross-correlograms suggested that interspecific facilitation occurred during the study. Nevertheless, it is difficult to ascertain from correlograms alone whether facilitation was unidirectional (commensal) or bidirectional (mutualistic). Several points aid in interpreting these interspecific interactions. First, *S. portoricensis*, the specialist frugivore, which consumed mostly *Schefflera morototoni*, tended to forage consistently in the same areas, while the gregarious generalist, *N. speculiferus*, tended to forage in different cells in consecutive months. In Puerto Rico, mixed-species flocks often form following the loud calls of *N. speculiferus* (Pérez-Rivera 1994; Recher and Recher 1966; Willis 1973). *S. portoricensis*, although often foraging solitarily or in pairs, does join these flocks. From the variable locations of *N. speculiferus* foraging, as well as its loud flock calls, *S. portoricensis* probably benefited from finding new foraging locations discovered by this species. We have observed *S. portoricensis* mimicking the foraging behavior of *N.*

speculiferus while in flocks, and on at least one occasion this practice has led to *S. portoricensis* individuals “testing” food items that are generally not included in their diet, such as *Guarea guidonia* fruits (J.F.S., personal observation). Thus, the interaction was likely commensal, with *S. portoricensis* benefiting from joining *N. speculiferus* feeding aggregations.

Our study is not unique in suggesting that birds that join flocks benefit by finding new resource patches. In fact, many empirical and theoretical studies have supported this notion (e.g., Krebs et al. 1972; Krebs 1973; Giraldeau 1984). However, to our knowledge, ours is the first study to suggest the spatial scales at which such indirect resource monitoring may occur. Benefits of indirect resource monitoring and group foraging may be particularly important for highly frugivorous birds because the distribution of fruit patches, relative to other resources utilized by small forest birds (e.g., insects), is often especially heterogeneous in space and time (van Schaik et al. 1993). Fruit is often “superabundant” within these patches and so costs of group foraging (Hutto 1988) by frugivorous birds may be especially low (Willis 1966). Support for this idea for Puerto Rican forests comes both from Cruz’s (1980) finding that foraging niches of birds overlap broadly when feeding on fruits, and our own observations that suggest interspecific aggression (in contrast to intraspecific aggregation) between frugivores in these forests is uncommon (J.F.S., unpublished data).

Our results have important implications for understanding the ways in which organisms that share resources interact. For the specific case of tropical frugivorous birds, Fleming (1979) suggested that seasonal fruit shortages yield situations conducive to interspecific competition. However, birds may in fact be particularly reliant on one another under such conditions to find fruit, acting more as facilitators than competitors. Our results are consistent with this idea, and we suggest that such reliance may help explain such phenomena as the formation of ephemeral mixed-species flocks. Facilitative interactions between species could be a critical factor enabling the co-occurrence of potential competitors, particularly in circumstances where the shared resources are ephemeral and patchily distributed.

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