Local bird traits match fruit traits of two alien plants in urban fruit-frugivore interactions

Facundo X. Palacio✉ & Diego Montalti

Sección Ornitología, División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo. La Plata, Buenos Aires, Argentina.

Abstract. Bird-mediated seed dispersal enhances invasions of many alien plant species. Typically, this mutualism is composed of a generalist assemblage of frugivorous birds in which morphological trait matching between bird and plant species is often thought to be poor due to low reciprocal adaptation. Despite this long-held notion, trait matching between local birds and alien plants has not been investigated. Here, we assessed trait matching by comparing functional traits in multidimensional space for local birds (bill, wing and tarsus size) and two alien invasive plants (fruit and seed size, fruit and seed shape) in an urban area. To do this, we measured bird functional traits in museum specimens and plant functional traits in individuals located in the study area. We found significant trait matching between birds and alien invasive plants (i.e., frugivorous birds interacted with morphologically corresponding invasive plant species). In addition, we detected a positive correlation between morphological and functional specialization of bird species so that extreme morphologies played specialized functional roles. Contrary to the idea that alien plant mutualisms are mediated by generalized seed dispersers without a close match between bird and alien plant traits, our results indicate that species with different morphologies forage on distinct plant species. These findings highlight the importance of studying the functional role of local birds in mutualistic interactions with alien invasive plants, and how these functional roles may promote invasion processes.

[Keywords: seed dispersal, invasive species, frugivory]

Resumen. **Los rasgos de las aves locales coinciden con rasgos de los frutos de dos plantas exóticas en interacciones fruto-frugívoro urbanas.** La dispersión mediada por aves promueve la invasión de muchas especies de plantas exóticas. Típicamente, este mutualismo se compone de un ensamble generalista de aves frugívoras en el cual el acople de rasgos morfológicos entre especies de aves y plantas se considera pobre como resultado de una baja adaptación recíproca. A pesar de esta idea de larga data, el acople de rasgos entre aves locales y plantas exóticas no ha sido investigado. Evaluamos el acople de caracteres mediante la comparación de rasgos funcionales en un espacio multidimensional para aves frugívoras locales (tamaño del pico, ala y tarso) y dos plantas invasoras (tamaño del fruto y semilla, forma del fruto y semilla) en un área urbana. Para esto, medimos los rasgos funcionales de las aves en especímenes de museo y los rasgos funcionales de las plantas en individuos localizados en el área de estudio. Encontramos un acople de rasgos significativo entre las aves y las plantas invasoras (las aves frugívoras interactuaron con aquellas especies de plantas invasoras correspondientes en términos morfológicos), y una correlación positiva entre la especialización morfológica y la funcional de las especies de aves (morfologías extremas tuvieron roles funcionales especializados). Contrario a la idea de que los mutualismos de plantas invasoras son mediados por dispersores de semillas generalistas sin un ajuste fino entre rasgos de las aves y plantas, nuestros resultados indican que especies con diferentes morfologías se alimentan de especies de plantas distintivas. Estos resultados resaltan la importancia de estudiar el rol funcional de las aves locales en interacciones mutualistas con especies de plantas exóticas, y cómo estos roles funcionales pueden promover los procesos de invasión.

[Palabras clave: dispersión de semillas, especie invasora, frugivoría]

Introduction

Seed dispersal by vertebrates is recognized as a major mechanism of plant invasion (Gosper et al. 2005; Buckley et al. 2006). In a novel environment, alien invasive plants (*sensu* Richardson et al. 2000) can disrupt mutualistic plant-frugivore interactions by establishing new links with local birds and impairing previous ones between birds and native plants (Traveset and Richardson 2006). For instance, Spotswood et al. (2012) found that the alien invasive *Miconia calvescens* shifted diets of local birds decreasing fruit consumption of native plants in French Polynesia. Consequently, this species severely altered seed dispersal assemblages in the most invaded sites (Spotswood et al. 2012). In two studies, Heleno et al. (2013a,b) found a higher integration of alien plants and simplified frugivore assemblages in plant-frugivore networks from insular systems. Alternatively, invasive plants can also facilitate fruit removal

of native species via the attraction of seed dispersers. For instance, Vergara-Tabares et al. (2021) found that fruiting availability of invasive *Pyracantha* shrub species increased frugivory by seed dispersers of native plant species in Argentina. Despite these potential negative and positive effects of alien plants on plant-frugivore interactions, whether fine-tuned morphological matching between plants and birds exists in bird-alien plants networks remains poorly tested.

Broad patterns found in alien invasive plant-frugivore interactions include: 1) alien plants benefiting from the seed dispersal service provided by local birds, and 2) alien plants spreading mediated by generalist frugivore assemblages (Gosper et al. 2005; Traveset and Richardson 2006; García et al. 2014; Ramaswami et al. 2016). Under these scenarios, fine-tuned matching between local and alien invasive species traits relevant for the interaction is thought to be poor, as the interaction is relatively recent to promote reciprocal adaptation (Traveset and Richardson 2006). However, a generalist seed dispersal system should not necessarily lead to a mismatch between plant and bird traits. This is because some bird species, despite being generalists, preferentially interact with some plant species (Jordano et al. 2003). This, in turn, may be driven or constrained by morphological traits (González-Castro et al. 2015; Bender et al. 2018). For instance, Burns (2013) found that average size of consumed fruits increased with maximum bird gape width in plant-frugivore interactions in New Zealand. In another study, Dehling et al. (2016) found that bird species with different morphologies foraged on distinct groups of plant species in Andean plant-frugivore assemblages. However, the long-held notion that alien invasive plant mutualisms are composed of generalist seed dispersers without a close match between bird and alien invasive plant traits has not been investigated in plant-frugivore mutualisms yet.

Here, we assessed whether morphological trait matching between local (native and alien) birds and two alien invasive plant species (*Melia azedarach* and *Ligustrum lucidum*) occur in plant-frugivore interactions in an urban area. Our hypothesis is that trait matching between birds and alien invasive plants is poor, under the assumption that a generalist bird assemblage is not locally adapted to alien invasive plant traits. To test this, we compared bird and fruit functional traits

relevant for this mutualism and analyzed how these traits relate to interaction patterns between birds and plants. We also analyzed whether morphologically specialized birds correlated with specialized functional roles in the interaction.

Materials and Methods

Study site and species

The study was carried out in La Plata city (34°55' S - 57°57' W), northeast Buenos Aires province, Argentina. The study area is ~16 km² (183798 inhabitants) (Lódola and Brigo 2011), and two major habitat types can be recognized: a) built-up areas including a densely built-up city center and residential areas with numerous gardens and tree avenues (main tree species are *Jacaranda mimosifolia*, *Melia azedarach*, *Citrus aurantium*, *Platanus acerifolia*, *Tilia×moltkei*, *Acer negundo* and *Ligustrum lucidum*), and b) parks regularly distributed over the study area composed mainly of mature trees (de Paula 1987), such as *Phytolacca dioica*, *Chorisia speciosa*, *Jacaranda mimosifolia*, *Erythrina christagalli*, *Cyca revoluta*, *Pinus pinaster*, *Cupressus sempervirens*, *M. azedarach*, *L. lucidum* and *Phoenix canarensis*. The average annual rainfall is 1062 mm and the average annual temperature is 15.9 °C.

The Chinaberry tree *Melia azedarach* L. (Meliaceae) is a deciduous tree, reaching between 10 and 15 m in height. The wild form originates from southern Asia and northern Australia and has been introduced to many parts of the world (e.g., North and South America, Mediterranean basin, Africa) as an ornamental and shade tree (Mabberley 1984; Thakur et al. 2016; Bhatt et al. 2021). Fruits are yellow fleshy drupes (12-13 mm) that contain one seed (Bitani et al. 2020) dispersed by birds and bats (Corlett 2005; Voigt et al. 2011; Jordaan et al. 2012). In Argentina, the Chinaberry tree was introduced with the European colonization, and now is an alien invasive species in the Pampas Region (Ghersa et al. 2002). The Glossy Privet *Ligustrum lucidum* W.T. Aiton (Oleaceae) is an evergreen tree native to China reaching up to 15 m in height considered alien invasive in Australia, New Zealand, North America and Argentina (Fernández et al. 2021). This tree produces two-seeded bluish-black fruits (~5-8 mm diameter) whose seeds are dispersed by birds (Montaldo 1993; Rougès and Blake 2001). Like the Chinaberry tree, the Glossy Privet was introduced around the 1900's as an ornamental species and has

invaded several regions in Argentina, with negative impacts on both native plant and bird diversity (Montaldo 2005; Aragón and Morales 2003; Ayup et al. 2014; Fernández et al. 2020). Both alien species are invasive in the study area and have extended fruiting seasons (May to October) (Piccolo and Gregolim 1980; Montaldo 1993) and are ones of few species fruiting throughout the winter in the study area. They thus represent an important food supply for birds, a property that facilitates invasion success (Gosper et al. 2005; Aguirre-Acosta et al. 2013). As the Glossy Privet and the Chinaberry Tree occur at high densities in La Plata (F.X.P personal observation) and the frugivorous bird assemblage is composed of a set of generalist species (Montalti and Kopij 2001), the study site provides a suitable system to test our hypothesis.

Field sampling

Fieldwork was carried out during 13 days (September 26th to October 7th, 2016). We estimated Chinaberry tree and Glossy Privet abundance in 40 line transects (500-m long and 20-m wide) located randomly in the study area. To this end, we first placed 40 random points on a Google Earth image, and the nearest street was selected. This location represented the beginning of a given transect. We then selected a random orientation using two numbers (two possible directions on a given street). Only those individuals with ripe fruits were counted.

Fruit and bird measurements

To characterize fruits, we randomly selected 10 Chinaberry trees and 7 Glossy Privet trees, and collected 10 and 15 fruits per plant, respectively. Diameter, length, area and circularity were measured for each fruit and seed on scaled photographs using the software ImageJ 1.4 g (Rasband 1997). Circularity was estimated as $(4\pi \times Area)/(Perimeter)^2$. A total of 100 fruits and 100 seeds were measured for the Chinaberry tree, and 105 fruits and 206 seeds were measured for the Glossy Privet. Photographs were taken with a Canon EOS 550D digital camera (18.0 megapixels).

We also measured traits relevant for the foraging behavior of 13 bird species consuming fruits common in the city and nearby surrounding areas (Montalti and Kopij 2001; Palacio and Montalti 2013). These species were: Rufous-bellied Thrush (*Turdus rufiventris*), Creamy-bellied Thrush (*T. amaurochalinus*), Chalked-browed Mockingbird (*Mimus saturninus*), Great Kiskadee (*Pitangus sulphuratus*), Rufous-collared Sparrow (*Zonotrichia capensis*), Picazuro Pigeon (*Patagioenas picazuro*), European Starling (*Sturnus vulgaris*), Monk Parakeet (*Myiopsitta monachus*), Turquoise-fronted Parrot (*Amazona aestiva*), Maroon-bellied Parakeet (*Pyrrhura frontalis*), Scaly-headed Parrot (*Pionus maximiliani*), White-eyed Parakeet (*Psittacara leucophthalmus*) and Mitred Parakeet (*P. mitratus*). The European Starling is an alien invasive species introduced from Europe in the late 1980's (Ibáñez et al. 2016; Palacio et al. 2016). The Turquoise-fronted Parrot, Maroon-bellied Parakeet (*Pyrrhura frontalis*), Scaly-headed Parrot (*Pionus maximiliani*), White-eyed Parakeet (*Psittacara leucophthalmus*), and Mitred Parakeet (*P. mitratus*) are parrots introduced from northern Argentina in the early 2000's which are expanding their distributions (Ibáñez et al. 2014; Scheffer et al. 2015). Although parrots have been typically considered as antagonists due to seed destroying, recent studies have shown that they also act as key seed dispersers (recorded for all these species, including the Monk Parakeet) (Tella et al. 2015, 2019; Blanco et al. 2016). We measured six bird traits on 5-22 specimens (adults, males and females) housed at the Ornithology collection of Museo de La Plata (La Plata, Argentina) with a digital caliper (nearest 0.01 mm). The traits measured were: mandibula length, culmen length, gape width, bill depth, tarsus length, and wing chord. Bill traits (mandibula length, culmen length, gape width, bill depth) influence a bird's ability to handle fruits by constraining fruit size (Wheelwright 1985; Palacio et al. 2017), while tarsus length and wing chord relate to foraging substrate and maneuver (Miles and Ricklefs 1984). All measurements were made on the right side of each bird because some species show bilateral asymmetry (one side of the body was larger than the other) (McNeil and Martínez 1967). We recorded the sex and age of each specimen from the museum tag. Specimens from the study area (Buenos Aires province) were measured for native species and the European Starling, whereas specimens from part of their original distribution range (northwestern Argentina) were also measured for alien parrots. This was because parrot populations in the study area are from this region (Scheffer et al. 2015). The use of museum specimens to measure bird morphology has been shown to be a suitable approach to describe birds' functional roles

in biological communities (Dehling et al. 2016; Pigot et al. 2016). Finally, we built a presence-absence network based on fruit-bird interactions recorded in published sources (Montaldo 1993; de la Peña 2001; Perchivale and Lucero 2013; Frutos et al. 2014; Ibáñez et al. 2014; Scheffer et al. 2015; Benavidez et al. 2018) and personal observations of the authors (for Rufous-Bellied Thrush, European Starling, Picazuro Pigeon, and Scaly-headed Parrot).

Data analysis

We assessed the functional role of species by analyzing the traits of the species they interact with following the approach of Dehling et al. (2016). This framework characterizes the functional role of a species by analyzing the traits of interacting species in a multidimensional trait space (Dehling et al. 2016). First, two functional trait spaces are built, one for birds and another for plants, using a dimensionality reduction technique (e.g., principal component analysis), and species are projected into their respective trait spaces. Second, bird species are projected into the plant trait space by computing their interaction centroids (resulting from a plant-bird interaction network). This bird interaction centroid is the mean position of the set of plants that each bird consumes, in plant trait space (Dehling et al. 2016). The position of bird species in bird trait space and their bird interaction centroids in plant trait space are compared with Procrustes rotation and a Mantel test (Dehling et al. 2016). This allows a direct association between trait combinations of interacting species partners. Thus, for each trait matrix (fruits and birds), a principal component analysis (PCA) was performed (functional trait spaces) and the bird species centroids were computed (Palacio et al. 2020). We retained the first two components for both ordinations, accounting for >89% of explained variance. Then, bird species were projected into the plant trait space by computing their interaction centroids. As the network was built using presence-absence data, interaction centroids were represented by the un-weighted averages of PC scores in plant trait space. The relative position of birds in bird trait space and the bird interaction centroids in plan trait space were compared with Procrustes rotation (superimposing both ordinations until the best fit is reached) and a Mantel test (correlating the pairwise distances between bird species in bird trait space with the pairwise distances between their interaction centroids in plant trait space)

(Dehling et al. 2016). To test whether test results were expected by chance, interactions between species in the networks were randomized (10000 iterations). A significant result (P<0.05) indicates matching between bird and plant functional traits (Dehling et al. 2016).

In addition, to test if morphologically extreme species played specialized functional roles in the interaction, we computed the degree of morphological specialization of bird and plant species as the degree to which their morphology differed from those of other species in the assemblage. For this purpose, we computed morphological originality and morphological uniqueness (Dehling et al. 2016). Morphological originality represents the distance of a bird species in trait space to the overall centroid of the trait space (Dehling et al. 2016). A species far apart from the centroid of the trait space can be considered morphologically original. In contrast, morphological uniqueness is the distance of a bird species in trait space to its nearest neighbor (Dehling et al. 2016). Therefore, a species far apart from any other species is considered as morphologically unique. Similarly, functional specialization was computed as functional originality (distance of an interaction centroid to the overall interaction centroid in plant trait space) and functional uniqueness (distance of an interaction centroid to its nearest neighbor in plant trait space). A species' interaction centroid far apart from the mean interaction centroid in plan trait space describes a species functionally specialized, and a species' interaction centroid far apart from the next similar species in plant trait space represents a species functionally unique (Dehling et al. 2016). Therefore, a species functionally original plays a functional role (in terms of its interactions with plants) not played by most species, whereas a species functionally unique plays a functional role not played by any other species. To test whether morphological specialization was related to functional specialization, we first standardized originality and uniqueness to the range 0-1 and fitted a beta regression model with a logit-link function (Douma and Weedon 2019).

All analyses and graphs were run in R v.4.0.2 (R Core Team 2020) using the packages doBy (function summaryBy) (Højsgaard and Halekoh 2020), vegan (function protest) (Oksanen et al. 2018), ade4 (function mantel.rtest) (Dray and Dufour 2007) and

betareg (function betareg) (Cribari-Neto and Zeleis 2010).

RESULTS

Fruiting individuals of the Glossy Privet (mean density=0.75 individuals/ha, 95% confidence interval=0.32-1.73, n=40, overall estimated abundance=2025 individuals) were more abundant than fruiting individuals of the Chinaberry tree (mean density=0.40 individuals/ha, 95% confidence interval=0.15-1.06, n=40, overall estimated abundance=1080 individuals) in the study area in Spring-Summer. Both PCA accounted for high variation in the first two axes (90.88% and 89.50%, for birds and fruits, respectively). For birds, PC1 represented a dimension of bill and body size variation positively related to culmen length, gape width, bill depth, and wing chord, while PC2 represented a dimension of tarsus and mandibula length positively related to these traits (Figure 1a). Mostly, PC1 separated Psittacidae from Passeriformes, while the Picazuro Pigeon (Columbidae) showed mean trait values (Figure 1a). The largest species were the Turquoise-fronted Amazon, Scaly-headed Parrot, White-eyed Parakeet, and Mitred Parakeet (Table 1). The Picazuro Pigeon was also a large species, but had a relatively small bill (Table 1). For fruits, PC1 represented an axis of fruit and seed size variation positively associated with fruit and seed diameter, length, and area, whereas PC2 represented an axis of fruit and seed shape variation

positively associated with fruit and seed circularity (Figure 1b). Fruits of *M. azedarach* showed higher trait variation than fruits of *L. lucidum*, but fruit and seed circularity was nearly equal for both species, showing quite rounded fruits and seeds (Table 2).

The relative position of bird species in bird trait space correlated significantly with the relative position of bird interaction centroids in plant trait space (Procrustes sum of squares = 0.54, Procrustes r=0.68, P=0.003; Mantel r=0.47, P=0.002). Therefore, different bird species interacted with Chinaberry tree and Glossy Privet according to their morphology (Figure 1c). Moreover, morphological

Table 2. Fruit and seed measurements for the invasive Chinaberry tree (*Melia azedarach*) (n=100 fruits and 100 seeds) and Glossy Privet (*Ligustrum lucidum*) (n=105 fruits and 206 seeds) from La Plata city, east-central Argentina. Mean±1 standard deviation is shown.

Tabla 2. Medidas de frutos y semillas de las invasoras Paraíso (*Melia azedarach*) (n=100 frutos y 100 semillas) y Ligustro (*Ligustrum lucidum*) (n=105 frutos y 206 semillas) de la ciudad de La Plata, centro-este de Argentina. Se muestra la media±1 desviación estándar.

Trait	*Melia azedarach*	*Ligustrum lucidum*
Fruit length (mm)	13.5±1.4	7.0±0.6
Fruit diameter (mm)	12.5±1.0	5.9±0.7
Fruit area (mm^2)	142.3±20.0	34.9±5.6
Fruit circularity	0.8±0.1	0.8±0.1
Seed length (mm)	11.7±1.3	5.5±0.6
Seed diameter (mm)	10.0±1.1	3.4±0.4
Seed area (mm^2)	96.8±18.5	15.6±3.4
Seed circularity	0.7±0.1	0.7±0.1

Table 1. Bird measurements of 13 species consuming fruits of the invasive Chinaberry tree (*Melia azedarach*) and Glossy Privet (*Ligustrum lucidum*) in La Plata city, east-central Argentina. Data are presented in mm as mean±1 standard deviation.

Tabla 1. Medidas de 13 especies de aves que consumen frutos de las invasoras Paraíso (*Melia azedarach*) y Ligustro (*Ligustrum lucidum*) en la ciudad de La Plata, centro-este de Argentina. Los datos se presentan en mm como media±1 desviación estándar.

Species	Family	Mandibula length	Culmen length	Gape width	Bill depth	Tarsus length	Wing chord	Sample size
Amazona aestiva	Psittacidae	18.4±1.3	33.7±2.1	19.4±0.8	32.0±1.2	13.1±1.2	224.0±8.0	11
Mimus saturninus	Mimidae	25.1±1.8	17.6±0.8	11.2±0.5	6.8±0.4	35.1±1.6	116.0±4.0	20
Myiopsitta monachus	Psittacidae	12.1±0.9	19.8±0.9	14.0±0.6	20.6±0.9	13.053±1.1	147.0±5.0	22
Patagioenas picazuro	Columbidae	25.9±1.4	19.2±0.9	10.7±1.1	7.6±0.8	24.1±2.7	227.0±8.0	5
Pionus maximiliani	Psittacidae	15.7±1.5	27.8±1.4	17.4±0.8	27.2±1.5	12.2±1.1	188.0±7.0	16
Pitangus sulphuratus	Tyrannidae	36.3±1.5	6.9±1.7	16.9±1.6	10.4±0.6	25.6±1.9	11.8±0.5	20
Psittacara leucophthalmus	Psittacidae	16.1±2.1	27.7±1.5	19.2±1.3	31.5±1.8	12.0±1.4	179.0±5.0	12
Psittacara mitrata	Psittacidae	16.1±1.4	31.5±1.5	19.8±0.5	35.9±1.3	12.6±1.3	199.0±6.0	9
Pyrrhura frontalis	Psittacidae	11.8±1.0	16.7±1.3	12.5±0.4	18.1±1.2	10.9±1.5	132.0±2.0	8
Sturnus vulgaris	Sturnidae	29.0±1.0	23.7±1.2	11.0±0.7	7.06±0.6	25.9±1.2	12.0±0.5	13
Turdus amaurochalinus	Turdidae	25.1±2.0	17.2±1.0	12.2±0.7	6.8±0.3	31.4±1.0	11.5±0.4	20
Turdus rufiventris	Turdidae	25.9±1.8	19.5±1.2	12.2±0.7	7.5±0.5	34.6±2.5	11.7±0.4	20
Zonotrichia capensis	Passerellidae	13.1±1.2	10.2±0.8	8.6±0.6	6.8±0.4	19.4±1.4	6.5±0.2	20

(a)

(b)

(c)

Turr (n) Tura (n) Patp (n) Myim (n) Piom (a)

Mims (n)

Amaa (a)

Pits (n)

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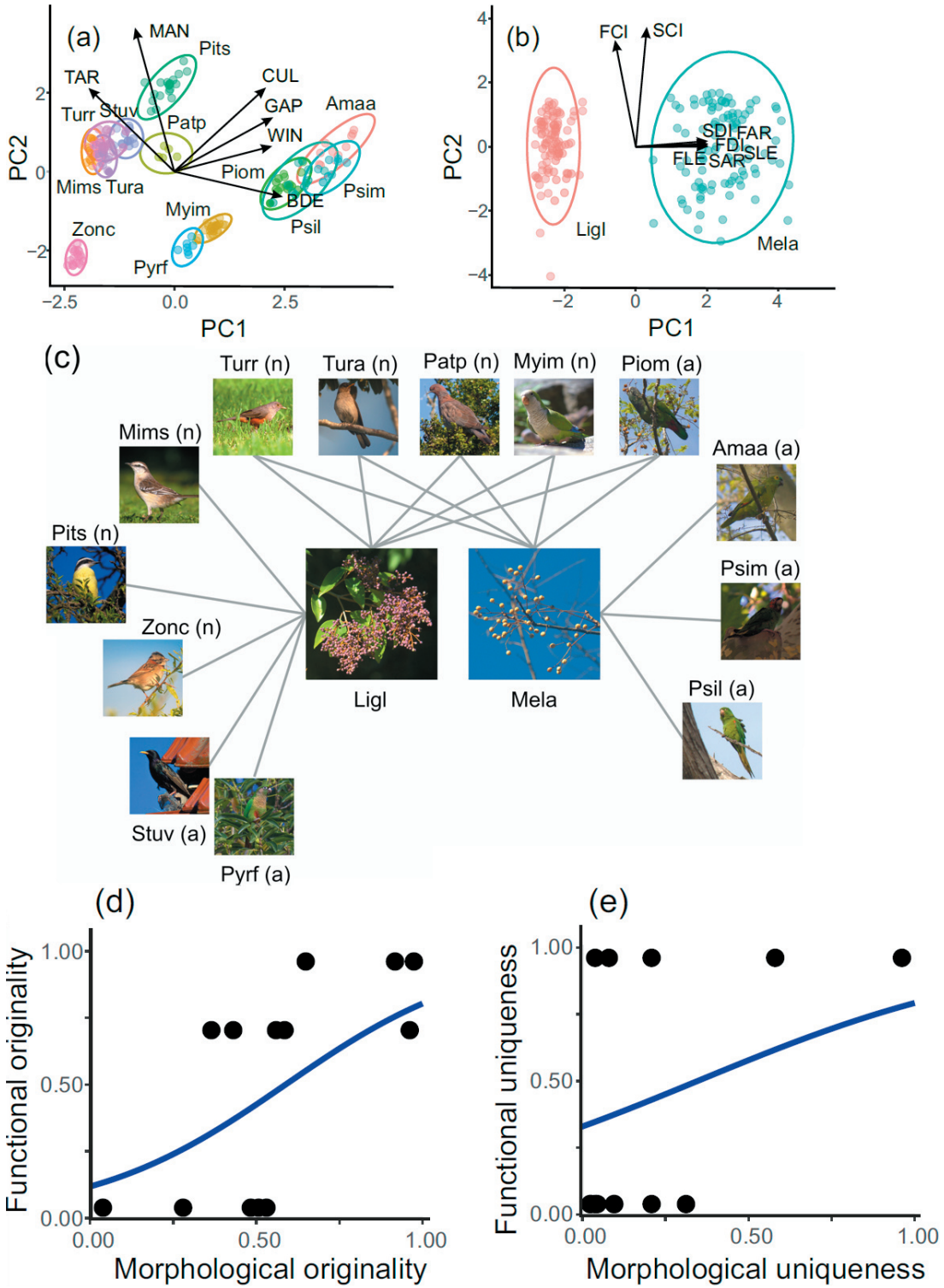Ligl   Mela

Psil (a)

Stuv (a)

Pyrf (a)

(d)

(e)

Figure 1. Trait matching between birds, Chinaberry tree (*Melia azedarach*) and Glossy Privet (*Ligustrum lucidum*) in La Plata City, Argentina. (a) Bird trait space (principal component analysis) based on morphological traits (arrows). Colors and confidence ellipses depict different species. Amaa: *Amazona aestiva*, Mims: *Mimus saturninus*, Myim: *Myiopsitta monachus*, Patp: *Patagioenas picazuro*, Piom: *Pionus maximiliani*, Pits: *Pitangus sulphuratus*, Psil: *Psittacara leucophtalmus*, Psim: *Psittacara mitrata*, Pyrf: *Pyrrhura frontalis*, Stuv: *Sturnus vulgaris*, Tura: *Turdus amaurochalinus*, Turr: *Turdus rufiventris*, Zonc: *Zonotrichia capensis*, CUL: culmen length, GAP: gape width, WIN: wing chord, BDE: bill depth, MAN: mandibula length, TAR: tarsus length. (b) Plant trait space (principal component analysis) based on fruit and seed morphological traits (arrows). Colors and confidence ellipses (95%) depict each species. Ligl: *Ligustrum lucidum*, Mela: *Melia azedarach*, SDIA: seed diameter, FDIA: fruit diameter, FLEN: fruit length, SARE: seed area, SLEN: seed length, FCI: fruit circularity, SCI: seed circularity. (c) Fruit-frugivore interactions between birds, Chinaberry tree and Glossy Privet based on published and personal data. Photographs: F.X. Palacio. (d-e) Relationship between morphological and functional specialization. Points show observed values, and lines depict predictions from beta regression models. a: alien bird species, n: native bird species.

Figura 1. Acople de rasgos entre aves, Paraíso (*Melia azedarach*) y Ligustro (*Ligustrum lucidum*) en la ciudad de La Plata, Argentina. (a) Espacio de caracteres de las aves (análisis de componentes principales) basado en rasgos morfológicos (flechas). Los colores y las elipses de confianza indican especies diferentes. Amaa: *Amazona aestiva*, Mims: *Mimus saturninus*, Myim: *Myiopsitta monachus*, Patp: *Patagioenas picazuro*, Piom: *Pionus maximiliani*, Pits: *Pitangus sulphuratus*, Psil: *Psittacara leucophtalmus*, Psim: *Psittacara mitrata*, Pyrf: *Pyrrhura frontalis*, Stuv: *Sturnus vulgaris*, Tura: *Turdus amaurochalinus*, Turr: *Turdus rufiventris*, Zonc: *Zonotrichia capensis*, CUL: longitud del culmen, GAP: ancho de fauces, WIN: cuerda del ala, BDE: altura del pico, MAN: longitud de la mandíbula, TAR: longitud del tarso. (b) Espacio de caracteres de las plantas (análisis de componentes principales) basado en rasgos morfológicos de frutos y semillas. Los colores y las elipses de confianza (95%) indican cada una de las especies. Ligl: *Ligustrum lucidum*, Mela: *Melia azedarach*, SDIA: diámetro de la semilla, FDIA: diámetro del fruto, FLEN: longitud del fruto, SARE: área de la semilla, SLEN: longitud de la semilla, FCI: circularidad del fruto, SCI: circularidad de la semilla. (c) Interacciones fruto-frugívoro entre aves, Paraíso y Ligustro basadas en datos publicados y personales. Fotografías: F.X. Palacio. (d-e) Relación entre especialización morfológica y funcional. Los puntos muestran los valores observados y las líneas indican las predicciones de modelos de regresión beta. a: especie de ave exótica, n: especie de ave nativa.

originality was positively related to functional originality (beta regression coefficient=3.42, SE=1.29, pseudo-R^2=0.46, n=13, P=0.008), indicating that bird species with specialized morphologies played specialized functional roles in the bird assemblage (Figure 1d). In particular, large alien parrots tended to interact with the Chinaberry tree (larger fruits) whereas relatively small-sized birds (mainly Passeriformes) tended to interact with the Glossy Privet (smaller fruits). By contrast, morphological uniqueness was not related to functional uniqueness (beta regression coefficient=2.06, SE=1.34, pseudo-R^2=0.24, n=13, P=0.12) (Figure 1e).

Discussion

We show that local frugivorous birds interact with morphologically corresponding alien invasive plant species in an urban area. Moreover, morphological specialization correlated with functional specialization, indicating that birds with extreme morphologies played specialized functional roles for the interaction. For instance, relatively small-sized native species (Passeriformes) tended to interact only with the Glossy Privet (a small fruit). Similarly, large alien parrots tended to interact only with the Chinaberry tree (a large fruit) and occupied an area of the functional trait space not previously occupied by native bird species, suggesting the emergence of new functional roles in the community of invasive plant-frugivore

interactions (e.g., Palacio et al. 2016). This contrasts with García et al. (2014), who found that alien frugivorous birds increased generalization of interaction networks and that bird species abundances determined the patterns of interactions in plant-frugivore assemblages rather than trait-matching constraints. Our results support the idea that the introduction of alien birds promoted specialized interactions supporting trait matching between interacting partners (Vázquez et al. 2009). Therefore, our results suggest that a typically generalized bird assemblage may differentially interact with alien plant species, which in turn respond to morphological differences between bird species.

The trait matching observed between birds and alien invasive plants could have strong consequences for plant invasion. At our study area, alien parrots are rapidly expanding throughout the region (Ibáñez et al. 2014; Scheffer et al. 2015). As matching traits define a species' functional role in an interaction network (Dehling et al. 2016), the functionally specialized role of the alien parrots interacting with the Chinaberry tree may accelerate the spread of this species. Similarly, the specialized functional role of Passerines interacting with the Glossy Privet leads to the high dispersal and colonization ability of this highly invasive species (Fernández et al. 2021). In a recent study, Sperry et al. (2021) found that traits increasing the probability of encounter and the

ability to be consumed were more important for dispersal by alien frugivores than traits associated with fruit preferences in Hawaii. As a consequence, these traits are driving the spread of invasive species and limiting dispersal of some native species (Sperry et al. 2021). Given that the Chinaberry tree and the Glossy Privet have extended fruiting seasons during months in which most native fruits are not available, trait matching along with phenological matching may explain the high invasive potential of these plant species.

Two limitations of our study are the use of museum specimens to describe birds' morphology and considering that some interactions occurred based on the presence of the species and previous records in the literature. Although the use of museum specimens and databases to extract morphological and species interaction information is a common practice in functional ecology, it is more appropriate to quantify functional traits and species interactions in the community under study (Cordlandwehr et al. 2013). This is because mean trait values in a given population do not necessarily correspond with those measured in other populations, and because we have not seen some interactions described here. Since we measured individuals collected in a region larger than our study area and we did not confirm some interactions in the field, our results should be taken with caution.

Our findings suggest that functional groups of species linked by exclusive or frequent interactions ('mutualistic compartments') (Traveset and Richardson 2006) between local birds and alien plants would have consequences on invasion success by enhancing seed dispersal via groups of specialized bird species. Overall, we highlight the importance of studying the morphology and functional role of local birds in mutualistic interactions with alien invasive plants, and how these functional roles may promote invasion processes.

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