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

Mariki Y. Zietsman,¹ Norberto H. Montaldo¹ and Mariano Devoto ²,∗

¹Facultad de Agronomía, Cátedra de Botánica General, Universidad de Buenos Aires, Av. San Martín 4453, C. A. de Buenos Aires C1417DSE, Argentina and ²Consejo 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...
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, Wenry, 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, Ramírez, 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-fruit 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 m², 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, Pitrangus 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°C 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 518 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 Degenini 1995; Bertolini and Caminha 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 Guittán 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 x 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
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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

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.

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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).

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, \( r = 0.28 \) and \( P = 0.427, n = 10 \) months) nor when considering only preferred fruit species (\( r = 0.43 \) 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 \( C. \) picazuro (Columbidae). Two plant species were common to the two habitats: the native \( P. \) dioica and the exotic \( M. \) 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
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 of 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 this species is known to thrive in highly urbanized areas, it is also able to adapt to a variety of landscapes and habitats. This behaviour may be due to the bird’s strong foraging ability, which allows it to exploit a wide range of food resources. In our study, *T. rufiventris* was found to be the most abundant species in the reserve, followed by *L. sinense*. Both species are known to be generalist feeders, able to consume a wide range of fruits and insects. In our study, we found that the abundance of both species was highest during the months of April and May, which may be related to the availability of fruits such as *L. sinense* and *T. rufiventris*.

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).

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.
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. picazo* 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.

**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 (Volenc 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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