



Scale-Dependent Spatial Match between Fruits and Fruit-eating Birds during the Breeding Season in Yungas Andean Forests

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ABSTRACT

The multi-scale spatial match between bird and food abundances is a main driver of the structure of fruit-eating bird assemblages. We explored how the activity of fruit-eating birds was influenced by the abundance of fruits at the local and landscape scales in Andean mountain forests during the breeding season, when most birds forage close to their nest. We measured: (1) the spatial scale of variation in the abundance of fruits, (2) the spatial scale of variation in the activity of fruit-eating birds, and (3) the spatial match between both variables. The sampling design consisted of eleven 1.2-ha sites, each subdivided into 30 cells of 20 × 20 m, where we sampled fruits and fruit-eating birds. We found that fruit consumption, and to a lesser extent bird abundance, were associated with local spatial variation in abundance of selected fruit species. However, fruit-eating birds did not modify their spatial distribution in the landscape following changes in availability of these fruits. Our study shows that fruit-eating birds detect local spatial variation in fruit availability in their home breeding ranges, and exploit patches with large clusters of selected fruits. However, it may be unprofitable for breeding birds to stray too far from their nests to exploit fruit-rich patches, accounting for the absence of fruit tracking at larger spatial scales.

Abstract in Spanish is available with online material.

Key words: Andean mountain forests; food tracking; frugivory; fruit–frugivore link; Neotropics; seed dispersal; Southern Yungas.

CHANGES IN FOOD SUPPLY AFFECT BIRD MOVEMENTS AND REGULATE BIRD POPULATIONS (*e.g.*, Newton 1998, Cortés-Avizanda *et al.* 2011, Côrtes & Uriarte 2013, Wolfe *et al.* 2014). Food abundance and distribution affect the ability of individuals to find food and acquire nutrients and energy for growth, maintenance, and reproduction. Hence, changes in the availability of food may drive bird movements in time and space. Birds must allocate a significant proportion of their daily energy expenditure to food-related activities (Goldstein 1988, Weimerskirch *et al.* 2003), and have evolved strategies to cope with food fluctuations at multiple scales. Birds perceive and respond to the non-random distribution of resources, *e.g.*, patches differing in quantity and quality of available food (Kotliar & Wiens 1990, Johnson *et al.* 2002, García *et al.* 2011, Greenberg *et al.* 2012). Migratory birds can exploit heterogeneous spatial patterns of food supply during migration, and in wintering areas can distribute themselves in response to variation in food availability (Loiselle & Blake 1991, Johnson & Sherry 2001, Tellería *et al.* 2014, Wolfe *et al.* 2014). During the breeding period, foraging movements of parent birds are expected to be more constrained than at other times of their life cycle (Côtés & Uriarte 2013, Slagsvold *et al.* 2013, Lenz *et al.*

2015). Breeding birds typically have stationary home ranges, while non-breeding birds can modify the location of their daily ranges, even without changing the range size (Mueller & Fagan 2008, Lenz *et al.* 2015). At small spatial scales, birds revisit predictable food sources within their territories, and may even memorize the spatial location of feeding sites and use this knowledge in their foraging decisions (Henderson *et al.* 2006, Salwiczek *et al.* 2010). Thus, birds are able to adjust their activity to the spatial arrangement of food supply across several scales, from large regional scales to small differences within individual territories.

The spatial match between food resources and consumers could be defined as the positive relationship between the abundance of consumers and the availability of food, which can enhance the efficiency of food exploitation (Blendinger *et al.* 2012). The multi-scale aspect of the spatial match between bird and food abundances is a main driver of community structure and ecosystem function, described in the mutualism among fruiting plants and fruit-eating birds (Rey 1995, Tellería & Pérez-Tris 2003, Burns 2004, García & Ortiz-Pulido 2004, García *et al.* 2011). Spatial heterogeneity in fruit availability occurs along a gradient of scales: from the arrangement and clumping of ripe fruits in the crown of a plant to the difference among crop sizes of neighboring plants, or among habitat patches that differ in composition and density of fruiting plants, up to differences between

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landscapes at the regional level. To cope with the scale-dependent heterogeneity in fruit availability, fruit-eating birds display distinct behaviors and life-history traits believed to be adaptations related to their foraging habits. At large spatial scales, birds can track fruit abundance and adjust their own distribution and abundance to match that of the fruits (Burns 2003, Guitián & Munilla 2008, Tellería *et al.* 2014). At smaller scales, adjustments in the abundance of fruit-eating birds may reflect individual decisions of food search in the short term, such as bird attraction to plants with heavy crops, or movements related to multiple cues of social attraction and gathering of public information (*e.g.*, birds benefit from following the activity of other frugivores to find new foraging locations [Doligez *et al.* 2004, Saracco *et al.* 2005, Valone 2007]). Defective adjustments can occur, *e.g.*, from imperfect knowledge of the distribution of fruits, overabundance of fruit relative to consumer demand, or monopolization of resources by dominant frugivores (Martin 1985, Daily & Ehrlich 1994, Shochat *et al.* 2002, Hampe 2008). Moreover, given fruit scarcity, fruit-eating birds can switch to other types of food to meet their energy requirements instead of tracking fruits (Herrera *et al.* 2005, Carnicer *et al.* 2008). In turn, the scales relevant to understanding birds' spatial responses to changes in food availability may vary with the tradeoffs and constraints imposed by different fitness-related activities that also vary during the bird's life cycle. For example, changing from non-breeding to breeding social behaviors modifies the rules governing fruit tracking (Tellería & Pérez-Tris 2003).

In this study, we explored the spatial scale of the match between fruit availability and fruit-eating birds in the Southern Andean Yungas. We assessed this relationship at two spatial scales, one at a local ($<1 \text{ km}^2$), fine-grained (tens of meters) extent, and the other at the landscape level ($<100 \text{ km}^2$), with a spatial resolution on the order of a hectare. We conducted the study during the peak of the breeding season, when most birds are likely central-place foragers constrained to explore resource abundance in the surroundings of the nest (Orians & Pearson 1979, Lenz *et al.* 2015). On average, fruit-eating species have a breeding season shorter than 2 months, during which the females invest two-thirds of the daylight hours in nest attentiveness during incubation and both adults feed and care for nestlings, with high nestling feeding rates close to ten visits per hour (Auer *et al.* 2007). Fruit-eating birds track fruit availability across the year in the forests of the Southern Yungas (Blendinger *et al.* 2012, Blendinger *et al.* 2015). They also respond to the local spatial variation in fruit availability, although the strength of this match is considerably lower than the strength of the temporal fruit tracking. Accordingly, the fruit–frugivore match is predicted to be stronger with increasing variability in fruit availability (Blendinger *et al.* 2012). To test this prediction, we first described the composition of fruit and fruit-eating bird assemblages in several sites of the Southern Yungas. We then evaluated the spatial variation at the local and landscape scales in: (1) the composition and abundance of fruit assemblages and (2) the activity (fruit consumption and bird abundance) of fruit-eating birds. Finally, (3) we measured the spatial match between the

variation in fruit abundance and the activity of fruit-eating birds as a group. We expected that the spatial match at the local scale would be stronger than at the landscape scale, as restrictions on bird movements imposed by the location of the nest would prevent fruit-eating birds from freely tracking the changes in fruit availability that occur at the landscape scale throughout the breeding season.

METHODS

STUDY AREA.—We conducted the study in the lower montane forest of the Southern Yungas (Brown *et al.* 2001), in the San Javier and Yerba Huasi mountain ranges of Tucumán, Argentina (Fig. S1), which comprise an orographic unit extending around 37 km from north to south. Climate is subtropical with dry winters (May to September) and wet summers (November to March). Average annual rainfall is 1300–1500 mm, of which 80 percent is concentrated in summer; average annual temperature is 19°C (Minetti *et al.* 2005). For a representative sample of the forest heterogeneity in vegetation composition and fruit ripening phenology at the landscape scale, we chose 11 sampling sites with an altitudinal range of 500 m (550–1050 m a.s.l.; Table 1) placed at the bottom of ravines, slopes of different exposures, and ridges. All sampling sites had a continuous canopy with natural treefall gaps. We included mature forest sites and sites with old secondary growth (Table 1), with low and moderate levels of human intervention, respectively. Six sites were located in a protected area (Parque Sierra de San Javier) with more than 30 yr of effective protection. The forest canopy was characterized by *Cinamomum porphyrium*, *Anadenanthera colubrina*, *Parapiptadenia excelsa*, *Juglans australis*, *Blepharocalyx salicifolius*, *Pisonia zapallo*, *Cedrela angustifolia*, and *Handroanthus impetiginosus*. Vines and epiphytes were common, and there was a dense shrub understory. Species of exotic invasive plants (*Morus alba*, *Ligustrum lucidum*) were more frequent in secondary growth forests. In San Javier and Yerba Huasi lower montane forests, ripe fruit abundance peaks between July and October, mainly due to the massive fructification of *Pyrcobotria carthagenensis*. November to January is the period of maximum diversity of ripe fruit, while March to June are months of low abundance and diversity of ripe fruit (Blendinger *et al.* 2012, Blendinger *et al.* 2015).

The median distance among sampling sites was 7.64 km (range: 0.64 to 22.58 km). In each sampling site, we established a 40 m \times 300 m plot, split in a grid of 30 cells of 20 m \times 20 m each. Individual cells were the sampling units for all counts of fruits and fruit-eating birds. Each cell in the grid was assigned a position with respect to a corner of the grid with arbitrary coordinates (1, 1). We conducted fieldwork in late spring, between mid-November and mid-December 2012. Birds and fruits were counted on the same days. M. G. Nazaro *et al.* (unpubl. data) mist-netted birds simultaneously with our fruit–frugivore samplings. They found that 86.2 percent of 65 adults of the species we studied had brood patches or cloacal protuberances (reliable indicators of reproductive condition in passerines; *e.g.*, Wolfson 1952, Gill 2007). All species included in the assemblage of fruit-eating birds regularly consume

TABLE 1. Name and location of sampling sites, with acronyms in brackets. For each site, the number and abundance of total fruit species, the number and abundance of fruit species selected by birds, and the number of bird species recorded eating fruits are given. Fruit abundance is expressed in grams of dry pulp mass.

Site	Elevation (m asl)	Location (°S, °W)	Forest type	Fruit abundance		Fruit species selected		Fruit-eating species N
				N	g/ha	N	g/ha ^a	
Antayacu (An)	985	26.76199, 65.33315	MF (PSSJ)	12	418.5	6	140.0	6
Arroyo Tañi (AT)	906	26.71587, 65.29707	OGF	15	712.4	7	181.9	7
Frontino (Fr)	679	26.79658, 65.33544	OGF (PSSJ)	18	598.6	4	274.5	8
Funicular abajo (FAB)	756	26.78572, 65.33844	MF (PSSJ)	12	161.8	5	54.5	7
Funicular arriba (FAR)	1022	26.77688, 65.34530	MF (PSSJ)	16	278.5	6	10.7	8
Loma Bola (LB)	987	26.82569, 65.35680	MF	15	1576.1	8	340.2	6
Mundo Nuevo (MN)	723	26.85415, 65.35313	OGF	15	1190.9	7	800.8	5
Puerta del Cielo (PC)	995	26.78261, 65.34545	MF (PSSJ)	11	341.0	7	62.4	7
Quebrada de Lules (QL)	562	26.89477, 65.38284	MF	12	519.5	6	376.6	8
Río Las Cañas (RC)	805	26.77339, 65.33474	MF (PSSJ)	14	766.6	6	57.7	6
Yerba Huasi (YH)	1049	26.89908, 65.39644	OGF	16	929.9	5	111.9	5

N, number of species; MF, mature forest; OGF, old growth forest; PSSJ, sites in the protected area Parque Sierra de San Javier.

^aCumulative values of the eight fruit species selected by birds.

fleshy fruits in addition to varying amounts of insects and other invertebrates (Giannini 1999).

FRUIT COUNTS.—In each sampling site, we counted the abundance of ripe fruit of all bird-dispersed plants in each of the 30 grid cells. We counted ripe fruits per plant from 1 to 10 in units, from 11 to 100 in tens, from 101 to 1000 in hundreds, and for more than 1000 in thousands of fruits. The only exception was *Psychotria carthagenensis* with extremely high density, for which we used five 4-m² quadrats randomly located in each cell, and extrapolated to the surface area of the cell. We determined fruit ripeness based on previous observations about the condition in which fruits are usually eaten by birds. We expressed fruit abundance as dry mass of ripe fruit pulp, calculated for each species as the number of ripe fruits recorded times the mean pulp dry mass in grams. We obtained pulp dry mass from healthy fresh ripe fruits, dried at 60°C for 72 h (Blendinger *et al.* 2015). For each cell and sampling site, we assessed fruit abundance in two ways: (1) as the sum of dry mass of all fleshy fruit species and (2) as the summed dry mass of those species selected by fruit-eating birds. We called ‘selected fruits’ those species consumed well above the expected values according to their availability (see below).

BIRD COUNTS.—We began bird counts at sunrise and completed them within 4 h. Observers traversed each block of 10 × 2 contiguous cells, recording all fruit-eating birds seen or heard within the cell, and their fruit-consuming behaviors, for 20 min per cell. We repeated the same sampling protocol for 3 days, starting on different cells each day to switch the sampling time of each sector. The small size of the sampling unit allowed us to obtain highly reliable data of bird presence in the cell, despite the potential temporal and between-species differences in detectability, and to

follow bird movements well enough to prevent double counts. We followed the location and displacement of individual birds as far as possible, while remaining within the cell, which gave us a comparative measure of plot-use intensity (hereafter ‘bird abundance’). The number of fruit-eating birds recorded in the cell was used as the measure of cell-use intensity. We also recorded every event of fruit consumption detected (defined as any visit by a fruit-eating bird to a plant in which it was directly observed to eat fruit), noting the bird species and the fruit consumed. In a few cases with restricted visibility, we also included birds noted entering a part of the plant with ripe fruit and remaining in there for a length of time consistent with fruit consumption (Saracco *et al.* 2005, Blendinger *et al.* 2012). We considered consecutive visits to different plants as separate events; likewise, we considered each individual of a flock consuming fruits a separate frugivory event.

STATISTICAL ANALYSES.—We used univariate analysis of variance (ANOVA) to evaluate the effects of sampling sites (*i.e.*, ‘landscape’) on the variation in the dry mass of all fleshy fruit species as the dependent variable. To compare the intra-site (*i.e.*, ‘local’) variation in fruit dry mass among sampling sites, we used the coefficient of variation (%) in fruit dry mass as a proxy of the local heterogeneity and patchy distribution in fruit abundance. Then, we used linear and polynomial regressions to explore the relationship between the local heterogeneity in fruit abundance and the overall fruit abundance in the site. Selection of the best regression model was based on the Akaike information criterion adjusted for small sample size (AICc), considering that models with differences in AICc values of two or less ($\Delta\text{AICc} < 2$) have a similar level of empirical support. We considered only the best set of models competitive for inference and reported them in the results.

We ran separate regression models to assess how variations in fruit consumption and fruit-eating bird abundance respectively responded to fruit abundance at the landscape scale. We used Moran's I correlograms (Rangel *et al.* 2010) to evaluate the occurrence of spatial patterns in the dependent variables and in the residuals from fruit–bird simple regression models. We constructed correlograms such that the first interval included most distances between nearest neighbors and intervals had equal numbers of pairs of sites ($N = 102$ comparisons), resulting in five distance increments (centered in 1.5, 4.4, 7.0, 10.3, and 16.8 km). In the absence of spatial autocorrelation, we conducted simple regressions; when model residuals were spatially autocorrelated, we conducted spatial autoregressive models (SAR), which fit a variance–covariance matrix based on the spatial observations. For the ANOVA and regression models, we $\log_{10}(1 + x)$ transformed variables before the analysis. We checked regression residuals for the fulfillment of assumptions of normality and homogeneity of variance prior to model acceptance.

We used Spatial Analysis by Distance Indices (SADIE, Perry & Dixon 2002) to assess the local spatial covariation between fruit abundance and fruit consumption, and between fruit and fruit-eating bird abundances. We compared the quantity of records by cell of each dataset in a site. As SADIE was developed to analyze spatially referenced counts, we rounded data of dry pulp mass (originally fruit counts) to the nearest integer value. The SADIE system estimates an 'overall association' index X based on the correlation between cluster indices of two datasets, equivalent to a simple correlation coefficient (Winder *et al.* 2001). A positive value of X indicates that the two datasets are associated, with patches coinciding spatially (a negative value indicates spatial dissociation, interpreted as evidence of segregation); thus, we assume that a greater positive value of X indicates greater coupling between datasets. The significance of X was tested with a randomization test that included a Dutilleul adjustment for spatial autocorrelation (Perry & Dixon 2002). According to our hypothesis of spatial match, we used one-tailed significance to test predictions of association. SADIE also allows calculation of a measure of 'local association' χ for each sample unit (*i.e.*, cell). We used χ to identify cells with large measures of local association, defined as those falling outside the 95% critical interval (Perry & Dixon 2002), and to create contour maps of the local spatial association between fruit and bird variables.

RESULTS

FRUIT ASSEMBLAGES.—We found 11–18 fleshy-fruited species per site (mean \pm SD = 14.18 ± 2.18 ; Table S1) out of 37 recorded at all sites (Table S2). Fruit composition (Appendix S1) and abundance varied among sites (ANOVA; $F_{10,319} = 12.71$, $P < 0.001$). Sites explained 28.5 percent of the variation in fruit abundance; the large residual variation indicates relatively high local variation.

The intra-site coefficient of variation in fruit abundance fit a quadratic regression with total fruit abundance per site ($R^2 = 0.72$, $df = 8$, $P = 0.006$). This local heterogeneity in fruit abundance diminished with the increase in the overall fruit abun-

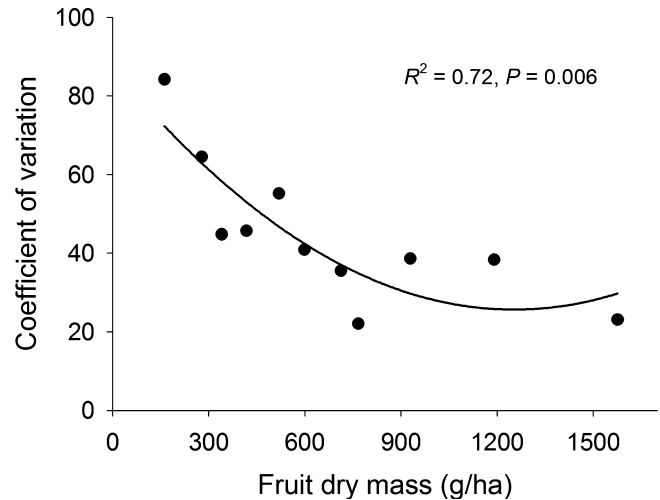


FIGURE 1. Relationship between the coefficient of variation in $\log_{10}(1 + x)$ fruit abundance recorded in 30 grid cells of 400 m² and total fruit abundance recorded at the site in 11 forest sites sampled in San Javier-Yerba Huasi mountain range.

dance in the site (Fig. 1), indicating a more patchy fruit distribution in less productive sites. Local variation in fruit abundance (CV median = 40.9, interquartile range = 35.5–55.2, $N = 11$ sites) was greater than at the landscape scale (CV = 26.9%, $N = 1$ landscape).

FRUIT CONSUMPTION.—Fruit-eating birds consumed 22 of the 37 fruit species recorded. Non-consumed fruit species were infrequent (with fruits being present in 1–3 sites, except *Piper hieronymi*, which was present in 6), with low regional abundance (<3 g/ha pulp dry mass), except for three species, which were abundant, but primarily dispersed by mammals: *P. hieronymi* (42.3 g/ha), *Solanum betaceum* (18.4 g/ha), and *S. trichoneuron* (11.7 g/ha). These three species, plus *P. tucumanum*, *P. carthagenensis*, and *Morus alba*, were consumed at rates well below those expected in relation to their abundance (Fig. 2).

Consumed fruit species were recorded in 1–11 sites (mean \pm SD = 5.77 ± 3.22). Fruit productivity of particular species varied among sites (median = 6.45 g/ha, range = 0.48–134.7 g/ha). Some fruit species that were consumed well above the expected values (*i.e.*, 'selected' species) were abundant (*Allophylus edulis*, *Cinnamomum porphyrium*) and others had more scarce relative fruit abundances (4.1–1.2%; *P. falcifrons*, *R. floccosa*, *Mysine coriacea*, *Cissus striata*, *Xylosma pubescens*, and *Cupania vernalis*) (Fig. 2).

FRUIT-EATING BIRD ASSEMBLAGES.—Assemblages of fruit-eating birds were similar in species richness, but variable in composition and in the relative importance of the major fruit consumers. We recorded 5–8 bird species consuming fruits per site (mean \pm SD = 6.64 ± 1.12) out of 17 recorded at all sites (Table 1). Six bird species were recorded in more than half of the sites (*Turdus rufiventris* and *Chlorospingus ophthalmicus* in 11;

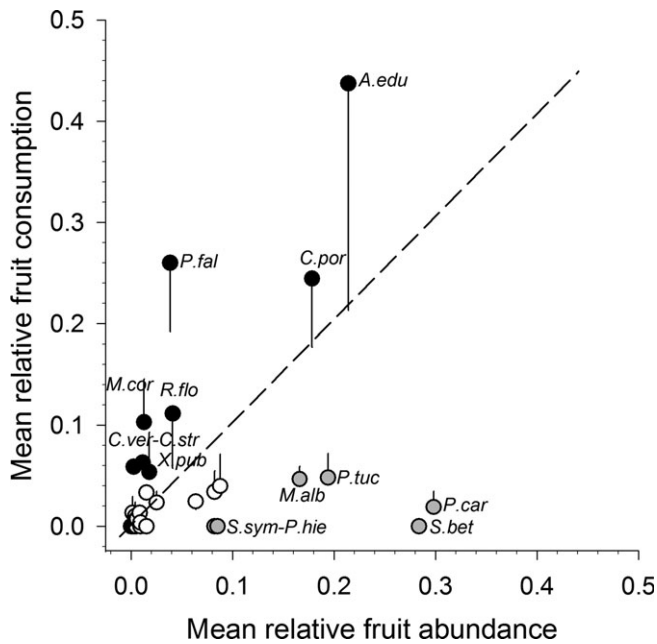


FIGURE 2. Scatterplot showing the relationship between fruit consumption by birds and fruit abundance of fleshy-fruited species in late spring in forests of the San Javier-Yerba Huasi mountain range. Relative values of fruit consumption and fruit abundance per species were estimated with respect to the total values recorded per site. Circles show mean values and vertical bars indicate standard deviation for species consumed in more than one site; sites without records of ripe fruits were not considered when estimating relative values. Black and gray circles highlight fruit species consumed at rates well above or below expected given their abundance, respectively; the remaining species in white circles. Abbreviations: *A.edu* *Allophylus edulis*, *C.por* *Cinnamomum porphyrium*, *C.str* *Cissus striata*, *C.ver* *Cupania vernalis*, *M.alb* *Morus alba*, *M.cqr* *Myrsine coriacea*, *P.car* *Psychotria carthagenensis*, *P.fal* *Phoradendron falcifrons*, *P.hie* *Piper hieronimi*, *P.tuc* *Piper tucumanum*, *R.flo* *Rhipsalis floccosa*, *S.bet* *Solanum betaceum*, *S.tri* *Solanum trichoneuron*, *X.pub* *Xylosma pubescens*.

Thraupis sayaca in 10; *Catharus ustulatus*, *Turdus nigricaps* and *Euphonia chlorotica* in 7), and together comprised 90.9 percent of all consumption events ($N = 374$; Table S1). The importance of these species as fruit consumers varied among sites (Fig. 3). The consumption of fruit species across fruit-eating birds was asymmetric; few bird species ate many fruits and many bird species consumed few fruits (Table S1). *Turdus rufiventris* and *T. sayaca* consumed 16 and 14 fruit species respectively, *C. ustulatus* 8, *T. nigricaps* 6, and the rest of the birds 4 or less. Fruits consumed by the rest of the fruit-eating birds were a subset of the fruit species consumed by the six main frugivores (Table S1).

FRUIT-FRUGIVORE SPATIAL MATCH.—Fruit consumption at the landscape scale was not related to total fruit abundance (simple regression model: $R^2 = 0.01$, $N = 11$, $b = 0.04$, $P = 0.72$) nor to the abundance of selected fruit species (simple regression model: $R^2 = 0.16$, $N = 11$, $b = 0.07$, $P = 0.22$). Moran's I correlograms revealed a positive spatial autocorrelation in bird abundances on

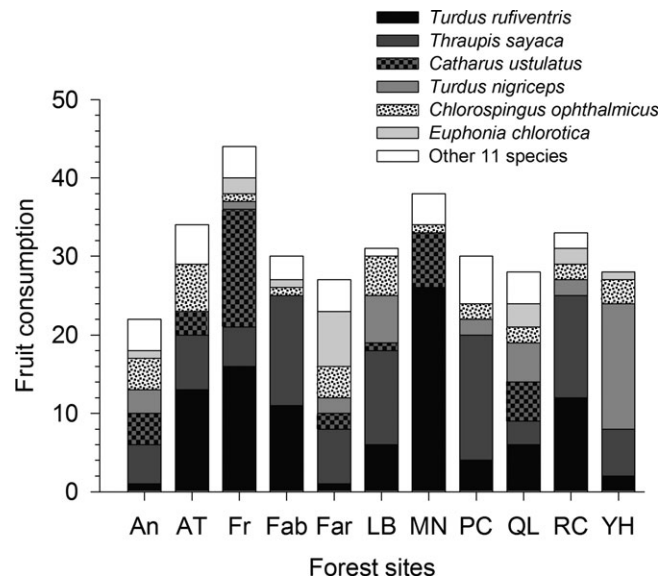


FIGURE 3. Number of fruit consumption events by fruit-eating birds recorded in 11 forest sites in the San Javier-Yerba Huasi mountain range. Site acronyms are the same as in Table 1.

a scale of <5 km and negative autocorrelation at 10–12 km between sites, justifying the use of SAR models. We did not find support for the expected positive association between fruit-eating bird abundance and total fruit abundance (SAR model: $R^2 = 0.07$, $N = 11$, $b = -0.15$, $P = 0.29$) or the abundance of selected fruit species (SAR model: $R^2 = 0.41$, $N = 11$, $b = -0.23$, $P = 0.03$).

Local spatial analysis showed clear overall association (X indices) between the abundance of selected fruits and fruit consumption in nine of 11 sites (Table 2). The strength of the overall association between fruit and fruit-eating bird abundances was variable across sites, with a strong significant relationship in one site ($P < 0.01$) and moderately significant relationships in four ($P < 0.05$) (Table 2). Overall, there were few (1–3) small patches showing large values of local association between fruit and bird variables in the 1.2-ha plots (Fig. 4; Fig. S2). While fruits selected by birds were recorded in almost all (96%) 400-m² cells, large local association values (χ) mostly occurred in cells of greater selected fruit abundance (Fig. 5A and B). Such association weakened in most cases when total fruit abundance was considered, as was found by conducting similar analyses (not reported) exploring the relationships of bird abundances and fruit consumption with total fruit abundances.

DISCUSSION

The spatial match between bird and fruit abundances is a straightforward prediction of the seed dispersal mutualism, an understanding of which requires the consideration of multiple spatial scales (Burns 2004, García *et al.* 2011). In the Southern Yungas forests, fruit consumption by birds was strongly associated with

TABLE 2. *Spatial covariation between the abundance of selected fruit species and the number of fruit consumption events, or the abundance of fruit-eating birds recorded in 30 cells of 0.04 ha.*

Sites	Fruit consumption		Bird abundance	
	X	<i>P</i> adjusted	X	<i>P</i> adjusted
Antayacu (An)	0.5666	0.004	−0.1429	0.76
Arroyo Tañi (AT)	0.5011	0.015	0.4037	0.030
Frontino (Fr)	0.4414	0.025	0.3499	0.041
Funicular abajo (FAB)	0.4625	0.011	0.4610	0.012
Funicular arriba (FAR)	0.5014	0.010	0.3146	0.042
Loma Bola (LB)	0.5734	0.006	0.5279	0.003
Mundo Nuevo (MN)	0.5219	0.004	0.2978	0.07
Puerta del Cielo (PC)	−0.0893	0.63	0.1218	0.21
Quebrada de Lules (QL)	0.6942	0.005	0.2997	0.09
Río Las Cañas (RC)	−0.1654	0.77	−0.2110	0.85
Yerba Huasi (YH)	0.5413	0.017	0.2769	0.09

X: overall association index; to provide *P*-values a Dutilleul adjustment procedure was included to randomization tests.

the abundance of selected fruit species at the local scale, but spatial changes in bird activity (*i.e.*, fruit consumption and frugivore abundance) were not related to variations in fruit abundance at the landscape level. Although fruit and fruit-eating bird assemblages were variable in composition and abundance at the landscape scale, spatial variation in fruit abundance was greater locally. Frugivores selected several fruit species, including some with relatively high local fruit abundance. At the local scale, the strongest associations between fruit abundance and fruit consumption occurred in small patches of great abundance of selected fruits. Together, these results indicate that fruit-eating birds did not track fruit abundance in the landscape during the breeding season, but chose to feed in small patches of high abundance of selected fruit species. Our results provide insight into the mechanisms that determine the scale dependence of mutualistic relationships between fruiting plants and frugivores. Fruit tracking at large spatial scales may involve mainly non-breeding birds, while small-scale fruit–bird adjustments, regulated by reproductive activity, might reflect the information breeding birds have regarding the location of fruit resources within their home ranges.

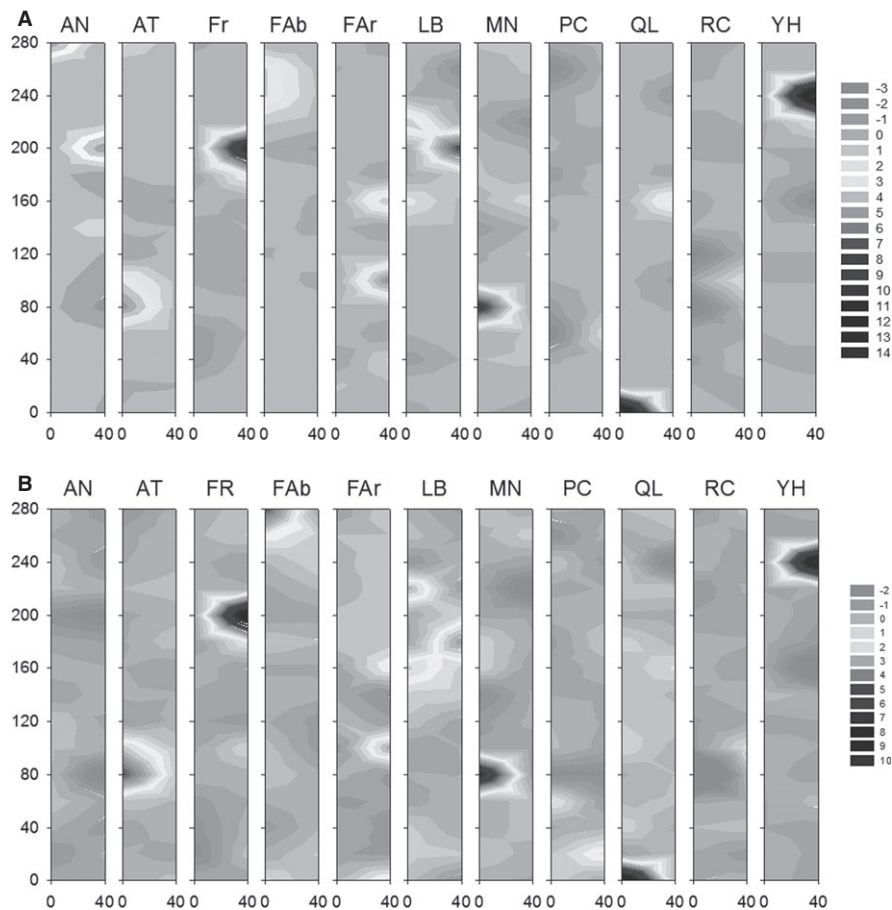


FIGURE 4. Contour maps of the local spatial association between the abundance of fruit species selected by birds and (A) the consumption of fruits by birds and (B) the abundance of fruit-eating birds in 1.2-ha plots split in grids of 30 cells of 20 × 20 m each. Maps are based in the 'local association' measure (χ) for each cell available in SADIE (Perry & Dixon 2002). Large positive values indicate areas of strong spatial association. Sampling site acronyms as in Table 1.

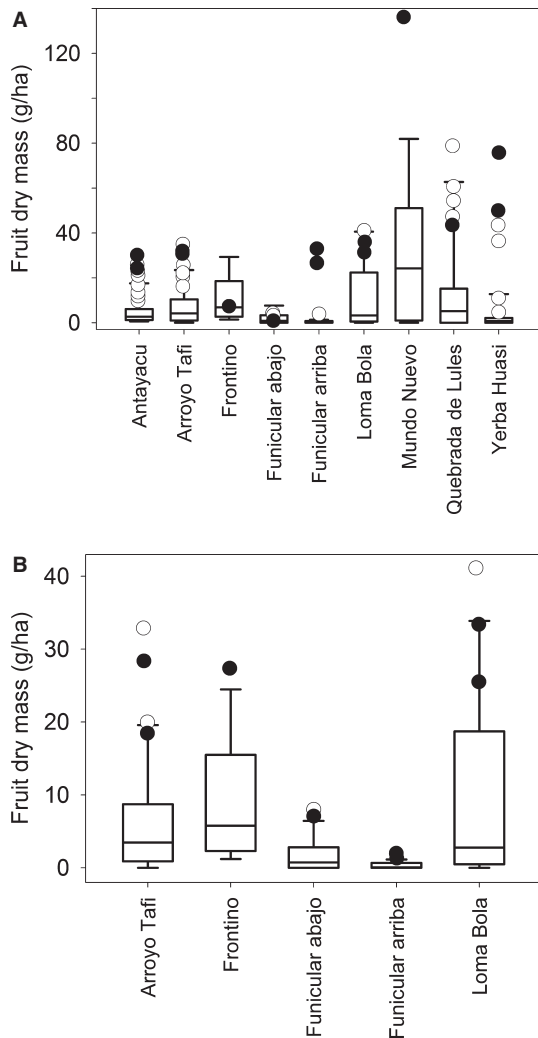


FIGURE 5. Boxplots describing the abundance of fruit species selected by birds in 30 cells of 20×20 m at several forest sites sampled in San Javier-Yerba Huasi mountain range. Black circles show cells with large values of 'local association' (χ^2) between fruit abundance and (A) fruit consumption in sites ($N = 9$ of 11) with significant 'overall association' (X indices) between fruit abundance and consumption, (B) fruit-eating bird abundance in sites ($N = 5$ of 11) with significant overall association (X indices) between fruit and bird abundances. Cells with large measures of local association (χ^2) were defined as those falling outside the 95% critical interval in their randomized distributions of local association values.

Experimental and observational studies support matching patterns in bird and fruit abundances (e.g., Loiselle & Blake 1991, Burns 2003, Moegenburg & Levey 2003, Borgmann *et al.* 2004, Blending *et al.* 2012). The high mobility of birds allows them to track fruits over large land tracts, such as landscapes or regions, but the establishment of territories and the care of the offspring must confine frugivore movements to areas close to the nest (Lenz *et al.* 2015). Most studies reporting bird–fruit adjustments at large spatial scales assessed non-breeding temperate birds, either during migration (Mudrzyński & Norment

2013, Wolfe *et al.* 2014) or in wintering grounds (e.g., Rey 1995, Tellería & Pérez-Tris 2003, García & Ortiz-Pulido 2004, Kwit *et al.* 2004, Guitián & Munilla 2008, García *et al.* 2011, Tellería *et al.* 2014). When the spatial match in fruit–bird abundances was evaluated at the local and landscape scales, most cases cited above found stronger adjustments at larger spatial extents (but see Rey 1995), interpreted as a mechanism of spatial escape from fruit scarcity. These temperate wintering birds are characterized by strong vagility, a tendency to aggregate in flocks, and a highly fruit-based diet, all of which would promote fruit tracking throughout the landscape (García *et al.* 2011).

Unlike previous studies, we found that fruit availability was an important factor affecting the spatial patterns of breeding fruit-eating birds at the local scale but not at the landscape scale. The discordance among local and landscape scales allows scale-specific patterns to link to processes occurring at the same scale (Perry & Dixon 2002). García and Ortiz-Pulido (2004) proposed that the context in which fruit availability is presented across patches and the spatial distribution of fruit patches could determine local or landscape responses in bird activity. In their study site in central eastern Mexico, a larger contrast in fruit abundance at the local scale than at the landscape scale was explained by birds searching for individual *Bursera fagaroides* plants with a large crop size and not for fruit-rich sites. Greater variation in fruit availability at the local than at the landscape scale could prevent birds from perceiving landscape heterogeneity as an option to overcome local fruit shortage. However, we consider this unlikely in our study system, as local fruit assemblages differed significantly in composition and abundance despite their small differences in total fruit availability. Processes underpinning adaptive fruit tracking could be found in behavioral and ecological responses to fruit heterogeneity, which may in turn be affected by scale-dependent factors other than the distribution of food resources (García & Ortiz-Pulido 2004, Lehouk *et al.* 2009). Our study suggests that in markedly seasonal environments, where birds have a distinct breeding season, nesting activities prevent birds from compensating for reductions in food availability using tracking behavior.

Changes in fruit–frugivore abundances did not match at the landscape level, though resource abundance is a major driver of bird choice for breeding territories (Martin 1987, Wiens 1989). Nonetheless, the fruits available during the establishment of territories in the Southern Yungas are not reliable indicators of fruits available later, when birds are raising nestlings. In the lower montane forest, resident populations of fruit-eating birds establish breeding territories early in the spring and most species start laying eggs after mid-October (Auer *et al.* 2007, Lomáscolo *et al.* 2010), 1–2 mo before our field sampling was conducted. Breeding season coincides with a period of high abundance and maximum diversity of ripe fruits in these sites (Blending *et al.* 2015, E. Martín *et al.*, unpubl. data). However, the local availability of ripe fruits changes rapidly: in a previous study, Blending *et al.* (2012) found an absence of temporal autocorrelation in fruit availability over 2-mo periods, meaning that the abundance of

fruits available at any one site does not predict its abundance 2 mo later. Therefore, the distribution of the abundance of fruit-eating birds in the landscape may depend upon factors unrelated to fruit availability during the breeding season. Besides their breeding behavior, interactions with other birds, predation risk, and density dependent processes of habitat occupation also affect the spatial distribution of bird abundances (Kennedy & Gray 1993, Tellería *et al.* 2014). Moreover, if fruit availability does not limit frugivore density, fruit tracking becomes unnecessary; the absence of fruit tracking at the landscape scale may result from an oversupply of fruits (but see Hampe 2008), when birds would be reluctant to move to other sites given the additional costs of moving, such as risk of predation, competitive interactions, and uncertainty in the energy intake at these new sites. Most limitations outlined above are aligned with arguments invoked to explain imperfect spatial matches predicted by the ideal free distribution model (*e.g.*, Kennedy & Gray 1993, Shochat *et al.* 2002, Matsumura *et al.* 2010), which proposes that organisms distribute themselves across habitats according to the distribution of resources (Fretwell & Lucas 1970). Our study does not support this density dependent selection of resource patches, although it must be interpreted with caution as we did not measure bird density. Particularly, our study suggests that organism distribution among habitats/resource patches is not free, as breeding fruit-eating birds cannot move without restriction from one patch to another.

Unlike the ideal free distribution model, Blendinger *et al.* (2012) showed that both bird abundance and fruit consumption must covary with fruit availability to be considered a consequence of fruit tracking. Even in the absence of fruit tracking, the frequency of fruit consumption may match changes in the availability of fruits, regardless of change in the abundance of fruit-eating birds. For example, species showing no significant food abundance relationships could switch between resource types, consuming mostly fruits when they are abundant and other resources, such as arthropods, when fruits are scarce (Carnicer *et al.* 2008, Blendinger *et al.* 2015). At a local spatial scale, birds can display spatial feeding patterns linked to variation in food availability without changing their abundance. This is the case for birds taking foraging trips but consistently returning to a focal location, such as nests and lek sites (Ryder *et al.* 2006, Lenz *et al.* 2015). The concentration of feeding activity at resource-rich places within the home range of breeding birds would favor a reduction in costs associated with distance, as predicted by the theory of central-place foraging (Orians & Pearson 1979, Stanton *et al.* 2014). Our results reveal such a process in the fruit-seed disperser system of the Southern Yungas forests, where the spatial arrangement of fruit availability affected the birds' foraging activity in local fruit-eating assemblages. Fruit consumption peaked in small, fruit-rich patches, which represent reliable places to find food. Notably, these birds selected certain fruit species with large crop sizes (*e.g.*, *A. edulis*, *C. porphyrium*) or which were densely clustered (*e.g.*, *R. floccosa*, *P. falcifrons*). Furthermore, as attractors of fruit-eating birds, small patches of selected fruit species may be seed dispersal foci, driving the contagious deposition of

heterospecific seeds below them, resulting in bird-made fruit orchards (Clark *et al.* 2004, Lázaro *et al.* 2005, Blendinger *et al.* 2011).

Although the spatial foraging patterns of frugivores fit the local distribution of fruits, much of the spatial variation in patterns of consumption could not be explained by fruit availability. Part of this unexplained variation may be due to intrinsic attributes, either of frugivores, such as morphological constraints and nutritional ecology, or their fruit resources, such as nutritional compounds and secondary metabolites (Witmer & Van Soest 1998, Levey & Martínez del Río 2001, Saldaña-Vázquez 2014). We already know that different species in the fruit-eating assemblages of the Southern Yungas forests differ in their criteria for fruit selection and in response to the availability and composition of fruit species (Blendinger & Villegas 2011; E. Martín *et al.*, unpubl. data), which can obscure community-level responses. The value of selected fruit species is also expected to change with their spatial arrangement relative to the nest. One intriguing question is how fruit aggregation and distance to the nest are combined to determine foraging decisions and fruit selection during the breeding season.

CONCLUSIONS

Fruit-eating birds were able to detect local spatial variation in fruit availability and exploited places within their home ranges with large clusters of selected fruit species. Frugivores did not modify their spatial distribution in the landscape in accordance with changes in fruit availability during the breeding season. The absence of fruit tracking at the landscape level may be determined by the inability of breeding birds to respond to deep short-term changes that characterize the abundance of local fruit assemblages. Because breeding birds must repeatedly return to the nest after each foraging bout, the value of sites with high fruit availability should decrease as distance increases from this central place, owing to the added costs to reach fruits at these greater distances (Kacelnik 1984). Tracking and exploiting fruit-rich patches would no longer be profitable when they are located too far from the nest, which could explain why many studies found effective fruit tracking at the landscape scale in non-breeding birds (*e.g.*, Rey 1995, Kwit *et al.* 2004, Guitián & Munilla 2008, García *et al.* 2011), but the absence of it among breeding birds, as found in this study.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

APPENDIX S1. Composition of fruit assemblages.

TABLE S1. *Events of fruit consumption by fruit-eating birds recorded in 11 sampling sites.*

TABLE S2. *List of plant species with ripe fleshy fruits recorded during the study period.*

FIGURE S1. Map of the study area showing the location of 11 sampling sites in the San Javier-Yerba Huasi mountain range in Tucumán province, Argentina.

FIGURE S2. Color contour maps of the local spatial association between bird abundance and fruit consumption with the abundance of fruit species selected by birds.

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