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Ecologia da invasão dos suídeos asselvajados *Sus scrofa* no Brasil

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Orientador: Dr. Mauro Galetti Rodrigues

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ecologia e Biodiversidade.

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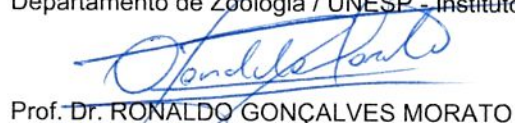
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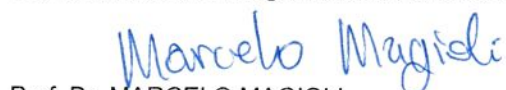
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Resumo

Invasões biológicas são uma das principais ameaças à biodiversidade, razão pela qual é campo de interesse de investigações científicas dos ecólogos. Os Neotrópicos abrigam uma das maiores riquezas de espécies do planeta e ao longo dos últimos anos vem sofrendo um aumento expressivo no número de introduções de espécies exóticas. Uma delas é o javali *Sus scrofa* e suas raças cruzadas com porcos domésticos, que em sua forma silvestre e de vida livre chamamos suídeos asselvajados. Ao longo dessa tese procuro investigar algumas das consequências ecológicas da invasão dessa espécie, assim como apresentar um panorama do controle populacional empregado hoje no Brasil, buscando sempre que possível fazer uma discussão dos resultados aplicada ao manejo da espécie. No Capítulo 1 mostro como a introdução acentuada dessa espécie ocorrida nos últimos 20 anos no Brasil fez com que ela se distribuisse amplamente por todo território nacional, principalmente nas regiões Sul, Sudeste e Centro-Oeste. No Capítulo 2 eu procurei fazer uma avaliação da efetividade do papel ecológico de frugivoria e dispersão de sementes prestado por esses animais. O Capítulo 3 mostra como as paisagens agrícolas estão subsidiando a invasão dos suídeos asselvajados potencializando a expansão da espécie e no Capítulo 4 busco revelar o papel do invasor no deslocamento do nicho trófico dos pecarídeos nativos. Já o Capítulo 5 apresenta um breve relato da interação entre os suídeos asselvajados e morcegos vampiros e, ao final, o Capítulo 6 traça um perfil dos métodos e motivações dos controladores da espécie hoje no Brasil. Em síntese, essa tese mostra que 1) os suídeos asselvajados desempenham papel ecológico de frugívoros e dispersores de sementes de plantas nativas e exóticas, 2) papel comparável – mas não equivalente – ao desempenhado pelas antas, 3) por também serem onívoros, são ao mesmo tempo subsidiados e grande problema para as atividades agrícolas além de 4) poderem competir por recursos com espécies que ocupam nicho similares como os catetos/caititus (*Pecari tajacu*) e queixadas (*Tayassu pecari*) e 5) servirem de presas para morcegos vampiros; além disso, 6) o controle populacional da espécie hoje no Brasil é feito em sua maioria por caçadores motivados pela defesa da propriedade e consumo da carne. O controle populacional da espécie é necessário como forma de frear a expansão populacional e diminuir os impactos negativos ecológicos e econômicos.

Palavras-chave: Javali, Mata Atlântica, Antropoceno, Espécie exótica, Frugivoria, Manejo de fauna

Abstract

Biological invasions are one of the main threats to biodiversity, which is why it is a field of interest for scientific investigations by ecologists. The Neotropics are home to one of the planet's greatest species richness, and over the last few years it has been experiencing a significant increase in the number of exotic species introduction. One of them is the wild boar *Sus scrofa* and their crossed-breeds with domestic pigs, that in its free-living wild-form we call wild pigs. My effort throughout this thesis is to investigate some of the ecological consequences of the invasion of this species, as well as present an outlook of the population control employed in Brazil, always seeking to make a discussion of the results applied to the management of the species. In Chapter 1 I show how the severe introduction of this species that occurred in the last 20 years in Brazil has made it widely distributed throughout the country, especially in the South, Southeast and Midwest regions. In Chapter 2 I evaluated the effectiveness of the ecological role of frugivory and seed dispersal provided by these animals. Chapter 3 shows how agricultural landscapes are subsidizing the invasion of wild pigs enhancing the species' expansion. In Chapter 4 I seek to reveal the role of the invader in displacing the trophic niche of native peccaries and Chapter 5 presents a brief account of the interaction between wild pigs and vampire bats. In the end, Chapter 6 outlines a profile of the methods and motivations of the species controllers in Brazil today. In summary, this thesis shows that 1) wild pig plays the ecological role of frugivores and seed dispersers of native and exotic plants, 2) comparable role – but not equivalent – to that played by tapirs, 3) because they are also omnivorous, they are both subsidized and a major problem for agricultural activities, 4) being able to compete for resources with similar niche species such as collared peccary (*Pecari tajacu*) and white-lipped peccary (*Tayassu pecari*) and 5) are serving as prey for vampire bats; in addition, 6) the population control of the species today in Brazil is made mostly by hunters motivated by property defense and meat consumption. Population control of the species is necessary to stop population expansion and mitigate the ecological and economic negative impacts.

Keywords: Wild boar, Atlantic forest, Anthropocene, Exotic species, Frugivory, Wildlife management

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INTRODUÇÃO

Assim como todas as espécies da família Suidae, os porcos *Sus scrofa* não são nativos das Américas (Melletti e Meijaard, 2018). Os porcos-do-mato nativos dos Neotrópicos são da família Tayassuidae (caititu/cateto *Pecari tajacu*, queixada *Tayassu pecari* e tagua *Catagonus wagneri*) e sua relação evolutiva com os Suidae data de 35 milhões de anos atrás, tempo aproximado do início da divergência das espécies de porcos com o ancestral comum às duas famílias (Randi *et al.*, 1996). Apesar dos porcos-do-mato Neotropicais também serem considerados suiformes, apenas os Suidae *S. scrofa* podem ser chamados de suídeos (Fig 1, Groves e Grubb, 2011).



Figura 1. Porco-monteiro (suídeo, acima), cateto/caititu e queixada (pecarídeos, abaixo e à esquerda e direita, respectivamente) no Pantanal. Os porcos-monteiros do Pantanal são os mais antigos suídeos asselvajados do Brasil. Fonte da foto: Galetti *et al.* 2015a.

Talvez os representantes mais emblemáticos dos suídeos sejam os porcos domésticos e os javalis. Os porcos domésticos que conhecemos hoje tiveram origem na domesticação de javalis europeus e asiáticos ocorrida em múltiplos centros de

domesticação entre 11 e 8 mil anos atrás (Larson *et al.*, 2005). Trata-se de um dos poucos exemplos de espécie animal domesticada pelo homem que ainda possui ancestral selvagem amplamente distribuído na natureza. O mais interessante é que tanto javalis Euroasiáticos selvagens quanto porcos domésticos pertencem à mesma espécie *S. scrofa*, ou seja, não há barreira reprodutiva entre eles e o cruzamento gera descendentes férteis (Gimenez *et al.*, 2003).

Desde o início de sua domesticação, porcos domésticos, javalis e descendentes do cruzamento dos dois, vem sendo introduzidos em toda parte do mundo, seja para criação em cativeiro ou soltura na natureza para caça, mas sempre com a mesma finalidade: fonte de proteína animal para subsistência humana (Tisdell, 1982; Weeks e Packard, 2009). Por serem animais que se alimentam de praticamente qualquer coisa (Ballari e Barrios-García, 2014) e que naturalmente ocorrem em ambientes climáticos diversos (Sales *et al.*, 2017), bastam poucos animais para formarem rapidamente populações numerosas em quase qualquer lugar que seja introduzido (Bieber e Ruf, 2005; Tabak *et al.*, 2018).

Porcos domésticos criados parcialmente soltos em boa parte do mundo eventualmente escapam e passam a viver por conta própria na natureza, voltando ao estado selvagem, e nesse caso dá-se o nome de porco asselvajado (ou feral). Javalis que escapam ou são liberados de criadores ou são introduzidos intencionalmente com finalidade de caça, continuam recebendo o mesmo nome. As raças cruzadas de javali com porcos domésticos ora são chamadas de porcos ferais ou javaporcos, ora de javalis e apesar de haver semelhanças fenotípicas, apenas análises cromossômicas podem diferenciar com segurança javalis puros 36N (provenientes de populações Euroasiáticas) de suas raças cruzadas 37N ou 38N (Gimenez *et al.*, 2003; García *et al.*, 2011; Sagua *et al.*, 2018). Para evitar confusão com denominação inapropriada da origem (se doméstico, ou javali Euroasiático ou cruzado), o termo mais apropriado para designar porcos *S. scrofa* de vida livre fora de sua distribuição natural – e que não se encontram sob supervisão humana – é Suídeo Asselvajado (em inglês wild pig *S. scrofa*, Keiter *et al.*, 2016). E este é exatamente o caso dos diversos tipos de *S. scrofa* de vida livre hoje no Brasil (Figs 2 e 3, Salvador e Fernandez, 2018).



Figura 2. Um suídeo asselvajado fêmea com seus filhotes capturados por armadilha fotográfica em Rio Claro-SP – Brasil. Nessa região são chamados popularmente de javaporco. Note que os filhotes possuem um padrão de pelagem típico dos encontrados nos javalis Euroasiáticos 36N, no entanto, como o próprio nome popular indica, trata-se de uma raça cruzada com porcos domésticos, provavelmente 37N.

O Brasil possui populações de porcos domésticos asselvajados, como por exemplo o porco monteiro do Pantanal (Mourão *et al.*, 2002), possui raças cruzadas, como por exemplo os javaporcos (Salvador and Fernandez 2018) e possui javalis (Deberdt e Scherer, 2007). É claro que as denominações de *S. scrofa* de vida livre variam muito, tanto no uso comum como na literatura científica (javali, javaporco, porco monteiro, javonteiro, suídeo asselvajado, porco feral, feral pig, feral hog, feral swine, wild boar, wild pig, etc), refletindo não só as diferenças regionais de designação como também as diferenças fenotípicas encontradas nas diversas raças de suídeos asselvajados. Por isso, os diferentes termos existentes para designar os suídeos asselvajados também são válidos. Porcos-monteiros do pantanal são bem distintos dos javalis do RS ou dos javaporcos de SP (Figs 1, 2 e 3). No entanto, apesar da diferença fenotípica entre algumas raças, acredito que sua plasticidade fisiológica, ecológica e comportamental permanecem quase as mesmas em todas as cruzas de vida livre (Melletti e Meijaard, 2018) – daí o sentido em nos referirmos à todas elas como suídeos asselvajados – mas este é um campo que merece ser melhor investigado (Salvador and Fernandez 2018).

As introduções desses animais com finalidade de produção comercial e caça no Brasil e ao redor do mundo acentuaram-se no século XX e o crescimento e a expansão populacional a partir dessas introduções não demonstram tendências de diminuição ou retração no século corrente (Long, 2003; Bengsen *et al.*, 2014; McClure *et al.*, 2015; Lewis *et al.*, 2017; Rosa *et al.*, 2017; Snow *et al.*, 2017; Tabak *et al.*, 2017; Melletti e Meijaard, 2018). Por esse motivo, hoje os suídeos asselvajados são considerados uma das espécies de mamífero terrestre com a distribuição mais ampla do planeta (Lowe *et al.*, 2000; Barrios-García e Ballari, 2012). Há uma vasta literatura documentando as consequências negativas das invasões dos suídeos asselvajados, tanto ecológicas – como competição por recurso alimentar, alteração de microhabitats e predação da fauna – quanto sócio-econômicas – como a destruição de culturas agrícolas, danos à infra-estrutura, acidentes de trânsito, destruição de sítios arqueológicos, degradação da terra e predação de bezerros e cordeiros (Challies, 1975; Hone, 1980; Campbell e Rudge, 1984; Tisdell, 1984; Lacki e Lancia, 1986; O'brien, 1987; Kotaten, 1995; Choquenot *et al.*, 1997; Mayer *et al.*, 2000; Zivin *et al.*, 2000; Drake, 2001; Hone, 2002; Roemer *et al.*, 2002; Sicuro e Oliveira, 2002; Herrero e De Luco, 2003; Cushman *et al.*, 2004; Engeman *et al.*, 2004; Geisser e Reyer, 2004; Ickes *et al.*, 2005; Desbiez *et al.*, 2009; Oliveira-Santos *et al.*, 2011; Barrios-García e Ballari, 2012; Hegel e Marini, 2013; Barrios-García *et al.*, 2014; Mendina Filho *et al.*, 2015; Pedrosa *et al.*, 2015; Graitson *et al.*, 2018; Rosa *et al.*, 2018). Suídeos asselvajados são onívoros e fuçadores do solo, duas das principais características associadas aos impactos ecológico e sócio-econômicos que lhes são atribuídos (Barrios-García e Ballari, 2012). Outra característica que age de maneira sinérgica com as anteriores é o fato de não possuírem glândulas sudoríparas e por isso dependem da proximidade com corpos d'água para manter o equilíbrio térmico favorável em ambientes quentes, impactando ambientes brejosos e úmidos (Barrett, 1978; Baber e Coblenz, 1986; Ilse e Hellgren, 1995a; Dexter, 1998; Choquenot e Ruscoe, 2003; Luskin *et al.*, 2017; Cordeiro *et al.*, 2018). Além disso, esses animais também são considerados reservatórios de doenças infecciosas de importância econômica e para saúde humana (zoonoses), como por exemplo – e apenas citando algumas – brucelose, tuberculose, toxoplasmose e peste suína clássica (Pech e Hone, 1988; Pech e Mcilroy, 1990; Hahn *et al.*, 1997; Doran, 2005; Herrera *et al.*, 2005; Corner, 2006; Hampton *et al.*, 2006; Ruiz-Fons *et al.*, 2007; Herrera *et al.*, 2008; Ruiz-

Fons, 2017; Trevisol *et al.*, 2017; Silva *et al.*, 2017 ; Boklund *et al.*, 2018; Maciel *et al.*, 2018). Por estas razões, o controle populacional dos suídeos asselvajados se faz necessário e é recomendado em todos os lugares do mundo afetados pela invasão desses animais (Hone, 1983; Coblenz e Baber, 1987; O'brien, 1987; Saunders e Bryant, 1988; Hone e Stone, 1989; Mcilroy e Saillard, 1989; Anderson e Stone, 1993; Choquenot *et al.*, 1996; Finlayson *et al.*, 1997; Eason *et al.*, 1999; Zivin *et al.*, 2000; Cruz *et al.*, 2005; Hone, 2006; Massei *et al.*, 2011; Ditchkoff *et al.*, 2012; Bengsen *et al.*, 2014; Boklund *et al.*, 2018).



Figura 3. Suídeo asselvajado se alimentando de frutos de jatobá *Hymenaea courbaril*, em Rio Claro-SP, Brasil.

Nem por isso pesquisas em história natural e ecologia desses animais se tornam menos relevantes. Pelo contrário, ainda há muito que entender sobre os efeitos desses animais sobre os ambientes naturais e antrópicos Neotropicais. Nos capítulos que se seguem, eu procuro desvendar alguns dos aspectos relacionados às interações ecológicas dos suídeos asselvajados no Brasil, mais especificamente frugivoria e dispersão de sementes e ecologia trófica, assim como discutir o manejo da espécie no contexto brasileiro. Todos os capítulos foram escritos em formato de artigo e possuem portanto *introduções* próprias que aprofundam e servem de extensão aos assuntos introduzidos nesta seção. Preferi, portanto, abordar nesta introdução assuntos que, pelo formato exigido nas revistas, não puderam receber o

devido espaço no contexto dos artigos, mas que não poderiam ser ignorados e acredito receberam a devida atenção aqui. Ainda na linha do formato que se buscou construir essa tese, todos os capítulos contaram com a colaboração de outros pesquisadores e colegas, conforme informado na página inicial dos capítulos (1,2,3,5 e 6) ou nos agradecimentos (capítulo 4).

Visto a imensa similaridade no nicho ecológico que esses animais têm com algumas espécies da fauna nativa, realizei experimentos de campo e laboratório e usei algumas ferramentas de análise disponíveis para, à luz do conhecimento atual, aprofundar uma investigação nesse sentido. Debrucei-me também sobre o tema do controle populacional dos suídeos asselvajados, traçando um perfil dos controladores brasileiros e dos métodos empregados por eles hoje no Brasil. Portanto, o que se segue ao longo dessa tese foi norteado por uma questão geral: qual papel desempenha uma espécie exótica em ambientes altamente biodiversos e ao mesmo tempo antropizados como os encontrados no Brasil e como nós brasileiros estamos lidando com ela?

CAPÍTULO 1*

Current distribution of invasive wild[†] pigs in Brazil: economic impacts and ecological uncertainty

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[†] Eu mudei o termo “feral”, originalmente usado na publicação, por “wild”, no título e em todo o texto, pois notei posteriormente que teria sido mais apropriado

Introduction of species beyond their natural geographic distribution is a major concern for both human well-being and health ecosystems. One of those species is the wild pig *Sus scrofa*. Wild pigs figure amongst the harmful alien invasive species (Lowe *et al.*, 2000), because of its impacts on natural and agricultural ecosystems. It has the wider distribution among all terrestrial mammals in the world, and its effects on ecosystem functioning have been broadly recognized (Barrios-García e Ballari, 2012). A set of traits such as plasticity in feeding behavior (Ballari e Barrios-García, 2014) and high reproductive rates (Dzieciółowski *et al.*, 1992), are associated to the ability of wild pigs to thrive wherever they are introduced.

In Brazil, wild pigs first invaded Pantanal ecosystems. They are locally known as “porco-monteiro”, a breed of domestic pig that escaped into the wild more than 200 years ago (Desbiez *et al.*, 2011). The second wave of invasion of wild pigs in Brazil took place in 1989, coming from Uruguay, when wild boars invaded the south part of Rio Grande do Sul, south of Brazil (Deberdt e Scherer, 2007). The third wave differs from the two others by context and magnitude. Wild boars were imported in the 1990’s from Europe and Canada by swine farmers which trusted in a new commercial appeal, sold to them as “the blue blood in the pigpen”, referring to the suppose royalty origin of the species as being a meat of a higher quality (Fig 1, GloboRural, 1994; 1996). The commercial promises proved unprofitable. Trying to save the business, many farmers bred wild boars with domestic pigs, intending a fattest pig. In fact, the breed resulted a half-bred *S. scrofa*, bigger than and skittish as pure wild boars, known as “javaporco”. By the end of the same decade, the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) suspended the importation and stopped to concede operating permits to established “exotic” swine farmers (IBAMA, 1998b; a). What followed was a widespread intentional (in some cases unintentional) release of half-bred wild pigs (and pure wild boars), in discontinued locations, inaugurating a continental scale invasion (Fig. 2).

We encouraged a broad network of people attentive to the issue of wild pigs in Brazil to participate in the effort to gather information on the location of incidence of these animals (aquitemjavali.com.br). This effort took place from May to December 2014. Legalized wild pig hunters accounted for the majority of the gathered records. They felt comfortable in sharing information, because since 2013 a new rule from IBAMA (IN 03/2013) allow for the persecution and slaughter of wild pigs aiming at

controlling their population size. It was surprising to note that there are many wild pig hunters in activity and aware that the impacts caused by these animals may get out of control. To avoid misleading information from the collaborative network, the only valid information considered was from reports accompanied by pictures from slaughtered or sighted animals.



Figure 1. The wild boar and wild pigs were the cover of 'Globo Rural' magazine in two editions in the mid-1990's (*Globo Rural*, 1994; 1996), a national circulation magazine of around 100,000 copies, with a strong impact and call for agricultural production in the country. This figure is not found in the original publication of the article.

Along with that, we collected data together with São Paulo State Environment Secretariat (SMA). The SMA of São Paulo implemented the Work Group in Exotic Species, which efforts resulted in an up to date publication about alien species invasion in the state (SMA, 2013). We also checked processes from IBAMA sent to SMA in the year of 2014, from citizens of São Paulo requesting authorization to control wild pig in third land, and these processes provided new records to us. The media also contributed, since the news about crop damage and other troubles associated to wild pig activity became recurrent, thereby we also accounted the publicized places.

We found that wild pigs are present in 472 Brazilian municipalities, in four of the five political regions of the country, presenting a pattern of regionally isolated populations (Fig 1 and supplementary information). The most affected region is the southeast (253 municipalities), followed by south (133), midwest (75) and northeast region (9). São Paulo is the most affected state (156 municipalities) followed by Minas Gerais (91) and Rio Grande do Sul (55) (see supplementary material). Our records represent an increase of five times on the number of locations invaded since Deberdt e Scherer (2007; 91 municipalities). We are watching an unforeseen invasion (Trovati e Munerato, 2013; Kaizer *et al.*, 2014).

It is well recognized that wild pigs might cause several economic losses, whether damaging crop fields and attacking livestock or causing indirect losses associated to the budget involved in control programs (Pimentel *et al.*, 2005; Deberdt e Scherer, 2007). An important agro-industry from São Paulo reported us its losses: 340 ha of maize crop in a year, equivalent to 2.84 thousand tons of grains or around R\$1.25 million (\$430.000 dollars). The most reported ecological impacts of wild pig invasions are related with its rooting and wallowing behavior, which may reduce the cover and diversity of plant species (Hone, 2002), affect soil properties (Barrios-García *et al.*, 2014) and also assist the spread of diseases to wildlife (Pejchar e Mooney, 2009). Wild pigs also contributes to the spread of invasive plants (Dovrat *et al.*, 2012).

In fact, the federal plan to control wild pig populations, the IN 03/2013, was edited primarily to protect macro-economic interests. The Brazilian swine business earns 1.5 billion dollars annually from international markets (ABPA, 2014), and the invasion of wild pigs put that market at risk. The World Organization for Animal Health (OIE) modified the rules and procedures to certify the country members as classical swine fever (CSF) free zones (OIE, 2013). Before 2015, CSF was an auto declared disease and the Brazilian Ministry of Agriculture (MAPA) recognized most of the country as CSF free zone (MAPA IN 52/2013), but now it needs an official recognition from OIE, otherwise Brazilian swine products cannot be exported. The national recognition of CSF free zones emerged from MAPA through the Swine Health National Program (MAPA, 2012), and since 2012 the Brazilian Corporation for Agricultural Research (EMBRAPA) implemented the epidemiological surveillance in wild pigs (EMBRAPA, 2012), attending to an official request from MAPA. Including EMBRAPA expertise in the CSF question is strategic to assure international recognition and keep

the market. Therefore, the main motivation to promote and authorize control of wild pigs in Brazil is to prevent a rupture in both ongoing and future commercial relations with international markets.

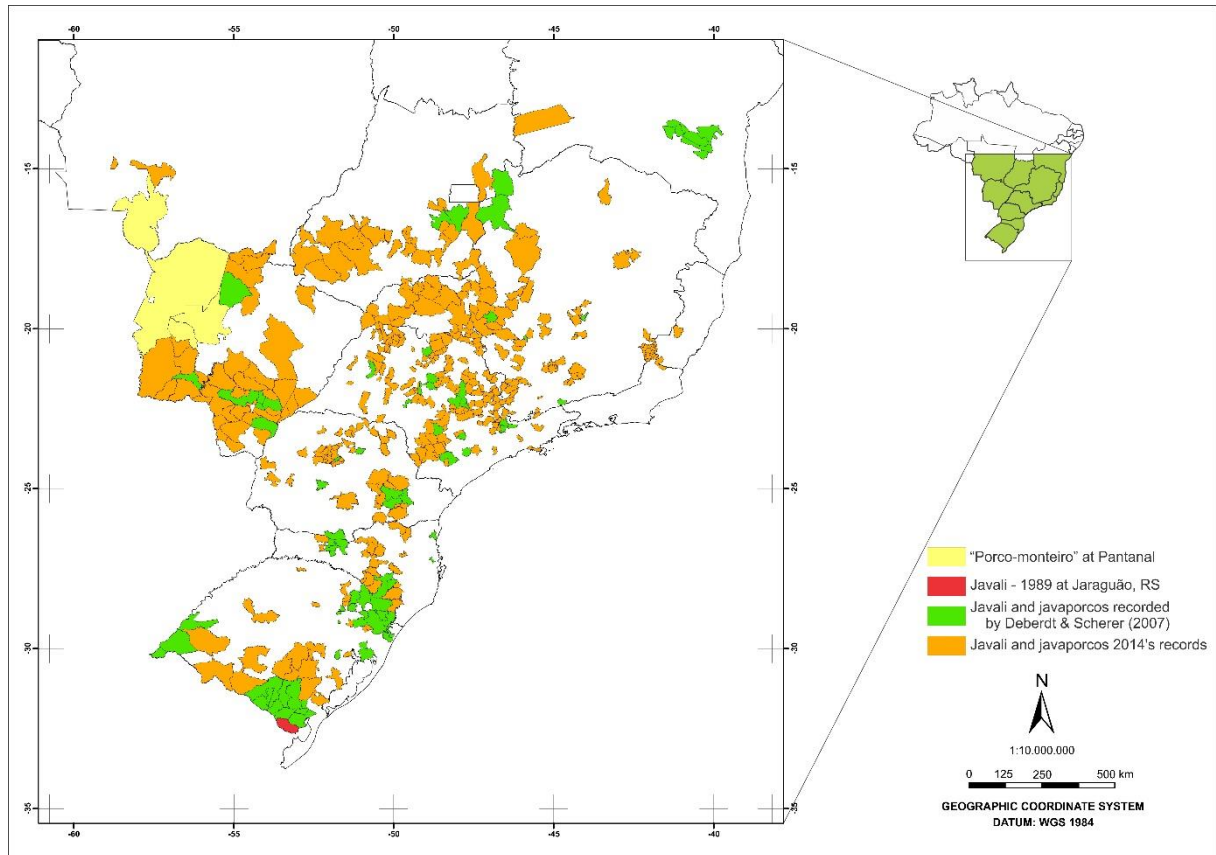


Figure 2. Distribution of wild pig populations and its varieties in Brazil. It first invaded Pantanal ecosystem; they are locally known as "porco-monteiro" a breed of domestic pigs escaped to the wild 200 years ago (yellow). Wild boars appear in Jaguarão-RS in 1989 (red), coming from Uruguay. The records from 2007 (green) are from Deberdt e Scherer (2007) and indicate all wild swine forms. The present work gathered records in the year of 2014 (orange). For complete list of the municipalities, see supplementary material.

There is a perception that the harmful effects of wild pigs are associated to high densities in both native and introduced ranges (Ickes, 2001; Hone, 2002), suggesting a threshold of pig densities above which they become noxious. Does this threshold really exist? If so, how to measure it? Below which threshold will wild pig become harmless to economic interests and to biodiversity and ecosystem services? Is the economic and ecological threshold similar? Given the speed of invasion throughout new ranges presented here, we believe that control or eradication programs are necessary, despite being difficult to implement. Most of eradication success programs come from islands (Cruz *et al.*, 2005; Parkes *et al.*, 2010 and references therein), and

continental programs fail to eradicate due to the high capacity that wild pigs have to recover and learn to avoid persecution (Morrison *et al.*, 2007).

Finally, the IN 03/2013 relies on the action of hunters to stop the advance of wild pigs in Brazil. This leads to an awkward situation: on the one hand wild pigs may be acting as a shield to other mammals, since they are favorite species of locals for food ingestion (Desbiez *et al.*, 2011), but there is also an evident concern about the increase in wildlife persecution, because most Brazilian ecosystems are highly defaunated due to illegal hunting (Peres e Palacios, 2007; Galetti *et al.*, 2009). Even if in near future a new rule determines the prohibition of wild pig control, hunters may keep doing it, as they have been doing before the legalization. What becomes evident is the need for a regulation on the hunting activity, as it will be a critical part in management of wild pig and other invasive species in near future. For instance, the hare *Lepus europaeus*, another invasive species (Auricchio e Olmos, 1999) are affecting the economy of small vegetable producers and cannot be legally controlled. The Brazilian Law 5197/1967, historically assumed by the epithet “Fauna Protection Law”, in fact does not prohibit hunting activity. The law 5197/1967 is also known as “Hunting Code” and is a bottleneck in biodiversity conservation policy, by neglecting to understand technically and scientifically the ecological and economic aspects of the potential game species present in Brazil.

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Supplementary Information

List of municipalities affected by wild pig populations in the year 2014, by alphabetical order by state.

BA	Barra da Estiva, Boa Nova, Contendas do Sincorá, Correntina, Ituaçu, Jequié, Manoel Vitorino, Mirante, Poções
ES	Afonso Claudio, Dores do Rio Preto, São José do Calçado
GO	Abadiania, Alexania, Cachoeira Dourada, Caiapônia, Caldas Novas, Catalão, Cristalina, Cromínia, Edeia, Formosa, Guapo, Ivolandia, Jandaia, Jataí, Luziania, Maripotaba, Mineiros, Montividiu, Morrinhos, Orizona, Paraúna, Pires do Rio, Pontalina, Rio Verde, Serranópolis, Silvania, Varjão, Vianópolis
MG	Água Comprida, Alterosa, Alto Caparaó, Araxá, Bom Despacho, Bom Sucesso, Botelhos, Brasilândia de Minas, Brumadinho, Buritit, Caiana, Caldas, Campestre, Campina Verde, Canápolis, Caparaó, Capelinha, Capim Branco, Capinópolis, Capitólio, Carangola, Carmo do Paranaíba, Carmo do Rio Claro, Carneirinho, Centralina, Conceição das Pedras, Conquista, Coromandel, Divino, Doresópolis, Esmeraldas, Espera Feliz, Estrela do Sul, Faria Lemos, Fortunas de Minas, Ibiá, Iguatama, Ijaci, Indianópolis, Itamarandiba, Itamonte, Ituiutaba, Iturama, Jacutinga, Janaúba, Jequitibá, João Pinheiro, Lavras, Limeira do Oeste, Machado, Madre de Deus de Minas, Manhuaçu, Manhumirim, Minduri, Monte Alegre de Minas, Monte Carmelo, Munhoz, Nepomuceno, Orizânia, Ouro Fino, Passos, Patrocínio, Pedra Dourada, Pedro Leopoldo, Perdizes, Perdões, Piedade do Rio Grande, Piranguçu, Piumhi, Poços de Caldas, Prata, Ribeirão Vermelho, Rio Manso, Rio Paranaíba, Sacramento, Santa Juliana, Santa Rita de Caldas, Santo Antonio do Monte, São Francisco de Sales, São Joao Del Rei, São Roque de Minas, São Vicente de Minas, Serrania, Sete Lagoas, Tapira, Tiros, Tombos, Tupaciguara, Uberaba, Uberlândia, Unaí, Varjão de Minas
MS	Amambaí, Anaurilândia, Angélica, Antonio João, Aquidauana, Aral Moreira, Bataypora, Bela Vista, Bodoquena, Bonito, Caarapó, Caracol, Chapadão do Sul, Coronel Sapucaia, Corumbá, Coxim, Deodópolis, Douradina, Dourados, Fátima do Sul, Glória de Dourados, Guia Lopes da Laguna, Itapora, Itaquiraí, Ivinhema, Jardim, Jateí, Juti, Laguna Carapa, Maracaju, Miranda, Navirai, Nova Alvorada do Sul, Nova Andradina, Novo Horizonte do Sul, Pedro Gomes, Ponta Porã, Porto Murtinho, Ribas do Rio Pardo, Rio Brilhante, Rio Verde de Mato Grosso, São Gabriel do Oeste, Sidrolândia, Sonora, Tacuru, Taquarussu
MT	Barra do Bugres, Cáceres
PR	Apucarana, Astorga, Balsa Nova, Barbosa Ferraz, Bom Sucesso, Cambé, Campo Largo, Campo Mourão, Carambei, Castro, Corbélia, Cornélio Procópio, Corumbataí do Sul, Engenheiro Beltrão, Fênix, Fernandes Pinheiro, Godoy Moreira, Guarapuava, Ibaiti, Ipiranga, Itambé, Jandaia do Sul, Jardim Alegre, Jundiá do Sul, Lapa, Lidianópolis, Lunardelli, Marilândia do Sul, Nova Esperança, Palmas, Palmeira, Palmital, Palotina, Peabiru, Ponta Grossa, Porto Amazonas, Quinta do Sol, Ribeirão do Pinhal, Rolândia, Santo Antonio da Platina, São Joao do Ivaí, São Mateus do Sul, São Pedro do Ivaí, Sertaneja, Sertanópolis, Tamarana, Teixeira Soares, Terra Roxa, Tibagi, Toledo, Tuneiras do Oeste
RJ	Bom Jesus do Itabapoana, Porciuncula, Varre Sai
RS	Aceguá, Alegrete, André da Rocha, Arroio dos Ratos, Arroio Grande, Bagé, Barra do Quaraí, Bom Jesus, Caçapava do Sul, Cachoeira do Sul, Camaquã, Cambará do Sul, Candiota, Canela, Canguçu, Caxias do Sul, Cerrito, Dom Pedrito, Encruzilhada do Sul, Fagundes Varela, Farroupilha, Gramado, Gravataí, Guaíba, Herval, Hulha Negra, Ibirapuita, Ipê, Itaqui, Itati, Jaguarão, Jaquirana, Lagoa Vermelha, Maquiné, Muitos Capões, Nova Prata, Pedras Altas, Pedro Osório, Pelotas, Pinheiro Machado, Piratini, Rio Pardo, Santa Tereza, Santana da Boa Vista, Santana do Livramento, São Francisco de Paula, São Gabriel, São José dos Ausentes, São Miguel das Missões, Terra de Areia, Trindade do Sul, Tupancireta, Uruguaiana, Vacária, Viamão
SC	Abelardo Luz, Água Doce, Araquari, Calmon, Campo Belo do Sul, Canelinha, Capão Alto, Cerro Negro, Curitibaanos, Faxinal dos Guedes, Fraiburgo, Irani, Lages, Lebon Regis, Mafra, Otacílio Costa, Pained, Passos Maia, Ponte Serrada, Presidente Getúlio, Rio Negrinho, Santa Cecilia, São Cristovão do Sul, São Joaquim, São Jose do Cerrito, Timbó Grande, Urupema
SP	Aguai, Alto Alegre, Alvares Florence, Americana, Américo de Campos, Amparo, Angatuba, Araçatuba, Araraquara, Araras, Atibaia, Avaí, Avaré, Balbinos, Barretos, Bauru, Birigui, Botucatu, Braganca Paulista, Brotas, Buri, Buritizal, Cafelândia, Cajobi, Campina do Monte Alegre, Campinas, Campos do Jordão, Candido Mota, Capão Bonito, Cardoso, Catanduva, Cesário Lange, Charqueada, Clementina, Colina, Colômbia, Conchal, Cosmorama, Cravinhos, Cristais Paulistas, Descalvado, Dobrada, Elisiário, Embaúba, Embu Guaçu, Espírito Santo do Pinhal, Estrela do Oeste, Fernandópolis, Flora Rica, Floreal, Franca, Gália, General Salgado, Getulina, Guaira, Guaraçaí, Guarani do Oeste, Guararapes, Guararema, Ibaté, Ibirá, Ibitinga, Igarapava, Ipeúna, Ipirá, Iracemópolis, Irapuã, Itaberá, Itai, Itapeçerica da Serra, Itapeva, Itapira, Itápolis, Itararé, Itatiba, Itatinga, Itirapina, Ituverava, Jaborandi, Jaboticabal, Jardinópolis, Jarinu, Jundiá, Limeira, Luís Antonio, Magda, Matão, Meridiano, Miguelópolis, Mineiros do Tiete, Mira Estrela, Mocóca, Mogi Guaçu, Monte Azul Paulista, Monte Mor, Morungaba, Nova Europa, Olímpia, Oscar Bressane, Ouroeste, Paraíso, Paranapanema, Paranaçu, Pardinho, Parisi, Patrocínio Paulista, Pederneiras, Pedranópolis, Pedregulho, Penápolis, Piedade, Pilar do Sul, Pinhalzinho, Piracaia, Piracicaba, Pirajuí, Pirassununga, Pitangueiras, Pompéia, Pontes Gestal, Populina, Quadra, Rancharia, Reginópolis, Ribeirão Corrente, Ribeirão Grande, Rio Claro, Santa Cruz das Palmeiras, Santa Maria da Serra, Santa Rita do Passa Quatro, Santo Antonio do Aracanguá, Santo Antonio de Posse, São Carlos, São Joao da Boa Vista, São Jose do Rio Pardo, São Manuel, São Pedro, São Sebastiao, São Simao, Severínia, Socorro, Tabapuã, Tabatinga, Taquaritinga, Taquaritiba, Taquarivaí, Tatuí, Taubaté, Torrinhã, Tuiuti, Turmalina, Urânia, Valentim Gentil, Vargem Grande do Sul, Viradouro, Votuporanga

CAPÍTULO 2

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

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Abstract

Animal-dispersed plants are increasingly reliant on limited seed dispersal effectiveness 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 5186 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 terms of the quantity of seeds removed and gut retention time was 70 ± 23 h, indicating that they 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 were defecated intact, for which we observed a positive or neutral effect on germination relative to manually de-pulped seeds. Finally, deposition of seeds were four times more frequent in unsuitable than suitable sites for seedling recruitment and establishment. Thus, 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.

Key words: Alien species, Anthropocene, Atlantic Forest, feral pig, fragmentation, frugivory, ecosystem services, *Sus scrofa*

INTRODUCTION

Many animal-dispersed plants are strongly dependent upon large-bodied ground-foraging frugivores to disperse their seeds (Campos-Arceiz e Blake, 2011; O'Farrill *et al.*, 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 *et al.*, 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 e Peres, 2013) and carbon sequestration (Bello *et al.*, 2015; Peres *et al.*, 2016) even before frugivore populations go extinct (McConkey e O'farrill, 2016). Moreover, dispersal limitation hinders seed-mediated gene flow (Giombini *et al.*, 2017), affecting the evolutionary dynamics of the dispersed plants (Galetti *et al.*, 2013).

Defaunation processes, the loss of large-bodied vertebrates due to anthropogenic causes (mainly 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 *et al.*, 2018). Some of these smaller-bodied species are effective in connecting plant populations between isolated habitat fragments (Corvidae birds and carnivores Canidae and Mustelidae; González-Varo *et al.*, 2013; Pesendorfer *et al.*, 2016), 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 *et al.*, 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 *et al.* 2010, Schupp *et al.* 2017). For extant frugivores in such landscape contexts, their effectiveness as seed-dispersal agents is affected by internal and external factors (Nathan *et al.*, 2008a ; Schupp *et al.*, 2010), such as gape size and gut retention time (Traveset e 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 permeability of the surrounding matrix to move among isolated patches (Delciellos *et al.*, 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 e 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 e Fragoso, 2003). Movement limitation may also exert constraints to seed dispersal in fragmented landscapes, because daily range scales with body mass (Carbone *et al.*, 2005), and although certain groups of mammalian frugivores may not have limited 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 *et al.*, 2018).

Although defaunation is ubiquitous in the tropics (Dirzo *et al.* 2014), a large-bodied invasive mammal, the wild pig *Sus scrofa*, is expanding its distribution throughout fragmented Neotropical forests (Rosa *et al.*, 2017). Wild pigs are omnivores and fruits are a permanent component of their diets in its native and introduced ranges (Fedriani e Delibes, 2009; Ballari e Barrios-García, 2014). The negative effects of invasive wild pigs to agriculture and ecosystems are largely documented (Barrios-García e Ballari, 2012). Even though they facilitate the spread of invasive plant species (Lynes e Campbell, 2000; Dovrat *et al.*, 2012) they could potentially serve as a surrogate for replacing lost seed-dispersal services of native zoochorous plants (Donatti *et al.*, 2007; O'Connor e Kelly, 2012). However, to determine the role of this invasive species as a seed disperser in defaunated and fragmented landscapes a thorough analysis of their interaction patterns, interaction frequencies, seed viability and characteristics of the seed shadows they produce is required. Given the large body size of wild pigs, which can weight an average of 89 ± 31 kg as adults (F Pedrosa, unpublished data), and resilience of populations to overharvest (Bieber e 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 modelling to conduct an in-depth characterization of the role of invasive 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; Schupp *et al.*, 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.

METHODS

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 *et al.*, 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 1441 m (Ribeiro *et al.*, 2009). In this biome, up to 89% of woody plant species rely on frugivores to disperse their propagules (Almeida-Neto *et al.*, 2008). Seed dispersal and gene flow of these zoochorous plants is potentially constrained due to the widespread extirpation of large frugivorous vertebrates (Bogoni *et al.*, 2018). Alien plants are also present within or surrounding natural areas of Atlantic Forest (Zenni e Ziller, 2011) and may increase their invasion as a result of interaction with seed dispersers.

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, Fig 1) 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 5 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 48h. 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 65x 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.

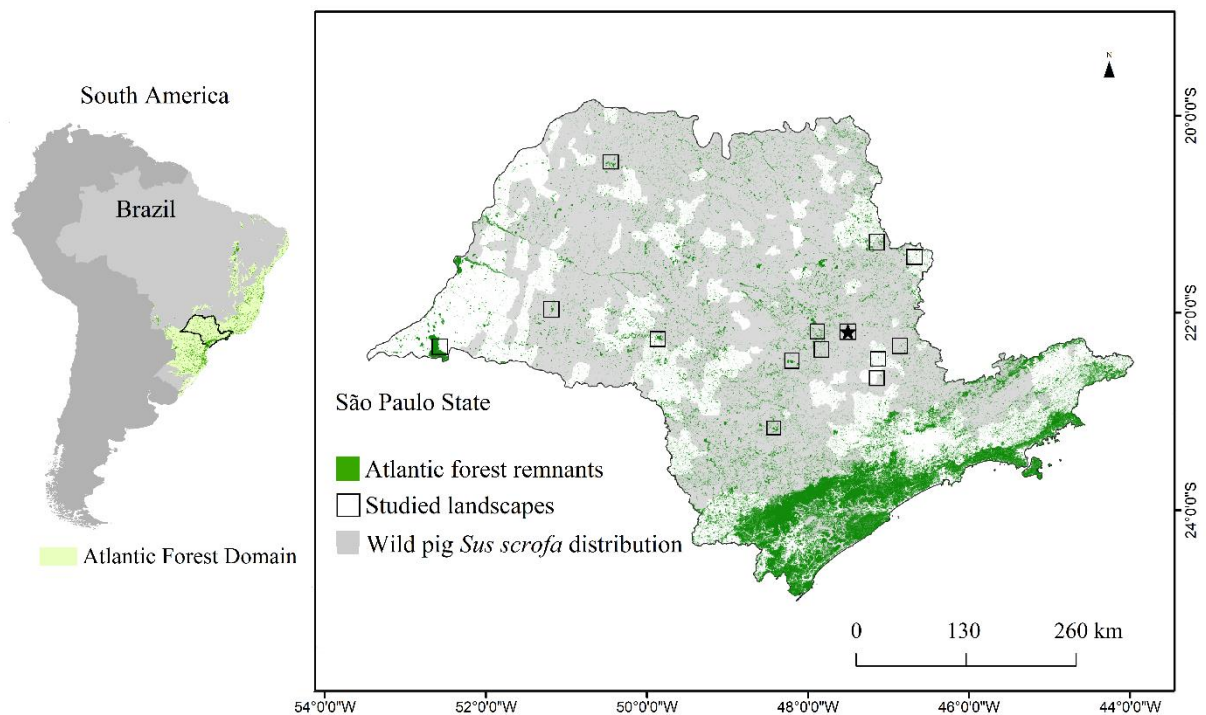


Figure 1. Study area. South America depicting Atlantic Forest domain and São Paulo state in Brazil. Study sites (solid squares) where we conducted the experiments on quantitative seed dispersal effectiveness (SDE) with large-fruited plant species (*Syagrus romanzoffiana*, *Guazuma ulmifolia* and *Hymenaea courbaril*). Stomachs and scats came from the Rio Claro region (solid square filled with black star). Dark green indicates Atlantic forest remnants, and the light grey indicates wild pig *Sus scrofa* distribution in São Paulo state (updated from Pedrosa *et al.* 2015).

We also collected scats opportunistically within forest fragments during 19 field surveys between February 2014 and August 2015 and then systematically from one to three days every month from April 2017 to March 2018 within both forest fragments and plantations, in 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.

were identified with the help of botanical specialists.

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 (Fig 1) 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 e Eaton 2008). *H. 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 fruit, each plant producing hundreds of fruits 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. *H. courbaril* and *G. ulmifolia* present a peculiar smell 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 to 80 ripe fruits of one plant species placed in front of one camera trap (Bushnell NatureView HD Essential®) positioned 1.5 to 2 m away from the fruits and approximately 45 cm from the ground. We set the cameras to operate in video mode (15 seconds length, 1 second delay between videos), which allowed us 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 *et al.* 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 more than one video, 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): (1) scatterhoarders, (2) primarily seed predators, (3) frugivores that may not swallow large seeds and (4) frugivores that may swallow both large and small seeds.

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: (1) the quality of seed deposition sites and (2) 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 forested patches of 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), 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). *S. 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 and Ziller 2011). See SI Table S1 for a summary of fruit and seed traits.

We offered 627 fruits of *S. romanzoffiana* (accounting for 627 seeds, collected from 7 different individuals), 107 fruits of *H. courbaril* (accounting for 321 seeds, from 2 different individuals), 10 fruits of *G. ulmifolia* (750 seeds, from 2 different individuals), 4 fruits of *G. americana* (684 seeds, from 2 individuals), 15 fruits of *J. spinosa* (735 seeds, from 1 individual), 23 fruits of *A. aculeata* (23 seeds from 2 different individuals), 12 fruits of *A. phalerata* (12 seeds from 1 individual), 60 fruits of *E. edulis* (60 seeds from 3 individuals), 9 fruits of *S. oleracea* (9 seeds of 2 individuals), 30 fruits of *S. cumini* (30 seeds from 1 individual), 80 fruits of *I. laurina* (unknown number of seeds from 1 individual), 200 seeds of *L. leucocephala* (from 5 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 SI Table S1 for a summary on fruit and seed traits). The two animals, a male and a female, were isolated from each other in 3x3m sheltered bays, food was offered once a day and water was available *ad libitum*. Ripe and undamaged fruits of a given plant species were offered 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. If intact fruits and seeds remained untouched in the bay after 1 hour, they were retrieved to avoid confusion with seeds from pig stool or seeds that were spat

out. Spat out seeds were recovered immediately after observing this behavior. During the following 7 days, pig stool was collected twice daily, kept in a 50L bucket and checked for intact seeds by washing it over a mesh of 4×4mm.

Intact seeds found in the pig stool (or spat out) were set to germinate in a greenhouse with irrigation twice daily and natural light and temperature variation. The seeds set to germinate at the greenhouse were observed daily and considered as germinated when at least 2mm 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. We assessed minimum days of seed dormancy (T_0 , the time lapse until first seed germinate), mean days of seed dormancy (MdD, the mean time elapsed until germination of all seeds) and seed germinability (the final proportion of seeds germinated after 180 days) (Reid e Armesto 2011). We used the Mann-Whitney U-test to test for differences among treatments (Reid e 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.

KERNELS OF SEED DISPERSAL DISTANCES – To quantify the potential for wild pigs and extant frugivores 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 *et al.*, 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 *et al.* 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 *et al.*, 2008b) as events of seed deposition greater than 1441 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 mean 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 fruit-feeding trials). We modeled seed retention time as a gamma distribution with the same mean and variance obtained from the empirical retention times. 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 retention time with body mass (Pires *et al.* 2018).

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 *et al.*, 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 combine 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.

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 ¹		Frequency % (n)	
	Stomachs	Scats	Stomachs	Scats	Stomachs	Scats
Zoochoric syndrome	10671	4657	11	8	36.9 (41)	62.2 (51)
Natives	6618	430	9	5	18.9 (21)	41.4 (34)
Aliens	529	30	1	2	4.5 (5)	8.5 (7)
Unknown	3524	4197	1	1	19.8 (22)	28 (23)
Non-zoochoric syndrome²	37	20	2	1	2.7 (3)	7.3 (6)
Poaceae	4142	297	7*	1*	18 (20)	46.3 (38)
Unknown	4379	509	13	15	24.3 (27)	57.3 (47)
Total	15087	5186	26	24	55.9 (62)	90.2 (74)
Natives	6618	430	9	5	19.9 (22)	41.4 (34)
Aliens	566	50	3	3	7.2% (8)	35.4 (29)

¹See Supplementary Information Tables S2 and S3 for taxonomic information of plant species. ²All non-zoochoric are alien species. *Morphospecies.

RESULTS

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 (9 natives, 1 alien and 1 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 only once in just one stomach but accounted for 1/3 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 5186 seeds. From those, at least 89.8% (4,657 seeds) were from zoochoric plants of eight different plant species (5 natives, 2 aliens and 1 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, 4197 seeds) *S. romanzoffiana* (Arecaceae, native species, 401 seeds), and Poaceae (unknown origin, 297 seeds) 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 (Fig. 2 and see SI Table S2 and S3 for taxonomic and trait information of plant species found in stomachs and scats);

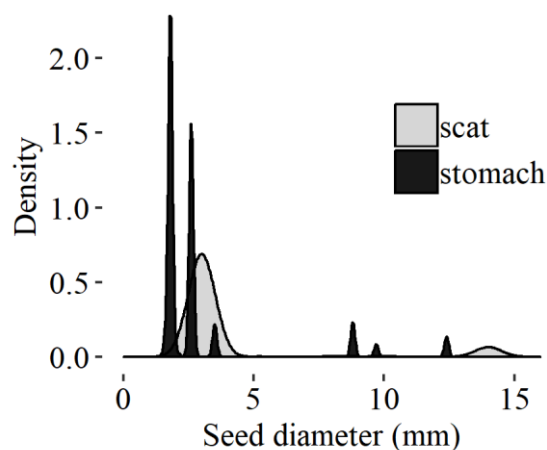


Figure 2 Probability density distribution of the size of all intact seeds of zoochoric plant species found in stomach and scats (see SI Tables S2 and S3 for details).

SEED DISPERSAL EFFECTIVENESS: THE QUANTITATIVE COMPONENT – We recorded 21 frugivorous species interacting with fruits in the 14 studied sites (17

mammal species, three bird species and one lizard, SI Fig. S1). 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 the white-lipped peccary (*Tayassu pecari*, seed predator), agoutis (*Dasyprocta azarae*, scatter-hoarder), wild pigs (which swallow both small and large seeds) and opossums (*Dideplhis aurita* and *D. albiventris*, may swallow only small seeds and thief pulp from large-seeded fruits; Fig. 3, SI Table S4). Tapirs (*T. terrestris*) were detected on cameras at 3 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 $\tau = 0.23$, $P = 0.16$).

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 4 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. (SI Fig. S2). 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 neither were spat out intact. We found a positive relationship between seed size and proportion of seed survival (linear regression: $R^2 = 0.46$, $p=0.008$, Fig 4).

Germination of *G. americana* occurred only for seeds that received gut passage treatment, with maximum germination of 63.5% of defecated seeds (Fig. 5). 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 $W=189$ $P=0.1193$, $W=664$ $P=0.459$ and $W=8.5$ $P=1$, respectively. Table 2), but handling and gut passage enhanced the speed of germination relative to

manually defleshed seeds, in terms of both T_0 and MdD (Wilcoxon signed rank test $W=240$ $P<0.001$, $W=468$ $P<0.001$ and $W=16$ $P=0.029$ for *J. spinosa*, *G. ulmifolia* and *H. courbaril* respectively. Results were identical for both response variables). Seeds of *A. aculeata*, *A. phalerata*, *S. oleracea*, *S. romanzoffiana* and *Cordia* sp. did not germinate in either the defecated or control treatments.

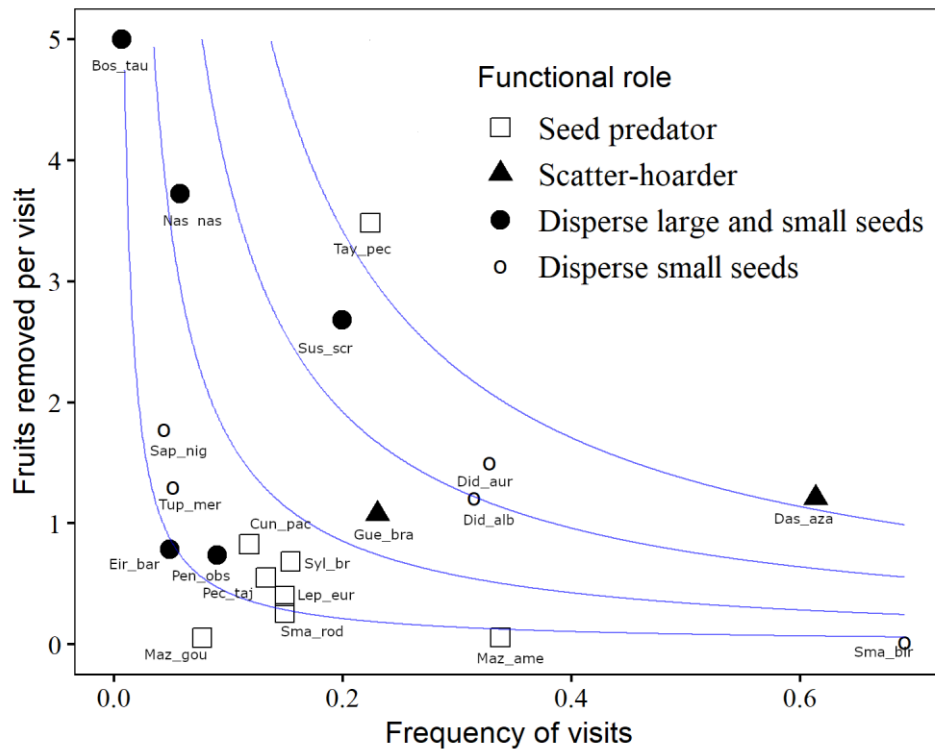


Figure 3. Overall quantitative component of seed dispersal effectiveness (SDE) of frugivore species to large-fruited plants *Syagrus romanzoffiana*, *Hymenaea courbaril* and *Guazuma ulmifolia* in the fragmented Atlantic Forest. Quantity component (QC) scores are the product of the subcomponents frequency 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 *D. albiventris* (Did alb), capuchin monkey *Sapajus nigritus* (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), grey brocket deer *Mazama gouazoubira* (Maz gou), red brocket deer *M. americana* (Maz ame), paca *Cuniculus paca* (Cun pac), small rodents (Sma rod, Echimidæ), 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 Supporting Information Table S4 for a complete QC score, rate of fruit removal of all species and references that based the classification of the frugivores' role.

Germination of seeds from scats found in the field were successful for 11 species but failed for another 13 (see SI Table S3). Among the identified plant species,

Syzigium cumini (alien) and *Psidium* spp. had the 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%). *S. romanzoffiana* seeds, the second most common plant found in the scats, had only 1% germination rate (4 of 401).

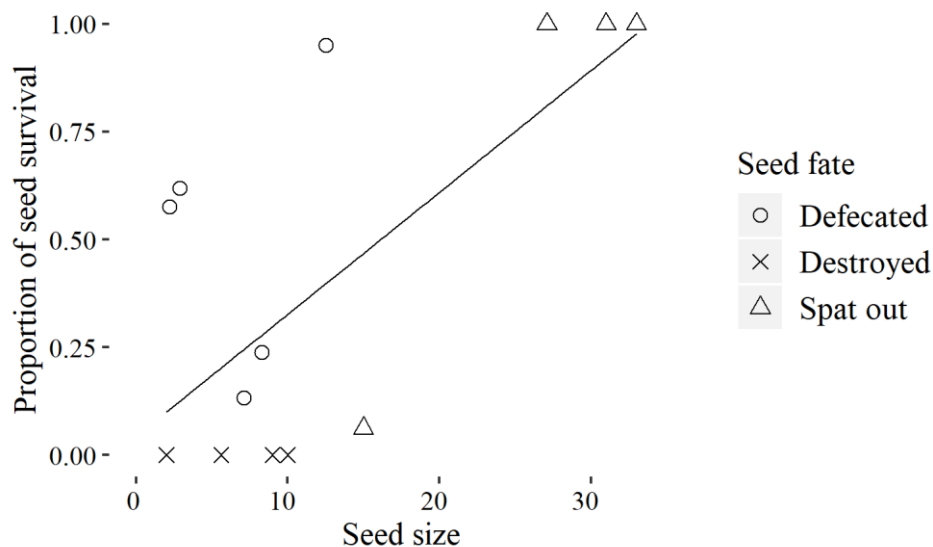


Figure 4. Proportion of seeds that survived (remained intact either after defecation or spat out) or were destroyed after fruit handling and gut passage by wild pigs *Sus scrofa* in captivity, as a function of seed size. The black line depicts the linear regression of this relationship ($R^2 = 0.48$, $p = 0.008$).

KERNELS OF SEED DISPERSAL DISTANCES – Wild pigs in captivity ingested and swallowed 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 h. (SI Fig. S3). No seeds were observed in the scats for any of the plant species in the first 24h for and the maximum length of time we observed seeds in the scats was 168 h 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 1367 m (upper 95th percentile) with a median of 605 m under a Brownian movement model and 3454 m (upper 95th percentile) with a median of 1194 m under a Levy walk movement model (Fig. 6) considering 100 simulations.

Among the other 20 frugivore species recorded removing fruits, 10 of them can swallow the seeds and deposit them intact (see SI Table S4, Belo *et al.* 2017). Most of these species have similar body sizes weighting between 1-5 kg (coatis *Nasua nasua*,

white-eared opossum *D. albiventris*, black-eared opossum *D. aurita*, tayra *Eira barbara* and capuchin monkey *Sapajus nigritus*, see SI Table S4). We thus used the seed dispersal model to generate seed-dispersal kernels considering an average body mass of 5kg, an upper bound for these small to medium-sized mammal species. Simulations for these frugivores 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 (Fig. 6).

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 1447 m (upper 95th percentile) with a median of 615 m and 3465 m (upper 95th percentile) with a median of 1168 when considering Levy walk model (Fig. 6).

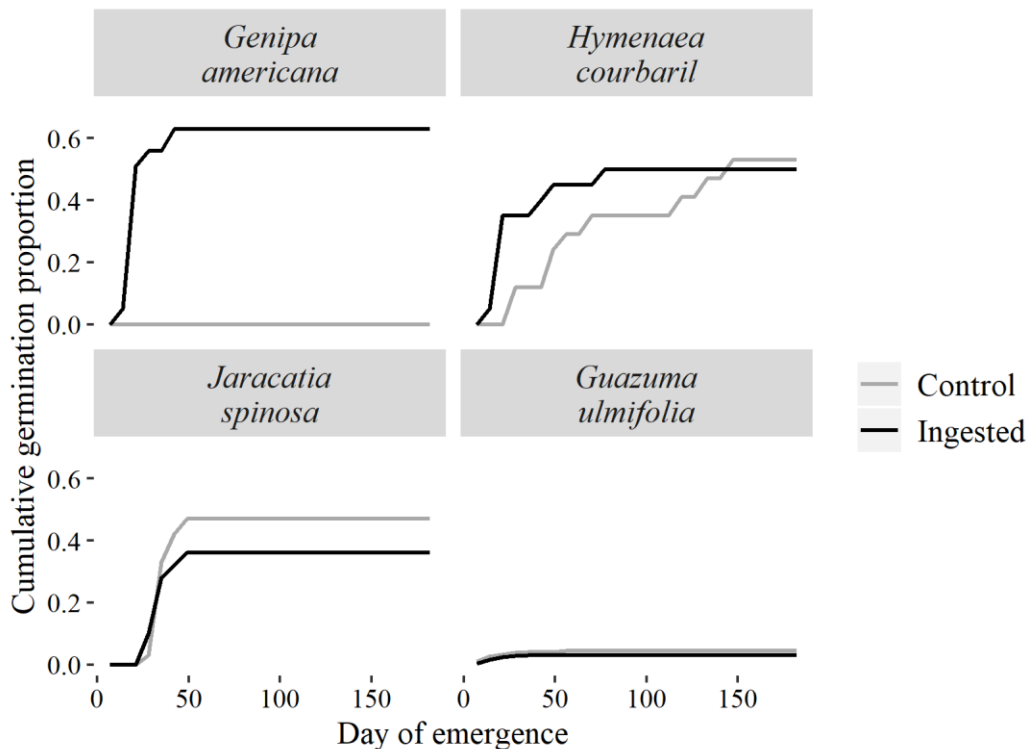


Figure 5. Germination of seeds. Cumulative proportion of germinated seeds through time for four plant species. Control seeds (manually defleshed seeds, grey line) were compared to ingested seeds (dark line) by wild pigs *Sus scrofa* in captivity. Ingested seeds were either defecated (*Genipa americana*, *Jaracatia spinosa* and *Guazuma ulmifolia*) or spat out (*Hymenaea courbaril*).

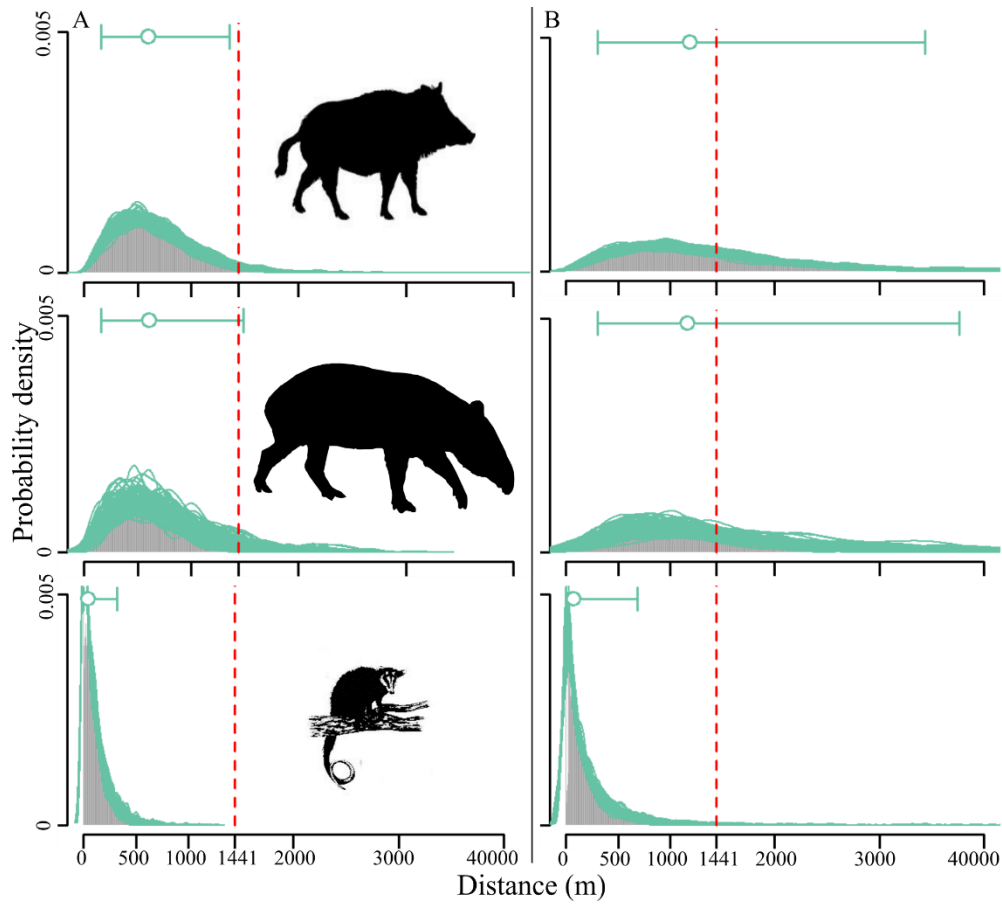


Figure 6. Kernel of seed dispersal distances simulating Brownian (A) and Levy (B) walk models for wild pigs (upper), tapirs (middle) and for other mammalian frugivores with maximum body weight of 5kg (lower). We depict the median distances (empty green circle) and the range (determined by the 5th and 95th percentiles, solid green line) in which 90% of seeds were estimated to drop. We highlighted 1441 meters (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).

DISCUSSION

Our data indicate that wild pigs can provide effective seed dispersal services in terms of the quantity of seeds dispersed. However, the quality of this service varies depending on the plant species. Although seed removal rate was high, our data show that plant species with 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 *et al.* 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 later. One of the differences among both 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 e Verdú 2002). Wild pigs defecated viable seeds and although we did not compared germination with the whole fruit – which simulate lack of dispersal – germinability was improved by gut passage for *G. americana* and speed up germination for three other plants tested. 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 *et al.* 2015).

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 1441 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, 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 *et al.* 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-Garcia 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. 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 e 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 invasive species restoring lost ecological interactions, such as seed dispersal, and functioning as surrogates of extinct or extirpated biota is not new (Gawel *et al.*, 2018; Lundgren *et al.*, 2018). For example, frugivorous alien birds in New Zealand may be rescuing native zoochoric flora from population collapse due to extinction of native bird species (García *et al.*, 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 e 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 bovids do not compensate for either the quantity nor the quality of the services provided by elephants (Sekar *et al.*, 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 overlaps with ~ 56% of the remaining distribution of the forest fragments in the Atlantic forest of São Paulo state (Pedrosa et al 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 (Lynes e Campbell, 2000; Dovrat *et al.*, 2012), driving changes in the structure of the ecosystem (Barrios-Garcia e Ballari 2012). 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 e Ziller 2011). In addition, invasive wild pigs have one of the highest reproductive rates among ungulates (Bieber e 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 offset by a negative role at latter recruitment stages (Ickes *et al.*, 2005). Furthermore, wild pigs host important zoonotic and livestock pathogens (Galetti *et al.*, 2016; Ruiz-Fons, 2017; Trevisol *et al.*, 2017) and are responsible for crop destruction causing negative socioeconomic impacts where their populations grow unchecked (Barrios-García e Ballari, 2012). Therefore, management plan of invasive 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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Ethics statement

All applicable institutional and national guidelines for the care and use of animals were followed, with permission given by IBAMA (authorization #46150) and the Scientific Animal-Ethic Committee from UNESP-Rio Claro (protocol #9396).

Supplementary Information

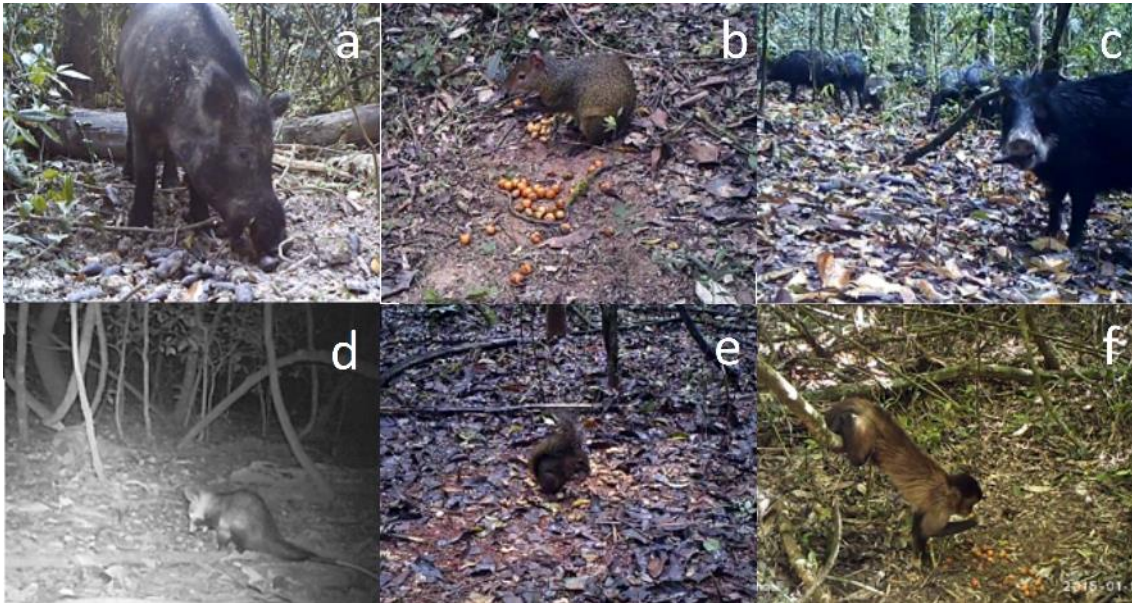


Figure S1. Still images from camera traps of six frugivore species recorded removing fruits within forest remnants of the fragmented Atlantic forest. (a) An adult male of the wild pig *Sus scrofa* feeding upon fruits of *Hymenaea courbaril* (the large pods on the ground in front of the animal), (b) Agouti *Dasyprocta azarae* gnawing a fruit of *Syagrus romanzoffiana*, (c), white-lipped peccary (*Tayassu pecari*) feeding upon fruits of *H. courbaril*, (d) white-eared opossum *Didelphis albiventris* chewing a fruit of *S. romanzoffiana*, (e) Ingram's squirrel *Guerlinguetus brasiliensis* gnawing a fruit of *S. romanzoffiana* and (f) capuchin monkey *Sapajus nigritus* picking up a fruit of *S. romanzoffiana*.

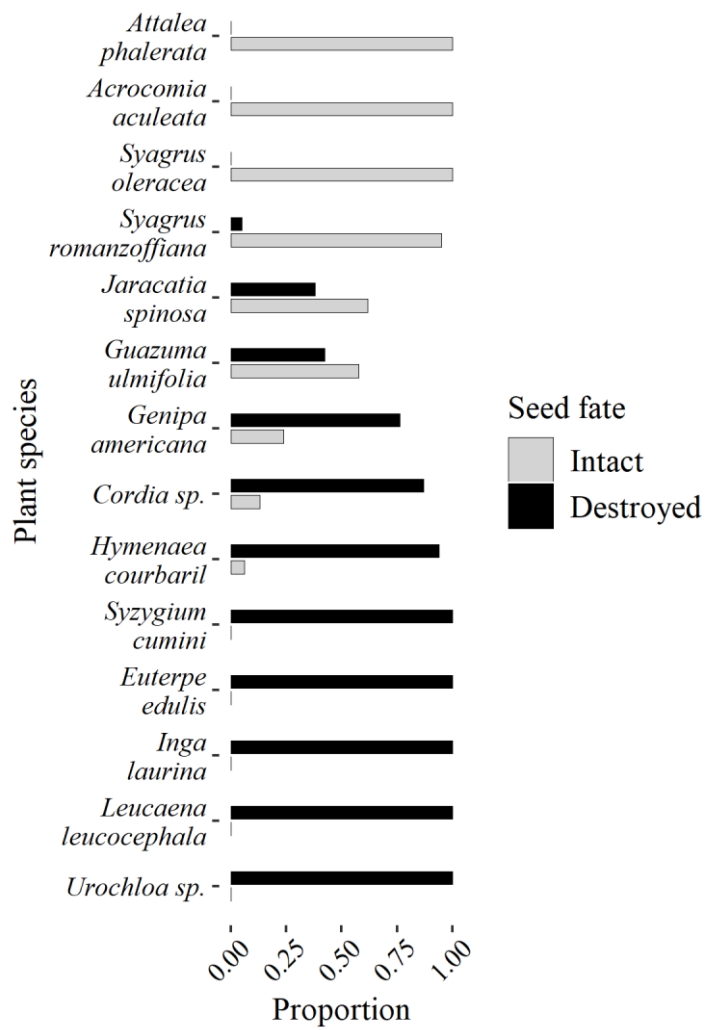


Figure S2. Proportion of seeds that remained intact or were destroyed for each plant species after fruit and seed handling and gut passage by wild pigs *Sus scrofa* in captivity. Seeds of plant species that survived were either spat out (*A. phalerata*, *A. aculeata*, *S. oleracea* and *H. courbaril*) or defecated intact (*S. romanzoffiana*, *J. spinosa*, *G. ulmifolia*, *G. americana* and *Cordia sp.*).

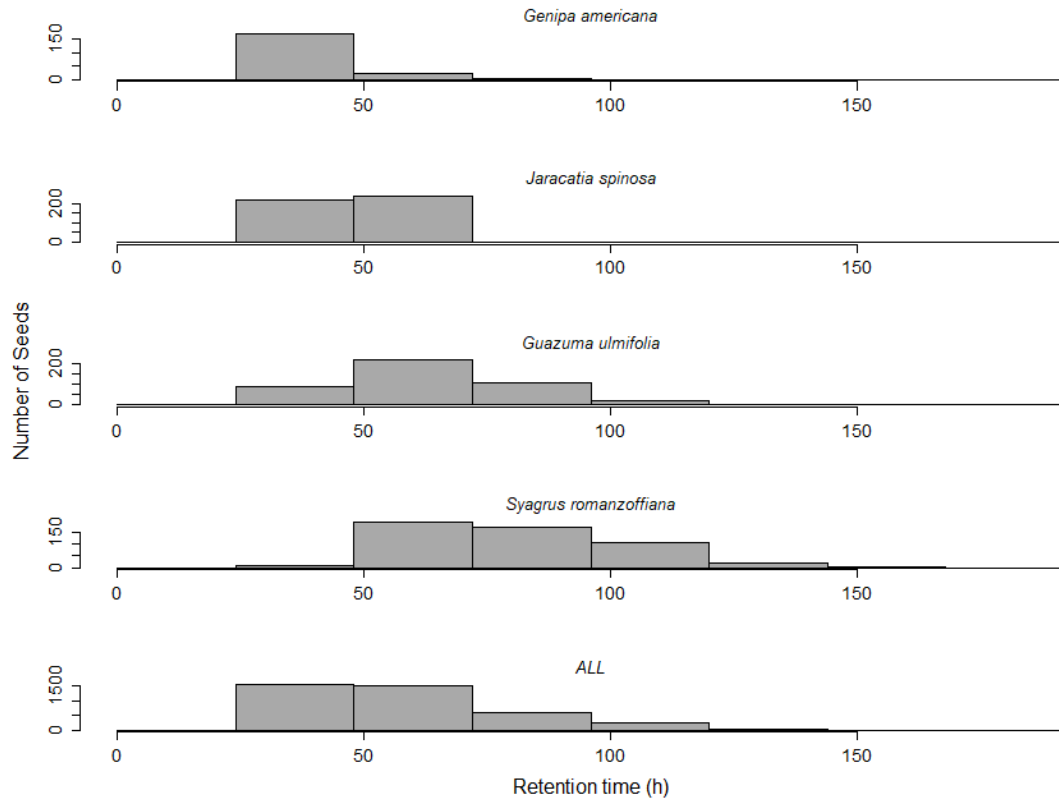


Figure S3. Gut retention time of seeds of four plants species for wild pigs *Sus scrofa*, ordered by the shorter (top) to longer (bottom) retention time – ALL means the mean retention time of all plant species. Fruits were offered to captive animals at once and pig stool was checked for intact seeds every 24 h for 7 consecutive days.

Table S1. Seed and fruit trait of plant species employed in the experiments that assessed the quantitative component of Seed Dispersal Effectiveness (qSDE) and the effect of seed handling and gut passage on seed survival and germination (GUT). Fruit traits and seed diameter were estimated by measuring the collected fruits and seeds employed in the experiments of this study, except *Inga laurina*, for which we refer to Farah *et al.*, 2017. Values of traits are in mm.

Plant family	Plant species	Dispersal syndrome	Fruit traits (n of fruits measured)			Seed diameter (n of seeds measured)	Experiment employed
			Fruit length	Fruit diameter	Number of seeds per fruit		
	<i>Acrocomia aculeata</i>	Zoochoric	37.3 ±1.9 (n = 35)	39.4 ±2.6 (n = 35)	1	26.9 ±1.6 (n = 29)	GUT
	<i>Attalea phalerata</i>	Zoochoric	65.7 ±2.5 (n = 41)	36 ±2.3 (n = 41)	1	31	GUT
Arecaceae	<i>Euterpe edulis</i>	Zoochoric	-	-	1	10	GUT
	<i>Syagrus oleracea</i>	Zoochoric	49.4 ±2.3 (n = 8)	37.9 ±3.9 (n = 8)	1	33	GUT
	<i>Syagrus romanzoffiana</i>	Zoochoric	-	18.6 ±1.6 (n = 20)	1	12.6 ±1.2 (n = 20)	qSDE, GUT
Boraginaceae	<i>Cordia</i> sp.	Zoochoric	12.6 ±0.8 (n = 15)	12 ±1 (n = 15)	1	7.1 ±0.8 (n = 10)	GUT
Caricaceae	<i>Jaracatia spinosa</i>	Zoochoric	55.8 ±4.3 (n = 17)	32.3 ±3.2 (n = 17)	49 ±12 (n = 3)	2.9 ±0.1 (n = 10)	GUT
	<i>Hymenaea courbaril</i>	Zoochoric	101.7 ±14.3 (n = 32)	41 ±3.7 (n = 32)	3 ±2 (n = 32)	15 ±1.7 (n = 74)	qSDE, GUT
Fabaceae	<i>Inga laurina</i>	Zoochoric	130	22	-	10	GUT
	<i>Leucaena leucocephala</i>	Autochoric	-	-	-	5.6	GUT
Malvaceae	<i>Guazuma ulmifolia</i>	Zoochoric	24 ±2.1 (n = 68)	26.2 ±2.7 (n = 68)	75 ±17 (n = 18)	2.2 ±0.2 (n = 30)	qSDE, GUT
Myrtaceae	<i>Syzygium cumini</i>	Zoochoric	-	-	1	9	GUT
Poaceae	<i>Urochloa</i> spp.	Autochoric	-	-	-	2	GUT
Rubiaceae	<i>Genipa americana</i>	Zoochoric	85.2 ±4.8 (n = 8)	67.9 ±4.9 (n = 8)	171 ±14 (n = 3)	8.3 ±0.6 (n = 10)	GUT

Table S2. Plant species, number of intact seeds, frequency (and number of stomachs), dispersal syndrome, origin and mean seed diameter of the intact seeds found in 111 stomachs of wild pigs.

Plant family	Plant species	Dispersal Syndrome	Origin	Number of intact seeds	Frequency % (n)	Mean seed diameter (mm)
Myrtaceae	<i>Psidium</i> sp.	Zoochoric	Unknown	3524	19.8 (22)	2.6
	<i>Syzygium cumini</i>	Zoochoric	Exotic	529	4.5 (5)	8.8
	<i>Psidium rufum</i>	Zoochoric	Native	510	1.8 (2)	3.5
Arecaceae	<i>Syagrus romanzoffiana</i>	Zoochoric	Native	319	9 (10)	12.4
Cannabaceae	<i>Celtis iguanaea</i>	Zoochoric	Native	198	5.4 (6)	9.66
Solanaceae	<i>Solanum americanum</i>	Zoochoric	Native	5300	1.8 (2)	1.77
	<i>Solanum mauritanum</i>	Zoochoric	Native	210	1.8 (2)	1.64
Malvaceae	<i>Guazuma ulmifolia</i>	Zoochoric	Native	60	0.9 (1)	2.14
Malpighiaceae	<i>Byrsonima sericea</i>	Zoochoric	Native	15	0.9 (1)	5.16
Rubiaceae	<i>Genipa americana</i>	Zoochoric	Native	4	0.9 (1)	4.72
Sapotaceae	<i>Chrysophyllum</i> sp.	Zoochoric	Native	2	0.9 (1)	6.37
Fabaceae	<i>Leucaena leucocephala</i>	Autochoric	Exotic	36	2.7 (3)	5.65
	<i>Acacia</i> sp.	Autochoric	Exotic	1	0.9 (1)	NE*
Poaceae	morfo sp 1	Unknown	Unknown	1020	6.3 (7)	NE
	morfo sp 5	Unknown	Unknown	200	4.5 (5)	NE
	morfo sp 6	Unknown	Unknown	250	3.6 (4)	NE
	morfo sp 2	Unknown	Unknown	580	2.7 (3)	NE
	morfo sp 4	Unknown	Unknown	320	2.7 (3)	NE
	morfo sp 7	Unknown	Unknown	1762	0.9 (1)	NE
	morfo sp 3	Unknown	Unknown	10	0.9 (1)	NE
Unknown	ni5	Unknown	Unknown	116	2.7 (3)	0.71
	ni8	Unknown	Unknown	40	0.9 (1)	1.17
	ni11	Unknown	Unknown	40	0.9 (1)	0.5
	ni4	Unknown	Unknown	30	0.9 (1)	4.33
	ni10	Unknown	Unknown	10	0.9 (1)	0.9
	ni7	Unknown	Unknown	1	0.9 (1)	3.22

*NE: Not evaluated

Table S3. Plant species, number of intact seeds, frequency (and number of scats), dispersal syndrome, origin, rate of germination and mean seed diameter of the intact seeds found in 82 scats of wild pigs.

Plant family	Plant species	Dispersal Syndrome	Origin	Intact seeds	Freq. % (n)	% of germination	Mean seed diameter (mm)
Myrtaceae	<i>Psidium</i> sp.	Zoochoric	Unknown	4197	28 (23)	75.7	3
	<i>Syzygium cumini</i>	Zoochoric	Exotic	26	4.9 (4)	80.8	10
Arecaceae	<i>Syagrus romanzoffiana</i>	Zoochoric	Native	401	32.9 (27)	1	14
Cannabaceae	<i>Celtis iguanaea</i>	Zoochoric	Native	12	3.7 (3)	33.3	8.6
Solanaceae	<i>Solanum</i> sp.1	Zoochoric	Native	10	4.9 (4)	-	1
	<i>Solanum</i> sp.2	Zoochoric	Native	3	1.2 (1)	-	1
Urticaceae	<i>Cecropia pachystachya</i>	Zoochoric	Native	4	1.2 (1)	75	1.8
Rutaceae	<i>Citrus</i> sp.	Zoochoric	Exotic	4	3.7 (3)	-	5
Fabaceae	<i>Leucena leucocephala</i>	Autochoric	Exotic	20	7.3 (6)	35	5.5
Poaceae	Sp1	unknown	unknown	297	46.3 (38)	2	2
Unknown	Sp2	unknown	unknown	1	1.2 (1)	-	3
	Sp5	unknown	unknown	9	2.4 (2)	33.3	2
	Sp6	unknown	unknown	4	1.2 (1)	-	2
	Sp7	unknown	unknown	109	11 (9)	-	3
	Sp9	unknown	unknown	10	6.1 (5)	-	1
	Sp10	unknown	unknown	26	12.2 (10)	-	1.5
	Sp11	unknown	unknown	27	3.7 (3)	-	1.5
	Sp12	unknown	unknown	16	1.2 (1)	43.7	2
	Sp13	unknown	unknown	1	1.2 (1)	-	2
	Sp15	unknown	unknown	4	3.7 (3)	25	1
	Sp16	unknown	unknown	2	2.4 (2)	-	1.8
	Sp17	unknown	unknown	1	1.2 (1)	100	1
	Sp18	unknown	unknown	1	1.2 (1)	-	1.5
	Sp19	unknown	unknown	1	1.2 (1)	-	1

Table S4. Frugivores recorded removing large fruits in the Atlantic forest remnants. Rate of removal was calculated as the sum of fruits removed by each frugivore species divided by total number of fruits removed in all stations by all frugivores. Quantitative component score (QC-score) is the multiplication of the two quantity subcomponents of seed dispersal effectiveness (Frequency of Visits *Fruits Removed per Visit, Schupp et al 2017, see methods for details).

Class	Order	Family	Species	Role*	Body mass ¹ (g)	Rate of removal	QCscore
Mammalia	Didelphimorphia	Didelphidae	<i>Didelphis aurita</i>	Swallow small seeds	870	0.070	0.49
			<i>Didelphis albiventris</i>	Swallow small seeds	1300	0.117	0.38
	Rodentia	Dasyproctidae	<i>Dasyprocta azarae</i>	Scatter-hoarder	3200	0.370	0.74
		Sciuridae	<i>Guerlinguetus brasiliensis</i>	Seed predator	170	0.061	0.25
		Cuniculidae	<i>Cuniculus paca</i>	Seed predator	6100	0.026	0.10
		Echimyidae	Small rodents ²	Seed predator	50	0.012	0.04
	Artiodactyla	Tayassuidae	<i>Tayassu pecari</i>	Seed predator	34000	0.130	0.78
			<i>Pecari tajacu</i>	Seed predator	17000	0.014	0.07
		Suidae	<i>Sus scrofa</i>	Swallow large and small seeds	89000 ³	0.103	0.53
		Cervidae	<i>Mazama americana</i>	Seed predator	35000	0.001	0.02
			<i>Mazama gouazoubira</i>	Seed predator	16000	0.001	<0.01
	Bovidae	<i>Bos taurus</i>	Swallow large and small seeds	600000	0.001	0.03	
	Carnivora	Procyonidae	<i>Nasua nasua</i>	Swallow large and small seeds	4500	0.029	0.21
		Mustelidae	<i>Eira barbara</i>	Swallow large and small seeds	5000	0.006	0.04
	Primates	Cebidae	<i>Sapajus nigritus</i>	Swallow small seeds	2600	0.026	0.08
Lagomorpha	Leporidae	<i>Sylvilagus brasiliensis</i>	Seed predator	670	0.018	0.11	
		<i>Lepus europaeus</i>	Seed predator	3000	0.001	0.06	
Aves	Galliformes	Cracidae	<i>Penelope obscura</i>	Swallow large and small seeds	1700	0.009	0.07
	Passeriformes		Corvidae	<i>Cyanocorax</i> sp.	Swallow small seeds	170	0.002
	Coraciiformes	Momotidae	<i>Baryphthengus ruficapilus</i>	Swallow small seeds	140		
Reptilia	Squamata	Teiidea	<i>Tupinambis merianae</i>	Swallow small seeds	2000	0.004	0.07

*We based our classification of the role of species that 1) swallow small and large seeds on Bello *et al.* (2017) and references therein, 2) seed predators on Smythe (1986), Vieira and Monteiro-Filho (2003), Beck (2005), Dobust and Henry (2006), Keuroghlian and Eaton (2008) and Galetti *et al.* (2015b) and 3) scatter-hoarders on Hallwachs (1986), Pascoal and Galetti (1995) and Jansen *et al.* (2012).

¹Average body mass of adults. Source (Gonçalves *et al.*, 2018)

² Small rodents could not be identified at species level.

³ This work (n=71 adult wild pigs)

Cyanocorax sp. and *Baryphthengus ruficapilus* are referred as Small birds and both Rate of fruit removal and QC score were grouped together.

CAPÍTULO 3

Large scale agriculture is subsidizing the invasion of wild pigs in Brazil

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Contribuição dos autores: FP e MG conceberam e planejaram o estudo; FP e WB coletaram os dados; FP, WB e VEC realizaram as análises dos dados; FP e WB escreveram o artigo com contribuições significativas de TL e MG.

ABSTRACT

Understanding the mechanisms by which alien species become invasive is critical to assure successful control programs and mitigate their impacts. Invasive wild pigs *Sus scrofa* has been sharply expanding their distribution throughout all regions of Brazil in the last few years, becoming the most abundant terrestrial mammal in anthropogenic landscapes. Here we demonstrate that large monoculture plantations provide the primary resource subsidies to invasive wild pigs in Brazil. We analyzed 106 stomach contents and carbon stable isotopes ($\delta^{13}\text{C}$) of 50 hair samples of wild pigs from a population immersed in a landscape dominated by agriculture. Stomach contents were dominated by maize (40.6%), sugarcane (28.5%), vegetal matter (all other vegetation other than crops, 26.9%) and animal matter (vertebrates and invertebrates, 4%). Bayesian mixing model analysis of $\delta^{13}\text{C}$ showed that food sources from C₄ photosynthetic pathway (represented by maize and sugarcane) accounted for 93.8% of the long-term diet, while C₃ food sources for only 6.2%. A landscape composed of agricultural crops and forest fragments are subsidizing wild pigs and may thus fuel population growth. Given that Brazil is a major agricultural producer and a hotspot of biodiversity, it is concerning that extensive food sources may accelerate the expansion of this invasive species resulting in economic losses and cascading effects on natural habitats. To increase the efficiency of culling programs designed to reduce the abundance of wild pigs, managers should fine-tune culling strategies to plantation cycles and its specific environmental characteristics incentivizing the involvement of farmers, hunters and the community.

Key words: Alien species, Anthropocene, Atlantic forest, feral swine, wild boar

INTRODUCTION

The drivers of invasion success by alien vertebrate species have long been debated in ecology (Elton, 1958; Vázquez, 2005). Among mammals, the best predictors of invasiveness are a combination of propagule pressure, broad native climatic range, broad diet breadth, size and frequency of litters, human affiliation and status as a game species (Jeschke e Strayer, 2006; Capellini *et al.*, 2015). The invasive wild pig, *Sus scrofa*, is a paradigmatic case of a widespread invasive species exemplifying such traits (Bengsen *et al.*, 2014; Lewis *et al.*, 2017; Sales *et al.*, 2017; Tabak *et al.*, 2018). Wild pigs are among the most widespread and one of the most destructive invasive terrestrial mammals on earth (Lowe *et al.*, 2000; Ballari e Barrios-García, 2014), inflicting high costs in the form of habitat and crop destruction and the implementation of control measures to mitigate their impacts (Pimentel *et al.*, 2005).

The population increase of wild pigs is largely explained by their plasticity in acquiring food resources (Bieber e Ruf, 2005; Luskin *et al.*, 2017; Tabak *et al.*, 2018). When nutritional resources are plentiful, population growth is twice the rate than under poor conditions (Bieber e Ruf, 2005; Tabak *et al.*, 2018). If populations are overabundant (Ickes *et al.*, 2001) rooting and digging behavior affect soil properties (Barrios-García *et al.* 2014), jeopardize seedling establishment in forest ecosystems (Barrios-García e Ballari, 2012; Luskin *et al.*, 2017) and represent a major risk for several small-bodied vertebrate species via destruction of microhabitats or depletion of prey (Wilcox e Van Vuren, 2009; Graitson *et al.*, 2018). Therefore, understanding the key spatiotemporal pattern of trophic subsidies that support wild pig populations is important for planning cost-effective control measures (Ditchkoff *et al.*, 2012; Montecino-Latorre e San Martín, 2018).

Combining seasonal stomach contents and stable isotopes of carbon ($\delta^{13}\text{C}$) from hair samples is a very comprehensive way to identify the key nutritional resources of wild pigs (Kelly, 2000; Ben-David e Flaherty, 2012). Although stomachs provide a precise but “snapshot” information of individual’s recent diet, all tissues of an animal carry the isotopic composition of their food sources at the time of synthesis and $\delta^{13}\text{C}$ of keratinous tissue that remain inert after formation is particularly useful to distinguish between carbon fixed by terrestrial C_4 crops and C_3 natural forest (Deniro e Epstein, 1978; Cerling *et al.*, 1997) and reflect the diet of a longer time period (Phillips *et al.* 2014). While much emphasis is given to the role of propagule pressure and lack of

competitors, predators and natural enemies in determining successful biological invasions (Kennedy *et al.*, 2002; Simberloff *et al.*, 2013), here we investigate the degree to which an agricultural trophic-subsidy is promoting the invasion of wild pigs in anthropogenic modified landscapes in Brazil. Although the invasion of wild pigs in Brazil is not recent (Rosa *et al.*, 2017), it has been expanding dramatically all over the country in the last 25 years (Pedrosa *et al.*, 2015) and are becoming the most abundant terrestrial mammal in anthropogenic landscapes (Beca *et al.*, 2017).

MATERIAL AND METHODS

STUDY AREA – The study area is located in Rio Claro region, São Paulo, southeast of Brazil (22°30'S, 47°30'W, Fig 1), with mean annual temperature and precipitation of 20.3°C and 1290 mm respectively. The climate is Cwa according to Köppen and Geiger classification, with wet summers (October to March) and dry winters (April to September). The landscape is dominated by extensive biofuel plantations of sugarcane, annual crops (mainly maize), perennial crops (mainly orange and coffee) and remnants of natural vegetation formed by semideciduous forest (Martinelli e Filoso, 2008; Lapola *et al.*, 2014). In the studied region, the first records of wild pigs were in 2010 (M. Galetti, unpubl. data). Control measures to stop population expansion were implemented nationwide in 2013 (under IBAMA's IN03/2013) with hunting serving as the primary method of population control (Rosa *et al.*, 2018).

Using satellite images with 1m or less resolution available in the Basemap (ArcGIS 10.2) and Open Layer (QGIS 1.8.0) extensions, we built a map of land cover of our study area. We assign 4 classes of land cover: sugarcane (that include full grown, initial growth stage, and bare soil from a recent plantation), natural areas (forests and swamps not used by agriculture), crops other than sugarcane, and other land cover (cattle pastures, water bodies, highways and rural or urban or mining facilities). We then calculated the proportion of each land use category within the total mapped area (Fig 1).

Natural forested habitats in the tropics are predominantly constituted of plants that capture carbon via C₃ photosynthetic pathways while agricultural monocultures in Brazil contain a large proportion of grasses, such as sugarcane and maize, that operate under a C₄ photosynthetic pathway (Cerling *et al.* 1997). Plants that follow a C₃ photosynthetic pathway discriminate more strongly against the heavier ¹³C isotope of CO₂ molecules (Bender, 1971), which creates a unique carbon isotope signature of

C₃ plants, presenting $\delta^{13}\text{C}$ values that range from -18 to -34‰ (Cerling *et al.*, 1997). In contrast, the outcome of the C₄ photosynthetic pathway in plants creates heavier molecules of CO₂ relative to C₃ plants, and the carbon isotope signature of C₄ plants presents $\delta^{13}\text{C}$ values from -9‰ to -20‰ (Cerling *et al.* 1997). Therefore, $\delta^{13}\text{C}$ acts as a tracer to differentiate among food sources of two distinct habitats – C₄ crops and C₃ natural forested areas.

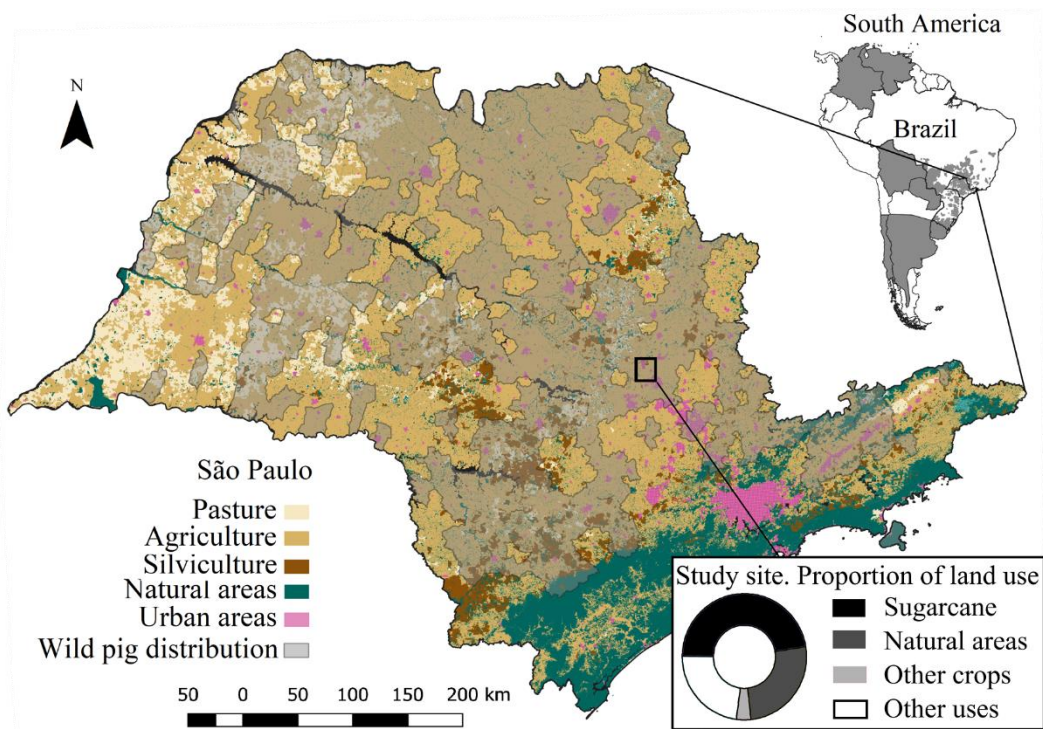


Figure 1. Location of the study area in São Paulo State-Brazil where 106 stomachs and 50 hair samples of invasive wild pigs *Sus scrofa* were collected to reconstruct the diet of the species. Land cover of São Paulo state was based on IBGE (<https://portaldemapas.ibge.gov.br/portal.php#mapa220605>) and the distribution of wild pigs in South America and Brazil is based on Pedrosa *et al.* (2015) and Barrios-García e Ballari (2012)

SAMPLE COLLECTION: STOMACHS – We took advantage of current control regulations to obtain stomachs of the animals from wild pig hunters. We collected 106 stomachs from wild pigs inhabiting our study area between September 2014 and February 2016. Following the method adapted from (Korschgen, 1987), each stomach was opened and the entire contents were removed and washed over 5 meshes of different sizes (5, 2, 1, 0.8 and 0.4 mm). The washed content was dried at 60°C for 48 h. Large and intact items recognized within the stomachs were separated. We homogenized and weighed the dry material of each stomach separately, then split (by weight) a subsample of 10% to be carefully examined with a 65x magnifying glass. We then extrapolated the

contents within the 10% subsample to the total stomach contents, assuming it was representative of total content. We identified the food items to the highest taxonomic level as possible. Later, we grouped food items in four distinct categories, sugarcane, maize, vegetal matter (fruits, seeds, leaves and roots other than crops) and animal matter (vertebrates and invertebrates).

SAMPLE COLLECTION: STABLE ISOTOPES – We collected and analyzed $\delta^{13}\text{C}$ of 50 hair samples from wild pigs, 46 of which were from individuals that provided the stomachs and 4 hair samples were collected inside a forest remnant within our study area on four different occasions during 2015. Each individual sample was composed of hairs (14 ± 12 hairs per sample) extracted directly from the fur (the case of the 46 individuals) or from trees used by wild pigs for scrubbing after mud baths (the case of the other 4 samples). We measured the length of each hair of each sample, which gave us an average of 5.31 ± 2.66 cm of hair length per sample. According to Hola *et al.* (2015), the rate of hair growth of wild pigs is 0.1 cm per day, suggesting that our samples integrate dietary information over 53 ± 26 days per hair. Asynchronous hair growth among the ~ 14 hairs per sample likely integrates dietary information over a longer time period.

We prepared the hair samples for analysis by first washing with distilled water to remove dust, followed by soaking each sample within a 2:1 solution of chloroform:methanol in 2ml individual plastic jars, shaking the jars for 30s using an electronic shaker. We repeated this procedure twice for each hair sample. We then rinsed the samples using distilled water and dried them at 55°C for 24 hours.

To categorize the isotopic composition of food sources, we sampled food items found inside the stomachs of the hunted animals. Given that wild pigs are omnivores, food items found in their stomachs are composed of several vegetal matter items (from crops and grasses to fruits and seeds) and different animal prey (vertebrates and invertebrates from multiple taxa). In order to lower the cost of analysis and guarantee each sample was heavy enough to be processed and analyzed, we pooled subsamples from a given category into one sample (Phillips *et al.*, 2005). These categories were: maize, sugarcane, invertebrate, vertebrate (feather, bone, fur), fruit pulp, seed, grass-leaf, and leaf (other than grass). We selected only intact food items from the stomachs (those that appeared unaltered by gastric juice), washed them thoroughly with distilled water, and then dried them at 55°C for 24h. We created

replicates of each category combining items from different stomachs to better characterize food sources both spatially and temporally (Phillips *et al.*, 2014).

DATA ANALYSIS: STOMACHS – For each category of food item we designated the following metrics: 1) frequency of occurrence (FO), which is the number of stomachs where a given category was found divided by total number of stomachs; 2) dry weight (DW), which is the dry weight of a given food category relative to the total dry weight of the stomach contents; and 3) index of relative importance (IRI) adapted from (Hyslop, 1980). IRI aims to estimate a degree of importance of each food category in the diet considering both the frequency of occurrence and the proportion in dry weight, and is determined by:

$$IRI = 100(FO_i DW_i) / \sum_{i=1}^n FO_i DW_i \quad (1)$$

where FO_i is the FO of food item i and DW_i is the DW of food item i . We also evaluated the seasonality of food consumption considering the mean DW of food items for each month.

DATA ANALYSIS: STABLE ISOTOPES – The stable isotope analysis was performed at Stable Isotopes Center – CIE in São Paulo State University, Botucatu facility. Both hair and resources were powdered using cryogenic grinder, model Spex Sample – Geno Grinder 2010 under -196 °C. Each one of the samples were individually packed in polycarbonate jars containing three stainless steel spheres. Both jars and steel spheres were previously cleaned with distilled water. The jars with the samples were then immersed in liquid nitrogen for 5 minutes and placed into the grinder. After powdered, the samples were weighted in tin capsules, employing a high sensitivity analytical scale (Mettler Toledo XP6). We determined the isotopic ratios using a continuous flux isotopic ratio mass spectrometer system (CF-IRMS, Thermo Scientific – Delta V Advantage Isotope Ratio MS) coupled to an elemental analyzer (Thermo Scientific – Flash 2000 Organic Elementar Analyzer). The IRMS determine the carbon isotopic ratio value ($^{13}\text{C}/^{12}\text{C}$) of the samples, which is converted to relative difference of isotope ratio ($\delta^{13}\text{C}$) in permil (‰), according to,

$$\delta^{13}\text{C} = \left(\frac{R_{sample}}{R_{std}} - 1 \right) \cdot 1000 \quad (2)$$

where R_{std} is the isotopic ratio of the international standard Vienna Peedee Belemnite (VPDB) and R_{sample} is the isotopic ratio of the sample.

ISOTOPE MIXING MODELS – We used a Bayesian stable isotope mixing model to estimate the contribution of food sources in the diet of wild pigs (Parnell *et al.*, 2013) using MixSIAR in R with a burn-in period of 25,000 and a chain length of 50,000 (Stock e Semmens, 2013; Stock *et al.*, 2018). One important aspect of mixing models that optimize the estimation of proportional contribution of sources (food) to a mixture (animal tissue) is that the n of sources should be $n+1$ number of tracers (Phillips *et al.*, 2014). Estimations of the proportion of several food items to the diet employing one isotope tracer ($\delta^{13}\text{C}$) will be largely imprecise. This aspect is especially critical for omnivorous diets as in the case of wild pigs that feed on several food sources. We thus grouped sources based on their functional similarities (Phillips *et al.*, 2005). We aggregated our sources into two distinct groups, C_3 and C_4 , based on the photosynthetic pathways of potential food sources. Therefore, we solved the statistical problem of too many sources in mixing models while offering a clear-cut estimation of two opposing sources to the diet, agriculture vs. natural forest areas.

S. scrofa is one of few species for which specific trophic discrimination factors (TDF) values have been experimentally established (Nardoto *et al.*, 2006; Hola *et al.*, 2015). Given that TDF values are largely determined by diet type (Caut *et al.*, 2008; Kurle *et al.*, 2014), we used $\delta^{13}\text{C}$ TDF values of 0.2‰, considering hair tissue reported in (Nardoto *et al.*, 2006).

RESULTS

STOMACHS – Agriculture food sources were the most important item in the diet of wild pigs according to stomach analysis (Table 1). Maize was the most important item in the diet (IRI = 40.6%), occurring in 33% of the stomachs, representing 61.7% of all dry weight found. The second most important item was sugarcane (IRI = 28.5%), present in 90.6% of the stomachs corresponding to 15.8% of the total dry weight. Vegetal matter (fruits, seeds, leaves and roots) was very similar to sugarcane in importance for wild pigs (IRI = 26.9%), present in 70% of the stomachs and corresponding to 19.1% total dry weight. Fruits represented 69% of total dry weight of vegetal matter and occurred in 50% of stomachs (Table1). Most of the fruit component was represented by seeds from both invasive (*Leucaena leucocephala*, *Syzygium cumini*, *Acacia* sp., *Urochloa* spp.) and native species (*Byrsonima sericea*, *Celtis iguanaea* *Genipa americana*, *Guazuma ulmifolia*, *Psidium rufum* *Solanum americanum*, *S. mauritanum*

and *Syagrus romanzoffiana*, Pedrosa et al in prep.). Animal matter had minor importance in the diet (IRI = 4%, Table 1), and although more frequently found than maize, its dry weight was low (3.3%). Among vertebrate items we found evidence of small rodent fur, bird leather, reptile skin and a paw from another wild pig. Among the invertebrates, Coleoptera and Chilopoda were the taxa most frequently found. A detailed description of the highest taxonomic level of animal items found in the stomachs is presented in the Supplementary material.

Table 1. Summary of the diet composition of wild pigs *Sus scrofa* based on stomach contents. Frequency of occurrence (FO), proportion of total dry weight (DW) and index of relative importance (IRI) are related to food items found in stomachs. Vegetal matter includes fruits (pulp and seeds), leaves and roots. Animal matter includes vertebrates and invertebrates

Item	FO (%)	DW (%)	IRI (%)
Maize	33.0	61.7	40.6
Sugarcane	90.6	15.8	28.5
Vegetal matter	70.8	19.1	26.9
<i>Fruits (pulp & seeds)</i>	<i>50.0</i>	<i>13.1</i>	<i>14.8</i>
<i>Leaves</i>	<i>44.3</i>	<i>3.5</i>	<i>3.5</i>
<i>Roots</i>	<i>3.7</i>	<i>2.5</i>	<i>0.2</i>
Animal matter	60.4	3.3	4.0
<i>Vertebrates</i>	<i>28.3</i>	<i>1.3</i>	<i>0.9</i>
<i>Invertebrates</i>	<i>48.1</i>	<i>2.0</i>	<i>2.2</i>

The consumption of food items varied seasonally (Fig 2). Maize was predominant during six months of the year, from February to April and from September to November. Sugarcane and animal matter were the only items consistently present throughout the year despite minor importance of the later. Sugarcane was most important in the months of May, July, August and December, while vegetal matter was the most important in the months of January and June (Fig 2).

ISOTOPES – The range in mean $\delta^{13}\text{C}$ values of C_3 and C_4 food sources were from -26.00‰ and -14.55‰, respectively (Table 2). Sugarcane and maize fell within the C_4 group, as expected, and both vegetal matter and animal matter had samples that represented C_3 and C_4 groups (Table 2). All fruit samples were within the C_3 group with mean $\delta^{13}\text{C}$ values of -27.71‰. Wild pig's hairs had carbon isotope signature of C_4 feeders (Fig 3). Reconstruction of diet employing mixing models indicated that C_4 food sources accounted for $93.8\% \pm 3.4$ (86.4 – 99.6 95% credible interval) of wild pig diets while C_3 food sources accounted for only $6.2\% \pm 3.4$ (0.4 – 13.6 95% CI). Our Markov

chain had good convergence properties. The Gelman and Rubin diagnostics showed very low deviance of the variances of the Markov chains (all variable <1.001), indicating proper convergence.

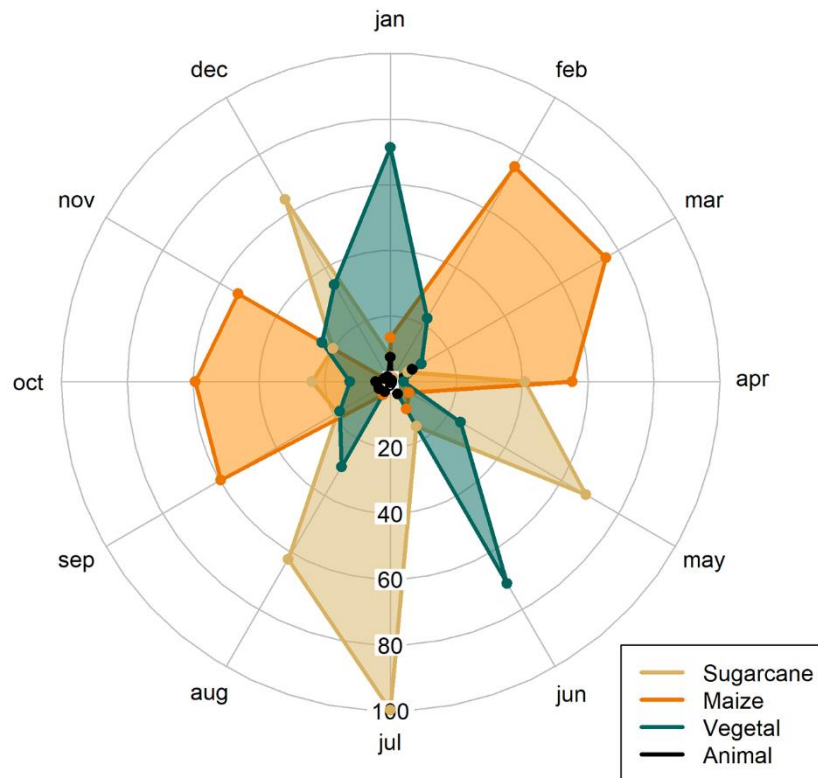


Figure 2. Seasonality of food consumption by invasive wild pigs *Sus scrofa* in Rio Claro-SP, Brazil

DISCUSSION

Both short term (stomachs) and long-term (isotopes) analyses of the diet of wild pigs indicate that they feed overwhelmingly on agricultural crops. Wild pigs consumed sugarcane year-round and exhibited selection towards high-quality maize forage disproportionate to its availability on the landscape. Such extensive agricultural subsidies are an important driver of elevated pig densities (Schley e Roper, 2003; Herrero *et al.*, 2006; Luskin *et al.*, 2017), which may have cascading effects on natural habitats by hindering plant regeneration and destroying microhabitats through uprooting of seedlings, saplings and topsoil (Ickes *et al.*, 2005; Cuevas *et al.*, 2010; Graitson *et al.*, 2018).

Although crops provide resource subsidies, natural areas remain important to wild pigs for foraging opportunities, shelter, and as a thermal refuge for managing heat stress under warm tropical temperatures (Choquenot e Ruscoe, 2003; Cordeiro *et al.*,

2018). Within this wildland-agriculture interface, wild pigs act as seed dispersers of native plant species, which can connect plant populations among forest fragments in the absence of extirpated tapirs, but also act as substantial seed dispersers for invasive plants (Pedrosa *et al.* in prep., chapter 2). Animal matter from both agricultural and natural areas was found in low quantities but at high frequency in the diet of wild pigs. In contrast to ruminant ungulates that absorb nutrients relatively efficiently from green vegetation (Hofmann, 1989), wild pigs are monogastric omnivores with animal matter constituting an essential source of protein (Fournier-Chambrillon *et al.*, 1995; Sáenz De Buruaga, 1995). We found traces of mammals, birds and reptiles among the vertebrates, which may come from both scavenging animal carcasses and predation. Most of the invertebrates present in the diet were Coleoptera and Chilopoda of fossorial habits, suggesting that wild pigs actively sought for them by revolving and digging the soil. Therefore, anthropogenic landscapes composed of forest fragments and agricultural crops likely fuel rapid growth of wild pig populations.

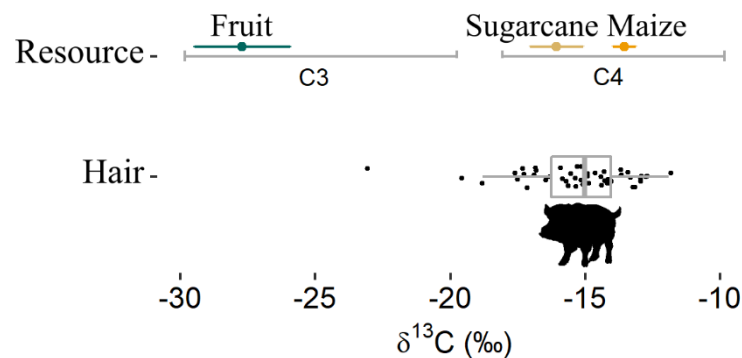


Figure 3. Plot of the $\delta^{13}\text{C}$ values of C₃ and C₄ food resources (range), depicting fruits, sugarcane and maize (mean and SD's values). Black dots are the 50 individual hair samples of wild pigs *Sus scrofa* (corrected for discrimination factor) with the boxplot highlighting median distribution of the $\delta^{13}\text{C}$ values.

Plantations other than sugarcane comprised less than 5% of the land cover within our study site, which contrasts with the importance of maize in wild pig stomachs. It is likely that supplementary feeding from traps and bait stations set up by trappers and hunters is playing a role as additional source of maize other than that available in the crop fields (Rosa *et al.*, 2018). The maize-“state” of some stomachs resembled pure dry grain while others resembled fresh maize (Cellina, 2008). When dry maize is

chewed, the shell of the grain tends to stick on the pieces, whereas if it is soft when chewed (fresh maize from crop fields), the "content" of the grains is squeezed out of the shell (Cellina, 2008). But a confusion factor is that baits are also set using fresh maize (whole corn cob), therefore we cannot provide a precise estimate of one or another source of maize in pig's diet. However, most of our stomachs came from pigs that were hunted using active search with dogs, which we believe reduce the bias of catching baited-pigs. Supplementary feeding is used as a short-term strategy to diminish wild pig impact on agriculture with the intention to attract pigs away from crops (Geisser e Reyer, 2004), although the long term outcome of this method can be the opposite of desired as it may increase the reproductive output (Massei *et al.*, 2011).

Table 2. Means and SD's of $\delta^{13}\text{C}$ values of food resources and individual hair samples of wild pigs *Sus scrofa*. Both animal matter and vegetal matter were comprised by samples representatives of carbon stable isotope signatures of C3 and C4 photosynthetic pathways. Values for hair samples are corrected for trophic discrimination factor.

Sample Type		<i>n</i>	Mean $\delta^{13}\text{C}$ ‰ (SD)
Resource	C3	16	-26.00 (3.05)
	Animal matter	4	-21.86 (4.38)
	Vegetal matter	12	-27.38 (6.10)
	Fruits	10	-27.71 (1.79)
	C4	26	-14.55 (1.95)
	Animal matter	9	-13.93 (2.73)
	Vegetal matter	4	-14.19 (0.41)
	Maize	5	-13.54 (0.47)
	Sugarcane	8	-16.06 (0.98)
Hair	50	-15.29 (1.99)	

Population growth of wild pigs is highly determined by their plasticity in acquiring food resources, which can increase twice faster under favorable conditions (Bieber e Ruf, 2005; Tabak *et al.*, 2018). Resource pulses from mast trees fruits are the major component of wild pig diet in its native range, playing an important role in wild pig fitness (Cutini *et al.*, 2013). In agricultural areas, crops may substitute mast tree fruits as main food item, which combined with lack of predators, create a perfect situation for population expansion (Snow *et al.*, 2017). High population densities of wild pigs may cause severe impacts on ecosystems (Ickes *et al.*, 2005; Luskin *et al.*, 2017), harm human well-being (Ruiz-Fons, 2017; Trevisol *et al.*, 2017) and compromise economic activities (Barrios-García e Ballari, 2012). In Brazil a mid-sized farm can lose US\$300,000 annually due to crop damage on maize plantations and silage (Pedrosa *et al.* 2015). In the United States annual losses to agriculture caused by wild pigs exceed US\$800 million (Pimentel *et al.*, 2005).

Extensive agricultural monocultures in Brazil appear to be the primary resource subsidy that is fueling the invasion of wild pigs. Reducing crop accessibility is likely to decrease the abundance of wild pigs. However, fencing crops may be economically impractical as a large-scale strategy. To increase the efficiency of culling programs designed to reduce the abundance of wild pigs, managers should incentivize year-round hunting effort and adjust the use of corral-traps to take place subsequently to crop harvest, which increases the chance of capturing the whole sounder (Massei *et al.*, 2011). Fine-tuning culling strategies to plantation cycles and its specific environmental characteristics together with involvement of farmers, hunters and the community is likely to increase the chance of success to mitigate the impacts caused by wild pigs.

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Compliance with ethical standards: The authors declare that they have no conflict of interest.

Ethics statement: All applicable institutional and national guidelines for the care and use of animals were followed, with permission given by IBAMA (authorization #46150) and the Scientific Animal-Ethic Committee from UNESP-Rio Claro (protocol #9396).

CAPÍTULO 4

Are invasive wild pigs altering the isotopic niche of native peccaries in the Neotropics?

Abstract

Introduction of species beyond their natural range is a concern for conservation, especially if it becomes invasive and occupy niches that overlaps with those of native biota. In such cases, ecological theory predicts that species may shift some dimension of their niche to avoid competitive exclusion. In that sense, invasion of wild pigs in the neotropical region is a good model to test this prediction. We analyzed stable isotopes of C and N of wild pigs and native peccaries (white-lipped and collared peccary) in three distinct scenarios: 1) natives and the invasive in sympatry, 2) natives alone and 3) wild pigs alone. Peccaries presented wider isotopic niches when inhabiting with wild pigs than when inhabiting in the absence of the invasive species, although small sample size for collared peccary make the findings to be questionable. The isotopic niche of wild pigs did not change in size either inhabiting with peccaries or alone, but their isotopic values were distinct for each scenario, especially $\delta^{13}\text{C}$, showing they are C3 and C4 feeders depending on the landscape they inhabit. The difference in isotopic values of peccaries and wild pigs suggest that there is more resemblance among peccaries themselves than between wild pigs and the peccaries. Our study highlights that invasive wild pigs and peccaries may be using several mechanisms to avoid direct competition for resources when in sympatry, increasing their isotopic niche breadth.

Key words: Invasive species, niche breadth, competition, feral swine, feral pig, wild boar, *Tayassu pecari*, *Pecari tajacu*, *Sus scrofa*,

INTRODUCTION

Invasion ecology is one of the leading fields of community ecology, because of its inherent interest as a test case of how much we understand community interactions. The classical niche theory propose that species will occupy larger realised niches in the absence of interspecific competition and species can only have a small degree of resource overlap before the competitive exclusion happens (Hutchinson, 1957; Pianka, 1974). Similarly, Charles Elton (1958) proposed that invasive species can out-compete native competitors by occupying a wider niche. For example, native deer species in North America faced reduction in their fitness due to competition with exotic deer species (Putman e Putman, 1996). Mechanisms underlying such outcome may be related with the niche constriction (dietary, habitat use) faced by subordinate species (Harrington *et al.*, 2009; Jackson *et al.*, 2016). On the other hand, to avoid competitive exclusion, competing species must shift some dimension of their niche, enabling coexistence (Rosenzweig, 1981). It means that if two or more sympatric species share preferences in resource use, the subordinate species must include less-preferred resources in order to coexist. Consequently, niche breadths of subordinate species shall be wider in the presence of competitor, as an outcome of using less-preferred resources (Rosenzweig, 1981; Codron *et al.*, 2011). In that sense, the invasion of wild pigs *S. scrofa* in Brazilian ecosystems provide a good model to test this hypothesis.

Domestic pigs were first brought to Pantanal in Brazil about 300 years ago (Deberdt e Scherer, 2007; Pedrosa *et al.*, 2015). They became feral and spread through this ecosystem as settlers abandoned their lands due to Brazil-Paraguay war during the second half of the 19th century. Since then, they spread over the region (Mourão *et al.*, 2002) where they co-occur widely with native peccaries (white-lipped *Tayassu pecari* and collared *Pecari tajacu*) (Alho *et al.*, 2011a). Invasive wild pigs (IWP) in Pantanal are highly frugivorous (Donatti *et al.*, 2007) as they are worldwide (Setter *et al.*, 2002; Fedriani e Delibes, 2009; Fujinuma e Harrison, 2012) and given they have similar foraging habits than that of peccaries, researches were impelled to investigate for potential competition between the alien and the native species (Desbiez *et al.*, 2009; Oliveira-Santos *et al.*, 2011). Desbiez *et al.* (2009) showed that overlaps in food resources and habitat use between IWP and native peccaries were lower than expected. In fact, niche overlap was highest between the native species (Desbiez *et al.*, 2009). Oliveira-Santos *et al.* (2011) argued for no evidence of interference

competition among the IWP and the two native peccary species in Pantanal. More recently, Galetti *et al.* (2015a) found that IWP may alter the foraging period of both peccaries and also showed high diet overlap between white-lipped peccaries (WLP) and IWP, but low overlap between collared peccaries (CP) and IWP (Fig 1).

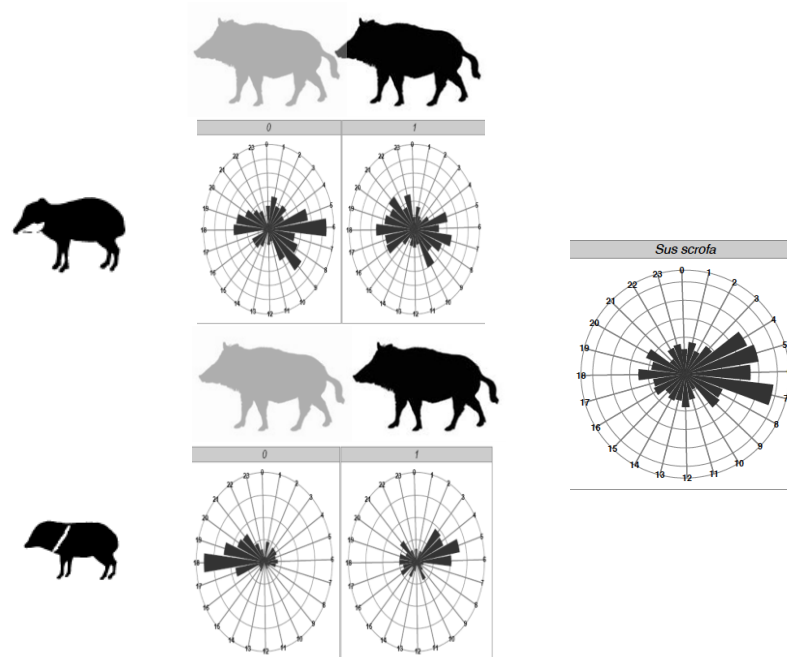


Figure 1. Extracted from Galetti *et al.* (2015a). Temporal differences in the foraging activity periods under fruiting trees of native peccaries in relation to invasive wild pigs (right) in the Brazilian Pantanal. On top: white lipped peccaries (*Tayassu pecari*) in the absence and presence of invasive wild pigs (*Sus scrofa*). Bottom: Collared peccaries (*Pecari tajacu*).

CP are smaller in group number and body size (Desbiez *et al.*, 2010) and perhaps they are subordinate species in this system. Although IWP are larger than WLP the later assemble large herds up to 100 animals/group (while the former constitute on average of 8.6 animals/group), probably offsetting the disadvantage of smaller body size when competing for resources with IWP. Nevertheless, WLP resemble a lot with IWP in type of fruit consumed, spreading the period of activity along the day, avoiding the presence of IWP, and may thus be considered subordinate species too (Galetti *et al.*, 2015a) (Fig 1). Therefore, it is expected a gradient of narrow-to-wide niche breadth for IWP, WLP and CP, respectively, in systems that three species co-occur, as subordinate species need to explore non-preferred resources as a mechanism to coexist, amplifying their niche breadth (Rosenzweig 1981, Codron *et al.* 2011, Fig. 2).

One way to measure niche breadth is analyzing the diet of the species employing stable isotopes analysis (Layman *et al.*, 2007). Stable isotope of carbon and nitrogen from animal tissues and their food sources is a powerful method to investigate trophic ecology and habitat use of wildlife (Kelly, 2000; Ben-David e Flaherty, 2012). All tissues of an animal carries the isotopic signatures of the resources, serving as natural tracers of food consumption and habitat exploitation (Martínez Del Rio e Carleton, 2012). Photosynthesis creates distinct carbon-isotope marks that can be used to distinguish carbon fixed by terrestrial C₃ and C₄ plants (Deniro e Epstein, 1978) and the difference in $\delta^{13}\text{C}$ values between terrestrial C₃ and C₄ plants provide a natural evidence of the herbivores diet (Ben-David e Flaherty, 2012). For example, the introduced gemsbok *Oryx gazelle* exhibited an isotopic shift in carbon when compared to its native range in Africa, and it was found by looking at the $\delta^{13}\text{C}$ values, which are the result of distinct photosynthetic pathway present in C₃ and C₄ plants that trace CO₂ with less or more ¹³C, respectively (Marquez e Boecklen, 2010).

This difference in isotopic traces of $\delta^{13}\text{C}$ among different energy sources of the consumers percolate through successive trophic levels, even after the consumption and absorption of the consumers by predators (Martínez Del Rio e Carleton, 2012). In the case of the heavy isotope of nitrogen (¹⁵N), there is a cumulative enrichment of ¹⁵N at each trophic level. Consequently, the measure of $\delta^{15}\text{N}$ values in animal tissues indicate trophic position of the consumer (Kelly, 2000) and, therefore, the demonstration of the ellipse area built from the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot may characterize the isotopic niches of different species (Newsome *et al.*, 2007).

Our goal in this work was to test what is acknowledged by theory through the comparison of the isotopic niche breadth of IWP and the peccaries, conducting stable isotopes analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the hair tissue of the focal species. We compared three distinct scenarios: a) areas where peccaries and IWP live in sympatry, b) areas where peccaries inhabit without the IWP and c) areas where IWP live without peccaries. Our hypothesis is that CP will have the wider isotopic niche, regardless of inhabiting with both competing species or only with WLP. On the other hand, IWP will experience the wider niche breadth in the absence of peccaries, as a result of competitive release (Fig 2).

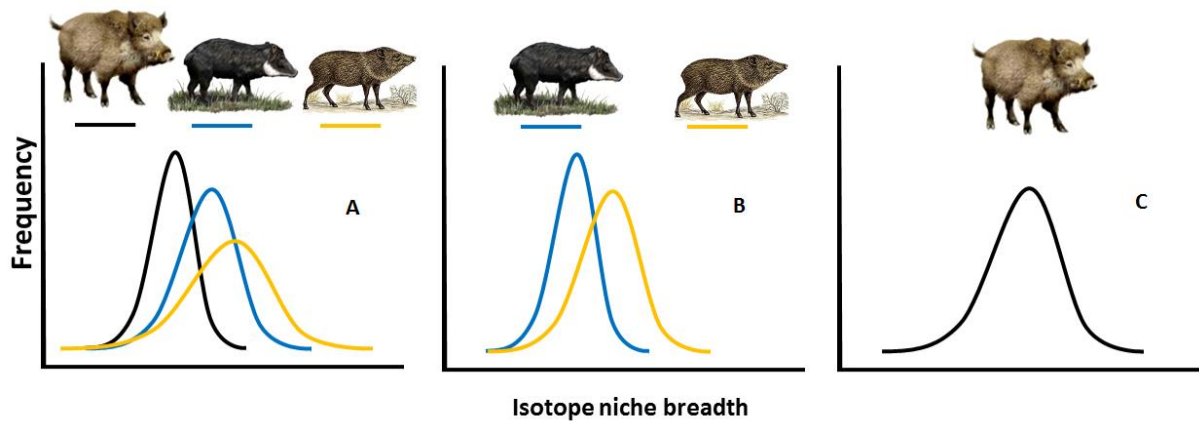


Figure 2. Conceptual design of expected results, showing the narrow-to-wide niche breadth of dominant-to-subordinate species, respectively, as a result of niche shift to avoid competitive exclusion, in a system of interacting species that share preferred resources. In A) a system where the three focus species live in sympatry (collared peccary is subordinate to white-lipped peccary that is subordinate to wild pigs); in B) a system inhabited by peccary species only (collared peccary subordinate to white-lipped peccary) and C) a system inhabited only by wild pigs.

METHODS

STUDY DESIGN – We selected three distinct scenarios of occurrence of CP, WLP and IWP: Pantanal, Bacury Farm and Rio Claro. The three species co-occur in Pantanal, while Bacury Farm is inhabited only by CP and WLP and Rio Claro is inhabited only by wild pigs. The Pantanal is one of the largest floodplains in the world (14° to 22° S and 53° to 66° W), a complex mosaic of tropical forest, savanna, and aquatic environments and supports a highly productive and diverse assemblage of neotropical flora and fauna (Junk *et al.*, 2006). Domestic pigs were introduced by European colonists to the Pantanal in the mid-1500s and became feral and invasive during the 19th century (Alho *et al.*, 2011b). IWP in Pantanal have average group size of 8.6 animals/group and they reach a densities of 1.5 to 11 individual/km² and mean body size of 60 kg, CP forage in small herds (mean of 4 animals/group) with a density 0.7 to 6.6 individual/km² and mean body size of 20 kg and WLP forage in large herds (up to 100 animals/group) reaching a density of 3 to 13.7 individual/km² and mean body size is 35 kg (Desbiez *et al.*, 2010 and Galetti *et al.* unpublished data). Bacury Farm ($22^{\circ}41'S$, $48^{\circ}06'W$) is a private cattle ranch and encompasses a large forest fragment (~1,500 ha), responsible for harboring one of the last remnants of peccary population in the Atlantic Forest (Lima *et al.*, 2017). Rio Claro ($22^{\circ}30'S$, $47^{\circ}30'W$) is about 75 km distant from Bacury Farm and was invaded by wild pigs during the beginning of the 2010's. Peccaries were extirpated from Rio Claro since the 2nd half of the past century

(Dean, 1997; Briani *et al.*, 2001). Both Bacury Farm and Rio Claro are characterized by a landscape of forest fragments immersed in monoculture of biofuel plantations (Martinelli e Filoso, 2008; Beca *et al.*, 2017).

DATA COLLECTION – We collected and analyzed 147 hair samples of WP, CP and IWP in Pantanal, Bacury Farm and Rio Claro (under SISBIO license #31088, #46150 and #46131). Hair of CP and WLP were collected during the years 2014 and 2015 in Pantanal and 2016 in Bacury Farm with the use of hair traps, active search following animal's track and used mud or live capture. Except for live capture collection, hairs collected in a same location within the sites (i.e, hair traps) were assembled together to avoid duplicates of sampling the same individual. Hair of IWP in Pantanal were collected during the years of 2003 to 2013 and in Rio Claro in 2014 to 2016. Except for 4 hair samples of Rio Claro, all other IWP hair samples were from live capture or hunted animals (See Table 1 for sample size of each species in each site and Chapter 3).

We characterized the isotopic baseline by collecting food resources that may consist of dietary items of peccaries and IWP in Pantanal, Bacury and Rio Claro, during the years of 2015 and 2016 (Layman *et al.*, 2007; Keuroghlian e Eaton, 2008; 2009). This include plant parts (leaf, fruit pulp seed, root) as well as animal prey (invertebrates such as but not limited to beetles, gastropods and chilopods) and fungi. Animal prey were collected from topsoil, mimicking prey that are consumed when these animals search for food. We included samples from different habitats, such as forest, grasslands, riparian environments and agriculture (sugarcane and maze). The goal was to provide an isotopic-picture of potential resources available in the study areas rather than the amount of the resources (Layman *et al.* 2007). See chapter 3 for details on resource sampling of Rio Claro.

SAMPLE PROCESSING AND ISOTOPE ANALYSIS – We first washed the hairs with distilled water to remove dust and then soaked each sample within a 2:1 solution of chloroform:methanol in 2ml individual plastic jars, shaking the jars for 30s using an electronic shaker. This procedure was repeated twice for each hair sample, after which we rinsed the samples with distilled water and dried them at 55°C for 24 hours.

We performed the stable isotope analysis at Stable Isotopes Center – CIE in São Paulo State University, Botucatu facility. We powdered the samples using cryogenic grinder, model Spex Sample – Geno Grinder 2010 under -196 °C, by

individually packing the samples in cleaned polycarbonate jars containing three stainless steel spheres. We weighted the powdered samples in tin capsules, using a high sensitivity analytical scale (Mettler Toledo XP6). A continuous flux isotopic ratio mass spectrometer system (CF-IRMS, Thermo Scientific – Delta V Advantage Isotope Ratio MS) was used to determine the isotopic ratio coupled to an elemental analyzer (Thermo Scientific – Flash 2000 Organic Elemental Analyzer). The IRMS determine the carbon and nitrogen isotopic ratio value ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$, respectively) of the samples, which is converted to relative difference of isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in permil (‰), according to, $\delta_{\text{Sample}} = [R_{\text{Sample}} / (R_{\text{Standard}}) - 1] \times 1000$, where R_{Sample} is the isotopic ratio ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) of the sample and R_{Std} is the isotopic ratio of the international standard Vienna Peedee Belemnite (VPDB).

Table 1. Sample size and summary of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of analyzed hair samples.

Species	Pantanal			Bacury			Rio Claro		
	<i>n</i> hair	$\delta^{13}\text{C}$ mean (SD)	$\delta^{15}\text{N}$ mean (SD)	<i>n</i> hair	$\delta^{13}\text{C}$ mean (SD)	$\delta^{15}\text{N}$ mean (SD)	<i>n</i> hair	$\delta^{13}\text{C}$ mean (SD)	$\delta^{15}\text{N}$ mean (SD)
Collared peccary	5	-24.16 (5.52)	2.70 (1.32)	7	-22.99 (0.60)	4.68 (0.29)	-	-	-
White-lipped peccary	41	-26.02 (0.51)	2.84 (0.88)	6	-23.30 (0.66)	5.13 (0.18)	-	-	-
Invasive wild pigs	42	-22.05 (1.54)	4.94 (1.16)	-	-	-	46	-15.09 (1.66)	6.38 (0.98)

Table 2. Sample size and minimum and maximum values of $\delta^{13}\text{C}$ $\delta^{15}\text{N}$ of analyzed resource samples.

Location	<i>n</i> samples	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		Min	Max	Min	Max
Pantanal	59	-33.33	-4.93	-0.53	10.51
Bacury	18	-35.35	-15.45	-0.34	7.26
Rio Claro	43	-29.84	-9.83	-1.67	11.23

DATA ANALYSIS – We employed a geometric approach (Newsome *et al.*, 2012) using the Standard Ellipse Area (SEA) as a metric to quantify and compare the niche widths among species (Layman *et al.*, 2007; Jackson *et al.*, 2011). SEA is the representation of deviation of bivariate $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ data and was inferred within a Bayesian approach, which gives a portrayal of the size of the occupied niche (SEA_b, Jackson *et al.* 2011).

This approach represent estimates of SEA in the form of posterior distributions (the SEA_b), reflecting uncertainty from the data. Even though smaller samples sizes are coupled with larger uncertainty, the resulting ellipses can be compared in a quantitative way that returns a robust probability with reference to differences between the samples (Jackson *et al.*, 2011). We also calculated two community metrics proposed by Layman *et al.* (2007), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges, which represents the variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within the community. While $\delta^{13}\text{C}$ range indicate the degree of which species are exploring different basal resources in the community, $\delta^{15}\text{N}$ variation indicate the extent of trophic level separation (Layman *et al.* 2007). We performed our analysis using SIBER package in R (Jackson, *et al.* 2011). We corrected the isotope ratios for trophic discrimination factors (TDF), using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TDF values of 0.2‰ and 2.7‰, respectively, considering hair tissue reported for *S. scrofa* in (Nardoto *et al.*, 2006).

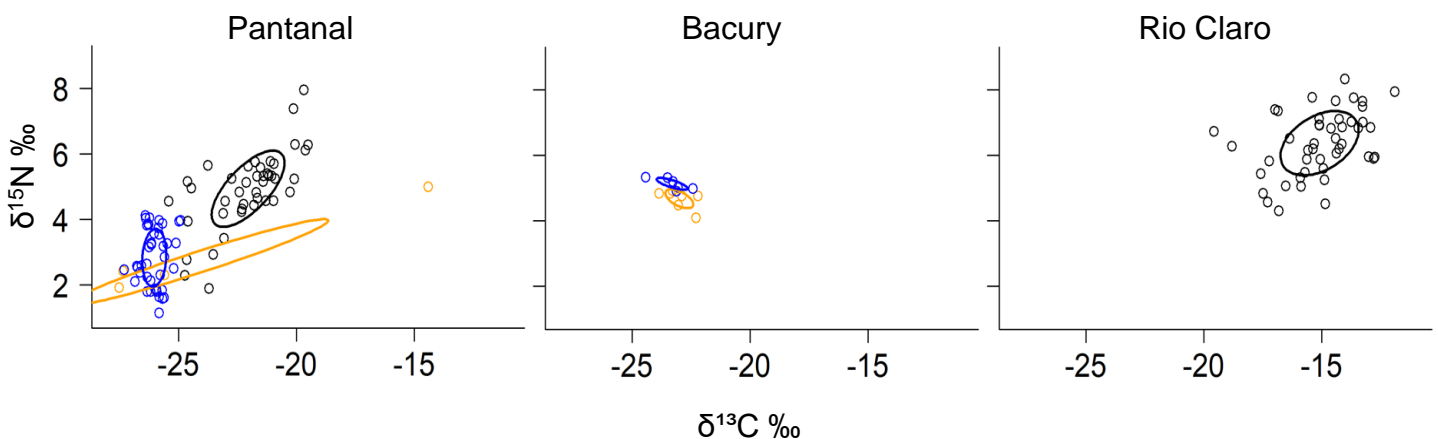


Figure 3. Isotopic niche of collared peccary (orange), white-lipped peccary (blue) and invasive wild pigs (black) in Pantanal, Bacury Farm and Rio Claro. The standard ellipses drawn represent ~40% of the data distribution.

RESULTS

The mean $\delta^{13}\text{C}$ values of peccaries was typical than that of C3 feeders in Pantanal and Bacury, with the exception of an outlier CP in Pantanal that seems to be C4 feeder (Table 1 and Fig 3). IWP are exploring C4 resources in Rio Claro and C3 in Pantanal and presented similar SEA_b sizes in both places (Figs 3 and 4). The highest SEA_b value was for CP in Pantanal. The SEA_b of WLP in Pantanal was the smaller

among the three species. In Bacury, the SEA_b of CP was larger than that of WLP, but for both species it was the smaller SEA_b of the study (Fig 4). The range of $\delta^{13}C$ values in Pantanal was 3.54 to 4.43‰ (95% Bayesian credible interval – CrdI) and in Bacury was 0 to 1.40‰ (95% CrdI, Fig 5). The range of $\delta^{15}N$ values was 1.72 to 3.22‰ (95% CrdI) in Pantanal and 0 to 1.56 (95% CrdI) in Bacury (Fig 5). The characterization of the baseline showed that the variation in $\delta^{13}C$ and $\delta^{15}N$ values of resources was similar in all study areas, with both isotopes ranging from low to high values (Table 2).

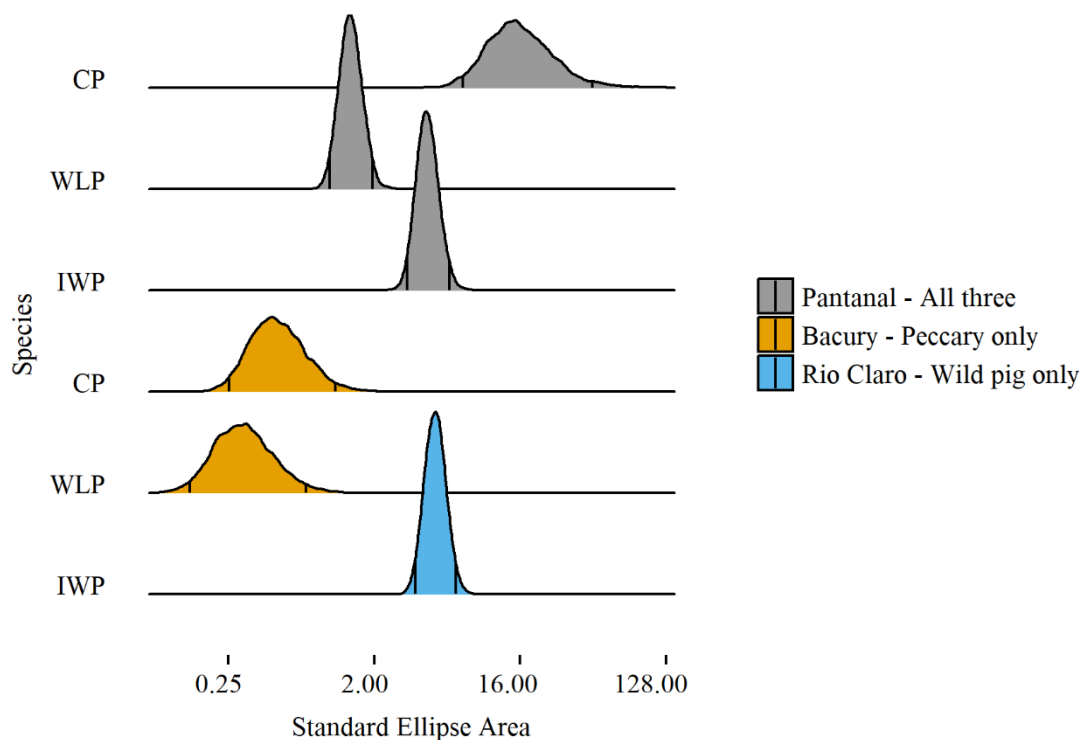


Figure 4. Posterior distributions of values of the Bayesian standard ellipses areas (SEA_b) for collared peccary (CP), white-lipped peccary (WLP) and invasive wild pigs (IWP) derived from bivariate $\delta^{13}C$ - $\delta^{15}N$ stable isotopes. Vertical black lines within the ellipses represent the 95% credible interval. Values of the SEA_b are in ‰² and were log2 transformed for best visualization.

DISCUSSION

Although the results indicate what we expected for CP – the subordinate species of the system, we cannot say it corroborate the hypotheses, because of the low sample size of hair of CP and the presence of an outlier within the samples this species in Pantanal. IWP also presented large isotopic niches in both systems, evidencing their dietary plasticity. WLP is occupying a narrow isotopic niche regardless

of co-occurring with IWP or not. In the Pantanal we saw the larger variance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, indicating that co-occurring species may be exploiting a wide range of basal resources from different trophic levels as a mechanism to coexist, amplifying thus their niche breadth. In the opposite, Bacury showed lower variance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, suggesting that, in the absence of IWP, peccaries may accommodate resource exploitation according to their preferences, without the interference of a competitively superior species. Therefore, differently from niche constriction hypotheses in which subordinate species experience narrow niches in face of competition (Harrington *et al.*, 2009; Jackson *et al.*, 2016), our study showed that niche breadths of subordinate species was wider in the presence of a competitor (Rosenzweig, 1981; Codron *et al.*, 2011).

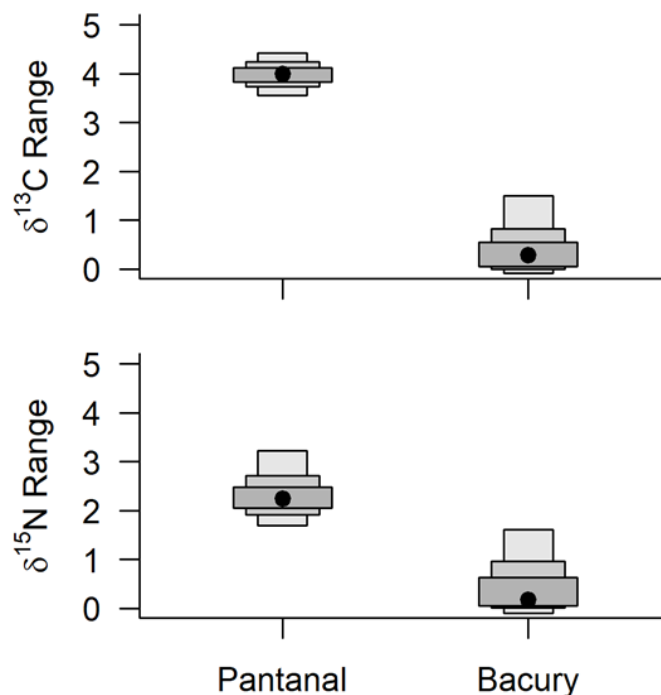


Figure 5. Posterior distribution of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges in Pantanal and Bacury. The upper and lower limits of the grey-shaded rectangles represents the Bayesian credible intervals (95%, 75% and 50%).

Although we cannot measure exactly the amount of resources each species are consuming, stable isotopes of hair integrate foraging activity information of months, therefore, the size of the isotopic ellipses represents the long-term diversification of foraging strategies – but the CP result should be interpreted with caution, as mentioned above. For example, Galetti *et al.* (2015a) showed that CP drastically changes its

period of activity when in the presence of WLP and IWP. Because CP and IWP bears little resemblance in type of fruit use, CP can forage in similar periods of time of IWP when the alien is present, avoiding competition with WLP. Bite force has also been hypothesized as a mechanism of niche partitioning among these three species, enabling them to access different parts of similar food sources (Kiltie, 1982; Desbiez e Keuroghlian, 2009). The difference in isotopic values of CP, WLP and IWP suggest that there is more resemblance among CP and WLP than between IWP and the peccaries, strengthening the previous findings regarding niche partitioning of the three species in Pantanal. IWP occupies a distinct isotopic niche than that occupied by peccaries in Pantanal, with low overlap of isotopic values among the invasive and the peccaries – mainly $\delta^{13}\text{C}$, indicating the incorporation both C3 and C4 resources in the diet, while CP and WLP are feeding predominantly on C3 resources.

IWP possess an efficient morphology and behavior for food acquisition and are expected to impact native species with similar niches, as documented for CP in southern Texas (Ilse e Hellgren, 1995b). For instance, the range of IWP in the Neotropics is increasingly overlapping with that of the peccaries, particularly in Brazil (Lima *et al.*, 2017; Rosa *et al.*, 2017). Therefore, although IWP, CP and WLP are coexisting for a long time in Pantanal (Oliveira-Santos *et al.*, 2011) and may be using several mechanisms to avoid direct competition (Galetti *et al.*, 2015a), the increasing niche breadth of native species observed here indicate that are experiencing long-term competition for resources.

Aknowledgements

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CAPÍTULO 5*

Liquid lunch – vampire bats feeding on invasive wild[†] pigs and native ungulates

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Contribuição dos autores: MG concebeu e planejou o estudo; MG, FP e AK coletaram os dados; FP realizou a análise dos dados; MG escreveu o artigo com contribuições significativas de FP, AK e IS.

[†] Eu mudei o termo “feral”, originalmente usado na publicação, por “wild”, no título e em todo o texto, pois acredito que teria sido mais apropriado

Vampire bats have long captivated the imagination of humans worldwide. Although often associate with myths about Dracula-like creatures (Mayen, 2003), only three of the about 1,200 known bat species – *Desmodus rotundus*, *Diaemus youngi*, and *Diphylla ecaudata*), all of them restricted to the New World – feed exclusively on blood (Turner, 1975). Of these, the common vampire bat (*D rotundus*) has the widest distribution, extending from Mexico to Argentina. This species feeds mostly on livestock and poultry (Greenhall *et al.*, 1983), but has also been documented preying on native mammals (Catenazzi e Donnelly, 2008; Sánchez-Cordero *et al.*, 2011).

We have used camera traps to monitor mammals in the Brazilian Pantanal and Atlantic Forest for the past 12 years. After checking 10,529 photos and videos of several terrestrial mammals, we saw several examples of *D rotundus* feeding on invasive wild pigs (*Sus scrofa*; six instances), free-ranging cattle (two instances), and native ungulates (four instances) including lowland tapirs (*Tapirus terrestris*) and red brocket deer (*Mazama americana*). See WebVideos 1–5 as Supplementary information for examples of bat feeding behavior and a thwarted attack on native and non-native mammals.

Because vampire bats feed nocturnally, we also analyzed a subset of the 10,529 records that included only nighttime photos and videos (from 18:00 pm to 6:00 am) showing tapirs, brocket deer, and wild pigs. To estimate the frequency of encounters between bats and these three ungulates, we considered each night (12-hour period) as an independent event. From the 4629 night records available, we logged 158 independent events in the Pantanal (101 for wild pigs, 38 for deer, and 19 for tapirs) and 87 independent events in the Atlantic Forest (35 for wild pigs, 29 for deer, and 23 for tapirs). Based on these encounters between vampire bats and each of the prey species, we estimated that the chances of an ungulate being attacked by a vampire bat in the Pantanal were 2% for wild pigs, 11% for tapirs, and 3% for brocket deer. In the Atlantic Forest, we found only wild pigs and brocket deer being attacked by bats, with a probability of 11% and 7%, respectively.

Wild pigs and brocket deer were the only ungulates recorded with vampire bats in both the Pantanal and Atlantic Forest. The frequency of encounters between bats and wild pigs is fivefold higher in the Atlantic Forest than in the Pantanal. However, our sample does not capture vampire bat–prey interactions when the prey is not foraging

or moving. Consequently, the actual encounter frequency between bats and ungulates is probably higher than our estimates.



Figure 1. A common vampire bat (*Desmodus rotundus*) rides a sow of the invasive wild pig (*Sus scrofa*) (Brazilian Pantanal, Photo A. Keuroghlian).

About 1.4% of vampire bats are infected with rabies virus in the Atlantic Forest (Scheffer *et al.*, 2007), but this may reach up to 10% in the Peruvian Amazon (Streicker *et al.*, 2012). Based on a vampire bat–rabies prevalence of 0.014 (Scheffer *et al.* 2007), the probability of rabies transfer to tapirs and deer by bats in the Pantanal is 0.15% and 0.04%, respectively, and is 0.09% for deer in the Atlantic Forest. Based on the same data, rabies transmission to wild pigs is 5.3 times as high in the Atlantic Forest (0.16%) as in the Pantanal (0.03%). Vampire bat-transmission of rabies is a major concern for livestock owners in Brazil, even in areas where cattle are routinely vaccinated (Ito *et al.*, 2001; Kobayashi *et al.*, 2006), but wild animals – including wild pigs – are not vaccinated and may therefore pose a serious threat by spreading the disease.

Besides attaching themselves to wild pigs' bodies to feed (Figure 1), the vampire bats were also seen hopping along on the ground in an attempt to catch the pigs and

take blood from their feet when they stopped to root through or dig into the forest floor (SI WebVideos 1 and 2). On one occasion, two vampire bats fed on a wild pig while another bat hovered nearby (SI WebVideo 3). Vampire bats are able to dodge branches and other obstacles while riding the pigs or chasing after them on the forest floor. Similar behavior was recorded for a vampire bat feeding on a lowland tapir in the Pantanal, as the bat skillfully avoided being trampled while feeding from the tapir's foot (SI WebVideo 4). Vampire bats have also been seen chasing capybaras (*Hydrochoerus hydrochaeris*) at Anchieta Island, Atlantic Forest (VB Zipparro, unpublished data).

We recorded unsuccessful attacks on an adult female brocket deer in the Atlantic Forest (SI WebVideo 5). In response to the approaching bats, the brocket deer kicked out with its hind legs, charging at bats near or on the ground and snapping its jaw at one flying close-by. In most of the videos, more than one bat attacked the prey, but the vigorous avoidance behavior of the brocket deer successfully kept the bats at bay.



Figure 2. A common vampire bat (*Desmodus rotundus*) takes blood from the ear of a resting domestic pig (*Sus scrofa*) in a subsistence farm (Photo W. Uieda).

The population density of *D rotundus* is usually high in areas with domestic animals, especially cattle (Turner, 1975). Land-use change converted the area's natural ecosystems into pasture for livestock, which may have boosted vampire bat

populations due to food abundance (Turner 1975). However, conversion of pastures into sugar cane agriculture in most of southeastern Brazil during the past few decades (Rudorff *et al.*, 2010) and the severe defaunation of the Atlantic forest (Jorge *et al.*, 2013) may have forced the bats to switch from the formerly abundant cattle to an alternative food source – the wild pigs.

In the Pantanal, where cattle density can reach 1.4 head per hectare, *D rotundus* is the seventh most abundant bat, with a 4% capture frequency (Alho *et al.*, 2011c), whereas in the Atlantic forest they represent <1% of the captures (Gorresen e Willig, 2004). The growing population of wild pigs in the Atlantic Forest (Pedrosa *et al.*, 2015), make them ideal prey substitutes for the bats (Figure 2), as pigs are among the preferred prey of this species (Figure 2, and Mialhe, 2014; Bobrowiec *et al.*, 2015). Under the human-induced environmental changes described above, vampire populations may increase due to the widespread invasion of wild pigs, mostly in in Brazil's southern regions (Pedrosa *et al.* 2015), and our findings on the encounter frequency between vampire bats and wild pigs support this suggestion.

The common vampire bat is a major reservoir of rabies virus and is well known for spreading this deadly disease to several mammals upon which it feeds (Turner, 1975; Anderson *et al.*, 2014). The rabies virus is transmitted through the saliva of infected bats (Aguilar-Setien *et al.*, 2005), and exposure to saliva through small wounds or scratches may occasionally result in rabies infection (Rupprecht *et al.*, 2002). Bushmeat hunters are exposed to saliva and other bodily fluids from their kills when they cut up the carcasses (Desbiez *et al.*, 2011). Rabies-infected wild pigs may also occasionally bite hunters, their dogs, or even other predators of pigs (Jorge, *et al.* 2010). There is therefore a danger of the virus being transmitted to hunters and dogs via wild pigs (Nociti *et al.*, 2009; Pessoa *et al.*, 2011).

D rotundus is also a reservoir for other viruses, including hantavirus, coronavirus, and adenovirus (Brandão *et al.*, 2008; Lima *et al.*, 2013 ; Sabino-Santos *et al.*, 2015). Human-induced changes in the environment are linked to an increasing occurrence of emerging infectious diseases (Kuzmin *et al.*, 2011) including spillover of viruses from bats to humans and other mammals (Plowright *et al.*, 2015). Vampire bats feeding on the constantly spreading wild pigs may therefore be viewed as a potential risk to wildlife, livestock, and humans.

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Supplementary Information

Web Videos 1 to 5 can be found here:

<http://onlinelibrary.wiley.com/doi/10.1002/fee.1431/suppinfo>

Video 1: Wild pig with two vampire bats on its back and one on the forest floor in the Brazilian Atlantic forest.

Video 2: Wild pig chased by a vampire bat on the forest floor in the Brazilian Atlantic forest.

Video 3: Two vampire bats feeding on wild pigs while one hover and leave.

Video 4: Lowland tapir chased by a vampire bat on the forest floor in the Brazilian Pantanal.

Video 5: Brocket deer repelling attacks of vampire bats in the Brazilian Atlantic forest.

CAPÍTULO 6*

Hunting as the Main Technique Used to Control Wild Pigs in Brazil

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ABSTRACT

Wild Pigs (*Sus scrofa*) have expanded their range in Brazil since late 1980's, with reports of damage becoming more frequent in recent years. In 2013, the use of lethal methods for wild pig control was legalized by the federal environmental agency. However, several restrictions related to the purchase and transportation of guns and ammunition hamper our ability to evaluate the effectiveness of control measures. Nevertheless, many citizens engaged in wild pig control in Brazil do not officially report their control activities, as required by the legislation. Our goal was to characterize the profile of wild pig controllers in Brazil to understand their methods and motivations estimate the number of wild pigs killed per person per year and evaluate the current regulations regarding their applicability to the situations observed in the field. We formulated and distributed a structured questionnaire to wild pig controllers (N = 172), including both hunters and non-hunters. A total of 2389 wild pigs were reported killed, each of the respondents killing a mean of 17.2 (SE = 24.8) pigs per year, with males and females killed in the same proportion. We found that 40% were acting illegally, and most of the control is being done by hunters for property defence in third party properties. Since most of the effort for controlling wild pigs in Brazil is done by volunteers, and farmers suffer most of the impacts, we believe that adjusting hunting method to crop season (e.g. hunting after harvesting the crops or an integrated program of hunters and traps placed around crops) could be an important new management tool for reducing wild pig population and crop damage. Further, to enhance wild pig control we recommend incentivizing use of corral traps and cages because such techniques have the greatest effect on reducing wild pig population.

Key words: Brazil, citizen science, feral pigs, feral swine, harvest, invasion biology, wild boar.

INTRODUCTION

Wild boars (*Sus scrofa* L.), originally from Eurasia and northern Africa, were one of the first animals domesticated by humans. Pigs, the domesticated form of wild boars, were commonly introduced by European explorers in colonies and constituted an important source of protein, due to rapid growth and reproductive rates and high adaptive capacity to new environments. These same traits resulted in wild pigs (see Keiter *et al.*, 2016 for correct terminology of nonnative *Sus scrofa*) being one of the most widely distributed alien mammal species in the world (Long, 2003; Lewis *et al.*, 2017). In South America, Spaniards and Portuguese settlers introduced pigs in the 16th century. In the early 1900's, the wild boars were brought to Argentina for game purposes; they were subsequently taken to Chile and Uruguay. Wild boars eventually escaped from hunting ranches and dispersed throughout the continent (Jaksic *et al.*, 2002; Lombardi *et al.*, 2015). By the 1990's, around 10% of Southern America had already been invaded by wild pigs; rates of expansion were much higher than would be expected naturally, possibly due to human-assisted transportation to establishing hunting grounds and favourable environmental conditions (Salvador, 2012).

In Brazil, wild pigs were first recorded in 1989 near the border with Uruguay (Deberdt e Scherer, 2007), although unofficial reports from old hunters date back to the 1970's. Their popularity as game species and exotic meat grew in the 1990's, when several wild boar farms, both legal and illegal, were established in the south and southeast regions of Brazil. New genetic (pure) lineages were even brought from Europe and used to establish commercial herds. Economic issues and a government ban on new farms in 1998 [IBAMA ordinance 102/98, IBAMA is Portuguese acronym for Brazilian Institute for Environment and Renewable Natural Resources] led to a generalized release of wild boars into the environment during 2000-2005 (Salvador 2012). Currently, wild pig range is expanding rapidly due to translocations and introductions between different places for hunting or meat production, and crossbreeding with free-ranging domestic pigs. Wild pigs are already present in all five political regions in Brazil, with major concentration in the South and Southeast regions (Pedrosa *et al.* 2015), where estimated population density ranges from 0.22 (Salvador 2012) to 22.3 individual/km² (Puertas, 2015).

Since the late 20th century, conflicts between wild pigs and humans have been increasing in Brazil, resulting in severe economic losses (Salvador 2012, Pedrosa *et al.* 2015), decline of water resource quality (Rosa, 2016), disturbance of natural environments (Hegel e Marini, 2013) and threats to commercial pig operations. Timely but unsuccessful control efforts were conducted in the southern states in the 2000's. Such efforts consisted primarily of short-term (3 to 12 months) targeted efforts, where groups of hunters, accompanied by federal environmental agents, performed one or more incursions in specific areas where wild pigs had been reported. Lack of expertise from both agents and hunters, deficiency of the techniques being used (only hunting), and lack of a continuous effort were determinant factors negatively affecting efficiency (Deberdt and Scherer 2007). After 24 years of the first report of wild pigs in Brazil, lethal methods for population control was authorized nationwide by the IBAMA. The Normative Instruction 03/2013 (NI 03/2013) declared wild pigs a noxious species, and allowed population control in all Brazilian territory, by any citizen, with no control season or bag limit. This normative does not acknowledge recreational hunting, but declares that lethal control of wild pigs can be done using firearms, knife or crossbow, with or without the aid of dogs. The use of live trapping techniques (e.g. box and corral traps) is another alternative technique permitted by the normative, but requires extensive documentation. Depending on how it is applied hunting can either function as population-enhancing technique or for population control. For example, trophy hunting (killing adult males for the best trophy, e.g. teeth or head) has been largely used as management tool for enhancing wildlife populations with the goal of increasing or maintaining population growth rates and density to facilitate sustainable recreational hunting opportunity (Heffelfinger *et al.*, 2013). On the other hand, hunting for purposes of population control targets all animal sex- and age-categories (juveniles, females, males) and results in reduced survival rates of juveniles and females. This approach has a strong negative impact on population numbers and is of little interest to recreational/trophy hunters (Seward *et al.*, 2004; Bieber e Ruf, 2005; Tabak *et al.*, 2018).

The NI 03/2013 is the first regulation for large vertebrate population control in Brazil and permits the use hunting techniques for invasive animals. In fact, it is the first hunting-like regulation nationwide since the federal law 5197 from 1967 (Table S1 in Supporting Information) – a law that regulates fauna protection and reserves the use

of wildlife for a select subset of the human population (e.g. native Brazilians). Consequently, there is no information about the use of control techniques for large invasive vertebrates in Brazil. Therefore, to evaluate the effectiveness of NI 03/2013, we applied a questionnaire to hunters and non-hunters, involved in wild pig control in Brazil. The goal of this study was to characterize the profile of controllers by: 1) identifying the main techniques used for wild pigs control since 2013, 2) assessing the personal motivations involved (crop/livestock protection, sport or subsistence), 3) estimating the number of wild pigs killed per person per year, and 4) describing the involvement of controllers in the legal procedures required by NI 03/2013.

METHODS

We distributed questionnaires to hunters or any person involved on wild pig control in Brazil (e.g. landowners, Figure 1). Our questionnaire captured the general profile of wild pig controllers (origin, age, education level and income); methods employed (hunting and traps); motivation for control (property defence, trophy/sport, food for humans); type of property where the control was done (private, third party or public land); number and category of wild pigs killed in one year (adult males, adult females and piglets). We also asked if the participants followed the legal procedures required by the NI 03/2013. We provided multiple-choice questions, in which participants could choose more than one answer. In addition, there were closed questions (yes/no answers) and open questions, in which participants could answer freely (see Supporting Information for detailed questionnaire). The questionnaires were applied with the authorization of Research Ethics Committee of Federal University of Lavras (number 48788115.4.0000.5148), in accordance with Brazilian System of Ethics in Research.

We applied the questionnaire using two techniques: in-person surveys (face-to face interviews) using snowball-sampling technique (Browne, 2005; Sheu *et al.*, 2009) and an online questionnaire (Google Forms®). Since we aimed to capture both legal and illegal activities, respondents had no obligation to identify themselves or to answer all questions. During January to March 2014, we conducted 38 in-person surveys in Itamonte (IT) (MG state, 22°21 S; 44°47 W; Figure 1), in the rainforest of southeast Brazil. During 2015 we conducted eight in-person surveys in Santana do Livramento (SL) (RS state, 30°53 S; 55°31 W; Figure 1), in the grasslands of southern Brazil.

Before each interview, our research goals were explained. Since wild pig control is frequently performed irregularly, especially in rural communities (i.e. controllers do not have all required documents), only the number and category of wild pigs harvested and method were asked in the in-person survey.

From June to August 2015, 126 respondents answered online questionnaires. This technique had national coverage with the support of @aquitemjavali, and was advertised in hunting clubs, blogs and social networks for the participation of wild pig controllers. Prior to the online survey, @aquitemjavali network promoted an online conference between our research group and hunters, for explaining the goals of this research and the importance of answering the questionnaire. The conference was held via Google Hangout and available online on @aquitemjavali YouTube™ account throughout the year of 2015. The main results of the survey were later presented on the @aquitemjavali blog to provide feedback for the respondents. We choose this approach by @aquitemjavali, because the network is one of the most popular channels in Brazil managed by and for hunters, where they discuss and exchange experiences associated with wild pig hunting; we believe this approach increased the reliability of respondents answers.

We pooled the data from online and in-person surveys, and used each respondent as sampling unit within each question category. We categorize control techniques into traps and hunting. We further categorize hunting techniques into active hunting or stand, where the former refers to all forms of hunting involving persecution and catch of pig, done on foot, horseback or vehicle, with or without use of dogs. Stands consists of choosing a place naturally used or visited by wild pigs (previously recognized by searching for signs near feeding sites or wallows), or by setting artificial places or baits for attracting wild pigs. Temporary structures or fixed platforms high off the ground are commonly used for concealment and protection. Because respondents had no obligation to answer all questions, the number of sampling units differed between questions. We evaluated if there was a difference in the number of males and females killed by one respondent per year, using Kruskal-Wallis test ($\alpha = 0.05$ significance level) on BioEstat 5.0 (Ayres *et al.*, 2007).

RESULTS

We obtained 172 responses for both questionnaires combined. Overall, we documented harvest of 2,389 pigs including 1017 adult males and 1131 adult females; we did not find statistically significant difference in the average number of adult males and adult females killed by one hunter per year ($P = 0.5876$). The mean number of wild pigs harvested per controller was 17 (Standard error = 24.8; Max = 150; Min = 0). Only respondents of the online survey reported killing piglets (13.5% of 2180 pigs harvested from online responses) and pregnant females (27.6% of 931 sows from online reports). Nine (5.2%) respondents, all from the online survey, reported no wild pig harvest. Almost half of the respondents (42.4% of 172) reported only one individual killed per month (12 wild pigs per year). Only 29 (16.8%) respondents harvested more than 30 pigs per year. Most respondents (83%) of online questionnaires were from south and southeast Brazil. Most controllers sampled had high levels of education (61% with college degrees and 38% with high-school) and high income (21% with monthly wages > \$2,850.00; and only 3% earning minimum wage of around \$270.00) (Table S2, available online in supporting information).

Control technique was reported by 142 respondents and active hunting the most commonly used method (74.6% of the responses), whereas only 7% reported exclusively using traps; 17.9% used both hunting and traps (Table 1). Active hunting was reported being the sole technique used by 42.9% of the respondents but 92.2% of respondents practice it. Stands was practiced by 41.5% of respondents and exclusively used by only 4.9% of respondents. Using dogs was the most popular form of active hunting, being practiced by 86.6% of the 142 respondents. We divided traps in two categories: live traps (including corral traps, small cages and trench traps) and snares. Trench trap was a local method developed in IT, which consisted of adapting empty silage trenches to work as corral traps. The use of live traps were reported in 21.1% of the responses, but respondents that reported using this technique also hunted. Snares were used in 4.9% of the cases, despite being prohibited by the NI 03/2013. Regarding disposal method, respondents (N = 124) reported using both firearms (70.2%) and cold steel weapons (74.2%; Table 1). Of those using cold steel weapons (N = 92), most used knives (64.5%) or archery (38.7%), which has been an increasing choice because of difficulty on getting all required documents for firearms permits.

When asked about the main motivations for controlling wild pigs, most of the respondents (56.4% of 117 responses) had multiple motivations (Table 1), choosing one or more alternatives in the questionnaire. Property defence was declared as the motivation by 81.2% of respondents but was the exclusive motivation for 24.8%; sport (trophy) was reported by 68.4% but was the exclusive motivation for 11.9%; and meat consumption was reported by 63.2% but was the exclusive motivation for 6.8% of respondents (Table1). Meat consumption was the third ranked main motivation, yet all respondents reported meat consumption as the final destination for the carcasses (See questions details in S1). In terms of property ownership, 79.4% of controllers reported hunting wild pigs on their own property, 94.3% on third-party properties and only 7.6% in state or federal protected areas (Table 1).

Table 1: Number of respondents (bold parentheses) and percentage of responses obtained in both questionnaires (online and in-person) to each category of question (Multiple-choice and Yes-or-No questions). Number of respondents to each question is in parentheses. Some of the respondents assigned only one choice within a certain category of question in Multiple-choice questions, which was highlighted in the column Exclusively.

Multiple-Choice Questions	Total	Exclusively
Control technique (N = 142)		
Hunting	93.0% (132)	74.6% (106)
Active hunting	92.2% (131)	42.9% (61)
Hunting with dogs	86.6% (123)	
Stands	41.5% (59)	4.9% (7)
Traps	25.4% (36)	7% (10)
Live traps	21.1% (30)	
Snares	4.9% (7)	
Disposing method (N = 124)		
Firearms	70.2% (87)	
Cold steel weapons	74.2% (92)	
Knives	64.5% (80)	
Archery	38.7% (48)	
Primary motivation (N = 117)		
Propriety defense	81.2% (95)	24.8% (29)
Trophy/sport	68.4% (80)	11.9% (14)
Meat consumption	63.2% (74)	6.8% (8)
Yes-or-No Questions	Yes	No
Propriety ownership		
Own propriety (N=126)	79.4% (100)	20.6% (26)
Third-party propriety (N= 124)	94.3% (117)	5.7% (7)
Protected areas (State or Federal) (N=105)	7.6% (8)	92.4% (97)
Legal paperwork		
IBAMA (control license) (N=126)	60.3% (76)	39.7% (50)
Army (firearms) (N= 103)	66.0% (68)	34.0% (35)

Most of the respondents reported being registered in both IBAMA (60% of 126 respondents) and Brazilian Army (66% of 103 respondents) for using firearms during controlling activities. Of the respondents that were not legalized, only 45 declared reasons for the lack of IBAMA's authorization - bureaucracy (46%) and lack of information about the authorization process (33%) were the main causes for lack of compliance. Many stressed the need for an electronic system to facilitate license distribution and declaration processes; currently the process is required to be done in person with printed-paper at the IBAMA offices. The need for extending the license expiration date for one year instead of three months was one of the main requests. At the time of the survey, the Army's authorization for gun transportation was linked to this document and should be renewed four times in the year.

In addition to the main questions, local residents of both counties in the in-person survey reported economic losses caused by wild pigs, but exact amount of losses was hard to assess and were not the focus of our survey. Nevertheless, this is an important subject to mention because there are no previous broad-scale reports relating to damage by wild pigs in the country. In Itamonte, 100% of respondents reported losses on agricultural production, particularly sugarcane, corn and cassava. They also reported wild pigs approaching houses, attacking gardens, destroying springs, feeding on livestock carcasses and crossbreeding with domestic pigs. In Santana do L farmers reported losses between 10 and 50% of lamb production and, in one case, 250 lambs were reportedly predated by pigs; an estimated in loss of U\$7,600.00.

DISCUSSION

Our sampling effort focused on both the rural and urban population sector, enabling us to identify two profiles of wild pig controllers in Brazil: the producer, aiming to protect livestock and crops, and the recreational hunter that values wild pigs as an opportunity for legal hunting. However, because most of respondents completed online surveys, our responses were biased towards sport hunters that may have personal interests in hunting wild pigs (El Bizri *et al.*, 2015). Our online survey did not reach producers that live in rural areas and are the most affected by wild pigs. However, all respondents of our in-person survey are producers and reported losses by wild pigs and are in the field controlling wild pigs. Hunting was the main technique used for

controlling wild pigs since 2013 because of readily available tools and expertise, even after nationwide prohibition of 1967 Federal Law (5197/1967; but see Deberdt and Scherer 2007 for specific game species in southern Brazil). Wild pig controllers used the same techniques (stand and persecution with dogs) as for poaching native species (Alves *et al.*, 2016), probably because hunting culture was maintained through generations, especially in the rural areas (Fernandes-Ferreira e Da Nóbrega Alves, 2014; Alves *et al.*, 2016). In many cases, poachers are the same individuals now involved on wild pig control (Desbiez *et al.*, 2011).

Recreational hunting is still a tool being used to help reduce wild pig population numbers, including Europe (Nores *et al.*, 2008; Acevedo *et al.*, 2009; Massei *et al.*, 2015) and the United States (Heffelfinger *et al.* 2013). Hunting with dogs is one of the main techniques applied for sport hunting and pest population control worldwide (Maillard e Fournier, 2014; Sparkes *et al.*, 2016). In Brazil, the use of dogs was the most viable way to deal with the wild pig problem initially, and still is the dominant technique used by many controllers. The main reasons leading the use of dogs are the reduced amount of documentation requirements (especially when compared with guns) and availability of trained animals. Furthermore, there is still a very strong, traditional dog hunting culture, especially in the border with Uruguay. Dogs generally assist by detecting, flushing, bailing, lugging and/or retrieving prey, increasing the probability of success (Godwin *et al.*, 2013; Koster e Noss, 2014). They are very efficient in removing residual wild pig populations after other more efficient methods (e.g. trapping) have been used, or where other methods of hunting or pest control are ineffective because of rough or steep terrain and thick vegetative cover (Sternler e Barrett, 1991; Caley e Ottley, 1995; Mowbray, 2002; Parkes *et al.*, 2002). However, if used alone, hunting with dogs is less effective for large-scale reductions in population (Caley and Ottley 1995), potentially facilitating species dispersal. Caley and Ottley (1995) stated that an increasing number of pigs in a sounder do not correspond to an increased number of pigs caught by dogs, which generally capture less than 3 pigs per encounter, independent of sounder size. Despite the benefits of hunting with dogs, domestic dogs can also pose a risk to human and wildlife health through the transfer of diseases (Hughes e Macdonald, 2013) or wounding and displacing non-target wildlife species (Godwin *et al.*, 2013). To reduce those risks, many hunters worldwide collared dogs with GPS tracking devices, monitoring them during hunting activities

(Maillard e Fournier, 2014; Sparkes *et al.*, 2016). However, in the current scenario, high cost of the equipment and lack of expertise with the technology make GPS-collared dogs unfeasible for most of Brazilian hunters operating at large spatial scales, especially in small communities in rural areas. In addition, using hunting as the main technique for controlling pigs can be a problem if the possible increase in movement and space use by wild pigs results in increases in crop damages (Keuling *et al.*, 2008; Servanty *et al.*, 2011; Thurfjell *et al.*, 2013). Nevertheless, when integrated with other control techniques, such as trapping, aerial shooting and baiting, hunting has been successfully applied to eradicate island populations and control continental populations of wild pigs (Parkes *et al.*, 2010; McIlroy, 2014).

Despite the higher efficiency and practicality of traps (Sterner and Barrett 1991, Caley and Ottley 1995), which was expected to be the most common method among rural communities (Doughty *et al.*, 2015), it was the least used by controllers in our survey. Our sampling was composed mainly by sport hunters which responded to the online survey and were not interested in using traps. Still, even within the group of respondents from the in-person survey, which included a larger proportion of farmers, the use of traps was not commonly reported. Most farmers are unfamiliar with the excessive documentation required by IBAMA, or lack expertise on implementing the technique, many times causing it to fail and to be regarded as inefficient, or even targeting native species, stressing and possibly injuring them (Gannon e Sikes, 2007). The success of the trapping programs depends on a variety of factors, such as topography, season, type of trap, trapping location, effort (number and density of traps and number of days) and financial resources available (Coblentz e Baber, 1987; Massei *et al.*, 2011). The use of traps can be effective to reduce populations in areas of high wild pig density, removing up to 70% of a feral population in a short period of time (McCann e Garcelon, 2008; Massei *et al.*, 2011). However, at low density, wild pigs are more likely to develop trap-aversion behaviour. Also, monitoring and maintaining traps is costly in terms of money, time and human labour. Therefore, traps are usually applied and become very effective in small areas or areas where they can be easily incorporated into the daily routine or integrated in a multi-techniques program (Massei *et al.* 2011). Management programs that used traps as the main control method were very efficient when incorporating other techniques (e.g. stands or hunting

with dogs) to eliminate residual and trap-shy animals (McCann e Garcelon, 2008; Campbell e Long, 2009; Massei *et al.*, 2011).

Overall, effective wild pig control depends on a multitechnique approach because traps can be difficult to manage in remote areas (e.g., mountain areas of Brazil with no trafficable roads), and wild pigs learn to avoid traps and escape and take refuge from hunters (Thurfjell *et al.* 2013, McIlroy 2014). Sport hunters in Brazil spend large sums of money buying equipment (Bizri *et al.* 2015), which is important for properly performing wild pig population control (e.g., GPS-collared dogs, high-caliber guns). Sport hunting can be used as a tool to minimize crop damages by adjusting hunting effort to crop seasons (Braga *et al.*, 2010). When hunted by dogs, wild pigs tend to seek refuge in crops and riparian forests, possibly expanding their home range (Thurfjell *et al.* 2013). Thus, hunting with dogs should be done after crop harvest and integrated with mass-capture techniques applied during cropping season, to avoid encouraging wild pigs to access agricultural land or livestock (Geisser e Reyer, 2004; Braga *et al.*, 2010; Thurfjell *et al.*, 2013). However, when trapping and hunting techniques are used together in a stakeholder program management, positive effects in reducing population and damage of wild pigs can be achieved (Massei *et al.* 2011). Traps can be highly effective for quick reduction of wild pig populations, especially in small areas (Massei *et al.* 2011), and should be greatly incentivized in Brazil, especially in rural areas where trap maintenance can be included in property management routine. If traps are checked at least once per day, the technique is considered a humane method of wild pig control and nontarget species can be released immediately when captured. Preliminary research conducted by the Environmental Police in Santa Catarina state in southern Brazil showed that if the farmers are trained to install and maintain the traps, wild pig control might be enhanced without threat to native species or relying on off-farm help from hunters. Trapping is the only technique allowed in Brazil as an alternative to hunting, especially for farmers that do not hunt or allow hunter access to their property. In addition, this is the main technique accepted by animal welfare organizations and the general population in Brazil, and public support is important for the success of control and eradication programs (Hulme *et al.*, 2009).

We do not have information about population demographics of wild pigs, so we cannot make conclusions about how selectivity of control affects gender or age category. Prevalence of a specific gender in hunting bags could be either selectivity or

a simply characteristic of the sex ratio of wild pig population (Korytin *et al.* 2002). However, controllers killed both males and females at the same proportion, including pregnant females and piglets, which enhances effectiveness of population control (Bieber and Ruf 2005, Desbiez *et al.* 2009). Brazilian controllers are motivated by the same reasons as are native species poachers —the thrill of chasing target species and consuming game meat (Bizri *et al.* 2015, Alves *et al.* 2016). Even when the main objective is property defense, controllers were using wild pigs as a resource by consuming the meat as a protein complement; in some cases, they reported preference for females and piglets over adult males for meat quality. Transportation and destination of carcasses and meat is still one of the most discussed and polemic subjects related to wild pig control. The NI 03/2013 strictly prohibits the transportation of live wild pigs, and stipulates that carcasses and meat transportation should follow state's sanitary legislation. Despite not addressing meat consumption, NI 03/2013 technically allows meat to be used only on site. Some hunters reported being penalized by government agents because they had transported wild pig meat or carcass. The lack of technical understanding and broad-perspective analysis from regulatory officials and other players involved in legal discussions (e.g., Farmers' Federation, animal protection societies, hunter's representatives) is a recurring matter that adds more instability to discussions regarding wild pig control in the country. Sport hunting, as carried out by volunteers, is the dominant tool for wild pig control in Brazil. These volunteers found that the wild pig population control program is a legal way to hunt, despite that activity not being explicitly allowed by Brazilian laws. In addition, many illegal controllers showed interest in applying for authorization to avoid legal prosecution. Legally, the Brazilian government treats wild pigs only as a problem, but it is inevitable that the government consider them as a resource because demand for game meat tends to exceed supply in the tropics (Tisdell, 1982; Robinson e Bennett, 2004). If Brazil did treat wild pigs as a resource, high-pressure hunting on wild pigs could eventually decrease poaching pressure on native species (Desbiez *et al.*, 2011). However, recreational hunting could represent a double-edged sword because the objectives of hunting to control alien populations are different from those for trophy hunting (Engeman *et al.*, 2007). In addition, establishment of a legal wild pig market with commercial hunting grounds and commerce of live-trapped wild pigs for slaughter

have been identified as major factors negatively influencing effectiveness of population control in Texas, USA (Bodenchuk e Vercauteren, 2016).

MANAGEMENT IMPLICATIONS

There was a 24-year gap between wild pig invasion and legalization of wild pig control in Brazil, which potentially helped increase wild pig populations and their conflicts with human activities (Massei *et al.*, 2015). Government investment and involvement in the matter has been insignificant so far; therefore, we support sport hunting of wild pigs in Brazil as a means to control populations. Sport hunting should focus on priority areas and seasons and be aligned with needs of stakeholder groups to facilitate a feasible strategy for keeping wild pig populations at low levels. There is also a need to adapt the NI 03/2013 to simplify the process of legalizing and encouraging use of traps for stakeholders, and toward implementation of a simple online system for reports. Finally, effects of control techniques for wild pig have been well-studied worldwide (e.g., Parkes *et al.* 2010, McIlroy 2014); however, we need more studies to evaluate the efficacy and selectivity of the different methods in Brazil. Brazil has the highest biodiversity in the world and supports several species with ecological niches and requirements (e.g., peccaries [*Pecari tajacu*, *Tayassu pecari*]) similar to those of wild pigs. Thus, it is important to evaluate whether control techniques being used for wild pigs are affecting native fauna by killing, injuring, or stressing them.

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Supplementary Information

Questionnaire

Assessment questionnaire for control methods and regulation processes related to wild pig control in Brazil.

GENERAL INFORMATIONS – PROFILE OF WILD PIG CONTROLLERS

I. Current city and state: _____

II. Age: _____

III. Education level: () Primary () High school () Undergraduate degree () Graduate degree

IV. Monthly income:

() Up to US\$242.00 () Up to US\$358.00 () Up to US\$510.00 () Up to US\$835.00

() Up to US\$1,637.00 () Up to US\$2,894.00 () Above US\$2,894.00

QUESTIONS

1. How many wild pigs did you kill in the last 12 months??

2. From those that you killed, how many were: ____ Females
____ Males ____ Piglets

3. From those that you killed, was any female pregnant? () No () Yes.
How many? _____

4. Did you perform wild pig control in your own property? () Yes. () No

5. Did you perform wild pig control in third-party property? () Yes. () No

6. Did you perform wild pig control in Environmental Protection Areas?

() No. () Yes.
Which? _____

7. Which method did you use to control wild pig?

- Active search on horse Alone In group
 Active search on foot Alone In group
 Active search on vehicle Alone In group
 Active search with dogs Alone In group
 Stand hunting
 Corral trap for several individuals
 Cage trap for one or few individuals
 Snare
 Others.
Specify: _____

8. If you performed wild pig control in group, specify the mean number of people involved: _____

9. Which method did you employ to slaughter wild pigs?

- Firearm Calibers: _____
 Knife Spear/Javelin Cross-bow Archery
 Others. Specify: _____

10. What was your main motivation to perform wild pig control?

- Trophy. Which: _____
 Private property defense Public property defense
 Food Subsistence Complementary protein
 Commercial (sell meat, leather, carcass)
 Commercial (Private company or citizen that perform the control of wild pig as a professional)
 Other _____
—

11. Did you have the IBAMA license, in accordance to the Normative Instruction #03/2013, to control wild pig (CTF-CR of IBAMA)?

- No. Yes. How long? _____

If you check "No", why?

- I started the process but I did not have all required documentation
- I started the process but I did not have financial resources to keep the license
- Lack of time to renew the license
- I started the process but I give up because the bureaucracy
- I started the process but I was unaware on how to keep the license
- I did not start the process because I have no interest that it become regulated
- I did not start the process because I do not know how to do
- I did not start the process because I was uninformed about the regulation and about the IBAMA rules
- Other_____

12. Did you use a registered firearm?

- Yes. In which Authority? Federal Police Army Other:_____
- No I used a non-registered firearm.

Table S1. Summary of laws regarding wild pig lethal control in Brazil until October 2016. Abbreviations: RS - Rio Grande do Sul, SC - Santa Catarina, PR - Paraná and MS - Mato Grosso do Sul states; IBAMA - Environmental Agency, NI - Normative Instruction, SAR – Fisheries and Agriculture State Office of SC, IAP – Environmental Institute of PR, SEMAC – Environmental State Office of MS, SEAPI – Agriculture, Livestock and Irrigation State Office of RS.

Year	Regulations	Context and coverage
1995	IBAMA Ordinance 7/95	Authorized in 11 counties of RS state, for 3.5 months.
2002	IBAMA Ordinance 138/02	Authorized in 11 counties of RS, for one year.
2004	IBAMA NI 25/04	Authorized capture and harvest in all RS, for one year.
2005	IBAMA NI 71/05	Authorized in RS, for undetermined period of time
2007	SAR Ordinance 010/07	Authorized only stands and feeders, forbidding traps and dogs in SC state.
2009	IAP Ordinance 98/09	Authorizes within the Vila Velha State Park in PR state.
2008	IBAMA NI 08/2010	Prohibited the control nationwide in Brazil
2010	SAR Ordinance 1/10	Authorization extended in all SC, maintaining restrictions towards traps and dogs.
2010	SMAC Ordinance 001/10	Partially authorized in MS state, actions restricted to an emergencial Intervention Group
2010	SAR Ordinance 20/10	Authorized in all SC, without restrictions.
2010	SEAPI Ordinance 183/10	Authorized in RS, for undetermined period of time
2013	IBAMA NI 3/13	Authorized nationwide in Brazil, for undetermined period of time.

Table S2: Profile of controllers from online survey

State	Age	Education level	Income
Bahia	46	High school	Above US\$2,894.00
Goiás	29	College degree	Above US\$2,894.00
Goiás	18	High school	Above US\$2,894.00
Goiás	22	High school	Up to US\$358.00
Goiás	21	High school	Up to US\$358.00
Goiás	29	College degree	Up to US\$835.00
Goiás	34	College degree	Up to US\$1,637.00
Goiás	31	High school	Up to US\$1,637.00
Goiás	44	College degree	Up to US\$1,637.00
Goiás	28	Graduate degree	Up to US\$1,637.00
Goiás	46	High school	Up to US\$1,637.00
Goiás	21	College degree	Up to US\$242.00
Goiás	39	College degree	Up to US\$2,894.00
Goiás	31	Graduate degree	Up to US\$2,894.00
Goiás	32	College degree	-
Minas Gerais	51	College degree	Above US\$2,894.00
Minas Gerais	31	Graduate degree	Above US\$2,894.00
Minas Gerais	44	Graduate degree	Above US\$2,894.00
Minas Gerais	41	Graduate degree	Above US\$2,894.00
Minas Gerais	31	College degree	Up to US\$358.00
Minas Gerais	26	High school	Up to US\$358.00
Minas Gerais	25	High school	Up to US\$358.00
Minas Gerais	43	High school	Up to US\$510.00
Minas Gerais	20	College degree	Up to US\$510.00
Minas Gerais	56	High school	Up to US\$835.00
Minas Gerais	27	College degree	Up to US\$835.00
Minas Gerais	-	College degree	Up to US\$835.00
Minas Gerais	37	High school	Up to US\$835.00
Minas Gerais	45	High school	Up to US\$835.00
Minas Gerais	41	College degree	Up to US\$1,637.00
Minas Gerais	33	Graduate degree	Up to US\$1,637.00
Minas Gerais	27	College degree	Up to US\$1,637.00

Minas Gerais	54	College degree	Up to US\$1,637.00
Minas Gerais	26	High school	Up to US\$1,637.00
Minas Gerais	32	College degree	Up to US\$1,637.00
Minas Gerais	20	-	Up to US\$1,637.00
Minas Gerais	30	College degree	Up to US\$1,637.00
Minas Gerais	21	High school	Up to US\$1,637.00
Minas Gerais	24	College degree	Up to US\$242.00
Minas Gerais	27	College degree	Up to US\$2,894.00
Minas Gerais	35	College degree	Up to US\$2,894.00
Minas Gerais	34	Graduate degree	Up to US\$2,894.00
Minas Gerais	29	College degree	Up to US\$2,894.00
Minas Gerais	32	College degree	Up to US\$2,894.00
Minas Gerais	25	College degree	Up to US\$2,894.00
Mato Grosso do Sul	36	High school	Above US\$2,894.00
Mato Grosso do Sul	41	Graduate degree	Above US\$2,894.00
Mato Grosso do Sul	33	College degree	Up to US\$1,637.00
Mato Grosso do Sul	34	Graduate degree	Up to US\$2,894.00
Mato Grosso	28	College degree	Up to US\$510.00
Mato Grosso	57	College degree	Up to US\$1,637.00
-	67	Graduate degree	Above US\$2,894.00
-	-	College degree	Up to US\$242.00
Pará	41	Graduate degree	Above US\$2,894.00
Paraná	29	Graduate degree	Above US\$2,894.00
Paraná	46	College degree	Above US\$2,894.00
Paraná	31	College degree	Above US\$2,894.00
Paraná	19	High school	Up to US\$358.00
Paraná	36	College degree	Up to US\$510.00
Paraná	27	High school	Up to US\$510.00
Paraná	39	College degree	Up to US\$510.00
Paraná	40	High school	Up to US\$835.00
Paraná	37	High school	Up to US\$835.00
Paraná	25	College degree	Up to US\$835.00
Paraná	31	College degree	Up to US\$1,637.00
Paraná	29	High school	Up to US\$1,637.00

Rio de Janeiro	51	Graduate degree	Above US\$2,894.00
Rio de Janeiro	44	College degree	Above US\$2,894.00
Rondônia	19	High school	Up to US\$1,637.00
Rio Grande do Sul	27	High school	Above US\$2,894.00
Rio Grande do Sul	38	Graduate degree	Above US\$2,894.00
Rio Grande do Sul	39	Graduate degree	Above US\$2,894.00
Rio Grande do Sul	37	College degree	Above US\$2,894.00
Rio Grande do Sul	19	High school	Up to US\$358.00
Rio Grande do Sul	32	College degree	Up to US\$510.00
Rio Grande do Sul	40	High school	Up to US\$835.00
Rio Grande do Sul	35	High school	Up to US\$835.00
Rio Grande do Sul	29	College degree	Up to US\$835.00
Rio Grande do Sul	34	High school	Up to US\$835.00
Rio Grande do Sul	25	College degree	Up to US\$835.00
Rio Grande do Sul	28	College degree	Up to US\$1,637.00
Rio Grande do Sul	-	High school	Up to US\$1,637.00
Rio Grande do Sul	18	High school	Up to US\$1,637.00
Rio Grande do Sul	36	Graduate degree	Up to US\$1,637.00
Rio Grande do Sul	34	College degree	Up to US\$1,637.00
Rio Grande do Sul	37	High school	Up to US\$1,637.00
Rio Grande do Sul	-	College degree	Up to US\$1,637.00
Rio Grande do Sul	25	Graduate degree	Up to US\$2,894.00
Santa Catari-	35	College degree	Above US\$2,894.00
Santa Catari-	36	Graduate degree	Above US\$2,894.00
Santa Catari-	29	Graduate degree	Above US\$2,894.00
Santa Catari-	22	High school	Up to US\$510.00
Santa Catari-	-	High school	Up to US\$835.00
Santa Catari-	37	High school	Up to US\$835.00
Santa Catari-	30	College degree	Up to US\$1,637.00
Santa Catari-	31	College degree	Up to US\$1,637.00
Santa Catari-	36	College degree	Up to US\$1,637.00
Santa Catari-	30	College degree	Up to US\$1,637.00
Santa Catari-	19	Graduate degree	Up to US\$242.00
Santa Catari-	27	High school	-

São Paulo	36	College degree	Above US\$2,894.00
São Paulo	59	College degree	Above US\$2,894.00
São Paulo	33	College degree	Above US\$2,894.00
São Paulo	47	High school	Above US\$2,894.00
São Paulo	34	High school	Up to US\$358.00
São Paulo	18	High school	Up to US\$358.00
São Paulo	31	Primary school	Up to US\$358.00
São Paulo	20	High school	Up to US\$358.00
São Paulo	23	High school	Up to US\$358.00
São Paulo	22	High school	Up to US\$510.00
São Paulo	23	High school	Up to US\$510.00
São Paulo	47	Primary school	Up to US\$510.00
São Paulo	24	High school	Up to US\$510.00
São Paulo	25	High school	Up to US\$510.00
São Paulo	29	High school	Up to US\$835.00
São Paulo	23	College degree	Up to US\$835.00
São Paulo	31	College degree	Up to US\$835.00
São Paulo	47	College degree	Up to US\$835.00
São Paulo	24	High school	Up to US\$835.00
São Paulo	39	College degree	Up to US\$1,637.00
São Paulo	41	College degree	Up to US\$1,637.00
São Paulo	29	High school	Up to US\$1,637.00
São Paulo	37	High school	Up to US\$1,637.00
São Paulo	28	College degree	Up to US\$1,637.00
São Paulo	27	Graduate degree	Up to US\$1,637.00
São Paulo	35	Graduate degree	Up to US\$1,637.00
São Paulo	47	High school	Up to US\$1,637.00
São Paulo	57	College degree	Up to US\$2,894.00

CONCLUSÃO

Atualmente os suídeos asselvajados encontram-se distribuídos amplamente no Brasil e em algumas regiões já constituem a principal biomassa de vertebrados silvestres (Beca *et al.*, 2017; Brocardo *et al.*, 2018). Dados de 2016 do Plano Nacional de Prevenção, Controle e Monitoramento do Javali (*Sus scrofa*) no Brasil (PAN-Javali, 2017) apontavam ocorrência em 563 municípios e 45 Unidades de Conservação. Dados mais atuais do Ministério da Agricultura referentes ao ano de 2018 apontam presença de suídeos asselvajados em 1135 municípios em todas as regiões e biomas do país (Fig 1, MAPA, 2019), número quase 2.5 vezes maior do que aquele levantado em 2014 (Capítulo 1, Pedrosa *et al.* 2015). Só o estado de São Paulo viu saltar de 17 o número de municípios com ocorrência em 2007 para mais de 300 em 2018 (dados de acesso público da SMA-SP).

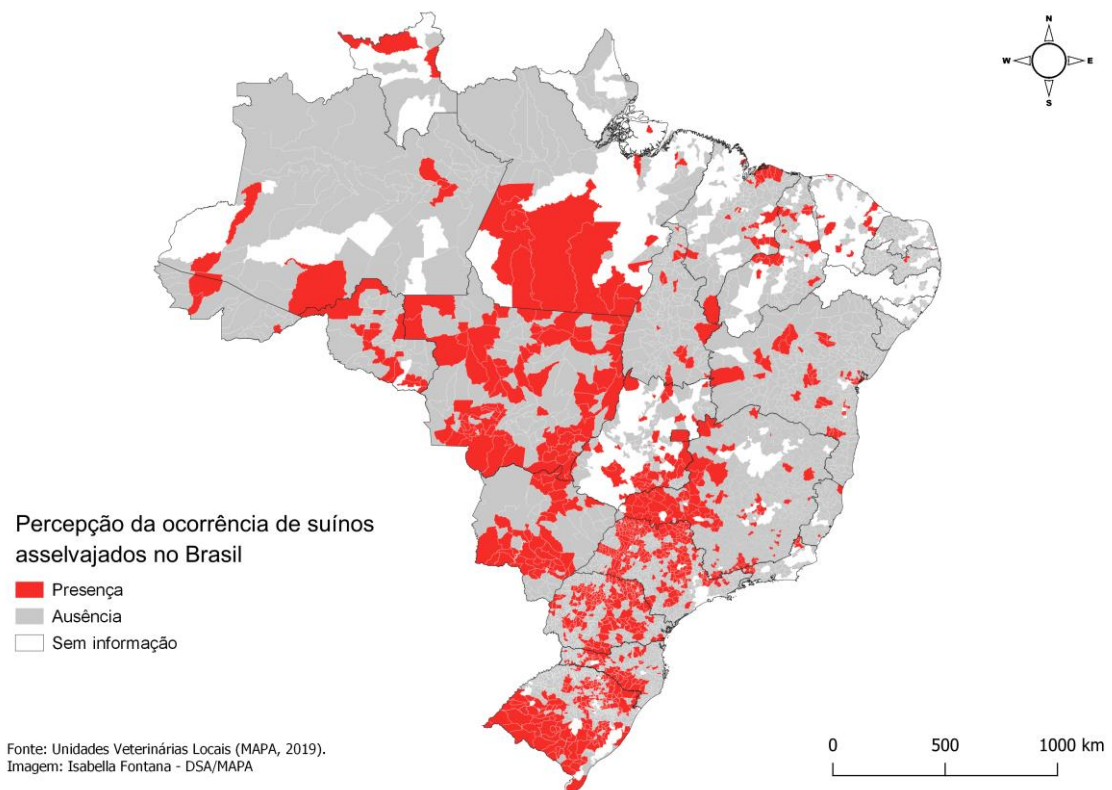


Figura 1. Percepção da ocorrência de suídeos asselvajados no Brasil, obtidos mediante aplicação de questionário eletrônico, elaborado pelo Departamento de Saúde Animal e Insumos Pecuários – DSA/MAPA e pela EMBRAPA Suínos e Aves, às Unidade Veterinárias Locais do Serviço Veterinário Oficial. Fonte: MAPA, 2019.

Como visto ao longo dessa tese, os suídeos asselvajados podem desempenhar papéis positivos e negativos nos ecossistemas brasileiros, embora não equivalentes. São mega-frugívoros e dispersam sementes de plantas nativas e exóticas, algumas altamente invasoras. Apesar da quantidade de sementes e a variedade de espécies dispersadas ser inquestionável e possuir potencial de dispersar sementes à longas distâncias, característica comparável apenas ao maior frugívoro terrestre Neotropical – a anta –, a qualidade do serviço é bastante variada dependendo da espécie de planta consumida.

Se a semelhança dos suídeos asselvajados com a anta no aspecto quantitativo da dispersão de sementes parece próxima (O'Farrill *et al.*, 2013), o mesmo não pode ser dito para as posições tróficas ocupadas pelo invasor e o ungulado nativo. As antas são essencialmente herbívoros de ambientes florestais (Talamoni e Assis, 2009), já os suídeos são onívoros que, apesar de também utilizarem habitats florestais onde consomem frutos, estão sendo amplamente subsidiados pelas paisagens agrícolas. Este atributo trófico nos ajuda a compreender um aspecto diferencial da qualidade do serviço de dispersão de sementes prestado por essas duas espécies: enquanto as sementes ingeridas por antas são em sua maioria defecadas no interior das florestas (Bueno *et al.*, 2013) – habitat adequado ao recrutamento e estabelecimento de plântulas – sementes ingeridas pelos suídeos asselvajados vivendo em meio à paisagens agrícolas são defecadas em sua maioria em locais inadequados à regeneração florestal.

Em sua distribuição nativa, as populações dos suídeos asselvajados (os javalis) crescem a uma taxa de 5% a 15% anual (Massei *et al.*, 2015), o que significaria uma população 2 vezes maior do que é hoje em apenas 5 a 15 anos. Diferentemente da Europa, o Brasil possui em sua maioria híbridos do cruzamento com o porco doméstico (Gimenez *et al.*, 2003) que podem ter herdado deste a capacidade de gerar proles mais numerosas (Bosse *et al.*, 2014). Aliado à isso, a farta oferta de recursos alimentares presentes nas monoculturas de grãos e biocombustíveis e nos rebanhos brasileiros proporcionam alimento em abundância o ano todo que, somado aos fragmentos de habitats florestais e áreas úmidas que funcionam de refúgio térmico e alternativa de forrageamento na entre-safra, serão de fato o combustível da invasão dos suídeos asselvajados nos próximos anos.

Uma das consequências dessa expansão pode ser o avanço de ocorrência sobre áreas habitadas pelos pecarídeos. Pecarídeos e suídeos asselvajados possuem certa sobreposição de nicho alimentar, de nicho espacial e período de atividade, e em áreas de co-ocorrência poderiam deslocar os nativos, forçando-os a explorar recursos alimentares menos preferenciais, com consequências ainda pouco exploradas. Outra consequência da expansão dos suídeos asselvajados pode ser o aumento nos surtos de raiva (Galetti *et al.*, 2016). Morcegos vampiros são hospedeiros e vetores do vírus da raiva e encontram nos suídeos asselvajados uma presa fácil. Se os suídeos asselvajados prosperarem, assim também poderão prosperar os morcegos vampiros. Ataques à pessoas no campo e acidentes rodoviários são outras consequências que serão mais frequentes com o aumento populacional da espécie (Oliveira *et al.* 2018). Para frear o crescimento populacional dos suídeos asselvajados estima-se que seja necessário uma remoção anual acima de 65% dos indivíduos de uma população (Keuling *et al.*, 2013).

O controle populacional efetuado hoje no Brasil está ocorrendo em sua maioria por caçadores, motivados pela defesa da propriedade, por esporte e consumo da carne (Rosa *et al.* 2018). O IBAMA possui hoje (fevereiro de 2018) cerca de 36.000 CPF's inscritos no Cadastro Técnico Federal código 21-58 (CTF 21-58 – manejo de fauna exótica invasora). Esse número de controladores de suídeos asselvajados são irrisórios se comparados aos de outros países (Sharp e Wollscheid 2009, Finch *et al.*, 2014; Massei *et al.*, 2015). São cerca de 7.5 milhões de caçadores em toda Europa, 13 milhões nos EUA e outras centenas de milhares na Austrália (Sharp e Wollscheid 2009, (Sharp e Wollscheid 2009, Finch *et al.*, 2014; Massei *et al.*, 2015). Muito se especula sobre o aumento da caça de espécies nativas frente à liberação da caça dessa espécie exótica. O fato é que onde se testou essa hipótese viu-se justamente o contrário, suídeos asselvajados funcionando como escudo para a fauna nativa (Desbiez *et al.*, 2011). O conflito de interesses envolvido na estratégia da caça como instrumento de controle é evidente: caçadores não estão interessados no extermínio da população, o que poderia significar o fim de sua atividade (Bengsen e Sparkes, 2016). Porém, assim como a caça descontrolada pode levar populações da fauna ao declínio e mesmo à extinção (Peres e Palacios, 2007; Benítez-López *et al.*, 2017), a caça dos suídeos asselvajados pode ter efeito similar na redução da densidade e crescimento populacional. Talvez por isso a EFSA (a autoridade europeia em saúde

animal) recomende o recrutamento de mais caçadores como estratégia para diminuir as densidades populacionais dessa espécie (Boklund *et al.*, 2018). Apesar do custo financeiro para o Estado ser baixíssimo com a adoção desse método – afinal os caçadores são voluntários – o custo político em se defender publicamente a caça é alto, pois caça é tido como atividade nefasta e cruel contra animais (Bengsen e Sparkes, 2016). O debate sobre se essa conduta é ética ou não está longe de chegar a um consenso, mesmo em casos de controle de espécies nocivas como os suídeos asselvajados, e, portanto, políticas públicas nesse sentido estarão sempre sujeitas a embates judiciais e ao sabor de orientações políticas diversas.

Não existe bala de prata no combate aos suídeos asselvajados (Massei *et al.*, 2011), e se hoje a caça é permitida, não deve ser encarada como a única forma de controle desses animais, muito menos ser proibida no futuro quando novos governantes assumirem a responsabilidade pela gestão do problema. Como alternativa à caça, o uso de armadilhas do tipo bretes e currais que visem a captura do maior número de indivíduos de uma única vez se apresenta como método eticamente aceitável, pois oferece a possibilidade de abate dos animais com o mínimo de sofrimento animal (Massei *et al.*, 2011). O uso de armadilhas do tipo bretes e currais devem ser estimulados, seja na forma de condicionantes para licenciamentos ambientais ou como incentivos financeiros para treinamento de recursos humanos e desenvolvimento tecnológico, a fim de que se capacitem profissionais para lidar com o planejamento e operação das armadilhas e se aprimorem a efetividade da captura – hoje em baixo número e mau utilizados. Tecnologias hoje disponíveis apenas para Exército e demais forças de segurança pública, como binóculos com visão noturna termal e silenciadores de armas de fogo deveriam fazer parte do rol de ferramentas disponíveis para quem pretende fazer o controle populacional de suídeos asselvajados, pois aumentariam bastante a efetividade das ações.

A biodiversidade brasileira é uma das mais ricas do planeta (Myers *et al.*, 2000). Ao mesmo tempo o Brasil é um gigante da produção agrícola. Tendo em vista as ameaças inerentes à biodiversidade e à produção decorrentes de um descontrole populacional que se torna cada vez mais iminente, o manejo de suídeos asselvajados não deveria ser assunto exclusivo de uma pasta ministerial ou de outra. Nos estados que possuem acordo de cooperação em gestão de fauna com o IBAMA, como em SP por exemplo, só existem departamentos e serviços de fauna silvestre dentro da pasta

do Meio Ambiente. Outras pastas deveriam tomar pra si a responsabilidade do assunto, criar serviços semelhantes e somar esforços. A gestão do problema deveria sempre basear-se em informações técnicas, usando a experiência adquirida nos últimos anos de regulamentação do controle populacional em diferentes estados e o que se sabe de sucesso e fracasso no controle populacional da espécie em outros países e ser auxiliado por um corpo técnico capacitado no assunto específico dos suídeos asselvajados. Um dos principais desafios é conciliar interesses dos diversos agentes envolvidos e afetados direta e indiretamente pelo problema e não apenas de grupos de interesse específicos, a fim de criar alianças que facilitem a resolução dos conflitos, caso contrário correremos o risco de aprofundar o problema se forem adotadas políticas públicas equivocadas.

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