

## Fine-tuning the fruit-tracking hypothesis: spatiotemporal links between fruit availability and fruit consumption by birds in Andean mountain forests

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### Summary

1. The fruit-tracking hypothesis predicts spatiotemporal links between changes in the abundance of fruit-eating birds and the abundance of their fleshy-fruit resources.
2. While the spatial scale of plant–frugivore interactions has been explored to understand mismatches between observed and expected fruit–frugivore patterns, methodological issues such as the consequences of measuring fruit and frugivore abundance rather than fruit availability and fruit consumption have not been evaluated.
3. Here, we explored whether predicted fruit–frugivore spatiotemporal links can be captured with higher accuracy by proximate measurements of interaction strength. We used a 6-ha grided plot in an Andean subtropical forest to study the link between (i) fruit and fruit-eating bird abundances; (ii) fruit availability and frequency of fruit consumption; and (iii) covariation between frugivore abundance and frequency of frugivory. We evaluated these links for the entire frugivore assemblage and for the four most important species using data gathered bimonthly along a 2-year period.
4. Fleshy-fruit availability and abundance varied sharply temporally and were patchily distributed in mosaics that differed in fruit quantity. Fruit availability and abundance also varied along spatial gradients extended over the whole study plot. We found a strong response of the entire frugivorous bird assemblage to fruit availability over time, and a weakly significant relationship over space at the local scale. The main frugivore species widely differed in their responses to changes in fruit abundance in such a way that response at the assemblage level cannot be seen as the sum of individual responses of each species. Our results suggest that fruit tracking in frugivorous–insectivorous birds may be largely explained by species-specific responses to changes in the availability of fruits and alternative resources.
5. In agreement with our prediction, more accurate measurements of interaction strength described fruit–frugivore relationships better than traditional measurements. Moreover, we show that covariation between frugivore abundance, frequency of fruit consumption and fruit availability must be included in the fruit-tracking hypothesis framework to demonstrate (or reject) spatiotemporal fruit tracking. We propose that estimation of nutrient and energy availability in fruits could be a new frontier to understanding the forces driving foraging decisions that lead to fruit tracking.

**Key-words:** frugivore assemblage, fruit tracking, fruit-eating birds, resource tracking, seed dispersers, Southern Yungas forest

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## Introduction

Mutualistic interactions between fleshy-fruited plants and their seed dispersers involve up to 90% of woody plant species of tropical and subtropical forests and a large proportion of fruit-eating birds (Fleming, Breitwisch & Whitesides 1987; Kissling, Böhning-Gaese & Jetz 2009). These interactions play an essential role in the maintenance of biodiversity; the multiple mechanisms through which seed dispersal is realized are of particular interest given their influence on the success and structure of these mutualistic interactions and their conservation

(Bascompte, Jordano & Olesen 2006; Kiers *et al.* 2010). One such mechanism is the ability of fruit-eating bird species to track fruit production that varies both spatially and temporally, which in turn should lead to increased seed dispersal and spatial positive feedbacks in plant recruitment (Lázaro, Mark & Olesen 2005; Blendinger, Blake & Loiselle 2011). The fruit-tracking hypothesis predicts that changes in the abundance of fruit-eating birds are linked to changes in the abundance of fruit resources in time and space (Rey 1995; Burns 2004). Ideally, frugivores track fruits to increase their food intake, selecting on a hierarchy of spatial and temporal scales on the basis of fruit quantity and quality (Rey 1995; Mayor *et al.* 2009; Vergara *et al.* 2010). Several studies, both experimental (Rey 1995; Moegenburg & Levey 2003; Borgmann *et al.* 2004) and correlational (e.g. Levey 1988; Loiselle & Blake 1991; García & Ortiz-Pulido 2004; Saracco, Collazo & Groom 2004; Crampton *et al.* 2011), have shown spatiotemporal changes in the local abundance of fruit-eating bird species linked to changes in the abundance of fleshy fruits. The match between fruit and frugivore abundances has been recorded across different spatial scales, from within home-range locations reflecting small-scale variation in food availability (Brown & Sherry 2008) to the regional scale in relation to migratory behaviour (Izhaki & Safriel 1985; Loiselle & Blake 1991; Tellería & Pérez-Tris 2003). Also, temporal links between changes in fleshy-fruit abundance and number of frugivores have been recorded from biweekly to annual periods (Rey 1995; Tellería, Ramirez & Pérez-Tris 2008).

Other studies have found partial or no evidence of correlated bird–fruit abundance patterns (e.g. Herrera 1998; Malizia 2001; Guitián & Munilla 2008). Studies in which support for the fruit-tracking hypothesis was lacking have suggested mismatches because of either (i) independence of the processes regulating the populations of fruits and birds, which in turn act at different spatial scales (e.g. Herrera 1998); or (ii) behavioural constraints on the side of birds and their social life which may have prevented the expected link, such as those determined by agonistic interactions between territorial birds or by incomplete knowledge of the spatial distribution of fruits (Shochat *et al.* 2002; Brown & Long 2006). The failure to detect a pattern could also be a consequence of varying species-specific responses to changes in the abundance of fruits (Borgmann *et al.* 2004; Tellería, Ramirez &

Pérez-Tris 2008). For example, there could be interspecific differences in the preference for subsets of the fruit pool or for alternative food that becomes important when fruits are scarce (e.g. arthropods vs. seeds). Besides, the spatial scale at which frugivores perceive and exploit fruit abundance has received particular attention in regard to inconsistencies between the observed and expected fruit–frugivore patterns (Burns 2004; García & Ortiz-Pulido 2004; García, Zamora & Amico 2011), and consequences of the metric and the methodology used to quantify fruit and frugivore abundances have been much less investigated. In particular, food abundance does not necessarily correspond with food availability for foraging birds (Wiens 1989): the latter takes into account the constraints (of the bird, of the fruit, and from the environment) imposed on the task of obtaining fruits. While fruit abundance was measured with a great diversity of techniques (e.g. by extrapolation from pictures, Vergara *et al.* 2010), most studies did not actually assess fruit availability, that is, the abundance of fruit species actually consumed (e.g. Kinnaird, O'Brien & Suryadi 1996; Herrera 1998; Malizia 2001; Saracco, Collazo & Groom 2004), probably because food availability is very difficult to measure (Wiens 1989). Similarly, most studies have estimated frugivore abundance rather than fruit consumption, which is a more proper measurement to test hypotheses on interactions between fruit-eating birds and fruits.

To test the fruit-tracking hypothesis, we analysed the spatiotemporal fruit–frugivore link at the local scale in a subtropical Andean mountain forest, focusing on two ecological levels of fruit-eating birds: (i) for the entire frugivore assemblage and (ii) for the chief seed dispersers. Very little is known on how fruit-tracking patterns move up and down from community to species and *vice versa* (García & Ortiz-Pulido 2004; Tellería, Ramirez & Pérez-Tris 2008). Assembly-wide responses could be the consequence of diffuse co-evolutionary interactions between groups of plants and birds (Burns 2002); still, fluctuations in total fruit resources may not explain changes in the abundance of each coexisting population of fruit-eating bird (Kinnaird, O'Brien & Suryadi 1996). Here, we used two different measurements of interaction strength to test the fruit–frugivore link at both the assembly and species levels. Specifically, we pursued three goals: determining the relationship between (i) abundance of ornithochorous fruits and abundance of fruit-eating birds; (ii) fruit availability and frequency of fruit consumption; and finally (iii) comparing the spatial and temporal covariation between the abundance of fruit-eating birds, the frequency of frugivory and the availability of fruits. Assembly-wide responses may mirror the temporal or spatial fingerprint generated by a few numerically dominant species (Tellería, Ramirez & Pérez-Tris 2008), even more so if highly fruit-based diets promote spatial matching between fruits and birds (García, Zamora & Amico 2011). Thus, we discussed the results considering whether fruit tracking was stronger in more frugivorous species, and

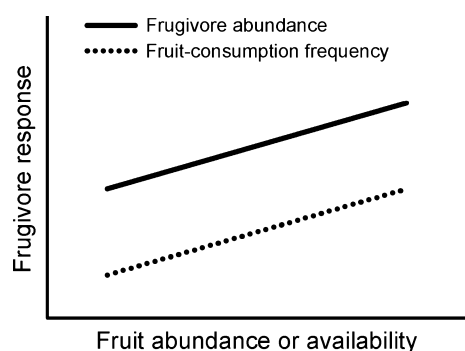
whether single species affects fruit-tracking patterns of the whole frugivore assemblage.

Measurements of abundance were widely used to explore the spatiotemporal links between fruits and frugivores (Loiselle & Blake 1991; Herrera 1998; Malizia 2001; Burns 2002; Kwit *et al.* 2004; Haugaasen & Peres 2007; Guitián & Munilla 2008). Correlations of bird abundance with the abundance of the entire assemblage of fruits or with the abundance of a single fruit species could be too simplistic to detect covariation, so the complexity of food preferences must be included in the analysis to understand the link of frugivores with fruit production (Levey & Benkman 1999). Fruit availability and the frequency of fruit consumption are more accurate measurements of the interaction strength than are the abundance of interacting partners. To our knowledge, these measurements have not yet been considered together in the context of testing the fruit-tracking hypothesis. Our expectation was that the spatial and temporal links predicted by the fruit-tracking hypothesis would be captured with higher accuracy by proximate measurements of the interaction strength, such as fruit availability and frequency of fruit consumption. However, change neither in frugivore abundance nor in frugivory frequency affords enough evidence of fruit tracking by themselves, given that both may change because of causes unrelated to fruit variability. Thus, evidence of covariation between frugivore abundance and frequency of frugivory linked to fruit abundance or availability (Fig. 1) should contribute to our understanding of the factors that determine whether and why fruit tracking is only expressed at particular times.

## Materials and methods

### STUDY SITE AND ARRANGEMENT OF SAMPLING UNITS

We conducted this study in Parque Sierra de San Javier, Tucumán province, NW Argentina. This is a 14 000-ha protected



**Fig. 1.** Expected covariation between frugivore abundance, frequency of fruit consumption and fruit abundance or availability within the fruit-tracking hypothesis framework. Covariation is illustrated by a parallelism of the functions of each response variable to the fruit abundance or availability (the absence of covariation between response variables shown in the lack of parallelism indicates changes in frugivores not related to fruit tracking).

area with subtropical Andean mountain forests known as the Southern Yungas. Climate is subtropical with dry winters (May to September) and wet summers (November to March; Hunzinger 1997). Average annual rainfall varies between 1300 and 1500 mm across the mountain range, and average annual temperature is 18 °C (Hunzinger 1997). The natural regime of disturbance includes tree fall gaps and landslides allowing secondary vegetation growth inside the forest (Grau 2002). The study site (27°30' S, 65°40' W, 970 m asl) belongs to the elevational belt of vegetation known as 'Selva Montana' or lower montane forest and is located on the upper part of a slope with SE exposure in mature forest. This site was altered by very selective logging until 50 years ago. Vegetation features emergent trees 25–30 m in height of *Cinnamomum porphyrium* (Lauraceae) and *Blepharocalyx salicifolius* (Myrtaceae); an upper canopy layer composed mainly of *Parapiptadenia excelsa* (Fabaceae), *Myrcianthes pungens* (Myrtaceae), *Pisonia zapallo* (Nyctaginaceae) and *Terminalia triflora* (Combretaceae); a lower canopy dominated by 5- to 12-m-height small trees of *Piper tucumanum* (Piperaceae), *Eugenia uniflora* (Myrtaceae), *Allophylus edulis* (Sapindaceae) and *Solanum riparium* (Solanaceae); and a dense understory dominated by the shrub *Psychotria carthagenensis* (Rubiaceae) (Blendinger & Villegas 2011). Typical vines and epiphytes include *Cissus striata* (Vitaceae), *Celtis iguanaea* (Cannabaceae), *Aechmea distichantha* (Bromeliaceae) and *Rhipsalis floccosa* (Cactaceae). Field work was carried out in a permanent 200 × 300 m plot, split in a grid of 150 cells of 20 × 20 m each; individual cells were the sampling units for all counts of both fruits and frugivores. A (x, y) coordinate system was set such that each cell in the grid was assigned a position with respect to a corner of the grid with arbitrary coordinates (1, 1).

### BIRD COUNTS

We sampled fruit-eating birds bimonthly from September 2008 to August 2010, totalling 12 sampling periods with each sampling conducted during the last week of the month. Bird counts began at sunrise and were completed within 4 h. On a sampling day, each one of five observers traversed a block of 10 × 2 contiguous cells, walking slowly and recording all fruit-eating birds and their fruit-consuming behaviours during 20 min per cell. The same sampling protocol was repeated for 3 days, starting on different cells to switch the sampling times of each sector within the block. In this way, each cell had two 20-min samples on different days and hours. The assignment of observers to the cell blocks was randomized, with the restriction that observers must rotate during successive sampling periods. Each block was assigned at least one sampling period to each observer.

In each cell, we recorded all fruit-eating birds seen or heard during a 20-min period, which gave us a comparative measure of cell use intensity (not an estimate of frugivore density). We also recorded each and every event of fruit consumption detected, noting the frugivore species and the fruit consumed. Following Saracco, Collazo & Groom (2004), an event of fruit consumption was defined as any visit by a fruit-eating bird to a plant in which the bird was either directly observed to eat fruit or noted entering a part of the plant with ripe fruit, remaining in there for a length of time consistent with fruit consumption. As we were interested in the ecological consequences of the interaction, consecutive visits to different individual plants by the same bird were considered as separate events; likewise, each individual of a flock consuming fruits was considered a separate event of frugivory. However, we

did not count the number of fruits consumed per bird per plant because of reduced visibility inside the forest.

All species included in the frugivore assemblage regularly consume fleshy fruits in addition to varying amounts of insects and other invertebrates (Giannini 1999; Rougès 2004; Blendinger & Giannini 2010). According to the treatment given to the fruits, frugivores can be roughly classified in 'pulp mashers' and 'fruit gulpers' (Levey 1987; Blendinger & Villegas 2011), but all of them swallow and disperse the smaller seeds (e.g. species in Cactaceae and Viscaceae). *Turdus rufiventris* (Turdidae), *Thraupis sayaca* (Thraupidae), *Chlorospingus ophthalmicus* (Emberizidae) and *Euphonia cyanocephala* (Fringillidae) accounted for most fruit consumption events (83% of all records); these species were the ones included in the analyses at the species level.

#### FRUIT COUNTS

During a sampling period, we counted the abundance of ripe fruit of all bird-dispersed plants in each of the 150 grid cells. One or two researchers walked carefully across every cell recording all plants (trees, shrubs, vines and epiphytes) with ripe fruits. The abundance of ripe fruits per plant was assigned to one of the following categories: 1–5, 6–10, 11–50, 51–100, 101–500, 501–1000 and 1001–5000 fruits. The only exception was *P. carthagenensis*, a very common shrub in the understory. To estimate fruit abundance in *P. carthagenensis*, we counted ripe fruit abundance inside of five 4-m<sup>2</sup> quadrats randomly located in each cell. The density so obtained was then extrapolated to the surface area of the cell. For canopy trees with large crown volume, we estimated ripe fruit abundance on a portion of the canopy, extrapolating this estimate to the remainder of the tree. We estimated fruit abundance of epiphytic plants by direct counting whenever possible; alternatively, we assigned these plants the average value for the species at the corresponding sampling period. Fruit ripeness of all species was determined on the basis of previous observations about the condition in which fruits are usually eaten by birds. To reduce observer bias in counting fruit and determining fruit ripeness, all observers were trained and their performance compared prior to the actual sampling. We followed the same protocol as for the bird counts in assigning observers to cells.

For all analyses, fruit abundance was expressed 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 of healthy ripe fruits. Pulp dry mass was calculated by the difference between mean fruit weight and mean weighed seeds and water content of the pulp; water content was calculated by the difference before and after heating weighed fresh pulp (to the nearest 0.1 mg) in an oven at 60 °C during 4 days (the time period that yielded constant mass in consecutive half-day measurement intervals; N. P. Giannini & P. G. Blendinger, unpublished data). For each sampling period, fruit abundance was assessed in two ways: (i) as the sum of dry mass recorded in a given period of all ornithochorous fruit species (hereafter 'fruit abundance') and (ii) as the summed dry mass estimated by sampling period of fruit species consumed by frugivores during the entire study (hereafter 'fruit availability' for the entire assemblage of frugivorous birds), or as the total dry mass by sampling period of the fruits each bird species consumed through the entire study ('fruit availability' for the species level).

#### STATISTICAL ANALYSIS

We analysed the link in time and space between the full assemblage of frugivores and between the major fruit-eating species of birds with the ripe fruit dry mass. We first considered fruit and bird abundances, and then fruit availability and frequency of fruit-eating events. At the level of assemblage, we included all species that interacted during the study (26 plants and 19 birds; Table S1, Supporting information) to analyse fruit–bird abundance relationships; in fruit availability analyses, we excluded fruits sporadically consumed by the entire assemblage of frugivores. At the species level, we considered for each analysis all fruit species consumed during the study by the focus frugivore species, except those 'sporadically consumed'. The last category was determined when the following three criteria were met: (i) it represented <5% in dry mass of the frugivorous diet of the focus species; (ii) it was part of the higher quartile of fruit abundance during the periods in which it was consumed; and (iii) it was not a preferred species in the sampling period when its consumption by the focus frugivore reached its maximum value. We defined a preference ratio simply as the proportion of consumption divided by the proportion of abundance of a given fruit; preference ratio <1 indicated non-preference.

#### TEMPORAL PATTERNS

The time series of 12 sampling periods was used in a temporal analysis. A single value per sampling period was used for each variable. For any given variable, this value was obtained by adding up all observations recorded in the 150 cells. Site fidelity, territoriality and migratory movements may cause temporal autocorrelations (bird abundance in a given sampling period might depend on its abundance in the previous sampling period). Short-term temporal autocorrelation could be more closely linked to life history and ecological attributes of birds relevant to fruit tracking than annual cycles mostly determined (directly and indirectly) by climate. Thus, seasonal patterns of frugivore abundance and frequency of fruit consumption were analysed with autocorrelations of the time series shifted by a lag of one (i.e. consecutive sampling periods taken at bimonthly intervals). Serial correlation coefficients and their standard errors were estimated at the established lag, and the significance of the coefficient difference from randomness at  $\alpha = 0.05$  was determined with the Box-Ljung  $Q$  statistic (Ljung & Box 1978). In the absence of temporal autocorrelation between successive sampling periods, we conducted ordinary least squares regressions (OLS) between fruit and bird abundances, and between fruit availability and fruit consumption. As we did not record frugivory events by *E. cyanocephala* in some consecutive sampling periods, only temporal autocorrelation in abundance was analysed. All variables were transformed using the  $(\log_{10} + 1)$  function to improve normality of residuals and alleviate potential problems caused by fitting regression lines with outliers.

#### SPATIAL PATTERNS

In the spatial analyses, we included only sampling periods with  $\geq 20$  records of frugivory, specifically nine of 12 sampling periods at the assemblage level (excluding March 2009, February 2010 and August 2010) and 1–8 periods at the species level (depending on the species). We analysed the spatial relationship between



birds and fruits at the cell scale with regression models. As this relationship could be influenced by spatial structures in resources and their consumers, we checked for spatial autocorrelation in the data. Spatial autocorrelation in the response variable (i.e. when values recorded at a given location are not independent from values at other locations in the vicinity) violates the assumption of independently and identically distributed errors in OLS models and hence inflates type I errors (Dormann *et al.* 2007). First, we used Moran's I correlograms to explore spatial autocorrelation in the ( $\log_{10} + 1$ ) transformed fruit and frugivore variables, with the 20-m side of a cell as distance class and with significance set at  $\alpha = 0.05$ . Correlograms allowed us to evaluate autocorrelation intensity, size of influence area and type of spatial pattern of the study variable. To analyse frugivore–fruit relationships in the presence of spatial autocorrelation, we used spatial autoregressive models (SAR). These models assume a response that is a function of both the explanatory variables and the response values at neighbouring locations, allowing for the correction of spatial autocorrelation effects (Lichstein *et al.* 2002; Dormann *et al.* 2007). In the absence of spatial autocorrelation, we fitted OLS models to fruit abundance and fruit availability for the frugivore assemblage and for each fruit-eating species. For all regression models, the response variable was the  $\log_{10}$ -transformed total count of each species or assemblage. Regression models were fit using the program SAM v4.0 (Rangel, Diniz-Filho & Bini 2010). Bonferroni corrections were applied for multiple tests within a single sampling period.

## Results

### TEMPORAL LINK BETWEEN FRUGIVORES AND FRUITS

Total abundance and availability of ripe fruits, frugivore abundance and frequency of fruit consumption varied in a similar fashion during the time frame captured by our data (Fig. 2; Table S2, Supporting information). Fruit consumption and frugivore abundance covaried both at the assemblage (Pearson correlation,  $r = 0.85$ ,  $P < 0.001$ ) and species level (*E. cyanocephala*:  $r = 0.77$ ,  $P = 0.01$ ; *T. sayaca*:  $r = 0.87$ ,  $P < 0.001$ ; *T. rufiventris*:  $r = 0.83$ ,  $P < 0.001$ ), except for *C. ophthalmicus* ( $r = 0.33$ ,  $P = 0.28$ ).

Neither abundance of fruit-eating birds recorded in the plot nor the frequency of fruit consumption was temporally autocorrelated at both the assemblage and species levels (Box-Ljung  $Q$  statistic,  $P > 0.05$  in all cases; Table S3, Supporting information). The abundance of frugivores in the assemblage and their frequency of fruit consumption were positively related to fruit abundance and availability, respectively, throughout the 2-year period (OLS,  $P < 0.01$ ; Fig. 3). At the species level, the links between a frugivorous species with fruit abundance were variable. The abundance of *T. sayaca* recorded in the plot was positively related to the abundance of fruits ( $P < 0.01$ ), but we did not detect a statistically significant relationship ( $P > 0.05$ ) in temporal patterns of abundances of fruit-eating species and fruits (Fig. 3). The frequency of fruit consumption in *T. sayaca* and *C. ophthalmicus* was more strongly related ( $P < 0.001$ ) to fruit availability than in *E. cyanocephala* and *T. rufiventris* ( $P < 0.05$ ; Fig. 3).

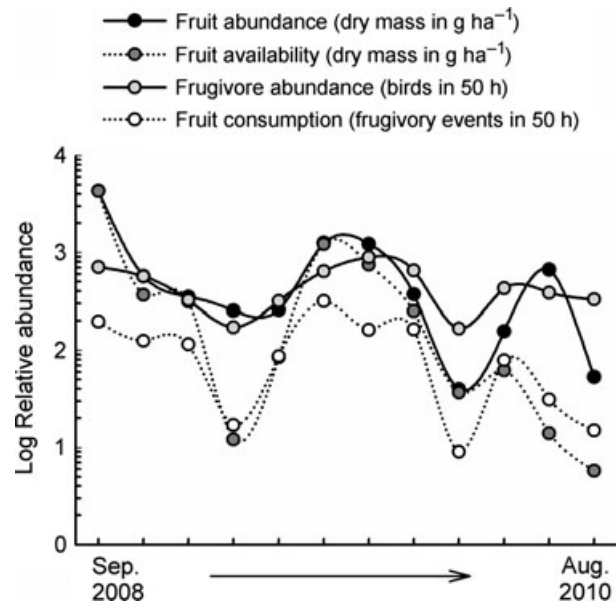


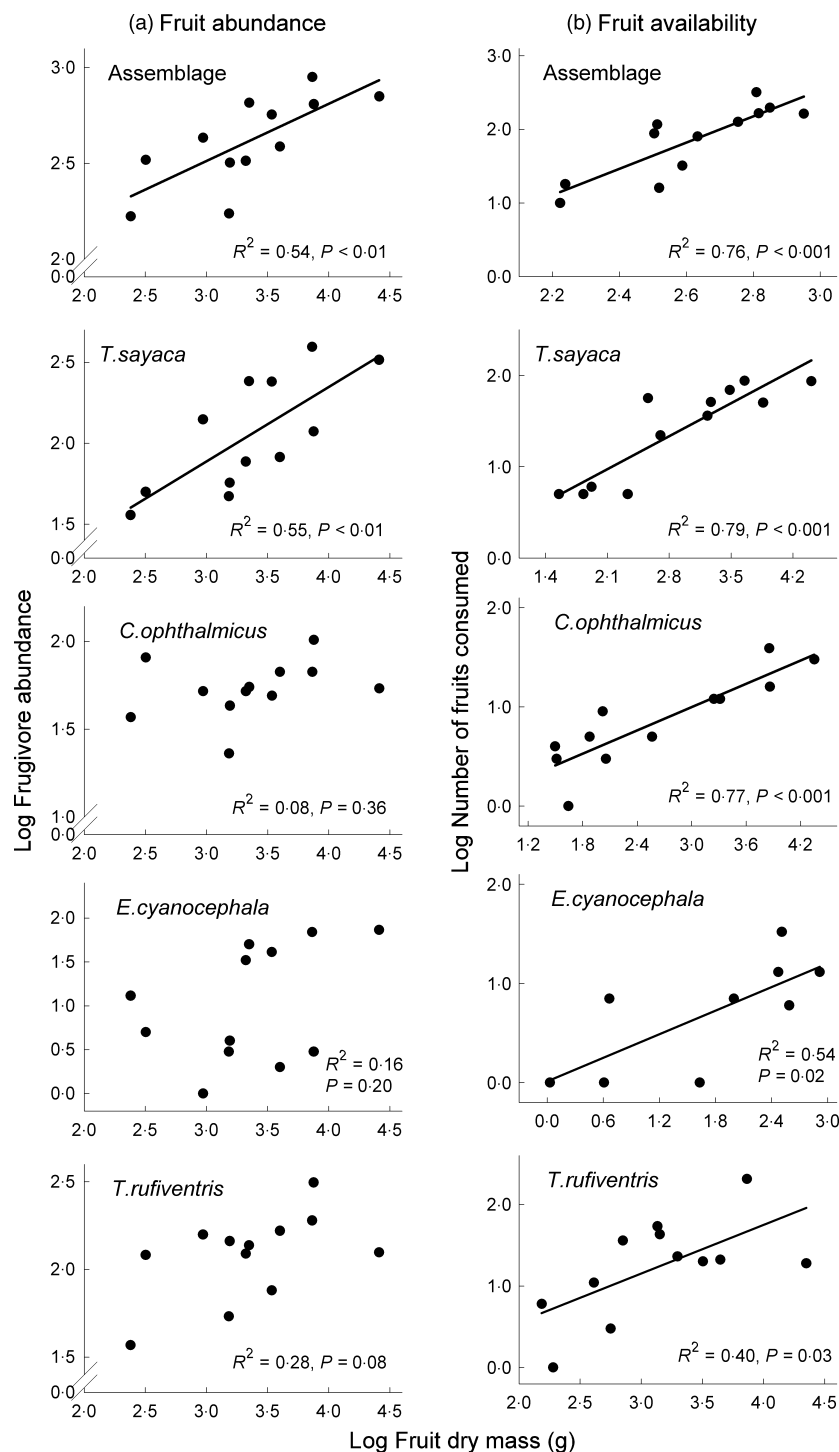
Fig. 2. Temporal variation in fruit abundance and availability, abundance of frugivores and frequency of fruit consumption recorded over a 2-year period sampled bimonthly in a 6-ha plot in an Andean mountain forest of NW Argentina.

In only three of five cases, frugivore abundance covaried with the availability of fruits (assemblage:  $R^2 = 0.54$ ,  $P < 0.01$ ; *T. sayaca*:  $R^2 = 0.61$ ,  $P < 0.01$ ; *C. ophthalmicus*:  $R^2 = 0.22$ ,  $P = 0.12$ ; *E. chlorotica*:  $R^2 = 0.78$ ,  $P < 0.001$ ; *T. rufiventris*:  $R^2 = 0.28$ ,  $P = 0.08$ ); in four of these cases, the relationship was weaker than that recorded between fruit availability and frequency of fruit consumption (Fig. 3).

### SPATIAL LINK BETWEEN FRUGIVORES AND FRUITS

#### Entire study period

The total abundance of fruit-eating birds recorded per cell along the study period varied between 12 and 58 ( $n = 4949$ ) and tended to be distributed in small patches, as displayed in the plot map (Fig. 4a). This is also suggested by a positive and significant spatial autocorrelation found at short distances (Fig. 4b). The total abundance of fruits for the assemblage showed a marked spatial structure through the gradient of distances in the plot (Fig. 4a–b). The SAR model of the relationship between fruit and frugivore abundance was not significant ( $R^2 = 0.11$ ,  $F_{1,150} = 3.15$ ,  $P = 0.08$ ; Fig. 4c) and had a lower AICc (Akaike Information Criterion corrected for sample size) value than a OLS model ( $R^2 = 0.03$ ,  $F_{1,150} = 3.88$ ,  $P = 0.05$ ). The total fruit availability for the fruit-eating assemblage also showed a strong spatial gradient (Fig. 5a), but the frequency of frugivory per cell (range, 0–29;  $n = 1272$ ) had a very weak spatial structure (Fig. 5b), and no spatial structure was found in the residuals of a OLS model. Nevertheless, fruit consumption was positively related to fruit availability (Fig. 5c;  $R^2 = 0.09$ ,  $F_{1,150} = 14.84$ ,  $P < 0.001$ ).

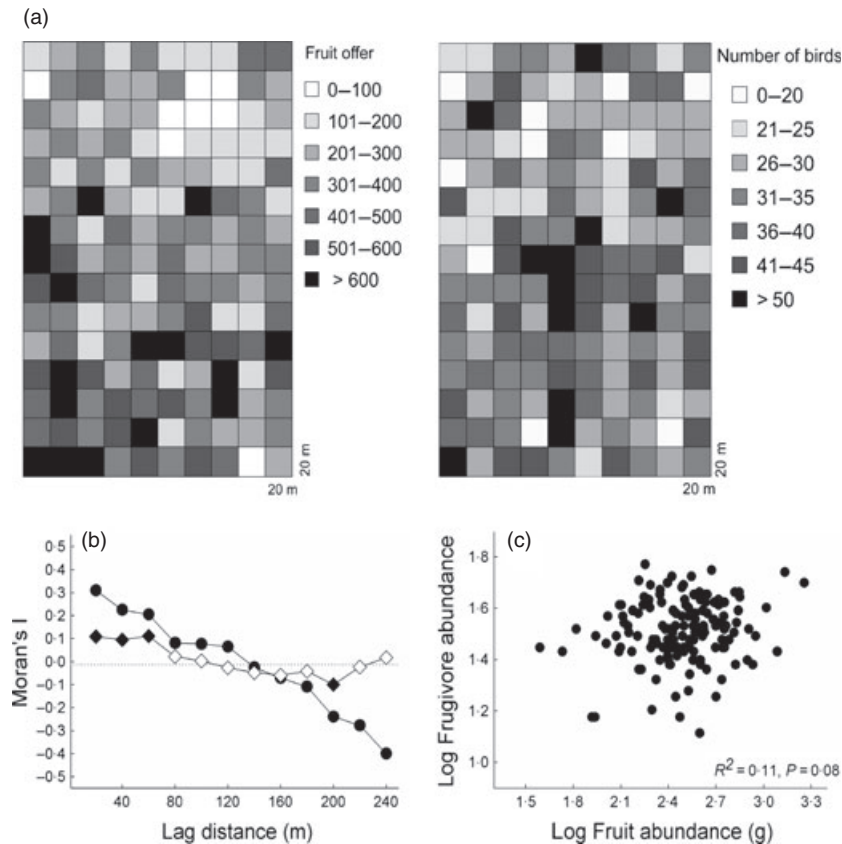


**Fig. 3.** Ordinary least squares regressions of fruit-eating birds on fruit abundance along a series of 12 consecutive bimonthly sampling periods. Relationship between (a) abundance of fruit-eating birds and fruit abundance of all species consumed by frugivorous birds during the 2-year period; (b) frequency of fruit consumption and availability of fruits consumed by frugivorous birds during the 2-year period.

#### Single sampling periods

The general trend in spatial distributions observed over the entire study period remained when each sampling period was analysed separately: fruit abundance and availability were spatially structured in gradients or patches,

and frugivore abundance and fruit consumption showed weak or no spatial structure. A significant and positive response of frugivore abundance to fruit abundance and between fruit consumption and availability was found at the assemblage level in five of nine sampling periods. However, only in three cases, frugivore abundance and



**Fig. 4.** Spatial structure of fruit abundance and frugivore abundance at the bird assemblage level. (a) Maps showing the spatial distribution of total fruit abundance (estimated as the pulp dry mass in grams) and abundance of frugivores recorded in the 6-ha study plot during 2 years. (b) Correlograms of fruit abundance (circles) and total abundance of fruit-eating birds (diamonds) recorded during 2 years in  $20 \times 20$  m cells; filled symbols show lag distances with a significant ( $P < 0.05$ ) Moran's I value. (c) Scatter plot of frugivore and fruit abundances by cell and their relationship estimated with a spatial autoregressive model (SAR).

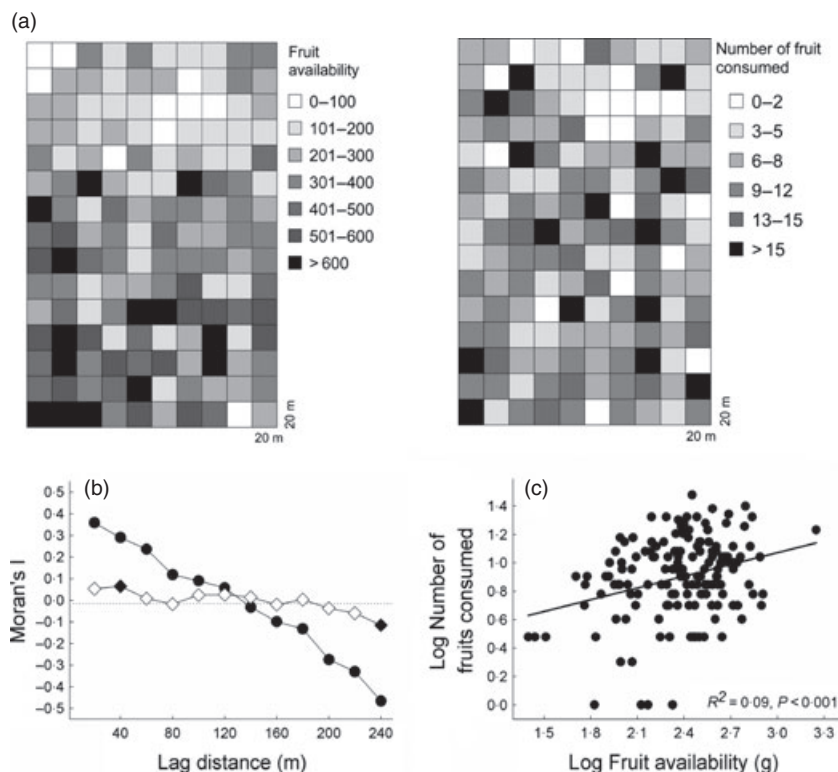
fruit consumption were significantly related to fruit availability at the same period (Table 1). In all these cases, fruit abundance was explained between 12% and 35% of frugivore abundances at the cell scale, and between 12% and 22% of fruit consumption by the assemblage (Table 1).

At the species level, we did not find significant relationships between birds and fruits for *E. cyanocephala* and *C. ophthalmicus* (in one and two sampling periods analysed, respectively; Table 1). In *T. sayaca*, bird abundance and fruit consumption showed a positive and significant response to fruit abundance and availability, respectively, at the same four sampling periods (Table 1). Finally, of six sampling periods analysed for *T. rufiventris*, its abundance was positively and significantly related to fruit abundance in one period, and fruit consumption and availability were related in three periods. In eight of the nine significant cases, frugivore abundance and frequency of fruit consumption covaried with the availability of fruit (Table 1).

## Discussion

The fruit-tracking hypothesis predicts that changes in the abundance of fruit-eating birds should respond in time

and space to changes in fruit abundance (Rey 1995; Burns 2004). We demonstrate that the use of more accurate metrics of the interaction, along with taking into account covariation in frugivory and abundance of fruit-eating birds in response to fruit availability, should be included within the fruit-tracking hypothesis framework for a better understanding of frugivore–fruit links. Our 2-year study of the spatial links between fruit availability and the entire frugivore assemblage or selected fruit-eating species affords correlational support to this hypothesis in an Andean subtropical forest, the Southern Yungas. However, the principal fruit-eating species differed in their responses to temporal and spatial changes in fruit availability. Only some of these species seemed to track the temporal changes in local availability of fruits. In turn, fruit availability played a relatively minor role in explaining the local spatial differences in fruit consumption. In agreement with our prediction, the fruit–bird link was better explained by fruit availability and consumption than by the mere abundance of fruits and frugivores. Fruit consumption and frugivore abundances strongly covaried with fruit availability at the assemblage level, but only sometimes at the species level, pointing to changes in bird abundances not related to fruit tracking. This study



**Fig. 5.** Spatial structure of fruit availability and frequency of fruit consumption at the bird assemblage level. (a) Maps showing the spatial distribution of fruit availability (estimated as pulp dry mass in grams) and all events of fruit consumption recorded in the 6-ha study plot during 2 years. (b) Correlograms of fruit availability (circles) and frequency of fruit consumption (diamonds) recorded during 2 years in  $20 \times 20$  m cells; filled symbols show lag distances with significant ( $P < 0.05$ ) Moran's  $I$  value. (c) Scatter plot of frequency of fruit consumption and fruit availability per cell and their relationship estimated with an ordinary least squares regressions model.

showed that cases with weak or null support for the fruit-tracking hypothesis may be largely explained by both species-specific responses to changes in availability and composition of fruits, and inaccurate measurement of fruit tracking.

#### FRUIT TRACKING BY THE FRUGIVORE ASSEMBLAGE

Previous studies on fruit tracking by birds showed conflicting results. Some mismatches can be explained by dependence on the spatiotemporal scale at which birds track fruits, even when there seems to be no emerging scale at which positive links might occur, or if the scale is species specific. At the assemblage level, contrasting results were reported within and between spatial and temporal scales; some studies found positive matches to monthly (Loiselle & Blake 1991; Hampe 2008) and yearly variation (Gutián & Munilla 2008), while others did not (Levey 1988; Herrera 1998; Haugaasen & Peres 2007). Similarly, there is evidence for spatial matches at the local (Malizia 2001; García & Ortiz-Pulido 2004) or landscape scales (García & Ortiz-Pulido 2004; Gutián & Munilla 2008; Hampe 2008). However, the same authors failed to find spatial links between fruit and frugivore abundances at another spatial scale. Malizia (2001) found no conclusive evidence for correlations between monthly fruit

abundance (number of plant species with ripe fruits and a fruit phenology index) and capture rates of frugivores at the local scale (*c.* 50 ha), concluding that frugivores are not strongly tied to fruit abundance in this Southern Yungas forest. The forest and the frugivore assemblage composition studied by Malizia (2001) was similar to those reported in this study, in which we found that frugivores as a group did track temporal changes in fruit availability. As discussed earlier, the use of different measurements to assess the fruit–frugivore interaction strength probably explains contrasting conclusions on fruit tracking by birds reached by both studies conducted in the Southern Yungas.

Matching changes in fruit abundance by the whole frugivore assemblage could also be improved by shared ecologies among frugivores, such as strategies to track fruit resources (Shochat *et al.* 2002). The temporal link between fruit availability and frugivory was strong in the Southern Yungas site, which hardly could be the consequence of shared fruit-tracking strategies. The number of species eating fruits (range, 4–11) changed across sampling periods, and frugivores included latitudinal migrants in spring and summer, altitudinal migrants in autumn and winter and resident species (Vides-Almonacid 1992; Rougès 2004; Capllonch & Lobo 2005), all together responsible for short-term fluctuations in abundances not



**Table 1.** Ordinary least squares regressions (OLS) or spatial autoregression (SAR) models between fruit-eating birds and fruit abundance variables at 20 × 20 m contiguous cells in a 6-ha plot. Significant values in bold

	Frugivore abundance vs. fruit abundance			Frugivore abundance vs. fruit availability				Fruit consumption vs. fruit availability			
	$R^2$	$F_{1,150}$	$P$	$R^2$	$F_{1,150}$	$P$	Model	$R^2$	$F_{1,150}$	$P$	Model
<b>Frugivore assemblage</b>											
September 2008	0.16	13.58	<b>&lt;0.001</b>	0.16	13.69	<b>&lt;0.001</b>	SAR	0.04	5.41	0.02 <sup>a</sup>	OLS
November 2008	0.17	8.05	<b>0.005</b>	0.16	6.07	<b>0.01</b>	SAR	0.05	0.17	0.68	SAR
January 2009	0.21	27.95	<b>&lt;0.001</b>	0.27	46.89	<b>&lt;0.001</b>	SAR	0.17	22.08	<b>&lt;0.001</b>	OLS
May 2009	0.01	1.18	0.34	0.02	3.39	0.07	OLS	0.20	21.73	<b>&lt;0.001</b>	SAR
July 2009	0.10	0.02	0.90	0.11	0.03	0.86	SAR	0.11	0.25	0.62	SAR
October 2009	0.27	0.02	0.90	0.27	0.02	0.90	SAR	0.22	7.10	<b>0.009</b>	SAR
December 2009	0.35	24.44	<b>&lt;0.001</b>	0.29	14.51	<b>&lt;0.001</b>	SAR	0.12	21.05	<b>&lt;0.001</b>	OLS
April 2010	0.12	13.89	<b>&lt;0.001</b>	0.10	13.12	<b>&lt;0.001</b>	SAR	0.18	19.31	<b>&lt;0.001</b>	SAR
June 2010	0.00	0.35	0.56	0.00	0.03	0.85	OLS	0.01	1.63	0.16	OLS
<b><i>Turdus rufiventris</i></b>											
November 2008	0.01	0.98	0.32	0.01	1.67	0.20	OLS	0.09	0.07	0.79	SAR
January 2009	0.07	10.71	<b>0.001</b>	0.11	18.88	<b>&lt;0.001</b>	OLS	0.15	26.24	<b>&lt;0.001</b>	OLS
May 2009	0.01	0.01	0.92	0.01	0.15	0.29	OLS	0.14	10.96	<b>0.001</b>	SAR
July 2009	0.12	0.02	0.90	0.12	0.02	0.90	SAR	0.14	3.89	0.05 <sup>a</sup>	SAR
October 2009	0.11	0.02	0.90	0.11	0.02	0.90	SAR	0.00	0.05	0.82	OLS
December 2009	0.02	3.63	0.06	0.06	8.81	<b>0.004</b>	OLS	0.08	13.14	<b>&lt;0.001</b>	OLS
<b><i>Thraupis sayaca</i></b>											
September 2008	0.10	10.47	<b>0.001</b>	0.10	11.09	<b>0.001</b>	SAR	0.05	7.05	<b>0.009</b>	OLS
November 2008	0.10	2.72	0.10	0.10	3.93	0.05 <sup>a</sup>	SAR	0.04	0.02	0.90	SAR
January 2009	0.12	9.72	<b>0.002</b>	0.12	8.89	<b>0.003</b>	SAR	0.06	8.60	<b>0.004</b>	OLS
May 2009	0.00	0.34	0.56	0.01	1.81	0.18	OLS	0.04	5.34	0.02 <sup>a</sup>	OLS
July 2009	0.05	0.29	0.59	0.07	1.56	0.21	SAR	0.00	0.03	0.87	OLS
October 2009	0.21	0.68	0.41	0.21	0.02	0.90	SAR	0.01	1.62	0.21	OLS
December 2009	0.15	25.86	<b>&lt;0.001</b>	0.11	17.28	<b>&lt;0.001</b>	OLS	0.06	8.53	<b>0.004</b>	OLS
April 2010	0.06	10.14	<b>0.002</b>	0.10	17.08	<b>&lt;0.001</b>	OLS	0.16	17.33	<b>&lt;0.001</b>	SAR
<b><i>Chlorospingus ophthalmicus</i></b>											
September 2008	0.21	4.39	0.04 <sup>a</sup>	0.22	5.51	0.02 <sup>a</sup>	SAR	0.01	0.76	0.38	OLS
July 2009	0.06	0.02	0.90	0.06	0.02	0.90	SAR	0.01	0.99	0.32	OLS
<b><i>Euphonia cyanocephala</i></b>											
September 2008	0.00	0.00	0.99	0.00	0.00	0.96	OLS	0.07	3.20	0.08	SAR

SAR models were selected after detection of spatial autocorrelation in the response variable; in these cases, SAR models always fitted better than OLS models according to the AIC<sub>c</sub>. <sup>a</sup>Not significant after a Bonferroni correction for multiple testing within a single sampling period.

related with the breeding output. Alternatively, a match between changes in abundance of fruits and the whole frugivore assemblage could result from the combination of independent fruit-tracking responses by the more abundant species (Tellería, Ramirez & Pérez-Tris 2008). However, temporal links between fruits and the frugivore assemblage were not a result of added responses of single species, as the four major fruit-eating species differed in their temporal patterns of response to fruit availability.

Assembly-wide changes in abundance linked to changes in fruit availability may reflect mechanisms operating above the species level, with strong evolutionary consequences on the plant species consumed. A meta-analysis showed a positive association between monthly peaks of fruit production and the total fruit-eating bird abundances in localities from four continents (mostly in temperate northern hemisphere), which could be consequence of diffuse co-evolutionary interactions between groups of plants and birds (Burns 2002). The ability of birds as a

group to track fruit abundance could promote this fruit–bird phenological synchrony. For example, abundance peaks of autumn migrants were proposed as an evolutionary driver of the phenology of temperate bird-dispersed plants (Thompson & Willson 1979; Eriksson & Ehrlén 1998; Hanya 2005), whereas co-evolution between plants and frugivores leads to greater availability of frugivores through the year and more extended fruit-ripening phenologies in lower than high latitudes (Thompson & Willson 1979). From a plant's perspective growing in subtropical and temperate environments where climate plays an important role determining the reproductive phenology, efficient tracking of fruit availability by birds implies that ripening fruits during periods of increased total supply of fleshy fruits would not be penalized by decreasing fruit removal. Nevertheless, total proportion of available fruits consumed was lower in periods of high fruit availability ( $r = -0.56$ ,  $n = 12$ ,  $P < 0.06$ ) in the Southern Yungas, pointing out inefficient fruit tracking as

a potential selective force that can promote asynchronous fruit ripening at the community level.

#### FRUIT TRACKING BY FRUIT-EATING BIRD SPECIES

Mismatches between fruit and frugivore abundance patterns may be caused by design and methodological flaws, or by frugivore inability or lack of necessity to track fruits. To the best of our knowledge, methodological issues addressed here have not been previously considered even though relevant variables of frugivores and their resources have been measured by means of a variety of techniques to infer fruit tracking by birds. As we expected, fruit–frugivore temporal links were captured with higher accuracy by proximate measurements of interaction strength. The abundance of *E. cyanocephala*, *C. ophthalmicus* and *T. rufiventris* was not related to fruit abundance, but a significant response (positive link) occurred when considering fruit availability and frequency of fruit consumption. Unlike temporal matches, most cases of local spatial links between fruits and frugivores were not captured more accurately by fruit availability and consumption than by fruit and frugivore abundances.

Maintaining a frugivorous diet throughout the year requires the ability to move to new sites when fruit supply gets depleted (Loiselle & Blake 1991). In highly frugivorous birds, the selection of a fruit-tracking strategy may have been related to the ability to perform nomadic movements or partial or full migration (Levey & Stiles 1992; Tellería & Pérez-Tris 2003), coupled with a predictable probability of finding other sites with fruits, enabling long-term selective pressures conducive to the evolution of this mutualism-related trait. Predictability of resources was also considered crucial in the evolution of nomadism of desert birds and in life-history strategies linked to resource tracking in raptors (Dean 1997; Sergio *et al.* 2011). However, fruit tracking is part of trade-offs between costs and benefits subject to natural selection. While frugivores may track fruits to increase their resource intake, other concurrent mechanisms could dilute the expected link between fruits and frugivores. For example, predation risk could modify foraging decisions because it is a stronger constraint on fitness than temporary food shortages (Mayor *et al.* 2009). We demonstrated that resource tracking is a viable strategy in the Southern Yungas, while its non-occurrence in similar instances (e.g. in the same species at the same area and spatial scale) suggests a temporal alternancy in the strength of competing mechanisms acting at a similar spatial scale.

Most temperate and subtropical biomes are characterized by heterogeneous assemblages of bird species that include variable proportions of fruits in their diets, and by the almost complete absence of strict frugivores. Interspecific differences in frugivore responses to fruit characteristics (e.g. Moermond & Denslow 1985) suggest that community-wide fluctuations in fruit resources may not explain changes in the abundance of each coexisting

species of fruit-eating birds. Unlike highly frugivorous species, other phenotypic traits (as switching behaviour between alternative resources; Carnicer, Jordano & Melián 2009) could be as or more important than fruit tracking to deal with spatial or temporal shortage of fruits among opportunistic frugivores. Observational and experimental studies have found clear positive responses to changes in fruit abundance by some fruit-eating bird species, whereas other bird species failed to respond (Rey 1995, 2011; Malizia 2001; Borgmann *et al.* 2004; Tellería, Ramirez & Pérez-Tris 2008). Regional species abundance and the presence of nomadism or regional migration have been related to the capacity to track fruit abundance, despite dissimilar strategies of the use of space. In the Southern Yungas, interspecific differences in the dietary proportion of fruit vs. invertebrates, in fruit preferences and in frugivorous dietary breadth (Giannini 1999; Rougès 2004; E. Martín, P. G. Blendinger, O. Osinaga Acosta, R. A. Ruggera, M. G. Núñez Montellano, L. Macchi *et al.*, unpublished manuscript) suggest mismatches in fruit–frugivore abundances promoted by idiosyncratic species responses to fruit availability. For example, the two numerically dominant frugivores, *T. sayaca* and *T. rufiventris*, accounted for 37% and 34% of total fruit consumption events, respectively; abundance of the former was strongly related to fruit abundance (and track temporal changes in fruit availability), whereas the latter did not. These two bird species consume most of ornithochorous fruits available in the Southern Yungas forests, but *T. sayaca* includes a larger fraction of fruits in its diet over the year (Rougès 2004). Also, different responses of *T. sayaca* and *T. rufiventris* to fruit availability of *Eugenia uniflora* (Myrtaceae) were attributed to their preferences for different fruit species (Blendinger & Villegas 2011). Further, *T. sayaca* is considered a regional migrant whose populations display local movements and experience greater seasonal fluctuations than *T. rufiventris* (Giannini 1999; Rougès 2004). As a consequence, *T. sayaca* might be more influenced by, and could more closely match, the changes in fruit availability relative to *T. rufiventris*, as was observed in this study.

#### COVARIATION BETWEEN BIRD ABUNDANCE AND FRUIT CONSUMPTION

The strong temporal response of frugivore abundance and fruit consumption found at the levels of assemblage and species (i.e. *T. sayaca* and *E. cyanocephala*; also in *T. rufiventris* at the spatial scale), linked in turn to changes in fruit availability, supports the influence of fruit tracking on changes in some frugivore abundance. It is worth noting that positive links between fruit availability and abundance of fruit-eating birds or frequency of fruit consumption not necessarily imply fruit tracking and can be misleading regarding the processes involved. These frugivore variables alone did not lead always to similar conclusions on spatiotemporal fruit–frugivore links (at species

and assemblage levels, both over time and space). Besides fruits, shelter, nesting sites, search for other foods, interactions with other birds, territorial behaviour and predation risk, among other factors, also may influence local bird distribution. Similarly, fluctuations in the frequency of fruit consumption may be correlated with responses to availability of alternative resources or may reflect seasonal shifts between alternative resources not necessarily related to food abundance (Carnicer, Jordano & Melián 2009).

We showed above that frugivore abundance and fruit consumption always change in the same way in relation to fruit availability in *T. sayaca*, but only sometimes in *T. rufiventris*. In *E. cyanocephala*, the significant temporal link of its abundance with fruit availability was largely a result of a positive relationship ( $R^2 = 0.74$ ;  $P < 0.001$ ) with the availability of mistletoe fruits (*Phoradendron falcifrons* and *P. tucumanense*). Fruit consumption by *E. cyanocephala*, only recorded during periods of its highest abundance, included mostly mistletoe berries (*Phoradendron falcifrons* and *P. tucumanense*; 85% of fruit consumption records). Species of *Euphonia* have shown a strong preference for mistletoe berries (Snow 1981; Carlo, Collazo & Groom 2003) and a reliance on a highly frugivorous diet to fulfil their nutrient requirements (Herrera, Rodríguez & Hernández 2009). Finally, lack of temporal and spatial matching between *C. ophthalmicus* abundance and fruit availability was not surprising, because it is less frugivorous than the other species here compared (Giannini 1999; Rougès 2004). Carnicer, Jordano & Melián (2009) found that most frugivore–insectivore species inhabiting sclerophyllous shrublands in Spain shift to a more frugivorous diet when insects are scarce and relative fruit supply increases. Although temporal changes in frequency of fruit consumption were tightly linked to fruit availability in *C. ophthalmicus*, the lack of covariation between bird abundance and frequency of frugivory in this species did not support expectations of the fruit-tracking hypothesis. *C. ophthalmicus* abundance was fairly constant and varied much less (CV = 9.6%) than its frequency of fruit consumption (CV = 53.0%) throughout the time period of this study, suggesting that the strong difference between both measures of plant–frugivore links might be explained by seasonal shifts in the relative importance of arthropods and fruits in the diet rather than by population fluctuations. According to our expectations, fruit tracking was more frequent in birds more specialized in a frugivores diet, suggesting that temporal fruit tracking may not be an important strategy for frugivorous species which also consume large amounts of insects or other foods, at least when switching behaviour allows them to exploit alternative food resources when fruits become scarce.

## Conclusions

The ability to track fruits is a strategy of frugivorous birds extended from the tropics to temperate forests of

higher latitudes. However, the study of fruit tracking is affected by methodological and scale issues and the co-occurrence of other mechanisms. As we predicted, fruit–frugivore spatiotemporal links can be captured with higher accuracy by proximate measurements of interaction strength, whose measurement in the field does not require much additional effort to be undertaken in other studies. Most importantly, we show that covariation in frugivory and abundance of fruit-eating birds in response to fruit availability should be taken into account for a better understanding of frugivore–fruit links. In their study on the response of species richness of frugivorous bird to fruit availability, Peters *et al.* (2010) recognized the need of improving the measurement of fruit abundance and estimate the availability of energy in fruits. We propose that further inclusion of not just fruit quantity but also fruit quality estimation within the fruit-tracking hypothesis framework will make significant progress toward understanding how nutrient and energy intake determine bird decisions that lead to tracking fruits.

In the Southern Yungas, the temporal fluctuations in species abundances matching fruit availability were much stronger than local fruit–bird spatial links. Local fruit availability changed much more between than within sampling periods; thus, we expect that more pronounced spatial tracking might occur at larger spatial scales with increasing spatial variability in fruit availability. Spatial fruit–frugivore links were mostly recorded at landscape and regional scales (e.g. Guitián & Munilla 2008; Hampe 2008; Tellería, Ramirez & Pérez-Tris 2008; Vergara *et al.* 2010; Crampton *et al.* 2011). Animals often must deal with food components at a diversity of scales. To do it, they can track the distribution of resources at several scales, using search strategies that may reflect the hierarchical properties of the resources (Fauchald, Erikstad & Skarsfjord 2000; García & Ortiz-Pulido 2004). While fruit tracking implies that birds must move to sites with enough fruit resources to meet nutritional and energy requirements, animals face trade-offs among multiple factors that may modify foraging decisions. Fruit tracking by the entire frugivore assemblage extends to several but not all fruit-eating species; among them, positive links between resource–consumer abundances may be frequent in animals with a specialized diet. Nevertheless, fruit tracking has been always tested in birds that depend on additional food types to balance their diets. For these eclectic fruit-eating birds, which may switch spatially and temporally between alternative resources, fruit availability by itself may not lead to matches as predicted by the fruit-tracking hypothesis. Its occurrence in frugivorous–insectivorous birds may be largely dependent on species-specific responses to changes in availability of fruits on gradients of variation in this and alternative resources. Future theoretical development of fruit-tracking hypothesis should evaluate ecological and evolutionary consequences of resource tracking by frugivores. For example, the ability of birds to track fruit abundance could exert

top-down controlling influence on ecosystem functional integrity and may drive seed dispersal resilience to habitat fragmentation (García *et al.* 2012), and dispersers loss (Loiselle *et al.* 2007) and promote fruiting phenological patterns of plants (Eriksson & Ehrlén 1998).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Species of interacting fleshy-fruited plants and fruit-eating birds recorded during the 2-years study in a 6-ha plot of subtropical Andean mountain forests known as Southern Yungas.

**Table S2.** Number of fruits, frugivores, and fruit consumption events recorded in a 6-ha plot on 12 periods sampled from September 2008 to August 2010.

**Table S3.** Temporal autocorrelation between consecutive sampling periods of fruit-eating birds (number of birds and frequency of fruit consumption recorded at bimonthly intervals) in a 12-period series.

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