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ORIGINAL PAPER

Influence of secondary dispersal by ants on invasive processes of exotic species with fleshy fruits

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Abstract Invasive alien plant species (IAPS) are severely changing ecosystems on earth. Studying the interactions that allow IAPS to establish and spread in the new regions is crucial. Ants can disperse exotic fleshy fruits. We asked the following questions at three different sites of Chaco Mountain Forest (Córdoba, Argentina): (1) Do ants disperse diaspores of native, neonative and IAPS differentially? (2) Which is the ant species assemblage and their role in the secondary dispersal of each of the selected plant species? (3) Do ants interact in different ways with intact and manipulated fruits, and these interactions vary within plant species origin? and (4) Are diaspore traits different among the plant species considered? We selected four plant species: *Celtis ehrenbergiana* (native), *Lantana camara* (neonative), *Pyracantha angustifolia* and *Ligustrum lucidum* (IAPS). Two experiments were performed: (1) To disentangle the contribution of ants to the secondary dispersal process, and (2) To investigate the ant behavior of ground-foraging ant species when they encountered the fruits. Additionally, we measured fruit mass and the number of seeds per fruit. Ants were the main diaspore dispersers on the Chaco Mountain Forest ground. Twelve ant species interacted with the fruits; the native presented the higher number, followed by the neonative, and the two IAPS. Only *Acromyrmex crassispinus* and *Pheidole cordyceps* removed diaspores. Furthermore, the fruits differed in their mass and also in the number of seeds. Our results highlight the importance of ants and also diaspores traits in these diffuse mutualisms, and enhance their role in plant-invasive processes in subtropical ecosystems.

Keywords Ant assemblage · Caging experiment · Chaco Mountain Forest · Diaspore mass · Invasive alien plant species · Mutualism

Introduction

Humans have been modifying nature since they appeared on earth (Diamond and Ordunio 1999). However, in recent decades this process has been accelerated and the distribution of several species from different taxa worldwide has been reshaped (Sala et al. 2000; Corlett 2015). In their new

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distribution areas, species of some plant taxa are capable of establishing and spreading along the new landscapes (Richardson et al. 2000b). The invasive process is complex and encounters several filters at different temporal and spatial scales that the plant species have to surpass. These filters include abiotic and biotic interactions in their new habitats. For plants depending on animal vectors for pollination and dispersal, mutualisms are key to facilitate the invasive process (Richardson et al. 2000a, b; Dietz and Edwards 2006; Blackburn et al. 2011; Traveset and Richardson 2014). Nevertheless, invasive alien plant species (hereafter IAPS) are distributed along diverse regions of the world (Rejmánek and Richardson 2013; Seebens et al. 2017; Turbelin et al. 2017), causing different kinds of problems in the new ecosystems they invade (Vilà et al. 2011; Diagne et al. 2021).

Most of the research previously performed on invasive species has focused on negative interactions (e.g., Elton 1958), but it has been shown that positive interactions are also relevant for plant establishment and dispersal (e.g., mutualist interactions; Richardson et al. 2000a; Traveset and Richardson 2014). In particular, the dispersal process of diaspores (i.e., the unit of dispersal; Van der Pijl 1982) is a key component for the establishment and the spreading phases of IAPS (Theodarides and Dukes 2007). In the case of plants dispersed by animals, the possibility of successful dispersal depends on the presence of animal vectors in the new distribution areas (Richardson et al. 2000a), mainly native generalist species (Traveset and Richardson 2014). Plant species that have fleshy fruits depend on the presence of frugivorous animals to be dispersed (Cronk and Fuller 1995). In general, most studies have been performed considering the prevailing biotic dispersal syndrome and consequently the main group of organisms involved (Richardson et al. 2000a). However, two-phase dispersal processes also occur involving other secondary dispersal agents, that could also be relevant for the whole dispersal process and the establishment and spreading of IAPS in the new sites (Holmes 1990a, b; Amodeo et al. 2017).

Ants establish several relevant interactions with plants, including primary and secondary diaspore dispersal (Rico-Gray and Oliveira 2007). Myrmechocory involve plants having diaspores with particular seed structures (e.g., elaiosomes) for rewarding ant dispersers (Rico-Gray and Oliveira 2007). Myrmecochorous plants can be primary dispersed by ants, but this group of plants is also composed by diplochorous plant species (Gorb and Gorb 2003; Lengyel et al. 2010). Diplochory is a seed dispersal process with two phases, involving two or more different abiotic/biotic agents (Vander wall and Longland 2004). This two-phase process normally occurs when a primary agent, as vertebrates or processes as ballistic dispersal, remove the diaspore directly from the parent plant. Then, a secondary agent (such as ants) may complement seed dispersal, usually from the ground (Vander wall and Longland 2004). Secondary dispersal by ants involves escape from ground predation and the possibility to reach safe sites that ensure germination and establishment (Vander wall and Longland 2004). They can also perform a process known as directed dispersal, directly conducting seeds to safe sites (Schupp 1995; Richardson et al. 2000a). Small ant species can also benefit plants by removing fruit pulp, impeding fungus colonization of fruits and enhancing seed survival and germination (Oliveira et al. 1995; Leal and Oliveira 1998; Ohkawara and Akino 2005). Furthermore, previous evidence has shown that some diaspore traits (e.g., diaspore mass and seed number per diaspore) are relevant for secondary dispersal by ants. For instance, small-sized diaspores have higher chances of being removed in comparison to medium and large-sized diaspores (Pizo and Oliveira 2001; Anjos et al. 2020), while seed number can be relevant for seed dispersal effectiveness (Schupp et al. 2010). In addition, there is evidence showing that the condition of the fruit on the ground can influence subsequent interaction with ants, especially previous handling by avian frugivores (in primarily bird-dispersed species), enhancing subsequent secondary dispersal (Bieber et al. 2013; Guerra et al. 2018).

Recent evidence shows that highly invasive species are more dependent on mutualisms than previously expected (Moyano et al. 2020). It is very important to consider the relevance of diffuse mutualisms (i.e., a focal species depends on multiple agents) (Janzen 1985; Richardson et al. 2000a), such as seed-dispersal mutualisms. For instance, native ants in the genera *Anoplolepis* and *Pheidole* disperse seeds of the IAPS *Acacia cyclops* A. Cunn. ex G. Don and *A. saligna* (Labill.) H.L. Wendl. in Western Cape (South Africa) at short distances, rendering the diaspores less vulnerable to rodent predation (Holmes 1990a, b). Native and invasive ant species contribute to the spread of *Chelidonium majus* L. seeds, a fast-growing European perennial herb, introduced into North America (Prior et al. 2014). Ants can also disperse fleshy fruits of IAPS, such as the shrub *Murraya paniculata* (L.) Jack by *Acromyrmex niger* in Brazil (Smith, 1858) (Pikart et al. 2011). In Argentina, some studies have shown that native ant species disperse seeds of IAPS (Sanhueza et al. 2008; Pirk and Lopez de Casenave 2017; Ortiz et al. 2021). Despite the wide distribution of the IAPS in some regions, including South America, knowledge of secondary dispersal by ants of fleshy diaspores is incipient and the consequences of the invasive potential of these plant species is not well known (Giorgis and Tecco 2014). The selection of plants with different origins (i.e., native, exotic-invasive, and neonative) would allow us to analyze if the native ant assemblage selects or not diaspores according to the history of the interaction. Neonative designates plants that have recently expanded their range as a consequence of environmental changes generated by human-activities (Essl et al. 2019). Neonative plants have an eco-evolutionary history more similar to native species compared to IAPS, and this could result in a gradient of preferences (i.e., secondary dispersal) between ant and diaspores of plants with different origins.

In the present work we ask the following questions: (1) Do ants disperse diaspores of native, neonative and invasive alien plant species differentially? (2) Which is the ant species assemblage and their role in the secondary dispersal of each of the selected plant species? (3) Do ants interact in different ways with intact and manipulated fruits (i.e., simulating previous manipulation by birds), and these interactions vary within plant species origin? and (4) Are diaspore traits (i.e., diaspore mass and number of seeds per fruit) different among the plant species considered? Considering the history of interaction, we expect a higher number of ants interacting and removing fruits of the native plant species, but this would be constrained by diaspore mass. Regarding the fruit type, we expect a higher number of interactions with previously manipulated fruits independent of plant origin.

Materials and methods

Study site

We performed our study near the localities of Río Ceballos and Salsipuedes in Córdoba Province (central Argentina), during summer months (November 2017-March 2018). We selected three different sites corresponding to the Chaco Mountain Forest phytogeographical region (31° 09′ S and 64° 17′ W; 640–753 m a.s.l.; Cabrera 1976; Oyarzabal et al. 2018). We deliberately selected sites where the neonative species and the two IAPS were already present. In a regional context (i.e., several vegetation units of the Chaco Mountain Forest), the neonative species and also the two IAPS are in high abundance and therefore causing several ecological problems (Hoyos et al. 2010; Ferreras et al. 2015, 2019; Whitworth-Hulse et al. 2020).

The vegetation of the study area is a mosaic of physiognomies, from grasslands and low open shrublands to locally closed forests, with a total cover between 80 and 100%. Tree species such as *Lithraea molleoides* (Vell.) Engl. (Anacardiaceae), *Condalia buxifolia* Reissek (Rhamnaceae) and *Zanthoxylum coco* Gillies ex Hook. f. & Arn. (Rutaceae) together with some shrubs and vines are among the dominant species (Giorgis et al. 2017; Cabido et al. 2018). An open shrub layer is formed by *Croton lachnostachyus* Baill. (Euphorbiaceae) and other species; in the herb layer, the grasses *Oplismenus hirtellus* (L.) P. Beauv., *Setaria oblongata* (Griseb.) Parodi and *Gouinia latifolia* (Griseb.) Vasey var. *latifolia* (Poaceae) occur with the highest frequency (Cabido et al. 2018). Mean annual precipitation between October and May is 750 mm (Luti et al. 1979; Moglia and Giménez 1998).

Plant species

We selected four plant species: one native, one neonative (Richardson 2001; Essl et al. 2019) and two considered IAPS for this region (Giorgis and Tecco 2014; Giorgis et al. 2017; Cabido et al. 2018). All of them are woody species with fleshy fruits primarily dispersed by birds (Ferreras et al. 2008; Ponce et al. 2012; Vergara-Tabares et al. 2016; Díaz Vélez et al. 2017; Chari et al. 2020).

The native species *Celtis ehrenbergiana* (Klotszch) Liebm. (Cannabaceae), is a thorny tree producing fruits from November to April. This species is usually found in dry forests and scrubs from the southern USA to central Argentina (Berg and Dahlberg 2001; Cabido et al. 2018). The shrub species *Lantana camara* L. (Verbenaceae) has a fruiting phenology between January and May (Díaz Vélez et al. 2017), and is considered a neonative species (sensu Essl et al. 2019) for this region (Chaco Mountain Forest), because it is originally from other phytogeographical regions of South America (Richardson 2001). These two species have evidence that ants have interacted with their fruits (Grilli and Galetto 2009; Osunkoya and Perrett 2011; Palacio et al. 2020). Moreover, there is no record of human introduction of *L. camara* in the southern region of the continent (central Argentina), so probably it colonized this region due to human-induced changes of the biophysical environment (Essl et al. 2019). However, nowadays this plant species is commonly used as ornamental. In addition, other authors have considered this plant species as a native invader species because it is native from Argentina (northeast) but it became an invader in the Córdoba Province (Giorgis and Tecco 2014; Torres and Galetto 2014).

The two IAPS are *Pyracantha angustifolia* (Franch.) C.K. Schneid. (Rosaceae) (hereafter IAPS-P) and *Ligustrum lucidum* W.T. Aiton (Oleaceae) (hereafter IAPS-L). The former is a thorny evergreen shrub native to Asia that produces fruits throughout the whole year, mainly in autumn and winter months (Tecco et al. 2006). *Ligustrum lucidum* is an evergreen and shade-tolerant Chinese tree. The fruiting period of IAPS-L in low Chaco Mountain Forest ranges from May to the end of November (Ferreras et al. 2008). Both IAPS have been introduced as ornamental and are widely used in landscaping and gardening (Novara 1993; Giorgis and Tecco 2014). In the Chaco Mountain Forest of Córdoba, IAPSL was introduced at the beginning of the twentieth century, whereas the first occurrence of IAPS-P has been recorded in 1984 (Delucchi 1991; Hoyos et al. 2010; Giorgis et al. 2011). Afterwards, they spread throughout the region (Giorgis et al. 2017; Cabido et al. 2018). *Ligustrum lucidum* has evidence that ants have interacted with their fruits (Ferreras et al. 2008). Furthermore, while most native species disperse in the warm and rainy season, mostly from November to April, both IAPS disperse their fruits also in the cold and dry season (Gurvich et al. 2005; Tecco et al. 2013).

Fruit harvest and measurements

To perform the experiments described in the following sections, we collected mature fruits from at least five different plant individuals on the previous day of the beginning of the experiments. In this way, we created fruit pools from each species that were maintained in the fridge between 3 and 5 °C prior to the experiments. We selected 100 diaspores from the fruit pool of each plant species to determine fresh diaspore mass using a precision balance (0.0001 g) in the laboratory. It has been previously documented that fruit variables (i.e., fruit size and fruit mass) are highly correlated (Flörchinger et al. 2010). Additionally, for all species we counted the number of seeds per fruit from 100 fruits.

Caging experiment

In order to disentangle the contribution of ants to the secondary dispersal process of the selected plant species, we designed a paired experiment: some fruits were exposed to all potential dispersers and others were excluded from vertebrates. Vertebrates were excluded from diaspores using wire cages ($15 \times 10 \times 10$ cm; 1.5 cm mesh) that impeded vertebrates to make contact with fruits but allowed ants to freely go in and out. Each experimental pair consisted of a set of 10 intact fruits on white filter paper placed directly on the ground inside a wire cage (experimental treatment: vertebrates excluded), and an exposed set of diaspores placed outside the cage, 10 m away (open control: ants and vertebrates allowed) (Figs. 1a; 2). Previous studies showed that the filter paper apparently has neither effect on ant behavior nor on other potential seed dispersers (e.g., Byre and Levey 1993; Pizo and Oliveira 2000; Passos and Oliveira 2002). One transect of each kind was placed in each selected site with five paired stations (i.e., experimental treatment and open control) for each plant species. Fruits were set out at 09:00 a.m. and after 24 h, we recorded the number of fruits removed in each experimental category. We settled the experiment during a 24 h period, based on evidence from previous studies using a similar approach (e.g., Passos and Oliveira

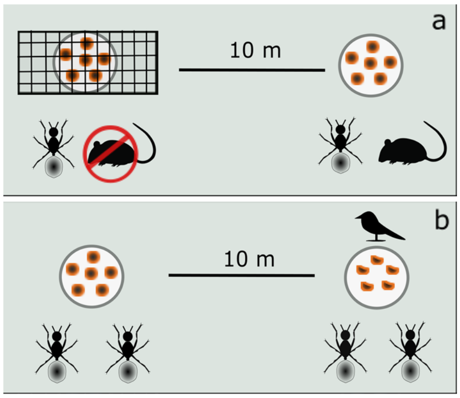

Fig. 1 Conceptual diagram showing the two experiments performed: **a** caging experiment showing a paired station with fruits on white filter paper, inside wire cages (left) and exposed (right) and **b** fruit manipulation experiment showing a paired station with fruits on white filter paper, intact (left) and manipulated (right) simulating previous manipulation by avian frugivores. Each transect contained five paired stations (separated by 10 m) for each plant species; it is important to consider that the experiments were carried out with ten fruits per species, only five are shown schematically in the figure

2002; Christianini et al. 2007; Christianini and Oliveira 2010; Camargo et al. 2016). A given fruit was considered removed if it was not found within 30 cm of its original location. Before establishing the transects, all fruits from any of the selected plant species were removed from the area. Also, it is important to mention that during the experiment, apart from ants no invertebrate species were seen at caged fruits, nor rodents at exposed ones.

Fruit manipulation experiment

To register the ant species assemblage interacting with diaspores, as well as the kind of interaction established with the four plant species selected, in each site we placed two transects with five diaspore depots in each one (depots were 10 m from one another). In one transect, on each diaspore depot we placed 10 intact fruits on white filter paper. In the other transect, in each diaspore depot we placed 10 fruits that were manipulated with forceps to simulate pecking by bird's beak (i.e., imitating fallen fruits beneath trees after manipulation by birds) (Fig. 1b). Transects were also separated at least by 10 m. Diaspores were set at 08:00 a.m. until 20:00 p.m. on sunny days and checked at 15 min intervals over 1 h, allowing us to record ant activity during all day. We registered the species and number of ants at each diaspore depot and their behavior towards the diaspores of selected plant species in three different categories, based and adapted from previous studies: (1) Inspect/collect liquids (IC-L): this include ants that contact the fruits with their mandibles, antennae or legs but do not remove them, and ants that collect liquid from the fleshy diaspore (mainly fruits with the pulp exposed, simulating previous handling by frugivores); (2) Consume/remove fruit pulp (CR-FP): this include ants that consume fruit pulp at the diaspore depot, and ants that remove small pieces of fruit pulp; and (3) Remove diaspores (RD): ants that grab the fruits and carry them away from the diaspore depots (Pizo and Oliveira 1998; Passos Oliveira 2002; 2004; Aranda-Rickert and Fracchia 2011; Pirk and Lopez de Casenave 2017) (Fig. 3). These three types of behaviours towards the diaspores were treated as ant-diaspore interactions in the present study. When

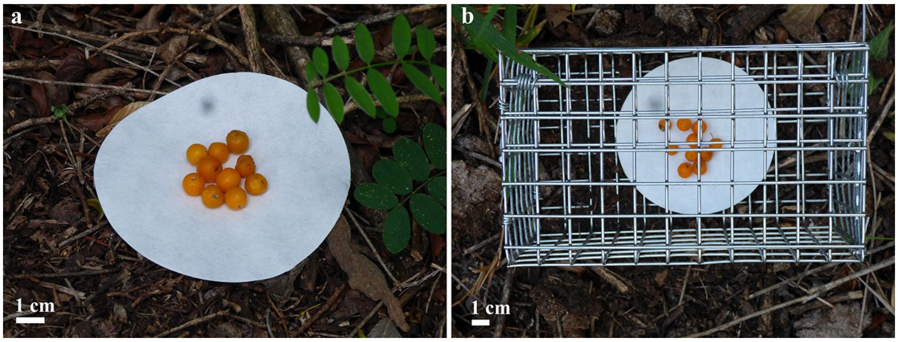

Fig. 2 Intact fruits of the native species *Celtis ehrenbergiana* on white filter paper, **a** exposed and **b** inside wire cages

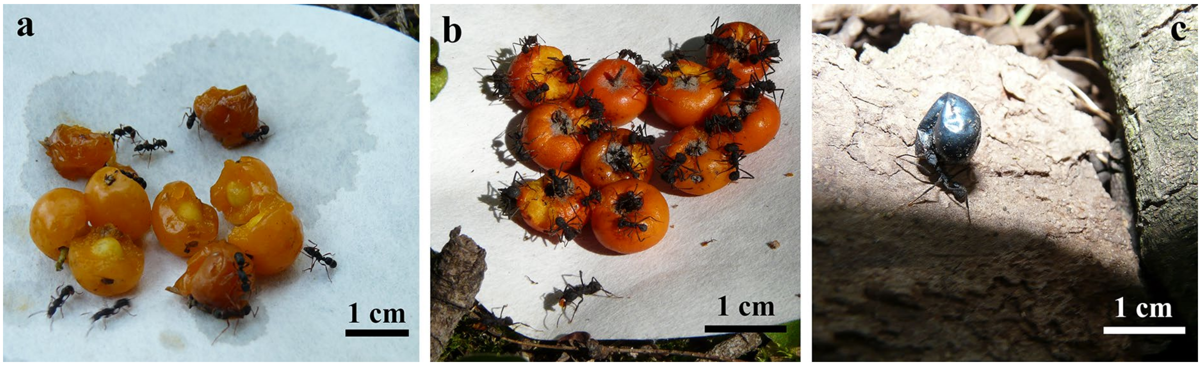

Fig. 3 Types of behaviors performed by ants towards the diaspores: **a** ants performing diaspore inspection or liquid collection on the diaspore depot (i.e. *Gnamptogenys striatula* on *Celtis eherenbergiana*), **b** ants consuming and removing fruit pulp (i.e. *Acromyrmex crassispinus* on *Pyracantha angustifolia*), and **c** ants removing diaspores (i.e., *Acromyrmex crassispinus* removing a fruit of *Lantana camara*)

we could not identify the ant species in the field, we collected and preserved them in 96% ethanol for further identification. Code numbers assigned to morphospecies apply only to this study. A full collection of voucher specimens was deposited at Instituto Multidisciplinario de Biología Vegetal (UNC-CONICET).

Data analyses

We used the data from the caging experiment to analyze if ants remove fruits from each of the selected plant species. For this analysis, we performed Generalized Mixed Effect Models (GLMM) using '*MASS*' package (Ripley et al. 2013). We used 'glmmPQL' function with quassibinomial distribution as the data were overdispersed. The model was constructed with Site as random effect, and Treatment (open control and vertebrates excluded) and Species origin (native, neonative, IAPS-L and IAPS-P) as explanatory variables. The ant assemblage was visualized through a Venn Diagramm using 'venn.diagram' function from '*VennDiagram*' package (Chen and Boutros 2011). The dataset from the fruit manipulation experiment was used to test the effects of Fruit condition (intact vs. manipulated) and Species origin as well as Fruit condition (intact vs. manipulated) and Type of interaction on the response variable: Number of ants visiting diaspore depots. In both cases, we performed a GLMM using '*MASS*' package with Poisson distribution. The model was constructed with Site as random effect, and Fruit condition, Type of interaction and Species origin as explanatory variables.

To evaluate if diaspore mass and seed number differed among species, we performed a GLM using the 'glm' function with a Gaussian and Poisson distribution, respectively; and then compared with the null model using the 'anova' function. For all models performed, we tested for differences between factor levels using 'lsmeans' function from '*emmeans'* package (Lenth et al. 2018). All the analyses and graphics were performed using R version 2020 (R Core Team 2020); except the first diagram performed entirely in Inkscape (2020).

Results

The caging experiments revealed that the quantity of diaspores removed within 24 h in the enclosure and the control is similar for all plant species ($\chi^2=0.91$; Df = 1; P = 0.33; Table 1; Fig. 4), suggesting that ants are the main dispersers of the diaspores on the Chaco Mountain Forest ground. However, the analysis also showed meaningful differences in the removal rate among the plant species ($\chi^2=12.22$; Df = 3; $P=0.006$; Fig. 4). Diaspores of the neonative species had higher removal rates in both type of conditions (exposed and wired cages) compared with the native species (Estimate = 1.43; Std error = 0.55; *t* ratio = 2.63; $P=0.04$) and IAPS-P (Estimate = 1.72; Std error = 0.55; *t* ratio = 3.12; P = 0.01).

From the fruit manipulation experiment, we observed that the ant species assemblage interacting

Table 1 Variation in the number of diaspores removed in relation to plant species and type of treatment (exposed vs. wire cages) in Chaco Mountain Forest in Córdoba, central Argentina

Plant species	*N*	Exposed	Wire cages	*P*
Celtis ehrenbergiana (Native)	14	3.71 ± 4.03	2 ± 3.57	ns
Lantana camara (Neonative)	15	6.47 ± 4.66	5.87 ± 4.53	ns
Ligustrum lucidum (IAPS-L)	15	5.13 ± 4.85	3.53 ± 4.79	ns
Pyracantha angustifolia (IAPS-P)	15	1.87 ± 3.76	2.67 ± 4.58	ns

Ten diaspores of each species were set out under a wire cage (i.e., free access to ants; vertebrates excluded) paired with an open control (access to all kinds of animals). The number of diaspores removed was recorded after 24 h. *N* refers to the number of replicates; ns indicates no significant difference ($P > 0.05$) between exposed and wire cages

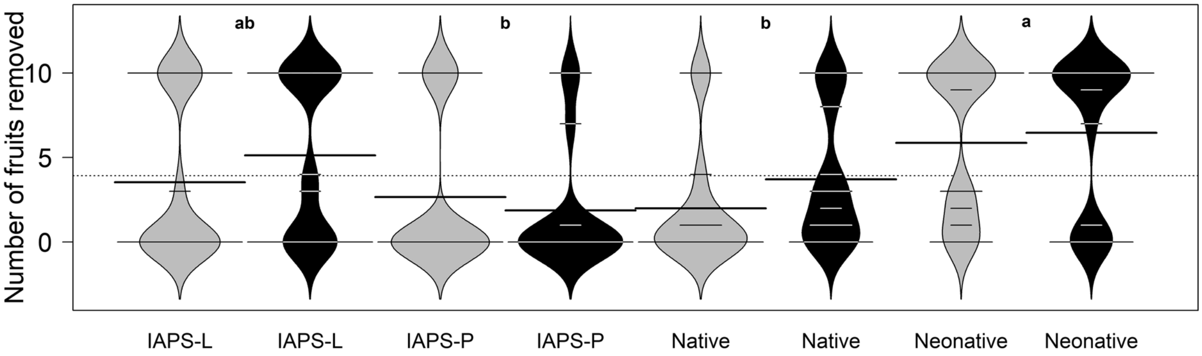

Fig. 4 Number of fruits removed per plant species (IAPS-L, *Ligustrum lucidum;* IAPS-P, *Pyracantha angustifolia;* Native, *Celtis ehrenbergiana* and Neonative, *Lantana camara*) considering fruits exposed (black) and inside wire cages (gray) in three sites of Chaco Mountain Forest (Córdoba, central Argentina). Black continuous lines indicate individual values, if there are two identical values, the line is drawn twice as long; the dashed line represents the mean; different letters indicate differences between plant species

Table 2 Ant species assemblage and behavior (i.e., IC-L, inspect/collect liquids; CR-FP, consume/remove fruit pulp; and RD, remove diaspores) registered in the fruit manipulation experiment with the four plant species selected (a- *Celtis ehrenbergiana*, b- *Lantana camara*, c- *Ligustrum lucidum* and d- *Pyracantha angustifolia*) in three different sites of Chaco Mountain Forest in Córdoba, central Argentina

Subfamily	Ant species	IC-L	CR-FP	RD
Myrmicinae	*Acromyrmex crassispinus* Forel, 1909	*x* (a, d)	*x* (a, c, d)	*x* (a, b, c, d)
	Crematogaster sp.	*x* (c, d)		
	Pheidole cordiceps Mayr, 1868	*x* (a, b, c)	*x* (a, b)	*x* (b)
	Pheidole radoszkowskii Mayr, 1884	*x* (a, b)	*x* (b)	
	Pheidole sp. 1	*x* (a)	*x* (a)	
	Wasmannia auropunctata Roger, 1863	*x* (a, d)		
Formicinae	*Brachymyrmex* sp.	*x* (c)		
	Camponotus mus Roger, 1863	*x* (a, b, c, d)	*x* (b)	
	Camponotus rufipes Fabricius, 1775	*x* (a)		
	Nylanderia sp.	*x* (a)	*x* (a)	
Ectatomminae	*Gnamptogenys striatula* Mayr, 1884	*x* (a, b)	*x* (a)	
Dolichoderinae	*Linephitema gallardoi* Brèthes, 1914	*x* (a, b)		

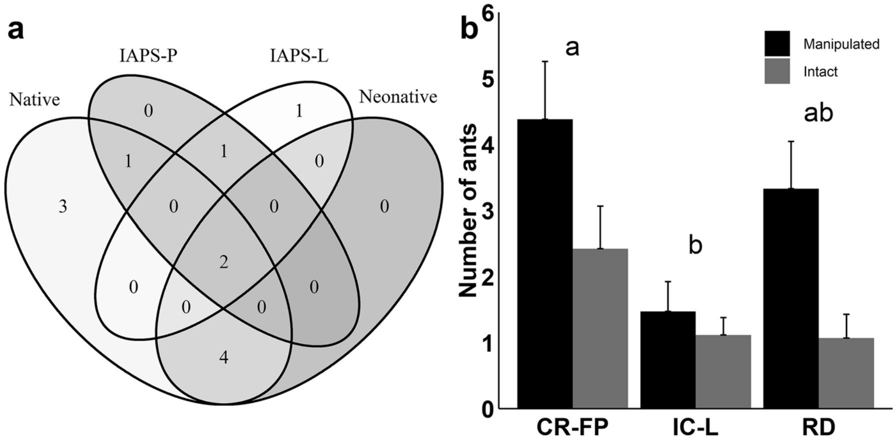

Fig. 5 **a** Venn diagram showing the ant species assemblage and **b** barplot of the number of ants in relation to the type of interaction (i.e., consume/remove fruit pulp (CR-FP), inspect/collect liquids (IC-L) and remove diaspores (RD)) and the fruit condition: manipulated (black) and intact (gray) of native (*Celtis ehrenbergiana*), neonative (*Lantana camara*), IAPS-L (*Ligustrum lucidum*) and IAPS-P (*Pyracantha angustifolia*) in three sites of Chaco Mountain Forest in Córdoba, central Argentina; different letters indicate significant differences

with diaspores was composed of 12 native species belonging to four subfamilies: Formicinae, Myrmicinae, Ectatomminae and Dolichoderinae (Table 2). We found a greater number of ant species interacting with the native species *Celtis ehrenbergiana* (10 species) compared with the neonative and both IAPS: *Lantana camara* (6), *Ligustrum lucidum* (4) and *Pyracantha angustifolia* (4), respectively (Fig. 5a). Moreover, the native plant species presented the higher number of exclusive ant species interacting with their diaspores (3) (Fig. 5a), while two ant species were observed interacting exclusively with IAPS-P and IAPS-L (Fig. 5a; Table 2). All ant species inspected the fruits or collected liquid from them (Table 2). Seven species consumed fruit pulp on the diaspore depots and/or removed it; including *Gnamptogenys striatula* (mainly an arthropod predator; Latkke 1990). However, only two ant species removed diaspores, *Acromyrmex crassispinus* and *Pheidole cordiceps* (Table 2). While the former removed diaspores of all plant species, *P. cordiceps* only removed diaspores of *Lantana camara* (we followed one individual of each species; > 15 m and up to 5 m, respectively).

The model performed between fruit condition (i.e., intact or manipulated) and species origin from the fruit manipulation experiment did not show a significant interaction term ($\chi^2 = 5.79$; Df = 3; $P = 0.12$). The number of ants visiting diaspore depots was different among plant species with different origins ($\chi^2 = 31.89$; Df = 3; $P \leq 0.0001$). IAPS-L had significantly less ants visiting their fruits compared with the other three plant species selected, whereas no significant differences was found among the latter. Moreover, we detected meaningful differences concerning fruit condition ($\chi^2 = 18.3$; Df = 1; $P \leq 0.0001$), with a higher number of ants visiting diaspore depots with manipulated fruits (3.06 ± 7.45; mean ± SD) compared to diaspore depots with intact fruits (1.53 ± 4.77).

We did not detect an interaction between fruit condition and type of interaction ($\chi^2 = 2.1$; Df = 2; P = 0.38). But we detect differences between type of interactions ($\chi^2 = 13.1$; Df = 2; P = 0.001); inspect/collect liquid was different from consume/remove fruit pulp (Estimate = -0.93; Std error = 0.27; t value = -3.41; P = 0.002; Fig. 5b). The other type of interactions did not differ between them. Moreover, we ran an analysis to evaluate variation in the type of treatment by ants to each plant species considered (Supplementary Information Appendix 1). For the native plant species, we did not detect differences in the number of ants performing the different type of interactions, but the IC-L seems the most frequent interaction. In the neonative plant species, RD was the interaction most frequently observed, and it differed significantly from CR-FP and IC-L. For IAPS-L and IAPS-P, CR-FP was the most frequent ant

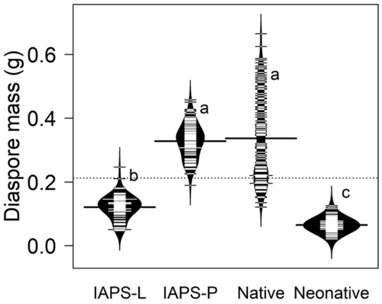

Fig. 6 Beanplot (the dashed line represents the mean) showing diaspore mass of 100 fruits of the Native (*Celtis ehrenbergiana*), IAPS-P (*Pyracantha angustifolia*), IAPS-L (*Ligustrum lucidum*) and Neonative (*Lantana camara*) plants selected in this study. Black continuous lines indicate individual values, if there are two identical values, the line is drawn twice as long. Different letters indicate significant differences between diaspore mass

behavior toward fruits (Supplementary Information Appendix 1).

Diaspore mass differed significantly among selected plant species ($\chi^2 = 1027.1$; Df = 3; $P \leq 0.0001$). The neonative plant species presented the lowest diaspore mass compared with the other species (Fig. 6). The native plant species and IAPS-P presented the highest mass but did not differ from one another (Fig. 6). The native plant species presented a higher variability in diaspore mass data compared with the other species. Overall, selected plant species differed significantly in the number of seeds per fruit ($\chi^2 = 415.62$; Df = 3; $P \leq 0.0001$), but only IAPS-P was meaningful different from the other plant species. The number of seeds per fruit (mean ± SD) was 4.97 ± 0.48 for IAPS-P, followed by 1.38 ± 0.49 for neonative, 1.25 ± 0.17 for IAPS-L, and 1 ± 0 for native species.

Discussion

Our results highlight the role of ants in the secondary dispersal processes of native, neonative and IAPS with fleshy fruits in seasonally dry forests of central Argentina, as it has been observed in other regions of the world (Rico-Gray and Oliveira 2007). Additionally, our results reveal that ants could also be important in primary dispersal processes (i.e., removing fruits without necessarily being previously manipulated by a primary disperser). Twelve native ant species interacted with the fleshy fruits; the native plant species presented a higher number of ant species interacting with their fruits, followed by the neonative species and the two IAPS. *Acromyrmex crassispinus* and *Pheidole cordyceps* were the only two species removing diaspores. Furthermore, the fleshy fruits of selected plant species differed in their mass and in the number of seeds per fruit, two important traits that could influence the likelihood of being removed by the ants. The plant species with fruits with a lesser mass (i.e., neonative) had higher rates of removal. These results highlight the importance that ants and diaspore traits have in these diffuse mutualisms as well as in the invasive processes of plants in subtropical ecosystems.

Although in central Argentina we lack large ponerines that are well-known for their role as secondary dispersers in the Brazilian Atlantic rainforest and Cerrado savanna (e.g., *Odontomachus*, *Pachycondyla* and *Dinoponera*; Pizo and Oliveira 1998; 2000; Passos and Oliveira 2002; 2004; Christianini et al. 2012; Magalhães et al. 2018), our results indicate that ants in Argentine seasonally dry forests can remove diaspores from different plant species. The results obtained in the cage experiments (i.e., similar removal rates in caged and exposed fruits) indicate that ants are the main diaspore dispersers of the selected plant species on the ground of Chaco Mountain Forest. This result is consistent with previous studies in Neotropical forests and savannas, where ants have been reported as the main secondary dispersers of fleshy diaspores primarily dispersed by vertebrates (Oliveira et al. 2017, and included references). Indeed, our removal rates in cage *vs.* exposed treatments are similar to those found for primarily bird-dispersed plants in Cerrado savanna such as *Ocotea pulchella* (Nees & Mart.) Mez and *Erythroxylum pelleterianum* A. St.-Hil. (Christianini et al. 2007). Furthermore, a previous study performed with *Erythroxylum ambiguum* Peyr. in Brazil, showed that ants and birds had the same quantitative importance for seed dispersal effectiveness, highlighting the importance of diplochory for several non-myrmechocorus species (Camargo et al. 2016).

In accordance with other studies, we registered a higher number of interactions and visitation by ants to plant species whose fruits were treated with the forceps simulating a previous bird manipulation.

Bieber et al. (2013) found a higher frequency of ant visits when fruits were mandibulated or embedded in bird faces, and Guerra et al. (2018) showed that partially defleshed fruits were more removed than intact fruits. Mandibulated fruits are more accessible to ants because previous handling by frugivores increases exposure of the fleshy pulp (Bieber et al. 2013). In our study, the native plant species had a higher number of native ants interacting with its diaspores, suggesting that the ant species are more acquainted with these fruits compared to other diaspores that are relatively new in the ecosystems when considering a temporal scale (i.e., neonative and both IAPS; Thompson 1999). Some species interacted on the diaspore depot with the fruits, only inspecting them or performing liquid collection (e.g., *Brachymyrmex* sp., *Crematogaster* sp., *Linephitema gallardoi*, *Wasmannia auropunctata*, *Camponotus rufipes*). All these are small ants, except for *C. rufipes,* that has been reported to feed mainly on liquid rewards (Ronque et al. 2018). Other ant species consumed and removed fruit pulp, although the seeds remained on the diaspore depot. This kind of behavior could not only reduce the fungal attack but also facilitate seed germination, as previously reported for other plant species (Oliveira et al. 1995; Leal and Oliveira 1998). *Gnamptogenys striatula* was one of the ant species observed performing this task, and in Brazil this species was seen removing fruits of the shrub *Erythroxylum ambiguum* to their nests (Camargo et al. 2016). Only two ant species dispersed diaspores in our study: *Acromyrmex crassispinus* and *Pheidole cordiceps*. The small *P. cordiceps* only removed diaspores of the neonative species (i.e., with less diaspore mass). Indeed, *P. cordiceps* recruits nestmates to carry fruits as a group, as observed in other ant species (i.e., *Pheidole bergi* Mayr, 1887 in Monte Desert; Pirk et al. 2009), this constitutes a flexible mechanism for simulating a larger-bodied forager (Traniello 1989) that could broaden the range of food size that ants can carry. On the other hand, *Acromyrmex crassispinus* removed diaspores of all the plant species selected for this study (see also Calheiros et al. 2019, on *A. subterraneus* (Forel 1893) in Cerrado savanna). We also saw some seedlings of the selected plant species (as well as other species with fleshy fruits) growing in refuse dumps of *A. crassispinus*. Similar effects on plant recruitment by *Atta* and *Acromyrmex* were previously documented by Farji-Brener and Silva (1996) and Farji-Brener et al. (2017) in southern Argentina, and Dalling and Wirth (1998) in Panamanian rainforest. In grasslands of Argentina, Amodeo et al. (2017) found a higher germination rate by invasive alien *Prunus mahaleb* L. after their seeds had their pulp removed by *Acromyrmex lundii* (Guérin-Méneville 1838) and were deposited near the nest. This behavior was also observed in *A. crassispinus* in the present study, indicating that further investigation is needed with germination tests after ant manipulation of the seeds (see Leal and Oliveira 1998; Christianini and Oliveira 2009).

From the point of view of the invasive process, our results confirm the relevance of native ant species as dispersal agents of the IAPS selected in the present study. As previously mentioned, former studies revealed that these plant species are dispersed by birds (i.e., *Pyracantha angustifolia*, *Ligustrum lucidum*, see Ferreras et al. 2008; Vergara-Tabares et al. 2016). Although dispersal mutualisms are important to ensure the establishment of some IAPS, diaspore dispersal is most relevant during the spread phase (Theodarides and Dukes 2007; Traveset and Richardson 2014). The removal of fallen fleshy diaspores by ants can benefit plants in different ways. By removing the diaspores to their nests, ants could provide favorable microsites for seed germination and seedling establishment (Passos and Oliveira 2002; 2004; Christianini et al. 2007; Christianini and Oliveira 2009). If the diaspores do not reach the nest, the seeds can get lost on the way and be dropped in favorable microsites for seedling recruitment (Horvitz 1981; Vander Wall and Longland 2005). Additionally, ants could diminish seed predation and seedling competition by moving seeds away from parent trees (Pizo 1997; Pizo and Oliveira 1998; Vander Wall and Longland 2005). Furthermore, the ant-induced movements can rearrange the seed rain generated primarily by vertebrate dispersers (Robert and Heithaus 1986; Horvitz and Le Corff 1993; Pizo and Oliveira 1999; Pizo et al. 2005). Just as fruit removal has several positive effects on plants, it can also benefit ant colonies. Indeed, there is evidence that consumption of lipid-rich aril improves larval development in predominantly carnivorous ponerines such as *Odontomachus chelifer* (Latreille, 1802) (Bottcher and Oliveira 2014). Given that some of the IAPS in our study have a wider fruiting period than native species (Tecco et al. 2006), increased availability of fallen fleshy diaspores in periods of food scarcity in this subtropical forest may enhance dispersal by ants. Furthermore, we observed differences in the number of ants visiting the diaspore depots, being IAPS-L the plant species with less visits; this could be related to differences in the chemical attributes of the fruits, that would be interesting to study. For example, previous evidence has shown that ants prefer lipid rich diaspores (Pizo and Oliveira 2001).

Finally, it is well known that the dispersal process depends on fruit size relative to the body size of the frugivorous animal (Jordano 2000). Ants are not the exception, and it has been shown that small-sized diaspores are removed in greater numbers and to increased distances than medium and large-sized diaspores (Pizo and Oliveira 2001; Anjos et al. 2020). In this way, the differences in diaspore mass between species that we observed could be related to the higher removal rate that we found in the neonative plant species compared with the other plant species (in both conditions: treatment and control). The neonative plant species presented the lowest diaspore mass. Furthermore, the high variability in diaspore mass observed in native compared to non-native species, could allow a broader range of dispersal agents from different sizes (Jordano 2000). Despite the lower removal rate of IAPS-P, the diaspores of this plant species have more seeds than the other selected species, likely conferring an advantage to this invasive alien since seed number can be relevant for seed dispersal effectiveness (Schupp et al. 2010). These results highlight the importance of considering diaspore traits when plant–seed dispersal interactions are assessed.

Our results suggest that ants are relevant removal agents of native and invasive alien plant species in seasonally subtropical forests of the southernmost part of South America. This study is the first to describe the ant species assemblage attending diaspores, and to report secondary dispersal by ants in central Argentina. Our field account includes native plant species and plant species of different origins, highlighting the relevance of these ant-plant mutualisms for the invasive process (Richardson et al. 2000a, b). The Chaco Mountain Forest has a rich community of fleshy-fruited plants (i.e., native, neonative, exotic and invasive species) that could benefit from the litter-dwelling ant assemblage. Further investigation should focus on post dispersal processes resulting from ant-diaspore interactions, including experiments to find out if manipulation by ants enhances seed germination, as well as if ant-induced seed displacement improves seedling establishment in suitable sites (Horvitz 1981; Passos and Oliveira 2002). In this way, it would be possible to determine if ants contribute to the establishment of new seedlings in native communities and acquire a whole picture of the role of ants in the invasive process. Our study shows that ants can be considered relevant agents increasing the invasion success of alien fleshy-fruited plants in central Argentina. The relative contribution of ants versus birds in the spread stage of these plants remains to be assessed.

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Declarations

Conflict of interest The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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