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Effects of Rufous-Backed Robin (*Turdus rufopalliatus*) on Brazilian Pepper-Tree (*Schinus terebinthifolius*) Seed Germination and Dispersal in a Subtropical Peri-Urban Environment

Mauricio Ortega-Flores[1,2], Elisa Maya-Elizarrarás[2], and Jorge E. Schondube[2]

Abstract

Alien invasive species pose a major threat to socioecological systems worldwide. Native avian frugivores may enhance the dispersal and germination success of exotic plants introduced for ornamental motives. In this study, we investigated the role of the native Rufous-backed Robin (*Turdus rufopalliatus*) as a potential dispersal agent of the worldwide invasive Brazilian pepper-tree (*Schinus terebinthifolius*). We evaluated gut transit time and mean retention time for birds feeding on this plant fruits and compared the germination rate and germination probability of intact fruits, peeled seeds, scarified seeds, and seeds from bird fecal samples. Gut transit time varied from 1.26 to 13.65 min, while mean retention time varied from 3.4 to 11.3 min. Germination rates differed between the intact seeds and the other three treatments; however, we found no differences among the germination rates of peeled, scarified, and defecated seeds. We found no differences among the seed germination probabilities of all treatments using the survival analysis; however, intact seeds presented a lower germination probability. Few studies have evaluated the role of avian frugivore's gut transit time, mean retention time, germination rate, and germination probability on the seed germination of invasive plants. This study indicates that a native fruit-eating bird can play an important role dispersing the seeds of the Brazilian pepper-tree in an invasive range.

Keywords

avian frugivore, biotic seed dispersal, germination rate, gut transit time, invasive tree

Introduction

Invasive species generate negative socioecological impacts all over the world and are one of the main drivers of global change in the Anthropocene (Clavero & García-Berthou, 2005; Mooney & Cleland, 2001; Vitousek, Mooney, Lubchenco, & Melillo, 1997). They are considered as the second greatest threat to biodiversity, generating economic losses of thousands of millions of dollars per year (Holmes, Aukema, Von Holle, & Liebhold, 2009; Lowe, Browne, Boudjelas, & De Poorter, 2000; Pimentel, Zuñiga, & Morrison, 2005). The lack of strong biosecurity policies in most countries and recent globalization processes, like the development and growth of the world trade system, have increased the problems generated by invasive species by intensifying the rate at which introduction of exotic species occurs (Meyerson & Mooney, 2007; Perrings, Dehnen-Schmutz, Touza, & Williamson, 2005).

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Invasive plant species are known for having strong ecological impacts that include the modification of ecosystem functioning and structure, such as the alteration of fire regimes, nutrient cycling, and hydrology (Lambert, D'Antonio, & Dudley, 2010; Le Maitre, 2004; Weidenhamer & Callaway, 2010). By doing this, they can change the configuration of native biotic communities and ecosystems (Ehrenfeld, 2010; Liao et al., 2007; Vilà et al., 2011). The Brazilian pepper-tree (*Schinus terebinthifolius*) is an invasive tree member of the Anacardiaceae family native to Brazil, Argentina, Uruguay, and Paraguay (Morton, 1978; United States Department of Agriculture, Agricultural Research Service, 2012). It is a shrubby tree with narrow, compound leaves that grows 4 to 10 m tall, with a trunk 25 to 35 cm in diameter. It produces an abundance of small flowers formed in panicles that bear a great many small, red-colored, berry-like fruits (5–6 mm in diameter) that contain a single seed (Ferriter, 1997). It is used as an ornamental tree and can be found acting as an invasive species in Mediterranean Europe, North and South Africa, East Asia, Australia, South America outside its original range, parts of Central America, Bermuda, the Bahama Islands, Florida, California, Hawaii, and southern Arizona (Invasive Species Specialist Group, 2011; Morton, 1978; Panetta & McKee, 1997).

The Brazilian pepper-tree has caused important ecological effects on native ecosystems (Donelly, Green, & Walters, 2008; Ewe & Sternberg, 2002, 2003; Morton, 1978). It outcompetes native plants by forming a thick canopy that produces a dense shade and by releasing allelopathic substances (Donelly et al., 2008; Morgan & Overholt, 2005). The invasion success of this species can be attributed to its high tolerance to shade (Ewel, 1986; Invasive Species Specialist Group, 2011), its production of high quantities of fruits that are commonly consumed by native species of birds (Ewel, Ojima, Karl, & DeBusk, 1982; Panetta & McKee, 1997) and by physiological adaptations that allow it to survive in a wide range of pH, hydrology, and salinity conditions (Dawkins & Esiobu, 2016; Ewe & Sternberg, 2002; Mytinger & Williamson, 1987). It can also generate important impacts on native bird communities by reducing both bird density and diversity (Curnutt, 1989).

Avian frugivores are identified as important vectors of seed dispersal and germination of a large number of plants all over the world (Garcia, Zamora, & Guillermo, 2010; Medellin & Gaona, 1999; Snow, 1981). Several studies had demonstrated that seed transit through the digestive tract of birds can have a positive effect on seed germination, and the high mobility of these animals tend to dramatically increase seed rain (Izhaki & Safriel, 1990; Traveset, 1998). However, little is known about the invasion ecology of animal-dispersed plants and the role that native fruit-eating animals play in their establishment and spread into new environments (but see Bartuszevige & Gorchov, 2006; Richardson et al., 2000 as examples).

In Mexico, the Brazilian pepper-tree is recognized as an exotic species, however, is not included in the official government list of invasive species (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, 2016). To this date, there are no reports of this tree acting as an invader in the country. However, the species is becoming widely used as an ornamental plant inside urban environments in several regions of Mexico. In this study, we explore the potential effect that a native frugivore bird, the Rufous-backed Robin (*Turdus rufopalliatus*), has on its dispersal by measuring gut transit time and the effects that ingestion and defecation had on seed germination.

Methods

Birds Feeding on Brazilian Pepper-Tree Fruits, and Fruit Collection

We conducted 10 observation sessions to determine which birds were feeding on the fruits of the Brazilian pepper-tree at the campus of the National Autonomous University of Mexico in Morelia, Michoacan, Mexico (19°38′55.21″N, and 101°13′46.82″W). All sessions started at sunrise and lasted 6 hr and were conducted during a period of 3 weeks in the month of April 2016 when the trees were fruiting heavily. We observed three bird species feeding on the fruits of the Brazilian pepper-tree during this period: the Rufous-backed Robin (*Turdus rufopalliatus*), the spotted wren (*Campylorhynchus gularis*), and the yellow-bellied sapsucker (*Sphyrapicus varius*). From these species, the Rufous-backed Robin was observed ingesting fruits more frequently. We only used individuals of the Rufous-backed Robin for our experiments due to the fact that it includes more fruit in its diet than the other two species, it visited the trees more often, and adapts well to captivity. In addition to our observations, we collected whole fruits (≅400 fruits) from seven different individual trees and kept them at room temperature in Ziploc® bags to conserve freshness.

Gut Transit Time and Mean Retention Time of Brazilian Pepper-Tree Seeds

We assessed gut transit time and mean retention time of seeds ingested by four captive individual birds. Birds were obtained from a local pet shop and kept in cubic cages (60 × 60 × 60 cm), in a bioterium at Instituto de Investigaciones en Ecosistemas y Sustentabilidad in the National Autonomous University of Mexico campus mentioned earlier. Cages were lined with white paper cover with plastic and monitored with a camera system that recorded bird behavior with a resolution of

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30 frames/s (DIGIOPG2®, United States). We monitored the birds for three days before conducting our experimental trials. During this time, food was weighed in the mornings and the afternoons to determine food ingestion. The number of experimental birds was small due to experimental permit constraints.

We defined gut transit time as the time from ingestion of a marker to its first appearance in the feces (Van Soest, 1994; Warner, 1981). Mean retention time as defined by Van Soest (1994), is the time an average particle of the marker takes to be excreted after a pulse dose of the marker is ingested, and is the integrated average of the distribution of marker concentration in the feces after dosing. In this case, since each fruit of the Brazilian pepper-tree contains only one seed, we used individual seeds as markers. We conducted two trials daily per bird, during five consecutive days. The first trial started at sunrise, and the second trial started at 16:00 hours. Trials lasted as long as needed for the birds to defecate all ingested fruits. In each trial, we offered to individual birds 16 fruits and water. Maintenance diet was not offered to the birds during the trials but was available to them between trials. From the videos, we recorded the time of ingestion of each of the 16 fruits, and all defecation events until all the ingested seeds were excreted. We collected each one of the feces produced by the birds and weighted them. Mean retention time of seeds in the birds' guts was calculated for each individual bird with the formula:

$$MRT = \sum_{i=1}^{n} miti \sum_{i=1}^{n} mi$$

where *ti* is the mean retention time of seeds in the gut, and *mi* is the quantity of feces (g dry mass) excreted at time interval *ti* after feeding (Warner, 1981).

Germination Experiments

To consider the effects that passing through the gut of the Rufous-backed Robin had on the germination of Brazilian pepper-tree seeds, we conducted a germination experiment with four treatments: (a) intact fruits (whole fruits were set to germinate), (b) peeled seeds (fruit skin and pulp removed mechanically by hand), (c) scarified seeds (fruit skin and pulp removed mechanically by hand and seeds scarified by placing them in boiling water for 5 s; Barton, 1965; Roberts, 1972), and (d) seeds from fecal samples of captive birds. All collected fruits were mixed, and from this stock, we randomly selected the fruits used in each treatment. We placed 50 seeds per treatment in disposable trays covered with a pot-mix and located them in a room under natural light (mean temperature 27°C and ~12-hr light photoperiod). Humidity was maintained by adding water every day. Seeds were monitored every morning to determine the day of radicle emergence. We monitored them for 21 days following the day the seeds were placed on the germination trays (Day 0). Germination was expressed as seed germination rate (accumulative percentage of seeds that germinated vs. time) and germination probability at the end of the 21 days period.

Data Analysis

We determined the germination rate of the different treatments by obtaining the slope of the accumulative percentage of seeds that germinated versus time. Because these plots were not linear, we log-transformed the accumulative percentage of seeds that germinated to perform our statistical analyses. We compared the slopes of the germination rate among treatment using an analysis of covariance. In addition, we used survival analysis to describe and compare the germination probability of all the seed germination treatments (Muenchow, 1986). If a seed germinated, then it became censored data because it left the seed state to become a seedling. We used the Kaplan–Meier product limit nonparametric method for the computation of the probability that seeds had a germination difference after the start of the time (days) and use the log-rank (Mantel-Cox) statistic to test differences among germination treatments. Statistical analyses were conducted in the platform StatView 5.0 (Abacus Concepts, Inc., 1996).

Results

Gut Transit Time and Mean Retention Time

Gut transit time of the Brazilian pepper-tree seeds in the gut of Rufous-backed Robin varied from as low as 1.2 min up to 13.6 min (5.9 ± 4.4 min; mean $\pm$ *SD*). Mean retention time varied from 3.4 to 11.3 min (9.0 ± 5.7 min; mean $\pm$ *SD*). Birds varied widely in the time they needed to ingest and defecate the 16 fruits we offered them, from as low as 9.3 min up to 69.3 min.

Germination Rate and Seed Survival Analysis

No seeds from the intact fruit treatment germinated during the 21 days experimental period; however, seeds in the other three treatments did. The number of germinated seed was not very high and varied among treatments (peeled: 13 seeds, 32%; scarified: 7 seeds, 14%; defecated: 10 seeds, 20%). We found statistical differences among the germination rate of the intact seeds and the other three treatments (peeled seeds, scarified seeds, and seeds from bird's fecal samples; Figure 1 and Table 1). We found no statistical differences when we compared the germination probabilities of the four

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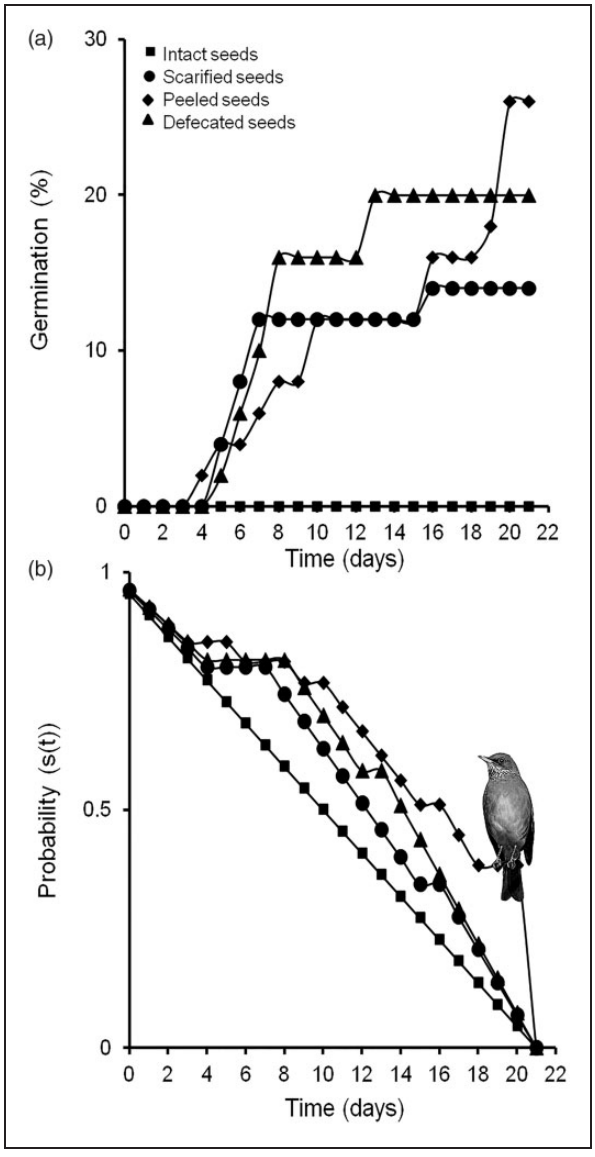


Figure 1. Germination rate and germination probability (from the survival analysis) of the Brazilian pepper-tree seeds. Seed germination ceased after Day 21 and germination did not occur for intact fruits as seen in both (a) and (b).

treatments, ($\chi^2 = 6.987$, $df = 3$, $p = .0726$). However, there is a pattern that shows a lower germination probability of the intact seeds (Figure 1). The intact seed treatment maintained a continuous change rate between the non-germinated seed stage and the seedling stage during the whole experimental time, diminishing the germination probability with each day that passed (Figure 1). The other three seed germination treatments started in a similar fashion during the first three days, however during the 4th and 8th days, peeled, scarified, and defecated seed treatments varied among them. However, when considering the complete experimental time, we found no significant differences in germination probability among these three treatments ($\chi^2 = 3.237$, $df = 2$, $p = .1982$). After the 18th day, only the peeled seed treatment maintained a higher germination probability than the other treatments (approximately 40% of probability; Figure 1).

Discussion

We found that the Rufous-backed Robin and two other resident bird species consumed fruits of Brazilian pepper-trees planted on gardens. The gut transit time and mean retention time of the seeds in the gut of the Rufous-backed Robin were relatively short. The germination rate varied for all four treatments, and the germination probability differed significantly between the intact fruits and the other three treatments. However, we found no statistical differences in the germination probability among mechanically peeled seeds, scarified seeds, and seeds from the fecal samples.

We only observed three bird species consuming the fruits of the Brazilian pepper-tree. This could be the result of the fruits of this plant species being dry and presenting little digestible matter; therefore they can be less preferred or consumed by native birds in relation to other food resources. However, another species of the same genus, the Peruvian pepper-tree (*Schinus molle*), which was brought to Mexico by the Spaniards in the 16th century, is consumed by a large number of bird

Table 1. ANCOVA Table Depicting Differences of Germination Rate Between the Interactions of All Four Different Treatments.

	Defecated	Peeled	Scarified
Intact	$F(3, 40)=115.7750$, $p < .0001$*	$F(3, 40)=201.5896$, $p < .0001$*	$F(3, 40)=92.6996$, $p < .0001$*
Defecated	–	$F(3, 40)=53.5153$, $p = .9258$	$F(3, 40)=34.2987$, $p = .2836$
Peeled	–	–	$F(3, 40)=45.2813$, $p = .2481$
Scarified	–	–	–

Note. Asterisk indicates statistically different values.

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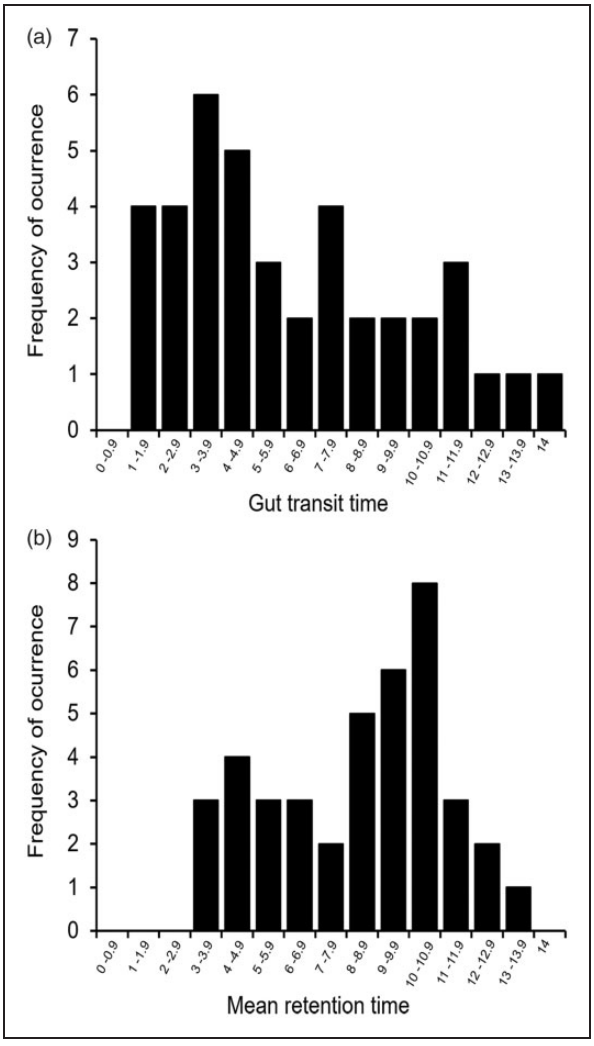


Figure 2. Frequency distribution graph that depicts the variation of gut transit time (a) and mean retention time (b) of Brazilian pepper-tree seeds passing through the digestive tract of Rufous-backed Robin individuals.

species in urban areas, and desertic and semidesertic regions of the country (Corkidi, Cacho, & Búrquez, 1991). This suggests that the Brazilian pepper-tree has the potential to be visited and its fruits ingested by more species of native birds in different ecological conditions. Therefore, it is necessary to conduct more field observations focusing on ecological systems where fruit quantity is limited, just like the cold or template semideserts of the central and northern part of the country (i.e., the Chihuahuan Desert), where this species has been planted as an ornamental tree in urban public spaces and has been found growing in the wild (Global Biodiversity Information Facility, 2017).

To what extent could the Rufous-backed Robin be considered as a good disperser of the Brazilian pepper-tree? Our observations indicate that individuals of this native bird species spent a small fraction of time in Brazilian pepper-trees and flew away after feeding of its fruits. When they visit this tree, this bird species tend to land on branches and fed rapidly on three to eight fruits before leaving. The gut transit time and mean retention time that we found for this bird species while feeding on the fruits of this tree were much shorter compared with those reported for other frugivorous birds (Witmer & Van Soest, 1998). These could be caused by the small amount of digestible matter present in the fruits of the Brazilian pepper-tree (Levey & del Río, 2001). However short, gut transit time values make possible for the birds to disperse the seeds of this plant away from the parent tree between short and intermediate distances. While there is no information on flying distances and flying speed of the Rufous-backed Trush, we know that a closely related species of similar body mass, morphology, and behavior (American Robin—*Turdus migratorius*) moves with a mean velocity of 40.5 km/h (Schnell & Hellack, 1978), so that in the time that a seed passes through the digestive tract of the Rufous-backed Robin, this bird could disperse it a distance up to 6 km.

In addition, telemetric observations of the American Robin show that this bird travels distances of 640 m a day in an urban environment (Graber & Wunderle, 1996). Although this species does not travel far distances in a given day in urban areas, flight traveling distances of robins are highly influenced by landscape composition (Da Silveira, Niebuhr, Muylaert, Ribeiro, & Pizo, 2016). Peri-urban areas are characterized by being the edges between urban and rural or natural environments, thus, acting as potential sources of invasive species propagules. Due to its flying capacities, Rufous-backed Robins could allow the dispersal of Brazilian pepper-trees outside urban environments when trees of this species with fruits are located in small settlements or in the gardens of peri-urban zones.

We found that the transit of seed through the digestive tract enhanced seed germination rate in relation to intact fruits. This is similar to the results of a study conducted in Brazil using the same plant species in which they found a higher germination rate of defecated seeds in relation to intact fruits (D'Avila, Gomes-Jr, Canary, & Bugoni, 2010). The lack of difference we found between the three treatments in which fruit manipulation was conducted (peeled seeds, scarified seeds, and defecated seeds) suggest that the presence of the pulp or skin of the fruits inhibits seed germination and that any process which removes the pulp improves seed germination. Therefore, non-granivorous birds that consume Brazilian pepper-tree fruits could enhance seed germination by digesting the seed cover. In addition, it has been suggested that the Brazilian pepper-tree have antibacterial effects, which could retard seed decomposition but also can inhibit seed germination (Silva et al., 2010). This finding supports our hypothesis that the fruits of this species only germinate when pulp or skin is removed. A study conducted in Australia, where this tree species is considered

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an invasive species, found similar results, with no statistical differences between the germination rates of bird defecated and peeled seeds (Panetta & McKee, 1997), supporting our claim.

In addition, a recent study conducted in South Africa by Dlamini, Zachariades, and Downs (2018) where gut transit time and germination experiments were conducted using three native bird species shows longer gut transit times than those of the Rufous-backed Robin. This suggests that the seed rain of the Brazilian pepper-tree can vary depending on the native bird frugivorous species that ingest it in different regions. Moreover, these authors found that seed germination started between Day 15 and Day 20 for the three South African bird species. This finding differs dramatically from our results, since we found that in seeds ingested and defected by the Robin germination started at Day 5. This difference could be explained by differences in gut morphology and physiology among the different bird species analyzed in the two studies.

Previous studies have indicated the role played by native birds in the invasion process of the Brazilian pepper-tree and the risks that its dispersal, establishment, and colonization may pose to native species and ecosystems (Mandon-Dalger, Clergeau, Tassin, Rivière, & Gatti, 2004; Stevens & Beckage, 2009; Williams, Muchugu, Overholt, & Cuda, 2007). Our data indicate that Mexico is a country where this species could become invasive, generating negative socioecological effects. Williams et al. (2004) indicated that stratified dispersal, explained as the combination of both local seed dispersal (caused by animal vectors) and long-distance jumps (caused by human transportation), is controlling the invasion success of the Brazilian pepper-tree in Florida, United States, a place, where this species is considered one of the most iconic invasive species (Ewel, 1986). Moreover, stratified dispersal increases the rate and distance of range expansion in a significant matter compared with diffuse dispersal (Higgins & Richardson, 1999). Since our study indicates that a native frugivore bird species enhance seed dispersal and germination of the Brazilian pepper-tree (local seed dispersal), and that different states and municipalities are using this tree species as an ornamental tree (long-distance jumps) in urban green spaces (Ayuntamiento de Zacatecas, 2011; Norma Estatal Ambiental-Secretaría de Medio Ambiente y Desarrollo Territorial, 2005; personal observation), there is an ongoing stratified dispersal that could trigger the rapid invasion success of the Brazilian pepper-tree in the country. In addition, *Turdus* spp. have been depicted as consumers and dispersers of invasive plants (Bartuszevige & Gorchov, 2006; Ewel, 1986), therefore our study reinforce the idea that birds in this genus could be acting as important animal vectors in the invasion success of some alien plant species.

In Mexico, this tree species has not been considered as an invasive species (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, 2016). This is shocking if we consider that this species acts as an invasive species in the United States in similar climatic conditions to the ones in which this species is found in Mexico. Not only that, but also the Peruvian pepper-tree, a similar and phylogenetically close species is also an invasive species in different regions of the country. This situation seems problematic since this species is being used as an ornamental tree in cities of different states of Mexico, such as Jalisco, Michoacán, Querétaro, San Luis Potosí, and Zacatecas (Ayuntamiento de Zacatecas, 2011; Norma Ambiental Estatal-Secretaría del Medio Ambiente para el Desarrollo Sustentable, 2005; personal observation). In addition, this fact indicates that Mexico national invasive species list is far from complete, lacking high-risk species being used at the present in the country. This lack of rigor of the national list of invasive species of the Federal government and the use of exotic invasive species by State Governments in urban gardens, parks, and streets add additional risks of invasive species to the ecological and socioeconomic welfare of one of the most biodiverse countries in the world.

Implication for Conservation

Despite the fact that the Brazilian pepper-tree is considered as one of the 100 world's worst invasive species (Lowe et al., 2000), and it is present in several states of Mexico, this species is not included on the official governmental list of invasive species and is promoted by different municipalities across the country as an ornamental plant species to be included in urban green spaces (Ayuntamiento de Zacatecas, 2011; Norma Ambiental Estatal-Secretaría del Medio Ambiente para el Desarrollo Sustentable, 2005). Our study indicates that native frugivorous species, such as the Rufous-backed Robin, can act as important seed dispersal agents of this invasive species, enabling its successful spread and establishment in different regions of the country. While we do not offer information on the possible role of other bird species in the dispersion, and establishment of this invasive tree, the Rufous-backed Robin by itself could generate an important problem dispersing this plant. A study conducted by Martínez-Morales and collaborators (2010) indicates that the Rufous-backed Robin abundances and distribution are increasing dramatically in the country. They predict that its geographic range should cover 40% of Mexico by 2025. The increase in the geographic distribution of this bird species, together with its predisposition to use urban environments, and the use of the Brazilian pepper-tree individuals in urban green spaces could help to expand the Brazilian pepper-tree geographic range too. We encourage local and national institutions to include the Brazilian pepper-tree on the official list of invasive species in order to stop the

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socioeconomic and ecological problems that its dispersal could generate. Studying the ecology of the Brazilian pepper-tree and its interactions with native bird frugivores is relevant to propose management strategies that could efficiently control it before it becomes a major conservation problem in a biodiverse country like Mexico.

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