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Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal

Received: 4 January 2002 / Accepted: 16 September 2002 / Published online: 31 October 2002
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Abstract Avian fruit consumption may ensure plant reproductive success when frugivores show consistent preference patterns and effectively remove and disperse seeds. In this study we examined avian fruit preferences and their seed-removal services at five study sites in north-central Puerto Rico. At each site, we documented the diet of seven common fruit-eating avian species from February to September 1998. Using foraging observations and area-based estimates of fruit abundance, we examined preference patterns of birds. We found that 7 out of 68 fleshy-fruited plant species were responsible for most of the fruit diet of birds. Seventeen plant species were preferred and four of them were repeatedly preferred across several study sites and times by at least one avian species. Preferred plant species comprised a small percentage of fleshy fruits at each site (<15% in four out of five study sites), but showed extended phenology patterns. The quantity of seeds removed by frugivore species was not strictly related to preferences. Some frugivores showing no preference could effectively remove more seeds from plants at some locations than species exhibiting constancy in their patterns of preference. Only two frugivores, *Euphonia musica* and *Vireo altiloquous*, removed most of the seeds of plants for which they exhibited repeated preference across the landscape. Preference patterns, particularly those exhibiting consistency in space and time for plant species having prolonged fruiting periods, may have important mecha-

nistic consequences for the persistence, succession, and regeneration of tropical plant communities.

Keywords Frugivory · Preference · Plant phenology · Seed dispersal · Puerto Rico

Introduction

Understanding fruit preference patterns of frugivorous animals is of special ecological importance when it is linked to the effective removal and dispersal of seeds. Once animals operate as seed dispersal agents, patterns of preference can couple with delimited foraging movements and produce non-random or *focal* spatial patterns of seed deposition (Wenny and Levey 1998; Schupp et al. 2002). A major consequence of focal seed rain can be the spatial aggregation and association among zoochorous plant species (Tewksbury et al. 1999; Aukema and Martínez del Rio 2002). Preferences are also potential generators of competitive and facilitative interactions among plants that share animal dispersers (Manasse and Howe 1983; Sargent 1990; Saracco 2001; Van Ommersen and Witham 2002).

Regardless of dietary dependence on fruit, avian frugivores do not consume fruits indiscriminately. Morphological features such as bill shape and size affect preference because they impose handling difficulties depending on fruit size, seed size, and seed to pulp ratios (Moermond and Denslow 1983; Wheelright 1985). Frugivore morphology also interacts with the architecture of fruit displays, affecting access to fruit (Moermond and Denslow 1985). Physiological traits also condition preferences when avian guts are nutritionally specialized (Martínez del Rio et al. 1988; Levey and Grajal 1991), or cannot deal with secondary metabolites that defend some fruits from predation (Cipollini and Levey 1997; Struempf et al. 1999). To further complicate fruit choice, the spatial aggregation of fruit resources (Manasse and Howe 1983; Denslow 1987; Sargent 1990), the distance between sources (Levey et al. 1984), and changing

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seasonal nutritional requirements (Herrera 1982; Wheelright 1988) have been shown to affect patterns of fruit use.

In addition to the multiplicity of factors affecting fruit selection, it is necessary that birds not only consume, but also effectively disperse the seeds of their food plants. Schupp (1993) identified major aspects of the seed dispersal process as quantity and quality parameters. Metrics such as the relative abundance of frugivores, the frequency of consumption of available fruiting species, the amount of seeds removed in viable state, and the deposition of seeds into suitable places for germination by frugivores, are all important contributors to the seed dispersal process. Among these parameters, the proportion of seeds effectively removed by frugivore species *in situ* stands as a major component of the dispersal process (Wheelright and Orians 1982; Jordano and Schupp 2000). However, the net contribution to plant recruitment may differ for bird species providing a similar quantity of seed removal due to directional patterns of dispersal (Wenny and Levey 1998) or microhabitat/habitat selection (Jordano and Schupp 2000). Differences in seed-deposition patterns among frugivore species are probably most important for plants whose life strategies require seeds to arrive at very specific places (e.g., gap-dependent plants; Murray 1988), or in harsh environments such as deserts where suitable places for germination are limiting (Callaway 1995).

Most field studies of preference and/or seed dispersal have been limited to single localities (Fuentes 1994; Herrera 1998). We remain largely ignorant about the temporal and spatial variability of frugivory patterns and how it may relate to plant seed dispersal. Jordano (1993) has stressed the need for landscape and regional approaches to the study of frugivore–plant interactions. Studies have shown how the distribution and abundance of fruit resources affect patterns of habitat use and movements of fruit-eating birds (Levey 1988; Loiselle and Blake 1991, 1993; Rey 1995; Kinnaird et al. 1996). Such changing fruit scenarios are inevitably presenting animals with new arrays on which to exercise fruit choice. Therefore, fruit preference patterns should be evaluated across both space and time when possible. Herrera (1998) documented a low coupling in yearly preference patterns and fruit–bird abundance relationships in a Mediterranean scrubland over twelve years; yet, the study was limited to a single locality. The use of separate locations in space may be more resilient to the influence of seasonal or supra-annual fluctuations in the production of fruits (e.g., masting; Herrera et al. 1998). Patterns that may be elusive at local scales may emerge at larger ones (Levin 1992). Landscape scales also provide an opportunity to examine the variability of seed-removal regimes that plant species experience at different localities.

In this study we assessed patterns of fruit use of several avian frugivores and their connection to seed removal of preferred fruiting plant species in the north-central region of Puerto Rico. Specifically, we asked: (1) How consistent are preference patterns across different sites and

times for a bird–plant species pair? (2) How variable is the relative quantity of seeds removed from a plant species by specific frugivores across sites and times? (3) What is the relationship between quantity of seed removal and fruit preference?

Materials and methods

This study was conducted in five study sites, three of which were moist subtropical secondary forests (one on lateritic and two on karstic soils; Ewel and Whitmore 1973), and two shaded coffee plantations–secondary forest sites (on lateritic soils) in north central Puerto Rico. In each site we set grids of 30×30 m cells demarcated by flagged points. The grids ranged in size from 4 to 10 ha. Forest sites were located at Cordillera (2027041 N, 1976699E UTM; 250 m), Dominguito (2036964 N, 19739558E UTM; 100 m), and Caguana (2023200 N, 191739643E UTM; 430 m). Shaded coffee sites were located at Frontón (2025343 N, 19758565E UTM; 300 m) and Cialitos (2018972 N, 19761130E; 650 m). The shaded coffee sites were a mosaic of coffee and forest patches, all included within the study grids.

Fruiting plant phenology

Once a month, from February through September 1998, we recorded the number of ripe fruits per plant for a total of 858 adults (epiphytes, parasites, shrubs, trees) among all sites. We monitored as many individuals as possible, trying to tag ten adults per site for each species. In some cases, however, rarity precluded achieving this sample size. Most of the species we monitored were within avian count stations (see bird abundance below). If a plant species was not found within count stations, we marked individuals haphazardly throughout the sites. The total number of tagged plants and number of species monitored per study site were Caguana ($n=117$, 23 plant species), Cialitos ($n=190$, 29 species), Frontón ($n=125$, 19 species), Cordillera ($n=180$, 45 species), and Dominguito ($n=201$, 59 species). We estimated the density of adult fruiting plants from a series of 11-m radius count stations randomly established across each study area (see Martin and Guepel 1993). The number of count stations at each site is listed below (see frugivore abundance below).

Eight categories were used to estimate each individual's monthly ripe and unripe fruit abundance (1=1–10, 2=11–50, 3=51–100, 4=101–500, 5=501–1,000, 6=1,001–5,000, 7=5,001–10,000, 8=>10,000). We used the ripe fruit average of the abundance categories' midpoints as our estimator of fruit abundance for each species within sites; for category eight (maximum possible), we arbitrarily used a value of 10,000. We multiplied each of these mean estimates by the corresponding plant species density/ha at each site to obtain a fruit abundance index (hereafter FAI), an estimate of ripe fruit/ha. Rare plant species that were not recorded in vegetation surveys or phenological samples but were observed to be consumed by birds were all assigned a mean FAI of 0.1. This ensured that when rank-transforming the FAI values, such rare plants obtained lower ranks of fruit abundance than species detected by our sampling scheme.

Frugivory and frugivore abundance

Foraging observations were recorded for 5 h/day, twice a week, 3 weeks per month/site (30 h/month), for 8 months, yielding a total of 1,200 sampling hours (240 h/site). Avian censuses (i.e., frugivores) were conducted once a month, from sunrise to 10:00, at randomly selected count stations (grid points) within each study site. Counts were made within a fixed radius of 30 m for 10 min. All birds seen or heard were recorded. Count stations were at least 120 m apart from each other. The number of count stations per

study site was Cialitos – 9, Frontón – 9, Cordillera – 7, Caguana – 5, Dominguito – 8.

To record foraging observations at study sites on sampling days, a start point was chosen at random from grid points. From such random point, the observer would move through the grid for 5 h, beginning an hour after sunrise, guided by visual and auditory cues from focal bird species. Focal species were common forest-dwelling birds: *Spindalis portoricensis*, *Euphonia musica*, *Nesospingus speculiferus*, *Vireo altiloquous*, *Turdus plumbeus*, and *Margarops fuscatus*; hereafter focal species. Once an individual was located, we followed it until feeding took place. We did not make sequential foraging observations on the same bird to avoid problems associated with non-independent data (Sallie et al. 1990). However, it is possible that on a given day we observed the same bird more than once, though most likely at a different location and time within a study site.

When feeding was observed, food was classified as fruit, arthropod, or other matters (e.g., anthers, nectar, leaf shoots). Our observation protocol was different for fruit than for other food items. When birds fed on fruits, we extended the observation bout until the frugivore abandoned the plant it was feeding on. Alternatively, if a focal species was observed eating any other food, we recorded just the food item and continued looking for different individuals of focal species. For frugivory observations we counted the number of fruits handled, number of bites per fruit (for piecemeal-eaten fruits like *Cecropia*), number of dropped seeds or fruit parts containing seeds (e.g., *Ficus*, *Miconia*, and *Cecropia* fruits), total time spent on the plant, and approximate distance flown by the bird after leaving the fruiting plant. However, it was often difficult to witness-fully all that occurred during a fruit-eating visit to a plant. In spite of the fact that many of our observations reflect only a fraction of what occurred during a frugivory visit to a plant, we believe that our method captured the main behavioral patterns of focal avian species.

Statistical analyses

All analyses were based on the foraging data, fruit abundance, and avian abundance obtained after we pooled data into two 4-month periods at each site (e.g., Caguana February–May, hereafter site-periods). We grouped the data into 4-month periods, and not smaller time spans, to avoid an excessive dilution of our sample sizes per site and a loss of statistical power. We did not obtain information for all bird species for all months. The within-site groupings were optimal time frames for our analyses because they both depicted distinct ripe-fruit species assemblages and accounted for a temporal change at local fruiting communities. Within-site temporal changes in ripe-fruit species assemblages need to be accounted for in the study of preference because new arrays of available ripe-fruit species have the potential to influence patterns of preference. Among all our site-periods, maximum ripe-fruit species overlap was only 60% and occurred between two different study sites (Cialitos February–May and Caguana February–May). The highest overlap within site-periods for any given study site ranged from 39% to 55%, revealing major changes in local ripe-fruit species assemblages. The ability of the analysis to detect avian preference on ephemeral fruiting species was not significantly affected by the 4-month blocking as we were able to detect preference for plant species with both short (≤ 1 month) and long (≥ 8 months) fruiting seasons (see Results). We used the site-periods to (1) test for non-proportional patterns of fruit use, and (2) to examine a synthetic measure of seed removal that avian species offered to selected plant species.

Fruit preference analyses

For fruit preference assessments of avian species at each site-period, we employed randomization tests using MATLAB software (Version 5.0, Math Works, 2001). The program randomized the N foraging observations per site period for each bird species (i). On

each iteration, N_i random numbers between 0 and 1 were generated. Each randomly generated number was then assigned to the plant species whose FAI interval contained the random number. Intervals were defined based on the proportion of ranked fruit abundance of each plant species at each site-period. Thus, plant species received a simulated number of feeding observations n_{si} that was random but allocated based on the proportion of abundance of fruit per species. This procedure was repeated for 10,000 iterations. To determine if there was preference, the program tallied the iterations in which the simulated value of consumption (n_{si}) was greater than the empirical (observed) value of use n_{ei} for the given plant species in the site-period (i.e., $n_{si} > n_{ei}$). The tally was then divided by total iterations (10,000) to generate a P value (Manly 1991). P values were interpreted as the probability of observing a bird (i) feeding n_{ei} times on the fruits of a plant species under the null hypothesis of proportional use. We used $\alpha=0.05$, Bonferroni-corrected for multiple comparisons (α /total fruiting species at each site-period). Notice that this analysis does not obscure preference for plants that did not fruit for the full span of the 4-month periods because fruit use is weighted by FAI rank.

Quantity of seed removal

We developed an index to estimate the relative contribution of focal avian species to the dispersal of selected plant species in our study sites (Schupp 1993). Our approach differs from others in that we used the foraging behavior of bird species, combined with their relative abundance on each site-period, to estimate their contribution to the seed removal of certain plant species in given site, rather than focusing on plant individuals. The removal index (hereafter RI) consisted of the product of three parameters that contribute to the quantity of seeds removed by a frugivore species from a plant species. First, we calculated S , the average number of seed-swallowing events per fruit-eating visit. Second, we used the mean number of detections N of each frugivore for each site-period. Third, we calculated the proportion of the fruit P in the diet for each site-period. We multiplied the parameters yielding the formula $RI = S \times N \times P$. We used parameters S , N , and P for each frugivore species on each site-period on plant species for which we gathered sufficient data.

Results

Patterns of fruit abundance

Fruit abundance differed markedly among sites and time. At higher elevations (i.e., above 500 m), the most abundant crops belonged to *Schefflera morototoni*, *Henriettea fascicularis*, *Ocotea* spp., *Guarea guidonia*, *Anthurium scandens*, *Dendropanax arboreous*, and *Phoradendron* spp. At lower elevations (i.e., 100–250 m) species with the highest fruit crops were *Zanthoxylum martinicense*, *Bucida buceras*, *Roystonea borinquena*, *Petitia dominguensis*, *Castilla elastica*, and *Casearia* spp. (we will keep referring to species only by genus to simplify both text and figures). Plants that produced non-fleshy (e.g., autochorous or wind-dispersed) fruits comprised $<1\%$ of the total fruits/ha and were represented by species such as *Cordia alliodora*, *Spathodea campanulata*, *Thouinia striata*, and *Ormosia krugii*. We found great variation in the span of the fruiting season among the 68 species that fruited during the study: 19% of all fruiting species bore ripe fruits for no more than 1 month, 25% for 2–3 months, 16% for 4–5 months, 10% for 6–7 months,

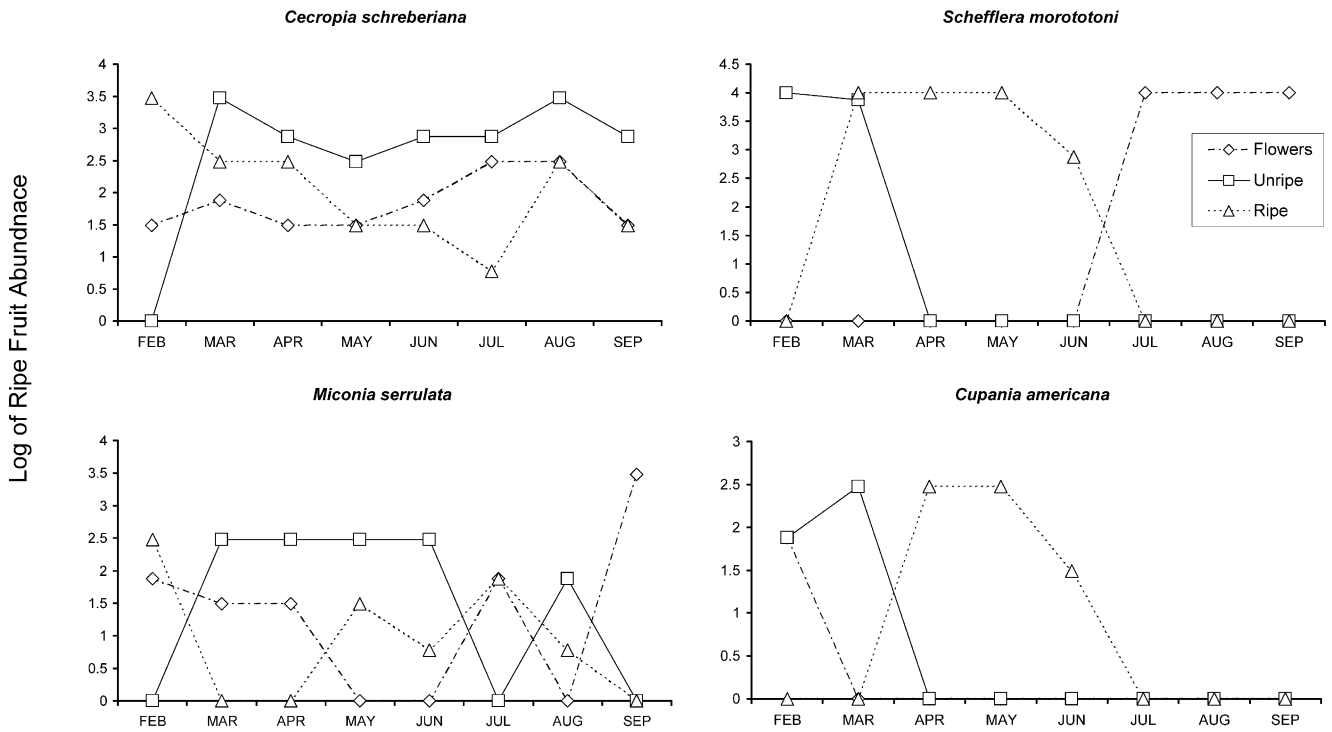


Fig. 1 Monthly phenological patterns of individuals of four plant species. The abundance of flowers and fruits was estimated using semi-logarithmic categories (see Materials and methods for details)

and 7% for the whole sampling period. Differences in the length of the fruiting periods were due to the diverse flowering and fruiting characteristics of species. For example, plants like *Cecropia schreberiana* and *Miconia serrulata* flowered and fruited repeatedly throughout many months (Fig. 1). Other species had sharply defined seasons but differed in that some (e.g., *Schefflera*; Fig. 1) started flowering immediately after ending a fruiting period while others showed a time lag (e.g., *Cupania americana*; Fig. 1). Among the species with extended fruiting periods were the most consumed plants (see Fruit preference below). In contrast, some species like *Eugenia monticola* were not recorded with fruit that year although they were observed fruiting in 1997 and 1999, suggesting that some plants in the region have supra-annual phenology cycles.

Fruit preference

Altogether, focal avian species were observed consuming the majority of the fleshy-fruited plants present at each site, with each species using over 20 different plant species. Each avian species differed in its relative consumption of arthropods, fruits, and other plant materials. Regardless of diet breadth, all bird species exhibited preferences, with significant preferences detected for 17 plant species (Table 1). Of the plants preferred by more than two avian species, not one shared the exact group of

birds and the resulting overlap in preference was low. Avian species shared preferred plants in 38% of cases, with 48% sharing one preferred plant and 14% two or more. *Cecropia*, *Guarea*, *Schefflera*, *Miconia* spp. (3 spp., Table 1), *Clusia*, and *Phoradendron* were the most used and preferred plants, and altogether accounted for half (50.3%) of frugivory observations. The relative abun-

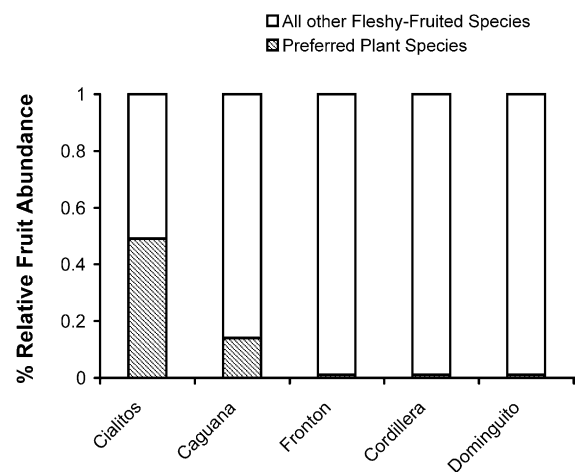


Fig. 2 Mean abundance of the fruits of preferred and non-preferred plants at each study site. *Schefflera* is excluded from this figure because in spite of its extreme abundance at some site-periods (comprising more than one-third of the total fruit abundance) it was preferred by only two bird species

Table 1 (continued)

Plant	Site	Month								Avian consumers	
		February	March	April	May	June	July	August	September	February–May	June–September
<i>Miconia prasina</i>	CA	—		—————						L	L; M; S**
	CO										
	CI										
	FR				—————						L; N; S; V
	DO										
<i>Miconia sp.</i>	CA						—				
	CO										
	CI			—————						N*; S	N*; S*; V
	FR										
	DO										
<i>Myrcine coriacea</i>	CA		—		—						
	CO									S; V	
	CI	—————								L; N**; V	
	FR										
	DO										
<i>Ocotea coriacea</i>	CA	—————									
	CO									M**; T*	
	CI										
	FR										
	DO	—————					—————			T	
<i>Phoradendron spp.</i>	CA	—————								E; L	E; S
	CO								—		E
	CI	—————								E**; L**; N; S**; V	E**
	FR										
	DO								—		E**
<i>Schefflera morototoni</i>	CA		—————							S*; T*; V	S
	CO										
	CI	—————								E; L; N; M; S**; V	S**
	FR		—————							S; T	S; T
	DO										

dance of fruits from plant species that were preferred was low in four out of five study sites, comprising no more than 15% of the average fleshy-fruit production (Fig. 2).

Frugivore species showed constancy in their patterns of preference across study sites. This is evident from the repeated instances of preference for the same bird-plant pairs at different site-periods (Table 1). For example, *Loxigilla* consumed *Guarea* in all study sites and preferred it in six out of ten site-periods, *Spindalis* preferred *Cecropia* fruits in four out of six, and *Vireo* preferred *Clusia* in every site-period where consumption was observed (Table 1). Other focal avian species repeatedly consumed specific plant species but statistically significant preference was detected in just a few site-periods. In many of such cases, sample sizes were low (i.e., less than 20; Carlo 1999) and it may have precluded the detection of preference. Examples are *Euphonia* and *Phoradendron*; *Nesospingus* and *Miconia*; and *Turdus* and *Ocotea*.

The use of preferred plant species was strongly influenced by the seasonal abundance of fruits. Birds were tracking peaks of fruit abundance of favorite species (Fig. 3). Some avian species concentrated frugivory on plant species having short and synchronous fruiting seasons. For example, *Spindalis* made heavy use of

Cordia in February in Cialitos, causing a proportionally low consumption of the abundant *Schefflera* (Fig. 3A). Similarly, *Loxigilla* significantly reduced the use of *Guarea* at Caguana and Cordillera during periods when *Cupania* fruited (Fig. 3B). Although *Cecropia* had smaller crops, peaks of abundance were smoother and it was well represented in the monthly diet of *Spindalis* at several sites (Fig. 3A). Preferences of *Euphonia* were less diverse. At Cialitos, *Euphonia* preferred the parasite *Phoradendron*, switching to consume the epiphytic *Anthurium* at the exhaustion of the former (Fig. 3C).

Seed removal

Seed removal by specific frugivores was highly variable across site-periods for most plants as shown by seed RIs (Fig. 4). Plant species such as *Cecropia*, and *Miconia* attracted many frugivores that had a variable contribution to the removal of seeds across the different study sites. Each bird species scored highest (>50%) in RI for at least one plant species in at least one site-period. *Euphonia* had the highest RIs for *Phoradendron* in all site-periods where the species coincided (Fig. 4). Similarly, *Vireo* had the highest RI values for *Clusia* for most sites. On the other

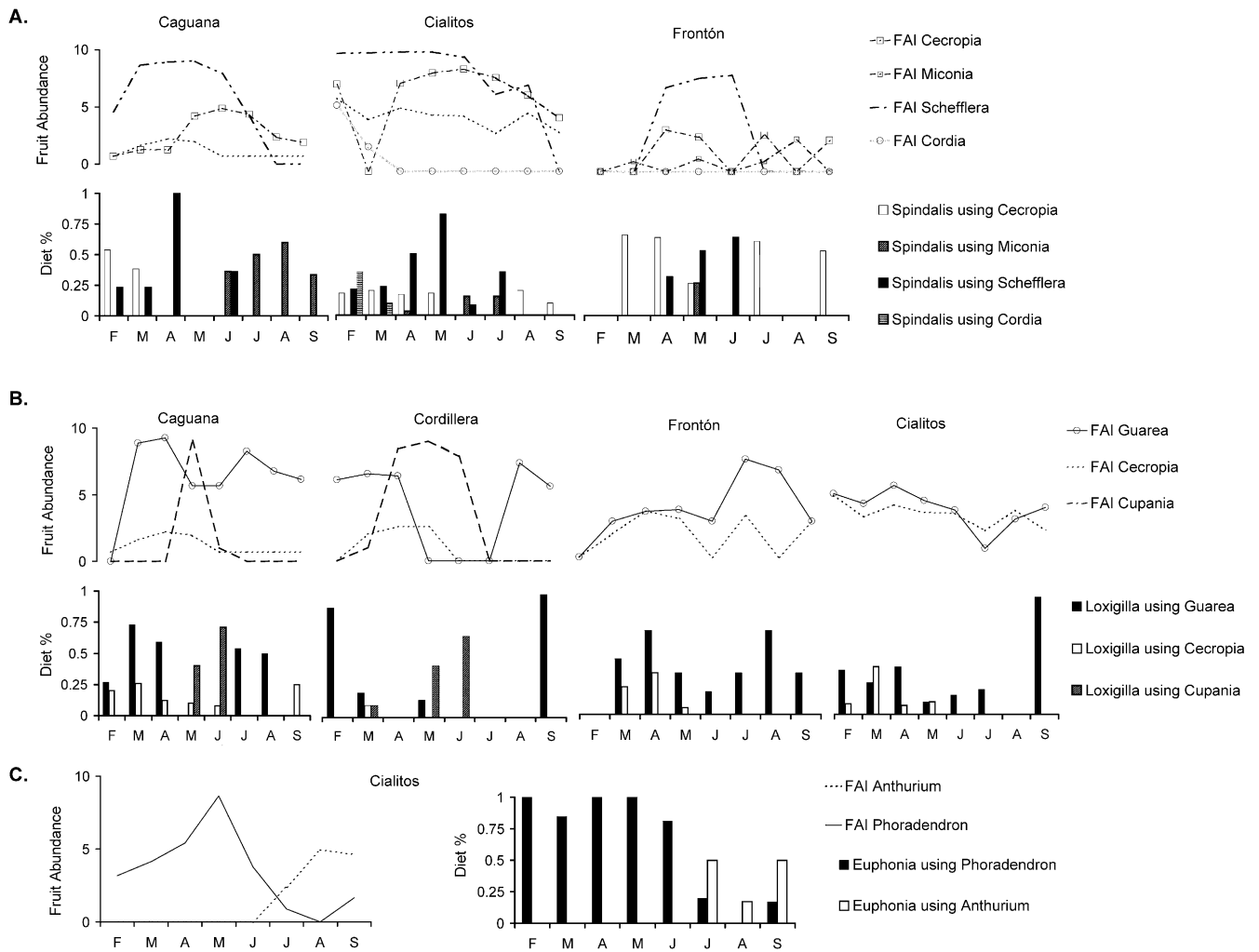


Fig. 3A–C Monthly abundance of preferred fruiting plant species and its use by focal frugivore species at several study sites. **A** *Spindalis*; **B** *Loxigilla*; **C** *Euphonia*. Fruit abundance is expressed at the plot level by the value of the fruit abundance index (FAI, see

Materials and methods for details) for each plant species at each site. Consumption is expressed as the proportion of each fruiting species in the observed monthly diet (all food items taken into consideration) for each avian species/site

hand, *Loxigilla* was the main consumer of *Guarea* but never removed any seeds effectively.

The variation in RI values was due to differences in seed ingestion events, changes in the proportion of fruiting plants in diets across site-periods, and/or the relative abundance of birds at site-periods (Appendix). For example, the large *Turdus* fed more frequently and removed more seeds per visit to *Schefflera* than the smaller *Spindalis*. Still, in several site-periods *Spindalis* obtained higher RI values due to its higher abundance (Appendix). Although we do not include the average time frugivores spent foraging on plants as a parameter of the RI, visits varied between 0.85 ± 0.2 (*Turdus*) and 2.06 ± 0.16 (*Euphonia*) minutes per visit. Such short times confirm that indeed ingested fruits were removed from parent plants because seed passage rates reported for birds of comparable size are much higher, usually over 15 min (Wahaj et al. 1998). Carlo (1999) collected seeds of the aforementioned plants in viable state in fecal samples

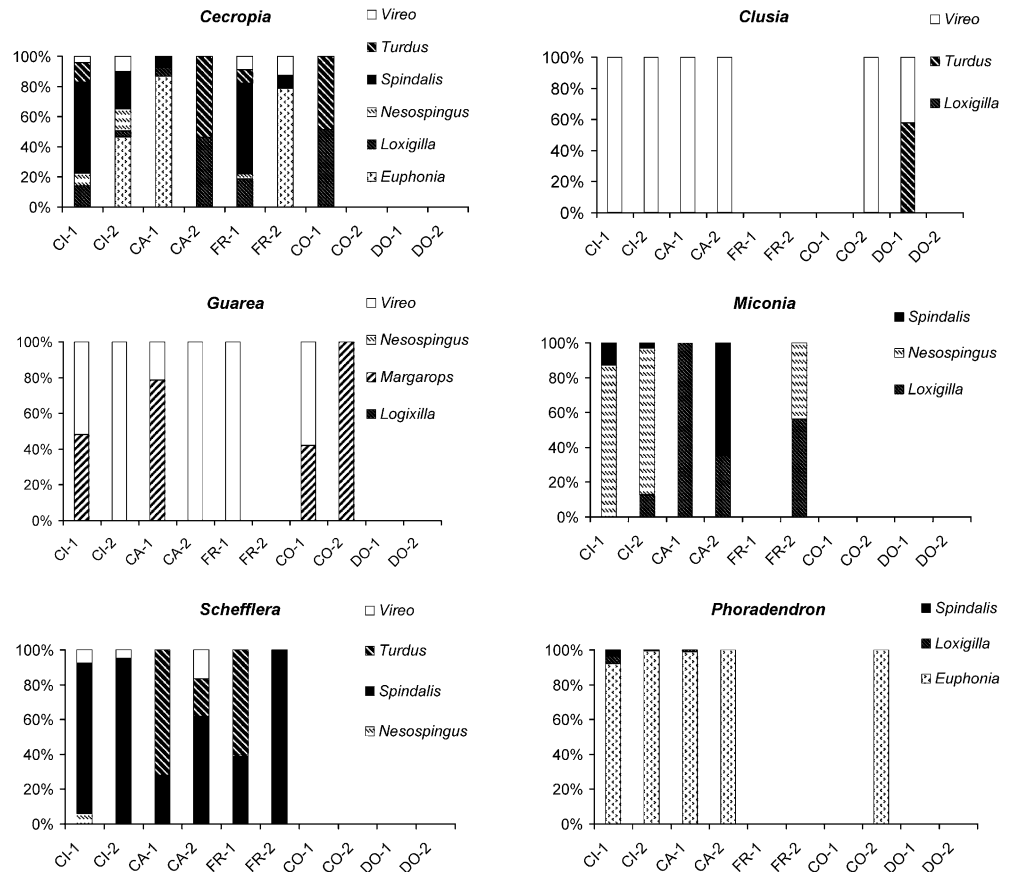
from each species, confirming that indeed the studied avian species are legitimate seed dispersers.

Discussion

Fruit preference

Patterns of fruit preference for some plant species were fairly constant across sites and time. This repetition in preference probably reflects the top-choices of each avian species in a hierarchy of fruit use. Although we sampled a reduced portion of a landscape for a relatively short time, we believe that the preference patterns we found show a remarkable strength given the multiplicity of factors that conspire against any consistency in avian fruit choices (Herrera 1982; Wheelright 1988), particularly in the floristically complex landscape of north-central Puerto Rico.

Fig. 4 Composite removal index (RI) that estimates the relative contribution of avian species to the dispersal of selected plant species at different sites and times (RI standardized to total to 100% for each plant species, see Materials and methods for details). *CI-1*, Cialitos February–May; *CI-2*, Cialitos June–September; *CA-1*, Caguana February–May; *CA-2*, Caguana June–September; *FR-1*, Frontón February–May; *FR-2*, Frontón June–September; *CO-1*, Cordillera February–May; *CO-2*, Cordillera June–September; *DO-1*, Dominguito February–May; *DO-2*, Dominguito June–September



Frugivores were opportunistic in the use of preferred fruit resources as they responded to the abundance peaks of preferred fruiting species. Such opportunism likely causes competitive interactions among plant species that share seed dispersers because consumption of one species becomes dependent upon the relative abundance of others. For example, *Cordia* fruited only in February in Cialitos and was highly preferred by *Spindalis*, representing 35% of observations for the month while composing less than 1% of the fruit abundance at the time. While *Cordia* fruited, 21% of observations for *Spindalis* were on *Schefflera*, but the fraction went up to 50% and 80% after *Cordia* fruits were exhausted. Because *Cordia* was less abundant than *Schefflera*, it seems that *Spindalis* is fonder of *Cordia* than *Schefflera*. We obtained data on *Cordia* for only one site and it is impossible for us to determine how consistent the pattern may be. A similar case was that of *Miconia* fruits, which were present at Caguana for all months, but *Spindalis* exhibited preference for it only in the June–September block, right after *Schefflera* fruits started to decline in abundance. However, it is possible that some preferred plant species are less prone to competitive interactions as they are consumed more predictably by some avian species, regardless of the crop abundance of other plant species. This is suggested by the cases of *Euphonia* using *Phoradendron*, and *Spindalis* using *Cecropia*. Invariably, *Euphonia* consumed and preferred *Phoradendron* fruits when present

and *Spindalis* made a more consistent use of *Cecropia* than any other of its preferred plant species. Temporal interactions among preferred plants like the case of *Miconia*, *Schefflera*, and *Cordia* are probably commonplace in fruiting species-rich tropical forests and may act as selective forces on fruit traits and on the time to fruit (Rathcke and Lacey 1985; van Schaik et al. 1993). A few other studies have also documented such “switches” in consumption, either due to the local exhaustion of a resource (Galetti and Aleixo 1998), or to changing nutritional needs in the annual cycle of frugivores (Wheelright 1988).

Plant-plant interactions regarding seed dispersal are accentuated when (1) frugivores show a tendency to concentrate their foraging efforts on a particular subset of available fruiting species, and (2) frugivores are a limited resource in the environment (i.e., plants compete for dispersers). The tendency to concentrate use on a small subset of the resources may be explained by factors such as the use of memory to guide foraging patterns (Sherry 1989), resource partitioning and competition (Hutchinson 1957), morphology (Moermond and Denslow 1985) and changing seasonal nutritional requirements (Wheelright 1988). It is puzzling why particular bird species may prefer some fruits so strongly and ignore others, but the unique morphology and physiology of each avian species are probable underlying factors (Moermond and Denslow 1983; Martínez del Río 1988). From a zoochorous plant

perspective, the existence of such patterns may have important reproductive and even evolutionary consequences. When plants compete for dispersers, seed-removal services may be subject to hierarchical regulation, with less preferred fruits removed only when fruits with a higher rank of preference are absent. Conversely, the interaction could be complementary with some plant species experiencing an increase in seed removal by facilitation, as preferred plant species act as magnets for frugivores (Van Ommen and Whitham 2002). This last case could favor the interspecific synchrony of fruiting cycles and even the coevolution of nutritional and complementary chemistry (i.e., secondary compounds) in fruits (Cipollini and Levey 1997) that may exert control over consumption. Definitive evidence for these hypotheses waits to be collected.

Several authors (Terborgh 1986; Gautier-Hion and Michaloud 1989; Vanschaick et al. 1993) have documented the importance of a small group of neotropical plant species in sustaining the frugivore community in times of scarcity due to having extended (or asynchronous) fruiting seasons. Terborgh (1986) has classified the use of such species as either peculiar or pervasive without entering in metrics of preference. Our findings of consistent patterns of preference are somewhat analogous to Terborgh's definition of a pervasively used species, while peculiar would apply to those exhibiting poor consistency across the landscape. In our study, repeatedly preferred plants had extended fruiting periods of at least 7 months (the remaining fruited for 4 months). The origin of extended phenological characteristics deserves further attention. It could be hypothesized that natural selection should favor plants that invest for longer periods in reproductive activities only if the removal of seeds is predictable (*sensu* Howe and Estabrook 1977). Alternatively, animals may specialize in the use of fruits that are available for longer periods. As long as the influence of developmental or environmental constraints on the length of fruiting seasons are accounted for, a comparative approach could be used to test the adaptive nature of extended phenology among plant species.

Seed removal

Our analyses show that in most cases seed-removal index scores (RI) and preference were not concordant, whether at the site-specific or across study sites. This is exemplified by the case of *Guarea*, where *Vireo* and *Margarops* removed most of its seeds in spite that *Loxigilla* was the main consumer with a robust consistency in preference. On the other hand, there were cases where preference and RI scores were tightly linked. For example, *Euphonia* consistently had the highest removal scores for *Phoradendron* and also exhibited strong preference for it. In addition to the relationship of *Euphonia* and *Phoradendron*, *Vireo* was found to be the most effective seed remover for *Clusia* in all but one site-period (Fig. 4), and exhibited preference for it throughout the landscape.

Clearly the importance of a species as a disperser is greatly enhanced when preference and high effectiveness scores converge, as in the case of *Vireo* and *Euphonia*. Our findings also showed how easy it could be to underestimate the role of a bird species when studies are designed based on presumed trophic relationships (e.g., insectivorous vs frugivores). Although *Vireo* feeds primarily on insects, it scored highest as a disperser for *Clusia* for most sites, and *Guarea* in some others. Other studies also have documented the importance of vireos as seed dispersers of other plant species (see Greenberg et al. 1995). Thus, from the plant's perspective, the functional behavior of *Vireo* may parallel that of a specialized frugivore.

For many plant species, the identity of the frugivore contributing the most to its removal of seeds changed across sites. For example, three bird species had the highest RI scores for *Cecropia* in different site-periods, not to mention that *Cecropia* is highly dispersed by bats (Charles-Dominique 1986). *Euphonia* and *Spindalis* each had the highest RI scores for *Cecropia* in three cases, whereas *Turdus* had the highest RI scores twice. Spatial changes in seed removal services can be viewed as dynamic substitution processes (Fleming et al. 1993). Such substitutions reduce the selective impact of individual frugivore species and link plants and frugivores in an evolutionary diffuse manner (Herrera 1982; Jordano 1993). The extended phenology of *Cecropia* may be related to both having multiple dispersers and of being dependent on unpredictable forest gaps to germinate (Brokaw 1998). A dual function of plants like *Cecropia* may arise because (1) they are used and preferred by many frugivores and (2) high visitation rates increase the seed rain of other plants species directly under and around such trees (Slocum 2001). Slocum (2001) has shown how fleshy-fruited species like *Cecropia* facilitate both succession and species diversity in Costa Rica. Our findings for a sister species of *Cecropia* in Puerto Rico give support to Slocum's (2001) findings from the seed-disperser perspective.

The emergence of consistent patterns of preference across multiple study sites indicates that preference could reach some predictability that is not easily captured using local-scale approaches. At a time when Neotropical forests are quickly vanishing and commonly replaced by non-zoochorous invasive species, fruit preference and seed-dispersal are key processes in the preservation of biodiversity (Howe 1984; Terborgh and Andresen 1998). A better understanding of preference patterns and seed dispersal services of frugivores to plants promise to provide tools for a feasible restoration and conservation efforts in tropical regions. It will be helpful to know more about the physiology behind fruit selectivity, as well as the role frugivore assemblages play on the reproduction of keystone fruiting plants that better attract animal dispersers. Such plants are likely to facilitate the dispersal of other (e.g., rare) plant species in the community as they serve as a focus of strong plant-frugivore interactions.

Acknowledgements This study was made possible by the effort of many people, among whom A. Jordán, M Vález., J.A. Colón, and J. Saracco were instrumental in the field. Revisions and meaningful comments and suggestions were made by E. Schupp, J. Aukema, C.Martínez del Río, J. Saracco, D. Levey, T. Wentworth, H. Heatwole, J. Walters, and an anonymous reviewer. Statistical help was given by J. M. Morales (Pájaro), K. Pollock and G. Brown. L. Miranda and his crew selected study sites and conducted censuses and vegetation surveys. Funding was provided by the Puerto Rico Department of Environmental and Natural Resources, U.S. Fish and Wildlife Service, North Carolina State University and the Biological Resources Division (USGS).

Appendix

Quantity parameters for seed removal offered by avian frugivores per plant species

CI-1, Cialitos February–May; *CI-2*, Cialitos June–September; *CA-1*, Caguana February–May; *CA-2*, Caguana June–September; *FR-1*, Frontón February–May, *FR-2*, Frontón June–September; *CO-1*, Cordillera February–May; *CO-2*, Cordillera June–September; *DO-1*, Dominguito February–May; *DO-2*, Dominguito June–September

Plant	Bird	Average seed removal per visit				Proportion of the plant in diet								Avian abundance (mean monthly relative detections)											
		N	(SE)	Time on plant (SE)	CI-1	CI-2	CA-1	CA-2	>FR-1	FR-1	FR-2	CO-1	CO-2	Do-1	DO-2	CI-1	CI-2	CA-1	CA-2	FR-1	FR-2	CO-1	CO-2	DO-1	DO-2
<i>Cecropia schreberiana</i>	<i>Euphonia</i>	6	16.83 (±7.19)	2.42 (±0.58)	0.00	0.05	0.50	0.00	0.00	1.00	0.00	0.00	0.00	0.00	1.07	1.83	1.58	0.47	0.81	0.08	0.00	0.14	0.00	0.06	
	<i>Loxigilla</i>	25	3.78 (±0.69)	1.10 (±0.21)	0.09	0.04	0.15	0.06	0.23	0.00	0.04	0.00	0.00	0.00	0.96	0.89	1.58	0.65	0.81	0.43	0.00	0.21	0.87	0.87	
	<i>Nesospingus</i>	26	3.77 (±0.39)	0.86 (±0.10)	0.08	0.17	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.74	0.80	1.00	0.00	0.07	0.01	0.00	0.00	0.00	0.00	
	<i>Spindalis</i>	85	5.99 (±0.88)	1.38 (±0.13)	0.17	0.15	0.36	0.00	0.52	0.29	0.00	0.00	0.00	0.00	1.44	0.97	0.46	0.41	0.74	0.09	0.00	0.00	0.00	0.00	
	<i>Turdus</i>	6	2.83 (±0.65)	0.75 (±0.25)	1.00	0.00	0.08	1.00	0.20	0.00	0.07	0.00	0.00	0.00	0.11	0.19	0.37	0.06	0.59	0.20	0.29	0.14	0.18	0.25	
	<i>Vireo</i>	17	2.60 (±0.45)	0.64 (±0.19)	0.02	0.1	0.01	0.00	0.06	0.04	0.00	0.00	0.00	0.00	1.74	1.41	1.70	1.00	2.22	1.97	0.61	0.14	0.87	0.69	
<i>Clusia rosea</i>	<i>Loxigilla</i>	12	0.00	1.14 (±0.17)	0.00	0.04	0.00	0.00	0.00	0.00	0.07	0.33	0.08	0.21	0.96	0.89	1.58	0.65	0.81	0.43	0.46	0.21	0.87	0.87	
	<i>Turdus</i>	11	8.00 (±4.00)	0.73 (±0.14)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.64	0.00	0.11	0.19	0.37	0.06	0.59	0.20	0.29	0.14	0.18	0.25	
	<i>Vireo</i>	66	2.98 (±0.39)	0.88 (±0.08)	0.06	0.34	0.09	0.06	0.00	0.00	0.00	0.45	0.26	0.00	1.74	1.41	1.70	1.00	2.22	1.97	0.61	0.14	0.87	0.69	
<i>Guarea guilandina</i>	<i>Loxigilla</i>	98	0.00	1.85 (±0.24)	0.23	0.17	0.43	0.26	0.41	0.40	0.39	0.33	0.06	0.00	0.96	0.89	1.58	0.65	0.81	0.43	0.46	0.21	0.87	0.87	
	<i>Margarops</i>	16	3.00 (±0.72)	0.86 (±0.22)	0.33	0.00	0.50	0.00	0.00	0.00	0.31	0.50	0.00	0.00	0.37	0.22	0.29	0.17	0.07	0.17	0.09	0.71	0.00	0.00	
	<i>Nesospingus</i>	6	0.00	0.68 (±0.23)	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.74	0.80	0.00	0.00	0.07	0.01	0.00	0.00	0.00	0.00	
	<i>Vireo</i>	35	1.34 (±0.17)	0.77 (±0.11)	0.17	0.01	0.05	0.12	0.08	0.00	0.14	0.00	0.00	0.00	1.74	1.41	1.70	1.00	2.22	1.97	0.61	0.14	0.87	0.69	
<i>Miconia prasina-affinis</i>	<i>Loxigilla</i>	18	1.38 (±0.32)	1.62 (±1.12)	0.00	0.04	0.07	0.16	0.00	0.06	0.00	0.00	0.00	0.00	0.96	0.89	1.58	0.65	0.81	0.43	0.46	0.21	0.87	0.87	
	<i>Nesospingus</i>	13	2.77 (±0.86)	0.58 (±0.07)	0.04	0.15	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.74	0.80	0.00	0.00	0.07	0.01	0.00	0.00	0.00	0.00	
	<i>Spindalis</i>	9	1.56 (±0.42)	1.11 (±0.16)	0.01	0.01	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.00	1.44	0.97	0.46	0.41	0.74	0.09	0.00	0.00	0.00	0.00	
<i>Schefflera morototomi</i>	<i>Nesospingus</i>	6	2.00 (±1.23)	0.46 (±0.1)	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.74	0.80	0.00	0.00	0.07	0.01	0.00	0.00	0.00	0.00	
	<i>Spindalis</i>	102	2.25 (±0.19)	1.07 (±0.07)	0.30	0.18	0.31	0.11	0.17	0.18	0.00	0.00	0.00	0.00	1.44	0.97	0.46	0.41	0.74	0.09	0.00	0.00	0.00	0.00	
	<i>Turdus</i>	23	2.96 (±0.50)	0.70 (±0.07)	0.00	0.00	0.76	0.20	0.25	0.00	0.00	0.00	0.00	0.00	0.11	0.19	0.37	0.06	0.59	0.20	0.29	0.14	0.18	0.25	
	<i>Vireo</i>	10	1.38 (±0.26)	0.50 (±0.26)	0.04	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	1.74	1.41	1.70	1.00	2.22	1.97	0.61	0.14	0.87	0.69	
<i>Phoradendron spp.</i>	<i>Euphonia</i>	52	15.58 (±2.17)	2.39 (±0.37)	0.91	0.35	0.50	0.66	0.00	0.00	0.00	1.00	0.00	0.00	1.07	1.83	1.58	0.47	0.81	0.08	0.00	0.14	0.00	0.06	
	<i>Loxigilla</i>	7	5.43 (±1.52)	1.15 (±0.45)	0.14	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.96	0.89	1.58	0.65	0.81	0.43	0.46	0.21	0.87	0.87	
	<i>Spindalis</i>	6	6.50 (±1.60)	1.25 (±0.35)	0.06	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.44	0.97	0.46	0.41	0.74	0.09	0.00	0.00	0.00	0.00	

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