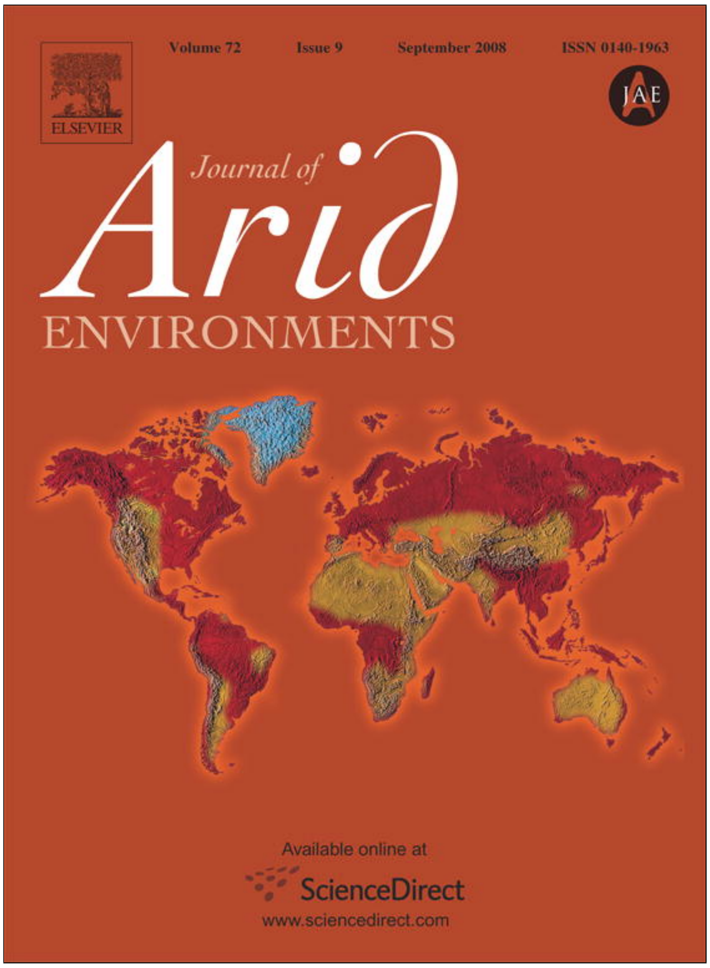
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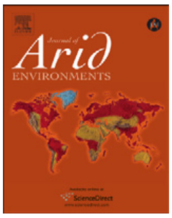

Fruit removal of an invasive exotic species (*Ligustrum lucidum*) in a fragmented landscape

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ABSTRACT

We evaluated if fruit removal of an exotic and invasive species—*Ligustrum lucidum* (Oleaceae)—varies between fragments of different sizes in the Chaco dry forests of Córdoba, Argentina. We considered densities of both *L. lucidum* and the other ornithochorous plant species that bear fruit simultaneously with *L. lucidum*, as variables that could influence fruit removal of this species. We sampled three small (0.5–5 ha), two medium fragments (10–30 ha), and two continuous forests (more than 1000 ha). The percentage of fruits removed per tree was higher in small fragments than in medium or large ones. We did not find significant differences in plant density between fragments of different size neither for *L. lucidum* nor for the other ornithochorous plant species. During the "effective" removal period of *L. lucidum* (i.e., when animals removed fruits), the other ornithochorous plant species did not offer fruits. This region is affected by an increasing fragmentation process, where continuous woodlands have been reduced to small fragments. Considering that the main result is higher fruit removal in small fragments, new studies on the ecology of this species are needed if Chaco dry forests are to be conserved.

1. Introduction

Many authors have considered invasive species as one of the most important modern ecological problems, because their proliferation affects biodiversity conservation and ecosystems functioning (Cohen, 2002; Pauchard et al., 2004). The establishment and reproduction of these species imply physical and biological changes in the communities, which might modify resource availability that may allow new exotic species to invade (Cohen, 2002; Davis et al., 2000). In general, the invasive process is related to human activities, mainly because men are responsible for many intentionally introductions and because of the modifications they cause to natural environments (Sakai et al., 2001). Some generalizations have been proposed about the relationships between the degree of habitat disturbance and the susceptibility of the habitat to be invaded. The ideas that invasive species are more successful in disturbed habitats (citations in Cohen, 2002), and that invasive species and the invaded landscapes have some characteristics that determine the invasion process have predominated during recent years (Williamson and Fitter, 1996; citations in Vázquez and Aragón, 2002). However, many exceptions to these generalizations have been reported (Davis et al., 2000; Heger and Trepl, 2003; Lodge, 1993). One of the main obstacles for the development of a solid theory about invasive species is the scarce knowledge about their ecology (Vázquez and Aragón, 2002).

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Studies on the biology of invasive species suggest that the introduction, establishment, and expansion of a species over its new geographical range are important steps for a successful invasion (Sakai et al., 2001). Fruit removal is a key process within these steps because of its relationship to the population density of a plant species (Lichstein et al., 2004; Lonsdale, 1999). Thus, to evaluate the progress of an eventual invasion process it is necessary to know which factors influence seed removal of an exotic species (Davis et al., 2000; Lonsdale, 1999; Sakai et al., 2001).

Most landscapes around the world are changing their configuration due to habitat fragmentation (Hoekstra et al., 2005). In general, semiarid environments are least susceptible to exotic invasive species than other kind of landscapes (Lonsdale, 1999), but recently appeared some reports about exotic invasive species in these ecosystems (Rejmánek et al., 2005; Ward et al., 2006). Habitat fragmentation is one of the most important factors promoting plant invasions in arid or semiarid environments (Rejmánek et al., 2005; Zak et al., 2004 and references therein). The performance of exotic species in fragmented landscapes may be increased by improving resource availability, germination, growth or seed set (With, 2002 and references therein). In particular, there are some studies remarking the importance of fruit dispersal ecology of invasive species in fragmented landscapes at a global scale (Hanski, 2001; Hobbs and Yates, 2003; With, 2002; and references therein).

In the semiarid environments of Argentina, and particularly in the Chaco forests region, the populations of some exotic and invasive species are growing (Marco et al., 2002) and consequently their area of distribution. In addition, this biogeographic region is suffering a fragmentation process (Cabido and Zak, 1999; Zak et al., 2004) that could be favoring the introduction and proliferation of exotic species. There are some studies connecting mutualistic animal–plant interactions (i.e., pollination) with habitat fragmentation in Argentinean semiarid landscapes (e.g., Aguilar and Galetto, 2004; Aizen and Feinsinger, 1994). Nevertheless, to our knowledge, this is the first study for the Chaco region relating fruit removal with habitat fragmentation.

Ligustrum lucidum W.T. Aiton (Oleaceae) was introduced as an ornamental tree in central Argentina and later some individuals were established in the nearest woodlands (Hoyos, 2007). It is a tree native to China that can reach up to 15 m. Each plant produces a high number of black-blue fruits (ca. 5–8 mm diameter) with synchronic maturation (Moltaldo, 1993; Parodi, 1980). Different species of birds have been reported as dispersal agents of this species for other regions of Argentina (Aragón and Morales, 2003; Montaldo, 1993, 2000). The genus *Ligustrum* has generated concern in terms of biological invasions in different countries of the world (Lake and Leishman, 2004; Morris et al., 2002; Richardson et al., 2000 and references therein). In Argentina, *L. lucidum* has proliferated in different regions reducing diversity of natural forests (Aragón and Morales, 2003; Cabrera, 1971; Gavier and Bucher, 2004; Montaldo, 1993, 2000). A study developed in a locality of central Argentina using satellite images showed that the fragments occupied by *Ligustrum* in 1983 were close to urban areas and compromised only 41 ha, but 15 years later the area covered by this species was extended to 1689 ha (Hoyos, 2007).

In this paper, as a first step, we investigated the reproductive phenology of *L. lucidum* and the removal agents. Considering that some traits of a species and the reproductive process can vary with habitat fragmentation (e.g., Debinski and Holt, 2000; Fahrig, 2003), we analyzed if fruit removal of *L. lucidum* varies between fragments of different sizes in the Chaco forests of Córdoba, Argentina. We also considered some aspects of the local habitat heterogeneity that could vary with habitat fragmentation and that can be related to *L. lucidum* invasive process and fruit removal. In particular, we measured plant densities of *L. lucidum* and of the other ornithochorous plant species that bear fruits simultaneously with *L. lucidum*.

2. Methodology

2.1. The study area

Based on Landsat TM5 images, seven forest fragments were selected with a minimum distance of 800 m between them. The criteria for fragment selection were (a) the presence of a minimum number of reproductive individuals of *L. lucidum*, (b) the regularity of some characteristics of the matrix (i.e., the cropped species, the minimum distance to the nearest fragment), and (c) the natural history (i.e., a minimum isolation period of 30 years; C. Torres unpublished data). We sampled three small (0.5–5 ha), two medium fragments (10–30 ha), and two continuous forests (more than 1000 ha). This criterion for fragment-size classes is based on previous studies about animal–plant interactions for this system, where functional differences were determined (e.g., Aguilar, 2005; Aguilar and Galetto, 2004 and references therein).

All the fragments are located in the Chaco region of the Province of Córdoba (Santa María and Colón Departments, over the east slope of the mountains, with altitudes ranging from 500 to 800 m a.s.l.), and have a comparable stratification of the vegetation. The mid annual temperature is 16 °C, with maximums of 45 °C and minimums of −9 °C (Capitanelli, 1979). Most precipitation falls from October to March (on average 578 mm per season). After the wet season, there is an extended dry season from April to September (on average 116 mm per season) with few precipitation events, which coincides with the period of low temperatures (Capitanelli, 1979). This region is considered a semiarid environment because of the high potential of evapo-transpiration which determines a water deficit during 11 months of the year (i.e., 69 and 97 mm of water deficit during the wet and dry seasons, respectively; Capitanelli, 1979). In addition, the beginning of the rainy season is unpredictable (i.e., it can occurs since September to January).

In the past, in general, forest canopy reached 20 m and different vegetation strata were present (Lorentz, 1876). At present, this ecosystem is characterized by secondary patch forests mixed with open areas with a canopy that covers 30–60% of the soil surface; it is greatly altered by human activities, showing a high rate (2.2%) of annual forest lost (Cabido and Zak, 1999; Zak et al., 2004). Natural vegetation includes trees—e.g., *Lithraea molleoides*, *Aspidosperma quebracho-blanco*, *Prosopis* spp., *Geoffroea decorticans, Zanthoxylum coco, Celtis* spp.— that usually reach 7–9 m tall, thorny shrubs—e.g. *Acacia caven, Schinus fasciculatus*—, cacti, herbs, as well as epiphytes and vines (Cabido and Zak, 1999; Luti et al., 1979). Many exotic tree species can be commonly found in the Chaco forests, such as *L. lucidum*, *Melia azederach*, *Broussonetia papyrifera*, *Gleditsia triacanthos*, *Morus* sp., *Ulmus* sp.

2.2. *L. lucidum* phenology

We randomly selected a maximum of 10-flowering individuals of *L. lucidum* in each fragment. To determine the flowering and fruiting periods, each focal plant was observed every 15 days from March to September 2004 recording the phenological phases. In order to estimate the average number of flowers/fruits produced per inflorescence/infructescence, we cut a minimum of five inflorescences/infructescences per tree with a telescoping pruner. Then, all the flowers/ripened fruits were counted.

2.3. Removal agents

We observed bird species that were consuming *L. lucidum* fruits on trees in each of the fragments. A minimum of three individuals of *L. lucidum* were randomly selected in each fragment (range 3–8 individuals, total number = 31 focal trees) to perform bird observations. Four observation periods (15 min) per tree were done on different days and times (i.e., two periods early in the morning and two in the afternoon). We completed a total observation period of 31 h (9, 9, and 13 h for the plants of the small, medium fragments, and continuous forests, respectively). We waited for 5 min before the initiation of observations to reduce bird intimidation. The observations were done with binoculars and birds were identified according to Narosky and Izurieta (2003).

2.4. Plant density of *L. lucidum* and of other ornithochorous plant species

Six plots of $2 \times 10\,\mathrm{m}^2$ were randomly established in each fragment at a minimum distance of 30 m from the forest edge. The number of adult individuals of *L. lucidum* (height over 1.5 m) and the number of other ornithochorous plant species that bear fruits simultaneously were counted in each plot. Three plots were examined at both the beginning and the end of the removal period (June–July, August–September, respectively). The end of the removal period in each fragment was determined following tagged infructescences. Visual and morphological traits of the diaspores were used to classify plant species of the community within the ornithochorous dispersal syndrome (Howe and Smallwood, 1982).

2.5. Fruit removal

The percentage of fruits removed per tree (%FRT) was calculated using the relationship between the number of fruits removed per tree (FRT) and the number of fruits offered per tree FOT

$$\%\mathrm{FRT} = \mathrm{FRT}/\mathrm{FOT} \times 100 \tag{1}$$

FRT was determined using the average number of fruits removed per infructescence $\bar{x}_{(\mathrm{FRI})}$, obtained from a minimum of five infructescences per tree and the mean number of infructescences per tree (NI; the total number of infructescences were counted on small and large trees; this number was calculated by multiplying the number of infructescences counted on a typical branch by the number of fruit-bearing branches of the tree):

$$\mathrm{FRT} = \bar{x}_{(\mathrm{FRI})} x \mathrm{NI} \tag{2}$$

The number of fruits removed per infructescence (FRI) was determined considering the mean number of fruits offered by the infructescence (FOI), the mean number of fruits that remained unremoved in the infructescences at the end of the removal period (FUI), and the mean number of fruits dropped from the infructescences (FDRI):

$$\mathrm{FRI} = \mathrm{FOI} - (\mathrm{FUI} + \mathrm{FDRI}) \tag{3}$$

To determine each of the terms of Eq. (3), a minimum of five infructescences per focal plant were removed with a telescoping pruner at different phenological moments. First, infructescences were collected before the fruits were completely ripened (i.e., when a fruit display a uniform black-violet color; Montaldo, 1993), all fruits were counted, and the rachis length of each one was measured. With these data, a regression analysis was performed to estimate later the number of fruits offered by each infructescence at the end of the removal period (i.e., this regression equation was used later to obtain FOI using rachis length data). Then, all the fruits that remained in the infructescences were counted to determine FUI, cutting five additional infructescences per focal plant at the end of the removal period. The rachis length was measured for each of these infructescences to estimate the total number of fruits offered (FOI) using the regression equation previously mentioned. FDRI was obtained from the number of fruits dropped within the tulle-bags of 59 infructescences from 40 different trees at the end of the removal period. FDRI is a mean value that represents the number of naturally dropped fruits of an infructescence. This method could prevent the access of frugivores that normally remove fruits and possibly generates an overestimation of the fruits dropped (FDRI). However, we found this approach as one of the most realistic ways to estimate both the number of dropped and removed fruits.

The mean number of fruits offered per tree (FOT; Eq. (1) was calculated by the product of the mean number of fruits offered per infructescence $\bar{x}_{(\mathrm{FOI})}$ and the mean number of infructescences per tree (NI): $\mathrm{FOT} = \bar{x}_{(\mathrm{FOI})} x\,\mathrm{NI}$.

2.6. Data analysis

Nested analyses of variance (ANOVAs) were used to evaluate differences in the percentage of fruits removed per tree (%FRT) among the three fragment-size classes, and in plant density of *L. lucidum* and of other ornithochorous plant species. Homocedasticity and normality of residuals were tested through Levene and Kolmogorov–Smirnov tests, respectively. Variable transformations were needed to meet assumptions (arcsine for %FDT and $\log_{10}(x+1)$ for plant density). A Tukey test was used to compare the differences between fragment-size classes. Parametric regression was performed to describe the relationship between the rachis length and the number of fruit offered per infructescence; the later variable was transformed to $\log_{10}(x+1)$. A non-parametric Spearman correlation was run between the mean percentage of fruits removed per tree and the density of the other ornithochorous plant species in each fragment.

3. Results

3.1. Reproductive phenology of L. lucidum

L. lucidum trees flowered from the beginning of February to the end of March 2004. Flowers are disposed in complex inflorescences that produce 406±248 flowers ($n = 192$ inflorescences), which were visited by different insects (e.g., honeybees, flies, butterflies). When mature, black-violet berries are 1–2 seeded, with a diameter of ca. 5 mm. Fruit development lasted from March to May. Plants displayed mature fruits from the middle of May to the end of September. The average number of inflorescences produced per tree was 312±433 ($n = 33$ trees). On average, 29% of the flowers initiated fruit development, but only 57% of these developing fruits could reach maturity.

3.2. Removal agents

Even though mature fruits of *L. lucidum* were available from the middle of May, animal removal occurred later, from late July to the end of September. As a result, we divided the dispersal period of this species into "potential" (May–September) and "effective" (July–September) removal periods. Three bird species were observed consuming fruits of *L. lucidum*: *Turdus chiguanco* (Turdidae), *Thraupis bonariensis* (Thraupidae) and *Pitangus sulphuratus* (Tyrannidae). Removal agents were observed in large- and medium-size fragments. These species were observed between 9:30 a.m. and 3:00 p.m. In addition, bird feces with seeds of *L. lucidum* were commonly observed in most of the fragments.

Ants (*Acromyrmex* sp., Formicidae, Myrmicinae) were also observed collecting fruits of *L. lucidum* from the ground. A large number of seeds without the fleshy pulp was observed near the ant nests, and between the refuse dumps. A few weeks later, many seedlings of *L. lucidum* were observed growing at these sites.

3.3. Plant density of L. lucidum and of other ornithochorous plant species

A nested ANOVA did not show significant differences in the plant density of *L. lucidum* neither between the three size-classes of fragments ($F_{[2;\,4]} = 1.12$; $P = 0.41$) nor between fragments of the same size-class ($F_{[4;\,35]} = 1.45$; $P = 0.24$; Table 1). Even though, the explained variance in the number of plants of *L. lucidum* was greater within than between size-classes (Table 1).

The mean number of the other ornithochorous plant species per 20 m^2 ranged from 0.17 to 3.5 plants. Larger differences were observed between the medium and large fragments (Table 1), but nested ANOVA showed that these differences were not statistically significant ($F_{[2;\,4]} = 0.81$; $P = 0.92$). In addition, differences between fragments nested within each size-class were not significant ($F_{[4;\,35]} = 1.08$; $P = 0.39$). Ornithochorous plant species that matured fruits simultaneously with *L. lucidum* were only found at the beginning of the "potential" removal period of *L. lucidum*. During the "effective" removal period of *L. lucidum*, the other ornithochorous plant species of the community did not offer fruits.

3.4. Relationships between the percentage of fruits removed, the area of the fragments, and the density of other ornithochorous plant species

The mean number of fruits offered per tree was 15 316±27 811. On average, a half (52%) of the mature fruits of a tree was removed (range from 12% to 83%; Fig. 2), a fifth (16.5±22%) dropped spontaneously, and a third (31.5%±23%) remained

Table 1
Plant density of adult individuals of *Ligustrum lucidum* and of other ornithochorous plant species with simultaneous fruiting periods, in fragments of different size of the Chaco forests

Fragment area (ha)	Fragment-size classes	PDLL[a]	PDO[b]
3.58	Small	0.5 ± 0.55	1.33 ± 2.16
3.48	Small	2 ± 1.41	2 ± 2.53
1.25	Small	2 ± 1.79	0.67 ± 1.03
Average	Small	**1.5 ± 1.47**	**1.33 ± 1.97**
29.53	Medium	1.17 ± 0.75	3.5 ± 7.15
13.77	Medium	1 ± 1.1	0.17 ± 0.41
Average	Medium	**1.08 ± 0.9**	**1.83 ± 5.13**
< 1000	Continuous	0.5 ± 0.55	1.17 ± 1.33
< 1000	Continuous	1 ± 1.55	0.83 ± 1.33
Average	Continuous	**0.75 ± 1.14**	**1 ± 1.28**

Bold numbers represent average values of PDLL and PDO for each fragment size class.

[a] PDLL: plant density of adult individuals of *L. lucidum* (mean ± standard deviations in 20 m^2).

[b] PDO: plant density of other ornithochorous plant species (mean ± standard deviations in 20 m^2).

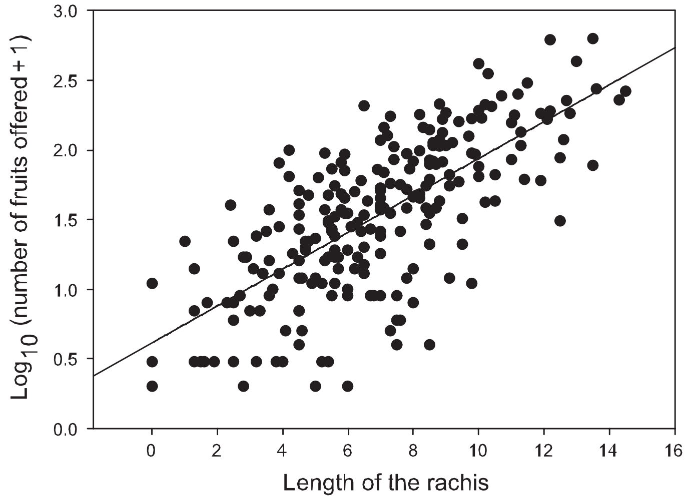

Fig. 1. Relationship between the rachis length and the number of fruits offered per infructescence in *Ligustrum lucidum*.

unremoved at the end of the removal period. The regression equation obtained to predict the number of fruits offered per infructescence was $y = 0.52+0.14X$ ($R^2 = 0.5$; $P<0.0001$), where X is the rachis's length of the infructescence (Fig. 1).

A nested ANOVA showed that the percentage of fruits removed per tree was significantly higher in small fragments than in medium or large ones ($F_{[2;\ 3.5]} = 11.51$; $P = 0.03$). There were no statistical differences between fragments nested within each size-class ($F_{[4;\ 24]} = 1.08$; $P = 0.39$; Fig. 2).

We did not run the correlation between the percentages of fruits removed of *L. lucidum* in each fragment and plant densities of the other ornithochorous plant species because these species did not bear fruits during the period of "effective" fruit removal of *L. lucidum*.

4. Discussion

We observed differences in fruit removal of *L. lucidum* in relation to the fragment size, but they were not related to the general availability of ornithochorous fruits offered in each fragment during the effective dispersal period of this exotic species. From a landscape perspective, the observed higher seed removal in small fragments could be explained if they are more isolated (With, 2002). However, satellite images showed that isolation is comparable for all the fragments used in this study. Data on bird richness/abundance within and between fragments are necessary to understand the process of fruit removal in this exotic species. For example, *L. lucidum* fruits could be an important source of water for birds, mainly during the drought period of this semiarid region when ornithochorous fruits of native species are not available.

4.1. Removal agents

Two of the three bird species (*P. sulphuratus* and *T. bonariensis*) that were observed removing fruits of *L. lucidum* are described as abundant for the Chaco region (Dardanelli, 2006). In the literature, there are some additional observations for

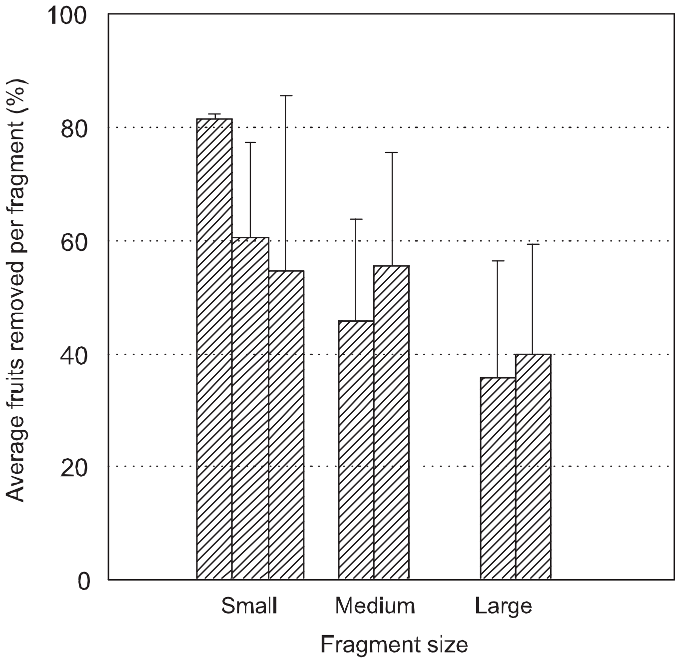

Fig. 2. Average fruit removal per tree (percentage) of *Ligustrum lucidum* in fragments of different size of the Chaco forests.

these bird species as dispersers. The omnivorous *P. sulphuratus* was reported dispersing fruits of ornithochorous plant species in the Brazilian Cerrado (Mercival and Galetti, 2002), and fruits of *L. lucidum* in SE Argentina (Punta Lara Reserve; Montaldo, 1993). In addition, two different Turdidae species (*Turdus amaurochalinus* and *T. rufiventris*) have been reported as legitimate seed dispersers of *L. lucidum* in SE Argentina (Montaldo, 1993). The lower richness of removal agents observed in the Chaco region compared to the Punta Lara Reserve (Montaldo, 1993) could be related to methodological differences. It is possible that other bird species are involved in fruit removal of *L. lucidum* in the Chaco region, considering the large number of fruits produced and removed per tree, the small fruit size that could be easily ingested by many bird species, and the local richness of birds (Montaldo, 2000; Richardson et al., 2000; Carlo et al., 2003; Dardanelli, 2006).

Ants were fortuitously seen carrying *L. lucidum* fruits and can be considered as secondary agents of seed dispersal. Secondary dispersal by ants was found in many exotic species in their new geographical range (e.g., Richardson et al., 2000). The ants deposited seeds without the fleshy pulp in the refuse piles. This process may reduce fungal seed infection, and could increase seed germination success, as was reported for some tree species (Pizo et al., 2005).

The role of dispersers seems to be very important for *L. lucidum* because experiments comparing seed germination between fruits with or without the fleshy pulp showed a significant increase when the fleshy pulp is manually removed (Panetta, 2000; Ferreras, unpublished data). This finding suggests that the removal of the fleshy pulp by dispersers could increase seed germination. Nevertheless, experiments comparing germination between seeds without fleshy pulp (manually removed) and seeds from bird's feces showed that the latter seeds had a significant lower germinability (Ferreras, unpublished data), suggesting a reduction in their viability. On the other hand, these results highlight the potential role of ants as important seed dispersal agents.

4.2. *Plant density of L. lucidum and of other ornithochorous plant species*

Plant density of the invasive species can be taken as an indirect measure of the state of the invasion. For example, in SE Argentina (Punta Lara Reserve) there was a dramatic increase in the population density of *L. lucidum* over the last 50 years (from 5% to 50%; Montaldo, 2000). In central Argentina, plant density values for *L. lucidum* and for the other ornithochorous plant species were comparable between fragments (from 0.5 to 2, and 0.17 to 3.5 individuals per 20 m^2, respectively). Comparable data (2 individuals of *L. lucidum* per 20 m^2) were found by Hoyos (2007) in a study developed in the same region. Considering that this species tends to develop monospecific woodlands (Gavier and Bucher, 2004), it is possible that actual values of population density in these forest fragments are indicating an initial phase of *L. lucidum* invasion.

4.3. *Linking the invasion process with reproductive traits of L. lucidum*

Fruit removal in *L. lucidum* occurs during a period of a low ornithochorous fruit offer by the native plant species of the community (i.e., in winter, during the dry season). This pattern was previously reported for ornithochorous plant species in different communities of Argentina (Aragón and Morales, 2003; Montaldo, 2000; Varela, 2004). Although a large number of fruits were offered per tree for many months, ripened fruits were effectively removed during the final phase of the "potential" removal period of this species. This trend could indicate (i) a low preference for these fruits by the removers (e.g., because fruits of this species are not of high nutritional value; Montaldo, 2000), and (ii) that the invasion process of this species in central Argentina is favored by a phenological window that maximizes fruit removal (i.e., fruits of *L. lucidum* constitute a food source during the dry season when fruits of other native ornithochorous species are not available).

L. lucidum displays a variety of traits that could be favoring the invasive process: (i) vegetative reproduction (Aragón and Groom, 2003; Lichstein et al., 2004), (ii) a high number of fruits is effectively removed and dispersed, (iii) seeds can be disseminated over large distances because fruit dispersers are birds, (iv) dropped fruits can be secondary dispersed by ants, (v) a high percentage of seed germination, and (vi) trees of small fragments showed the higher values of fruit removal. Many natural landscapes of the region—mainly those located near urban areas—are now monospecific woodland of *L. lucidum* (Gavier and Bucher, 2004). Exotic tree species are new components that could structurally and functionally change the composition of communities in Chaco forests remnants. New studies on the ecology of animal–plant interactions considering exotic species are needed if native vegetation of these forests is to be conserved particularly because, habitat fragmentation may be favoring the introduction and expansion of invasive species.

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