The role of avian frugivores on germination and potential seed dispersal of the Brazilian Pepper *Schinus terebinthifolius*

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Abstract: Frugivorous birds play a key role in seed dispersal and establishment of a range of plant species, including invasive weeds, such as the Brazilian Pepper *Schinus terebinthifolius*. The potential of seed dispersal of *Schinus* by birds with varied feeding behaviours was studied through seed-viability tests and germination experiments using seeds obtained from birds in the field and birds kept in captivity. It was found that seeds collected after gut passage in five bird species in the field had higher proportion of germination as well as higher germination rates compared to the control seeds. Viability of seeds ingested by the Blue-and-yellow Tanager *Thraupis bonariensis*, which mandibulates seeds before ingesting, was significantly lower than control seeds, while reduction in viability of seeds ingested by the Creamy-bellied Thrush *Turdus amaurochalinus* was nonsignificant. Seeds ingested by birds in captivity germinated earlier than the control seeds, within 1–2 weeks, and had proportion and germination rates higher than controls. Probably both mechanical and chemical effects play a role in enhancing germination of seeds. In Brazil where both *Schinus* and avian frugivores had evolved together, the dependence of *Schinus* on generalist frugivores had been demonstrated in this study, similar to other countries where the invasive *Schinus* is dependent on native or introduced avian species for its spreading. This finding has important implications for the restoration of human-altered areas in South America, were *Schinus* is a native pioneer species, as well as for the management and restoration of areas invaded by *Schinus* elsewhere.

Keywords: *frugivory, seed germination, invasive species, weed species, restoration.*

D'AVILA, G., GOMES-Jr., A., CANARY, A.C. & BUGONI, L. **O papel de aves frugívoras na germinação e potencial dispersão de sementes da Aroeira-vermelha *Schinus terebinthifolius***. Biota Neotrop. 10(3): http://www.biotaneotropica.org.br/v10n3/pt/abstract?article+bn00910032010.

Resumo: As aves frugívoras desempenham papel chave na dispersão de sementes e no estabelecimento de uma ampla gama de espécies de plantas, incluindo espécies invasoras como a Aroeira-vermelha *Schinus terebinthifolius*. O potencial de dispersão das sementes de Aroeira-vermelha pelas aves com diferentes tipos de comportamentos alimentares foi estudado através de testes de viabilidade de sementes e experimentos de germinação de sementes obtidas de aves em campo e de aves mantidas em cativeiro. Demonstrou-se que as sementes coletadas após a passagem pelo trato digestório de cinco espécies de aves em campo tiveram proporção de germinação mais alta e taxas de germinação semelhantes aos controles. A viabilidade das sementes ingeridas por *Thraupis bonariensis*, o qual mandibula as sementes antes de ingeri-las foi significativamente inferior ao controle, enquanto a redução na viabilidade das sementes ingeridas por *Turdus amaurochalinus* não foi significante. Sementes ingeridas por aves em cativeiro germinaram antes que seus controles, entre 1 e 2 semanas, e tiveram proporção e taxa de germinação mais altas que o controle. Provavelmente ambos os efeitos, químico e mecânico, desempenham papel no aumento da germinação das sementes. No Brasil, tanto a Aroeira-vermelha quanto as aves frugívoras estudadas evoluíram juntas, e foi demonstrado neste estudo a dependência que a aroeira tem das aves frugívoras para sua dispersão, semelhante a outros países onde esta árvore é dependente de espécies de aves nativas ou introduzidas para sua dispersão. Estes resultados têm importantes implicações para a recuperação de áreas alteradas por atividades antropogênicas na América do Sul, onde a Aroeira-vermelha é uma espécie pioneira nativa, assim como para o manejo e recuperação de áreas invadidas pela espécie em outros locais do planeta.

Palaras-chave: *frugivoria, germinação de sementes, espécies invasoras, espécie de planta daninha, recuperação.*

Introduction

The identification of recruitment pathways is one of the keys to understand dispersal mechanisms and establishing invasive plant-control strategies (Tassin et al. 2007). Frugivorous vertebrates frequently play a critical role in plant recruitment in native and invaded areas by dispersing seeds away from parent plants and by the effects of seed passage through their guts, thereby altering germination patterns (Samuels & Levey 2005). Seed passage through the gut of frugivores can, by varied ways, alter seed viability (i.e., cause mortality of the embryo = seed predation) and affect the germinability (the percentage of seeds that germinate) and the germination rate (or germination speed). Mechanical and chemical actions in the gut are common effects of frugivores on seeds, while release of germination inhibitors and high osmotic pressure in exocarp are less frequently mentioned effects (Traveset 1998, Samuels & Levey 2005).

The Brazilian Pepper *Schinus terebinthifolius* Raddi (Anacardiaceae), hereafter *Schinus*, is naturally distributed in tropical and subtropical South America from northeastern Brazil to Uruguay, Paraguay, and northeastern Argentina (Joly 1979). In Brazil, *Schinus* is found along the coast toward inland areas up to 2000 m above sea level, from Pernambuco State, near the Equator, to Southern Brazil where it is common and found virtually in any altered area (Joly 1979, Lenzi & Orth 2004a). Througout their range it occurs in areas in early stages of successional regeneration, forest edges, cities, dunes, drylands, marshes, and grasslands (Hasui & Höfling 1998, Backes & Irgang 2002, Ewe & Sternberg 2002, Tassin et al. 2007). As it is adapted to different environments, its appearance varies from arbustive sprawling shrub 2–3 m in height to trees up to 15 m (Lenzi & Orth 2004a). Crop of a single tree consists of large number of drupe-like fruits, bright red when ripe, with 3–5 mm in diameter enclosing a single internal seed. In Brazil, the fruiting period is from January to October (Jesus & Monteiro-Filho 2007). It is a dioecious plant, with pollination mediated by many native flies, wasps, and bees of over 10 families in a single area (Lenzi & Orth 2004b). Hence, it outcompetes native species, due to its tolerance to extreme moisture conditions, shaded environments, saline conditions, and allelopathic effects on neighboring plants (Cuda et al. 2005). It is an aggressive pioneer species, with rapid growth during sapling stages in nutrient-depleted soils (Souza et al. 2001) and rapidly occupies early and secondary successional stages, mainly due to high dispersion of seeds (Backes & Irgang 2002). It was introduced in over 20 countries of all continents, except Antarctica, currently with global distribution in two subtropical-temperate belts in both southern and northern hemispheres (Morton 1978, Mytinger & Williamson 1987). Introduced as ornamental in Florida, USA, during the ninetienth century *Schinus* extended its range to cover over 280,000 ha and is now regarded as the most widely found exotic woody species in Florida (Ewe & Sternberg 2002, Williams et al. 2005), listed as prohibited plant and noxious weed (Cuda et al. 2005). As a toxic weed which threatens biodiversity, it has been target of eradication and/or control activities by conventional and biological methods in the US mainland (Morton 1978, Cuda et al. 2005), as well as Hawaii (Hight et al. 2003). The high ecological plasticity of *Schinus* is a common feature of successful invaders (Cuda et al. 2005, Buckley et al. 2006, Donnelly et al. 2008).

Some of the most damaging invasive plants are dispersed by frugivores (Meisenburg & Fox 2002, Buckley et al. 2006) and *Schinus* is a typical example. A range of bird species have been recorded feeding on *Schinus* fruits in their natural-occurring or human-disturbed areas in Brazil (e.g., Hasui & Höfling 1998, Krügel & Behr 1998, Jesus & Monteiro-Filho 2007), and countries where it was introduced, such as Australia (Panetta & McKee 1997), United States (Mytinger & Williamson 1987), Reunion Island in the Indian Ocean (Tassin et al. 2007), Hawaiian Islands in the Pacific Ocean, and Bahamas in the Atlantic Ocean (Morton 1978). Among frugivorous birds, regarded as potential seed dispersers of *Schinus*, a variety of foraging tactics, bird morphology, and habitat uses are described (Hasui & Höfling 1998). Fruit-eating birds differ considerably in their effectiveness as seed dispersers (Cortês et al. 2009). Although the frequency of frugivorous visits is often considered the best predictor of dispersal ability of a given vertebrate (Schupp 1993, Vázquez et al. 2005), this relationship is not always true. For instance, Cortês et al. (2009) found that Emberizidae birds, including the primary visitor, the Sayaca Tanager *Thraupis sayaca* (Linnaeus, 1766), were inefficient seed dispersers. Despite presenting a high frequency of visits and fruit handling, they were unable to successfully remove fruits of *Eugenia umbelliflora* Berg. On the other hand, omnivorous or predominantly insectivorous birds such as thrushes (*Turdus* spp.) and the Great Kiskadee *Pitangus sulphuratus* (Linnaeus, 1766) were important dispersers. The quality of treatment these birds provide to the seeds they ingest (i.e., if they destroy or pass seeds intact through the gut or even if they alter the germination pattern) requires further investigation (Pizo 2004).

In addition to the role of avian frugivores in dispersing invasive plants, frugivores undertake a crucial importance in areas where endozoochory contributes toward regeneration of altered areas or maintenance of forests (Silva & Tabarelli 2000, Pizo 2004, Hansen & Galetti 2009). Thus, *Schinus* and their frugivores are particularly important for threatened vegetations, such as the 'restinga' formation, which historically have been the first area in the Atlantic rainforest to suffer the consequences of human expansion (Souza & Capellari-Jr 2004). This plant has been recommended to be used for the recovery of degraded and riparian areas and reforestation (Kageyama & Gandara 2000, Souza et al. 2001).

The fact that coevolution of fruiting plants and their dispersers has occurred is evidenced in the characteristics of fruit displays (van der Pilj 1972). The germination and potential seed dispersal of *Schinus* mediated by avian frugivores have been studied where both plant and birds are invasive (Reunion Is., Mandon-Dalger et al. 2004, Tassin et al. 2007), or where *Schinus* is invasive but dispersed by native birds (Australia, Panetta & McKee 1997). In both places the animal–plant mutualism is recent and coevolution probably has not played an important role. A better insight on the relationships of the *Schinus* with their dispersers in areas where they coevolved could potentially have important implications for the development of biologically-controlled strategies of this invasive tree elsewhere, as well as strategies for recovery of degraded areas within their native range. In order to understand the course of natural regeneration of degraded lands and properly manage this process, it becomes mandatory to know which bird species are the main seed dispersers in such environments (Pizo 2004). Moreover, a conclusive determination of endozoochoric seed dispersal by birds requires verification that the seeds are ingested, carried away from the parent plant, and voided in a viable condition (Meisenburg & Fox 2002). In this study, we investigated the effects of a range of bird species with different foraging methods (mandibulating tanagers; thrushes, mockingbirds, and the Great Kiskadee that ingest whole seeds) on the viability and germination of *Schinus* seeds. The role of avian frugivores in the recovery of altered areas where it naturally occurs and the dissemination of this invasive plant elsewhere is discussed.

Material and Methods

1. Study area

The Southern Brazilian restinga formation is on quaternary sand plain, covered by grasslands with small ponds, marshes, and patches of herbaceous and arboreous vegetation. The mosaic of different vegetation formations is characteristic of restinga, and is distributed in lowlands adjacent to the Atlantic rainforest in psamophylous and saline soils with variable humidity from northeastern to southern Brazil (Waechter 1985, Falkenberg 1999). *Schinus* though not an important component of well-preserved restinga formations, is commonly found in shrub patches or areas in intermediate or late successional stages (Waechter 1985, Falkenberg 1999), as well as at the edges of arboreal patches and virtually in any human-altered land, including cities (Hasui & Höfling 1998). An arboreous patch, composed mainly by *Schinus* trees, surrounded by grasslands and inserted in the urban area of Cassino beach, 500 m from the Atlantic Ocean, Southern Brazil (31° 11' S and 52° 09' W), was chosen for study. In order to capture birds, mist nets (12 × 2.5 m, 36 mm mesh size) were placed in July–August 2004 adjacent to trees with ripe fruits.

2. Field experiment

Fifty-nine birds were individually kept in cardboard boxes lined with white paper for 20–75 minutes (mean ± SD = 41.0 ± 13.8 minutes) and *Schinus* seeds were obtained from faeces of 28 birds. In total 300 seeds were collected from 19 Creamy-bellied Thrushes *Turdus amaurochalinus* (Cabanis 1850), 39 seeds from Great Kiskadees (*n* = 3 birds), 27 seeds from three Blue-and-yellow Tanagers *Thraupis bonariensis* (Gmelin 1789), 30 seeds from two Sayaca Tanagers, and 29 seeds from a single Chalk-browed Mockingbird *Mimus saturninus* (Lichtenstein 1823) in July and August 2004. Seeds were pooled according to species to obtain larger sample sizes. The control group was formed from seeds removed from trees in the same area. In Silvereyes *Zosterops lateralis* (Latham 1802) defecation of *Schinus* seeds ranged from 25 to 30 minutes after ingestion (Panetta & McKee 1997), or mean of 19.7 minutes in Red-whiskered Bulbul *Pycnonotus jocosus* (Linnaeus 1758) (Tassin et al. 2007), thus sampled birds could be defecating seeds ingested in nearby areas. Seeds collected from field, hereafter 'field experiment', had viability and germination rates tested in laboratory as described below. Body mass of birds was measured with Pesola® spring scales and banded with metal rings before being released in the capture place.

3. Captivity experiment

In an additional experiment, hereafter 'captivity experiment', two Creamy-bellied Thrushes and one male Blue-and-yellow Tanager were kept in cages under permission. Body mass was used as a proxy for adequate nutritional and health status, thus selected birds had high body mass compared to other birds captured in the same place. Birds were kept in individual cages (47 × 24 × 32 cm), supplied with ad libitum water with vitaminic supply, various fresh fruits, *Schinus* fruits, coleoptera larvae, and commercial food for passerine birds. Body mass was measured in intervals from 4 to 9 days during the first month (acclimation period). There was a decrease in body mass during the initial two weeks followed by stabilization or even increase toward the end of the acclimation period (data not shown). Experiments started after one month from the capture (i.e. early September), when birds were considered fully acclimated to captivity conditions. Birds were released at the end of the experiments.

During trials of the captivity experiment, *Schinus* fruits fed to birds and controls (whole fruits) were obtained from a single tree to minimize potential differences. In total, 100 and 200 seeds defecated by the two Creamy-bellied Thrushes, 200 from the Blue-and-yellow Tanager, and 200 from the tree for the control group were collected. Four replicates per treatment (i.e., per individual bird and control) were set for germination. As we aimed to test the effect of gut passage on germination, intact seeds were used as controls, after Samuels & Levey (2005) and Robertson et al. (2006).

4. Seed viability

Seed viability, defined as a seed with potential to germinate, was verified by tetrazolium test. By using a 1% tetrazolium chloride solution, the embryo of respiring tissues is stained pink/red (Sawma & Mohler 2002). Seeds (*n* = 100 for each group, i.e., control and birds) were cut in half and placed in a glass with tetrazolium solution covered by aluminium foil to avoid light and placed in an incubator at 50 °C for 2 hours. After draining the liquid, the stained half seeds were counted and the number divided by two to express the percentage of viable seeds. Differences in viability between the seeds defecated by birds and controls were compared by a two-tailed test for differences between two proportions (Statsoft Inc. 1998, Zar 2009).

5. Seed germination

Seeds/fruits from birds and control in both field and captivity experiments were rinsed in 96% ethanol for 2–5 minutes to avoid fungus, and later washed with distilled water; this procedure had shown no effect on *Schinus* germination (Panetta & McKee 1997). Seeds were set to germinate in petri dishes with cotton covered by filter paper, saturated with distilled water. Humidity was maintained by adding water every third day. In both field and captivity experiments and their controls, seeds were checked daily for germination, defined as the emergence of the radicle.

For the field experiment, number of seeds per dish varied from 1 to 29 according to the number of seeds obtained from faeces of every species in the previous morning. Seeds were set to germinate in the afternoon following collection and maintained in a germination chamber with temperatures at 20 °C day and 15 °C night, and photoperiod 14 hours light/10 hours dark. In addition, 100 seeds from one thrush were set to germinate in a cabinet with ambient temperature and the photoperiod 12/12 hours. Substrate and temperatures were those which maximize germination rates for *Schinus* (Medeiros & Zanon 1998).

Seeds from the captivity experiment and its control were set to germinate with four replicates (4 × 25 seeds) and maintained in germination chamber at temperatures 25 °C day, 20 °C night, and photoperiod 12/12 hours.

Germination was expressed as the percentage of germinated seeds at the end of the trial period (*G%*) and germination rate (*GR%*), which is also expressed as percentage but represents the rate (or speed) at which radicles emerged, calculated by the equation from Mugnisjah & Nakamura (1996): (Equation 1)

$$\mathrm{GR\%} = \left[\left(\frac{100}{\sum \mathrm{N_i}}\right) * \sum\left(\frac{\mathrm{N_i}}{\mathrm{T_i}}\right)\right] \tag{1}$$

where N = number of seeds germinated at the day *i* and T_i is the number of days since sowing.

For the field experiment, germination rate was tested between control and seeds defecated by birds through a two-tailed test of differences between two proportions (Statsoft Inc. 1998, Zar 2009). For the captivity experiment, as the number of tested seeds was set a priori (25 seeds) and with four replicates, comparison of means was possible. Thus, we used the non-parametric Kruskall–Wallis test, as values were not normal or homoscedastic (Zar 2009).

Results

Seeds were found in faeces of 47.5% of captured birds ($n = 59$). Mean number of seeds varied from 2.6 in Great Kiskadee ($n = 15$ birds) to 29 in the single Chalk-browed Mockingbird captured, with intermediate values for other birds (Table 1). Body mass of birds captured varied from 30.5 g in Sayaca Tanager to 70.8 g in Great Kiskadee. Foraging methods varied from birds, which mandibulated fruits before swallowing (Thraupidae tanagers), to species which ingest whole fruits (Turdidae thrushes, Mimidae mockingbird, and the Tyrannidae Great Kiskadee).

In the field experiment, germination of seeds defecated by all birds, both in germination chamber and on the bench, started earlier than controls. Radicle emergence occurred at days 6–7 for both tanagers species and thrush, to the day 10 in the mockingbird, while germination of control seeds started at the day 12 (Figure 1). Moreover, percentage of seeds germinated at the end of the experiment, as well as the germination rate, was higher for all bird species compared to controls (Table 1, Figure 1, difference between two proportions, $p < 0.001$). Only 7.0% of control seeds germinated in the field experiment, while seeds from all birds had higher G%, from 30.0 to 53.3% (Figure 1). Similarly, germination rate (*GR%*) was lower for control seeds (7.3%), while seeds which passed through birds' gut germinated at rates from 8.0 to 11.6% (Table 1). Seeds defecated by Sayaca and Blue-and-yellow Tanagers had highest germination rates in comparison to other birds and control in the field experiment (Table 1). In the captivity experiments *GR%* value of the Blue-and-yellow Tanager was intermediate between the two thrush individuals (Figure 2).

Thrushes, which ingest intact fruits without mandibulation, showed no reduction in seed viability compared to controls in both field and captivity experiments ($p = 0.2$ and $p = 0.7$, respectively), while a more pronounced and significant decrease in viability occurred in seeds ingested by Blue-and-yellow Tanager (Table 1).

Viability of control seeds from the field and the captivity experiments differed markedly, with 85.0 and 45.0%, respectively (Table 1). Germination started at days 8 and 10 for seeds collected from faeces of the two Creamy-bellied Thrushes, and at day 12 for the Blue-and-yellow Tanager (Figure 2). There was no seed germination after the day 23, and, moreover, germination did not occur at all in the control group. In accordance to the results of the viability test, percentage of germinated seeds was also lower in the captivity experiment in comparison to the field experiment (6.0 to 8.0%), while GR% was only slightly lower in captivity (6.6–9.1%), except for control seeds. In the captivity experiment, *G%* and *GR%* did not differ significantly between birds and control, as well as among birds (Kruskall–Wallis test, $p = 0.2$ for both *G%* and *GR%*).

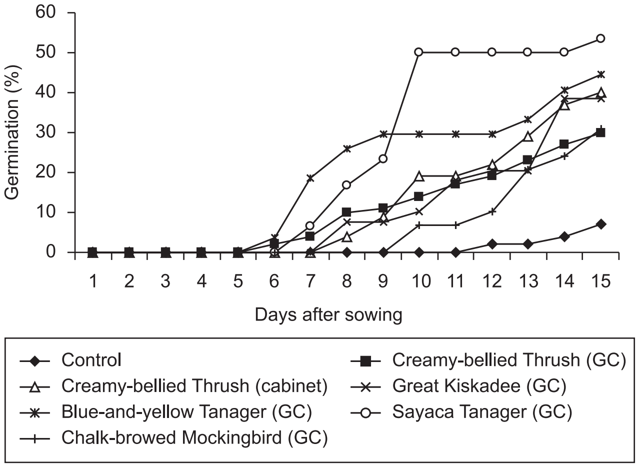

Figure 1. Daily cumulative percentage of germination seeds of Brazilian Pepper *Schinus terebinthifolius*. Control and seeds from bird faeces were obtained in field and maintained in Germination Chamber (GC). Seeds from one Creamy-bellied Thrush *Turdus amaurochalinus* were also set to germinate in cabinet.

Figura 1. Percentagem cumulativa diária de germinação de sementes da Aroeira-vermelha *Schinus terebinthifolius*. Sementes do grupo controle e das fezes das aves foram obtidas em campo e mantidas em câmara de germinação (GC). Sementes de um *Turdus amaurochalinus* foram também colocadas para germinar sobre a bancada.

Table 1. Viability (%), percentage of seeds germinated at the end of the experiment *(G%)*, and Germination Rate (*GR%*) of Brazilian Pepper *Schinus terebinthifolius*, collected from faeces of different bird species in field and captivity experiments. - not measured. Values statistically different are indicated with different letters.

Tabela 1. Viabilidade (%), percentagem de sementes germinadas ao final do experimento (*G%*), e taxa de germinação (*GR%*) de Aroeira-vermelha *Schinus terebinthifolius*, coletadas nas fezes de diferentes espécies de aves em campo e em experimentos em cativeiro. - dado não obtido. Valores estatisticamente diferentes são indicados com letras diferentes.

Species/Treatments	Seed ingestion technique	Mean No. of regurgitated seeds *(n)*	Viability *(%)*	Germination *(G%)*	Germination rate *(GR%)*
Field experiment					
Control		-	85.0^{a}	7.0^{a}	7.3^{a}
Creamy-bellied Thrush *Turdus amaurochalinus (*germination chamber)	Whole fruit	9.3 (37)	78.0^{a}	30.0^{b}	10.0^{b}
Creamy-bellied Thrush *Turdus amaurochalinus (*cabinet*)*	Whole fruit		78.0^{a}	40.0^{b}	9.0^{b}
Great Kiskadee *Pitangus sulphuratus*	Whole fruit	2.6 (15)	-	38.5^{b}	8.9^{b}
Blue-and-yellow Tanager *Thraupis bonariensis*	Mandibulate	6.8 (4)	-	44.4^{b}	11.6^{c}
Sayaca Tanager *Thraupis sayaca*	Mandibulate	14.5 (2)	-	53.3^{b}	10.9^{c}
Chalk-browed Mockingbird *Mimus saturninus*	Whole fruit	29.0 (1)	-	31.0^{b}	8.0^{b}
Captivity experiment					
Control		-	45.0^{a}	0	0^{a}
Creamy-bellied Thrush *Turdus amaurochalinus (*Bird A*)*	Whole fruit	-	-	6.0^{a}	9.1^{a}
Creamy-bellied Thrush *Turdus amaurochalinus (*Bird B*)*	Whole fruit	-	42.0^{a}	8.0^{a}	7.7^{a}
Blue-and-yellow Tanager *Thraupis bonariensis*	Mandibulate	-	25.0^{b}	7.0^{a}	6.6^{a}

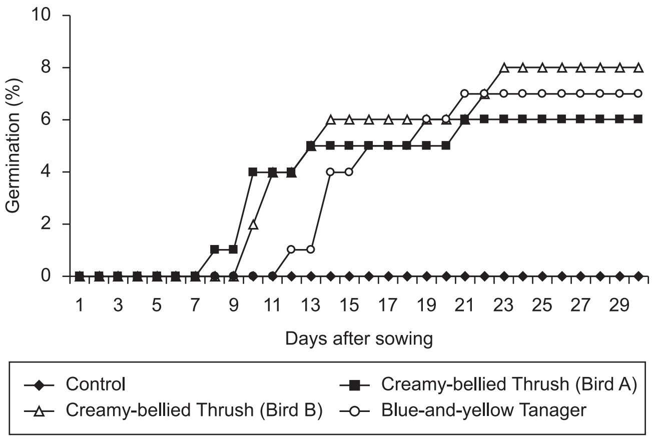

Figure 2. Daily cumulative percentage of germination seeds of Brazilian Pepper *Schinus terebinthifolius*. Control seeds and seeds from bird faeces were obtained from a single tree and birds kept in captivity, respectively. All seeds were set to germinate in germination chamber.

Figura 2. Percentagem de germinação cumulativa diária de sementes da Aroeira-vermelha *Schinus terebinthifolius*. Sementes do grupo controle foram obtidas de uma única árvore e das fezes das aves foram provenientes de aves mantidas em cativeiro. Todas as sementes foram colocadas para germinar em câmara de germinação.

Discussion

The present study demonstrated the potential dependency of *Schinus* on frugivores for dispersal and as mediators of the germination. Results on seed germination, viability, and potential dispersal of *Schinus* in natural-occurring areas (this study, Krügel & Behr 1998) as well as invaded areas (Panetta & McKee 1997, Mandon-Dalger et al. 2004, Tassin et al. 2007), are consistent, all studies reporting that *Schinus* is dependent upon generalist avian frugivores for establishment in new areas.

Most birds studied here (thrushes, mockingbirds, and Great Kiskadee) ingested whole fruits maintaining high levels of seed viability. Despite the reduction in seed viability in seeds ingested by tanagers, germination rate was high. All birds including tanagers, which madibulate fruits before swallowing, increased percentage of germinated seeds and germination rate. This apparently contradictory finding could be due to tanagers, by mandibulating fruits, mechanically enhancing germination rates by abrading the seed coat (Traveset 1998), despite destroying some seeds. Manual removal of exocarps had shown to maintain high germination rates in *Schinus* (Panetta & McKee 1997), while control seeds used here were intact fruits and had delayed and decreased germination, or even completely failed to germinate. The 'true control' of effects of gut passage on germination used in the present study (sensu Samuels & Levey 2005, Robertson et al. 2006) had demonstrated that bird gut passage enhance seed germination. It was also demonstrated that for a true control of effects of gut passage on seeds, intact fruits should be used as control, in agreement with Samuels & Levey (2005). Germination in *Schinus* could be prevented by the presence of chemical inhibitors in the pulp and blockage of permeability. An additional benefit of frugivores is increasing the speed of germination, as is widely accepted that rapid germination can be advantageous for plants because it reduces seed predation (Stevenson et al. 2002).

Contrasting differences found between field and captivity experiments in both seed viability and germination could be due to experiments taking place at different periods. In early spring when the captivity experiment was carried out, *Schinus* seeds were scarce in the study area, and thus suboptimal seeds at the end of the frutification period could be fed to birds and used as control. Moreover, the absence of germination of control seeds could be related to our inability to select good fruits and seeds, while birds are able to select better fruits, despite both control and birds fed fruits coming from the same tree. Tassin et al. (2007) demonstrated that stored *Schinus* seeds had reduced germination rates, thus seeds used in the captivity experiment, which were removed from trees later than in the field experiment could already had reduced potential for germination. An additional explanation for differences between both experiments could be the intrinsic differences in germination and viability between trees. Viable *Schinus* seeds could have reduced or null germination rates when intact and are dependent on mechanical and chemical scarification (this study, Panetta & McKee 1997). Thus, it can be suggested that passage of seeds through gut of birds which swallow whole seeds without mandibulating them is not enough to induce germination in all seeds as percentage of germination was much lower than viability in our captivity and field experiments. Mandibulating birds probably induce germination mechanically in some seeds, as well as chemically through gut passage, with an overall germination outcome similar in birds with different foraging methods. Flycatchers (Tyrannidae) and thrushes (Muscicapidae and Turdidae) usually ingest whole fruits, so are regarded as better dispersers than Emberizidae/Thraupidae, which usually mandibulate fruits before swallowing (Moermond & Denslow 1983). However, results shown in this study demonstrate an opposite view, with all studied species able to effectively disperse *Schinus* seeds, even mandibulating Emberizidae.

Schinus seeds were found in faeces of five abundant and opportunistic bird species, commonly found in human-altered areas and previously reported as being fed on *Schinus* fruits in Brazil (Belton 1994, Hasui & Höfling 1998, Krügel & Behr 1998). About half of the captured birds previously reported to feed on *Schinus* were found to defecate seeds, thereby confirming the importance of this plant as a food resource for a range of birds during winter months (Krügel & Behr 1998, Jesus & Monteiro-Filho 2007). The small size of *Schinus* fruits, attractive coloration, and exposed location on tree branches are typical characteristics of ornithochoric fruits (Moermond & Denslow 1985, Hasui & Höfling 1998). The ingestion of *Schinus* fruits by opportunistic species such as flycatchers, thrushes, mockingbirds, and tanagers, which move frequently among altered areas, contributes in improving seed dispersal and also toward natural recovery of vegetation (Hasui & Höfling 1998, Pizo 2004). While in several countries *Schinus* is a major invasive weed requiring control and management plans for reduction of effects over native species, and benefits from dispersal through ingestion by opportunistic frugivorous, in Brazil this species is an important tool for recovering vegetation altered by human activities (Souza et al. 2001).

The low or null germinability and germination rates and delayed germination of control seeds found in the experiments, which increase after passage by birds' gut, suggest that *Schinus* and frugivores coevolved in their areas of natural occurrence. In native areas in Southern Brazil, where *Schinus* is found in most altered areas frequently far from water, ornithochory is of vital importance for colonization of new areas and spreading of this tree, as found in Australia and USA (Ewel et al. 1982, Panetta & McKee 1997), but not in Reunion Island where suckering is advocated as more important for the recruitment process (Tassin et al. 2007). In both indigenous and introduced areas, *Schinus* may depends on generalist birds, indigenous or alien, for dispersal (Moermond & Denslow 1985). In areas invaded by *Schinus*, generalist avian frugivores were probably key factors in the dispersal of this weed (Panetta & McKee 1997, Mandon-Dalger et al. 2004) by transporting seeds among the matrix of the frugivores' preferred habitat within fragmented landscapes (Buckley et al. 2006). Mandon-Dalger et al. (2004) observed a possible synergistic interaction between alien birds and alien weeds, including *Schinus* in Reunion Island. Thus, it could be concluded that propagation of *Schinus* in areas where it invaded could be greatly accelerated by frugivores, as postulated for other plant–frugivorous pairs (e.g. Linnebjerg et al. 2009). Information on frugivores and the role of different dispersers should be considered at all stages of weed management (Buckley et al. 2006).

An opposite perspective rises in areas of natural occurrence of *Schinus* in South America. The long fruiting period, mainly during winter when insects are scarce, rapid germination after seed fall, i.e. within one or two weeks, could be important adaptations in *Schinus*, as sapling growth during spring, under higher temperatures and longer photoperiods, is expected to be enhanced (Souza et al. 2001). Furthermore, the dispersion of a large number of seeds produced by a single tree by avian dispersers with different morphologies and behaviours, and over an extended period, could increase the possibility of at least a few seeds reaching a favorable place for establishment. Habitat fragmentation has caused decline of frugivores, particularly medium sized to large ones, in the Atlantic rainforest, which in turn is expected to result in impoverishment of bird-dispersed trees (Silva & Tabarelli 2000, Pizo 2004, Hansen & Galetti 2009). While *Schinus* dispersal mediated by generalist avian frugivores has been suggested to play an important role in the natural recovery of degraded areas, by occupying nutrient-depleted soils and forest edges (Hasui & Höfling 1998, Pizo 2004), it is reasonable to suppose that alteration of forest formations in South America has benefited both *Schinus* and their dispersers. Furthermore, nowadays the severe threatened restinga ecosystem along the Brazilian coast is greatly benefited by the natural dispersion and colonization of *Schinus* trees, as this species is important during early successional stages. The use of *Schinus* for recovery of human-altered landscapes should be encouraged by benefiting a range of species feeding on fruits during winter months, as well as being beneficial in the natural recovery of the vegetation.

Overall, the current study demonstrates the role of avian frugivores as potential dispersers and mediators of the germination in *Schinus*. These results suggest that in areas within the natural range of the Brazilian Pepper, opportunistic birds greatly benefit from fruits as a food source, particularly in areas in early successional stages and cities, thus urban arborization with this tree is encouraged; restoration of degraded areas, particularly in the Atlantic rainforest, could be mediated by the pioneer *Schinus* and taking into account the presence of generalist avian frugivores; and the management of the invasive *Schinus* should consider the effects of seed dispersal by generalist avian frugivores to enhance effectiveness of control strategies.

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