Reunion overseas: introduced wild boars and cultivated orange trees interact in the Brazilian Atlantic Forest

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ABSTRACT. Introduction: Little is known concerning novel interactions between species that typically interact in their native range but, as a consequence of human activity, are also interacting out of their original distribution under new ecological conditions. **Objective:** We investigate the interaction between the orange tree and wild boar, both of which share Asian origins and have been introduced to the Americas (i.e. the overseas). **Methods:** Specifically, we assessed whether *i*) wild boars consume orange (*Citrus sinensis*) fruits and seeds in orchards adjacent to a remnant of the Atlantic Forest of Brazil, *ii*) the orange seeds are viable after passing through boar's digestive tract and *iii*) whether the orange tree may naturalise in the forest remnant assisted by wild boars. **Results:** Our camera surveys indicated that wild boar was by far the most frequent consumer of orange fruits (40.5 % of camera trap-days). A considerable proportion of sown orange seeds extracted from fresh boar feces emerged seedlings (27.8 %, N = 386) under controlled greenhouse conditions. Further, 37.6 % of sown seeds (N = 500) in the forest remnant emerged seedlings in July 2015; however, after ~4 years (March 2019) only 9 seedlings survived (i.e. 4.8 %, N = 188). Finally, 52 sweet orange seedlings were found during surveys within the forest remnant which is intensively used by wild boars. This study indicates a high potential of boars to act as effective seed dispersers of the sweet orange. However, harsh competition with native vegetation and the incidence of lethal diseases, which quickly kill sweet orange trees under non-agricultural conditions, could seriously limit orange tree establishment in the forest. **Conclusions:** Our results have important implications not only because the wild boar could be a vector of potential invasive species, but also because they disperse seeds of some native species (e.g. the queen palm, *Syagrus romanzofiana*) in defaunated forests, where large native seed dispersers are missing; thus, wild boars could exert critical ecological functions lost due to human activity.

Key words: agroecosystems; *Citrus*; frugivory; invasions; naturalization; novel interactions; seed dispersal; *Sus scrofa*.

Novel interactions usually take place between species that interact only because of human activity and would otherwise not even coexist (Hobbs et al., 2006; Turcotte, Araki, Karp, Poveda, & Whitehead, 2017). Thus, most typically novel interactions arise from 'introduced species' (i.e. those living outside their native distributional range due to human activity; Traveset & Richardson, 2014; Wood et al., 2015) as well as from interactions between native and crop species (Bhagwat, Willis, Birks, & Whittaker, 2008). Less studied are novel interactions between species that originally interact in their native range but, as consequence of human activity (domestication, hunt introductions, etc.; Parker & Gilbert, 2004), are now interacting out of their original distribution under new ecological conditions. Here, we report one such case focused on the interaction between sweet orange trees *Citrus sinensis* L. Osbeck, native to Asia but cultivated worldwide, and wild boar *Sus scrofa* L., which is native to Eurasian and has been introduced in the Americas (i.e. the overseas) as game species. Investigating this novel interaction is important to understand the chances of naturalization of sweet oranges mediated by introduced wild boars (e.g. García, Martínez, Stouffer, & Tylianajis, 2014).

The cultivation of citrus fruits is widespread worldwide in regions with optimal edaphoclimatic conditions for their development (30-40º North and South latitude). Although it is one of the most important fruit crops in the world, there are few studies about the basic ecology of citrus. Of particular interest is determining which animals eat their fruits and disperse their seeds. Only anecdotal evidence has been found about animals that consume cultivated citrus which has recently reviewed by Peris, Fedriani, and Peña (2015). Very little is known about whether the interactions between *Citrus* species and its fruit consumers (both native and introduced) are mutualistic (i.e. seed dispersal) or antagonistic (see predation; but see Gade, 1976; Ungar, 1993). For instance, we are not aware of any study that has evaluated whether *Citrus* seeds ingested by frugivores are viable, whether they emerge as seedlings, and how long they survive under the field conditions of non-native ranges. Such information is critical to assess the chances of *Citrus* species to become naturalized outside of its original range.

The wild boar has been naturalized in many countries after being introduced as a game species and due to escapes of domestic pigs with which it hybridizes (Gimenez et al., 2003). These naturalized populations are causing major environmental issues around the world (Barrios-García & Ballari, 2012; Pedrosa, Salernob, Padilhac, & Galetti, 2015). Wild boar adapts to a variety of habitat types and can rapidly increase its population (Massei & Genov, 2004). It is a threat to native species of flora and fauna (Bratton, 1974) and is considered one of the 100 most 'invasive species' (i.e. introduced species with a tendency to spread and to cause environmental damages; Lowe, Browne, & Boudjelas, 2000). The boar is omnivorous, eating everything from grain to carrion, including fruit and acting as seed disperser of many large-fruited plants (e.g. Fedriani & Delibes, 2009). Consequently, wild boar has great potential to act as an effective seed disperser (*sensu* Schupp, Jordano, & Gomez, 2010) of *Citrus* spp. and other cultivated species, exerting thus marked ecological impacts outside of its original geographical range. Nonetheless, introduced wild boars could also act as seed dispersers of some native plant species in areas where their regular seed dispersers have been extirpated (Dirzo et al., 2014) having thus potential positive effects for some plant populations.

In this study, we evaluate the potential of introduced wild boars to act as seed dispersers of *C. sinensis* in the Atlantic Forest of Brazil. *Citrus* are native to the tropical and subtropical regions of Southeast Asia (Webber, 1967), with edaphoclimatic conditions similar to those of Brazilian Atlantic Forest, indicating the suitability for *Citrus* in our study area (A. Juliano, unpublished data). To evaluate the importance of wild boars as consumers of *Citrus* fruits, we made camera surveys within a large orange

orchard adjacent to natural forest. Then, to evaluate whether boars disperse viable seeds within their feces, we conducted emergence trials with seeds extracted from boar feces under controlled greenhouse conditions. Finally, to assess orange seedlings recruitment and establishment under local field conditions we surveyed the forest remnant searching for putative orange seedlings, and also conducted seedling emergence and survival trials in the forest remnant. Specifically, we addressed the following three questions: (*i*) Are wild boars frequent consumers of orange fruits and their seeds? (*ii*) Do viable orange seeds appear after passing through boar's digestive tract? (*iii*) Is the forest remnant an appropriate habitat for orange seedling recruitment and establishment? Based on the opportunistic feeding habits of wild boars and in their known ability to disperser large-fruited species (e.g. Fedriani & Delibes, 2009), we hypothesized they will be effective dispersers of the sweet orange tree. However, because strong competition with native vegetation and because of the incidence of lethal diseases, which quickly kill sweet orange trees under non-agricultural conditions, we expected a low recruitment of sweet orange trees within the forest remnant.

MATERIALS AND METHODS

Study site and system: The study was carried out in Cambuhy Agrícola Ltda. (located at Matâo, Sâo Paulo, Southern Brazil; 21°38' S & 48°31' W, ~600 m.a.s.l.) between April 2014 and March 2019. The agricultural farm of Cambuhy has an area of 14 083 ha where sugarcane (*Saccharum officinarum* L.), rubber (*Hevea brasiliensis* (Willd. ex A., Juss.) Müll. Arg.), corn (*Zea mays* L.) and citrus are grown. A nature reserve of 2 168 ha is found inside the farm corresponding to the Cerrado and Atlantic forest domains, called Mata da Virgínia. The predominant native vegetation is the semi-deciduous seasonal forest with small portions of woodland savanna, Cerrado domain (Barros, Menezes, Falconi, & Giovanelli, 2017). The climate is warm and humid tropical with

a maximum temperature of 30.1 ± 0.37 ºC, a minimum temperature of 17.3 ± 0.52 ºC, and an average temperature of 22.8 ± 0.40 ºC (data obtained in the Cambuhy's weather station during 2014-2016). The annual rainfall during 2010-2016 was 1 386.5 + 61.06 mm, with a maximum of 1 601.1 mm (in 2015) and a minimum of 1 172.3 mm (in 2011).

The genus *Citrus* (Rutaceae) comprises perennial green trees originated in Southeast Asia. They produce hesperidium fleshy fruits divided into segments surrounded by peel that contains oil glands rich in volatile compounds. Orange is one of the most important fruit crops in the world. They are grown in more than 140 countries and, in 2015, the area planted with citrus fruits in the world was 8.7 million ha and citrus production was approximately 121 million tons (FAO statistics, 2016). An orange of the Pera cultivar matures between late May and June in Cambuhy, weighs 277.80 ± 21.37 g, measures 8.2 ± 0.12 cm in diameter and has a sugar pulp content of 9.67 ± 0.13 BRIX. The estimated production of a tree is 2 000 oranges per year. Our studies were performed when the fruit was already mature but just before operational harvesting for commercial activities of the farm. Sweet orange seeds are polyembryonic, recalcitrant, non-dormant, with sizes ranging from 1.2-1.8 cm in length (Spiegel-Roy & Goldschmidt, 1996).

Camera trap surveys of orange fruit consumers: To identify citrus frugivores and estimate their relative importance as fruit consumers, night-vision camera traps with motion sensors were installed on the trunks of orange trees and focused on mature oranges on the ground that had fallen from the tree in the cultivation plots near the forest remnant. The cameras (5 Bushnell Trophy Cam model 119446, USA and 1 Wildlife Trail model 02B, UK) were installed on cultivated trees along two rows with 3 cameras each at a distance of 6 and 76 m from the edge of the forest remnant, respectively. The cameras were checked daily to download the recorded images and verify their correct operation. Recording of frugivores was

done during April-May of 2014 and 2015 in 5 consecutive days periods. Since some cameras eventually failed, overall we undertook a sampling effort of 42 camera trap-days and attained 9 924 files (photos and videos) recording 679 vertebrate frugivores. Careful observations of all these files allowed us to estimate the relative importance of each recorded vertebrate as fruit consumer measured as the percentage of camera trap-days.

Occurrence viable orange seeds in boar feces and seedling emergence under controlled conditions: To estimate how often orange seeds occur in boar feces, during May 2014 we walked along three transect in the forest (two of 2 000 m and one of 1 500 m) located 5-8 m from the orchard. Each transect was searched for mammal feces once, and we covered a width of about 10 m (e.g. Suárez-Esteban, Delibes, & Fedriani, 2013). At the same time, feces were sought in the first 10 m of the forest remnant near these citrus orchards (two transects of 1000 meters). In total, 7.5 km in length were covered in 2014 (Appendix).

Fresh boar feces (N = 19) were identified (Bang & Vivó, 1975), bagged individually, and transferred to the laboratory the same day. They were measured, fresh weighed, and then sieved by a different-sized wire mesh sieves with warm water to extract the seeds (e.g. Fedriani, Fuller, & Sauvajot, 2001). Once cleaned, seeds were counted and stored in a refrigerator (4-6 ºC, to avoid deterioration and fungal infestation; e.g. King, Soetisma, & Roberts, 1981) for a maximum of 7 days. Then, they were sowed under greenhouse conditions in separate pots with citrus soil (50 % Sphagnum peat, 50 % coconut fiber), irrigated twice a week, 166 W/m^2 of natural irradiation, (average temperature of 23 ºC, with a minimum of 18 °C and a maximum of 28 °C), to evaluate their viability (e.g. Fedriani, Garrote, Delgado, & Penteriani, 2015). Together with citrus seeds, 53 seeds of queen palm (*Syagrus romanzofiana*) found within boar feces were sown.

Orange seedling recruitment and establishment in the forest remnant: We evaluated whether the forest remnant is an appropriate habitat for seedling recruitment and establishment by means of three approaches. Firstly, three people separated by three meters and walking in parallel straight lines through the forest remnant searched for citrus plants. During 2014, we walked two 900 m transects within the forest remnants (using machetes to open a path, see Appendix). During 2015, we surveyed a 3 km transect parallel to the line of citrus orchards but inside the forest remnant. In all cases, the width of the area surveyed along transects was 10 m approximately. Secondly, eight quadrants were made in the forest delimiting 60 m^2 (6 x 10 m) each, taking as a reference the method proposed by Braun-Blanquet (1979). To build the quadrants, four wooden stakes nailed to the ground were used, on which threads were tied to delimit the perimeter of the study. To facilitate the work, the threads were tied every 1.5 m lengthwise and every 1 m crosswise, forming a grid. In each grid a thorough analysis of the flora resembling citrus plants was performed. Eight quadrants were made, five in 2014 and three in 2015. Finally, we experimentally assessed whether orange seeds germinate and whether seedlings survive in the forest remnant. To this end, in May 2015, sweet orange fruits were collected from four fruiting trees. Seeds were extracted and washed to remove traces of pulp and dried for 1 day at room temperature. Seeds were sown in five quadrants (2 x 1 m each one) arranged along two lines 3 km apart. Whereas in the first line we set 3 quadrants at 0, 15, and 30 m inside the forest remnant, in the second one, due to logistic limitation, only two quadrants (at 0 and 15 m inside the forest) were set. As 500 seeds were required to perform this experiment, and it is extremely difficult to get those numbers from boar feces, we decided to use seeds extracted from fruits. Before seed sowing, the existing vegetation in each quadrant was removed and the soil was loosened with a hoe. The quadrants

were subdivided into 50 grids (20 x 20 cm). In each grid center, a hole of 1 cm in depth was made and 2 seeds were deposited, so a total of 100 seeds per quadrant were planted. Sown seeds were covered with the local soil (dried leaves were removed) and then watered every 2 weeks during the first 2 months after sowing. Thereafter, the sowings were subjected to natural conditions. Seedling emergence and growth was registered every two months.

Molecular typing of citrus plants found in the forest: A sample of three suspected *Citrus* seedlings found in the forest were subjected to microsatellite Simple Sequence Repeat analysis (following Pons, Navarro, Ollitrault, & Peña, 2011) to verify whether they belonged to the genus *Citrus*. As there was no unique marker to unequivocally distinguish among different citrus species, a multilocus analysis was made by choosing 3 different markers. These markers were *CIR07C07* (Froelicher et al., 2008), *CIR01C06* (Cuenca et al., 2011) and *mest86* (Luro, unpublished).

RESULTS

Relative importance of orange fruit consumers: Table 1 shows the percentage of camera trap-days in which each frugivore species was recorded, the mean number ($\pm$ 1 SE) of different individuals recorded per day and camera, the maximum number of individuals recorded, and the functional group of visitors (seed dispersers, seed predators, and pulp consumers). Among citrus seed dispersers, non-native wild boars were the most frequently recorded (40.5 %; Fig. 1), followed by Azara agouti (21.4 %) and Lowland agouti (16.7 %; Table 1), being these differences significant (χ^2 = 6.90, d.f. = 2, P < 0.05). Further, we detected up to 6 wild boars per day and per camera, while only up to 2 agoutis (Table 1). Thus, we considering the number of recorded individuals of each disperser species the predominance of wild boars as seed dispersers (58.9 %) when compared to Azara agouti (25.0 %) and Lowland agouti (16.1 %) was larger (χ^2 = 25.8, d.f. = 2, P < 0.0001). The most abundant pulp

Fig. 1. Wild boars (*Sus scrofa* L.) eating mature sweet orange fruits under the canopy of a tree in an orchard near the forest remnant. Because the species often hybridizes with domestic pigs, the possibility exists that the photographed individuals are hybrids.

consumers were unidentified small birds (that were recorded almost every camera trap-day) and that were often recorded consuming pulp and vesicle remains scattered by wild boars. Seed predators (small rodents, capybara, and tapeti) were infrequent visitors (Table 1).

The mean number of animals observed per day and per camera, the maximum number of animals recorded and the functional guild of each frugivore. Our sampling effort (42 camera trap-days) rendered 9 924 files (photos and videos) of 679 different vertebrate frugivores.

Wild boar dispersal of viable orange seeds: Most boar feces (68.4 %, N = 19) contained citrus seeds. The mean number of citrus seeds per boar feces was 29.1 ± 7.9, ranging from 4-101 (overall, 386 seeds in 14 feces). Citrus seedlings started to emerge one week after planting. Emergence percentage of citrus seedlings three months after sowing was 27.8 % (Table 2). No seedling emerged later than 3 months after planting. In addition to citrus seeds, two out of 53 seeds of queen palm found within boar feces emerged seedlings within the first 2 months after sowing (Table 2).

Orange seedling emergence and establishment in the forest remnant: No citrus seedlings were found in the three transects searched in 2014. However, 48 citrus seedlings were found within the 3-km transects searched in 2015 (they were grouped into 5 clusters within 50 m^2). The mean height of these seedlings (including roots) was 10.60 ± 1.53 cm, ranging from 5-40 cm. Their estimated age was between 6 months and 2 years. In addition, we found four seedlings in one (out of 8) 60 m^2 established quadrants. All 52 seedlings were taken to the laboratory, measured, and analysed to confirm their genetic identity.

Three of the presumed citrus seedlings found in the forest remnant were verified as citrus types based on molecular markers. Citrus seedlings were identified as sweet oranges according to their SSR profiles, clearly distinguishable for those of mandarin (*Citrus reshni* Hort. ex Tan.) and clementine (*Citrus*

TABLE 1

Percentage of animal observations in Cambuhy (Brazil) through the use of camera-traps

Species	% of days filmed	Mean±S.E.	Maximum	Functional group	Reference
Sus scrofa	40.5	1.94±2.5	6	Seed disperser	Barrios-García & Ballarri, 2012
Dasyprocta azarae	21.4	1.55±0.2	2	Seed disperser	Ribeiro and Vieira, 2014
Cuniculus paca	16.7	1.28±0.3	2	Seed disperser	Wenny, 2000
Nasua nasua	7.1	1±0.0	1	Seed disperser	Alves-Costa and Eterovick, 2007
Cerdocyon thous	4.8	1±0.0	1	Seed disperser	Rocha *et al.*, 2004
Small birds	97.6	11.63±11.6	50	Pulp feeders	Personal observation
Turdus leucomelas	76.2	1.71±1.8	4	Pulp feeders	Personal observation
Columbina talpacoti	59.5	1.84±2.2	4	Pulp feeders	Personal observation
Aramides cajaneus	28.6	1.91±0.1	3	Pulp feeders	Personal observation
Hydrochoerus hydrochaeris	2.4	10±0.0	10	Seed predator	Personal observation
Sylvilagus brasiliensis	4.8	1±0.0	1	Seed predator	Personal observation
Small rodents	4.8	1±0.0	1	Seed predator	Personal observation
Dasypus novemcinctus	2.4	1±0.0	1	Unknown	
Iguana spp.	2.4	1±0.0	1	Unknown	
Penelope spp.	2.4	1±0.0	1	Unknown	

TABLE 2

Fresh weight and number of seeds (*Citrus* sp., *Syagrus romanzofiana*, *Zea mays* and unidentified species)
found in wild boar feces collected at the grove-forest remnant ecotone. The emergence percentage
of citrus seedlings under greenhouse conditions is also shown

Sample	Fresh weight (g)	Number of seeds and plant species found				Citrus seedling emergence	
		Citrus sp.	*Syagrus romanzofiana*	*Zea mays*	Non-identified	Total	%
1	62.1	79				8	10.1
2	78.2	101	2			17	16.8
3	69.3	43				12	27.9
4	69.4	32				14	43.8
5	50.3	9			9	7	77.8
6	23.5	4	2			0	0
7	103.7	4	15			0	0
8	124.1	-	3			-	-
9	109.3	28				15	53.6
10	133.2	-				-	-
11	63.5	-		1		-	-
12	33.8	9				0	0
13	152.6	38	1	12		15	39.5
14	45.9	3				0	0
15	98.6	19				17	89.5
16	38.3	9				0	0
17	99.1	-	22			-	-
18	33.4	8				0	0
19	180.4	-	53			-	-

clementina Hort. ex Tan.) controls. This result is expected as citrus orchards at Cambuhy consisted basically of sweet orange trees.

Sweet orange sowing in the forest remnant: Two months after sowing seeds in the forest remnant (i.e. July 2015), 37.6 % of sown seeds (N = 500) emerged seedlings. Seedling survival rates decreased over the following years, being 72.3 % (N = 188) one year later (July 2016), 46.8 % (N = 188) two years later (March 2017) and 26.6 % after three years (May 2018) and 4.8 % after four years (March 2019). In May 2018, wild boars completely destroyed two quadrants. In March 2019, the 9 surviving orange seedlings were from 9 to 42 cm long, with an average height of 27.72 ± 3.41 cm.

DISCUSSION

Peris et al. (2015) recently reviewed citrus fruit vertebrate consumers and reported up to 28 vertebrate species. Other authors have detailed citrus fruit consumption by wild mammals and birds, as well as by livestock, both in areas where it is cultivated (e.g. Argentina, Dominica, Tanzania and Pakistan (Din & Ghazanfar, 1980; Shafi, Khan, & Hussain, 1986; Navarro, Martella, & Chediack, 1991; Wiley, 1993; Corp & Byrne, 2004; Stampella, Delucchi, Keller, & Hurrell, 2014) and where it is native (e.g. Torii, 1986; Ungar, 1993; Kitamura et al., 2002). Surprisingly, however, none of these studies have evaluated whether citrus frugivores acted as seed dispersers or as predators. To our knowledge, this is the first study evaluating the qualitative seed dispersal

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effectiveness (Schupp et al., 2010) of *Citrus* species, either in its native range or in areas where the species is cultivated. Based on our camera survey (Table 1) and field observations (e.g. fruit remains found underneath trees), wild boar was the only frequent species (40.5 %) that visited fruiting orange trees, consumed whole fruits, and that could act as an effective seed disperser (Fig. 1). Other mammals that could act as seed dispersers (e.g. Azara agouti, Lowland agouti, crab-eating fox) were much less frequent (5-21 %; Table 1). For example, Zuracatto, Carrara, & Franco (2010) documented Lowland agouti eating citrus fruits (including their seeds) in the Atlantic Forest of Brazil. For example Jansen et al. (2010) indicates that Central American agouti (*Dasyprocta punctata*) is of great ecological importance as seed predators and seed dispersers. Zuracatto et al. (2010) found that Lowland agouti consume both the endocarp and the seeds of *C. sinensis*, *Citrus limon* and *Citrus deliciosa*. However, Smythe (1978) indicate that agoutis (*Dasyprocta* spp.) eat, but do not disperse, seeds of certain Citrus species. In our study, we also very frequently recorded several bird species underneath orange trees; however, they were always picking pulp remains from fruits previously processed by boars or from fungus-infected fruits (which soften the fruit peel allowing birds to access the pulp; Peris, Rodríguez, Peña, & Fedriani, 2017) and no evidence of seed ingestion (and thus potential dispersal) was found during this study. Thus, the potential role of other mammals on citrus seed dispersal deserves further research.

The emergence experiments in the greenhouse and in the forest remnant, as well as our field surveys, where we found several citrus seedlings within the forest remnant, strongly support the conclusion that wild boars are acting as relatively effective dispersers of *C. sinensis* seeds. Surprisingly, however, we have not found any adult orange trees in the forest despite intensive searches, which could be explained in at least two ways. Firstly, since *C. sinensis* has a long period of juvenility, ranging from 7 to more than 10 years (Spiegel-Roy

& Goldschmidt, 1996), it could be due to a lack of time to recruit into adult trees. However, this seems unlikely since the orange tree orchards in Cambuhy Agrícola Ltda. were established in the 1970's. Secondly, although sweet orange seeds reach the forest, germinate, and seedlings emerge, perhaps they might not find the appropriate conditions to establish as adult individuals. Although the soil and climate conditions were optimal for the emergence and growth of citrus trees, competition with the abundant wild plants for water, light and nutrients could prevent citrus establishment. In addition, there are certain lethal and ubiquitous diseases for sweet orange trees such as Tristeza (caused by *Citrus tristeza* virus) or gummosis (caused by *Phytophthora* spp.) which quickly kill sweet orange trees under non-agricultural conditions (Spiegel-Roy & Goldschmidt, 1996; Moreno, Ambrós, Albiach-Martí, Guerri, & Peña, 2008). Indeed, most cases of citrus and Rutaceae naturalization have been reported in areas near their centers of origin and diversity, such as China and Southeast Asia (see Hong & Blackmore, 2015). In the Americas, as a result of their introduction for cultivation as a combination of rootstocks and scions of two different genotypes, only rootstock types have been found naturalized (Gade, 1979; Nesom, 2014). Therefore, it seems that the sweet orange has never been found naturalized in South America, which may explain the lack of success in our attempts either to find or to establish sweet orange adult in the forest remnants.

The wild boar is becoming a major matter of concern for the conservation of biodiversity in many areas around the world (Massei & Genov 2004; Barrios-García & Ballari, 2012; Pedrosa et al., 2015). In spite of its increasing distribution and density, there is a lack of information about their interactions with other species in the new distribution. Specifically, wild boars are becoming widespread and ubiquitous in several areas previously occupied by Atlantic forests of Brazil (Pedrosa et al., 2015). Here we show that they act as effective seed dispersers of the sweet orange tree in Southern Brazil, which could be environmental issue if this

exotic plant establish and become invasive. On the other hand, boars also acted as seed dispersers of the native queen palm. This finding could be especially relevant in defaunated areas of the Brazilian Atlantic forest (Chiarello, 1999; Galetti et al. 2017) where wild boars, through their novel interactions with native plants, could provide them with lost seed dispersal services. Boars could be dispersing many cultivated *Citrus* species in different areas of the world where both species have been introduced and favoured by human influences through citrus orchard abandonment, farming or lumbering practices (Gade, 1976). Thus, further studies concerning the pervasiveness and potential ecological outcomes of such novel interactions in other areas are clearly needed.

RESUMEN

Reunión en el extranjero: los jabalíes introducidos y los naranjos cultivados interactúan en el bosque atlántico brasileño. Introducción: Se conoce relativamente poco sobre las llamadas 'interacciones noveles' entre especies que típicamente interactúan en su área de distribución nativa pero que, como consecuencia de la actividad humana, también interactúan fuera de su distribución original bajo nuevas condiciones ecológicas. **Objetivo:** Investigamos la interacción entre el naranjo y el jabalí, ambos con origen asiático e introducidos en las Américas (es decir, del extranjero). **Métodos:** Específicamente, evaluamos si i) los jabalíes consumen frutas y semillas del naranjo (*Citrus sinensis*) en naranjales adyacentes a un parche remanente del bosque atlántico de Brasil, ii) las semillas de naranja son viables tras pasar por el tracto digestivo del jabalí, y iii) si el naranjo puede llegar a naturalizarse en el parche de bosque gracias a los jabalíes. **Resultados:** Los resultados de nuestro fototrampeo indicaron que el jabalí fue, con mucho, el consumidor más frecuente de las naranjas (40.5 % cámaras trampa-días). Una proporción considerable de semillas de naranjo extraídas de heces de jabalí frescas y sembradas emergieron plántulas bajo condiciones de invernadero controladas (27.8 %, N = 386). Además, del 37.6 % de las semillas sembradas (N = 500) en el parche remanente de bosque emergieron plántulas en julio 2015; sin embargo, después de ~ 4 años (marzo 2019) solo sobrevivieron 9 plántulas (es decir, 4.8 %, N = 188). Finalmente, se encontraron 52 plántulas de naranja dulce durante varias prospecciones dentro del parche de bosque que es utilizado intensivamente por los jabalíes. Este estudio indica un alto potencial de los jabalíes para actuar como dispersores de semillas eficaces del naranjo dulce. Sin embargo, la severa competencia con la abundante vegetación nativa y la incidencia de enfermedades letales, que matan rápidamente los naranjos dulces en condiciones no agrícolas, podrían limitar seriamente el establecimiento de naranjos en el bosque. **Conclusiones:** Nuestros resultados tienen implicaciones importantes no solo porque el jabalí podría ser un vector de posibles especies de plantas invasoras, sino también porque dispersan semillas de algunas especies nativas (p.e., la palmera reina, *Syagrus romanzofiana*) en estos bosques defaunados, donde faltan dispersores nativos de semillas de gran tamaño. Por ello, los jabalíes podrían ejercer funciones ecológicas críticas que se han perdido debido a la actividad humana.

Palabras clave: agroecosistemas; *Citrus*; frugivoría; invasiones; naturalización; interacciones noveles; dispersión de semillas; *Sus scrofa*.

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APPENDIX

Perimeter of the Cambuhy Farm, location of the citrus orchards, and details of the four transects made. The greenhouse is located in the farm, about 0.5-2 kilometers from transects.