

Seed dispersal effectiveness by a large-bodied invasive species in defaunated landscapes

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Abstract

Animal-dispersed plants are increasingly reliant on effective seed dispersal provided by small-bodied frugivores in defaunated habitats. In the Neotropical region, the non-native wild pig (*Sus scrofa*) is expanding its distribution and we hypothesized that they can be a surrogate for seed dispersal services lost by defaunation. We performed a thorough analysis of their interaction patterns, interaction frequencies, seed viability, and characteristics of the seed shadows they produce. We found 15,087 intact seeds in 56% of the stomachs and 5,186 intact seeds in 90% of the scats analyzed, 95% of which were smaller than 10 mm in diameter. Wild pigs were the third most effective disperser among 21 extant frugivore species in a feeding trail experiment in terms of quantity of seeds removed. Gut retention time was 70 ± 23 hr, indicating wild pigs can promote long-distance seed dispersal. Seed survival after seed handling and gut passage by wild pigs was positively related with seed size, but large seeds were spat out and only smaller seeds were defecated intact, for which we observed a positive or neutral effect on germination relative to manually de-pulped seeds. Finally, deposition of seeds was four times more frequent in unsuitable than suitable sites for seedling recruitment and establishment. Seed dispersal effectiveness by wild pigs is high in terms of the quantity of seeds dispersed but variable in terms of the quality of the service provided. Our study highlights that negative and positive effects delivered by non-native species should be examined in a case by case scenario.

Abstract in Portuguese is available with online material.

1 | INTRODUCTION

Many animal-dispersed plants are strongly dependent upon large-bodied, ground-foraging frugivores to disperse their seeds (Campos-Arceiz & Blake, 2011; O'Farrill, Galetti, & Campos-Arceiz, 2013). Those mammalian frugivores provide non-redundant dispersal services for zoochorous plant species by eating large numbers of fruits and dispersing their seeds over long distances, creating wide seed shadows across the landscape (Fragoso, Silvius, & Correa, 2003). This dependence is stronger

among large-seeded plants because smaller frugivores are unable to handle or ingest large-seeded fruits (Wheelwright, 1985). The loss of such seed dispersers can ultimately affect important ecosystem services, such as vegetation regeneration (Levi & Peres, 2013) and carbon sequestration (Bello et al., 2015; Peres, Emilio, Schietti, Desmoulière, & Levi, 2016), even before frugivore populations go extinct (McConkey & O'Farrill, 2016). Moreover, dispersal limitation hinders seed-mediated gene flow (Giombini, Bravo, Sica, & Tosto, 2017), affecting the evolutionary dynamics of the dispersed plants (Galetti et al., 2013).

Defaunation processes, the loss of animal species—especially large-bodied vertebrates—due to anthropogenic causes (mainly

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habitat loss and overhunting, Dirzo et al., 2014), act synergistically with habitat loss and fragmentation to constrain seed dispersal services. Small-bodied ground-foraging frugivores are resilient to defaunation and fragmentation and persist in disturbed landscapes (Bogoni, Pires, Graipel, Peroni, & Peres, 2018). Some of these smaller-bodied species, such as Corvid birds (Pesendorfer, Sillett, Koenig, & Morrison, 2016) and carnivorans such as canids and mustelids (González-Varo, López-Bao, & Guitián, 2013), are effective in connecting plant populations between isolated habitat fragments, but many fruit-eating species cannot swallow seeds above a modest size threshold or do not have sufficiently large ranges to connect fragments of habitats (Cramer, Mesquita, & Williamson, 2007). The effectiveness of a seed-dispersing frugivore is a function of complementary qualitative and quantitative components affecting the chances of success that removed seeds produce a new recruit (Schupp, Jordano, & Gómez, 2010, 2017). For extant frugivores in such landscape contexts, their effectiveness as seed dispersal agents is affected by internal and external factors (Nathan, Getz, et al., 2008; Schupp et al., 2010), such as gape size and gut retention time (Traveset & Verdú, 2002), fruit- and seed-handling behavior (e.g., scatter-hoarding, seed predation, ingestion and defecation, pulp-eating without ingestion, regurgitation, or spitting out, Simmons et al., 2018), and capacity to cross the surrounding matrix and move among isolated patches (Delciellos, Ribeiro, & Vieira, 2017).

Gape size limits the size of seeds ingested and retention time influences both the treatment given to seeds and the time of transport since the ingestion event (Traveset & Verdú, 2002). Ineffective seed dispersers may function primarily as seed predators or pulp thieves that spit rather than disperse seeds long distances via endozoochory (Simmons et al., 2018). Scatter-hoarders can be effective seed dispersal agents of large-seeded plant species (Jansen et al., 2012; Pesendorfer et al., 2016), but scatter-hoarding by terrestrial mammals is likely to create patchily distributed seed shadows with no connection among isolated habitats (Silvius & Fragoso, 2003). Movement limitation may also exert constraints to seed dispersal in fragmented landscapes, because daily range scales with body mass (Carbone, Cowlshaw, Isaac, & Rowcliffe, 2005), and although certain groups of mammalian frugivores may have navigation capacity to cross the surrounding matrix (González-Varo et al., 2013; Pesendorfer et al., 2016), other mammals may be more averse to traveling through the matrix (Delciellos et al., 2017). Consequently, extant small-bodied frugivores often have one or more traits that make them less likely to promote long-distance seed dispersal capable of connecting plant populations of isolated habitats (Pérez-Méndez, Jordano, & Valido, 2018).

Although defaunation is ubiquitous in the tropics (Dirzo et al., 2014), a large-bodied non-native mammal, the wild pig *Sus scrofa*, is expanding its distribution throughout fragmented Neotropical forests (da Rosa, de Almeida Curi, Puertas, & Passamani, 2017). Wild pigs are omnivores and fruits are a component of their diets in its native and introduced ranges (Ballari & Barrios-García, 2014; Fedriani & Delibes, 2009). The negative effects of non-native wild pigs to agriculture and ecosystems are well-documented

(Barrios-García & Ballari, 2012). Even though they facilitate the spread of invasive plant species (Dovrat, Perevolotsky, & Ne'eman, 2012; Lynes & Campbell, 2000), they could potentially serve as a surrogate for replacing lost seed dispersal services of native zoochorous plants (Donatti, Galetti, Pizo, Guimarães, & Jordano, 2007; O'Connor & Kelly, 2012). However, to determine the role of this non-native species as a seed disperser in defaunated and fragmented landscapes, a thorough analysis of their interaction patterns, interaction frequencies, seed viability after ingestion, and characteristics of the seed shadows they produce is required. Given the large body size of wild pigs, which can weigh an average of 89 ± 31 kg as adults (F. Pedrosa, unpublished data), and resilience of populations to overharvest (Bieber & Ruf, 2005), we hypothesized that wild pigs may be capable of restoring seed dispersal services to fragmented systems that are widely defaunated (Bogoni et al., 2018).

Here, we combine field data, experimental approaches, and modeling to conduct an in-depth characterization of the role of non-native wild pigs as seed dispersers in the highly fragmented and defaunated Atlantic Forest of Brazil. First, we assessed the frequency of endozoochorous seed dispersal by wild pigs using stomachs and scats analysis. Second, we assessed the quantitative component of seed dispersal effectiveness (SDE, Schupp et al., 2010, 2017), measuring fruit removal rates of large-fruited plants by frugivore species in fragmented landscapes. Third, we explored the qualitative component of SDE by examining the quality of seed deposition sites (suitable vs. unsuitable sites for seedling recruitment and establishment) and the effect of seed handling and gut passage on seed survival and germination. Finally, we modeled kernels of seed dispersal distances of wild pigs and extant frugivores to explore their potential role in promoting long-distance seed dispersal.

2 | METHODS

2.1 | Study system

The Atlantic rainforest of South America was once one of the largest rainforests in the world, originally covering an area of 150 million ha (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). By the beginning of the 21st century, only 12% of the original forest cover remained, 80% of which was composed of ~204,000 fragments smaller than 50 ha, with a mean isolation between fragments of 1,441 m (Ribeiro et al., 2009). In this biome, up to 89% of woody plant species rely on frugivores to disperse their propagules (Almeida-Neto, Campassi, Galetti, Jordano, & Oliveira-Filho, 2008). Seed dispersal and gene flow of these zoochorous plants are potentially constrained due to the widespread extirpation of large frugivorous vertebrates (for example, tapirs, southern, and northern muriquis, peccaries, and black-fronted piping guan, Bogoni et al., 2018). Alien plants are also present within or surrounding natural areas of Atlantic Forest (Zenni & Ziller, 2011) and may increase their invasion as a result of interaction with seed dispersers.

2.2 | Seed dispersal by wild pigs

To assess the frequency of endozoochorous seed dispersal, we collected stomachs from legally hunted wild pigs in the Rio Claro region (22°24'39"S 47°33'39"W, see Figure S1) from September 2014 to July 2016. The collection of stomachs from hunted animals was in accordance with the Brazilian law regarding ethics in using animals for scientific research. Following the method adapted from (Korschgen, 1987), the entire stomach content was removed and washed with running water over five meshes of different sizes (5, 2, 1, 0.8, and 0.4 mm). The washed stomach contents were set to dry at 60°C for 48 hr. Large and intact seeds easily recognizable within the stomachs and scat samples were separated during this first trial. To search for small seeds or seeds that were not found in the first scan, we homogenized and weighted the dry material of each stomach separately, then we took a subsample of 10% (by weight) to be examined carefully. We used a magnifying glass of 65× to search for seeds in the 10% subsamples. We then extrapolated what was found in the 10% subsample by multiplying it by 10, under the assumption that the sample was representative of total content.

We also collected scats opportunistically within forest fragments during 19 field surveys between February 2014 and August 2015 and then systematically from 1 to 3 days every month from April 2017 to March 2018 within both forest fragments and plantations, within the same study region, tracking back same trails. Scats of wild pigs are easily distinguishable from those of other mammal species, such as deer and carnivores, and other ungulates species are extirpated in the sampled areas. We used the same method of processing stomach samples described above for the collected scats, except that we did not dry the scat content. Seeds found in both stomachs and scats were identified with the help of botanical specialists.

2.3 | Seed dispersal effectiveness: The quantitative component

To evaluate the quantitative component of SDE (Schupp et al., 2010, 2017) of the assemblage of ground-foraging frugivores, we chose 14 study sites in fragmented Atlantic forest (Figure S1) and measured fruit removal rates of large-fruited plants. We focused on three large-fruited plant species that are broadly distributed in fragmented Atlantic forest remnants, *Syagrus romanzoffiana* (Arecaceae), *Hymenaea courbaril* (Fabaceae), and *Guazuma ulmifolia* (Malvaceae). The palm *S. romanzoffiana* is one of the most common and productive fruiting species in semideciduous Atlantic forest. It produces large (18.6 mm in diameter) single-seeded (12.6 mm in diameter) yellow fruits displayed at 2 ± 1 infructescences per tree containing hundreds of fruits each. Fruiting phenology is asynchronous, occurring year round, making *S. romanzoffiana* an important food resource for several frugivorous species (Keuroghlian & Eaton, 2008). *Hymenaea courbaril* is a masting leguminous fruiting tree, widely distributed in the Neotropics and produces large brown pods (101.7 mm in length and 41 mm in diameter), with 3 ± 2 large seeds (15 mm in diameter) per pod, each plant

producing hundreds of pods once every 2–3 years (Janzen, 1975), and *G. ulmifolia* fruits are round and black (26.2 mm in diameter) with 75 ± 17 small seeds (2.2 mm in diameter) per fruit and fruit phenology occurs at the end of the dry season. The fruits of all three species fall off from the tree when ripe, and *H. courbaril* and *G. ulmifolia* present a peculiar smell which is perhaps attractive to mammalian frugivores and are indehiscent (the flesh is covered by a tough exocarp), so their fruits need to be opened/crushed by a frugivorous species to release the seeds and allow germination.

We placed a known number of fruits from each of the three species in 145 sampling stations distributed inside forest remnants (median of 11 sampling stations in each study location). Each sampling station received 40–80 ripe fruits of one plant species placed in front of one camera trap (Bushnell NatureView HD Essential®) positioned 1.5–2 m away from the fruits and approximately 45 cm from the ground. We set the cameras to operate in video mode (15 s length, 1 s delay between videos), which allowed us to quantify fruit removal rates by each frugivorous species. We conducted these observations from October 2013 to October 2016 and from January to February 2018, always following the fruiting period and fruit availability of the plant species along these years. In our study sites, fruiting phenology of *S. romanzoffiana* occurs between January to March and July to October, for *H. courbaril* fruiting is between July and October, and *G. ulmifolia* fruits from September to November (Durigan, Franco, Saito, & Baitello, 2000 and F. Pedrosa pers. observ.).

Seed dispersal quantity component scores (QC) provide the basis to compare the subcomponents of the quantitative SDE among frugivore species by combining the effects of visitation rate and fruits removed per visit to estimate overall quantity of seeds dispersed (Schupp et al., 2010, 2017). Some stations had 100% fruit removal in just a few days, thus reducing monitoring effort in the calculation of the visitation rate. For sampling stations where fruit removal was under 100%, we considered 14 days for *S. romanzoffiana*, 31 days for *G. ulmifolia*, and 82 days for *H. courbaril* as the maximum monitoring effort based on field observations of the maximum length of time that each fruit takes to rot after reaching the forest floor. If visitation elapsed for more than one video (e.g., sequential videos recording the same individual), we considered a single visit to end when a frugivore left the station. Any subsequent return to the station was counted as a different visit. We classified frugivores into four main groups according to their functional role (Simmons et al., 2018): (a) primarily seed predators, (b) scatter-hoarders, (c) frugivores that can swallow only small seeds, and (d) frugivores that can swallow small and large seeds.

2.4 | Seed dispersal effectiveness: The qualitative component

We explored the qualitative component of SDE (Schupp et al., 2010, 2017) by examining two subcomponents that affect the final outcome of this component: (a) the quality of seed deposition sites and (b) the effect of seed handling and gut passage on seed survival (breakage and digestion) and germination.

We compared the proportion of scats found in suitable patches (forested habitats) relative to unsuitable large-scale mechanized plantations sites, roadsides, and cattle fields, from the systematic survey of scats described in the previous section. To control for variable effort among sites, we scaled the number of scats found at suitable and unsuitable sites by the search effort within each site type prior to calculating the proportion of scats deposited in suitable sites.

We assessed the effect of seed handling and gut passage on survival and germination of seeds for the native zoochorous plants *S. romanzoffiana*, *H. courbaril*, *G. ulmifolia*, *Acrocomia aculeata* (Arecaceae), *Attalea phalerata* (Arecaceae), *Euterpe edulis* (Arecaceae), *Syagrus oleracea* (Arecaceae), *Inga laurina* (Fabaceae), *Jaracatia spinosa* (Caricaceae), *Genipa americana* (Rubiaceae), and *Cordia* sp. (Boraginaceae), for the zoochoric non-native *Syzygium cumini* (Myrtaceae) and for the autochoric alien invaders *Leucaena leucocephala* (Fabaceae) and grass seeds of *Urochloa* genus (former *Brachiaria*, Poaceae). We choose these species because of (a) their ecological relevance to the study system we are investigating, both in terms of their importance (the case of animal-dispersed plants) and concern (the case of non-native and invasive plants), and (b) the availability of fruits and seeds to conduct the experimental feeding trials. All native plants used here are widespread in fragmented Atlantic forest (except *A. phalerata*, which distribution is along central and northern South America, Durigan et al., 2000; Farah et al., 2017). *Syzygium cumini* is native to Southeast Asia and is common in orchards, *L. leucocephala* is native to Central America but invasive in Brazil and grasses of the genus *Urochloa* are native to Paleotropical regions (Zenni & Ziller, 2011). See Table S1 for a summary of fruit and seed traits.

We offered 627 fruits of *S. romanzoffiana* (accounting for 627 seeds, collected from seven individuals), 107 fruits of *H. courbaril* (accounting for 321 seeds, from two individuals), 10 fruits of *G. ulmifolia* (750 seeds, from two individuals), four fruits of *G. americana* (684 seeds, from two individuals), 15 fruits of *J. spinosa* (735 seeds, from one individual), 60 fruits of *Cordia* sp. (60 seeds, from one individual) 23 fruits of *A. aculeata* (23 seeds from two individuals), 12 fruits of *A. phalerata* (12 seeds from one individual), 60 fruits of *E. edulis* (60 seeds from three individuals), nine fruits of *S. oleracea* (nine seeds of two individuals), 30 fruits of *S. cumini* (30 seeds from one individual), 80 fruits of *I. laurina* (unknown number of seeds from one individual), 200 seeds of *L. leucocephala* (from five individuals), and 350 seeds of *Urochloa* spp. (from several individuals) to two adult wild pigs kept in captivity. We estimated the number of seeds offered based on mean number of seeds found in each fruit (see Tables S1 and S2 for a summary on fruit and seed traits). We isolated two animals, a male and a female, from each other in 3 × 3 m sheltered bays, offering food once a day and water available ad libitum. We offered ripe and undamaged fruits of a given plant species at once to the animals during a single trial. Both pigs consumed fruits of all species, and we did not see differences in handling between male and female. We retrieved intact fruits and seeds if they remained untouched in the bay after 1 hr to avoid confusion with seeds from pig stool or seeds that were spat out. We recovered spat out seeds immediately after observing

this behavior. We collected pig stool during the following 7 days, twice daily, and checked for intact seeds by washing it over a mesh of 4 × 4 mm.

We set to germinate in a greenhouse intact seeds found in the pig stool (or spat out), with irrigation twice daily and natural light and temperature variation. We observed the seeds set to germinate at the greenhouse daily and considered as germinated when at least 2 mm of radicle was present. For comparison, we contemporaneously germinated manually defleshed seeds from fruits (control treatment) under the same conditions. Seeds of control treatment were from the same source and collected at the same time as the fruits offered to captive pigs. A total of 968 seeds were tested in individual pots unique to each treatment and plant species, each containing 1–10 seeds (see Table S2 for the number of seeds of each plant species set to germinate). We assessed minimum days of seed dormancy (T_0 , the time lapse until first seed germinate), mean days of seed dormancy (M_dD, the mean time elapsed until germination of all seeds) and seed germinability (the final proportion of seeds germinated after 180 days) (Reid & Armesto, 2011). We used the Mann–Whitney *U* test to test for differences among treatments (Reid & Armesto, 2011). We additionally estimated the germinability of seeds of scats found in the field. Seeds were set to germinate in greenhouse following the same protocol described above and checked for germination for 6 months.

2.5 | Kernels of seed dispersal distances

To quantify the potential for wild pigs and extant frugivores (determined via the seed removal experiment) to act as long-distance seed dispersers, we used an agent-based model that simulates seed dispersal considering ingestion, retention, movement, and deposition, resulting in the estimation of the seed dispersal kernels (Pires, Guimarães, Galetti, & Jordano, 2018). For example, dispersal distances of seeds provided by the fruit-eating *Casuaris casuaris* were estimated using their foraging activity (movement) and gut retention time of seeds (Westcott, Bentrupperbäumer, Bradford, & McKeown, 2005). Therefore, seed dispersal kernels represent the probability distributions of source-to-deposition distances (Westcott et al., 2005). We define long-distance seed dispersal (Nathan, Schurr, et al., 2008) as events of seed deposition greater than 1,441 m since this is the mean isolation distance among forest remnants in the Atlantic Forest (Ribeiro et al., 2009).

To estimate seed dispersal kernels for wild pigs, we first parameterized the model using empirical data on the average number of seeds ingested (based on the number of intact seeds found in stomachs of the hunted animals) and the observed seed-specific distribution of gut retention times in captive animals (from the results of the previous section on gut passage trials). We modeled seed retention time as a gamma distribution with the same mean and variance obtained from the empirical retention times (Guttal, Bartumeus, Hartvigsen, & Nevai, 2011). For other frugivores, ingestion and retention were based on available literature and parameterized accordingly. In the absence of estimates available in the literature, we used allometric relationships between seed ingestion and mean

TABLE 1 Summary of the intact seeds found in 111 stomachs and 82 scats of invasive wild pigs *Sus scrofa* in the Atlantic forest, according to dispersal characteristic of plant species

| Dispersal characteristic and origin | Number of intact seeds | | Number of plant species ^a | | Frequency % (n) | |
|-------------------------------------|------------------------|-------|--------------------------------------|----------------|-----------------|-----------|
| | Stomachs | Scats | Stomachs | Scats | Stomachs | Scats |
| Zoochoric syndrome | 10,671 | 4,657 | 11 | 8 | 36.9 (41) | 62.2 (51) |
| Natives | 6,618 | 430 | 9 | 5 | 18.9 (21) | 41.4 (34) |
| Aliens | 529 | 30 | 1 | 2 | 4.5 (5) | 8.5 (7) |
| Unknown | 3,524 | 4,197 | 1 | 1 | 19.8 (22) | 28 (23) |
| Non-zoochoric syndrome ^b | 37 | 20 | 2 | 1 | 2.7 (3) | 7.3 (6) |
| Poaceae | 4,142 | 297 | 7 ^c | 1 ^c | 18 (20) | 46.3 (38) |
| Unknown | 4,379 | 509 | 13 | 15 | 24.3 (27) | 57.3 (47) |
| Total | 15,087 | 5,186 | 26 | 24 | 55.9 (62) | 90.2 (74) |
| Natives | 6,618 | 430 | 9 | 5 | 19.9 (22) | 41.4 (34) |
| Aliens | 566 | 50 | 3 | 3 | 7.2 (8) | 35.4 (29) |

^aSee Tables S3 and S4 for taxonomic information of plant species. ^bAll non-zoochoric are alien species. ^cMorphospecies.

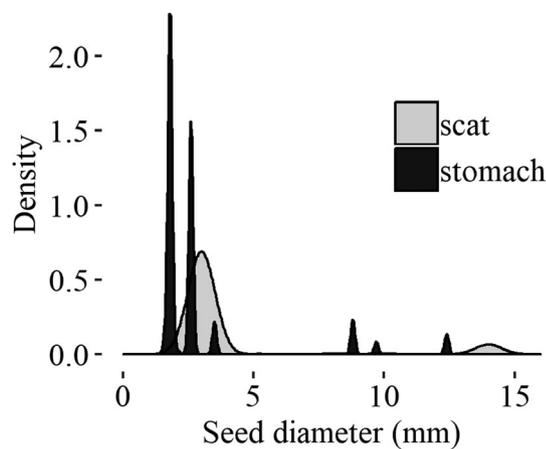


FIGURE 1 Probability density distribution of the size of all intact seeds of zoochoric plant species found in stomach and scats (see Tables S3 and S4 for details)

retention time with body mass (Pires et al., 2018). Because most of the remaining species have similar body sizes weighing between 1 and 5 kg (for example coatis *Nasua nasua*, white-eared opossum *Didelphis albiventris*, black-eared opossum *Dideplhis aurita*, tayra *Eira barbara*, and capuchin monkey *Sapajus nigritus*), we used the seed dispersal model to generate seed dispersal kernels considering an average body mass of 5 kg, an upper bound for these small- to medium-sized mammal species.

We used the allometric relationship between body mass and daily movement range (Carbone et al., 2005) to simulate movement using both Brownian and the Lévy walk models (Auger-Méthé, Derocher, Plank, Codling, & Lewis, 2015; Pires et al., 2018). These two models represent two extremes; the first generates shorter movement distances and the second allows movement over longer distances. The resulting model combines the number and retention time of ingested seeds with the simulated movement distance to build seed dispersal kernels (Pires et al., 2018). We performed one hundred replicates of the simulations.

3 | RESULTS

3.1 | Seed dispersal by wild pigs

We found 15,087 intact seeds in 111 stomachs of wild pigs, 55.9% ($n = 62$) of which had at least one seed (Table 1). Of all intact seeds, 70.7% (10,671) were from zoochoric fruits from 11 plant species (nine natives, one alien and one unknown origin), 27.5% (4,142) were from seven grass morphospecies (Poaceae), 1.6% (237) were from six unknown species, and 0.2% (37) from two non-zoochoric alien species. Seeds of *Solanum americanum* (Solanaceae, native) appeared in just one stomach but accounted for 1/3 (5,000) of all intact seeds found in all stomachs. Intact seeds also appeared in 90% (74) of the 82 scats collected in the field, which collectively contained 5,186 seeds. From those, at least 89.8% (4,657 seeds) were from zoochoric plants of eight different plant species (five natives, two aliens and one unknown origin), 0.4% (20 seeds) were from one autochoric alien species, and 9.8% (509 seeds) were from 15 unknown plant taxa. Intact seeds of *Psidium* spp. (Myrtaceae, unknown origin, 4,197 seeds, 81%) *S. romanzoffiana* (Arecaceae, native species, 401 seeds, 8%), and Poaceae (unknown origin, 297 seeds, 6%) were the most numerous and frequent plants found in the scats. Seeds smaller than 10 mm in diameter accounted for 98% and 92% of all seeds discovered in stomachs and scats, respectively, and the maximum seed size found was 19.7 mm (Figure 1 and see Tables S3 and S4 for taxonomic and trait information of plant species found in stomachs and scats).

3.2 | Seed dispersal effectiveness: The quantitative component

We recorded 21 ground-foraging frugivorous species interacting with fruits in the 14 studied sites in our fruit removal experiment (17 mammal species, three bird species and one lizard, Figure S2). The most effective frugivores in terms of fruit removal rate per frequency of visits (i.e., the highest scores in the QC of SDE) were

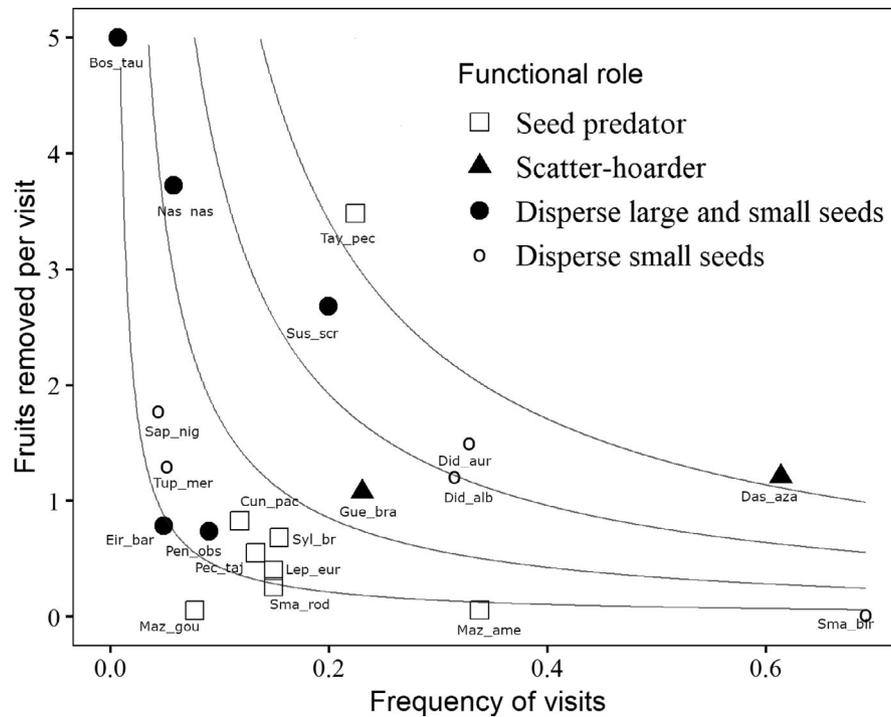


FIGURE 2 Overall quantitative component of seed dispersal effectiveness (SDE) of frugivore species to large-fruited plants *Syagrus romanzoffiana*, *Hymenaea courbaril*, and *Guazuma ulmifolia* in the fragmented Atlantic Forest. Quantity component (QC) scores are the product of the subcomponents frequency of visits and fruits removed per visit and define the quantitative SDE of the frugivores. Species symbols are assigned according to their functional role to seed dispersal service: Triangles are scatter-hoarders—agouti *Dasyprocta azarae* (Das aza) and ingrami squirrel *Guerlinguetus brasiliensis* (Gue bra); small circles may disperse only small seeds—black-eared opossum *Didelphis aurita* (Did aur), white-eared opossum *Didelphis albiventris* (Did alb), capuchin monkey *Sapajus nigratus* (Sap nig), tegu lizard *Tupinambis merianae* (Tup mer), and small birds (Sma bir, *Cyanocorax* sp. and *Baryphtengus ruficapilus*); black squares are primarily seed predators—white-lipped peccary *Tayassu pecari* (Tay pec), collared peccary *Pecari tajacu* (Pec taj), gray brocket deer *Mazama gouazoubira* (Maz gou), red brocket deer *Mazama americana* (Maz ame), paca *Cuniculus paca* (Cun pac), small rodents (Sma rod, Echimidae), Brazilian cottontail *Sylvilagus brasiliensis* (Syl bra), and European hare *Lepus europaeus* (Lep eur); large circles may swallow both large and small seeds—wild pig *Sus scrofa* (Sus scr), coati *Nasua nasua* (Nas nas), tayra *Eira barbara* (Eir bar), dusky-legged guan *Penelope obscura* (Pen obs), and cattle *Bos taurus* (Bos tau). See Table S5 for a complete QC score, rate of fruit removal of all species and references that based the classification of the frugivores' role

the white-lipped peccary (*Tayassu pecari*, seed predator), agoutis (*Dasyprocta azarae*, scatter-hoarder), wild pigs (which swallow both small and large seeds), and opossums (*D. aurita* and *D. albiventris*, may swallow only small seeds and thief pulp from large-seeded fruits; Figure 2, Table S5). Tapirs (*Tapirus terrestris*) were detected on cameras at three sites but were not recorded eating any fruit at the sampling stations. Although the number of fruits removed per visit is expected to be correlated with frugivore body size, our results did not indicate such correlation (using Ln of body mass, Kendall's correlation $\tau = .23$, $p = .16$).

3.3 | Seed dispersal effectiveness: The qualitative component

We found 24 scats in suitable sites and 58 in unsuitable sites after 28 and 17 days of survey effort, respectively. Deposition of scats in suitable sites was thus four times less frequent than in unsuitable sites, but accounted for 80% of all intact seeds found in the scats (mostly *Psidium* sp.). Scats found within sugarcane plantations represented 79% of the deposition events in unsuitable sites.

Wild pigs in captivity ingested and defecated intact 95% of the seeds of *S. romanzoffiana* (596 recovered intact), 57.6% (432) of the seeds of *G. ulmifolia*, 23.8% (163) of *G. americana*, 61.9% (455) of *J. spinosa* and 13.2% (10) of the seeds of *Cordia* sp. (Figure S3). Fruits of *A. aculeata*, *A. phalerata*, and *S. oleracea* were consumed, and 100% of their seeds were spat out intact. Captive pigs did not swallow and defecate intact seeds of *H. courbaril*, rather they destroyed 93.7% of the seeds and spat out intact 20 seeds (6.2%). None of the seeds of the other five plant species (*I. laurina*, *E. edulis*, *S. cumini*, *L. leucocephala*, and *Urochloa* spp.) were recovered intact in the pig stool of the captive wild pigs nor were spat out intact. We found a positive relationship between seed size and proportion of seed survival (linear regression: $R^2 = 0.46$, $p = .008$, Figure 3).

Germination of *G. americana* occurred only for seeds that received gut passage treatment, with maximum germination of 63.5% of defecated seeds (Figure 4). For *J. spinosa* and *G. ulmifolia* that received gut passage and *H. courbaril* that were spat out the final proportion of germinated seeds did not differ from control seeds (Wilcoxon signed-rank test $W = 189$ $p = .1193$, $W = 664$ $p = .459$ and $W = 8.5$ $p = 1$, respectively. Table 2), but handling and gut passage

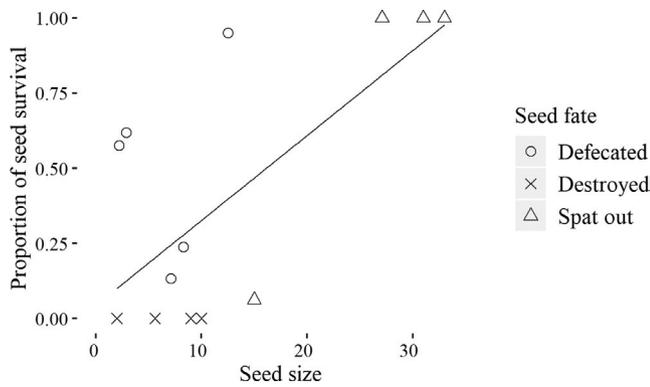


FIGURE 3 Proportion of seeds that survived (remained intact either after defecation or spat out) or were destroyed after fruit handling and gut passage by wild pigs *Sus scrofa* in captivity, as a function of seed size. The black line depict the linear regression of this relationship ($R^2 = 0.48, p = .008$)

enhanced the speed of germination relative to manually defleshed seeds, in terms of both T_0 and MdD (Wilcoxon signed-rank test $W = 240 p < .001, W = 468 p < .001, and W = 16 p = .029$ for *J. spinosa, G. ulmifolia* and *H. courbaril* respectively. Results were identical for both response variables). Seeds of *A. aculeata, A. phalerata, Syagrus oleracea, S. romanzoffiana,* and *Cordia* sp. did not germinate in either the defecated or control treatments.

Germination of seeds from scats found in the field was successful for 11 species but failed for another 13 (see Table S4). Among the identified plant species, *S. cumini* (alien) and *Psidium* spp. had the

TABLE 2 Minimum and mean days of seed dormancy (T_0 and MdD, respectively) and germinability (proportion of seeds germinated at the end of 180 days of experiment) for each plant species tested (number of samples within parentheses)

| | Treatment | Control |
|---------------------------------|----------------|----------------|
| <i>Genipa americana</i> | | |
| T_0^{NT} | 18 ± 7 (10) | 0 (11) |
| MdD ^{NT} | 20 ± 6 (10) | 0 (11) |
| Germinability (%) ^{NT} | 60.6 ± 28 (11) | 0 (11) |
| <i>Hymenaea courbaril</i> | | |
| T_0^* | 17 ± 2 (4) | 39 ± 14 (4) |
| MdD [*] | 26 ± 8 (4) | 71 ± 24 (4) |
| Germinability (%) ^{NS} | 50 ± 25.8 (4) | 52.5 ± 21 (4) |
| <i>Jaracatia spinosa</i> | | |
| T_0^{**} | 30 ± 6 (14) | 32 ± 3 (10) |
| MdD ^{**} | 32 ± 6 (14) | 35 ± 3 (10) |
| Germinability (%) ^{NS} | 33.3 ± 34 (24) | 47.3 ± 27 (12) |
| <i>Guazuma ulmifolia</i> | | |
| T_0^{**} | 15 ± 9 (11) | 17 ± 15 (13) |
| MdD ^{**} | 15 ± 9 (11) | 17 ± 15 (13) |
| Germinability (%) ^{NS} | 3.1 ± 4.7 (36) | 4.4 ± 6.6 (34) |

Abbreviations: NS, no significant statistical differences among treatments; NT, Not tested, given lack of germination on control seeds. * $p = .029; **p < .001$.

highest germination rate (80.8% and 75.7%, respectively), followed by the *Cecropia pachystachya* (75%), the alien *L. leucocephala* (35%), *Celtis iguanaea* (33.3%), and one unidentified species of Poaceae (2%). *Syagrus romanzoffiana* seeds, the second most common plant found in the scats, had only 1% germination rate (4 of 401).

3.4 | Kernels of seed dispersal distances

Wild pigs in captivity ingested and defecated intact the seeds of four plant species, *S. romanzoffiana, J. spinosa, G. americana,* and *G. ulmifolia* with a mean gut retention time of 70.4 ± 23.1 hr (Figure S4). No seeds were observed in the scats for any of the plant species in the first 24 hr for and the maximum length of time we observed seeds in the scats was 168 hr after the pigs had consumed the fruits. The simulations of seed dispersal distances given this distribution of gut retention times estimated that seed deposition for wild pigs can occur as far as 1,367 m (upper 95th percentile) with a median of 605 m under a Brownian movement model and 3,454 m (upper 95th percentile) with a median of 1,194 m under a Levy walk movement model (Figure 5) considering 100 simulations.

Among the other 20 frugivore species recorded removing fruits, at least 10 of them can swallow the seeds and deposit them intact (see Table S5, Bello et al., 2017). Simulations for frugivores that weighting up to 5 kg resulted in seed dispersal distances of 307 m (upper 95th percentile) with a median of 57 m when considering Brownian model and 663 m (upper 95th percentile) with a median of 96 m when considering Levy walk (Figure 5). Although we did not record tapirs removing fruits on cameras, which are rare or extirpated from much of the Atlantic Forest (Bogoni et al., 2018), we identified scats of the species filled with seeds of several plant species (*S. romanzoffiana, G. ulmifolia, F. Pedrosa* pers. observ.) at three different sites. We parameterized gut retention time for tapirs using information from (Clauss et al., 2010). Seed dispersal distances simulated for tapirs using a Brownian model resulted in 1,447 m (upper 95th percentile) with a median of 615 m and 3,465 m (upper 95th percentile) with a median of 1,168 when considering Levy walk model (Figure 5).

4 | DISCUSSION

Our data indicate that wild pigs can provide effective seed dispersal services in terms of the quantity of seeds dispersed. The number of intact seeds found in both stomachs and scats of wild pigs is only comparable to that observed for lowland tapirs (O’Farrill et al., 2013), the largest extant Neotropical mammal but extirpated in most of the Atlantic forest (Bogoni et al., 2018). The mean gut retention time of wild pigs recorded here is 1.5 times longer than that of tapirs (Clauss et al., 2010), making them potential promoters of long-distance seed dispersal. Considering that the mean isolation of Atlantic forest remnants is 1,441 m (Ribeiro et al., 2009), the estimated dispersal distances found here suggest that wild pigs may be able to promote seed dispersal among isolated forest fragments. Long-distance seed dispersal has consequences at landscape and regional scales,

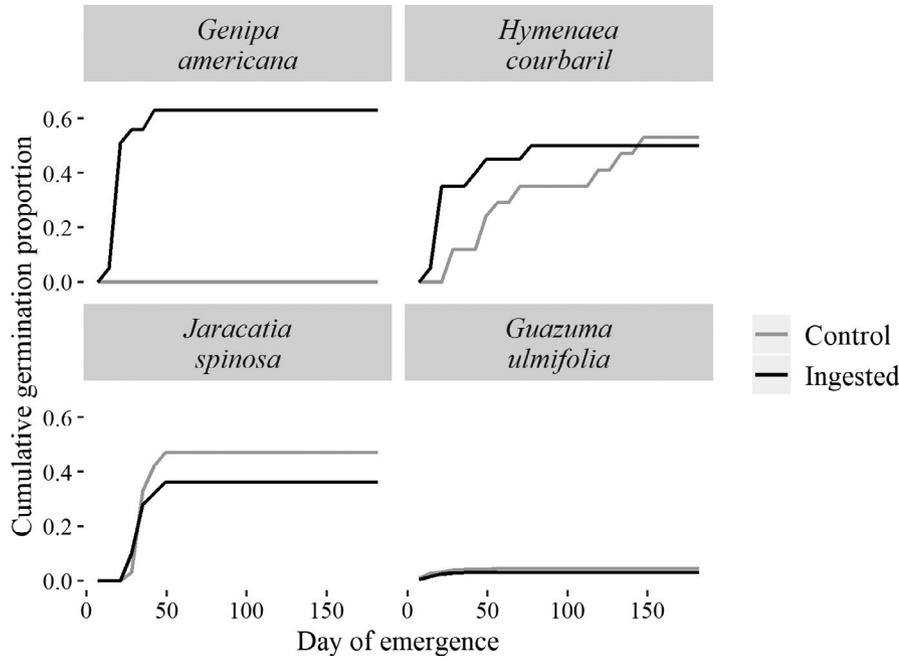


FIGURE 4 Germination of seeds. Cumulative proportion of germinated seeds through time for four plant species. Control seeds (manually defleshed seeds, gray line) were compared with ingested seeds (dark line) by wild pigs *Sus scrofa* in captivity. Ingested seeds were either defecated (*Genipa americana*, *Jaracatia spinosa*, and *Guazuma ulmifolia*) or spat out (*Hymenaea courbaril*)

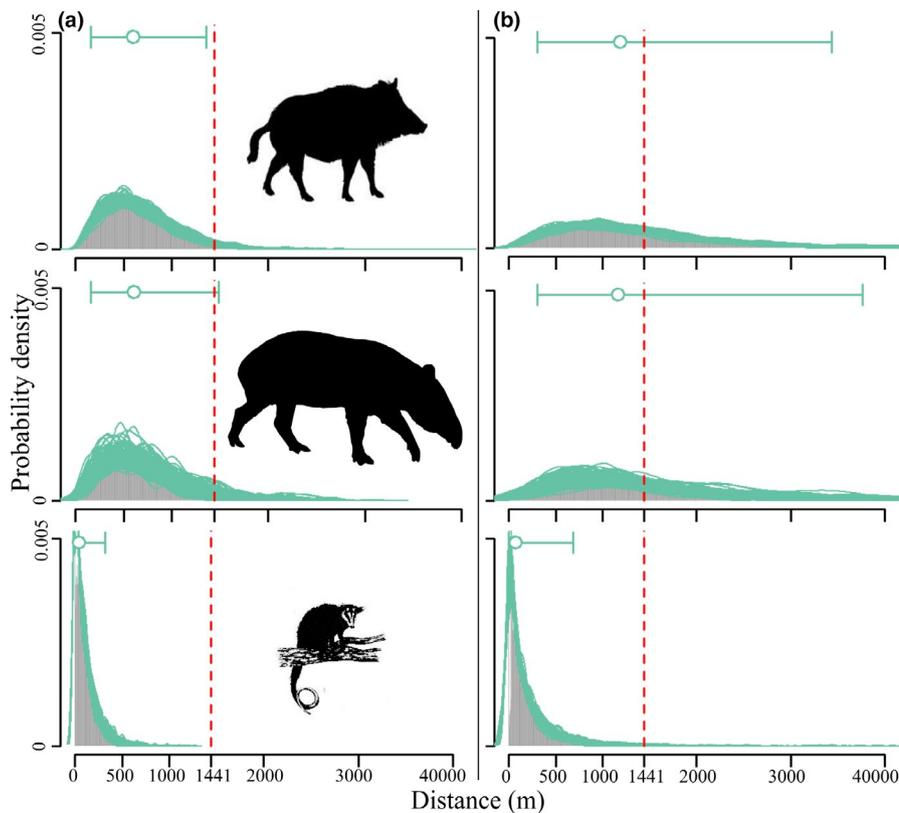


FIGURE 5 Kernel of seed dispersal distances simulating Brownian (a) and Levy (b) walk models for wild pigs (upper), tapirs (middle), and for other mammalian frugivores with maximum body weight of 5 kg (lower). We depict the median distances (empty green circle) and the range (determined by the 5th and 95th percentiles, solid green line) in which 90% of seeds were estimated to drop. We depict 1,441 m (red dashed line) as the threshold of long-distance seed dispersal (LDSD), since it is the mean isolation distance among forest remnants in Atlantic rainforest (Ribeiro et al., 2009)

since it mediates gene flow among forests remnants (Giombini et al., 2017), favors the colonization of unoccupied habitats such as restoration sites or abandoned agricultural areas (Fragoso et al., 2003), reinforces the persistence of species in fragmented landscapes (McConkey & O'Farrill, 2016) and is especially important in assisting the range shift of plant species distribution following climate change (Mokany, Prasad, & Westcott, 2014). Although similar on this regard to lowland tapirs, one key difference among wild pigs and this native

large-bodied ungulate concerns their trophic position. While wild pigs are omnivores and benefit from crops (Ballari & Barrios-García, 2014), lowland tapirs are essentially herbivores of forest environments (Talamoni & Assis, 2009), which ultimately may have consequences for seed deposition (O'Farrill et al., 2013). In fact, 3/4 of deposition events of seeds delivered by wild pigs are occurring more frequently in unsuitable than suitable sites for seedling recruitment and establishment.

Although wild pigs consume and remove high rates of seeds, our data show that the quality of this service varies depending on the plant species. Smaller seeds have a higher chance of being destroyed after handling and gut passage than plants with larger seeds. While the chance of seed survival increased with seed size, large seeds were those that were spat out and small seeds were those that were swallowed and defecated intact. We believe that along with seed size, there are other seed traits for which pigs may be beneficial or detrimental to the plants, such as seed coat thickness and hardness (likely related to the chance of being spat out or destroyed during handling), permeability and texture (likely related to the chance of being digested during gut passage, Traveset, Rodríguez-Pérez, & Pías, 2008). For example, *S. romanzoffiana* and *H. courbaril* have similar seed diameter, but the former resisted handling and gut passage, while the opposite was observed for the latter. One of the differences between species is the seed coat thickness, which is very thin in *H. courbaril* but thick in *S. romanzoffiana*. The three plant species that presented 100% survival after fruit and seed handling by captive pigs were the largest in seed size and possess the hardest seed coat among tested plants and were all spat out. Survival of only a subset of seeds after handling and gut passage is also seen for other large-bodied frugivores (Traveset & Verdú, 2002). Wild pigs defecated viable seeds and although we did not compare germination with the whole fruit—which simulate lack of dispersal—germinability was improved by gut passage for *G. americana* and sped up germination for three other plants tested. The largest benefit of gut passage may be removing the flesh (Fricke, Bender, Rehm, & Rogers, 2019) and the main positive effect of increasing the speed of germination is that it reduces the chance that the embryo is killed by seed predators (Hulme, 1998). Moreover, high growth rate may reduce seedling competition (Zhu, Comita, Hubbell, & Ma, 2015). In addition, another subcomponent of the qualitative SDE that would be valuable to consider—but not assessed by us—is the probability that a deposited seed will recruit and become a seedling (Schupp et al., 2010, 2017).

Most of the remaining native frugivore species may be ineffective in terms of their ability to move seeds across fragments. Seed dispersal effectiveness can be limited by gape size, which establishes an upper bound to the size of seeds that can be swallowed, gut retention times and movement ability, which constrain seed dispersal distance, and handling behavior upon fruits and seeds (pulp thieving, predation, spitting out, or scatter-hoarding), which affect the shape of seed shadows (Simmons et al., 2018). For example, the gape size and limited navigation capacity of white- and black-eared opossums limit the size of dispersed seeds as well as dispersal distance when compared to other frugivores (Cáceres, 2002; Delciellos et al., 2017). Similarly, scatter-hoarding rodents such as agoutis appeared to be among the most effective seed dispersers in terms of the quantity component of SDE in the analyzed sites, but they may not fully compensate for the loss of large-bodied frugivores in fragmented landscapes because the maximum recorded seed dispersal distance for agoutis is ~300 m (Jansen et al., 2012), far below the threshold of long-distance seed dispersal in fragmented Atlantic Forest. In addition, fragmentation of natural habitats creates barriers such as the

surrounding matrix and roads and it is unlikely that scatter-hoarders with small home ranges will connect isolated patches of forest via seed dispersal (Silvius & Fragoso, 2003). Although we did not record wild pigs dispersing seeds over 19 mm in diameter, they have been observed to swallow and disperse seeds as large as 30 mm (Donatti et al., 2007). Thus, wild pigs can potentially swallow large seeds and move long distances, cross the matrix connecting forest fragments and promote seed dispersal for several plant species.

The notion of non-native species restoring lost ecological interactions, such as seed dispersal, and functioning as surrogates of extinct or extirpated biota is not new (Gawel, Rogers, Miller, & Kerr, 2018; Lundgren, Ramp, Ripple, & Wallach, 2018). For example, frugivorous alien birds in New Zealand may be rescuing native zoophilic flora from population collapse due to extinction of native bird species (García, Martínez, Stouffer, & Tylianakis, 2014). Similarly, in Balearic Islands of the Mediterranean, where endemic frugivorous lizards went extinct, the alien carnivore *Martes martes* became the main seed dispersal agent of the shrub *Cneorum tricoccon* (Traveset, 1995). On the other hand, alien ecological surrogates are not always able to compensate for the services provided by native species (Lynes & Campbell, 2000). For example, the use of cattle and buffalo as replacements for threatened elephants for dispersal of large-seeded plants in continental India showed that bovines do not compensate for either the quantity nor the quality of the services provided by elephants (Sekar, Lee, & Sukumar, 2015). Yet, in the case of wild pigs, there are simply no large-bodied frugivores left in most of the Atlantic forest, and the seed dispersal services we uncover here would be limited if they were absent.

The distribution of wild pigs is mainly found in disturbed forest fragments in the Atlantic forest of São Paulo state (Pedrosa, Salerno, Padilha, & Galetti, 2015), highlighting the possibility that wild pigs may compensate for seed dispersal services lost due to the extirpation of large-bodied frugivores. However, a potential side effect of such seed dispersal services is the facilitation of rapid invasion by alien plant species (Dovrat et al., 2012; Lynes & Campbell, 2000), driving changes in the structure of the ecosystem (Barrios-García & Ballari, 2012), which is concerning as they disperse in the more intact forests (da Rosa et al., 2017). Two plant species found viable in the scats raise concern, *L. leucocephala* and *Urochloa* sp. Both were introduced as forage for livestock and are highly invasive, quickly colonizing open, and disturbed habitats after the deposition of a few viable seeds (Zenni & Ziller, 2011). In addition, non-native wild pigs have one of the highest reproductive rates among ungulates (Bieber & Ruf, 2005) and population growth in fragmented landscapes that is favored by abundant agriculture subsidies (Luskin et al., 2017) may cause pigs to be destructive through up-rooting seedlings and saplings and any positive role via seed dispersal may be off-set by a negative role at later recruitment stages (Ickes, Paciorek, & Thomas, 2005). Furthermore, wild pigs host important zoonotic and livestock pathogens (Galetti, Pedrosa, Keuroghlian, & Sazima, 2016; Ruiz-Fons, 2017; Trevisol, Kramer, Coldebella, & Santiago Silva, 2017) and are responsible for crop destruction causing negative

socioeconomic impacts where their populations grow unchecked (Barrios-García & Ballari, 2012). Therefore, management plan of non-native species for which eradication seems unachievable—the case of wild pigs—should envisage controlling the population to contain the negative impacts while inevitably benefiting from the positive ones. Our study highlights that a thorough evaluation of the services provided by alien surrogate species should be examined in a case by case scenario.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1f4h58f> (Pedrosa, Bercê, Levi, Pires, & Galetti, 2019).

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SUPPORTING INFORMATION

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