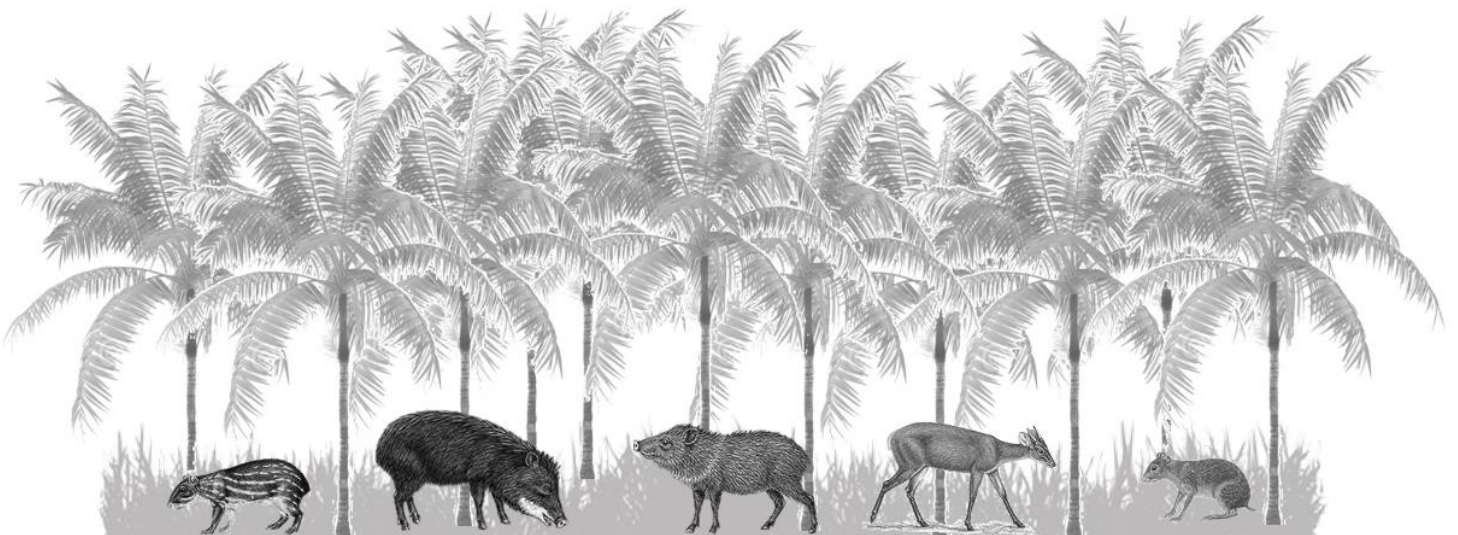# Interação ecológica entre mamíferos terrestres frugívoros e palmeiras neotropicais

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PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA)

INTERAÇÃO ECOLÓGICA ENTRE MAMÍFEROS TERRESTRES FRUGÍVOROS E PALMEIRAS NEOTROPICAIS

Paula Akkawi de Freitas

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SUMÁRIO

1. INTRODUÇÃO GERAL

Desde os primórdios da ecologia, cientistas tentam entender quais fatores levam uma dada espécie estar presente em um dado lugar. Desde Darwin (1859), em sua quase não conhecida obra "A origem das espécies", passando por estudos clássicos de Grinnell (1917), Hutchinson (1957) e (MACATHUR e LEVINS, 1964) o conceito de nicho veio se perpetuando ao longo da história. A teoria clássica de nicho lida essencialmente com competição, e tenta explicar a coexistência entre espécies e seu grau de similaridade (MACARTHUR e LEVINS, 1967; MACATHUR e LEVINS, 1964). Segundo ela, o "nicho" de uma determinada população é descrito como a frequência na utilização de recursos ordenados em uma ou mais dimensões (MACARTHUR e LEVINS, 1967). Entretanto, quando estes recursos se encontram limitados a competição entre co-específicos é esperada, e pode induzir a uma mudança de nicho das espécies, de forma a reduzir suas similaridades (HUTCHINSON, 1957; MACARTHUR e LEVINS, 1967; TILMAN, 1987).

De acordo com a teoria moderna de nicho, a coexistência entre populações similares depende do balanço das diferenças entre nichos e habilidades competitivas de cada espécie, e é o que definirá se tal relação de coexistência será ou não estável (CHESSON, 2000; LETTEN e colab., 2017). Muitas espécies buscam estabilizar tais relações através de mudanças comportamentais, que vão desde o uso diferencial do habitat, a variações na dieta, ou até mesmo em seus padrões de atividade (FINKE e SNYDER, 2008; TOKESHI, 1999). Quando tais alterações comportamentais permitem que duas espécies que possuem alta sobreposição de nicho coexistam, dizemos que naquele sistema há uma partição de nicho (Schoener 1974) .

Um dos primeiros cientistas a comprovar a relação competitiva experimentalmente foi o Gause (1934), estudando espécies diferentes de paramécios. Em seus experimento ele concluiu que quando duas espécies que ocupam o mesmo nicho são colocadas para crescerem na mesma cultura, uma tenderá a excluir a outra, e será denominada como a espécie superior. Desde então, centenas de trabalhos empíricos foram e vem sendo publicados ao longo dos anos, tentando entender e evidenciar relações de coexistência entre espécies similares em diferentes sistemas (Paine 1971, Jaeger 1972, Brown & Davidson 1979, Fleming 1979, Schoener 1983,

Tilman 1986, Bodmer 1991, Valeix et al. 2007, Head et al. 2012, Owen-Smith et al. 2015, Astete et al. 2017, Nagy-Reis et al. 2017).

Apesar de já existirem alguns estudos sobre a coexistência entre mamíferos frugivoros nas florestas tropicais (BODMER, 1991; DESBIEZ e colab., 2009; FERREGUETTI e colab., 2015, 2018; HEAD e colab., 2012; KILTIE, 1982), pouco ainda se sabe sobre como essas espécies se relacionam, principalmente em épocas de poucas chuvas onde os frutos são mais escassos. Além disso, a forte perda e fragmentação de habitat em grande parte dessas florestas faz com que as populações de muitas espécies vegetais sejam reduzidas, o que diminui também a quantidade de recursos disponíveis (HOBBS e YATES, 2003; TABARELLI e colab., 1999). Dessa forma, a sobreposição de nicho entre os mamíferos frugívoros pode acarretar em uma forte disputa por recursos dependendo da comunidade e principalmente da época do ano.

Em uma disputa por recursos entre espécies similares, geralmente uma se sobressairá em relação as outras, sendo portanto conhecida como a competidora dominante. (GAUSE, 1934). Entre espécies frugivoras, características dos frutos, como tamanho, cor, acessibilidade, peso, palatabilidade, nutrientes e fenologia, podem influenciar diretamente nessa inter-relações, e favorecer a exploração de alguns frugívoros em detrimento de outros (GAUTIER-HION e colab., 1985; VAN SCHAIK e colab., 1993). Características morfológicas dos próprios frugívoros também podem influenciar diretamente. Por exemplo estudos apontam que espécies com maiores tamanhos corporais tendem a se sobressair em uma disputa competitiva, em relação àquelas menores (BROWN e MAURER, 1986; HEAD e colab., 2012; VALEIX e colab., 2007). Dessa forma, a competição pode atuar como um forte processo ecológico selecionando taxas de exploração de recursos em frugívoros e determinando padrões de sobreposição e distribuição de espécies (ABRAMS e CHEN, 2002; LETTEN e colab., 2017; MACARTHUR e LEVINS, 1967; WIENS, 1977).

Este estudo levou em consideração a importância das palmeiras como recurso chave para a comunidade de mamíferos frugívoros, para entender como espécies que utilizam esses recursos coexistem. Recursos chaves são considerados pelos cientistas como àqueles que se retirados podem causar o colapso de diversas comunidades (MILLS e colab., 1993; PAINE, 1969; PERES, 2000). Para os mamíferos frugívoros, frutos de palmeiras, grupo vegetal pertencentes a família Arecaceae, podem ser considerados como um recurso alimentar chave, já que são responsáveis pela manutenção de diversas populações (GALETTI e ALEIXO, 1998; TERBORGH, 1986b). Com aproximadamente 500 espécies presentes nos Neotrópicos, e 350 apenas na América do Sul, seus frutos são altamente consumidos por uma variedade de animais

(HENDERSON e colab., 1995). Além de possuírem alta quantidade energética, estes frutos estão presentes em épocas de escassez alimentar, e também são produzidos em grandes quantidades (GALETTI e colab., 2011; GENINI e colab., 2009; STAGGEMEIER e colab., 2017). Em algumas regiões da Amazônia, por exemplo, estes frutos correspondem a 53% do peso de todos os frutos disponíveis, e tendem a ser bastante consumidos pela guilda dos mamíferos frugívoros (BODMER e WARD, 2006; FRAGOSO, 1998; TERBORGH, 1986a).

Nós optamos por utilizar os modelos de ocupação para duas espécies já que estes são considerados um bom método estatístico para se estudar a competição interespecífica entre espécies (FERREGUETTI e colab., 2015, 2018; NAGY-REIS e colab., 2017; WANG e colab., 2015) . Através de dados de presença/ausência, tais modelos permitem avaliar as probabilidades de presenças das espécies de forma independente, e em situações de influência de uma sobre a outra, levando em conta as detecções imperfeitas (falsas ausências) e a influência de covariáveis (MACKENZIE e colab., 2006, 2004; RICHMOND e colab., 2010). Os modelos de ocupação dividem a probabilidade de presença em dois parâmetros, um de ocupação que avalia a probabilidade de uma espécie estar presente em um sítio i, e um de detecção que avalia a probabilidades de uma espécie ser detectada em um sítio i em um tempo t, dado que ela está presente. Os modelos de ocupação para duas espécies utilizam destes dois parâmetros para estimar como a presença ou detecção de uma espécie pode afetar a detectabilidade de outra, expandindo para oito o números de parâmetros, e criando o que chamam de modelos condicionais (Fig. 1).

Nosso estudo utilizou os modelos de ocupação para duas espécies para avaliar como espécies similares de mamíferos frugívoros coexistem em duas áreas de Mata Atlântica, uma ilha de grande extensão situada no litoral sul do estado de São Paulo, e um remanescente menor, situado no interior do mesmo estado. Nosso objetivo foi comparar os padrões encontrados da inter-relação nestas duas áreas, tendo as palmeiras como recurso de possível disputa. Dessa forma, essa dissertação foi dividida em dois capítulos, cada qual apresentando os resultados de cada área.

ESSA DISSERTAÇÃO ESTÁ DIVIDIDA EM 2 CAPÍTULOS

1ºCapítulo: Quantificamos como três espécies de mamíferos terrestres frugívoros, Tayassu pecari, Pecari tajacu e Dasyprocta azarae coexistem e interagem com os frutos de três espécies de palmeiras, Euterpe edulis, Syagrus romamzoffiana e Syagrus oleracea, em um remanescente pequeno de floresta estacional semidecidual da Mata Atlântica.

2ºCapítulo: Quantificamos como uma comunidade de mamíferos terrestres frugívoros, Tayassu pecari, Pecari tajacu, Dasyprocta leporina, Cuniculus paca, e Mazama gouazoubira, coexistem entre si, e interagem com os frutos de uma espécies chave de palmeira, o palmito juçara (Euterpe edulis), em um grande remanescente de floresta ombrófila da Mata Atlântica.

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CAPÍTULO 1

PARTITIONING OF PALM RESOURCES AMONGST NEOTROPICAL FRUGIVOROUS MAMMALS

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ABSTRACT

Palm fruits are considered a key resource for tropical terrestrial forest-dwelling mammals. Yet, how hyper-diverse assemblies of frugivores in tropical forests exploit palm resources and coexist despite high diet overlap remains poorly understood. Here, we evaluate how three species of terrestrial frugivorous mammals, the white-lipped peccary (*Tayassu pecari*), their close relative the collared peccary (*Pecari tajacu*) and the agouti (*Dasyprocta azarae*), interact with each other, and with the fruits of three palm species in a tropical Atlantic Forest of Brazil. We used cameras-traps and occupancy models to examine competitive interactions amongst them. Contrary to our expectations, we found no evidence of competitive exclusion amongst these frugivores. White-lipped peccaries primarily exploited areas of large abundance of the hyper-dominant palm *Euterpe edulis*, whilst agoutis concentrated their foraging on areas with large abundances of *Syagrus oleracea* and, to a lesser extent, *Syagrus romamzoffiana*. White-lipped peccaries also responded positively to *Syagrus oleracea*, but only when agoutis were absent. Collared peccaries preferred areas of high abundance of *Syagrus romamzoffiana* where the other two species showed low detection or were absent. These results suggest that despite occupying similar habitats, being active during the same hours and sharing similar palm resources in an isolated forest fragment, behavioural strategies of these species allow them to coexist.

Keywords: Tropical forests; camera-trap; competition; co-occurrence; frugivores.

RESUMO

As palmeiras são consideradas um recurso chave para os mamíferos terrestres tropicais. Entretanto, como as hiper-diversas guildas de frugívoros das florestas tropicais exploram recursos de palmeiras e coexistem, ainda é pouco compreendido. Neste trabalho, avaliamos como três espécies de mamíferos frugívoros terrestres, o queixada (*Tayassu pecari*), seu parente próximo, o cateto (*Pecari tajacu*) e a cutia (*Dasyprocta azarae*) interagem entre si e com os frutos de três espécies de palmeiras em uma floresta tropical da Mata Atlântica do Brasil. Utilizamos armadilhas fotográficas e modelos de ocupação para examinar as interações competitivas entre eles. Ao contrário de nossas expectativas, não encontramos evidências de exclusão competitiva entre esses frugívoros. Os queixadas exploraram principalmente as áreas de grande abundância da palmeira hiper-dominante *Euterpe edulis*, enquanto as cutias concentraram seu forrageamento em áreas com grande abundância de *Syagrus oleracea* e, em menor escala, *Syagrus romamzoffiana*. Os queixadas também responderam positivamente a *Syagrus oleracea*, mas apenas na ausência de cutias. Os catetos preferiram áreas de alta abundância de *Syagrus romamzoffiana* onde as outras duas espécies apresentaram baixa detecção ou estavam ausentes. Estes resultados sugerem que, apesar de ocuparem habitats semelhantes, estarem ativos durante as mesmas horas e compartilharem recursos de palmeiras semelhantes, as estratégias comportamentais dessas espécies permitem que elas coexistam.

Palavras-chaves: Floresta tropical; armadilhas fotográficas; competição; modelos de ocupação; frugivoros.

1. INTRODUCTION

Tropical forests are an ideal natural laboratory to study species coexistence, as they hold hyper-diverse communities of animals and plants (Hubbell, 2001). Frugivory is ubiquitous component of tropical forests and diverse guilds of birds and mammals feed on a variety of fruits (Bello et al., 2017; Donatti et al., 2011). Fruits provide abundant resources to animals on the wet season, but during seasons when fruit production is low, shortage of resources can lead to diet overlap among frugivorous species and promote competition (Fleming, 1979; Head, Robbins, Mundry, Makaga, & Boesch, 2012; Smythe, 1986; Valeix, Chamaillé-Jammes, & Fritz, 2007).

How different frugivores explore different fruit species has been studied for a long time (Bodmer & Ward, 2006; Gautier-Hion et al., 1985; Smythe, 1986; Terborgh, 1986a), yet there is a lack of information on how similar frugivores share the same resources, especially when these are in shortage. Fruit traits such as seed size, display colour, accessibility, weight, palatability, nutrients and phenology, may favour exploitation by some frugivorous species over others in times of low availability, depending on frugivore morphological and physiological characteristics (Brown & Maurer, 1986; Gautier-Hion et al., 1985; Ilse & Hellgren, 1995; van Schaik, Terborgh, & Wright, 1993). Body mass, for instance, can be a major determinant of access to fruits at times of food shortage. For instance, forest African elephants exclude gorillas and chimpanzee from fruiting trees during periods of low fruit abundance in the rainforests of Gabon (Head et al., 2012). Morphology is also limiting: difference in bite force, for example, can directly influence exploitation of fruits and might promote niche partitioning and coexistence amongst peccary species in tropical forests (Kiltie, 1982). In this way, competition may act as a major ecological process selecting resource exploitation rates in frugivores and determining species overlap and distribution patterns.

Palm fruits are considered key resources for the maintenance of frugivores in tropical forests (Terborgh, 1986b). Palm species are among the most abundant arboreal elements in tropical forest (ter Steege et al., 2013) and their fruits are rich in energy and available in large quantities (Staggemeier, Cazetta, & Morellato, 2017). In some regions of the Amazon forest, palm fruits correspond to 53% of the weight of all fruits available, and many terrestrial frugivorous mammals tend to feed on them regularly (Bodmer & Ward, 2006; Fragoso, 1998; Terborgh, 1986b). This high diversity of frugivores feeding on palms however, causes diet overlap in different consumers (Muñoz, Trøjelsgaard, & Kissling, 2019), and might promote competition, especially in closely related species (Mayfield & Levine, 2010).

Here we assess whether three species of terrestrial frugivorous mammals, the white-lipped peccary - Tayassu pecari, collared peccary - Pecari tajacu and the agouti - Dasyprocta azarae, might be competing for palm fruits in a forest fragment in the Atlantic Forest of Brazil. These three mammal species are known to consume palm fruits regularly (Beck, 2006; Galetti, Zipparro, & Morellato, 1999; Keuroghlian & Eaton, 2008; Smythe, 1986). Previous studies have shown some degree of diet overlap and suggest spatial (Bodmer, 1991) and temporal avoidance (Galetti, Camargo, et al., 2015) between the peccary species, but whether this results from resource partitioning or competitive exclusion from a dominant peccary species on the other remains poorly understood (Ferreguetti, Davis, Tomas, & Bergallo, 2018; Fragoso, 1999). We examined how these frugivorous species exploit different species of palms and evaluated for competitive exclusion using occupancy modelling applied to camera trap data. We predicted that the white-lipped peccary, because of its larger body and group size (Beck, Keuroghlian, Reyna-Hurtado, Altrichter, & Gongora, 2017; Brown & Maurer, 1986; Kiltie & Terborgh, 1983), would overcompete the other two species at its core resource. Accordingly, we would expect that detection probabilities of the potentially subordinate collared peccary and agouti would decrease in palm resources exploited by white-lipped peccaries. We also evaluated for an effect of the collared peccary on the agouti, e.g. a hierarchy of dominance amongst peccaries.

2. MATERIALS AND METHODS

2a. Study site and palm species

The study was conducted at the Ecological Station of Caetetus, Gália, São Paulo, Brazil (hereafter ESC, 22º30' S, 49º45'W), an 2178 ha Atlantic Forest remnant (Fig. 1A) that holds a complete community of large and medium sized forest-dwelling frugivorous mammals (Table S1). Three palm species are present at ESC, whose fruits are consumed and dispersed by mammalian frugivores: Euterpe edulis, Syagrus romanzoffiana and Syagrus oleracea (Fig. 1B). E. edulis, commonly referred as "juçara", occurs in dense patches associated with water bodies, restricted to 1% of the area (Keuroghlian & Eaton, 2008). E. edulis are hyper-fecund (873-3365 fruits/bunch) that produce ~1 cm lipid rich fruits (Galetti et al., 2011; Paludo, da Silva, & dos Reis, 2012). Syagrus romanzoffiana and S. oleracea, commonly named as "jerivá" and "guariroba", are abundant across the study area, and occur in mature forest formations in both humid valleys and drier regions, which are the majority of ESC vegetation (Keuroghlian & Eaton, 2008). S. romanzoffiana produce ~562-1031 fruits/bunch of fibrous sugar-rich fruits,

while S. oleracea is the less fecund palm, 10~ 217 fruits/bunch of fibrous protein-rich fruits (Coimbra & Jorge, 2011; Dias, Laureano, & Ming, 2014; Galetti, Paschoal, & Pedroni, 1992).

2b.Terrestrial frugivorous community

We identified a subset of candidate frugivorous mammals likely to compete for palm fruits based on previous knowledge of their natural history: white lipped peccary Tayassu pecari – heareafter referred as WLP, mean body mass = 27.58 kg; collared peccary Pecari tajacu– heareafter referred as CP, mean body mass = 14.20 kg; agouti Dasyprocta azarae, mean body mass = 3.04 kg; tapir Tapirus terrestris, mean body mass= 220 kg; paca Cuniculus paca, mean body mass = 6.19 kg; and red brocket deer Mazama americana, mean body mass = 30.33 kg (Gonçalves et al., 2018). However, these six species presented different activity periods: whilst tapir, paca and red brocket deer were nocturnal/crepuscular, the two peccary species and agouti were diurnal (Fig. S1). We chose to evaluate competition for palm resources only among species that had the same period of activity because their activity period overlap might increase the likelihood of competition. We focused on the two peccary species and the agouti (Fig. 1C), because these three species have been reported consuming these palm fruits, with WLP in particular considered as a voracious palm consumer (Beck, 2006; da Silva, Begnini, Lopes, & Castellani, 2011; Galetti, Bovendorp, & Guevara, 2015; Keuroghlian & Eaton, 2008) In addition, this allowed us to examine competition between phylogenetically close (peccary-peccary) and distant (peccary-agouti) species.

2c.Camera traps across gradients of resource abundance

We distributed 29 cameras traps from March to September 2017 (Fig. 1A). We opted for a stratified sampling design that could encompass areas with different abundances of the three palm species, and with a minimum distance that could minimize the independence of our data (Fig. 1A). We distributed the cameras across ESC to cover the whole extent of the remnant but also to ensure that areas with different densities of the three palm trees were sufficiently represented in order to answer our study question. This sample design also allowed us to partially control for other factors that might influence the distribution of frugivores at large spatial scales across the study area, with a limited number of camera traps. Cameras were placed in trees stands, 45 cm above the ground. We estimated resource availability to frugivorous mammals by counting the number of fruit caches (attached to the tree) for each of the three palm species separately inside a circular buffer with 30 m of radius, using the camera trap as

the center (Fig. 1A). To ensure that the data collected was spatially independent, we performed a Moran's test using the package "ape " (Paradis, 2012; Paradis, Claude, & Strimmer, 2004; Popescu, Huber, & Paradis, 2012), available in R version 3.4.4 (R Core Team 2019). Moran's tests showed that the number of species recorded at every camera trap location were spatially independent across the scale of the study (Moran's test, z-value = -0.01, p=0.67).

2d.Evaluating competitive interactions through occupancy modelling

To assess the response of frugivorous mammals to palm resource availability, and to evaluate whether there is a competitive exclusion from palm resources among the frugivorous, we used the Two Species Conditional Occupancy Models (Richmond, Hines, & Beissinger, 2010), which is an extension of the occupancy models of MacKenzie et al. (2006). This approach allows the evaluation of how the occupancy and/or detection of a dominant species (species "A") can affect the occupancy and/or detectability of another (species "B"). The modelling framework is represented as a hierarchical tree of occupancy and detectability conditional probabilities, generating eight parameters (Table S2 and Fig. S2).

The analysis included three sets of occupancy models. First, we considered a model set with WLP as the dominant species (=A) and CP as subordinated (=B). WLPs live in large herds, often including more than 100 individuals, dominating ground-dwelling vertebrate biomass in the areas where they occur (Beck, 2006; Galetti, Guevara, et al., 2015; Kiltie & Terborgh, 1983) and physically intimidating other competing species (Keuroghlian & Eaton, 2008; Keuroghlian, Eaton, & Longland, 2004). Similarly, a second set kept WLP as the dominant species (A) and agouti as subordinated (B). Because we also considered that CP might compete for resources with agouti, we generated a third occupancy model set between these two species. In this case, the CP was considered the dominant species (A), due to its larger body size. To evaluate the hypothesis that a dominant species would exclude the subordinate from exploiting its preferred palm resource, the estimates of fruit caches of each palm species for each sampling point were add as covariates into the models. Due to camera trap malfunction and other logistical problems, some cameras traps had different sampling efforts (days of field operation). Therefore, we also introduced as covariate of each sampling point the effort of each camera trap. This, allowed us to verify if the detection estimates of the species were correlated with the number of days that each camera operated.

For every model set, we constructed models based on the following competitive/coexistence hypotheses: 1) competitive exclusion; 2) strict resource partitioning;

3) flexible resource partitioning with partial resource overlap but no competition. To evaluate these hypotheses we modelled the detection probabilities of frugivores as a function of the abundance of fruit caches of the three palms (separately and additively). We concentrated on detection probabilities because they reflect the daily foraging behaviour decisions and the frequency of visits to a certain palm resource, which are essential to evaluate a potential competition for the fruits among them. Occupancy probabilities are better suited for evaluating competitive interactions at the population level, e.g. where the large spatial scale of the study allows for variance in occupancy probabilities of potentially competing species (Mackenzie, Bailey, & Nichols, 2004). A very restricted number of herds of peccaries occur on our study site, occupying almost the entire extent of EEC (see results section), therefore preventing estimating competitive interactions at the population level by modelling variance in occupancy. Instead, variance in detection probabilities reflect how individuals respond to resources and presence of potential competitors. Under the competitive exclusion hypothesis, frugivores exploit the same palm resources areas, but the detection of the dominant species negatively interferes in the detection of the subordinate (pB>rBA/rBa, Fig. 2 and Table S2). Under the strict resource partitioning hypothesis, frugivores exploit different palm resources areas without any effect of the dominant species on the subordinate (pB=rBA/rBa or pB#rBA/rBa, but species do not overlap on the same palm resource area). Finally resource partitioning can also occur through partial resource overlap but no competition if different frugivores exploit palm areas with different intensity (pB=rBA/rBa or pB<rBA/rBa, and species showing different responses at every palm resource). In essence, the slope (beta parameter) of the detection probability of a frugivore in response to different palm resource availabilities describes the interaction strength between consumer and resource, and by using Two Species Conditional Occupancy Models we were able to evaluate how these change in the presence or absence of a potential competitor.

We used Program MARK to perform the analyses (MacKenzie et al. 2006). We constructed a matrix with a total encounter history of 167 occasions, each representing one day of camera trapping. To rank the best models, we used the Akaike's Information Criterion corrected for small sample sizes (AICc - Hook & Regal 1997). Those with ΔAICc < 2 and the highest AICc weight were considered the best models, because of their higher level of empirical support (Burnham & Anderson, 2004).

3. RESULTS

We accumulated a sampling effort of 3,216 traps/day and recorded 21 species of frugivorous mammals (Table S1). The WLP was the most common species, with 676 occasions

at 24 cameras traps (83% of all traps) and a high occupancy estimate (Table 1). CP were also recorded by 24 cameras traps, but less often (148 occasions), suggesting a similarly high use of the remnant but much lower frequency than WLP. In contrast, only 13 cameras (45% of all traps) recorded the agouti (104 occasions), suggesting a more restricted use in the fragment. The sampling effort of each trap did not influenced neither occupancy or detection estimates of the three frugivores in all the three sets of the Two Species Occupancy analyses.

We did not find any effect of WLP presence on the occupancy and detection parameters of the other two frugivorous species, or of CP on agouti occupancy and detection parameters (Table 1 and Table 2). The best models of the three occupancy analyses showed that the presence or detection of the dominant species did not change the parameters estimated for the subordinates (Table 2). On the contrary, we did find an influence of agouti presence on the detection estimation of both peccary species (Table 2). There was a higher probability of detecting CP at sites where agoutis were present ($pA<rA$ in model 3, Table 1), whilst agouti detection was not affected by CP detection ($pB=rBA=rBa$). This suggests that these species might partially share the same resources at ESC without competing for them (resource overlap without competition). For the WLP, the reverse occurred, so that WLP detection probability was higher at sites where agoutis were absent ($pA>rA$ in model 2, Table 1), whilst agouti detection was not affected by WLP detection ($pB=rBA=rBa$). Whilst this suggests that agoutis outcompeted WLPs where they co-occurred, the agouti was absent from one of the core resources of WLPs (Euterpe edulis) suggesting some degree of spatial segregation (habitat partitioning) between these species. Furthermore, despite wide spatial overlap, WLP detection did not change with the presence of CP ($pA=rA$ in model 1, Table 1), and vice versa ($pB=rBA=rBa$).

Regarding palm fruits, the best models revealed that the WLP responded positively to fruit production of all three palm species in both model sets (Table 2, Fig. 3). WLP response to E. edulis and S. romanzoffiana were the stronger whilst response to S. oleracea was the weakest, with detection rates reaching 0.75, 0.8 and 0.3, respectively, at areas with high fruit crop abundance (Fig. 3 and Fig S3). In contrast to the WLP, the CP showed a strong negative response to E. edulis, with detection estimates dropping to zero in areas of high concentration of this palm. Surprisingly, there was no record of agouti in areas with E. edulis palms, suggesting no or weak exploitation of this palm by agoutis in our study area. Thus, it appeared that E.edulis was an important resource for the WLP, but not for the other two species considered.

Both WLPs and agoutis showed a strong positive response to S. romanzoffiana and appeared to exploit this palm intensively. A positive response of WLPs to S. romanzoffiana fruits only occurred on locations where the agouti was present (Fig. 3), whilst in areas where agoutis were absent, the WLP responded negatively to S. romanzoffiana, having its detection lowered to nearly 0.2 (Fig. 3). In contrast, CP responded positively to S. romanzoffiana, but only in areas where agoutis were absent, and WLPs were rarely detected (Fig. 3). .

Agoutis showed the strongest positive response to S. oleracea, reaching a detection estimate of 0.8 (Fig. 3). WLP positive response to S. oleracea fruit production was very weak and only occurred in areas where the agouti was absent. CP showed no response whatsoever to this palm resource,yet this was the palm resource where CPs showed the largest absolute detection estimates, occurring in the presence of agoutis. Thus, S. oleracea emerged as an important resource for agoutis, and, only marginally, for WLPs, whilst CPs positively response to agoutis appeared mediated by the presence of this palm **.**

4. DISCUSSION

Our results show that terrestrial frugivorous mammals respond strongly to palm fruit production, discriminate between palm fruit resources, and suggest that resource partitioning might be an important process underlying species coexistence among the forest-dwelling tropical frugivores. As predicted from an scenario of resource overlap but no competition (Fig. 2), the three frugivorous species showed a partial overlap of resource use, however, each of them showed distinct resource exploitation strategies and interaction stenghts with their suit of palm resources that appeared to relax competition for resources. The WLP and the agouti largely overlapped on one core resource without competing for it, whilst strongly responded to alternative palm resources not or poorly exploited by the other. In contrast, the CP appeared to exploit palm resources less intensively and in a way that allowed avoiding competition with the other two species.

WLP demonstrated a strong preference for E. edulis patches, a pattern previously observed (Keuroghlian & Eaton, 2008; Keuroghlian et al., 2004). E. edulis palms produce fruits rich fruits with high lipid content, and provide a large amount of energy necessary to sustain large WLP groups (Galetti et al., 2011; Staggemeier et al., 2017), constituting a valuable resource for this species. This may explain the preference of WLP for E. edulis aggregates, even when other resources are available (Keuroghlian & Eaton, 2009). CP and agouti are also known to feed on E. edulis fruits in other forest remnants (Galetti et al 1999, Galetti et al 2015a). However, in ESC, we did not detect agoutis in Euterpe palm patches, and CP avoided them,

corroborating previous findings (Keuroghlian & Eaton, 2009) and suggesting some degree of context-dependent flexibility in the diet of these frugivores. The constant presence of WLP in E. edulis aggregates can be an explanation why CP showed negative response to this palm and agoutis were completely absent, so as to avoid competition with WLPs.

In the case of the CP, it is likely that CPs have developed a behavioural strategy to avoid competition with its a priori dominant close relative in areas where they coexist. Despite both peccary species occupied most of remnant, CP detection estimates were very low, and only showed a positive response to S. romanzoffiana palms when the other mammals were not exploiting that resource. The parameter estimates from our study show no interference between WLP and CP. In the same forest remnant, Keuroghlian et.al. (2004) reported that CP avoided contact with WLP. Diel activity shifts in CP have been recorded in the Pantanal region in the presence of WLP and invasive feral pigs (Desbiez, Santos, Keuroghlian, & Bodmer, 2009; Galetti, Camargo, et al., 2015). Keuroghlian and Eaton (2008) documented a wide spectrum of food items on the dry season for CP, including fruits from the Lauraceae family and native tubers. Other studies record a weak dependency of CP on fruits sources, especially of palms (Desbiez et al., 2009; Judas & Henry, 1999; Keuroghlian & Eaton, 2008). Taken together, this evidence strongly suggests that CPs have more flexible and broader diet breadths than their close WLP relatives (Galetti, Camargo, et al., 2015) allowing them to exploit alternative resources that minimize the probability of competition for food. Furthermore, WLPs showed a negative response to areas with high availability of S. romanzoffiana when agoutis were absent and CP was present, despite of evidence that fruits from this palm are amongst the most consumed by WLP during the dry season (Keuroghlian & Eaton, 2008, 2009). These patterns suggest behavioural avoidance rather than directinterference between the peccaries, and reinforce the hypothesis of resource partitioning between them, as previously suggested (Ferreguetti et al., 2018; Fragoso, 1999).How agouti selected their habitat is another evidence of resource partitioning among these three frugivorous mammals. In contrast to peccaries, agoutis occupied less than 50% of the study area, and were completely absent in the E. edulis aggregates, despite evidence of feeding on this fruit in other forests remnants (Galetti, Bovendorp, et al., 2015; Galetti et al., 1999). Conversely, agoutis showed a positive response to both Syagrus palms, especially S. oleracea. Although S. oleracea fruits present lower lipid content compared to E. edulis, this is higher than in S. romanzoffiana fruits, which have a higher sugar (i.e., carbohydrates) concentration (Borges et al., 2011; Coimbra & Jorge, 2011). Nutritionally, lipids provide more energy than carbohydrates (Coimbra & Jorge, 2011), which might explain agoutis foraging more where S. oleracea have higher densities. In contrast, WLPs

showed a marginal positive response to S. oleracea, and only when agoutis were completely absent. Thus, competition between WLPs and agoutis is discarded from E. edulis (strongly exploited by WLPs) and probably at S. oleracea patches (strongly exploited by agoutis). The fruit of S. romanzoffiana was an important palm resource for both frugivorous species, and the only palm resource where strong competition between these might have occurred.

Results suggest that where agoutis and WLPs co-occurred, detection probability of WLPs was reduced to 42% from where agoutis were absent, whilst agouti detection remained unaffected. Because both species showed strong positive responses to S. romanzoffiana it is possible that competition for these resource might have occurred, with agoutis outcompeting WLPs. However, it is also possible that the apparent negative effect of agouti presence on WLP detection might be precisely a consequence of the spatial segregation between WLPs and agoutis in S. olearacea and complete absence of agoutis from E. edulis aggregates. Furthermore, contrary to what it would be expected in the presence of strong competition, the absence of agoutis from aggregates of S. romanzoffiana indeed caused a negative response of WLP to these. Thus, WLP and agoutis showed partially alternative resource preferences and spatial segregation, and where they palm resource niche overlapped, there was few evidence of competition.

In contrast to the negative effect of agouti on WLP, the detection estimates of CPs when co-occurring with agoutis increased 350%, mostly due to the increase in average detection estimates on S. oleracea in the presence of agouti. This might be an indirect consequence of agoutis negative effect on WLP, or of the spatial segretation between WLP and agoutis, which might have favoured a positive response of CP on areas where agoutis are present so as to avoid WLPs. However, another possible interpretation is sa facilitating role of agouti scatter-hoarding on CPs in the reserve. According to Beck (2006), there is evidence of peccaries preferentially foraging near objects used by agoutis to stock their caches, which might indicate some sort of kleptoparasitism of peccaries upon agoutis. Therefore, agouti scattering behaviour may also influence CPs detection estimates, though this interpretation remains speculative.

Niche partitioning amongst frugivorous species has been already suggested in other studies. For instance, using dietary niches derived from stomach contents of ungulates on continuous areas of the Peruvian Amazon, Bodmer (1991) showed evidence of habitat partitioning between species with similar diets and resource partitioning among species with similar habitat use, at large spatial scales. Previous studies conducted in others tropical remnants, suggest that closely related species might avoid competition through shifting temporal activity patterns (Ferreguetti, Tomás, & Bergallo, 2015; Ferreguetti et al., 2018;

Galetti, Camargo, et al., 2015; Valeix et al., 2007). The species in our study occupied similar habitats, were active during same hours and shared similar palm resources (including two species of palms from the same genre- Syagrus). Even under those circumstances, they displayed a high degree of niche partitioning and spatial segregation that allowed them to avoid strong interference with each other. Of particular interest is the coexistence strategy of both peccary species. Because of their close phylogenetic origin, coexistence between these frugivores under these circumstances would be an a priori unlikely outcome of their interaction unless strong niche partitioning occurs (Mayfield & Levine, 2010). Our results suggest that intense exploitation of key resources by one of these species (e.g. E. edulis and S. romanzoffiana by WLP) and a broader less intense exploitation of a variety of resources by the other (CP) might promote coexistence amongst them, highlighting a critical role of context dependent interaction strengths between these consumers and their resources in promoting coexistence.

It is well known that remnant size and distance from larger and continuous undisturbed environments have a direct role in structuring communities (Chiarello, 1999; Chisholm, Lindo, & Gonzalez, 2011; Leibold et al., 2004; Magioli, Ribeiro, Ferraz, & Rodrigues, 2015). Despite of isolated and reduced area, ESC presents high abundance of food items maintaining a diverse community of frugivorous mammals, which seem to find behavioural strategies that allow them to coexist. A recent study (Beca et al., 2017) showed that the assembly of large mammals in tropical rainforest fragments immersed in a sugar-cane matrix remains intact despite varying degrees of fragmentation and isolation, against all expectations. On a global study, Beaudrot et al., 2019 found that tropical mammal species shower higher colonisation and lower extinction probabilities in areas of ecologically similar species along altitudinal gradients, suggesting positive interactions amongst many closely related herbivore species. In that context, our research adds up to a growing number of studies that suggest that consumer-resource interaction strengths are context dependent and relatively flexible, and therefore might at least partially buffer against strong competition on consumer-resource networks with high resource and spatial overlap. Future studies should assess the role of behavioural strategies and flexible interaction strengths in promoting coexistence amongst sympatric species under different scenarios of habitat fragmentation and isolation, and more generally, under environmental change.

5. ACKNOWLEDGEMENTS

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TABLES AND FIGURES

Table 1: Occupancy (ψ) and detection (p) real parameters of the best models of the three sets of Two Species Conditional Analyses: 1. *Tayassu pecari* vs. *Pecari tajacu, 2.Tayassu pecai* vs. *Dasyprocta azarae* and 3. *Pecari tajacu* vs. *Dasyprocta azarae.*

Real parameters model 1: *Tayassu pecari* vs. *Pecari tajacu*			
Species	Ψ^1	p and r ^{2}	
Tayassu pecari (A)	0.9 (SE=0.06)	pA=rA^3: 0.19 (SE=0.008)	
Pecari tajacu (B)	1* (SE=0.000006)*	pB=rBA=rBa^4: 0.03 (SE=0.005)	
Real parameters model 2: *Tayassu pecari* vs. *Dasyprocta azarae*			
Species	Ψ^1	p and r ^{2}	
Tayassu pecari (A)	0.9 (SE=0.06)	pA: 0.31 (SE=0.01)	rA: 0.13 (SE= 0.01)
Dasyprocta azarae (B)	0.51 (SE=0.09)	pB=rBA=rBa^4: 0.1 (SE=0.008)	
Real parameters model 3: *Pecari tajacu* vs. *Dasyprocta azarae*			
Species	Ψ^1	p and r ^{2}	
Pecari tajacu (A)	1* (SE=0.00001)	pA: 0.02 (SE=0.003)	rA: 0.07 (SE=0.006)
Dasyprocta azarae (B)	0.42 (SE=0.09)	pB=rBA=rBa^4: 0.1 (SE=0.01)	

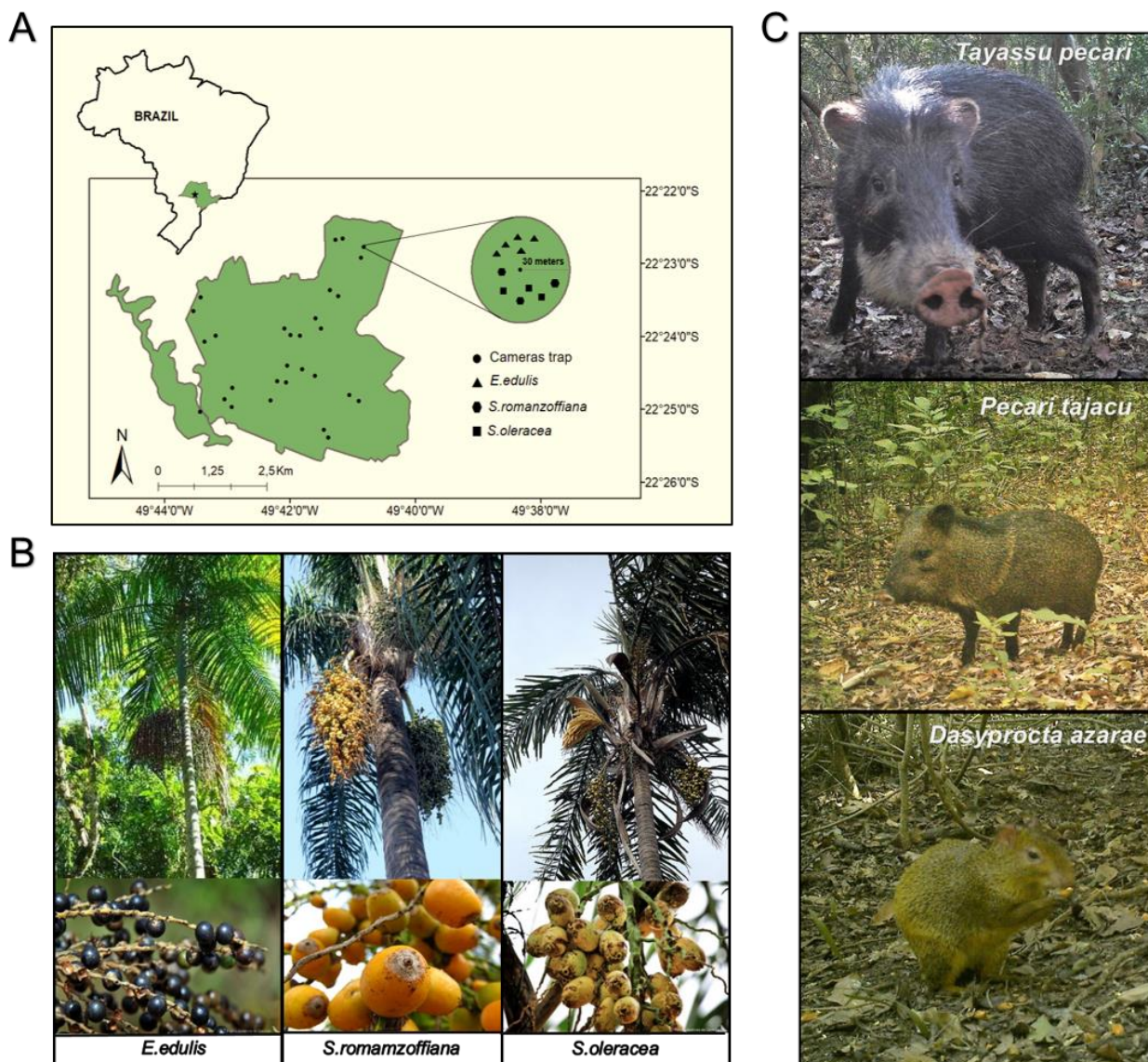[1] ψ = occupancy probabilities,

[2] p and r = detection probabilities

[3] pA=rA: detection probability by species A, considering that species B are absent (pA) is equal to detection probability by species A, considering that both species are present (rA)

[4] pB=rBA=rBa: detection probability by species B, considering that species A are absent (pB) is equal to the detection probability by species B, considering that both species are present, and species A is detected (rBA) and the detection probability by species B, considering that both species are present and species A is not detected (rBa).
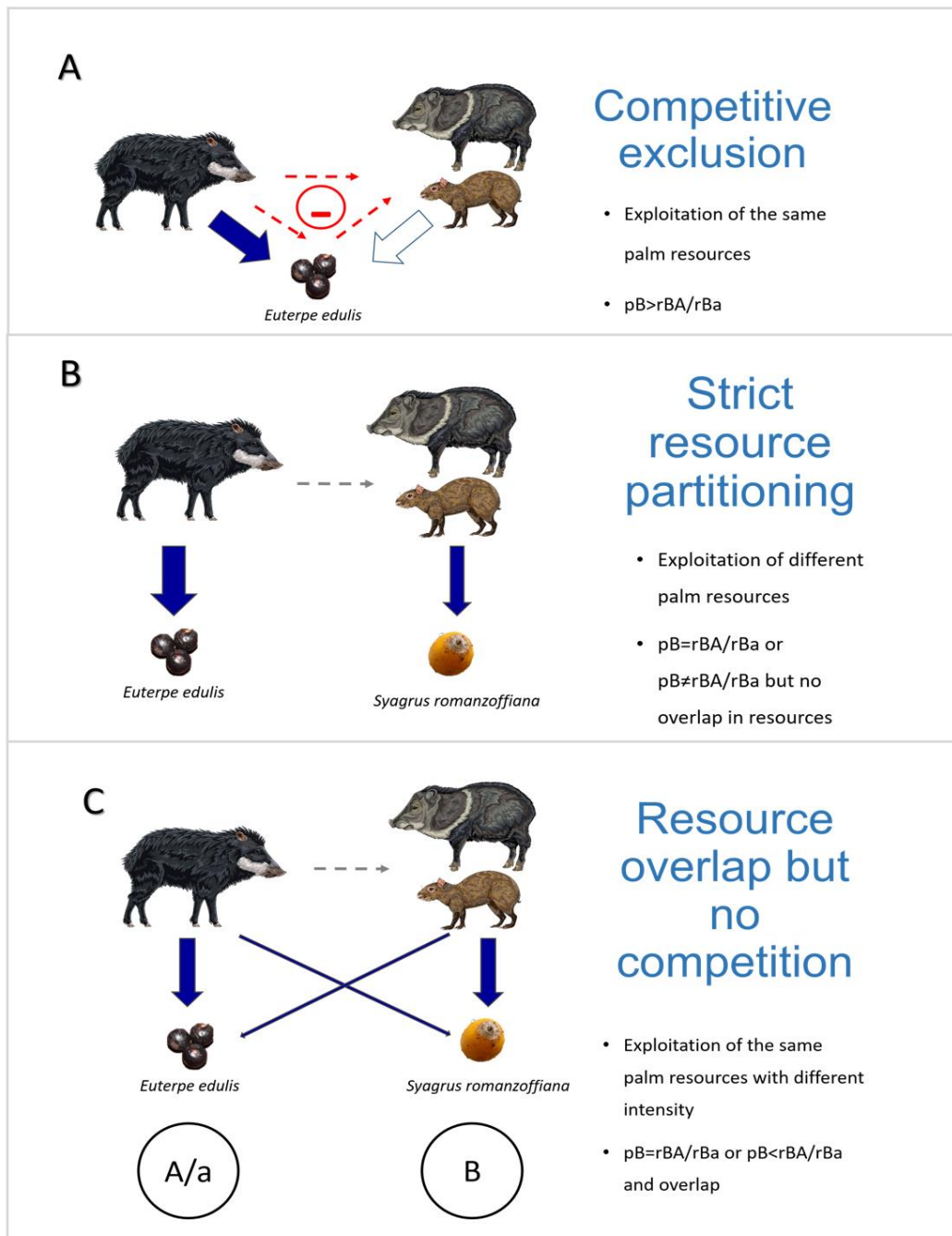
[*] The low detection estimate of *Pecari tajacu* inflated their occupancy probability and precluded the estimation of a sensible SE.

Table 2. Best five models of each of the three sets of Two Species Conditional Analyses: 1. *Tayassu pecari* vs *Pecari tajacu;* 2. *Tayassu pecari vs Dasyprocta azarae*; 3. *Pecari tajacu vs Dasyprocta azarae.* Palms: *juc= E. edulis; jer= S. romanzoffiana; ole= Syagrus oleracea.*
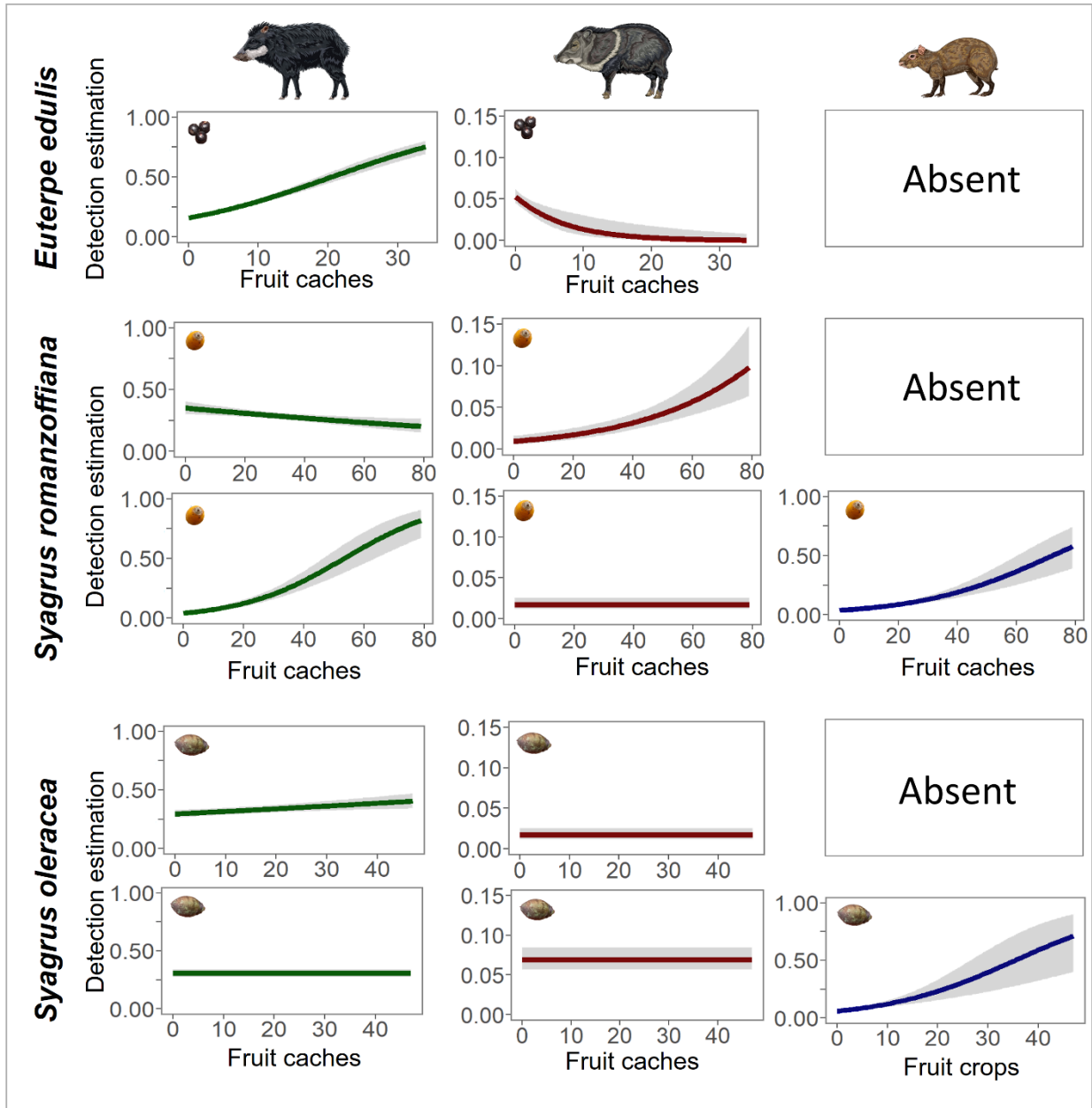
1. *Tayassu pecari* (A) vs. *Pecari tajacu* (B)	AICc	Delta AICc	AICc Weights	Num. Par	Deviance
ψA, ψBA=ψBa, pA= rA(juc+jer+ole), pB= rBA= rBa(jer+juc)	4049.2	0	0.76	9	4021.73
ψA, ψBA=ψBa, pA= rA(juc+jer+ole), pB= rBA= rBa(juc)	4053.25	4.05	0.09	8	4030.06
ψA, ψBA=ψBa, pA= rA(juc+jer+ole), pB= rBA= rBa(jer+juc+ole)	4053.94	4.74	0.07	10	4021.72
ψA, ψBA=ψBa(jer), pA= rA(juc+jer+ole),pB= rBA= rBa(jer+juc)	4053.95	4.75	0.07	10	4021.73
ψA, ψBA, ψBa, pA, rA(juc+jer+ole), pB, rBA= rBa(jer+juc)	4061.2	12	0.001	12	4017.71
2. *Tayassu pecari* (A) vs. *Dasyprocya azarae* (B)	AICc	Delta AICc	AICc Weights	Num. Par	Deviance
ψA, ψBA=ψBa, pA(juc+jer+ole), rA(jer), pB=rBA= rBa(jer+ole)	3457.8	0	0.68	11	3420.27
ψA, ψBA=ψBa, pA(juc+jer), rA(jer), pB=rBA= rBa(jer+ole)	3461.41	3.6	0.11	10	3429.18
ψA, ψBA=ψBa, pA(juc+ole), rA(jer), pB=rBA= rBa(jer+ole)	3461.51	3.71	0.11	10	3429.29
ψA, ψBA=ψBa, pA(juc+jer), rA(juc+jer), pB=rBA= rBa(jer+ole)	3463.01	5.21	0.05	11	3425.48
ψA, ψBA=ψBa, pA(juc+jer+ole), rA(jer+ole), pB=rBA= rBa(jer+ole)	3463.06	5.26	0.05	12	3419.56
3. *Pecari tajacu* (A) vs. *Dasyprocya azarae* (B)	AICc	Delta AICc	AICc Weights	Num. Par	Deviance
ψA, ψBA=ψBa, pA(juc+jer), rA, pB= rBA= rBa(jer+ole)	1880.99	0	0.57	9	1853.51
ψA, ψBA=ψBa, pA(jer), rA, pB= rBA= rBa(jer+ole)	1883.2	2.21	0.19	8	1859.99
ψA, ψBA=ψBa, pA(juc+jer), rA(juc), pB= rBA= rBa(jer+ole)	1885.61	4.62	0.05	10	1853.39
ψA, ψBA=ψBa, pA(juc+jer), rA(jer), pB= rBA= rBa(jer+ole)	1885.73	4.74	0.05	10	1853.51
ψA, ψBA=ψBa, pA(juc+jer), rA, pB, rBA= rBa(jer+ole)	1885.73	4.75	0.05	10	1853.51

Figure 1. A) Location of Ecological Station of Caetetus (ESC), Gália, São Paulo, Brazil. Points show the distribution of the 29 camera-traps across areas with different abundances of fruit caches of the three palm species, *Euterpe edulis, Syagrus romanzoffiana* and *Syagrus oleracea*. The circle shows an example of the distribution and abundance of the three palms species inside the circular buffer with 30 meters of radius measured from the camera-trap. B) The three palm species present in Ecological Station of Caetetus (ESC), and their respective fruits, which are heavily used by terrestrial frugivores: *Euterpe edulis, Syagrus romanzoffiana* and *Syagrus oleracea.* C) The three terrestrial frugivorous mammals of this study: *Tayassu pecari, Peccari tajacu* and *Dasyprocta azarae.*
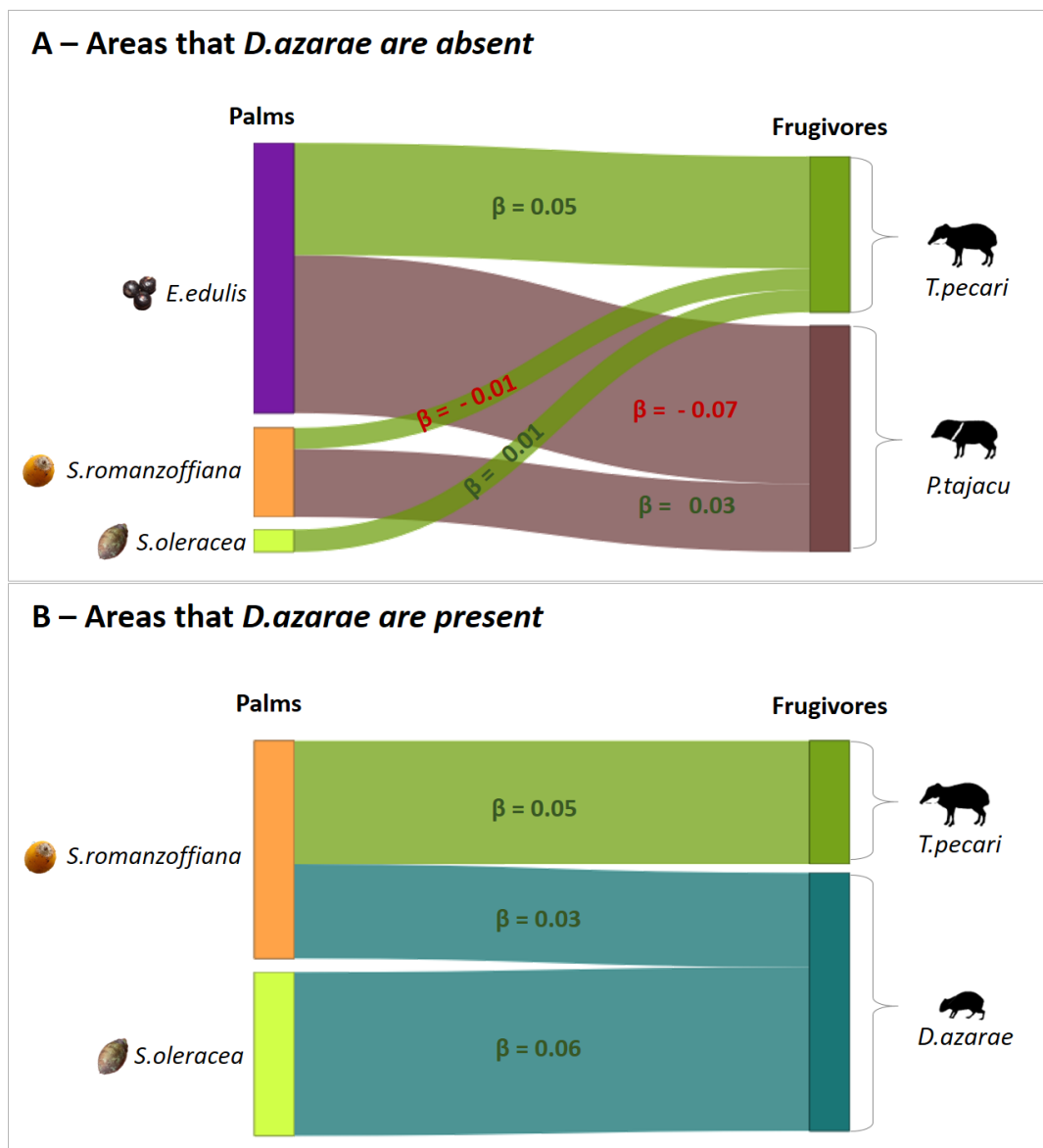
Figure 2. Conceptual representation of hypotheses. A shows competitive exclusion, B shows strict resource partitioning, and C resource overlap with no competition. The thickness of the arrows represents the intensity of the interaction (the thicker the arrow the greater the interaction). Blue arrows represents positive interactions, red arrowns are negative interactions and grey arrows are represents a lack of interaction. Different exploitative strategies and combinations of detection probabilities of a priori dominant or subordinate species in presence and/or absence of the other species can be used as probes to test for different competititive relationships (see methods section for details).

Figure 3. Summary of the relationship among the three species of palm *Euterpe edulis*, *Syagrus romanzoffiana* and *Syagrus oleracea* with the three frugivorous mammals, *Tayassu pecari* (green), *Pecari tajacu* (red) and *Dasyprocta azarae* (blue), in the sites with and without *D.azarae* presence. To see the full set of relationship of all three dominant-subordinate models see Fig S3.

Figure 4. Bipartite network of interactions amongst frugivores and palm species emerging from the Two Species Conditional Occupancy Analyses. The beta values representing interaction strengths (emphasized through the width of the interaction) are derived from best models of the three sets of dominant-subordinate models (see Table S3). Panels A and B represent the interactions in the areas that *D.azarae* did and did not occupy, respectively. Nodes on the left represent the palms *E.edulis* (purple), *S.romanzoffiana* (orange), *S.oleracea* (yellow), and nodes from the right represent the frugivorous mammals *T.pecari* (green), *P.tajacu* (red) and *D.azarae* (blue).

Table S1. Species recorded at Ecological Station of Caetetus (ESC), between March and September of 2017, the number of independent records (independence = 24 hours interval), and the Frequency of Occurrence = number of independent records (independence = 24 hours interval) / sample effort X 100.
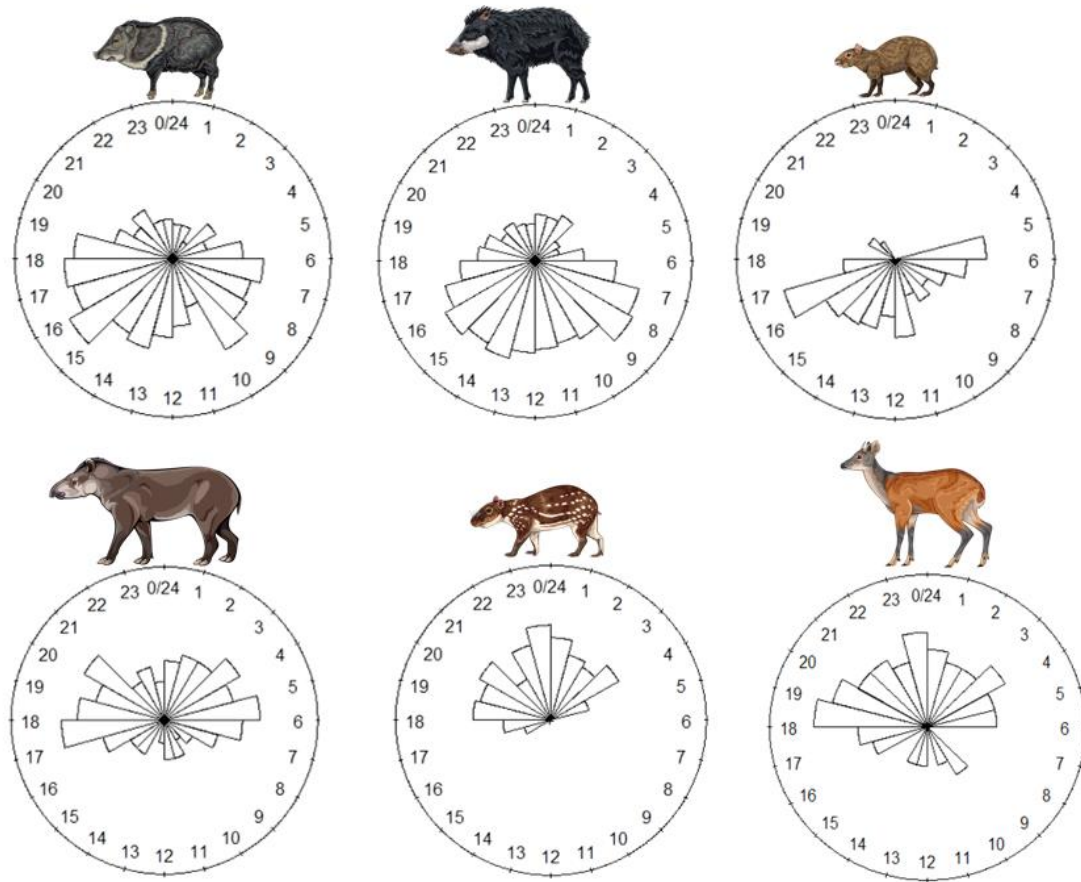
Scientific name	Common name	Independent records (24 hours)	Frequency of occurrence	Traps record
Tayassu pecari	White-lipped peccary	579	18.00	24
Pecari tajacu	Collared peccary	164	5.09	24
Tapirus terrestris	Tapir	142	4.41	24
Didelphis albiventris	White-eared opossum	133	4.13	18
Dasyprocta azarae	Agouti	118	3.67	13
Dasypus novemcinctus	Nine-banded Armadillo	117	3.64	22
Sylvilagus brasiliensis	Tapeti	80	2.49	9
Cuniculus paca	Spotted paca	66	2.05	12
Nasua nasua	South American Coati	51	1.58	17
Mazama americana	Red brocket deer	47	1.46	15
Guerlinguetus brasiliensis	Brazilian squirrel	25	0.78	7
Leopardus pardalis	Ocelot	18	0.56	10
Puma concolor	Puma	16	0.49	11
Eira barbara	Tayra	15	0.46	12
Cabassous unicinctus	Southern Naked-Tailed Armadillo	8	0.24	4
Canis lúpus familiaris	Dog	5	0.15	5
Tamandua tetradactyla	Southern Tamandua	4	0.12	2
Small rodents	Small rodents	4	0.12	2
Leopardus guttulus	Southern Little Spotted Cat	3	0.09	3
Puma yagouaroundi	Jaguarundi	1	0.03	1
Sapajus nigritus	Black-horned Capuchin	1	0.03	1

Table S2. Two Species Conditional Occupancy parameters: Ψ = occupancy; p and r= detection.
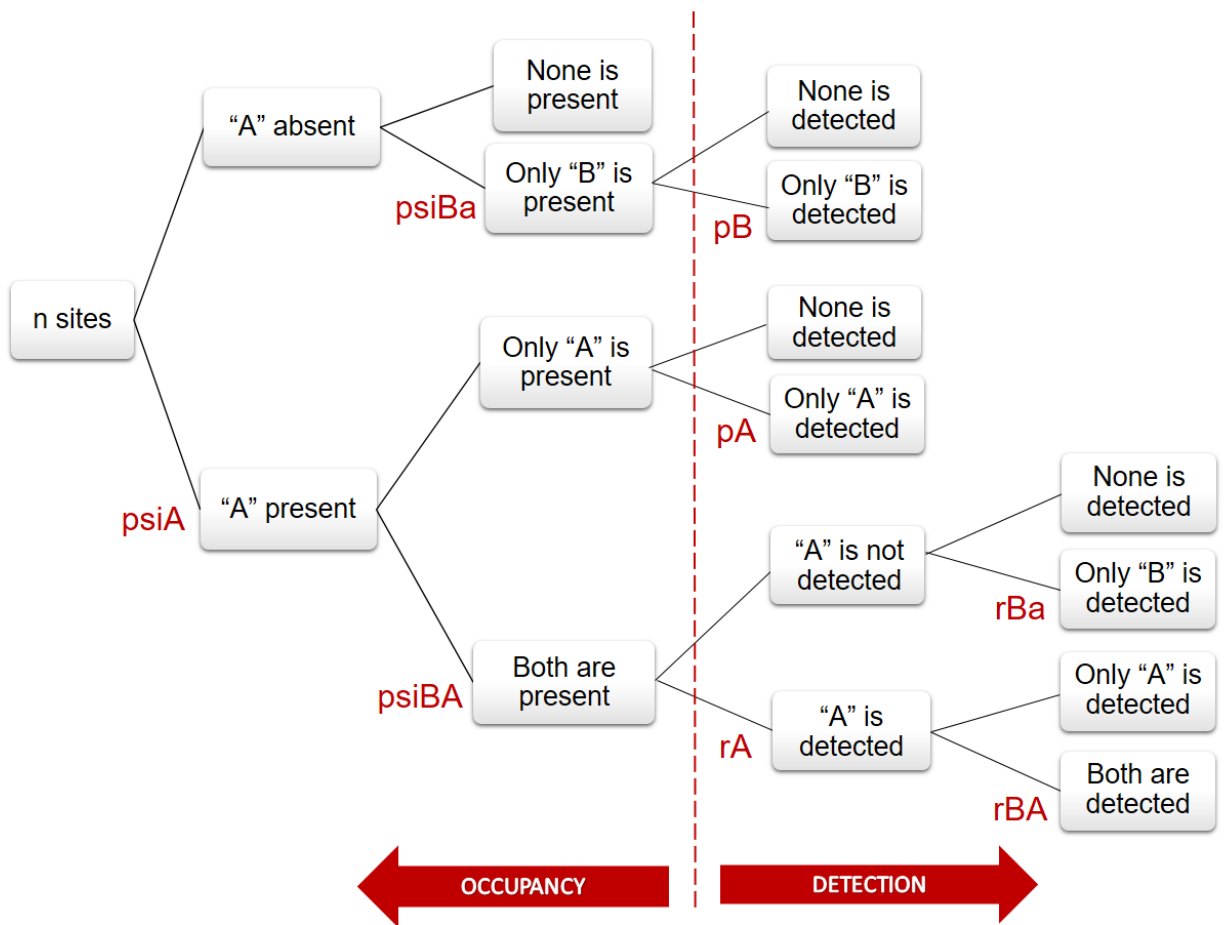
ψA	Occupancy probability by species A.
ψBA	Occupancy probability by species B, when species A is present.
ψBa	Occupancy probability by species B, when species A is absent.
pA	Detection probability of species A, considering that species B is absent.
pB	Detection probability of species B, considering that species A is absent.
rA	Detection probability of species A, considering that both species are present.
rBA	Detection probability of species B, considering that both species are present, and species A is detected.
rBa	Detection probability of species B, considering that both species are present, and species A is not detected.

Table S3. Beta parameters of the detections estimates (p and r) as a function of palms caches of the best models of the three sets of Two Species Conditional Analyses: 1. *Tayassu pecari* vs *Pecari tajacu, 2. Tayassu pecai vs Dasyprocta azarae* and 3. *Pecari tajacu vs Dasyprocta azarae.*
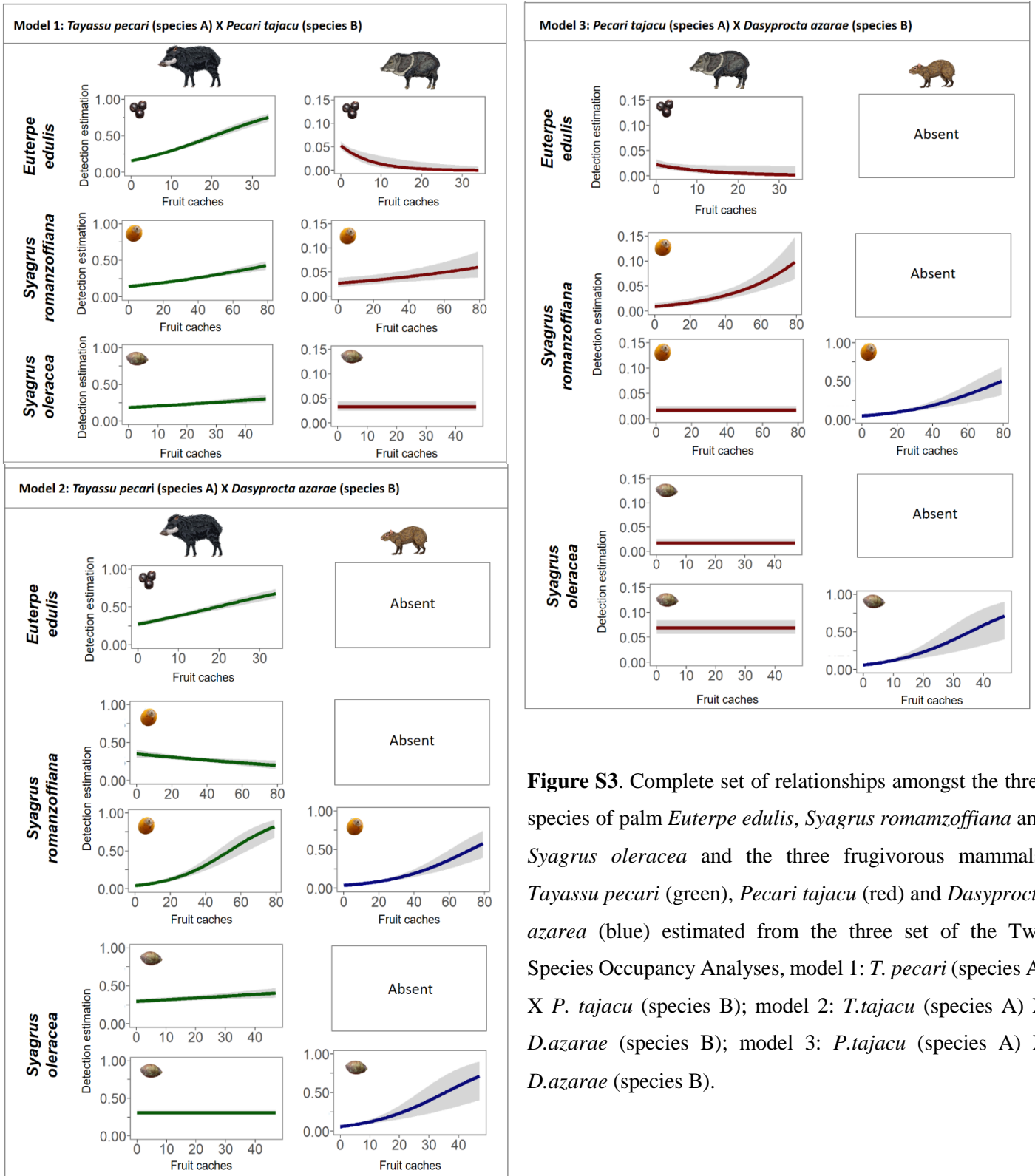
Model 1: *Tayassy pecari* (species A) X *Pecari tajacu* (species B)		
Parameters	Beta	SE
pA = rA X Juçara	0.08	0.00
pA = rA X Jerivá	0.02	0.00
pA = rA X Guariroba	0.01	0.00
pB = rBA = rBa X Jerivá	0.01	0.00
pB = rBA = rBa X Juçara	-0.13	0.04
Model 2: *Tayassu pecari* (species A) X *Dsyprocta azarae* (species B)		
Parameters	Beta	SE
pA X Juçara	0.05	0.01
pA X Jerivá	-0.01	0.00
pA X Guariroba	0.01	0.00
pB = rBA = rBa X Jerivá	0.04	0.01
pB = rBA = rBa X Guarioba	0.08	0.02
rA X Jerivá	0.06	0.00
Model 3: *Pecari tajacu* (species A) X *Dsyprocta azarae* (species B)		
Parameters	Beta	SE
pA X Juçara	-0.07	0.04
pA X Jerivá	0.03	0.01
pB = rBA = rBa x Jerivá	0.04	0.01
pB = rBA = rBa X Guarioba	0.06	0.02

Figure S1. Period of foraging activity of the main frugivorous record at Ecological Station of Caetetus, between March to September of 2017. From left to right: *Pecari tajacu, Tayassu pecari, Dasyprocta azarae, Tapirus terrestris, Cuniculus paca* and *Mazama americana*.

Figure S2. Representation of a hierarchical tree of occupancy and detectability conditional probabilities of the Two Species Occupancy Models, adapted from "http://phototrapping.blogspot.com/2012/01/tutorial-de-modelos-de-ocupacao-para.html" site.

Figure S3. Complete set of relationships amongst the three species of palm *Euterpe edulis*, *Syagrus romamzoffiana* and *Syagrus oleracea* and the three frugivorous mammals, *Tayassu pecari* (green), *Pecari tajacu* (red) and *Dasyprocta azarea* (blue) estimated from the three set of the Two Species Occupancy Analyses, model 1: *T. pecari* (species A) X *P. tajacu* (species B); model 2: *T.tajacu* (species A) X *D.azarae* (species B); model 3: *P.tajacu* (species A) X *D.azarae* (species B).

CAPÍTULO 2

HYPERDOMINANT PALM FRUITS MEDIATES NICHE PARTITIONING IN NEOTROPICAL FRUGIVOROUS MAMMALS

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ABSTRACT

Interspecific competition for resources is considered the main selective factor in distribution and structuring species within a community. Yet, for frugivorous mammals of tropical forests, this ecological relationship is still poorly understood. Here we evaluated how four species of terrestrial frugivorous mammal, white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), paca (*Cuniculus paca*) and grey brocket deer (*Mazama gouazoubira*), share palm patches of *Euterpe edulis,* a key food resource in the Atlantic Forest. We used cameras-traps and occupancy models to examine competitive interactions amongst them. Our results showed no evidence of competitive exclusion amongst these frugivores. White-lipped peccary interact positively with *E. edulis* only when coexisting with the other five species. In the areas where it does not have any competition, we did not find any interaction of the species with this palm. The other four frugivorous did not interact with *E. edulis* in any situation. Additionally, we have found that the probability of detecting white-lipped peccary is higher in the areas where the other frugivorous are absent. Together this evidence indicates that despite occupying similar habitats and sharing similar resources, niche partitioning might underlie the coexistence amongst forest-dwelling frugivorous species in this tropical forest remnant.

Keywords: *Tropical forests; camera-trap; competition; occupancy modelling; frugivores.*

RESUMO

A competição interespecífica por recursos é considerada o principal fator seletivo na distribuição e estruturação de espécies dentro de uma comunidade. No entanto, para mamíferos frugívoros de florestas tropicais, essa relação ecológica ainda é pouco compreendida. Aqui avaliamos como cinco espécies de mamíferos frugívoros terrestres, queixada (*Tayassu pecari*), cateto (*Pecari tajacu*), cutia (*Dasyprocta leporina*), paca (*Cuniculus paca*) e veado catingueiro (*Mazama gouazoubira*), compartilham as áreas de alta densidade da palmeira *Euterpe edulis*, um recurso chave da Mata Atlântica. Utilizamos armadilhas fotográficas e modelos de ocupação para examinar as interações competitivas entre eles. Nossos resultados não mostraram evidências de exclusão competitiva entre esses frugívoros. Os queixadas interagiram positivamente com *E. edulis* somente nas situações em que coexistiram com as outras quatro espécies. Nas áreas em que não disputam com outros coespecíficos não encontramos interação do queixada com essa palmeira. Já os outros quatro frugívoros não interagiram com *E. edulis* em nenhuma situação. Além disso, descobrimos que a probabilidade de detectar o queixada é maior nas áreas onde os outros frugívoros estão ausentes. Juntas, essas evidências sugerem que, apesar de ocupar habitats semelhantes e compartilhar recursos similares, a divisão de nicho pode estar subjacente à coexistência entre espécies frugívoras que habitam este remanescente de floresta tropical.

Palavras-chaves: Floresta tropical, armadilhas fotográficas, competição, modelos de ocupação, frugivoros.

1. INTRODUCTION

Many empirical studies have showed that species of the same guild tend to forage in different spaces or explore different resources (Astete et al., 2017; Bodmer, 1991; Murray & Brownt, 1993; Paine, 1971). Yet, competition is expected if resources are in shortage, and in that case, stronger competitors tend to exclude competitively the inferiors ones (Gause, 1934; Jaeger, 1972; Valeix, Chamaillé-Jammes, & Fritz, 2007). For frugivorous mammals of tropical forests, this ecological relationship is still poorly understood. Although the hyper-diversity community of fruits of this system, on seasons when fruit production is low, resources scarcity can lead to diet overlap and promote competition (Fleming, 1979; Head, Robbins, Mundry, Makaga, & Boesch, 2012; Smythe, 1986).

Interspecific competition among frugivorous mammals in tropical forest have been suggest by Head et al (2012), in which he verified that elephants excluded competitively two species of apes under low conditions of fruits and herbs at Loango National Park, Africa. However, niche partitioning among similar species is usually the most commonly scenario found (Barreto, Hernandez, & Ojasti, 1997; Bodmer, 1991; Ferreguetti, Davis, Tomas, & Bergallo, 2018; Ferreguetti, Tomás, & Bergallo, 2015; Mauro Galetti, Camargo, et al., 2015; Ilse & Hellgren, 1995; Kiltie, 1982). In Peruvian Amazonia, Bodmer (1991) showed evidence of habitat partitioning among frugivorous with similar diets and resource partitioning among frugivorous with similar habitat use, at large spatial scales. Nevertheless, how the species behave when coexisting with co-specifics is affected by many ecological and environmental factors, and therefore, will depend on the system that they are evolved (Chase & Leibold, 2003; Macarthur & Levins, 1967). For instance, the abundance variation of resources in space and time can trigger competitions scenarios that did not exist (Wiens, 1977). The plasticity of the species to foraging in different periods and habitats is another determinant factor (Schoener, 1974). Using the environment differently can be an outlet to avoid competition.

In the Atlantic forests of South America , one of the world's biodiversity hotspots, communities of frugivorous mammals are very diverse (Lima et al., 2017). A commonly resource regularly explored by them are the fruits of the palm Euterpe edulis (Mauro Galetti, Bovendorp, & Guevara, 2015; Mauro Galetti, Zipparro, & Patrícia c. Morellato, 1999; Keuroghlian & Eaton, 2009). This palm is considered a keystone resource (Mills, Soule, & Doak, 1993; Paine, 1971; Peres, 2000) because they normally are present in high quantities and

are rich in energy, as they have a high lipid content (Borges et al., 2011; Mauro Galetti, Pizo, & Morellato, 2011; Staggemeier, Cazetta, & Morellato, 2017). However, the species is highly targeted by palm harvesting, who seek their apical meristem, called "palmito", which is consumed in the Brazilian gastronomy (Mauro Galetti & Fernandez, 1998). Death is the destiny of the individuals that had their palmito cut out, and since a new adult palm tree will take at least 8 to 10 year to reach maturity and start fruiting (Carvalho, 1994), species that depend on their fruits are directly impacted (Mauro Galetti & Aleixo, 1998). In this way, the uncontrolled exploitation of this key resource might shift the behaviour of the frugivorous that depend on their fruits and change the way they related with similar species.

To amplify our understanding of interspecific relationship among terrestrial frugivorous mammals, we verified whether species of an Atlantic forest remnant compete for the fruits of the target palm Euterpe edulis. We assessed five species of terrestrial frugivorous mammals and evaluated for competitive exclusion amongst them at the palm resource using occupancy modelling. The species examined were the white-lipped peccary (Tayassu pecari), collared peccary (Pecari tajacu), agouti (Dasyprocta leporina), paca (Cuniculus paca) and grey brocket deer (Mazama gouazoubira). These five mammals species have been reported feeding on the Euterpe edulis fruits (Mauro Galetti, Bovendorp, et al., 2015; Mauro Galetti, Zipparro, & Morellato, 1999; Keuroghlian & Eaton, 2009). Additionally, previous studies have shown some degree of diet overlap and suggest spatial and temporal avoidance between both peccary species (Barreto et al., 1997; Bodmer, 1991; Mauro Galetti, Camargo, et al., 2015). Yet, whether these results from niche partitioning or competitive exclusion of a dominant peccary species remains poorly known (Ferreguetti et al., 2018; Fragoso, 1999). Our hypothesis is that the white-lipped peccary, because of its larger body and group size (Beck, Keuroghlian, Reyna-Hurtado, Altrichter, & Gongora, 2017; Brown & Maurer, 1986; Kiltie & Terborgh, 1983), would exclude the other four species as potential higher competitor from the areas of greater abundance of the palm Euterpe edulis (Fig. 1)

2. METHODS

2a. Site description

The study was carried out in Cardoso Island State Park (PEIC), Cananéia, SP, Brazil (48°05′W and 25°03′S), a protect park created in 1962. The PEIC is situated in the south coast, in the border with Paraná State, and consists of a total territory equal to 151 km2 (SMA, 2002 - Figure 2). It has superhumid climate, with an mean annual temperature of 23.8ºC and mean annual rainfall 2248 mm (Everaldo Rodrigo Castro, Corrêa Côrtes, Navarro, Galetti, & Morellato, 2012). It does not have a defined dry season, however there is a concentration of rains between December to March (Everaldo Rodrigo Castro et al., 2012). The topography is predominantly mountainous, mainly in the central region, which has elevations above 814 meters (SMA, 2002). The vegetation is majority composed of tropical rainforest, where the juçara palms are strongly present, although the intensive palm harvesting pressure. The remaining formations are mangroves, beaches and sand dunes.

2b. Camera traps across gradients of juçara abundance

We placed twenty-four photographic traps (Bushnell) in different parts of PEIC, that remained in field between February to May of 2016 (Fig. 2). We opted to conduct the study during this period due to E. edulis phenology, as literature showed that at Cardoso Island, its fruiting occurs between January to June, with ripe fruits peaking between April and May (E. R. Castro, Galetti, & Morellato, 2007). We stratified the experimental design aiming to cover as much of the island's territory as possible. We seek to place the cameras-trap at areas with different abundance of E. edulis, which allowed us to respond if the areas of higher palm concentrations had greater presences of frugivorous mammals. Palm sampling was done by counting the number of adult trees (diameter greater than 20 meters at chest height) that were inside a 10 meters radius buffer created around each camera site (Fig 2). The number of trees was a reference for the potential amount of fruits that each area might contained.

2c. Terrestrial frugivorous community

According to previous studies, there are a total of seven species of terrestrial frugivorous mammals inhabiting PEIC, which include both peccaries species Tayassu pecari (white-lipped peccaries - WLP) and Pecari tajacu (collared peccaries - CP), two large rodents Dasyprocta leporina (agouti) and Cuniculus paca (paca), two species of deers Mazama americana (red-brocket), Mazama gouazoubira (grey brocket) and the forest rabbit Sylvilagus brasiliensis

(forest rabbit) – (M. Galetti et al., 2016a; Lima et al., 2017; São Bernardo, 2004). The present study was able to detect five of these, the species M.americana and S. brasilienses were not recorded (see Table S1 and Fig.3). However, excluding the WLP, the other four frugivorous recorded had a very low detection rate, which make it impossible to analyze the competition among species individually. Therefore, we opted for joining the five species into a single group called "subordinate frugivorous", and verified if this group competes for E. edulis palm with the WLP. They were called as "subordinate frugivorous" because we supposed previously that WLP are the dominant species, since they live in large herds, often including more than 100 individuals, dominating ground-dwelling vertebrate biomass in the areas where they occur (Beck, 2006; Mauro Galetti, Guevara, et al., 2015; Kiltie & Terborgh, 1983) and physically intimidating other competing species (Keuroghlian & Eaton, 2008; Keuroghlian, Eaton, & Longland, 2004).

2d. Evaluating competitive interactions through occupancy modelling

We used the Two Species Conditional Occupancy Models (MacKenzie et al., 2006; Mackenzie, Bailey, & Nichols, 2004; Richmond, Hines, & Beissinger, 2010) to evaluate the response of frugivorous mammals to E. edulis availability, and to evaluate whether there is a proxy of competitive exclusion among the frugivorous at PEIC. This approach allows us to evaluate how the occupancy and/or detection of a dominant species (Tayassu pecari) can affect the occupancy and/or detectability of other (subordinate frugivorous). The modelling framework is represented as a hierarchical tree of occupancy and detectability conditional probabilities, generating eight parameters (Table 1 and S4). Occupancy parameters reflect the probability of the species being present in a site i, while the detection parameters reflect the probability of detecting a species in a site i, at a time t, giving that the species occurs in the area. From these parameters, it is possible to build different models, which will be assembled according to the hypothesis of the study: 1) species are exploring the fruits of E. edulis and the dominant WLP is negatively interfering in the detection of the subordinates frugivorous (competitive exclusion); 2 frugivorous exploit the space and the fruits of E. edulis distinctly without any effect of the dominant species on the subordinate (niche partitioning); 3) frugivorous share the fruits of E. edulis, but the dominant species has no effect on the detection of the subordinate (niche overlap, but no competition). To evaluate these hypotheses, we modelled the detection probabilities of frugivorous in function of the E. edulis abundance, while the occupancy parameters remained constant. The detection probabilities provide us the daily

foraging behaviour decisions of the species, which is essential to evaluate a possible competition for the palm among them.

We used the Program MARK to perform the analyses (MacKenzie et al., 2006), which evaluated the occurrence patterns of the species throughout a presence-absence matrix, categorized by the null model. We constructed a matrix with a total encounter history of 82 occasions, each representing one day of camera trapping. To rank the best models, we used the Akaike's Information Criterion corrected (AICc) for small samples (Hook & Regal, 1997). Those with ΔAICc < 2 and the highest AICc weight were consider the best models, because of their higher level of empirical support (Burnham & Anderson, 2004)

3. RESULTS

We accumulated a sampling effort of 1968 traps/days, and recorded a total of 14 medium and large mammals' species, being six of them fruit eaters (Table S1). WLP was the most detected species, being observed by 17 of 24 cameras-trap in 126 occasions, resulting in a naive occupancy probability (division of the number of sites the species were detected at least once into the total number of sites) of 71%, which suggested a broad use of the island. The four subordinate frugivorous detected - agouti, CP, paca and grey brocket deer - had very low detection rates, being together record by only 9 of 24 cameras-trap and in 18 occasions, resulting in a naive occupancy probability of 38%. Yet, even with the low detection history, the occupancy estimate of the subordinate species were high (Table 2), which means that the chances of occurring in those areas are very high.

Although the white-lipped peccary used much of the PEIC, the probability to detect the species was influenced by the presence of the subordinate frugivorous. There is a higher probability to detect WLP in the areas that the subordinate frugivorous mammals do not occur (Table 2). However, in the areas that they occur, the chances to detect WLP increases if these areas present a great abundance of E. edulis (Fig 4). In contrast, WLP did not influence neither on the occupancy and the detection probabilities of the subordinate frugivorous mammals, which indicated us a non-competitive scenario. Yet, the fact that E. edulis abundance did not influence the detection probabilities of the subordinates frugivorous, and also was not determinant to the WLP presence when the subordinate frugivorous were absent (Fig. 4), suggested that when all frugivorous mammals occupies the same areas, WLP tend to

concentrate in the areas that have greater E. edulis abundance. In disparity, when the species do not overlap spatially, WLP did not interact with E. edulis palms (Fig. 5).

4. DISCUSSION

Contrary to expectations, our results indicated that niche partitioning might underlie the coexistence amongst forest-dwelling frugivorous species in Cardoso Island. Although the subordinates frugivorous low encounter rate, we found that their presence directly affect the spatial exploitation strategy of the WLP. WLP had greater chances to be detected in the areas in which the subordinate frugivorous were absent. Additionally, they respond positively to E. edulis only at the areas in which they co-occur with the subordinated frugivorous. These outcomes, added to the null response of the subordinated frugivorous to the presence of E. edulis corroborated a niche partitioning assumption.

WLP strategy of foraging in situations in which it has null competition is not particularly of PEIC population, as previous studies have already atevaluateed such behaviour (Bodmer, 1991; Ferreguetti et al., 2018; Manuel & Fragoso, 1999). Yet, when coexisting with similar, the species dominated the areas of their preference resource, in this case fruits of E. edulis. The strong relationship of WLP and the fruits of this palm has been observed in other researches (Beck, 2006; Keuroghlian & Eaton, 2008, 2009). The high lipid-rich pulp biomass produced by this palm provide a huge amount of energy capable to sustain large WLP groups (Borges et al., 2011; Mauro Galetti et al., 2011; Staggemeier et al., 2017). However, the illegal extraction of the edible apical meristem of E. edulis, which has to be killed to have it removed, might be shifting their diet to others resources (Mauro Galetti & Aleixo, 1998).

Although, we did not find any influence of WLP on both occupancy and detections parameters of the subordinate frugivorous, the fact that these species did not interacted with E. edulis reinforces a niche partitioning scenario. CP, agouti and paca have been recorded consuming the fruits of E. edulis in others forests remnants (Mauro Galetti, Bovendorp, et al., 2015; Mauro Galetti, Zipparro, & Patrícia c. Morellato, 1999). Yet, the preference of the WLP to E. edulis fruits might be repelling the subordinate frugivorous away from these areas (Bodmer, 1991; Keuroghlian et al., 2004). Nevertheless, the subordinate frugivorous can overcome this situation by reducing their similarities. CP, agouti and grey brocket are able to occupy different types of habitats and be more generalist in their diets (Emmons & Feer, 1997; Ferreguetti et al., 2015; Judas & Henry, 1999; Keuroghlian & Eaton, 2009). On the other hand,

paca present a distinctive temporal activity period compared to the WLP. While it forage during the night, WLP is more activity during the day (Mauro Galetti, Camargo, et al., 2015; Jax, Marin, Rodríguez-Ferraro, & Isasi-Catalá, 2015).

Despite niche partitioning assumption, the low naive occupancy probability and encounter rate of the subordinate frugivorous might indicate that their population has been reduced due to competitive exclusion in the past (Lawlor, 1980). Mammalian surveys of previous studies have reported a high register frequency of the agouti in the Island (Jorge et al., n.d.; São Bernardo, 2004). CP and grey brocket deer also tend to be regularly recorded, and according to the local people, paca used to be very abundant (M. Galetti et al., 2016a). Their low detection estimates, however, designates that the scenario has changed, and WLP strong presence in the Island might be the reason why. According to unpublished data (Jorge et al., n.d.), the species populations have increased in the last decade, and our data have showed a high naive occupancy probability in the PEIC. Nonetheless, the direct impact of illegal hunting in the fauna cannot be dismissed, as is one of the main defaunation drivers and often practise in the protect area (Cullen, Bodmer, & Valladares Pádua, 2001; M. Galetti et al., 2016b; Hanazaki, Alves, & Begossi, 2009; São Bernardo, 2004).

Regardless the uncertainty in the interpretation of the results, our models show very interesting patterns, and suggest some hypotheses: 1- E. edulis proved to be an important resource for the WLP, however human presence can alter their behaviour against this interaction. Studies in areas with different anthropogenic pressures (e.g., areas with vs without poaching) may be interesting to investigate such behaviour and compare with the results of the present study; 2- There may be a separation of habitat between the subordinate frugivorous and the WLP in PEIC. This separation can be a response of the frugivores to the high presence of WLP, add to an avoidance behaviour of WLP themselves; 3 - There was a clear reduction of frugivorous in the PEIC, which can be justified by the increase in the population of the WLP and the high anthropic activity. However, continuous studies in the State Park of Cardoso Island are crucial for understanding the reason for their low presence in the region.

5. ACKNOWLEDGEMENTS

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TABLES AND FIGURES

Table 1: Two Species Conditional Occupancy parameters: Ψ = occupancy and p and r= detection.

ψA	Occupancy probability by species A.
ψBA	Occupancy probability by species B, and the species A are present.
ψBa	Occupancy probability by species B, and the species A are absent.
pA	Detection probability by species A, considering that species B are absent.
pB	Detection probability by species B, considering that species A are absent.
rA	Detection probability by species A, considering that both species are present.
rBA	Detection probability by species B, considering that both species are present, and species A is detected.
rBa	Detection probability by species B, considering that both species are present and species A is not detected.

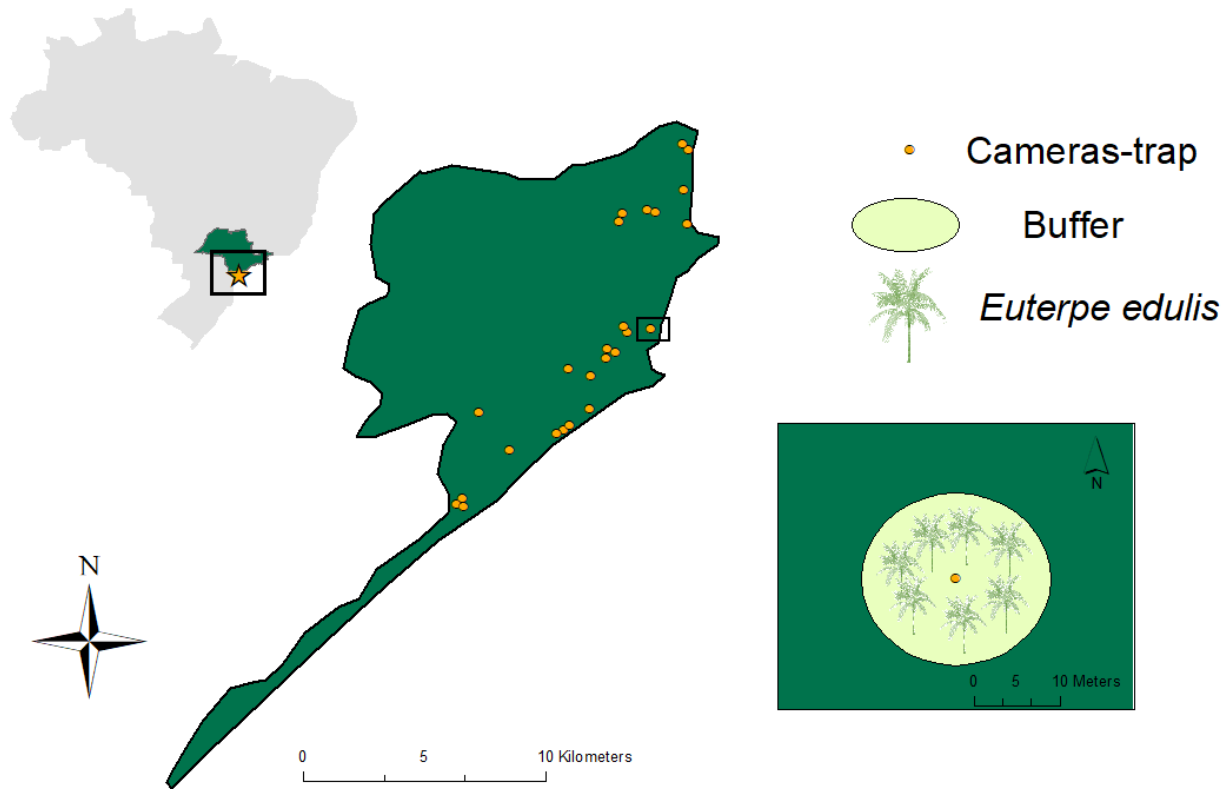**Table 2:** Occupancy (ψ) and detection (p) real parameters of the best models of the Two Species Conditional Analyses: *Tayassu pecari* vs subordinate frugivorous mammals (*Pecari tajacu, Cuniculus paca, Dasyprocta leporina and Mazama spp)*

Species	ψ	p	
Tayassu pecari	0.7837674 (SE = 0.1)	pA = 0.22 (SE = 0.02)	rA = 0.05 (SE=0.007)
Frugivorous mammals (*Pecari tajacu, Cuniculus paca, Dasyprocta leporina and Mazama gouazoubira)*	0.792075 (SE = 0.09)	pB/rBA/rBa = 0.01 (SE = 0.003)	

Table 3: Best models of the Two Species Conditional Analyses: *Tayassu pecari* vs subordinate frugivorous mammals (*Pecari tajacu, Cuniculus paca, Dasyprocta leporina and Mazama gouazoubira)*

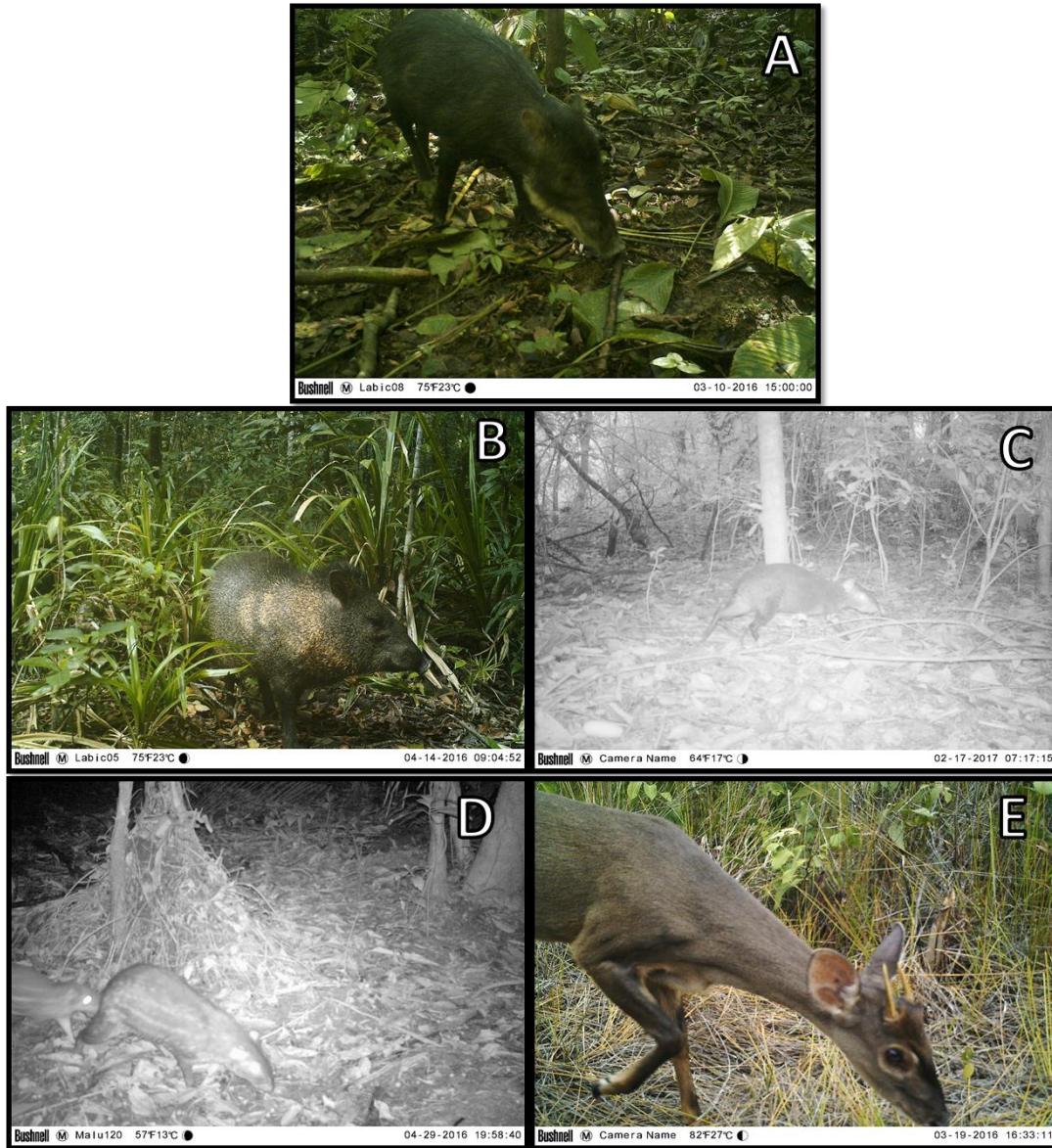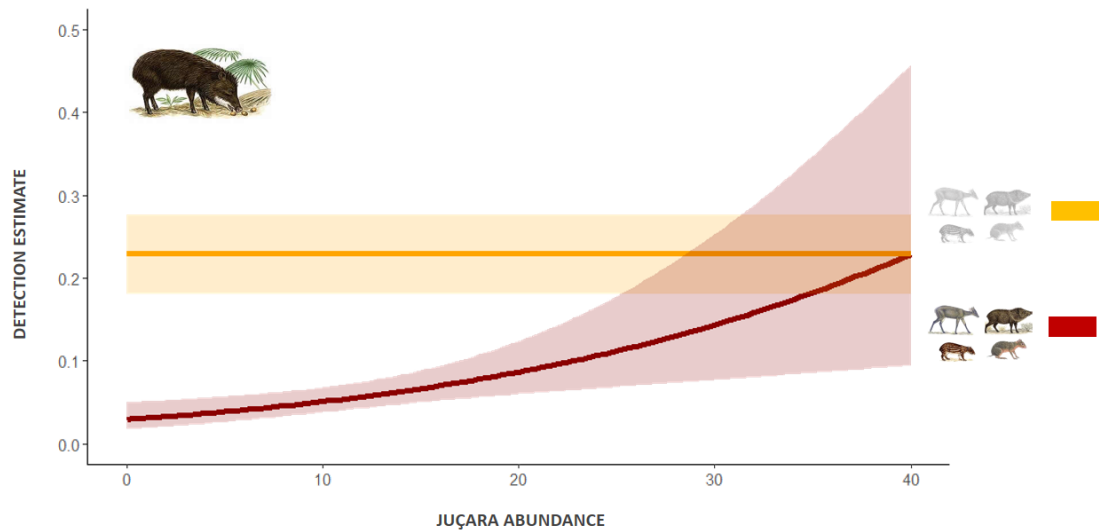| Tayassu pecari X frugivorous mammals (collared peccaries, agoutis and grey brocked deer)	AICc	Delta AICc	AICc Weights
ψA, ψBA=ψBa, pA, rA(juc), pB=rBA=rBa	989.0881	0	0.67921
ψA, ψBA=ψBa, pA, rA(juc), pB, rBa= rBA	992.8051	3.717	0.10589
ψA, ψBA=ψBa, pA, rA(juc), pB=rBa, rBA	993.0566	3.9685	0.09338
ψA, ψBA=ψBa, pA, rA(juc), pB=rBA=rBa(juc)	993.1122	4.0241	0.09082
ψA, ψBA=ψBa, pA, rA(juc), pB, rBa= rBA(juc)	996.406	7.3179	0.0175
ψA, ψBA=ψBa, pA, rA(juc), pB, rBA, rBa	997.3446	8.2565	0.01094
ψA, ψBA=ψBa, pA, rA, pB, rBA, rBa	1001.722	12.6339	0.00123
ψA, ψBA=ψBa, pA(juc), rAljuc), pB=rBA=rBa	1002.5427	13.4546	0.00081
ψA, ψBA, ψBa, pA, rA, pB, rBA, rBa	1005.4981	16.41	0.00019
ψA, ψBA=ψBa, pA, rA, pB=rBA=rBa	1009.9716	20.8835	0.00002

Figure 1: Conceptual representation of the terrestrial frugivorous mammals *Tayassu pecari, Pecari tajacu*, *Dasyprocta leporina, Cuniculus paca* and *Mazama gouazoubira* at Cardoso Island State Park according to the study hypothesis.

Figure 2: Location of Cardoso Island State Park (PEIC), Cananéia, SP, Brazil (48°05′W and 25°03′S). The distribution of the 24 camera-traps across areas with different abundances of the palm *Euterpe edulis*. On the tight below, the representation of the abundance of the palm species *Euterpe edulis* inside the circular buffer with 10 meters of radius measure from the trap sampling point.
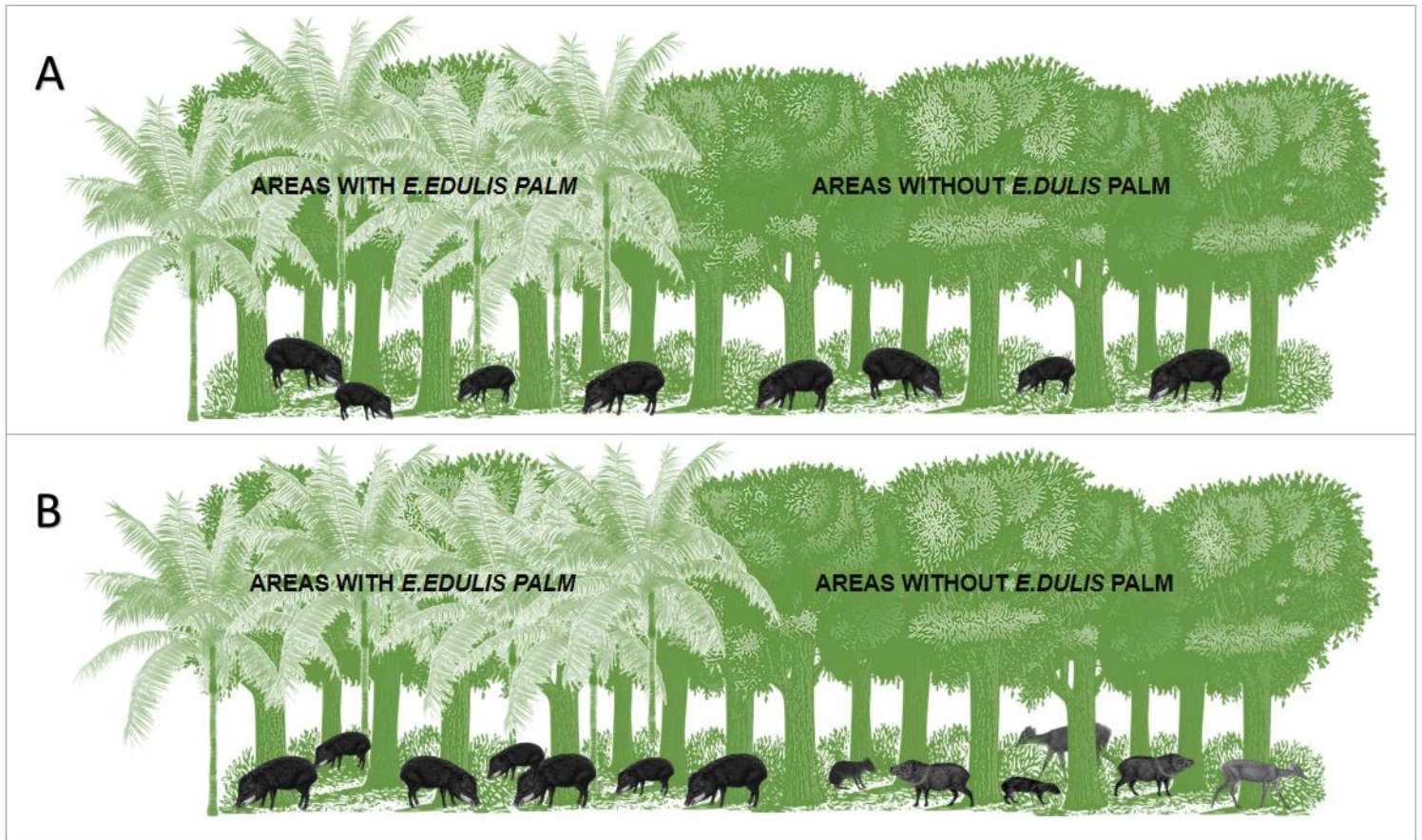
Figure 3: The five frugivorous mammals detected in the Cardoso Island State Park (PEIC), Cananéia, SP, Brazil (48°05′W and 25°03′S), A: *Tayassy pecari,* B: *Pecari tajacu,* C: *Dasyprocta leporina,* D: *Cuniculus paca,* E: *Mazama gouzoubira.*

Figure 4: Interaction between *Euterpe edulis* and *Tayassu pecari*: yellow – interaction in the areas where subordinate frugivorous (*Pecari tajacu,, Dasyprocta leporina, Cuniculus paca and* and *Mazama gouazoubira*) are absent; red – interaction in the areas where subordinate frugivorous (*Pecari tajacu, Dasyprocta leporina, Cuniculus paca* and *Mazama gouazoubira*) are present.
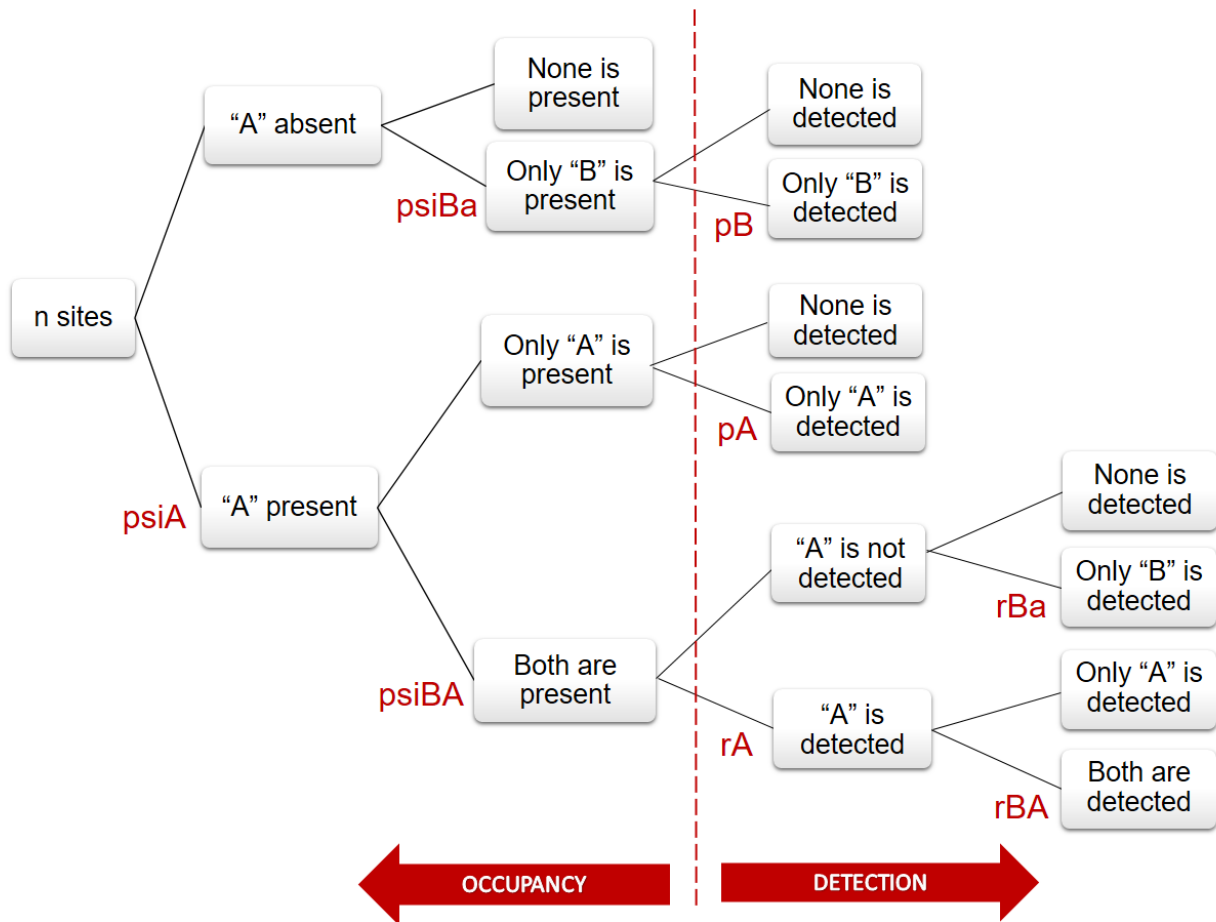
Figure 5: Conceptual representation of the terrestrial frugivorous mammals *Tayassu pecari, Pecari tajacu*, *Dasyprocta leporina, Cuniculus paca* and *Mazama gouazoubira* at Cardoso Island State Park. A: *T. pecari* distribution in the areas where the subordinate frugivorous are absent; B: *T. pecari* distribution in the areas where the subordinate frugivorous are present.

Table S1: Species registered in Cardoso Island State Park (PEIC), Cananéia, SP, Brazil (48°05′W and 25°03′S), between February and May of 2016. The number of independent records (independence = 24 hours interval), and the Frequency of Occurrence = number of independent records (independence = 24 hours interval) / sample effort X 100.

Species	Independent records (24 hours)	Frequency of occurrence
Tayassu pecari (White-lipped peccary)	107	5.37
Small rodents	22	1.1
Leopardus pardalis (Ocelot)	20	1
Didelphis aurita (Brazilian common opossum)	15	0.75
Dasypus novemcinctus (Nine-banded armadilho)	12	0.6
Cerdocyon thous (Crab-eating fox)	11	0.55
Mazama gouazoubira (Gray brocket deer)	10	0.5
Puma concolor (Puma)	5	0.25
Methachirus nudicaudatus (Brown four-eyed opossum)	4	0.2
Pecari tajacu (Collared peccary)	3	0.15
Dasyprocta leporina (Red-rumped agouti)	2	0.1
Cuniculus paca Paca	2	0.1
Eira barbara Tayra	2	0.1
Leopardus guttulus Southern tiger cat	1	0.05

Figure S2: Representation of a hierarchical tree of occupancy and detectability conditional probabilities of the Two Species Occupancy Models, adapted from "http://phototrapping.blogspot.com/2012/01/tutorial-de-modelos-de-ocupacao-para.html" site.

2. CONCLUSÕES GERAIS

Nessa dissertação foi possível explorar um pouco mais sobre como diferentes espécies de mamíferos frugívoros que habitam o mesmo local diferem na utilização de recursos. Apesar de alguns estudos já terem sido feitos nesse contexto, este trabalho traz avanços ao utilizar modelos de ocupação com o objetivo de entendermos mais sobre a inter-relação ecológica entre espécies que se sobrepõe na utilização de recursos. Tendo as palmeiras como foco de possível competição, visto sua importância ecológica, pudemos evidenciar como espécies similares de mamíferos frugívoros se inter-relacionam em dois diferentes sistemas de floresta tropicais.

No primeiro capítulo, ao estudarmos um pequeno remanescente de floresta tropical estacional semidecidual, demonstramos que as três espécies de mamíferos frugívoros, *Tayassu pecari, Pecari tajajcu* e *Dasyprocta azarae* apesar de ocuparem habitats semelhantes, estarem ativas durante as mesmas horas e compartilharem recursos de palmeiras semelhantes, possuem diferentes estratégias comportamentais que permitem que elas coexistam. Já no segundo capítulo, ao estudarmos um remanescente maior de Mata Atlântica composta por floresta ombrófila, encontramos forte indício de uma separação de habitat entre a espécie *Tayassu pecari* e outras quatro espécies de mamíferos frugívoros, *Pecari tajacu, Dasyprocta leporina, Cuniculus paca* e *Mazama gouazoubira.*

A partir dos resultados evidenciados nesse dois capítulo saímos com a conclusão que as espécies de mamíferos frugívoros de ambos os sistemas estudados conseguem evitar a competição e coexistir. Dessa forma, a partição de nicho parece reger as inter-relações entre essas espécies tanto no remanescente de floresta estacional semicidual, como no remanescente de floresta ombrófila. Entretanto, visto atual situação das florestas tropicais, de forte perda e fragmentação de habitat, esperamos que esteja havendo um aumento na sobreposição da exploração de recursos entre as espécies de mamíferos frugivoros remanescentes deste ecossistema. Desta forma, destacamos que mais estudos com o mesmo viés devem ser feitos em sistemas com diferentes pressões antrópicas (com e sem caça, por exemplo), de forma a elucidar melhor tal inter-relação, e comparar com os padrões encontrados nas duas áreas deste estudo.