UNIVERSIDADE ESTADUAL PAULISTA
“JÚLIO DE MESQUITA FILHO”
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

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PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS
(ZOOLOGIA)

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# EXTINÇÃO ECOLÓGICA DE GRANDES HERBÍVOROS E DIVERSIDADE DE PLANTAS EM UM GRADIENTE DE DEFAUNAÇÃO NA MATA ATLÂNTICA

**GABRIELA SCHMAEDECKE**

Dissertação apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Meste em Ciências Biológicas (Zoologia).

**Junho - 2013**

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Orientador: Prof. Dr. Mauro Galetti Rodrigues
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## CERTIFICADO DE APROVAÇÃO

**TÍTULO:** EXTINÇÃO ECOLÓGICA DE GRANDES HERBÍVOROS E DIVERSIDADE DE PLANTAS EM UM GRADIENTE DE DEFAUNAÇÃO NA MATA ATLÂNTICA

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*Aos meus pais Vera e Luiz (in memorian)*

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# RESUMO GERAL

O impacto humano sobre os ecossistemas tropicais tem um amplo efeito sobre a população dos grandes vertebrados. A ausência dos grandes mamíferos causa uma falta de seus processos fundamentais sobre comunidades de plantas como a herbivoria, o pisoteio, a predação e a dispersão de sementes. A perda de espécies resulta em perda de funções ecológicas o que altera o próprio funcionamento do ecossistema. Essa dissertação está organizada em dois capítulos: Primeiro (Capítulo I: A defaunação seletiva de mamíferos altera sua diversidade funcional em florestas atlânticas contínuas) nós analisamos como mudanças na riqueza e abundância de espécies de mamíferos de médio e grande porte afetam a diversidade funcional em Florestas Atlânticas tropicais brasileiras. Encontramos que, apesar das quatro áreas estudadas fazerem parte do mesmo contínuo de Floresta Atlântica, a riqueza e a abundância de espécies não são similares entre elas, e em uma das quatro áreas encontramos diversidade funcional alterada, o que revela a existência de comunidades de grandes mamíferos distintas nas áreas. Segundo (Capítulo II: Consequências da extinção de herbívoros sobre a diversidade de plantas em um gradiente de defaunação) nós investigamos se a ausência de grandes mamíferos altera a riqueza, densidade e beta diversidade de plântulas em florestas tropicais, a Floresta Atlântica Brasileira. Nós concluímos que apesar do fato de as quatro áreas fazerem parte de um mesmo contínuo de Floresta Atlântica, nós encontramos que em áreas com queixada, a presença dos grandes mamíferos herbívoros (parcelas abertas) causou uma tendência tanto no declínio na densidade de plântulas quanto no aumento da beta diversidade, como esperávamos, mas não encontramos um padrão para seu efeito sobre a riqueza de plântulas. Nas áreas sem queixada, a presença dos grandes mamíferos herbívoros (parcelas abertas) não causou mudanças na riqueza e na beta diversidade das plântulas, como esperávamos, mas não encontramos um padrão pra seu efeito sobre a densidade de plântulas. A extinção dos grandes mamíferos pode resultar em consequências preocupantes sobre comunidades de plantas, sendo o queixada, *Tayassu pecari*, o maior modificador de comunidades de plantas, o que torna a conservação do queixada fundamental para um melhor funcionamento do ecossistema. O conhecimento das consequências da extinção de espécies de mamíferos particulares permitirá um entendimento melhor de cada parte da teia alimentar dos mamíferos tropicais, e por sua vez, um melhor delineamento das estratégias de conservação.

**Palavras-chave**: Mata Atlântica, diversidade beta, diversidade funcional, cascatas tróficas.

# ABSTRACT

Human impact on tropical ecosystems has a pervasive effect on large bodied vertebrate populations. The absence of large mammals causes a lack of fundamental processes performed by them within the plant communities, such as herbivory, trampling, seed predation and seed dispersal. Species loss results in loss of ecological functions altering the proper functioning of the ecosystem. This dissertation is organized into two chapters. Firstly (Chapter I: Selective mammal defaunation changes functional diversity in continuous Atlantic rainforests) we analyzed how changes in species richness and abundance of mid and large forest-dwelling mammals affect functional diversity in a tropical forest, the Brazilian Atlantic Forest. We found that, despite the fact that the four studied sites compose the same Atlantic Forest continuum, species richness and abundance were not similar between sites and in one of four sites we found an alteration in functional diversity, which reveals the existence of distinct large mammal communities in these areas. Secondly (Chapter II: Consequences of herbivores extinction on plant diversity in a gradient of defaunation) we investigated whether the absence of large mammals alters seedling species richness, density and beta diversity in the same areas. We found that at peccary-present sites, the presence of large herbivorous mammals (open plots) causes a tendency of decrease in seedling density and a tendency of increase in beta diversity, but we found no pattern of their effect over seedling richness. At peccary-absent sites, the presence of large herbivorous mammals (open plots) causes no changes in seedling richness and in beta diversity, but we found no pattern of their effect over seedling density. The extinction of large mammals may result in worrying consequences over plant communities, being the white-lipped peccary, *Tayassu pecari*, the major driver of plant community changes, which makes white-lipped peccaries conservation fundamental for a healthy functioning of the ecosystem. Knowing the consequences of extinctions of particular mammal species will allow us to better understand the importance of each piece of tropical mammalian food webs and better delineate further conservation strategies.

**Key-words**: Atlantic forest, beta diversity, functional diversity, trophic cascades.

# SUMÁRIO

# CAPITULO I

## Selective mammal defaunation changes functional diversity in continuous Atlantic rainforests

# RESUMO

O impacto humano sobre os ecossistemas tropicais pode reduzir drasticamente a riqueza de espécies e alterar o funcionamento dos ecossistemas. Apesar de haver uma maior atenção para a compreensão dos efeitos da fragmentação sobre a diversidade dos mamíferos, ainda há pouca informação sobre como a diversidade funcional afeta a riqueza e abundância de espécies de mamíferos em florestas contínuas. Há menos informações ainda sobre como impactos sofridos por florestas contínuas afetam a diversidade funcional. Nesse estudo, analisamos as mudanças na riqueza e abundância de espécies de mamíferos de médio e grande porte em quatro áreas de floresta Atlântica contínua com diferentes níveis de defaunação, com o objetivo de entender os efeitos humanos sobre a diversidade funcional. A amostragem de mamíferos variou de nove a 13 espécies com um esforço de captura variando entre 416,16 e 555 armadilhas fotográficas-dia. As seguintes espécies foram as mais comuns em cada uma das quatro áreas: *Puma concolor, Leopardus pardalis* e *Didelphis aurita.* As espécies amostradas foram categorizadas em: predadores de topo, mesopredadores (hipercarnívoros e onívoros), herbívoros terrestres, herbívoros arborícolas e insetívoros terrestres. Não encontramos riqueza e abundância de espécies similares entre as comunidades de mamíferos de cada área, e em apenas uma das quatro áreas encontramos uma alteração na diversidade funcional, o que revela a existência de comunidades distintas de grandes mamíferos nessas áreas. Os herbívoros terrestres foram os mais representativos em três das quatro áreas, enquanto que em uma das áreas os predadores de topo e os mesopredadores (hipercarnívoros) foram mais comuns que os outros grupos funcionais. A perda de um padrão esperado para a diversidade funcional (como os herbívoros sendo mais abundantes que os carnívoros) pode resultar em perda de funções ecológicas alterando o próprio funcionamento dos ecossistemas. O entendimento dos efeitos de defaunação em florestas contínuas permitirá que pesquisadores possam predizer as consequências tróficas nesses ambientes.

**Palavras-chave:** Mata Atlântica, armadilha fotográfica, defaunação, diversidade funcional, *Tayassu pecari*.

# ABSTRACT

Human impacts on tropical ecosystems can greatly reduce species richness and ecosystem functioning. Despite the major attention to understand fragmentation effects on mammal diversity, we still have very little information on how functional diversity is affected by changes in mammal species richness and abundance in continuous forests. Even less is known about how human impacts on continuous forests affect functional diversity. Here, we sampled species richness and abundance of mid and large mammals in four continuous Atlantic forests with different levels of defaunation with the objective to understand human effects on functional diversity. Mammal sampling varied from nine to 13 species with a survey effort ranging from 416.16 to 555 camera-days. The following species were the most common in each of the four areas: *Puma concolor, Leopardus pardalis* and *Didelphis aurita.* Species were categorized as: top predators, mesopredators (hypercarnivores and omnivores), terrestrial herbivores, arboreal herbivores and terrestrial insectivores. We did not find similar species richness and abundance between sites and in just one of four sites we found an alteration in functional diversity, which reveals the existence of distinct large mammal communities in these areas. Terrestrial herbivores were the most representative in three of the four sites while in one of the sites top predators and mesopredators (hypercarnivores) were more common than the other functional groups. The loss of an expected pattern of functional diversity (such as herbivores being more abundant than carnivores) may result in the loss of ecological functions altering the proper functioning of ecosystems. The understanding of the effects of defaunation in continuous forests will enable researchers to predict trophic consequences in these habitats.

**Key words**: Atlantic forest, camera trap, defaunation, functional diversity, *Tayassu pecari.*

## 1. Introduction

In the last few years, researchers have concentrated their efforts on understanding the effects of fragmentation on the abundance and species richness of mammals (Quinn & Harrison 1988, Andrén 1994, Laurance 1994, Turner 1996, Chiarello 1999, Pardini 2004, Pardini et al. 2005, Prist et al. 2012), yet we have very insufficient information on how functional diversity is affected by changes in mammals species richness and abundance in continuous forests (Tilman et al. 1997, Flynn et al. 2009). Functional diversity was defined by Tilman (2001) as "the range and value of those species and organismal traits that influence ecosystem functioning". Therefore functional diversity is essential for the maintenance of ecosystem processes and properties (Tilman et al. 1997, Fragoso & Ruffman 2000, Núñez et al. 2000, Tilman 2001, Clark et al. 2012, Bueno et al. 2013).

Most of mid- and large-sized mammals are particularly likely to be negatively affected by fragmentation, habitat loss and illegal poaching (Bodmer et al. 1997, Peres 2000, 2001, Michalski & Peres 2007, Wright et al. 2007, Canale et al. 2012). The absence of large mammals causes changes of important processes that affect plant communities such as herbivory (Olff & Ritchie 1998, Yessoufou et al. 2013), trampling (Queenborough et al. 2012), seed predation and dispersal (Wright et al. 2000, Wright 2003, Galetti et al. 2006, Nuñez-Iturri & Howe 2007, Wright et al. 2007, Brodie et al. 2009, Farwig & Berens 2012, Bueno et al. 2013), which propagates alterations throughout the trophic levels in the ecosystem (Terborgh 1992, Wright et al. 2000). Due to these fundamental interactions among environmental components it is necessary to protect not only the species but also their ecological services (Anderson et al. 2011).

However even in large protected forests illegal hunting is common (Cullen Jr. et al. 2000, Peres 2000, Fa & Brown 2009, Laurance et al. 2012). Large continuous forests are still considered the best strategy to conserve the full diversity of mammal species (Peres 2005, Laurance 2005, Lopoukhine et al. 2012). One of these large protected forests occurs in the Brazilian Atlantic forest. The Atlantic forest is home to 73 endemic mammal species (Myers et al. 2000) and the Serra do Mar is the largest Atlantic forest corridor along the coast of Brazil with more than one million hectares of continuous forest (Ribeiro et al. 2009). Consequently, this corridor is the last refugee for large mammals, particularly jaguars, white-lipped peccaries and woolly spider monkeys (Jorge et al. 2013).

In this work we compared the species richness and abundance of terrestrial mammal communities in four continuous Atlantic Forest. Our objective was to understand how changes in abundance and species richness affect the functional diversity of mid- and large-sized mammals.

## 2. Material and Methods

### 2.1. Study sites

We carried out our study in four continuous protected areas of the Atlantic Forest along the Serra do Mar corridor (Aguiar et al. 2003) covered by ombrophylous rainforest (Instituto Florestal. 2006, Instituto Florestal 2008, Melo & Mantovani 1994). We have chosen these areas based on previous data on their importance for mammal conservation (Galetti et al. 2009). We sampled two areas in Serra do Mar State Park, Itamambuca Base (ITA) (45° 5’ W; 23° 19’ S) and Vargem Grande Base (VG) (45° 14’ 39” W; 23° 26’ S) and two other parks within this corridor, Carlos Botelho State Park (CB) (45° 14’ W, 23° 26’ S) and Ilha do Cardoso State Park (IC) (48º 01' W, 25º 12' S) (Figure 1).

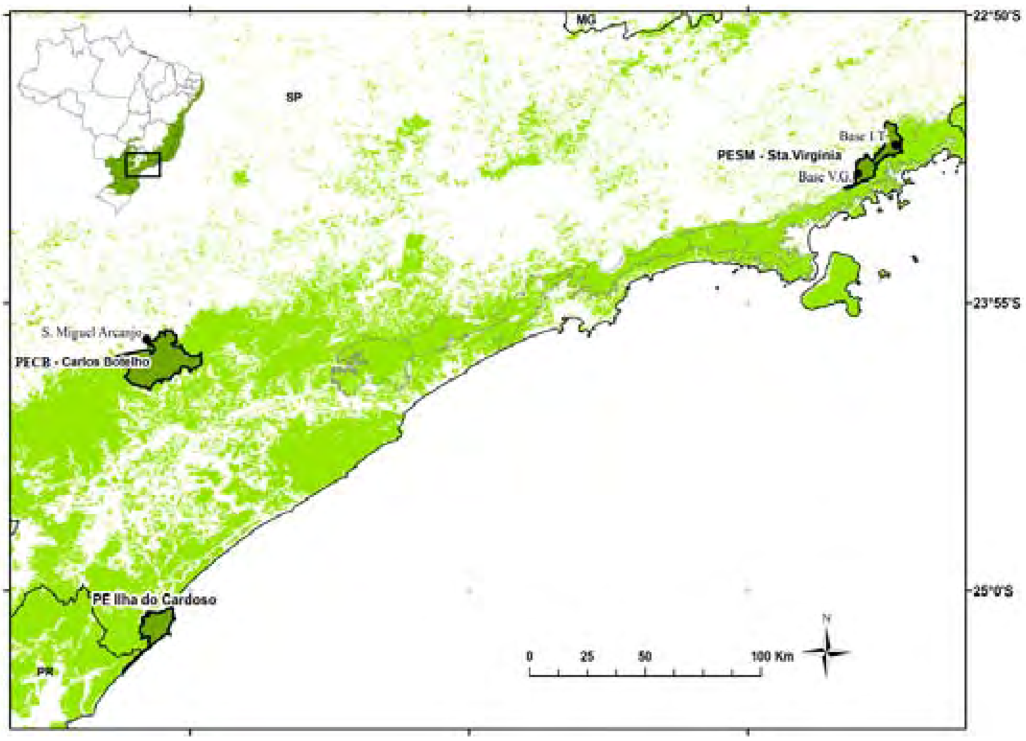

Figure 1. Location of study areas: Itamambuca Base (ITA) and Vargem Grande Base (VG) in Serra do Mar State Park (SMSP); Ilha do Cardoso State Park (ICSP) and Carlos Botelho State Park (CBSP), São Paulo, Brazil (Mapa: Bruno Borges).

## 2.2. Mammal surveys

There are several methods to sample mid- and large-sized mammals and we chose to use camera traps because they capture species affected by hunting such as apex predators, ungulates and large rodents (Srbek-Araujo & Chiarello 2005, Silveira et al. 2003), but primates (O'Brien et al. 2011). We surveyed mid- and large-sized mammals (> 1 kg) using camera traps with movement sensor models Reconyx® (model RC 55, Rapidfire Color IR, www.reconyx.com), Ecotone® (model HE-30, www.ecotone.pl) and Bushnell® (model 11-9600, www.bushnell.com). We used a total of 18 cameras at ITA, 16 at VG, 30 at IC and 49 at CB that were distributed across preexisting transects and trails throughout the areas including secondary and primary forest habitats, with a minimum distance of 200 m between each other (Table 1). The samples were taken from September 2011 to January 2012 at ITA, from September 2011 to June 2012 at VG, from August 2010 to September of 2011 at IC and from September 2009 to June 2010 at CB (Table 1).

We attached the cameras to trees approximately 50 cm above the ground with a small angle of inclination (Srbek-Araujo & Chiarello 2005, Tobler et al. 2008, O'Brien 2010). We removed the vegetation in front of the camera to increase the quality of the images. No bait or attractants were used. Cameras operated for 24 hours a day and were active from two to 32 days at ITA, from four to 40 days at VG, from five to 28 days at IC and from six to 16 days at CB per sampling (Table 1). Nomenclatures and the species body mass adhere to Paglia et al. (2012).

### 2.3. Data analysis

Sampling effort of mid- and large-sized mammals (> 1 kg) was calculated as the number of camera traps multiplied by the number of sampling days (1 day =24 h) (Srbek-Araujo & Chiarello 2005). The number of independent captures was obtained with respect to the following criteria: i) the organism was considered a new individual or group of individuals every 24 hours; ii) among the images obtained in these 24 hours interval, we chose the one with the largest number of individuals (adapted from Martins et al. 2007). We obtained the total abundance of each large mammal species through independent captures, and from this we calculated the relative abundance of species according to the formula: (number of independent captures/sampling effort) x 100 (Srbek-Araujo & Chiarello 2005). Relative biomass was obtained from the relative abundance multiplied by the weight (Galetti et al. 2009), again consulting Paglia et al. (2012) for weight measurements.

To compare mammal composition between the sites we used Bray-Curtis and Jaccard indexes, which are based on, respectively, species abundance (Bray & Curtis 1957) and the presence or absence of species (Chao et al. 2005) found in each site. These indexes were used to estimate dissimilarity matrices that jointly with the connection method UPGMA ("Unweighted Pair Group Method with Arithmaetic") permitted us to construct a cluster dendrogram.

Furthermore we analyzed the relationship between large mammal species richness and our sampling effort for all four sites. We then estimated the individual based rarefaction curve using the "specaccum" function and "exact" method; the result was compared with the prediction of the "First order jackknife" estimator by the "specpool." Both functions are found in the "vegan" package (http://cran.r-project.org/web/packages/vegan/index.html) in the R software 2.12.2 (Oksanen et al.

2011). The species accumulation rate was calculated by subtracting the species richness of the penultimate day from the species richness of the last day of sampling.

To analyze the most represented functional groups in each of the four sampling sites, the sampled species were categorized as: top predators, mesopredators (hypercarnivores), mesopredators (omnivores), terrestrial herbivores, arboreal herbivores and terrestrial insectivores.

## 3. Results

We obtained a total of 416 camera-days at ITA (9995 h), 416 camera-days at VG (9988 h), 497 camera-days at CB (11749 h) and 555 camera-days at IC (13320 h) (Table 1). From these efforts we captured nine species of mid- and large-sized mammals (> 1kg) at ITA, 10 species at VG, 11 species at IC and 13 species at CB (Table 2). The Guianan squirrel *Guerlinguetus ingrami* was the only species lighter than 1 kg considered in this research.

Table 1. Mid- and large-sized mammals (> 1 kg) samples using camera traps at Itamambuca (ITA), Vargem Grande (VG), Carlos Botelho (CB) and Ilha do Cardoso (IC).

| | ITA | VG | CB | IC |
|---|---|---|---|---|
| Sampling | Sep 2011 -<br>Jan 2012 | Sep 2011 -<br>June 2012 | Sep 2009 -<br>Jun 2010 | Aug 2010 -<br>Sep 2011 |
| Total cameras | 18 | 16 | 49 | 30 |
| Min-max of functional camera-days | 2 - 32 | 4 – 40 | 6 - 16 | 5 - 28 |
| Total hours | 9995h 45min | 9988h 7min | 11749h 57min | 13320h |
| Total camera-days | 416.45 | 416.16 | 489.54 | 555 |

Table 2. Mid- and large-sized mammals (>1 kg) from Itamambuca (ITA), Vargem Grande (VG), Carlos Botelho (CB) and Ilha do Cardoso (IC), São Paulo, Brazil.

| Order/Family/Species | Relative abundance* (relative biomass (kg)**) | | | | Threat Status |
|---|---|---|---|---|---|
| | ITA | VG | CB | IC | Reg[a]/Int[b] |
| **Artiodactyla** | | | | | |
| Cervidae | | | | | |
| *Mazama americana* | - | - | - | 0.19 (71.35) | VU/DD |
| *Mazama* spp.*** | - | - | 0.40 (10.86) | - | VU/DD |
| Tayassuidae | | | | | |
| *Tayassu pecari* | 28.12 (984.37) | - | - | 7.56 (264.86) | EN/NT |
| **Carnivora** | | | | | |
| Canidae | | | | | |
| *Cerdocyon thous* | - | - | 0.20 (1.30) | 0.16 (10.62) | LC/LC |
| Felidae | | | | | |
| *Leopardus pardalis* | 2.40 (22.83) | 4.32 (41.10) | 4.02 (38.22) | 3.24 (30.81) | VU/LC |
| *Leopardus tigrinus* | - | - | - | 0.36 (0.81) | VU/VU |
| *Leopardus wiedii* | - | - | 0.20 (1.20) | - | EN/NT |
| *Puma concolor* | 1.92 (88.46) | 4.56 (210.09) | 0.80 (37.03) | 0.36 (16.57) | VU/LC |
| *Puma yagouaroundi* | - | - | - | 0.18 (0.81) | LC/LC |
| Mustelidae | | | | | |
| *Eira Barbara* | - | 0.24 (1.68) | 0.40 (2.81) | 0.18 (1.26) | LC/LC |
| Procyonidae | | | | | |
| *Nasua nasua* | - | - | 0.80 (4.10) | - | LC/LC |
| *Procyon cancrivorus* | - | - | 1.40 (7.60) | - | LC/LC |
| **Cingulata** | | | | | |
| Dasypodidae | | | | | |
| *Cabassous unicinctus* | - | 0.48 (1.53) | - | - | NE/LC |
| *Cabassous tatouay* | - | - | 0.40 (2.15) | - | DD/LC |
| *Dasypus novemcinctus* | - | 0.48 (1.75) | - | - | LC/LC |
| **Didelphimorphia** | | | | | |
| Didelphidae | | | | | |

Continuation of Table 2

| | | | | | |
|---|---|---|---|---|---|
| *Didelphis aurita* | 1.20 (1.48) | 0.24 (0.29) | 1.00 (1.24) | 3.42 (4.22) | LC/LC |
| **Perissodactyla** | | | | | |
| Tapiridae | | | | | |
| *Tapirus terrestris* | 4.80 (1250.00) | 1.20 (312.50) | 4.42 (1151.02) | - | VU/VU |
| **Pilosa** | | | | | |
| Myrmecophagidae | | | | | |
| *Tamandua tetradactyla* | - | - | - | 0.36 (1.87) | LC/LC |
| **Rodentia** | | | | | |
| Caviidae | | | | | |
| *Hydrochoerus hydrochaeris* | 0.24 (12.01) | - | - | - | LC/LC |
| Cuniculidae | | | | | |
| *Cuniculus paca* | 1.44 (13.41) | 2.16 (20.12) | 0.60 (5.61) | - | NT/LC |
| Dasyproctidae | | | | | |
| *Dasyprocta leporina* | 1.68 (9.25) | - | - | 1.44 (7.92) | NE/LC |
| Erethizontidae | | | | | |
| *Coendou* cf. *spinosus* | - | 0.24 (0.43) | - | - | LC/LC |
| Sciuridae | | | | | |
| *Guerlinguetus ingrami* | 0.24 (0.041) | 0.48 (0.08) | 1.61 (0.27) | - | LC/NE |

[a] Threat status in the State of São Paulo (Bressan et al. 2009). EN = endangered, NE = not evaluated; [b] International threat status (IUCN 2011). LC = least concern, NT = near threatened, VU = vulnerable, DD = data deficient. *Relative abundance = (number of independent captures/sampling effort) x 100 (Srbek-Araujo & Chiarello 2005); **Relative biomass = relative abundance x weight (Galetti et al. 2009); ***Mean of the weights of *Mazama americana, M. bororo and M. gouazoubira.*

The mean rarefaction curve that estimated species richness per survey day did not reach an asymptote in any sites (Figure 2), with species continuing to accumulate at a rate of 0.04 species at ITA, 0.06 at VG and IC and 0.09 at CB after 45 survey days. Based on the First order jackknife the extrapolated species richness was between about eight to 14 species at ITA (estimate ± 95% CI = 10.96 ± 2.72), 10 to 16 species at VG (estimate ± 95% CI = 12.93 ± 3.32), 13 to 21 species at CB (estimate ± 95% CI = 16.93 ± 3.86) and 10 to 16 species at IC (estimate ± 95% CI = 12.96 ± 2.72).

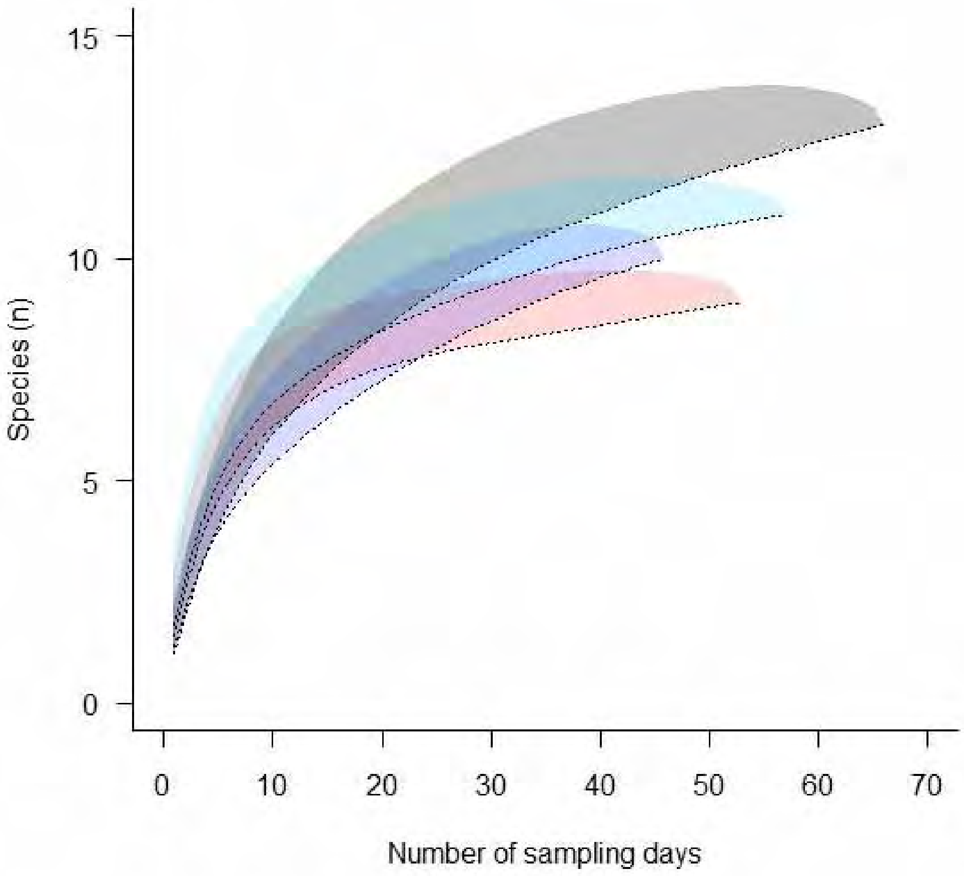

Figure 2. Mean rarefaction curve and 95% confidence interval of the expected number of mid- and large-sized mammals recorded with camera traps in Itamambuca (ITA; red) and Vargem Grande (VG; blue), Carlos Botelho (CB; grey), Ilha do Cardoso (IC; green).

The dendrograms showed that the four sites have similar large mammal richness but with a slightly higher similarity between the sites ITA and IC, and the sites CB and VG (Figure 3).

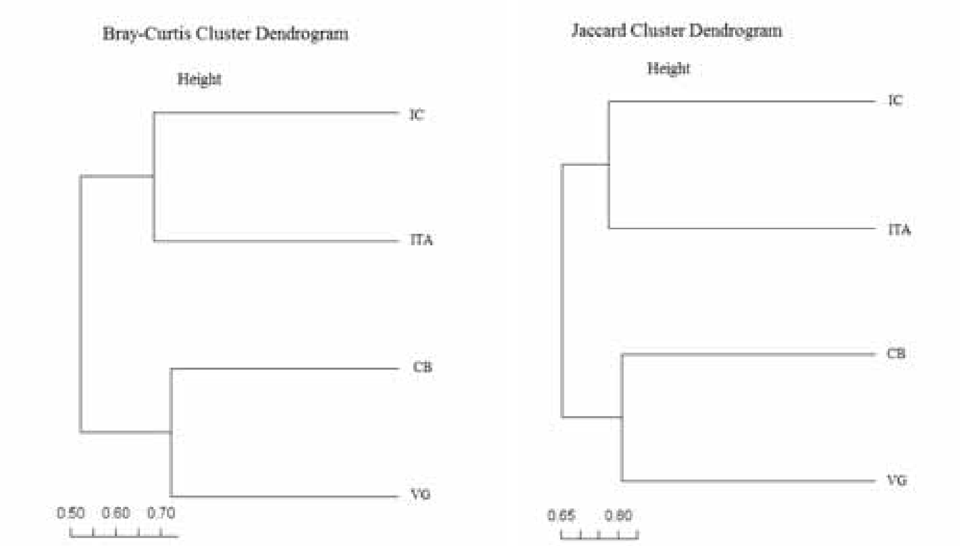
a. b.

Figure 3. Cluster dendrograms for Bray-Curtis (a) and Jaccard (b) Index for the measure of dissimilarity of mid- and large-mammals among the sites Itamambuca (ITA), Vargem Grande (VG), Carlos Botelho (CB) and Ilha do Cardoso (IC).

According to the functional groups of large mammals captured we found a predominance of terrestrial herbivores in ITA, IC and CB (relative abundance of 36.3 (independent captures/sampling effort) x 100, 9.2 and 5.5 respectively) with a predominance of *Tayassu pecari* (relative abundance of 28.12 and 7.56) at the two first sites and *Tapirus terrestres* (relative abundance of 4.42) at the last one. At VG the top predators (4.5) and mesopredators (hypercarnivores) (4.3) were more abundant the other functional groups (Table 3).

Table 3. Functional groups of mid- and large-sized mammals surveys at ITA, VG, IC and CB.

| **Functional groups** | **Relative abundance*** | | | | |
|---|---|---|---|---|---|
| | **Mean Body Mass (kg)**** | **ITA** | **VG** | **CB** | **IC** |
| **Top predators** | | **1.92** | **4.56** | **0.80** | **0.36** |
| *Puma concolor* | 46 | 1.92 | 4.56 | 0.80 | 0.36 |
| **Mesopredators (hypercarnivores)** | | **2.40** | **4.32** | **4.22** | **3.78** |
| *Leopardus pardalis* | 9.5 | 2.40 | 4.32 | 4.02 | 3.24 |
| *Leopardus wiedii* | 6 | - | - | 0.20 | - |
| *Leopardus tigrinus* | 2.25 | - | - | - | 0.36 |
| *Puma yagouaroundi* | 4.5 | - | - | - | 0.18 |
| **Mesopredators (omnivores)** | | **1.20** | **0.48** | **3.82** | **3.76** |
| *Cerdocyon thous* | 6.5 | - | - | 0.20 | 0.16 |
| *Didelphis aurita* | 2.47 | 1.20 | 0.24 | 1.00 | 3.42 |
| *Eira barbara* | 7 | - | 0.24 | 0.40 | 0.18 |
| *Nasua nasua* | 5.1 | - | - | 0.80 | - |
| *Procyon cancrivorus* | 5.4 | - | - | 1.40 | - |
| **Terrestrial herbivores** | | **36.29** | **3.36** | **5.43** | **9.20** |
| *Cuniculus paca* | 9.3 | 1.44 | 2.16 | 0.60 | - |
| *Dasyprocta leporina* | 5.5 | 1.68 | - | - | 1.44 |
| *Hydrochoerus hydrochaeris* | 50.5 | 0.24 | - | - | - |
| *Mazama americana* | 36 | - | - | - | 0.19 |
| *Mazama* spp. | 27 | - | - | 0.40 | - |
| *Tapirus terrestris* | 260 | 4.80 | 1.20 | 4.42 | - |
| *Tayassu pecari* | 35 | 28.12 | - | - | 7.56 |
| **Arboreal herbivores** | | **0.24** | **0.72** | **1.61** | **-** |
| *Coendou* cf. *spinosus* | 1.8 | - | 0.24 | - | - |
| *Guerlinguetus ingrami* | 0.17 | 0.24 | 0.48 | 1.61 | - |
| **Terrestrial insectivores** | | **-** | **0.96** | **0.40** | **0.36** |
| *Cabassous unicinctus* | 3.2 | - | 0.48 | - | - |
| *Cabassous tatouay* | 5.35 | - | - | 0.40 | - |
| *Dasypus novemcinctus* | 3.65 | - | 0.48 | - | - |
| *Tamandua tetradactyla* | 5.2 | - | - | - | 0.36 |

*Relative abundance = (number of independent captures/sampling effort) x 100 (Srbek-Araujo & Chiarello 2005). **From Paglia et al. 2012.

## 4. Discussion

Despite the fact that the four studied sites are located in the same Atlantic Forest continuum, we did not find a similar pattern of species richness and abundance between each site's large mammal communities and in just one of four sites we found an alteration in functional diversity, which illustrates the existence of distinct large mammal communities in this area.

Our samples were sufficient according to the extrapolated by the mean rarefaction curves and the First order jackknife. Of the nine species recorded at ITA, almost half (four species, 44% of the total) are considered threatened ("Vulnerable" or "Endangered") in the State of São Paulo (Bressan et al. 2009) and one species (11%) is considered threatened internationally (IUCN, 2011) (Table 2). Of the 10 species recorded at VG, three (30%) are considered threatened in the State of São Paulo and one (10%) globally. Of the 13 species recorded at CB, the numbers of threatened species are five (38%) and one (8%) according to the regional and international threat status, respectively. Lastly, of the 11 species recorded at IC, the threatened species are five (45%) and one (9%) respectively (Table 2).

Comparing the sites through the Bray-Curtis and Jaccard dendrograms, we found that mid- and large-mammals compositions between ITA and IC and between VG and CB are slightly more similar than other pairs of compositions. This trend can be partially explained by the predominance of certain functional groups of mammals in respective sites. At ITA we found a greater relative abundance of terrestrial herbivores (36.3 (independent captures/sampling effort) x 100), followed by mesopredators (hypercarnivores) (2.4) and top predator (2.0). The same pattern was observed for IC with more terrestrial herbivores (9.2), mesopredators (hypercarnivores) (3.8) and top predator (0.36) (Table 3). The high number of terrestrial herbivores in both sites can be explained by the prevalence of the white-lipped peccary, an important seed predator (Beck 2006, Keuroglian & Eaton 2009) and herbivore (Beck 2006) which lives in large herds (Jones et al. 1997, Altrichter & Almeida 2002, Silman et al. 2003) contributing to this huge portion of terrestrial herbivores abundance found in both sites. Moreover ITA and IC are the only ones among the four sites where we can find this species which may contribute to the similarity between both areas showed by the dendrogram.

CB and VG have the highest relative abundance of mesopredators (hypercarnivores) (4.2 and 4.3, respectively) when comparing this functional group abundance with the other sites. As previously stated, these sites hold the lowest relative abundance of terrestrial herbivores mostly represented there by *Tapirus terrestris* and *Cuniculus paca*. The lack of white-lipped peccary records in both areas justifies the low abundance of this functional group. According to local residents' reports, this species has been absent in CB since the end of 1980 (Brocardo 2012). Regarding the species recorded at the four sites, we had *Puma concolor*, the only top predator photographed, and the mesopredators *Leopardus pardalis* and *Didelphis aurita.* The first two species, *P. concolor* and *L. pardalis*, were more abundant at VG and the last one was more abundant at IC (Table 3).

Several studies suggest that human pressure caused by hunting generates predictable fauna communities where large mammals disappear (Cullen Jr et al. 2000, Peres 2001, Peres & Palacios 2007, Fa & Brown 2009). This is supported by Dobson et al. (2006), who concluded that the consequences of human exploitation affect firstly species of upper trophic levels due to their higher necessity of huge areas. Consequently, the ecological services provided by these species are lost before those provided by lower trophic levels. In our four continuous areas this pattern was not a rule. At these areas the mid- and large-mammals were not predictably affected by hunting.

We found that geographically close sites, ITA and VG, sustain completely distinct fauna composition with presence (ITA) and absence (VG) of such key species like *T. pecari*, which has a fundamental role in recruitment, demography and distribution of plants (Roldán & Simonetti 2001, Beck et al. 2005, Beck 2006, Keuroghlian & Eaton 2009). These distinct fauna compositions result in discrepant functional groups abundances in these areas (Table 3). In ITA, IC and CB we observed a well distributed relative abundance of the functional groups with lower abundance of top predators and mesopredators regulating a higher abundance of herbivores (Johnson et al. 2007, Estes et al. 2011). VG contrasts that pattern and reveals a lower abundance of terrestrial herbivores but still quite similar to that of top predators and mesopredators (hypercarnivores). In our view, this disparity at VG may result in higher pressure of predator control over the herbivore population, which consequently may result in changes within the plant communities, as suggested by several studies (Wright 2003, Galetti et al. 2006, Queenborough et al. 2012, Bueno et al. 2013, Yessoufou et al. 2013). However, longer-term studies are needed to confirm whether this high relative abundance of mesopredators (hypercarnivores) and top predators in VG is permanent or may result of population fluctuations reacting according to prey availability.

We can numerate several mechanisms that may explain this unpredictable fauna communities caused by human pressure which were found in the four sites, such as distinct history of human pressure, which mainly concerns the hunting pressure over time (Peres 2000, Nobre 2007), or distinct processes of species migration or epidemics (Fragoso 2004). On the other hand, the consequences of mammal defaunation may be very distinct, with greater or lesser impacts on other trophic levels, depending on which species is lost (Tilman et al. 1997). Extinction of keystone species will result in loss of their key and unique ecological functions, altering the proper functioning of the entire ecosystem (Terborgh 1992, Wright et al. 2000, Dobson et al. 2006, Flynn et al. 2009, Clark et al. 2012).

It is necessary to understand the effects of mammal absence on the trophic levels and the need for immediate action due to the fast increase of human impacts on natural areas. Beyond that such kind of studies will enable researchers to predict future patterns of extinction and consequently conservation directions for more effective strategies of biodiversity protection.

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# CAPITULO II

## Consequences of herbivores extinction on plant diversity in a gradient of defaunation

# RESUMO

A defaunação seletiva tem um amplo efeito sobre as populações de grandes vertebrados desencadeando diversos efeitos cascata. Apesar de termos um pobre entendimento dos efeitos “top down” sobre a composição de plantas, muitos estudos evidenciam a função de grandes herbívoros na formação das comunidades. No presente estudo, investigamos se as extinções funcionais dos grandes herbívoros alteram a riqueza, a densidade e a beta diversidade de plântulas em Florestas Atlânticas Brasileiras contínuas. Simulamos a defaunação experimentalmente em uma mesma área através de experimentos de exclusão, mas nós também replicamos nossos experimentos em quatro áreas distintas, todas as quatro com composição da fauna de grande porte conhecida. Nas áreas com presença de queixada, encontramos que a presença de grandes mamíferos herbívoros (parcelas abertas) causa uma tendência tanto ao declínio da densidade de plântulas quanto ao aumento da beta diversidade, como esperávamos, mas não encontramos um padrão para seu efeito sobre a riqueza de plântulas. Nas áreas com ausência de queixada, a presença dos grandes mamíferos herbívoros (parcelas abertas) não causou mudanças na riqueza e na beta diversidade das plântulas, e não encontramos um padrão para seu efeito sobre a densidade de plântulas. Concluímos que a extinção funcional de grandes mamíferos herbívoros pode resultar em consequências preocupantes sobre as comunidades vegetais, onde os queixadas, *Tayassu pecari*, são o maior modificador das comunidades vegetais. O conhecimento das consequências da extinção de determinadas espécies de mamíferos nos permitirá uma melhor compreensão da importância de cada parte da cadeia alimentar na qual os mamíferos tropicais se inserem, e um melhor delineamento das estratégias de conservação.

**Palavras-chave:** Diversidade beta, experimentos de exclusão, comunidade de mamíferos, plântulas, defaunação seletiva, *Tayassu pecari*, cascatas tróficas.

# ABSTRACT

Selective defaunation has a pervasive effect on the populations of large bodied vertebrates and triggers several trophic cascading effects. Although we have poor understanding of the top down effects on plant composition, several studies evidence the role of large herbivores in community assembly. In the present study, we investigated whether the functional extinction of large herbivores alters seedling species richness, density and beta diversity in the continuous Brazilian Atlantic Forest. We simulated defaunation experimentally within the same site through exclusion experiments, but we also replicated our experiments in four distinct sites, all four with a known large-bodied fauna composition. At peccary-present sites, we found that the presence of large herbivorous mammals (open plots) causes a decrease in seedling density and a tendency of increase in beta diversity as we expected, but we found no effect on seedling richness. At peccary-absent sites, the presence of large herbivorous mammals (open plots) causes no changes in seedling richness and in beta diversity as we predicted, but we found no pattern of their effect over seedling density. We concluded that the functional extinction of large herbivorous mammals may result in worrying consequences over plant communities, where the white-lipped peccary, *Tayassu pecari*, is the major driver of plant community changes. Knowing the consequences of extinctions of particular mammal species will allow us to better understand the importance of each piece of tropical mammalian food webs and better delineate further conservation strategies.

**Key-words:** Beta diversity, exclusion experiment, mammal community, seedlings, selective defaunation, *Tayassu pecari*. trophic cascades.

## 1. Introduction

Researchers have long recognized the importance of predation for the control of species abundance and on species coexistence and diversity (Hairston et al. 1960, Terborgh 1992, Terborgh et al. 2001, Ripple & Beschta 2006, Terborgh et al. 2006, Estes et al. 2011). In heavily hunted areas the large mammal communities are deeply disturbed by poachers (Bodmer et al. 1997, Peres 2000, Wright et al. 2007b, Canale et al. 2012, Galetti et al. 2009). The absence of large mammals prevents many fundamental processes in plant communities such as herbivory (Olff & Ritchie 1998, Yessoufou et al. 2013), trampling (Queenborough et al. 2012), seed predation and dispersal (Wright et al. 2000, Wright 2003, Galetti et al. 2006, Nuñez-Iturri & Howe 2007, Wright et al. 2007a, Brodie et al. 2009, Farwig & Berens 2012, Bueno et al. 2013), and the absence of those processes propagates throughout the other processes and other trophic levels in the ecosystem (Terborgh 1992, Wright et al. 2000, Culot et al. 2013).

Several studies aimed to elucidate the defaunation effects on plant diversity through the comparison of faunated forests and defaunated ones (Dirzo & Miranda 1991, Roldán & Simonetti 2001, Beckman & Muller-Landau 2007, Wright et al. 2007a, Effiom et al. 2013, Harrison et al. 2013) significantly contributing to our knowledge on the topic. However, comparing two sites without replication prevents researchers to fully determine whether differences in plant diversity are the result of mammal differences or some other differences that also exist between the two sites (Kurten *in press.).* Moreover, few of those studies present a measurement of large mammals' richness and abundance to correlate with the consequences on plant diversity (Kurten *in press*).

Our main objective was to determine whether the loss of large herbivorous mammals affects the seedling richness, density, and beta diversity. Furthermore, considering the limitations of previous studies, we proposed to investigate the effects of mid- and large-sized mammals on plant communities taking three points into considerations. First, instead of comparing a preserved site with a defaunated one, we simulated defaunation experimentally in the same site through exclusion plots, ensuring that biotic and abiotic conditions are more similar between control and mammal exclusion plots. Such design allowed us to minimize the effects of other factors such as historic events that may affect a site (logging, extraction of resources, weather events) and differences in the rainfall patterns (Beck et al. 2013). Second, we replicated the design in four sites located throughout the Serra do Mar, the largest Atlantic forest corridor along the coast of Brazil. Serra do Mar is the last refuge of large mammals, such as jaguars (*Panthera onca*), white-lipped peccaries (*Tayassu pecari*), tapirs (*Tapirus terrestris*) and woolly spider monkeys (genus *Brachyteles* spp.) (Jorge et al. 2013). Finally, our four areas of investigation have already been sampled for fauna composition and present a gradient of defaunation (see chapter 1 for definition, design and results), allowing us to correlate the presence and abundance of specific mammal species with seedling diversity, and to reinforce the results on effects of large mammals on plant community at two spatial levels (plot or local level, and site or regional level).

Following the Defaunation Hypothesis (Dirzo & Miranda 1991), our predictions were that in open plots (where the effects of mammals are still present) compared to closed ones, there would be (Figure 1):

(1) Higher seedling richness, smaller seedling density and higher beta diversity at sites with high mid and large herbivorous mammal's relative abundance (ITA and IC);

(2) Slight/no decrease in seedling richness, slight/no increase in density and slight/no decrease in beta diversity at sites with low mid and large mammal's relative abundance (CB and VG).

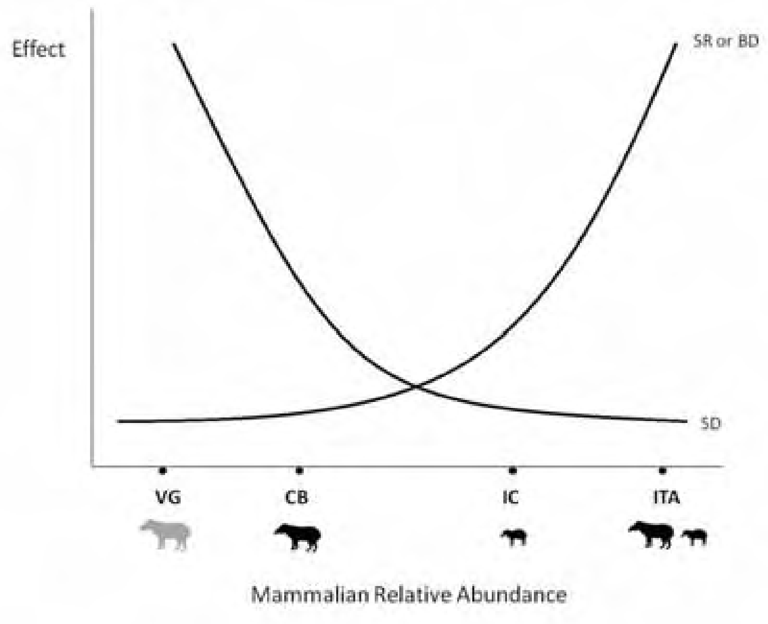

Figure 1. Conceptual hypothesis and predictions of the impact of defaunation in seedling richness (SR), seedling density (SD) and seedling $\beta$-Diversity (BD) at Vargem Grande (VG), Carlos Botelho (CB), Ilha do Cardoso (IC) and Itamambuca (ITA).

## 2. Material and Methods

### 2.1. Study site

We carried out our study in four continuous protected areas of the Atlantic Forest along the Serra do Mar corridor (Aguiar et al. 2003) covered by ombrophylous rainforest (Instituto Florestal. 2006, Instituto Florestal 2008, Melo & Mantovani 1994). We have chosen these areas based on previous data on their importance for mammal conservation (Galetti et al. 2009). We sampled two areas in Serra do Mar State Park, Itamambuca Base (ITA) (45° 5' W; 23° 19' S) and Vargem Grande Base (VG) (45° 14' 39" W; 23° 26' S) and two other parks within this corridor, Carlos Botelho State Park (CB) (45° 14' W, 23° 26' S) and Ilha do Cardoso State Park (IC) (48° 01' W, 25° 12' S) (Figure 2).

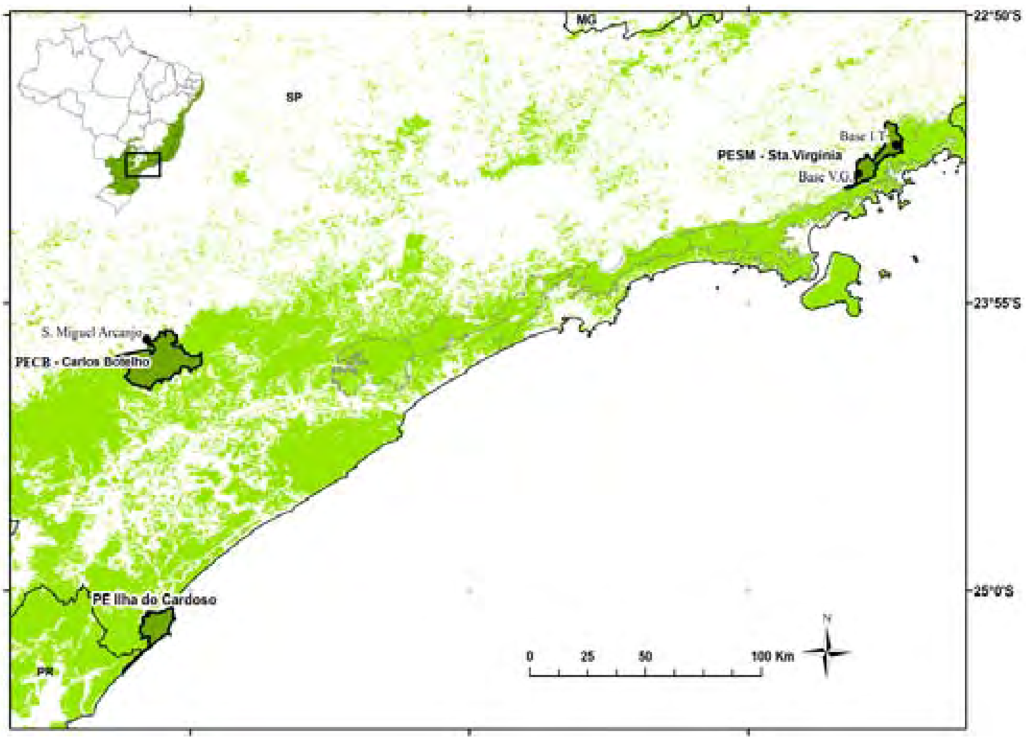

Figure 2. Location of study areas: Itamambuca Base (ITA) and Vargem Grande Base (VG), in Serra do Mar State Park (SMSP); Ilha do Cardoso State Park (ICSP) and Carlos Botelho State Park (CBSP), São Paulo, Brazil (mapa: Bruno Borges).

The four areas have already been sampled for fauna composition presenting mid and large terrestrial herbivorous mammal's total abundance of 36.29 (independent captures/sampling effort) x 100 at ITA, 9.20 at IC, 5.43 at CB and 3.36 at VG (see chapter 1, Table 3). More important, there are qualitative differences between the sites, such that there are white-lipped peccaries, *Tayassu pecari*, only at ITA and IC. We emphasize white-lipped peccaries because among Neotropical seed predators this species makes up the largest biomass (Silman et al. 2003, Beck et al. 2005, Beck 2006) where it occurs, as its individual body size ranges between 30-40kg and they can form large group sizes, up to hundreds of individuals (Altrichter & Almeida 2002, Beck 2006), greatly increasing their effect on seedlings where they are present. So according to the total abundance of large terrestrial herbivorous mammals and the sites' fauna composition we grouped ITA and IC as the sites with the highest total abundance of terrestrial herbivorous mammals and with peccaries (hereafter peccary-present sites) and VG and CB as the sites with the lowest total abundance of terrestrial herbivorous mammals and without peccaries (hereafter peccary-absent sites).

### 2.2. Seedling survival

We established 15 pairs of plots (3 x 5 m) at each of the four study sites. The pair of plots consisted of one exclusion plot (closed, simulating the absence of mammals) and one control plot (open, where all mammals had access). The exclusion plots were fenced off using a 1.5-m-high screen, only permitting the access of small rodents and invertebrates as well as sunlight (in order to not affect the plants' growth). The control plots remained open with their area delineated by poles (Brocardo et al. 2013, Beck et al. 2013). The open and closed plots were separated two to five meters from each other to ensure homogeneity between the environments, and there was a distance of at least 200 m between replicates at the same site.

We subdivided each plot into eight quadrants (1 $m^2$) and in three of them we conducted seedling-survival experiments during which we marked all seedlings between 10 cm to 1 m (DeMattia et al. 2004), identified and tracked their growth every six months for 24 months. Here we considered all plants with height between 10 cm to 1 m as a seedling. We left a border of 0.5 m in each plot to allow access into the plots without disturbing them too much and to avoid spurious results that could be related to the use of the borders as perches by birds. Seedlings were identified in species, genus or when could not be identified were grouped into morphospecies.

## 2.3. Data analysis

We evaluated the effect of defaunation on local seedling richness (total number of species per plot) and density (total number of individuals/m$^2$ per plot) through a Linear Mixed Models (LMM) using "lme" function in "nlme" package of R. For both analyses, the explanatory variable used was time (zero, six, 12, 18 and 24 months) and the random factor was the plots. We calculated the response variable (seedling richness or seedling density) through its difference between open and closed plots every six months until 24 months of experiment in each of the four sites.

We also calculated the beta diversity, defined by Anderson and collaborators (2006) as "the variability in species composition among sampling units for a given area at a given spatial scale." Beta diversity tends to increase in heterogeneous landscapes as few species are shared by these sample units, and decrease in homogeneous landscapes as the majority of species are shared between the sample units (Magurran 2004). To estimate the beta diversity we used the test for homogeneity of multivariate dispersions where an $F$-statistic was calculated to compare the average distance of the samples to their group centroid in a multivariate space through a chosen dissimilarity measure (Anderson et al. 2006). Then across permutation of least-squares residuals we obtained a $P$-value (Anderson et al. 2006).

The sample units used to calculate the beta diversity were the treatments, open and closed plots, in each study site every six months through 24 months of experiment. To construct beta diversity graphics the chosen dissimilarity measure was Bray-Curtis index which is based on the abundance of species (Chao et al. 2005) in each plot. Furthermore, for statistical tests we used the Monte Carlo randomization test with the Jaccard index, the Modified Gower dissimilarity measure (log 10), the Modified Gower measure (log 2), and the Bray-Curtis index (Anderson 2006). We ran the graphic analyses and the statistical tests in R software 2.12.2 (http://www.r-project.org/) using "betadisper" and "vegdist" functions of the "vegan" package for the graphics and the "betadisper" function of the "vegan" and "car" packages for the statistical test.

## 3. Results

At peccary-present sites, the presence of large herbivorous mammals (open plots) results in no changes (ITA) and decrease (IC) in seedling richness; tendency decrease in seedling density (ITA and IC); and increase (ITA) and no changes (IC) in seedling beta diversity. While at peccary-absent sites, in the presence of large herbivorous mammals (open plots) we found no changes in seedling richness (CB and VG); no changes (CB) and a slight decrease (VG) in seedling density; and no changes in beta diversity (CB and VG). In both cases our results corroborated partially with our predictions.

A Linear Mixed Models Analysis (LMM) for repeated measures showed a significant difference between seedling species richness of open and closed plots at IC, but not at ITA (Appendix - Table 1). Seedling species richness in open plots (mammal access) at ITA (peccary-present) did not change after 24 months of experiment while on closed plots (mammal exclusion) we found an increase in seedling richness (Figure 3a). At IC (peccary-presence) we noted a decrease in seedling species richness in open plots (mammal access) after six months of experiment while nothing changed in closed plots (Figure 3b). These results did not corroborate with our expectation of an increase in seedling richness in open plots of peccary-present sites. At CB and VG (peccary-absent) no differences between the treatments were observed for seedling richness (Figure 3c&d, Appendix - Table 1) corroborating with our prediction of a slight/no decrease of seedling richness in open plots of peccary-absent sites.

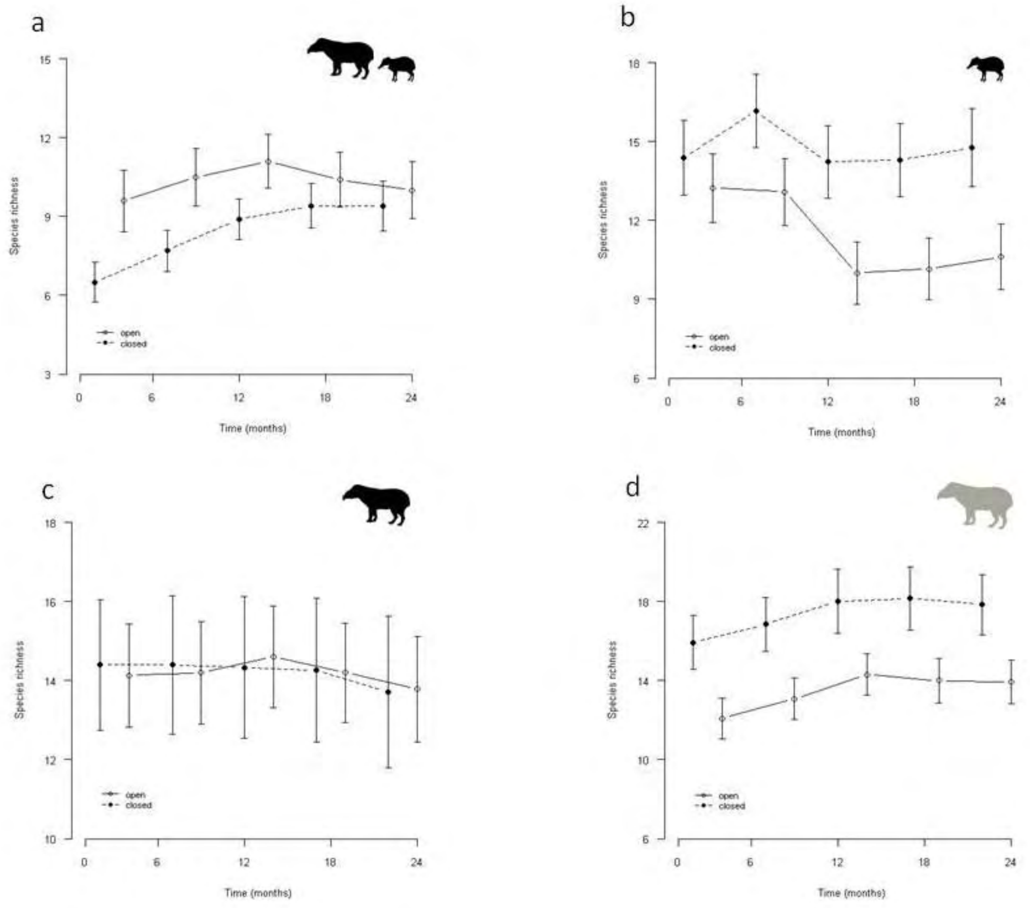

Figure 3. Species richness of seedling for open and closed plots at a gradient of mammal abundance: Itamambuca (a), Ilha do Cardoso (b), Carlos Botelho (c) and Vargem Grande (d) during 24 months of experiment.

Statistical test showed differences in seedling density between open and closed plots along the time of experiment in tree of the four sites. The difference between the treatments was found in ITA, IC and VG, but CB, which shows that large herbivorous mammals of the tree first sites have some effect over the density of seedlings while the large herbivorous mammals of CB have no effect (Appendix -Table 2). However, these statistical differences were not graphically evidenced (Figure 4). ITA and IC (peccary-present sites) have just a tendency in seedling density decrease in open plots corroborating partially with the seedling density decrease prediction for peccary-present sites, while CB had no changes and VG had a slight decrease in seedling density of open plots, corroborating partially with our predictions of a slight or no increase (Figure 4).

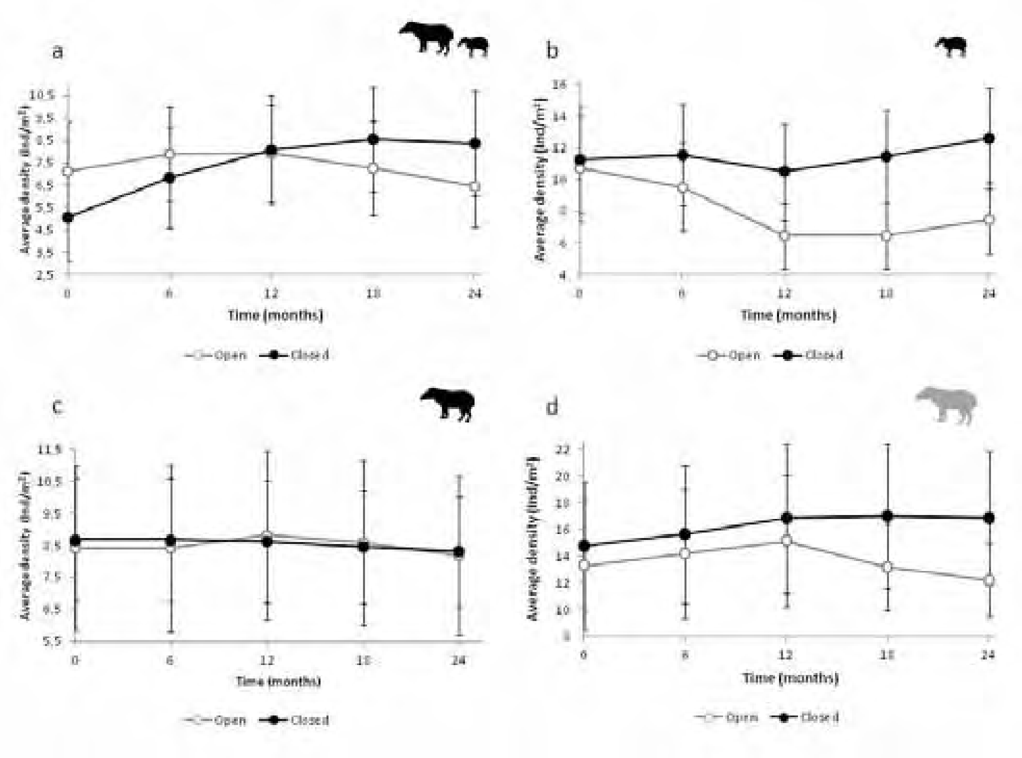

Figure 4. Average density (Individuals/m$^2$) of seedlings for open and closed plots at gradient of mammal abundance: Itamambuca (a), Ilha do Cardoso (b), Carlos Botelho (c) and Vargem Grande (d) during 24 months of experiment.

We also found no significant differences in statistical test of beta diversity between the treatments for the four indexes, at each interval of time for the four sites (Appendix - Table 3). Nevertheless, we found marginally significant differences between treatments at ITA after 24 months, and at IC after 12 months ($P\text{-value}_{\text{ITA24-Jac}} = 0.084$ and $P\text{-value}_{\text{IC12-BC}} = 0.083$, Appendix - Table 3). Those differences are more clearly seen when looking to the graphics of beta diversity. We noticed a slight divergence between open and closed plots at the 18 months marker at ITA, which becomes clearer at 24 months (Figure 5a). At IC the difference between the treatments starts at 12 months but decreases at 18 months, and disappears at 24 months of experiment (Figure 5b). So for peccary-present sites the results corroborated partially with our predictions of an increase in seedling beta diversity. For CB and VG no differences were observed between the treatments throughout the 24 months of experiment (Figure 5c&d) corroborating with the expectation of slight/ no decrease of large herbivorous mammals over seedling beta diversity.

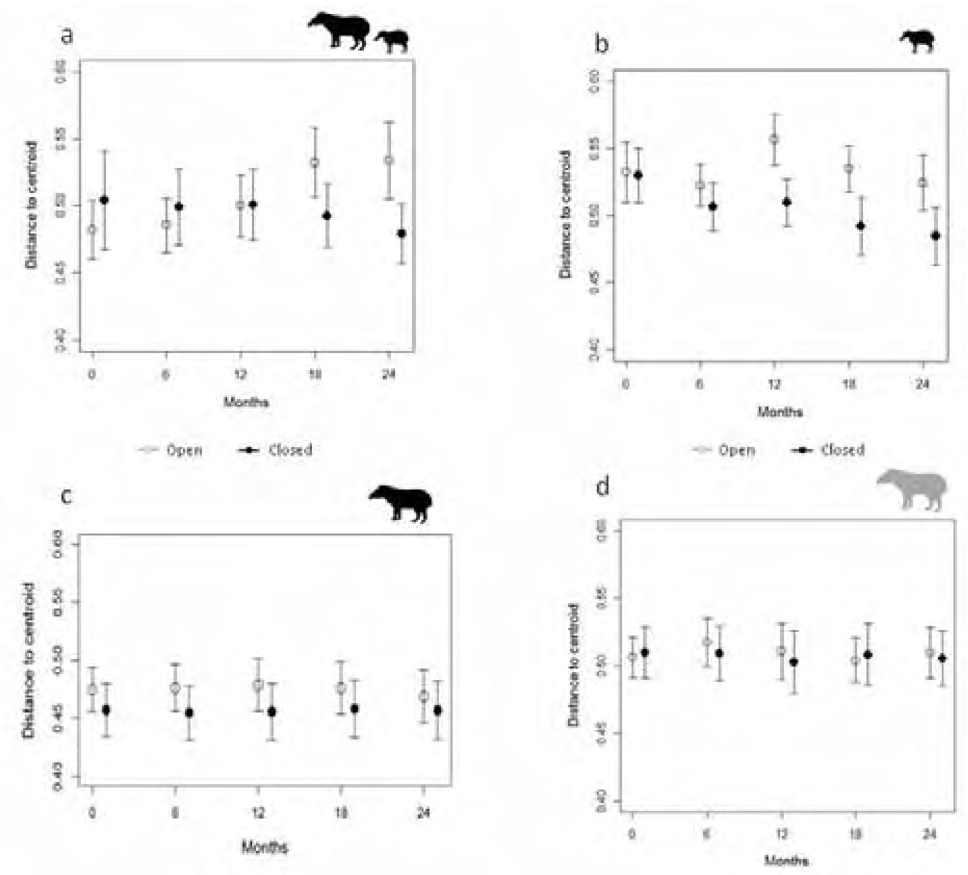

Figure 5. $\beta$-diversity (circles represent the mean value of distances to the centroid and the corresponding confidence intervals) for open and closed plots at a gradient of defaunation: Itamambuca (a), Ilha do Cardoso (b), Carlos Botelho (c) and Vargem Grande (d) during 24 months of experiment.

## 4. Discussion

Based on the Defaunation Hypothesis (Dirzo & Miranda 1991) we expected that in peccary-present sites, over time we would observe higher seedling species richness, smaller seedling density and higher beta diversity in open plots compared to closed ones, while in peccary-absent sites we would observe a slight/no decrease in seedling richness, slight/no increase in density and slight/no decrease in beta diversity.

At peccary-present sites, we found that the presence of large mammals (open plots) causes a decrease in seedling density and a tendency of increase in beta diversity as we expected, but we found no pattern of large mammal effects over seedling richness. At peccary-absent sites, the presence of large mammals (open plots) causes no changes in seedling richness and in beta diversity as we predicted, but we found no pattern of large mammal effects on seedling density.

At peccary-present sites (ITA and IC), seedling species richness did not increase over time of experiment, not corroborating with our predictions. At ITA, the presence of peccaries at the open plots did not increase seedling species richness. In fact, we did not observe a change over the 24 months of experiments. On the other hand, their absence in closed plots resulted in an increase in seedling richness (Figure 3a). At IC, we witnessed a decrease in seedling species richness in open plots and no change in the closed plots (Figure 3b). Keuroghlian & Eaton (2009) conducted a one-year exclusion plot experiment and found that excluding *T. pecari* greatly increased seedling abundance, with the exception of *Euterpe edulis*, but they did not analyze the peccary effect on seedling richness.

In peccary-present sites, we also expected to see a increase of seedling density at open plots as the presence of mammals would increase the impact on the seedlings (Dirzo & Miranda 1991). For both sites our results corroborated partially our predictions as it was observed a tendency in seedling density to decrease (Figure 4a&b). In peccary-absent sites, the results were consistent with our expectations showing no changes in seedling richness of open plots (Figure 3c&d). But for seedling density the results partially corroborated our predictions showing no changes (CB) and a decrease (VG) in open plots (Figure 4c&d). In the studies of Wright et al. (2000, 2007a) of how the absence of herbivorous mammals affected the density of two palms (*Attalea butyraceae* and *Astrocaryum standleyanum*) found no significant treatment effect.

The tree sites ITA ($P$-value$_{\text{ITA}}$ < 0.001), IC ($P$-value$_{\text{IC}}$ < 0.001) and VG ($P$-value$_{\text{VG}}$ < 0.001) showed differences in seedling density between the treatments along time of experiments (Appendix - Table 2), except CB ($P$-value = 0.1403). A possible hypothesis for this similar density between the treatments in CB along time of experiment, could be explained by the richness and density (Individuals/km$^2$) of primates found in CB, that is superior to the found at ITA, IC and VG (Brocardo 2011). This high concentration of primates in CB could cause equal probability of seed rain by primates in both treatments in CB, resulting in chances of equal recruitment of seedling in both treatments. Consequently the seed rain could lead to homogenized treatments resulting in similar seedling density between them as our results of CB demonstrated.

Dirzo & Miranda (1991) tested the hypothesis that defaunation alters patterns of forest understory herbivory and diversity by comparing faunated and defaunated sites. The defaunated site showed a decrease in species richness followed by an increase in seedling density, where fewer species dominated the scenario and that consequently led to a decrease in the diversity index of their plant community. However in a literature review of the consequences of defaunation on plants, Kurten (*in press*) found contradicting results concerning the effect of mammal absence on seedling density and diversity between studies with exclusion experiments and forest comparison. In some studies, exclusion experiments revealed a high density of seedlings in the absence of mammals (Ickes et al. 2001, Royo and Carson 2005) although Kurten (*in press*) did not find a clear pattern for seedling diversity. In studies that compared defaunated forest with non-defaunated, Kurten (*in press*) found that both seedling density and seedling diversity were generally lower in defaunated areas.

Until now our results indicate that a high abundance of large herbivorous mammals did not affect the seedling richness but have some effect on seedling density. Looking through a larger spatial scale using beta diversity we will be able to investigate the fauna effect over the seedling composition (Anderson et al. 2006).

Seedling beta diversity in open and closed plots was statistically similar at the four sites after 24 months (Appendix - Table 3). However, visually, we found a difference between seedling beta diversity of ITA after 24 months of experiment (Figure 5a). In the open plots of ITA, there was an increase in the seedling beta diversity showing that these plots shared fewer species and were more heterogeneous after 24 months of experiment. On the other hand, there was a decreasing trend of seedling beta diversity in closed plots, which indicates that plots became more similar to each other in terms of species diversity over time (Figure 5a). At IC, the trend is less evident. Open plots were more dissimilar amongst each other after 12 months, but became more homogeneous again after 24 months (Figure 5b). At peccary-absent sites we observed no differences between treatments in beta diversity over time (Figure 5c&d) which indicates that the fauna in these places did not influence seedling composition, as we had predicted. CB and VG do not have white-lipped peccaries but have other herbivores (tapirs and deer at CB, deer and very low abundances of tapir at VG) (more details at chapter 1). Tapirs provide a unique service as seed disperser of some plant species that produce medium and large seeds (Fragoso & Huffman 2000, Bueno et al. 2013, O'Farrill et al. 2012). Nevertheless, our study demonstrated that tapirs' effect on seedlings was not noticeable for any of our metrics: seedling richness (Figure 3c&d), density (Figure 4c&d) and composition (Figure 5c&d) over a period of 24 months of experiment.

Because white-lipped peccaries are the most abundant large mammal species in both sites (ITA and IC, Cap 1) we could detect some treatment effect on beta diversity, we can assume with caution that white-lipped peccaries may indeed have an important role to help maintaining the heterogeneity of the plant community. Previous studies have shown that white-lipped peccaries play an important role in the recruitment, demography and distribution of plants (Beck et al. 2005), especially with their trampling effects over seedlings (Roldán & Simonetti 2001, Beck 2006, Keuroghlian & Eaton 2009). Movement of herds can cause large perturbations on the understory and the forest floor and promote seedling diversity as they prevent some plant species to dominate the seedling community (Beck 2006), not to mention that large group formation (Altrichter & Almeida 2002, Beck 2006) intensifies their effects over seedlings, modifying the environment where they pass through (Silman et al. 2003, Beck et al. 2005, Beck 2006, 2007, Queenborought et al. 2012). These characteristics make the white-lipped peccary to be known as an “ecosystem engineer” (Jones et al. 1994, Jones et al. 1997).

The extinction of large herbivorous mammal species can cause worrying consequences on plant communities (Dirzo & Miranda 1991, Roldán & Simonetti 2001). In our case, it seems more evident that *T. pecari* has an important role as the major plant community modifier (Roldán & Simonetti 2001, Silman et al. 2003, Beck 2006, Keuroghlian & Eaton 2009). Maintenance of white-lipped peccary populations in those areas seems to be fundamental for a healthy functioning of the ecosystem. Nevertheless, our results highlight the importance of long-term studies as well as the importance of looking at larger spatial scales (such as beta diversity) to fully depict mammal effects on seedling community. Replications at other sites, with different and known large mammal composition and abundance are also necessary to allow us to understand which ecological functions are been lost and how they affect the plant community. Hopefully, such information will help delineate better and more efficient conservation and management strategies to prevent even more diversity loss over time.

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## 6. Appendix

Table 1. The differences of local seedling richness between the treatments (open and closed plots) calculated throw Linear Mixed Models (LMM) for Itamambuca (ITA), Ilha do Cardoso (IC), Carlos Botelho (CB) and Vargem Grande (VG) during 24 months of experiment.

| Área | num DF | den DF | *F*-value | *p*-value |
|---|---|---|---|---|
| Itamambuca | 1 | 39 | 0.8976 | 0.3492 |
| Ilha do Cardoso | 1 | 51 | 4.4084 | 0.0407 |
| Carlos Botelho | 1 | 59 | 0.0017 | 0.9671 |
| Vargem Grande | 1 | 51 | 0.1574 | 0.6932 |

Table 2. The differences of local seedling density between the treatments (open and closed plots) calculated throw Linear Mixed Models (LMM) for Itamambuca (ITA), Ilha do Cardoso (IC), Carlos Botelho (CB) and Vargem Grande (VG) during 24 months of experiment.

| Área | num DF | den DF | F-value | p-value |
|---|---|---|---|---|
| Itamambuca | 4 | 36 | 13.2585 | <.0001 |
| Ilha do Cardoso | 4 | 48 | 19.1802 | <.0001 |
| Carlos Botelho | 4 | 44 | 1.8291 | 0.1403 |
| Vargem Grande | 4 | 48 | 13.0287 | <.0001 |

Table 3. The differences of seedling composition ($\beta$-diversity) between the treatments (open and closed plots) calculated through Monte Carlo randomization test using Jaccard index, the Modified Gower dissimilarity measure (log 10), the Modified Gower measure (log 2), and the Bray-Curtis index, at Itamambuca (ITA), Ilha do Cardoso (IC), Carlos Botelho (CB) and Vargem Grande (VG) with six, 12, 18 and 24 months of experiment.

| | | Time (Months) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 0 | | | 6 | | | 12 | | | 18 | | | 24 | | |
| Sites | Indexes | DF | *F*-value | *p*-value | DF | *F*-value | *p*-value | DF | *F*-value | *p*-value | DF | *F*-value | *p*-value | DF | *F*-value | *p*-value |
| ITA | Jaccard | 1 | 0.7046 | 0.419 | 1 | 0.702 | 0.408 | 1 | 0.0964 | 0.737 | 1 | 0.8131 | 0.364 | 1 | 3.1565 | 0.084 |
| | Gower log 10 | 1 | 0.2442 | 0.627 | 1 | 0.4774 | 0.472 | 1 | 0.6273 | 0.421 | 1 | 0.0146 | 0.897 | 1 | 1e-04 | 0.994 |
| | Gower 2 | 1 | 0.2442 | 0.609 | 1 | 0.4774 | 0.505 | 1 | 0.6273 | 0.414 | 1 | 0.0146 | 0.909 | 1 | 1e-04 | 0.992 |
| | Bray-Curtis | 1 | 0.2414 | 0.653 | 1 | 0.158 | 0.686 | 1 | 2e-04 | 0.995 | 1 | 1.144 | 0.301 | 1 | 2.6965 | 0.128 |
| IC | Jaccard | 1 | 0.0559 | 0.815 | 1 | 0.0933 | 0.76 | 1 | 16.372 | 0.208 | 1 | 2.3181 | 0.152 | 1 | 1.1532 | 0.264 |
| | Gower log 10 | 1 | 0.1699 | 0.698 | 1 | 0.0813 | 0.779 | 1 | 0.2533 | 0.628 | 1 | 1.1739 | 0.32 | 1 | 0.1924 | 0.682 |
| | Gower 2 | 1 | 0.1699 | 0.673 | 1 | 0.0813 | 0.754 | 1 | 0.2533 | 0.639 | 1 | 1.1739 | 0.313 | 1 | 0.1924 | 0.669 |
| | Bray-Curtis | 1 | 0.007 | 0.928 | 1 | 0.4502 | 0.494 | 1 | 33.118 | 0.083 | 1 | 2.4282 | 0.13 | 1 | 1.7884 | 0.206 |
| CB | Jaccard | 1 | 0.0995 | 0.774 | 1 | 0.0995 | 0.755 | 1 | 0.0995 | 0.74 | 1 | 0.0995 | 0.761 | 1 | 0.0995 | 0.742 |
| | Gower log 10 | 1 | 0.6794 | 0.425 | 1 | 0.6794 | 0.44 | 1 | 0.6794 | 0.436 | 1 | 0.6794 | 0.402 | 1 | 0.6794 | 0.414 |
| | Gower 2 | 1 | 0.6794 | 0.412 | 1 | 0.6794 | 0.446 | 1 | 0.6794 | 0.439 | 1 | 0.6794 | 0.44 | 1 | 0.6794 | 0.447 |
| | Bray-Curtis | 1 | 0.199 | 0.662 | 1 | 0.199 | 0.651 | 1 | 0.199 | 0.665 | 1 | 0.199 | 0.672 | 1 | 0.199 | 0.659 |
| VG | Jaccard | 1 | 0.0271 | 0.867 | 1 | 0.0271 | 0.871 | 1 | 0.0271 | 0.863 | 1 | 0.0271 | 0.874 | 1 | 0.0271 | 0.873 |
| | Gower log 10 | 1 | 0.4454 | 0.508 | 1 | 0.4454 | 0.507 | 1 | 0.4454 | 0.507 | 1 | 0.4454 | 0.497 | 1 | 0.4454 | 0.496 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Gower 2 | 1 | 0.4454 | 0.484 | 1 | 0.4454 | 0.512 | 1 | 0.4454 | 0.518 | 1 | 0.4454 | 0.508 | 1 | 0.4454 | 0.515 |
| Bray-Curtis | 1 | 0.0254 | 0.865 | 1 | 0.0254 | 0.88 | 1 | 0.0254 | 0.892 | 1 | 0.0254 | 0.865 | 1 | 0.0254 | 0.879 |

Table 4. Total species and morphospecies sampled in the four continuous Atlantic forest sites: Itamambuca (ITA), Vargem Grande (VG), Carlos Botelho (CB) and Ilha do Cardoso (IC) along 24 months of experiment.

| Family | *Species* |
|---|---|
| Acanthaceae | Acanthaceae sp. 1 |
| Acanthaceae | Acanthaceae sp. 2 |
| Acanthaceae | *Aphelandra ornata* |
| Acanthaceae | *Aphelandra* sp. |
| Acanthaceae | *Justicia carnea* |
| Anacardiaceae | *Tapirira guianensis* |
| Annonaceae | *Annona* sp. |
| Annonaceae | *Guatteria australis* |
| Annonaceae | *Guatteria* sp. |
| Apocynaceae | Apocynaceae |
| Apocynaceae | *Malouetia cestroides* |
| Apocynaceae | *Peltastes peltatus* |
| Aquifoliaceae | *Ilex dumosa* |
| Araceae | *Anthurium* cf. *loefgrenii* |
| Araceae | *Anthurium* cf. *scandens* |
| Araceae | *Anthurium pentaphyllum* |
| Araceae | *Anthurium* sp. |
| Araceae | Araceae sp. 1 |
| Araceae | *Philodendon* sp. 1 |
| Araceae | *Philodendron* sp. 2 |
| Arecaceae | *Astrocaryum aculeatissimum* |
| Arecaceae | *Attalea dubia* |
| Arecaceae | *Attalea* sp. |
| Arecaceae | *Bactris setosa* |
| Arecaceae | *Euterpe edulis* |
| Arecaceae | *Geonoma elegans* |
| Arecaceae | *Geonoma gamiova* |
| Arecaceae | *Geonoma pauciflora* |
| Arecaceae | *Geonoma schottiana* |
| Arecaceae | *Geonoma* sp. |
| Arecaceae | *Syagrus romanzoffiana* |
| Aspleniaceae | *Asplenium* cf. *uniseriale* |
| Asteraceae | Asteraceae sp. 1 |
| Asteraceae | Asteraceae sp. 2 |
| Asteraceae | Asteraceae sp. 3 |
| Asteraceae | Asteraceae sp. 4 |
| Asteraceae | *Mikania* sp. 1 |
| Asteraceae | *Piptocarpha* sp. |
| Asteraceae | *Vernonia* sp. |
| Begoniaceae | *Begonia* sp. 1 |
| Begoniaceae | *Begonia* sp. 2 |

| | |
|---|---|
| Begoniaceae | *Begonia* sp. 3 |
| Bignoniaceae | Bignoniaceae sp. 1 |
| Bignoniaceae | Bignoniaceae sp. 2 |
| Bignoniaceae | Bignoniaceae sp. 3 |
| Blechnaceae | Blechnaceae sp. |
| Blechnaceae | *Blechnum* cf. *sampaioanum* |
| Blechnaceae | *Blechnum sampaioanum* |
| Boraginaceae | *Cordia sellowiana* |
| Bromeliaceae | *Bromeliaceae* sp. 1 |
| Bromeliaceae | *Bromeliaceae* sp. 2 |
| Bromeliaceae | *Bromeliaceae* sp. 3 |
| Bromeliaceae | *Nidularium* sp. 1 |
| Buseraceae | *Protium* sp. |
| Canellaceae | *Cinnamodendron dinisii* |
| Cardiopteridaceae | *Citronella paniculata* |
| Celastraceae | *Maytenus robusta* |
| Celastraceae | *Maytenus* sp. |
| Chrysobalanaceae | *Hirtella hebeclada* |
| Chrysobalanaceae | *Hirtella* sp. |
| Chrysobalanaceae | *Licania* cf. *hoehnei* |
| Chrysobalanaceae | *Parinari brasiliensis* |
| Chrysobalanaceae | *Parinari excelsa* |
| Clethraceae | *Clethra* sp. |
| Clusiaceae | *Calophyllum brasiliense* |
| Clusiaceae | *Garcinia gardneriana* |
| Commelinaceae | *Commelinaceae* sp. 1 |
| Commelinaceae | *Commelinaceae* sp. 2 |
| Commelinaceae | *Dichorisandra* cf. *thyrsiflora* |
| Commelinaceae | *Dichorisandra paranaensis* |
| Commelinaceae | *Dichorisandra pubescens* |
| Commelinaceae | *Dichorisandra* sp. |
| Connaraceae | *Connarus rostratus* |
| Cyperaceae | *Pleurostachys gaudichaudii* |
| Cyperaceae | *Pleurostachys* sp. 1 |
| Cyperaceae | *Pleurostachys* sp. 2 |
| Dilleniaceae | *Davilla rugosa* |
| Dryopteridaceae | *Ctenitis aspidioides* |
| Dryopteridaceae | *Ctenitis* sp. |
| Dryopteridaceae | *Ctenitis* cf. *aspidioides* |
| Dryopteridaceae | Dryopteridaceae sp. 1 |
| Dryopteridaceae | *Elaphoglossum glaziovii* |
| Dryopteridaceae | *Elaphoglossum* sp. 1 |
| Dryopteridaceae | *Elaphoglossum* sp. 2 |
| Dryopteridaceae | *Polybotrya cylindrica* |
| Elaeocarpaceae | *Sloanea guianensis* |
| Elaeocarpaceae | *Sloanea hirsuta* |

| | |
|---|---|
| Elaeocarpaceae | *Sloanea* sp. |
| Erythroxylaceae | *Erythroxylum* sp. |
| Erythroxylaceae | *Erythroxylun* cf. *ambiguum* |
| Euphorbiaceae | *Alchornea glandulosa* |
| Euphorbiaceae | *Alchornea triplinervia* |
| Euphorbiaceae | *Pausandra morisiana* |
| Fabaceae | *Abarema* sp. |
| Fabaceae | *Acacia* sp. |
| Fabaceae | *Andira anthelmia* |
| Fabaceae | *Bauhinia* sp. |
| Fabaceae | *Copaifera langsdorfii* |
| Fabaceae | *Copaifera trapezifolia* |
| Fabaceae | *Dahlstedtia pinnata* |
| Fabaceae | *Dalbergia frutescens* |
| Fabaceae | *Dalbergia* sp. |
| Fabaceae | Fabaceae sp. |
| Fabaceae | *Inga edulis* |
| Fabaceae | *Inga marginata* |
| Fabaceae | *Inga sellowiana* |
| Fabaceae | *Inga sessilis* |
| Fabaceae | *Inga* sp. |
| Fabaceae | *Myrocarpus frondosus* |
| Fabaceae | *Phanera microstachya* |
| Fabaceae | *Piptadenia* sp. |
| Fabaceae | *Pterocarpus rohrii* |
| Fabaceae | *Pterocarpus violaceus* |
| Fabaceae | *Zollernia ilicifolia* |
| Gesneriaceae | *Nemathantus* cf. *jolyanus* |
| Heliconiaceae | *Heliconia velloziana* |
| Hippocrateaceae | Hippocrateaceae sp. 1 |
| Hippocrateaceae | Hippocrateaceae sp. 2 |
| Indeterminada | Indeterminada sp. 1 |
| Indeterminada | Indeterminada sp. 2 |
| Indeterminada | Indeterminada sp. 3 |
| Indeterminada | Indeterminada sp. 4 |
| Indeterminada | Indeterminada sp. 5 |
| Indeterminada | Indeterminada sp. 6 |
| Indeterminada | Indeterminada sp. 7 |
| Indeterminada | Indeterminada sp. 8 |
| Indeterminada | Indeterminada sp. 9 |
| Indeterminada | Indeterminada sp. 10 |
| Indeterminada | Indeterminada sp. 11 |
| Indeterminada | Indeterminada sp. 12 |
| Indeterminada | Indeterminada sp. 13 |
| Indeterminada | Indeterminada sp. 14 |
| Indeterminada | Indeterminada sp. 15 |

| | |
|---|---|
| Indeterminada | Indeterminada sp. 16 |
| Indeterminada | Indeterminada sp. 17 |
| Iridaceae | *Neomarica candida* |
| Iridaceae | *Neomarica* sp. |
| Lacistemaceae | *Lacistema pubescens* |
| Lauraceae | *Aniba* sp. |
| Lauraceae | *Cryptocarya mandioccana* |
| Lauraceae | *Cryptocarya* sp. |
| Lauraceae | *Endlicheria paniculata* |
| Lauraceae | *Lauraceae* sp. 1 |
| Lauraceae | *Lauraceae* sp. 2 |
| Lauraceae | *Lauraceae* sp. 3 |
| Lauraceae | *Lauraceae* sp. 4 |
| Lauraceae | *Ocotea aciphylla* |
| Lauraceae | *Ocotea catharinensis* |
| Lauraceae | *Ocotea cf. dispersa* |
| Lauraceae | *Ocotea dispersa* |
| Lauraceae | *Ocotea odorifera* |
| Lauraceae | *Ocotea* sp. 1 |
| Lauraceae | *Ocotea* sp. 2 |
| Lauraceae | *Ocotea* sp. 3 |
| Lauraceae | *Ocotea* sp. 4 |
| Lauraceae | *Ocotea teleiandra* |
| Loganiaceae | *Strychnos trinervis* |
| Lygodiaceae | *Lygodium volubile* |
| Magnoliaceae | *Talauma ovata* |
| Malpighiaceae | *Heteropterys nitida* |
| Malpighiaceae | *Hirea* cf. *gaudichaudiana* |
| Malpighiaceae | Malpighiaceae sp. 1 |
| Malpighiaceae | Malpighiaceae sp. 2 |
| Marantaceae | *Calathea communis* |
| Marantaceae | *Calathea monophylla* |
| Marantaceae | *Calathea* sp. |
| Marantaceae | *Ctenanthe lanceolata* |
| Marantaceae | *Marantaceae* sp. |
| Marantaceae | *Stromanthe* sp. |
| Melastomataceae | *Bertolonia mosenii* |
| Melastomataceae | *Leandra acutiflora* |
| Melastomataceae | *Leandra cf. dasytricha* |
| Melastomataceae | *Leandra dasytricha* |
| Melastomataceae | *Leandra* sp. |
| Melastomataceae | Melastomataceae sp. 1 |
| Melastomataceae | Melastomataceae sp. 2 |
| Melastomataceae | Melastomataceae sp. 3 |
| Melastomataceae | Melastomataceae sp. 4 |
| Melastomataceae | Melastomataceae sp. 5 |

| | |
|---|---|
| Melastomataceae | *Miconia cabucu* |
| Melastomataceae | *Miconia* cf. *pusilliflora* |
| Melastomataceae | *Miconia cubatanensis* |
| Melastomataceae | *Miconia* sp. 1 |
| Melastomataceae | *Miconia* sp. 2 |
| Melastomataceae | *Ossaea sanguinea* |
| Melastomataceae | *Ossaea* sp. 1 |
| Meliaceae | *Cabralea canjerana* |
| Meliaceae | *Guarea macrophylla* |
| Meliaceae | *Trichilia* sp. |
| Menispermaceae | *Abuta selloana* |
| Monimiaceae | *Mollinedia* cf. *uleana* |
| Monimiaceae | *Mollinedia schottiana* |
| Monimiaceae | *Mollinedia* sp. |
| Moraceae | *Sorocea bonplandii* |
| Myristicaceae | *Virola bicuhyba* |
| Myrsinaceae | *Myrsine coriacea* |
| Myrtaceae | *Calycorectes* sp. |
| Myrtaceae | *Calyptranthes lanceolata* |
| Myrtaceae | *Campomanesia guaviroba* |
| Myrtaceae | *Eugenia aff. stigmatosa* |
| Myrtaceae | *Eugenia cerasiflora* |
| Myrtaceae | *Eugenia* cf. *capitulifera* |
| Myrtaceae | *Eugenia* cf. *handroana* |
| Myrtaceae | *Eugenia* cf. *stigmatosa* |
| Myrtaceae | *Eugenia cuprea* |
| Myrtaceae | *Eugenia melonogyna* |
| Myrtaceae | *Eugenia mosenii* |
| Myrtaceae | *Eugenia multicostata* |
| Myrtaceae | *Eugenia neoaustralis* |
| Myrtaceae | *Eugenia neoglomerata* |
| Myrtaceae | *Eugenia pruinosa* |
| Myrtaceae | *Eugenia riedeliana* |
| Myrtaceae | *Eugenia* sp. 1 |
| Myrtaceae | *Eugenia* sp. 2 |
| Myrtaceae | *Eugenia* sp. 3 |
| Myrtaceae | *Eugenia* sp. 4 |
| Myrtaceae | *Eugenia* sp. 5 |
| Myrtaceae | *Eugenia* sp. 6 |
| Myrtaceae | *Eugenia subavenia* |
| Myrtaceae | *Eugenia sulcata* |
| Myrtaceae | *Eugenia supraaxillaris* |
| Myrtaceae | *Marlierea obscura* |
| Myrtaceae | *Marlierea tomentosa* |
| Myrtaceae | *Myrceugenia cf. myrcioides* |
| Myrtaceae | *Myrceugenia myrcioides* |

| | |
|---|---|
| Myrtaceae | *Myrcia pubipetala* |
| Myrtaceae | *Myrcia sp.* |
| Myrtaceae | *Myrcia spectabilis* |
| Myrtaceae | *Myrcia splendens* |
| Myrtaceae | *Myrcia tenuivenosa* |
| Myrtaceae | *Myrcia tijucensis* |
| Myrtaceae | Myrtaceae sp. 1 |
| Myrtaceae | Myrtaceae sp. 2 |
| Myrtaceae | Myrtaceae sp. 3 |
| Myrtaceae | *Plinia* cf. *pseudodichasiantha* |
| Myrtaceae | *Plinia pseudodichasiantha* |
| Myrtaceae | *Plinia* sp. |
| Myrtaceae | *Calyptranthes* cf. *lucida* |
| Nyctaginaceae | *Guapira opposita* |
| Nyctaginaceae | *Guapira* sp. 1 |
| Nyctaginaceae | *Guapira* sp. 2 |
| Nyctaginaceae | *Pisonia ambigua* |
| Ochnaceae | *Ouratea parvifolia* |
| Olacaceae | *Heisteria silvianii* |
| Oleaceae | *Chionanthus filiformis* |
| Piperaceae | *Ottonia sp.* |
| Piperaceae | *Piper bowiei* |
| Piperaceae | *Piper* cf. *aduncum* |
| Piperaceae | *Piper* cf. *caldense* |
| Piperaceae | *Piper pseudopothifolium* |
| Piperaceae | *Piper setebarraense* |
| Piperaceae | *Piper* sp. 1 |
| Piperaceae | *Piper* sp. 2 |
| Piperaceae | Piperaceae sp. |
| Poaceae | *Chusquea* sp. 1 |
| Poaceae | *Chusquea* sp. 2 |
| Poaceae | *Merostachys* cf. *multiramea* |
| Poaceae | *Merostachys* sp. |
| Poaceae | *Parodiolyra* sp. |
| Poaceae | Poaceae sp. 1 |
| Poaceae | Poaceae sp. 2 |
| Poaceae | Poaceae sp. 3 |
| Poaceae | Poaceae sp. 4 |
| Polygonaceae | *Coccoloba* sp. |
| Polygonaceae | *Ruprechtia laxiflora* |
| Polypodiaceae | *Campyloneurum acrocarpon* |
| Polypodiaceae | Polypodiaceae sp. |
| Primulaceae | *Ardisia guianensis* |
| Primulaceae | *Myrsine* cf. *umbellata* |
| Primulaceae | *Myrsine* sp. 1 |
| Primulaceae | *Myrsine* sp. 2 |

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| Primulaceae | Primulaceae sp. |
| Pteridaceae | *Pteris* cf. *deflexa* |
| Rosaceae | *Prunus sellowii* |
| Rubiaceae | *Amaioua intermedia* |
| Rubiaceae | *Bathysa australis* |
| Rubiaceae | *Bathysa* sp. |
| Rubiaceae | *Becheria* sp. |
| Rubiaceae | cf. *Alibertia myrciifolia* |
| Rubiaceae | cf. *Borreria* sp. |
| Rubiaceae | *Coccocypselum* sp. |
| Rubiaceae | *Faramea* sp. |
| Rubiaceae | *Ixora* sp. |
| Rubiaceae | *Posoqueria acutifolia* |
| Rubiaceae | *Psychotria brachypoda* |
| Rubiaceae | *Psychotria* cf. *suterella* |
| Rubiaceae | *Psychotria leiocarpa* |
| Rubiaceae | *Psychotria mapourioides* |
| Rubiaceae | *Psychotria nemorosa* |
| Rubiaceae | *Psychotria nuda* |
| Rubiaceae | *Psychotria* sp. 1 |
| Rubiaceae | *Psychotria* sp. 2 |
| Rubiaceae | *Psychotria* sp. 3 |
| Rubiaceae | *Psychotria* sp. 4 |
| Rubiaceae | *Psychotria suterella* |
| Rubiaceae | *Rubiaceae* sp. 1 |
| Rubiaceae | *Rubiaceae* sp. 2 |
| Rubiaceae | *Rubiaceae* sp. 3 |
| Rubiaceae | *Rudgea jasminoides* |
| Rubiaceae | *Rudgea* sp. |
| Rutaceae | *Esenbeckia grandiflora* |
| Rutaceae | *Metrodorea nigra* |
| Sabiaceae | *Meliosma sellowii* |
| Salicaceae | *Casearia* cf. *sylvestris* |
| Salicaceae | *Casearia decandra* |
| Salicaceae | *Casearia obliqua* |
| Salicaceae | *Casearia* sp. |
| Salicaceae | *Xylosma* cf. *prockia* |
| Salicaceae | *Xylosma glaberrimum* |
| Sapindaceae | *Allophylus* sp. |
| Sapindaceae | *Cupania oblongifolia* |
| Sapindaceae | *Cupania vernalis* |
| Sapindaceae | *Matayba guianensis* |
| Sapindaceae | *Matayba* sp. 1 |
| Sapindaceae | *Matayba* sp. 2 |
| Sapindaceae | *Paulinia* sp. 1 |
| Sapindaceae | *Paulinia* sp. 2 |

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| Sapindaceae | *Paulinia* sp. 3 |
| Sapindaceae | *Paulinia* sp. 4 |
| Sapindaceae | Sapindaceae sp. |
| Sapindaceae | *Serjania communis* |
| Sapindaceae | *Serjania* sp. 1 |
| Sapindaceae | *Serjania* sp. 2 |
| Sapindaceae | *Serjania* sp. 3 |
| Sapotaceae | *Chrysophyllum flexuosum* |
| Sapotaceae | *Chrysophyllum inornatum* |
| Sapotaceae | *Diploon cuspidatum* |
| Sapotaceae | *Pouteria bullata* |
| Selaginellaceae | *Selaginella* sp. |
| Siparunaceae | *Siparuna* cf. *brasiliensis* |
| Smilacaceae | Smilacaceae sp. |
| Smilacaceae | *Smilax* sp. |
| Smilacaceae | *Smilax spicata* |
| Solanaceae | *Brunfelsia* sp. |
| Solanaceae | *Solanum* cf. *swartzianum* |
| Solanaceae | *Solanum* sp. |
| Symplocaceae | *Symplocos* sp. |
| Thymelaeaceae | *Daphnopsis schwackeana* |
| Urticaceae | *Pourouma guianensis* |
| Viteceae | *Cissus* sp. |
| Vochysiaceae | *Vochysia bifalcata* |
| Zingiberaceae | *Renealmia petasites* |