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Short note

SHORT NOTE

Plant–frugivore interactions in an urban nature reserve and its nearby gardens

Mariki Y. Zietsman,[1] Norberto H. Montaldo[1] and Mariano Devoto [1,2,*]

[1]Facultad de Agronomía, Cátedra de Botánica General, Universidad de Buenos Aires, Av. San Martín 4453, C. A. de Buenos Aires C1417DSE, Argentina and [2]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)

*Corresponding author. E-mail: mdevoto@agro.uba.ar

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Abstract

In the current global context of growing urbanization, urban nature reserves play a crucial role as habitats that serve educational, recreational and conservation purposes. Biodiversity conservation within urban reserves is a challenging task, particularly since connectivity between a reserve and its surrounding artificial green spaces (e.g. gardens and parks) may affect the ecological processes within the reserve in complex ways. In this context, we studied the feeding interactions between plants and birds to provide evidence that an urban nature reserve is connected to its surrounding artificial habitats by mobile organisms. We focused on fleshy-fruited plants and frugivorous birds, and we used a network approach to describe the feeding interactions between these two guilds. The most important connecting bird was *Turdus rufiventris*, an abundant and obligate frugivore, whose abundance was positively linked to fruit availability in most of the study sites. The apparent increase in the abundance of *T. rufiventris* in one habitat when it decreases in the other suggests that the two habitats may be complementary for this species. The nature reserve, with many native plants, however, seems to be the preferred site when both habitats offer an abundant fruit supply. Our results suggest changes in either habitat can have consequences in the other one, which has broad implications for the design of management plans of urban nature reserves.

Key words: plant–frugivore interactions, ecological network, functional connectivity, frugivory

Introduction

Habitat fragmentation and urbanization are major threats to biodiversity (Miller and Hobbs 2002; Wiens 2009). In cities, only a small proportion of land cover is green spaces, such as gardens and parks, and nature reserves are rare. Natural patches of flora and associated fauna are valuable for educational, recreational and even conservation purposes, but their value depends on the biodiversity they sustain (Savard, Clergeau, and Mennechez 2000; Sadler et al. 2010). The presence of a nature reserve in an urban setting poses a conservation challenge as it usually involves that habitats of different quality (sensu Hall, Krausman, and Morrison 1997) co-exist in close proximity and may affect each other in complex ways.

Urban nature reserves rarely maintain the original biodiversity that was present prior to urbanization; this degradation is the result of the many threats urban reserves suffer from their surroundings (e.g. pollution, visitors, invasive species and diseases; Wiens 2009). The effect that these pressures have on biodiversity partly depends on the size, shape and degree of isolation from other green spaces of the reserve (MacArthur, Wilson, and Wilson 1967; Turner 1989; Sadler et al. 2010). In particular, the degree of isolation of the reserve greatly depends

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directly on the connectivity of the surrounding landscape and the degree to which it facilitates the movement of animals among resource patches (Taylor et al. 1993; Tischendorf and Fahrig 2000; Fahrig et al. 2019).

Connectivity with nearby artificial green spaces (e.g. gardens and parks) may affect the biodiversity within an urban reserve in positive or negative ways (Turner 1989; Wiens 2009; Minor et al. 2009). For some species, connectivity can mean that they have a wider range of habitats from where to satisfy their resource requirements thus maintaining population densities higher or more stable in fragmented environments (Uezu, Metzger, and Vielliard 2005). On the down side, connectivity can also increase the risk of invasion of the reserve by alien plants or domesticated animals, which may then compete with or predate on native species (Minor et al. 2009; Shochat et al. 2010). Connectivity to other green spaces is therefore an important aspect to assess when designing management plans for nature reserves (Sadler et al. 2010).

Birds are generally extremely mobile and can use different habitats in different seasons (or different life stages) to meet their resource needs (Moermond and Denslow 1985), and can thus be considered mobile links that connect habitat patches (Lundberg and Moberg 2003; Whelan, Wenny, and Marquis 2008). Frugivorous birds, which depend on a year-round supply of fruit in their diets, need to be able to track fruit which can be patchily distributed (Moermond and Denslow 1985). In doing so, they transport seeds between patches from small to very large distances (Buckley et al. 2006), thus connecting these patches.

The fruit-tracking hypothesis predicts a correlation between changes in the abundance of fleshy-fruit resources and the abundance of fruit-eating birds (Rey 1995; Burns 2004; Blendinger et al. 2012). This correlation has both a spatial and a temporal component: it can occur between seasons or between years with variable resource abundances (Tellería, Ramirez, and Pérez-Tris 2008), between plants with different fruit abundances in a given habitat, and also between plots within the same or different habitats (Rey 1995; Tellería and Pérez-Tris 2003).

In this study, we assessed the spatial and seasonal variation in interactions between fleshy-fruited plants and the frugivorous birds that feed on them in an urban nature reserve and its surrounding gardens. We tackled three questions: (i) Is there seasonal complementarity between habitats (i.e. reserve vs gardens) in fleshy-fruit availability? (ii) Are there any fleshy-fruited plant species preferentially consumed by birds? (iii) Is there seasonal variation in frugivorous bird abundance in response to fruit abundance of preferred species?

We expect some degree of temporal complementarity (i.e. not total overlap) in fruit abundance between the reserve and the gardens. Given that highly frugivorous birds need to move between habitat patches when fruit supply runs low (Loiselle and Blake 1991), we expect to see a correlation across habitats between abundances of frugivore birds and of their preferred fruits, as predicted by the food-tracking hypothesis (Blendinger et al. 2012). In addition to giving an insight into how a nature reserve may connect with its surrounding anthropogenic habitat, our results could have implications for the reserve management as moving birds could increase the flow of seeds (particularly of alien plant species) between the two habitats (Reichard, Chalker-Scott, and Buchanan 2001; Gleditsch 2017).

Methods

Study site

We conducted the study in a 50-ha urban nature reserve (of which only 10 ha are terrestrial habitats) called Parque Natural Municipal Ribera Norte (hereafter PNMRN), and in three nearby private, residential gardens (see coordinates in the Supplementary Material) in the suburbs of the city of Buenos Aires, Argentina. In the context of this study we considered the reserve and the gardens as two different habitats. PNMRN is a relatively small nature reserve, immersed in a residential urban matrix, with a few hundred species of native plants and birds (see details below) which are sparsely represented in the area. The gardens, of 180, 250 and 870 m^2, were located at 180, 235 and 245 m away from the edge of the nature reserve, respectively. These distances are well within foraging distances of common frugivorous birds in the area, such as *Turdus rufiventris*, *Turdus amaurochalinus*, *Pitangus sulphuratus* and *Elaenia parvirostris* (Díaz Vélez et al. 2015; Da Silveira et al. 2016) which made flight between habitats possible, irrespective of whether the birds nest in the reserve, the gardens or in the street trees.

PNMRN is situated on the riverbank of Río de la Plata (34°28′7″S, 58°29′41″W). The climate of the area is temperate, with an average temperature of 16.7° and a mean annual rainfall of 1073 mm Servicio Meteorológico Nacional 1992). The reserve encompasses a variety of communities which are characteristic of two phytogeographic regions, the Pampa province in the Chaco domain and the Paraná province in the Amazon domain (Cabrera 1976; Kalesnik et al. 2005). These communities are composed of a total of 318 vascular plant species belonging to 66 families, of which 13% are alien (Dirección de Ecología y Conservación de la Biodiversidad 2011b). A total of 239 species of birds have been recorded in the nature reserve (Bertolini and Deginani 1995; Bertolini and Camiña 1996), of which 43 are obligate or occasional fruit-eaters (Del Hoyo 1992–2011).

Abundance of birds and fleshy-fruited plants, and plant–bird interactions

The abundance of frugivorous birds and fleshy fruits was registered during 10 months (from October 2011 until the end of July 2012) in PNMRN and the gardens using methods similar to Guitián and Munilla (2008). This period encompassed the fruiting seasons of all major fleshy-fruited plant species in the study sites. The frequency of interactions between birds and fleshy-fruited plants was also independently registered (see below).

Due to the differences in size, vegetation structure, visibility and heterogeneity between habitats, it was decided to do line transects in PNMRN and point counts in the gardens. Line transects were carried out along a circular path which passed through most of the woody environments of PNMRN. Two contiguous transects 560- and 330-m long, respectively, were established along a portion of the path. Transects were walked during the morning (9:00–12:00) from one to three times a month at a slow, set pace (ca. 40 and 20 min for the longest and shortest transect, respectively). The longest transect was sampled from October to July; the shortest one (which was established to include a few plant species that were not present in the first transect) was sampled from March until the end of July. In each transect, all fruit-eating birds seen (with 8 × 40 binoculars) or heard within a 10-m stripe either side of the path were recorded. A checklist of 43 bird species (Supplementary Table S1) that had been previously registered in PNMRN (Dirección de Ecología y Conservación de la Biodiversidad 2011a) and that are obligate or occasional fruit-eaters (Del Hoyo 1992–2011) was used as a reference.

In point counts, all birds seen or heard within the limits of the garden were recorded from a fixed position (which was visible to the birds). Each sampling lasted for 40 min, after an initial

5-min settling time. Bird densities were calculated for each habitat as the mean number of individuals of each species per month and per unit area.

The abundance of fleshy fruits in PNMRN (Montaldo 2000, 2005; Dirección de Ecología y Conservación de la Biodiversidad 2011b) was estimated at least once a month. After a bird count, the number of fruits of each species was counted in the 10-m stripe either side of the transect (see Supplementary Table S2), except for *Ligustrum sinense*, which was extremely abundant. For this species, five 5 × 4 m plots were assigned at random distances along the transects on each visit, and all the mature fruits were counted in them. In order to calculate fruit abundance each plant was partitioned in subunits based on the morphology of the plant (e.g. a branch, a frutescence or a quarter plant for symmetrical individuals) and the mean number of fruits per subunit was calculated by counting 10 subunits. The total fruit number of each plant was obtained from the product of the mean number of fruits per subunit and the number of observed subunits in a plant. Fruit counts in the gardens included all plant individuals.

Fruit abundance in each habitat was expressed as a mean volume per month and per unit area. The volume of fruit was obtained from the product of the mean volume of an individual fruit by the number of fruits counted. The mean volume per fruit was estimated on the assumption that they were spheres (in most cases) or cylinders (e.g. bananas). For spherical or nearly spherical fruit the greater and lesser diameters were measured on 20 fruits from 2 to 3 individuals of each species. Volume (V) was calculated from the mean diameter (D), using the following formula: $V = 4/3\pi(D/2)^3$. For cylindrical fruit, the length (L) and diameter (D) was measured and the volume (V) calculated using the equation: $V = L\pi(D/2)^2$ (see Supplementary Table S3). Measurements of the fruit size of two species (*Celtis ehrenbergiana* and *Prunus salicina*) were prevented by logistical problems, so they were obtained from the literature (Supplementary Table S3).

In both PNMRN and the nearby gardens, feeding events between frugivores and plants were recorded during the bird and fruit counts (Sutherland, Newton, and Green 2004). Approximately 75 h of observation of feeding events, evenly distributed among habitats, were carried out during the study. A feeding event was valid when the bird was seen to pick and swallow a part or the whole of at least one fruit. The frequency of interaction of a given pair of species was calculated as the total number of feeding events between them recorded throughout the study. Interaction frequencies were calculated separately for each habitat and month by pooling data from the three gardens on the one side and the two transects in the reserve on the other.

To characterize fruit–bird interactions, a bipartite network was constructed for each habitat, with plant species listed as rows and bird species listed as columns (Jordano 1987). Each cell in the matrix contained the interaction frequency of the corresponding pair of species in the given habitat. Bird species present in both networks were denominated ‘potential connecting species’ and were selected to test fruit-tracking.

Is there seasonal complementarity between habitats in fleshy-fruit availability?

If habitats were mutually complementary in terms of fruit availability, we expected fruit availability through time to be negatively correlated between habitats. For this analysis, we considered fruit abundance of *consumed* species and fruit abundance of *preferred* species. This distinction follows Blendinger et al. (2012), who showed that fruit-tracking is more evident when considering fruit abundance of those species that are actually eaten by birds rather than fruit abundance of the entire fleshy-fruited plant community, and Carlo, Collazo, and Groom (2003), who showed even greater evidence may be found if only the abundance of preferred fruits were considered (i.e. not including occasionally consumed species; see below for calculations of bird preferences).

Are there any fleshy-fruited plant species preferentially consumed by birds?

In order to establish preferred fruit species in each habitat, we performed a selectivity analysis based on the observed interaction networks. We carried out a Monte Carlo simulation generating null plant–frugivore interaction networks based on a matrix of expected interaction probabilities (Vázquez and Aizen 2003; Dormann et al. 2009). This probability matrix was generated by multiplying two vectors: one containing the total abundance of each consumed fruit species and the other containing the sum of feeding events of each bird species. After multiplying the vectors, the resulting matrices (of dimensions 8 plants × 8 birds for PNMRN, 5 plants × 7 birds for gardens) were normalized so that their elements added up to one, to transform them into probabilities (Dormann et al. 2009; Vázquez, Chacoff, and Cagnolo 2009). To build each random network an algorithm assigned interactions to an initially empty matrix until it reached the number of feeding events in the real, observed network of each habitat. For each habitat, 100 simulated networks were generated. To compare the observed interaction network with the simulated ones, the average frequency value and the 95% CI of each position in the matrix were calculated. This allowed to determine which plant species were preferred (observed value above CI) or avoided (observed value below CI) by birds in each habitat. We then excluded from further analyses the plant species which were avoided by the ‘potential connecting species’ defined earlier.

Is there seasonal variation in frugivorous bird abundance in response to preferred fruit abundance?

With the remaining plant species, we proceeded to evaluate with a Pearson correlation whether the abundance of each ‘potential connecting species’ correlated with fruit abundance of consumed or preferred species in each habitat (Blendinger et al. 2012). A significant positive correlation would provide evidence for active fruit-tracking by birds across habitats. Because fruit abundance varied by several orders of magnitude across species it was log-transformed to avoid large numbers having a disproportionate weight in the analyses. We did not consider the influence of other factors such as weather conditions or time of the day in the analyses. The reason was we did not have complete daily estimates of fruit abundance for all species, and also the records of plant–bird interactions were rather sparse (many species with zero daily interactions, and an overall average of *ca.* four feeding events per hour of observation) which would have resulted in a model with very low statistical power.

Data quality

In order to assess the quality of our field sampling we calculated the sampling completeness of the plant–frugivore network of interactions. For this analysis, we treated detected interactions as the ‘species’ being sampled, and we calculated the proportion of interactions detected relative to the number expected for

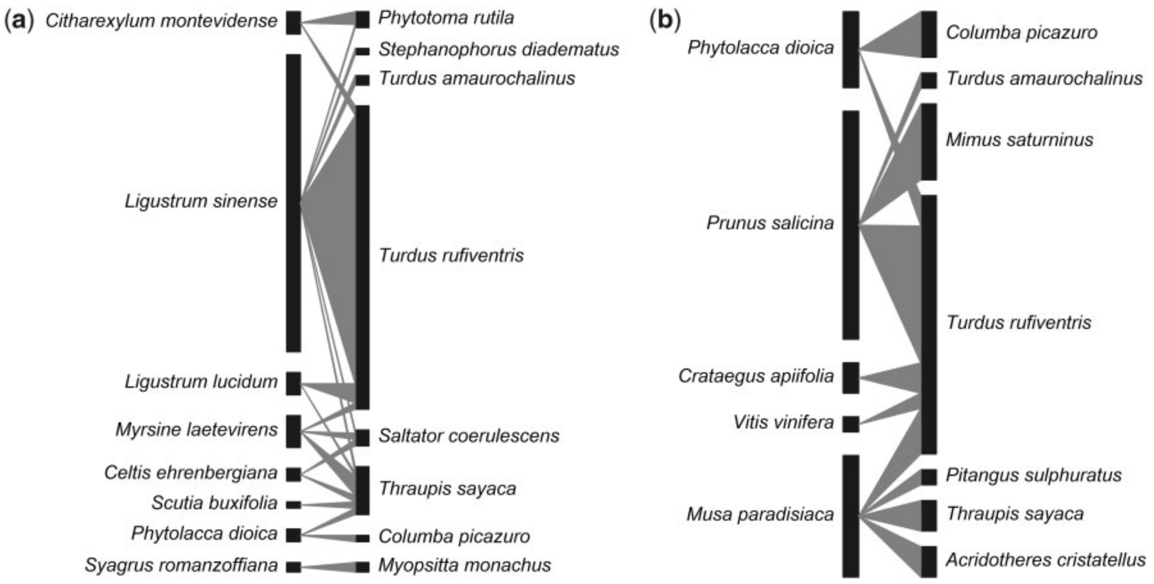

Figure 1: Plant–frugivore networks in (**a**) three urban gardens and (**b**) a nearby nature reserve. Each species of plant and bird is represented by a rectangle; the width of each rectangle represents the species' total number of interactions recorded throughout the study. The width of the arrow between species is proportional to their frequency of interaction at each place. Networks are drawn at different scales

each habitat. The number of expected interactions was estimated using the Chao 1 estimator (Chao 2005) following Devoto et al. (2012). Additionally, individual-based rarefaction curves of the number of feeding events detected in each environment were generated (Gotelli and Colwell 2001).

Results

Community description

In the nature reserve, a total of 1222 individuals belonging to 26 different occasional and obligate frugivore bird species were recorded (Supplementary Table S1). Of these, 134 individuals of 8 species were seen foraging on 6 native and 2 exotic plant species in PNMRN (Fig. 1b). Fruit abundance of exotic plants was 2.9 times higher than that of native plants. Accordingly, the fruits of *L. sinense* (the exotic and most abundant fleshy-fruited plant) were consumed by the greatest number of bird individuals (96 individuals) and species (6 species) although was seemingly avoided by two bird species and was never strongly preferred (Fig. 2a). In PNMRN, a total of 19 unique interactions (i.e. non-zero cells in the interaction matrix) were recorded between frugivore birds and plants, 8 of which were with the two exotic *Ligustrum* species (Fig. 1b).

In the gardens, a total of 198 individuals belonging to 14 frugivore species were recorded (Supplementary Table S1). Of these, 31 individuals of 7 species were seen foraging on the fleshy fruit of 4 exotic and 1 native plant species. In this habitat, 11 unique mutualistic interactions within the community of frugivore birds and plants were recorded (Fig. 1a). The most abundant fruits were *P. salicina* and *Phytolacca dioica*, which participated in 48.4 and 16.1% of the feeding events, respectively, although the latter seemed to be avoided by some bird species (Fig. 2b).

The most abundant frugivore species registered in PNMRN and the gardens was *T. rufiventris* (Fig. 3, species no. 24). This also was the species which interacted with the highest number of plant species in the gardens (Fig. 1a), whereas in PNMRN *Thraupis sayaca* interacted with the most plant species (Fig. 1b).

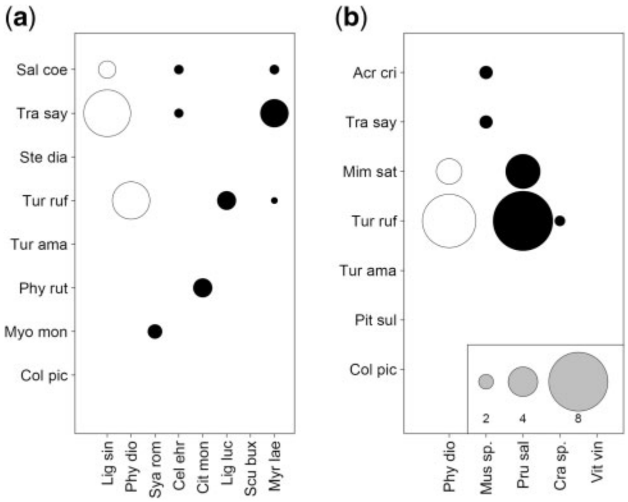

Figure 2: Fruit selectivity in (**a**) PNMRN and (**b**) the gardens. Solid circles represent preference of fruit species and empty circles represent avoidance. Circle size represents preference or avoidance intensity measured as the standardized (positive or negative) difference between predicted and observed values obtained from the preference test. Values range from −9.8 to 5.85 in PNMRN and from −7.25 to 8.08 in the gardens. Only significant values are shown (i.e. those above or below the 95% CI generated from 100 null webs in the preference test; see Methods section). The name of each species is shortened to the first three letters of the two parts of the Latin binomial

Evidence of fruit-tracking among birds

The abundance of consumed fruit species varied sharply during the sampling period in both PNMRN and the gardens, and the maximum values occurred in a different season in each habitat. A greater abundance of consumed fruit was found in the nature reserve in winter (Fig. 4a) whereas the gardens contained a greater abundance in summer. After removing the non-preferred species *L. sinense* and *P. dioica* from the analysis the abundance of preferred fruit peaked in the gardens in summer but remained similarly low in both habitats in winter (Fig. 4b).

Overall, no negative correlation in fruit abundance was found between habitats, neither when considering the whole guild of consumed fruit species (Pearson correlation, $\rho = 0.28$ and $P = 0.427$, $n = 10$ months) nor when considering only preferred fruit species ($\rho = 0.43$ and $P = 0.217$, $n = 10$ months).

A total of 12 frugivore bird species were common to both the nature reserve and the gardens (Supplementary Table S1) but only four were 'potential connecting species' seen feeding in both habitats. These were *T. rufiventris, T. amaurochalinus* (Turdidae), *T. sayaca* (Thraupidae) and *Columba picazuro* (Columbidae). Two plant species were common to the two habitats: the native *P. dioica* and the exotic *Musa* sp., although the latter never produced fully ripe fruits in PNMRN and consequently no interactions with it were recorded there. The only two potential connecting species which showed preferences for certain fruit species were *T. rufiventris* and *T. sayaca* ,which seemed to avoid the abundant *P. dioica* and *L. sinense*, respectively (Fig. 2).

A temporal correlation was found between monthly abundances of potential connecting species and total fruit abundances ($r = 0.19$ and $P = 0.0183$, $n = 10$ months). A similar trend was also found when the abundances of only consumed species were considered ($r = 0.20$ and $P = 0.0149$, $n = 10$), and a stronger correlation when only preferred fruit were considered ($r = 0.34$ and $P < 0.0001$, $n = 10$).

The abundance of *T. rufiventris* was significantly correlated with the abundance of preferred fruit in PNMRN (Pearson, $r = 0.68$, $P = 0.0008$, $n = 20$; Fig. 5a), but weakly correlated in the gardens (Pearson, $r = 0.34$, $P = 0.07$, $n = 28$; Fig. 5b). Correspondingly, the peaks in abundance of preferred fruit in each habitat coincided with peak abundances of *T. rufiventris* (Fig. 6). No significant correlations were found between the abundance of the other potential connecting species (*C. picazuro*, *T. amaurochalinus* and *T. sayaca*) and the abundance of consumed or preferred fruit in either habitat (results not shown).

The calculation of sampling completeness to assess data quality showed that 98.4 and 94.8% of the theoretically expected plant–bird interactions were detected in PNMRN and in the gardens, respectively.

Discussion

Globally, more people live in urban areas than in rural areas, with 55% of the world's population residing in urban areas in 2018, and a projected 68% to be urban by 2050 (United Nations, Department of Economic and Social Affairs, Population Division 2019). Such urban expansion threatens to destroy and fragment habitats in key biodiversity hotspots. As a result, patches of formerly natural habitat will become immersed in cities, and

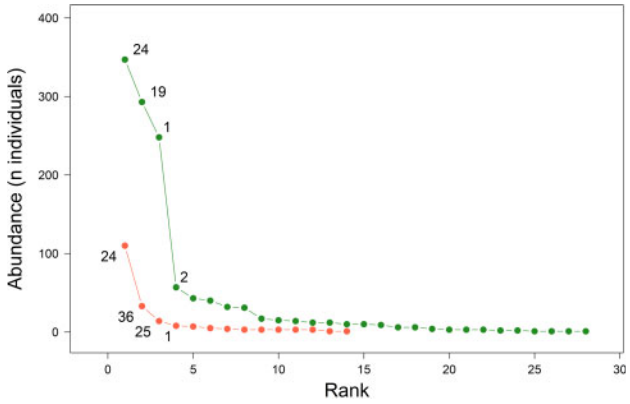

Figure 3: Rank-Abundance graphs of all frugivore bird species recorded in an urban nature reserve (in green) and three nearby garden (red). The four most abundant species in each habitat are labeled with their identifying code (Supplementary Table S1). Each point represents a species

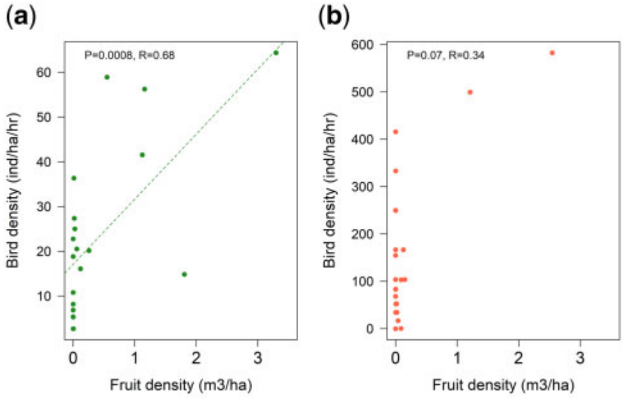

Figure 5: Correlation between the abundance of *T. rufiventris* and the abundance of preferred fruit in (**a**) an urban nature reserve and (**b**) three nearby gardens. Fruit abundance was log-transformed prior to analysis. Pearson correlation coefficients are shown

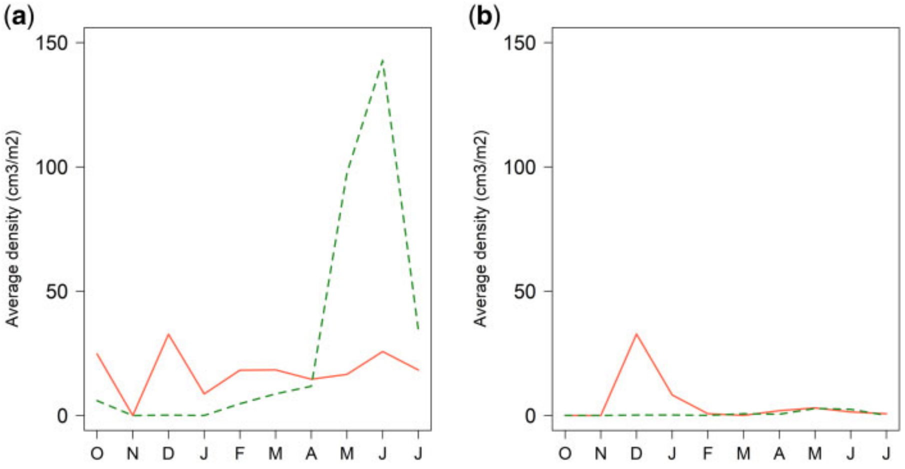

Figure 4: Abundance of (**a**) consumed and (**b**) preferred fruit in an urban nature reserve (in green) and three nearby gardens (in red)

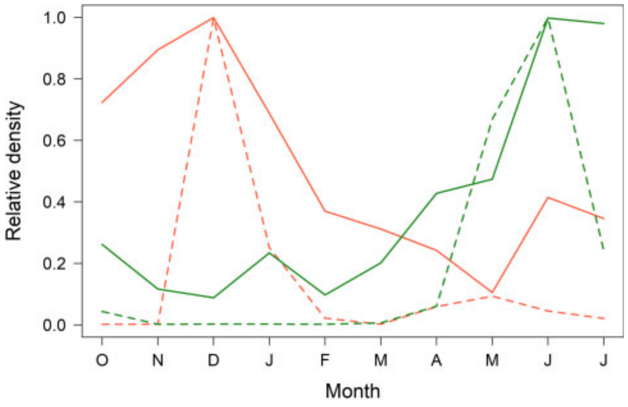

Figure 6: Relative abundances of *T. rufiventris* (solid lines) and its preferred fruit species (dashed lines) in PNMRN (green lines) and the gardens (red lines). In each habitat, the abundance of birds and fruits was divided by the maximum value recorded throughout the study

the urban green patches that previously existed will become even more isolated. This process poses a threat to the survival of a wide array of organisms, from plants to arthropods to vertebrates. Among birds, large frugivores are often one the guilds most vulnerable to the isolation imposed by urbanized landscapes (Franz, Cappelatti, and Barros 2010).

Urban reserves play a key role in preserving these novel, seminatural ecosystems and, in recent years, growing efforts have furthered our understanding of their structure (i.e. species diversity) and conservation status. However, few studies have attempted to understand their functioning, in particular the interactions between the species involved, which are the 'architecture of biodiversity' (Bascompte and Jordano 2007) upon which long-term species' persistence relies. This knowledge is critical for managing urban reserves in a sustainable way, preserving all their ecological complexity as living interconnected communities of species.

In this context, our study provides a description of the way frugivorous birds and fleshy-fruited plants interact in an urban nature reserve giving rise to a complex network of interactions. Furthermore, our results suggest these interactions go beyond the physical limits of the reserve and connect with plants in the surrounding nearby gardens, which may have implications for landscape planning.

Plant–bird interaction networks

The plant–frugivore interaction network of the reserve has a rather low species richness compared with published networks (Jordano 1987; Olesen and Jordano 2002; Jordano, Bascompte, and Olesen 2002; Bascompte and Jordano 2006, 2007; Rezende, Jordano, and Bascompte 2007) and is dominated by two species *T. rufiventris* and *L. sinense* that interact very strongly. This means the network is probably rather vulnerable to the loss or abrupt reduction in abundance of either of these two *hub* (sensu Olesen et al. 2007) species. These changes in abundance may be triggered by natural (e.g. storms or tidal surges) or man-made (e.g. aggressive management interventions) events.

Turdus rufiventris is the most abundant native bird. Although it is common that avian frugivores benefit from non-native plant species in urban environments (Reichard, Chalker-Scott, and Buchanan 2001) this bird seems to have notably was observed to use most potential interactions in the network. *Turdus rufiventris* seems to be resilient and adapted to several forms of environmental degradation and in previous studies it has shown a tendency to be an edge specialist (Da Silveira et al. 2016). Regionally, *T. rufiventris* it is one of the most abundant fruit consumers from south Brazil to central Argentina (Guix 2007; Franz, Cappelatti, and Barros 2010; Blendinger et al. 2012; Díaz Vélez et al. 2015; Da Silveira et al. 2016 and references therein; De la Peña and Pensiero 2017; Enedino, Loures-Ribeiro, and Santos 2018) and it is a legitimate seed disperser as it tends to defecate or regurgitate intact seeds from the fruit it eats, far away from the source plant (Montaldo 2005; Guix 2007).

The results suggest that *T. rufiventris* tracks fruit in the gardens in summer due to greater fruit availability than in PNMRN and remains in the reserve in winter when preferred fruit density in both environments is similar. *Turdus rufiventris* is thus connecting the reserve and the gardens by feeding alternately in each habitat, and not in a completely random pattern, but rather as a response to seasonal changes in fruit availability (Caula, Marty, and Martin 2008). A comparable, but seasonally reversed, behavior has been observed in forest fragments of several locations in Brazil: during winter months, if fruit availability in the forest is low, frugivore–insectivore birds enter urban areas to find alien plants that fructify abundantly (Guix 2007).

The fact that the main food source of *T. rufiventris* is the alien plant *L. sinense* suggests it may be contributing significantly to the invasion of species in the nature reserve (Williams 2006; Guix 2007). *Ligustrum sinense* is consumed by at least five other common bird species. This poses a challenge in terms of management as its large-scale removal may trigger a cascade of unwanted effects that could ripple across the entire system (Gleditsch 2017). In this sense, the network approach combined with the preference analysis provide clues as to which plants may act as alternative sources of 'appetizing' fruits to the bird community. For instance, *Myrsine laetevirens* is moderately preferred by three bird species and avoided by none (Fig. 2a), so it is a promising alternative food source to mitigate a large-scale removal of *L. sinense* from the nature reserve.

Other abundant species, however, were systematically avoided by birds. Such is the case of *P. dioica*. The reason for being avoided could be that this tree species contains secondary metabolites such as saponins (Cipollini and Levey 1997) which interfere with digestion (and may even be toxic for cows and chickens; Storie, McKenzie, and Fraser 1992), or that the fruits may have low nutritional value (Jordano 1992; Montaldo 2000) or may be difficult to eat (Moermond and Denslow 1985; Montaldo 2005).

Understanding the causes behind bird preferences, which in turn elicit the fruit-tracking behavior, is a complex problem. Blendinger et al. (2012) suggested that only fruit consumed rather than all fruit present should be used when testing the fruit-tracking hypothesis. We found this to be also true in our study site when testing correlations between abundance of consumed fruit and bird abundance. In fact, also eliminating species that were seldom selected by birds improved our fruit-tracking correlations. Fruit abundance as perceived by birds, however, may depend on intraspecific variations such as plant morphology and spatial arrangement, which affects birds' access to fruit, as well as interspecific variation, such as fruit nutritional values (Moermond and Denslow 1985).

Analyses of intensively sampled plant–frugivore communities have shown that network patterns are determined by short-term variation in abundance and seasonal variation in resource-switching behavior (Carnicer, Jordano, and Melián 2009), which is partly based on the birds' innate or acquired perception of fruit nutritional value. Although our results suggest both processes are present in our network, our understanding of the reserve-gardens system would certainly benefit from a more intense and spatially replicated sampling that would detect more interactions (particularly the rarer ones), and allow linking the fruiting phenologies, fruit nutritional values, the seasonal changes in bird abundances, the shifts in birds' feeding behavior and the short-term temporal changes in network structure. This mechanistic understanding of the system would allow fine tuning management decisions to an unprecedented degree.

Limitations

The two main sources of bias in this study are the lack of independent replicates and the difference in sampling techniques between habitats. Due to logistic constraints only one nature reserve and a small number of gardens were studied, in just one fruiting season. This limits the generality of our results. Also, because the two transects were contiguous, the possibility of double counting some of the individuals could not be completely discarded.

The use of different sampling techniques in the reserve and the gardens may bias the results in complex ways. There are two aspects to consider: the effect of sampling on the detection of birds and on the detection of their feeding interactions. In the reserve, an observer moving along a path is likely to underestimate bird richness as he may either scare away shy birds or miss individuals hiding in the woody, leafy surroundings. In the confined limits of the gardens, the observer, even though remained static, was still plainly visible to birds, so this may also lead to scaring shy species. In addition, the gardens are more open and more frequently disturbed than the reserve, so the shy species are probably altogether absent from that habitat.

The second aspect to consider is the way the sampling technique may have affected the detection of feeding interactions. To the best of our knowledge, there are no studies that compare the performance of sampling methods in the detection of plant–bird interactions. There is, however, a comparable study by Gibson et al (2011) on the way sampling methods affect the structure of plant–pollinator networks. When compared with transects, static timed observations achieve a higher detection of unique interaction. This is explained by the fact that timed observations are better at recording interactions in which rare or cryptic species are involved (Gibson et al. 2011). In this sense, it is likely that the actual networks of interactions of the reserve is more complex than we observed, both in terms of species and interactions as the transect sampling may have missed rare plants and rare (or shy) birds.

Interactions between species are shaped by a diverse array of mechanisms that operate at different temporal and spatial scales (Hastings 2004). In this context, our results have the limitations inherent to observational studies. The correlation between fruit and frugivore abundance does not necessarily mean that the mechanism of fruit-tracking is occurring as other factors could be involved in explaining frugivore dynamics. These could include the dynamics of other food or habitat resources, and those of predators and competitors, among others (Carnicer, Jordano, and Melián 2009). For instance, we did not consider the fruit available on the street habitat, which has lower local species richness and a typically linear spatial arrangement.

Finally, only one of the four potential connector species could be analyzed because too few individuals of the species *T. sayaca* and *T. amaurochalinus* were spotted and, although *C. picazuro* was very abundant, it was seldom seen feeding on fruit. This may be because our sampling method was not appropriate for this species and we missed feeding events. *C. picazuro* tends to feed early in the morning (N. H. Montaldo, pers. obs.) when we did not have access to the nature reserve, and it is rather shy and flies away when the observer approaches. For these species, a different sampling technique might be more appropriate in order to infer connectivity between environments, e.g. recording bird movements with radio transmitters, ringing birds in one habitat and recording its presence in the other or fecal sampling.

Conclusion

The reserve is a valuable refuge as it contains species and interactions that occur infrequently elsewhere in the surrounding urban matrix. However, the reserve may be extremely sensitive to management interventions because of the dominance exerted by a pair of tightly linked species.

Previous studies have highlighted that urban reserves both large (Enedino, Loures-Ribeiro, and Santos 2018) and small (Volenec and Dobson 2019) can make viable and significant contributions to bird conservation as habitat and by increasing landscape connectivity in metropolitan regions. Our results suggest that including gardens, particularly those near small reserves, into management strategies may have an additional positive impact on some bird species as they would provide alternative sources of food for large frugivore birds. This is consistent with previous studies that claim that non-reserve management may be just as important to maintain the functional connectivity of a landscape to aid species persistence (Uden et al. 2014). To effectively conserve biodiversity for future generations in landscapes fragmented by human development, large reserves, small reserves and private green spaces must be included in conservation planning.

Data availability

Data on plant–bird interactions will be uploaded to Web of Life Database (http://www.web-of-life.es/).

Supplementary data

Supplementary data are available at *JUECOL* online.

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