UNIVERSIDADE FEDERAL DO OESTE DO PARÁ
INSTITUTO DE CIÊNCIAS E TECNOLOGIA DAS ÁGUAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE

GABRIELA DA SILVA BATISTA

A DEFAUNAÇÃO INTERFERE NEGATIVAMENTE NO COMPORTAMENTO E FUNÇÕES ECOLÓGICAS DE MAMÍFEROS E AVES TERRESTRES NA AMAZÔNIA

SANTARÉM – PA

2023

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Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade da Universidade Federal do Oeste do Pará, como requisito para obtenção de grau de Mestre em Biodiversidade.
Orientador(a): Prof. Dr. Rodrigo Ferreira Fadini
Coorientador(a): Prof. Dr. Carlos Rodrigo Brocardo

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Mestranda

Dedico este trabalho aos meus
companheiros de vida e de pesquisa.

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RESUMO

A defaunação leva à alteração de funções ecológicas essenciais para os ecossistemas naturais, como predação, dispersão de sementes e ciclagem de nutrientes. Nas últimas décadas, os experimentos de exclusão se tornaram uma abordagem útil para investigar os impactos da perda de vida selvagem na diversidade de espécies de plântulas, mas pouco utilizado para avaliar o impacto da defaunação nas funções ecológicas. Nesse contexto, o objetivo deste estudo foi avaliar como as funções ecológicas em uma floresta netropical podem ser alteradas devido a mudanças na ocorrência e frequência de comportamentos exibidos por vertebrados terrestres em áreas com diferentes níveis de defaunação experimental: não defaunadas (controle), intermediárias (exclusão parcial) e severas (exclusão total). Além disso, questionamos se os comportamentos mudam mais sazonalmente em áreas não defaunadas do que em tratamentos experimentais defaunados. Registramos e quantificamos os comportamentos de vertebrados em diferentes tratamentos, usando armadilhas fotográficas, agrupando as espécies em grupos funcionais. Os comportamentos foram categorizados como alimentação, excreção ou defecação, bioturbação e pisoteio, ponderando-as pelo peso das espécies. Revelamos que a frequência ponderada de todos os comportamentos foi drasticamente reduzida (> 95% de redução para pisoteio, alimentação, bioturbação e defecação) em condições de defaunação severa. Durante a estação seca, houve um aumento no número de registros de comportamento, principalmente excreção e defecação, com ênfase em roedores grandes e pequenos mamíferos em tratamentos defaunados. Na estação chuvosa, os registros de aves se destacaram, principalmente nos comportamentos de bioturbação e alimentação. A remoção de mamíferos terrestres de médio e grande porte e aves levou a uma perda significativa de comportamentos, potencialmente reduzindo os serviços prestados pelas florestas tropicais como um todo.

Palavras-Chaves: FUNÇÃO ECOLÓGICA. EXPERIMENTOS. GRUPOS FUNCIONAIS. ETOGRAMA. NEOTROPICAL. VERTEBRADOS.

ABSTRACT

Defaunation leads to the alteration of ecological functions essential for natural ecosystems, such as predation, seed dispersal, and nutrient cycling. In recent decades, exclusion experiments have become a useful approach to investigate the impacts of wildlife loss on seedlings species diversity, but are seldom used to assess the impact of defaunation on ecological functions. In this context, we aimed to evaluate how ecological functions in a neotropical forest may be altered due to changes in the occurrence and frequency of behaviors exhibited by terrestrial vertebrates in areas simulating different levels of experimental defaunation: non-defaunated (control), intermediate (partial exclosure), and severe (total exclosure). Additionally, we questioned whether behaviors change more seasonally in non-defaunated areas than in defaunated experimental treatments. We recorded and quantified vertebrate behaviors within different treatments using camera traps, grouping species into functional groups. Behaviors were categorized as feeding, excretion or defecation, bioturbation, and trampling and weighted by species body size. We revealed that the weighted frequency of all behaviors was drastically reduced (> 95% reduction for trampling, feeding and bioturbation, and defecation) under severe defaunation conditions. During the dry season, there was an increase in the number of behavior records, mainly defecation or scent marking, with an emphasis on large rodents and small mammals in defaunated treatments. In the rainy season, bird records stood out, particularly in bioturbation and feeding behaviors. The removal of medium and large terrestrial mammals and birds led to a significant loss of behaviors, potentially reducing the services provided by tropical forests as a whole.

Key words/phases: ECOLOGICAL FUNCTION. EXPERIMENTS. FUNCTIONAL GROUPS. ETHOGRAM. NEOTROPICAL. VERTEBRATES.

LISTA DE ILUSTRAÇÕES

LISTA DE TABELAS

LISTA DE ABREVIATURAS E SIGLAS

WWF - World Wildlife Fund

EMMEANS – Estimated Marginal Means aka Least-Squares Means

GLMM – Generalized Linear Mixed Model

Sumário

INTRODUÇÃO GERAL

A DEFAUNAÇÃO INTERFERE NEGATIVAMENTE NO COMPORTAMENTO E FUNÇÕES ECOLÓGICAS DE MAMÍFEROS E AVES TERRESTRES NA AMAZÔNIA

Qual é o problema da pesquisa?

As florestas tropicais estão entre dos ecossistemas mais ricos e biodiversos do planeta, abrigando mais da metade das espécies do mundo. Contudo as atividades humanas que geram degradação e perda das florestas, a caça ilegal, doenças, introdução de espécies exóticas e os atropelamentos dos animais silvestres, levam a redução ou perda de populações da fauna silvestre, processo conhecido como defaunação.

Os vertebrados terrestres desempenham funções ecológicas decisivas para manutenção do meio ambiente, por exemplo, predação e dispersão de sementes, herbivoria, ciclagem de nutrientes no solo e regulação da abundância dos pequenos animais, através de comportamentos como alimentação, excreção, bioturbação e pisoteio. Por isso, é de suma importância entender como a perda dos vertebrados terrestres irá interferir no fornecimento das principais funções ecológicas prestadas por esses animais.

Para testar experimentalmente o impacto da defaunação nas funções ecológicas executadas por mamíferos e aves terrestres, utilizamos tratamentos de exclusão instaladas em uma unidade de conservação da Amazônia para simular diferentes níveis de defaunação, com objetivo de avaliar como as funções ecológicas serão alteradas devido a mudanças nos comportamentos desempenhados pelos vertebrados terrestres nos tratamentos e em diferentes períodos sazonais.

Onde e como a pesquisa foi realizada?

O estudo foi desenvolvido na Floresta Nacional do Tapajós (Flona Tapajós), unidade de conservação federal de uso sustentável, localizado no estado do Pará, na Amazonia brasileira. Os experimentos de exclusão consistiram em cercar áreas (5 x 10 m) com telas de aço de malha (5 x 10 cm) delimitadas por estacas, em três tipos de tratamentos experimentais: 1- exclusão total, com o objetivo de impedir o acesso no seu interior dos vertebrados terrestres de médio e grande porte, permitindo o acesso através da abertura da tela de aço dos animais pequenos (ratos e cuícas) e os arborícolas (assim simulando uma floresta com defaunação severa) (Figura 1A); 2- exclusão parcial, com o objetivo impedir o acesso no seu interior de vertebrados de grande porte como antas, queixadas e veados, mas não de pacas, cutias, roedores e marsupiais, por exemplo, devido a abertura de 20 centímetros entre tela de aço com o solo (simulando uma floresta com defaunação intermediária) (Figura 1B); 3- controle, com o objetivo de permitir a circulação de qualquer vertebrado no seu interior, sem cercas (como seria esperado em uma floresta com fauna intacta) (Figura 1C).

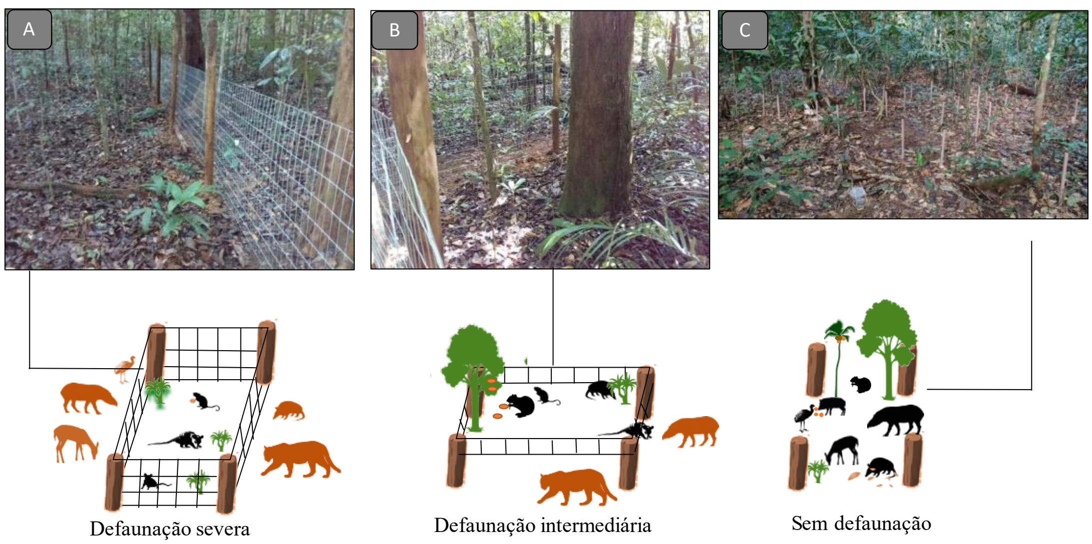

Figura: Esquema dos tratamentos de exclusão experimental, na Floresta Nacional do Tapajós.

Para monitorar os mamíferos e aves terrestres dentro dos tratamentos experimentais, utilizamos armadilhas fotográficas, programadas para gravar vídeos de 30 segundos, durante 30 dias. Com esses registros, categorizamos as identificações das espécies por uma combinação de características taxonômicas ou alimentares em oito grupos funcionais: aves, grandes roedores, insetívoros, marsupiais grandes, onívoros, pequenos felinos, pequenos mamíferos e ungulados.

Usando os vídeos das armadilhas fotográficas, obtivemos registros de diversos comportamentos desempenhados pelos animais, e dividimos em: [i] alimentação [ii] bioturbação [iii] pisoteio e [iv] defecação/excreção. A escolha desses comportamentos foi definida por serem essenciais em interações especificas entre plantas e animais, por exemplo, predação e dispersão de sementes e deposição de nutrientes no solo, e que representam os principais papéis ecológicos desempenhados por animais na natureza.

Combinando informações dos registros dos comportamentos com o peso e quantidade dos animais presente nos experimentos, foi possível utilizar métodos estatísticos para analisar a perda das funções ecológicas dos animais excluídos.

Qual a importância da pesquisa?

Houve uma drástica redução na quantidade de grupos funcionais presentes nas áreas defaunadas experimentalmente, e essa redução progressiva do conjunto de grupos funcionais causou diminuição dos comportamentos realizados pelos animais. Os comportamentos foram interrompidos em condições de defaunação severa no pisoteio em (95%), alimentação (97%), bioturbação (96%) e excreção e defecação (100%). No período de estiagem, houve um aumento do número de registros dos comportamentos, principalmente excreção e defecação, com destaque para os grandes roedores e pequenos mamíferos em áreas defaunadas.

Quantificar os comportamentos da fauna dentro dos tratamentos de exclusão é uma forma de demonstrar os possíveis efeitos de diferentes cenários de defaunação. Apesar de algumas espécies de grandes e pequenos roedores, predominantes nas áreas defaunadas, exercerem a funções ecológicas similares aos grandes herbívoros como predação e dispersão de sementes, os pequenos não podem compensar ou substituir totalmente os papéis ecológicos que os animais de grande porte fornecem. Reforçamos que florestas que seguirem esses padrões de defaunação e rodentização (predomínio de pequenos roedores em áreas defaunadas) irão impactar as diferentes propriedades dos ecossistemas, como dispersão de sementes, regulação de abundância de presas e disponibilização nutrientes no solo, que podem estar diretamente relacionadas com a recrutamento de plantas e dinâmica da floresta.

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CAPÍTULO ÚNICO

Artigo segue o modelo da Ecology

INTRODUCTION

Anthropogenic defaunation is a process that leads to the loss or reduction of wild species populations at various spatial (Dirzo et al., 2014) and temporal (Galetti et al., 2018) scales. According to the World Wildlife Fund (WWF) Living Planet Report, global populations of vertebrates declined by 69% between from1970 to 2018, with Latin America experiencing the highest impact, recording a 94% decline in the average abundance of these wild animal populations (Alkemade et al., 2022).

The main causes of defaunation are poaching (Benítez-López et al., 2017), habitat loss and degradation (Young et al., 2016), pollution (Wilcox et al., 2015) and climate change (Pecl et al., 2017). The primary consequences of defaunation, range from declines and rearrangements in ecosystem functions and services (Dirzo et al., 2014; Hooper et al., 2012), such as predation and seed dispersal (Brocardo et al., 2018), herbivory (Dirzo et al., 2020), soil biogeochemical cycling (Harrison, 2011), and causes several interferences throughout trophic levels (Beschta & Ripple, 2019). It is essential to quantify the consequences of defaunation to understand how the loss of animals will interfere on ecosystem dynamics. However, emprirical knowledge about the processes affected by defaunation is still limited, especially across tropical regions (Pringle et al., 2023; Bogoni et al., 2020).

Among vertebrates, large herbivores (folivores, frugivores, and granivores) comprise the most affected groups in tropical forests (Antunes et al., 2016; Galetti et al., 2015). Herbivores defaunation causes changes in plant diversity (Villar et al., 2020), with nutrient cycling (Villar et al., 2021), and ecosystem heterogeneity (Davies et al., 2018). For instance, a recent study simulating defaunation of large herbivores using exclusion experiments in the Atlantic Forest has shown that large herbivore removal reduced the availability of soil nitrogen (Villar et al., 2021). Defaunation has also been linked to alterations in Earth's climate regulation, as this functional group disperses large seeds formed mainly by species with large wood density, sequestering more carbon and reducing climate change (Bello et al., 2015; Peres et al., 2016).

In addition to herbivores, other functional groups of medium and large bodied vertebrates (e.g., rodents, mesopredators, insectivores, and omnivores) are also affected at different levels of defaunation. Yet the consequences of these depletions have been much less studied than those of large-bodied herbivores (Galetti & Dirzo, 2013; Stoner et al., 2007;). For example, the local extirpation of armadillos, one of the most hunted groups in the Neotropics, can alter nutrient cycling and soil properties due to their burrowing behavior (Rodrigues et al., 2020). The loss of medium-bodied rodents (e.g., pacas, agoutis, and acouchis) can affect several zoochory-dependent plant species, given that this functional group is widely responsible for both seed predation and dispersal, causing important changes in carbon storage through the behavior of hoarding dispersers (Galetti et al., 2010; Mittelman et al., 2021). These evidence reveals that besides the pervasive species loss, defaunation affects ecological functions due to the loss of species-specific behaviors.

Against the multiple consequences of defaunation for ecosystem functions and services, studying this phenomena under a observational approach still being a challenge for ecologists (Dirzo & Miranda, 1990; Putz & Wright, 1990). In this context, exclusion experiments, an approach that involves enclosing one (or several) plots to prevent contact of flora and other elements of biota with terrestrial vertebrates (e.g., Beck et al., 2013, Brocardo et al., 2013, Granados et al., 2018, Villar et al., 2020), allow for the experimental manipulation of defaunation of different-sized animal groups and functional groups. These experiments minimize the misinterpretation of environmental effects perse as results of defaunation, therefore providing insight to the potential consequences derived from the loss of ecological functions upon ecosystems functioning, patterns, mechanisms and services.

Some of the studies using exclusion experiments have used camera traps to quantify visiting animals (Kurten et al., 2015), but they have often focused on variation in species richness and not on the behaviors exhibited by them. A recent review concerning the use of camera-traps for behavioral studies of vertebrates do not provided an overview about how certain behaviors can be used as proxies for important ecological functions (Caravaggi et al., 2017. The definitions of ecological functions emphasize the idea of a trait-mediated function used to highlight those characteristics of living beings that come together to perform an ecosystem service (Cardinale et al., 2012). For example, animal defecation behavior can be directly linked to the functions of nutrient cycling and seed dispersal (Benbow et al., 2019), while the bioturbation behavior of armadillos and other vertebrates is related to nutrient cycling (Rodrigues et al., 2020; Pringle et al., 2023). Furthermore, feeding behavior can be related to diverse functions, such as seed predation, fruit consumption, predation, and herbivory (Estes et al., 2011; Ripple et al., 2015). These and other behaviors, captured by camera traps or other monitoring methods, are essential for describing the ecological functions provided by animals in nature (as proposed in this study).

Against this glaring gap about behaviours as proxies to ecological functions, we used exclusion experiments installed in a forest site in the Amazon to simulate both severe defaunation (i.e., preventing the access of medium- to large-bodied terrestrial vertebrates) and intermediate defaunation (i.e., only preventing the access of large-bodied terrestrial vertebrates), and used the records of terrestrial mammals and birds behaviors as a proxy for the ecological function performed, comparing these exclusion plots with a control that allows all those access of fauna. Initially, we characterized the behavior type recorded by camera-traps at any plot through an ethogram for each species and functional group. Our main question was: (1)- How ecosystem functions are altered due to changes in the occurrence and frequency of behaviors performed by terrestrial vertebrates in areas with different levels of experimental defaunation? Considering that the Amazon rainforest has a highly seasonal climate in some regions (Moraes et al., 2005; Nobre et al., 2013) and that this seasonality can affect the abundance, movement, and behavior of vertebrate species (Beever et al., 2017; Costa et al., 2018; Sales et al., 2019), we also derived an additional question: (2) How do seasonal features (i.e., dry and rainy periods) affect quantitatively the effect of experimental defaunation captured via species behaviors? Our hypothesis for question 1 (H1) is that various types of behaviors performed by terrestrial vertebrates, which can trigger physical, chemical, and structural changes in the environment, will be progressively reduced in environments with intermediate and severe defaunation,. For question 2, our hypothesis (H2) is that there will be little temporal variation in the set of behaviors performed by terrestrial vertebrates present under conditions of intermediate and severe defaunation (in that order), which could make the defaunated forest more temporally homogeneous.

MATERIALS AND METHODS

Study Area

The research was conducted in the Tapajós National Forest (Flona Tapajós), state of Pará, Brazil, located in the Amazon rainforest. The Flona Tapajós is a federal protected area of sustainable-use t covering an area of 527,319 hectares, with its main activities being research, tourism, and both timber and non-timber forest management (ICMBio, 2019). The predominant vegetation is the Dense Ombrophilous Forest of *terra firme*, with a prevalence of plant families such as Lauraceae, Lecythidaceae, Moraceae, and Fabaceae (Andrade et al., 2015; Espírito-Santo et al., 2005). The climate in the region is tropical humid, with an annual average temperature of 25°C (Am according to Köppen's classification) (Kottek et al., 2006). The annual average precipitation is around 1,820 mm, with a significant variation in rainfall throughout the year, with the highest precipitation occurring between January and May (Alvares et al., 2013). The diversity of medium and large terrestrial mammal species in Flona Tapajós is of 34 species, including large herbivores such as tapirs (*Tapirus terrestris*), deer (*Mazama* spp.), and peccaries (*Tayassu pecari*), as well as top predators like jaguars (*Panthera onca*) and pumas (*Puma concolor*) (Brocardo et al., 2023; Rosa et al., 2021). During the study period, white-lipped peccaries were not recorded, although they are known to occur locally (Sampaio et al., 2010).

Exclusion Experiment

Eleven experimental blocks were established, each located at a minimum distance of 400 m from the others (Figure 1), situated in *terra firme* forest in the central-southern part of the Tapajós National Forest (Rosa et al., 2021), and at least 2 km away from the nearest timber management area.

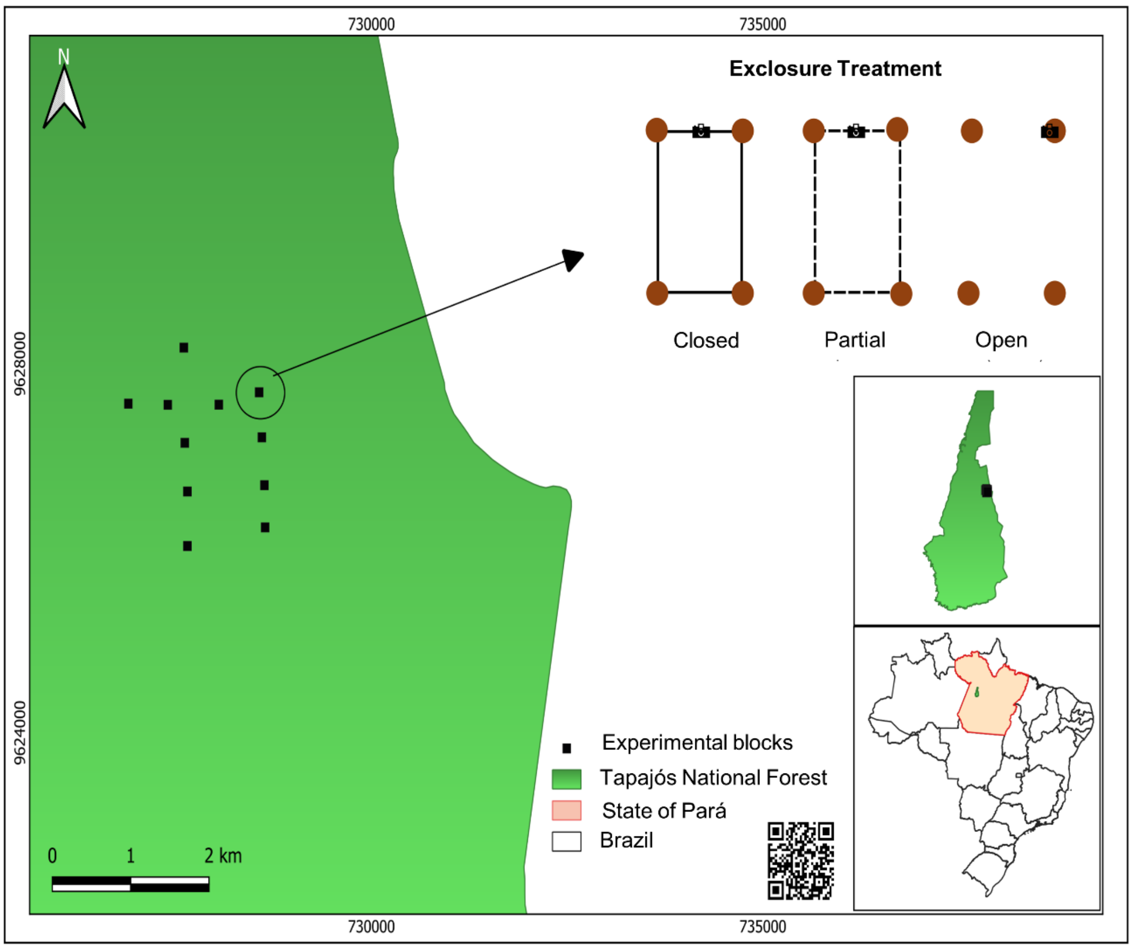


Figure 1: Study area location. Each black square represents an experimental block with three types of experimental treatments. Scan the QR Code on the map for more information about the Defaunation project in the Tapajós National Forest. This map was created with QGIS Desktop version 3.22.0 for Windows.

Each block contained three types of experimental treatments: 1- total exclusion, aiming to prevent access by medium and large terrestrial vertebrates, but not by small rodents and marsupials (simulating a forest with severe defaunation); 2- partial exclusion, aiming to prevent access by large vertebrates such as tapirs, peccaries, and deer, but not by medium mammals like pacas and agoutis, for example and small rodents and marsupials (simulating a forest with intermediate defaunation); 3- control, allowing the circulation of any vertebrates (as expected in a forest with intact fauna). Small mammals (rodents and marsupials $\leq$ 1kg) had free access in all treatment, as well as primates and other arboreal species. The average distance between the experimental plots within each block was approximately 30 meters, ensuring similar abiotic conditions between treatments at the start of the experiment. The assignment of treatment type to the plot in each block was randomly determined. Exclusion treatment consisted of enclosing an area (5 x 10 m) with steel mesh screens (5 x 10 cm). Wooden posts, 2 meters height, were placed every 2.5 meters in all treatments. For the 'total exclusion' treatment, the steel screens were nailed to the posts and buried 30 cm deep (Figure 2A). For the 'partial exclusion' treatment, the screens were nailed to the posts but kept 20 cm above the ground (Figure 2B). For the 'control' treatment, only the posts were kept to delineate the area (Figure 2C).

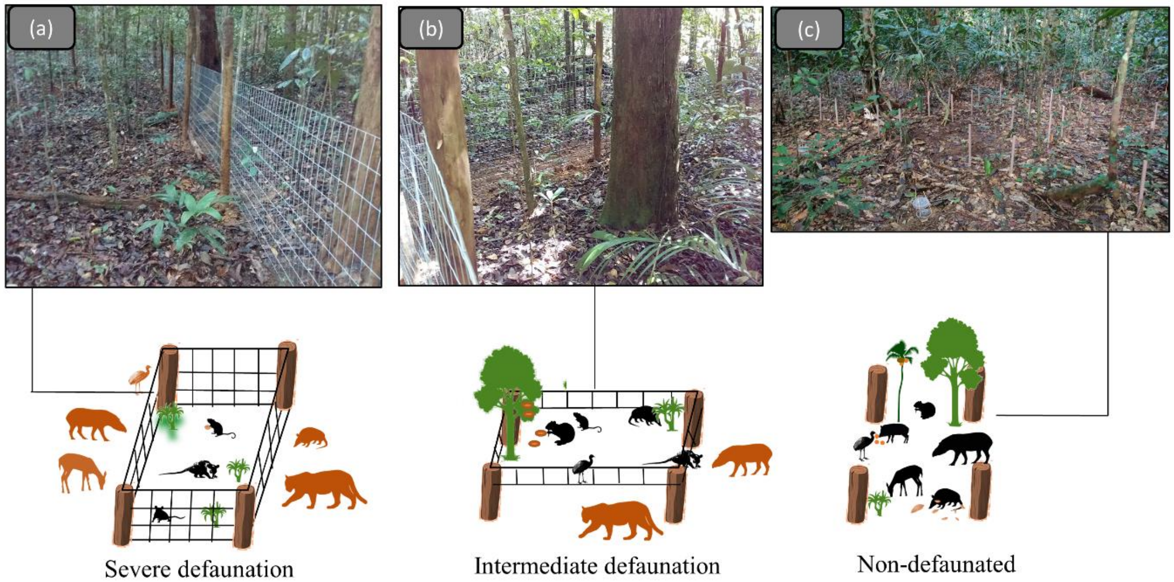


Figure 2: Figure of the sample design of the experimental treatments and their respective photos in the study area., (a) total exclusion treatment (b) partial exclusion treatment (c) control treatment (open).

Records of Terrestrial Vertebrates

To record mammal and bird behavior within each plot, we used non-baited digital trail cameras (Bushnell Prime 24MP model), programmed to record 30-second videos when remotely triggered by motion detected by the camera's motion sensor at one-minute intervals.. We installed one camera per treatment positioned at the ends of the plots and 40 cm above the ground covering the entire plot area. No plants were removed for these cameras to avoid affecting the ongoing seedling experiment. The cameras were used on two occasions, one during the rainy season (November 2021) and another during the transition between the rainy season and the dry season (hereafter 'dry season') (in June/and July 2022), for 30 days each time. Due to the limited availability of cameras in the November 2021 sampling, five experimental blocks were randomly selected for monitoring (n = 15) in both seasons of the year, and this data only addressed the seasonal analysis (question 2).

Species and Functional Groups

Species were identified to the lowest possible taxonomic level, with the assistance of field guides (Emmons, 1997; Reis et al., 2010; Sigrist, 2013) and support from an expert (C.R. Brocardo), and grouped the record species into eight functional groups. Functional groups are generally defined as a set of species that share similar responses to analogous environments or contribute to similar ecological functions (Brocardo et al., 2023, Laureto et al., 2015). Each functional group was formed by a combination of taxonomic or feeding characteristics: birds (A) (e.g., guans, trumpeters, tinamous, wood quails, among others), large rodents (GR) (agoutis and pacas), insectivores (I) (armadillos and anteaters), large marsupials (MG) (opossums ≥1 kg), omnivores (O) (e.g., tayras, bush dogs, and coatis), small felids (PF), small mammals (PM) (rodents and small marsupials ≤400g), and ungulates (U) (deer, tapirs, collared peccaries, and white-lipped peccaries) (Appendix S1: Table S1). Non-terrestrial birds, primates, and bats were excluded from our analyses. The taxonomic propositions of the Brazilian Committee of Ornithological Records (Pacheco et al., 2021) and the Taxonomy Committee of the Brazilian Society of Mammalogy (Abreu et al., 2022) were used to name the species.

Behavior Analysis

For the quantification of behaviors, all 30-second videos were considered without a minimum interval between them. Behavior is defined as the responses coordinated by whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes (Levitis et al., 2009), and behavioral category is defined as the description of a behavior that is distinguishable from other categories (Martin & Bateson, 1993).

We did not find studies that describe behaviors that encompass all different species within the functional groups of this research; therefore, the behavior recording was conducted in two stages. In the first stage, we observed animals *ad libitum* in camera videos for training. The second stage involved the development of a general ethogram for all recorded species, with a qualitative description of the behavioral repertoire in behavioral categories (Altmann, 1974; Martin & Bateson, 1993; Roll et al., 2006). In addition, the general descriptions were adjusted with specific bibliographies of ethograms or behavior descriptions by species or phylogenetically close species of the more general taxa.

We categorized the behaviors of all vertebrates into: [i] feeding (animal has its head facing the ground, chewing, or bringing leaves, fruits, seeds, or other animals to its mouth); [ii] bioturbation (animal inserts its head, beak, or snout into the litter, disturbing it, or removes the litter with its paws or tail); [iii] trampling (animal moves (running or walking) in front of the camera, rests, or interacts with another individual, trampling the area); [iv] defecation or scent marking (animal performs potential defecation or territory marking movements) (Detailed ethogram description in Appendix S2: Table S2).

These behaviors are essential in plant-animal interactions and are associated with important ecological functions, for example, feeding behavior is directly related to the ecological function of seed predation, fruit consumption, animal predation, and herbivory. Common International Classification of Ecosystem Services (CICES) v5.1 (Haines-Young & Potschin, 2018) (Refer to Appendix S3: Table S3). For the quantitative recording of behaviors, the focal animal method was used (Altmann, 1974; Martin & Bateson, 1993; Roll et al., 2006), recording the continuous time (in seconds) of each behavior of an individual (referring to the time recorded in the video). In this way, combining information on the frequency of activity and the duration of the behavior recorded by the cameras, we quantified the behaviors to assess the loss of behaviors in situations with different exclusion treatments.

Considering that the potential effects of terrestrial vertebrates on vegetation and soil, and animal species are influenced by both the duration of behavioral events and the body mass of individuals, we developed an index to quantify the potential effects of recorded behaviors, where the duration of the event is weighted by the body mass of the species involved in the behavior, such that:

$$I_{c,p} = \sum D_c m_i$$

where *c* represents a particular behavior, *p* refers to the monitored plot, *D* is the duration of the event c, and *m* is the average body mass (kg) of species *i* (see Appendix S1: Table S1). Data for species were grouped according to the functional group to which they belong. The body mass of mammals and birds followed the global compilation proposed by Wilman et al. (2014). For individuals identified to the genus level, an average weight of the species within the genus present in the region was calculated (Prado et al., 2022; Paglia et al., 2012).

Statistical Analyses

To analyze the influence of different levels of defaunation on the behavior index (dependent variable), we used generalized linear mixed models (GLMM) implemented with the glmmTMB package (Bolker, 2023). The predictor variables were treatment (control, partial exclusion, and total exclusion) and experimental block as random variable.

Question 1 - Model

$$Behavior\ index \sim treatment + (1|block)$$

For the seasonal analysis, season (rain vs. dry) was included as a predictor variable in the model. The experimental block and the plot id were treated as random variables for seasonal analysis.

Question 2 - Model

$$Behavior\ index \sim treatment + season + (1|block) + (1|plot\ ID)$$

We used the Gamma distribution with a log-link function, transforming the data by adding +1 to fit the distribution of residuals. The "DHARMa" package (Hartig & Lohse, 2022) was used for the model residual diagnostics. After finding significance in the GLMM results, *post hoc* analysis was conducted using the "emmeans" package (Russell et al., 2023). All analyses were performed in R software version 4.1 (R Core Team 2021).

RESULTS

We registered seven bird species and 19 mammals in the 33 plots, totaling a sampling effort of 990 trap-days. The number of species recorded in the 'control treatment' (26 species) was approximately twice as large as that recorded in the 'partial exclusion' treatment and four times larger in the 'total exclusion' treatment. There was a drastic reduction in the number of functional groups present in the "total exclusion" treatment (2 groups: large marsupials and small mammals) compared to the "partial exclusion" (6) and "control" (8) treatments (Appendix S1: Table S1). This progressive reduction in the set of functional groups led to a decrease in the behavior index in both exclusion treatments. In comparison to the control treatment, the “total exclusion” plots presented only 4% of the feeding, 9% of bioturbation, and 5% of trampling behavior. In “partial exclusion” plots, only 23% of the feeding, 16% of bioturbation, 7% of defecation or scent marking, and 30% of trampling behavior remained.

Effect of Experimental Defaunation on Behaviors

Trampling was three times higher in the control treatment than in the partial exclusion, but the difference was not significant ($p=0.2$), and twenty times higher than in total exclusion ($p<0.001$). The functional groups that contributed the most to this behavior in the control were large rodents (57%) and ungulates (23%). In partial exclusion, large rodents accounted for 84% of the index, followed by small mammals (7%). In total exclusion, the functional group of small mammals was responsible for 90%, followed by large marsupials (10%) (Figure 3).

Feeding was four times higher in the control treatment than in the partial exclusion without a significant difference ($p=0.9$) and twenty-seven times higher than in total exclusion ($p=0.005$). In the control, the functional groups of large rodents (48%) and ungulates (47%) were most important. In partial exclusion, large rodents (92%) made the greatest contribution. In total exclusion, the group of small mammals was 100% responsible for this behavior.

The mean index of defecation or scent marking was thirteen times higher in the control treatment than in the partial exclusion ($p=0.002$), this behavior was not recorded in the total exclusion treatment. The defecation or scent marking index were not observed by any functional group in the total exclusion treatment. In the partial exclusion treatment, only the group of small mammals (100%) contributed to the index. In the control, large rodents (88%) and small felids (12%) contributed to the index of this behavior.

Bioturbation was six times higher in the control treatment compared to partial exclusion ($p=0.01$) and twenty-three times higher than in total exclusion ($p<0.001$). Insectivores (53%) and birds (25%) contributed the most to this behavior in the control treatment, respectively. In partial exclusion, birds were responsible for 82% of the index, followed by small mammals (10%). In total exclusion, the only small mammals presented this behavior.

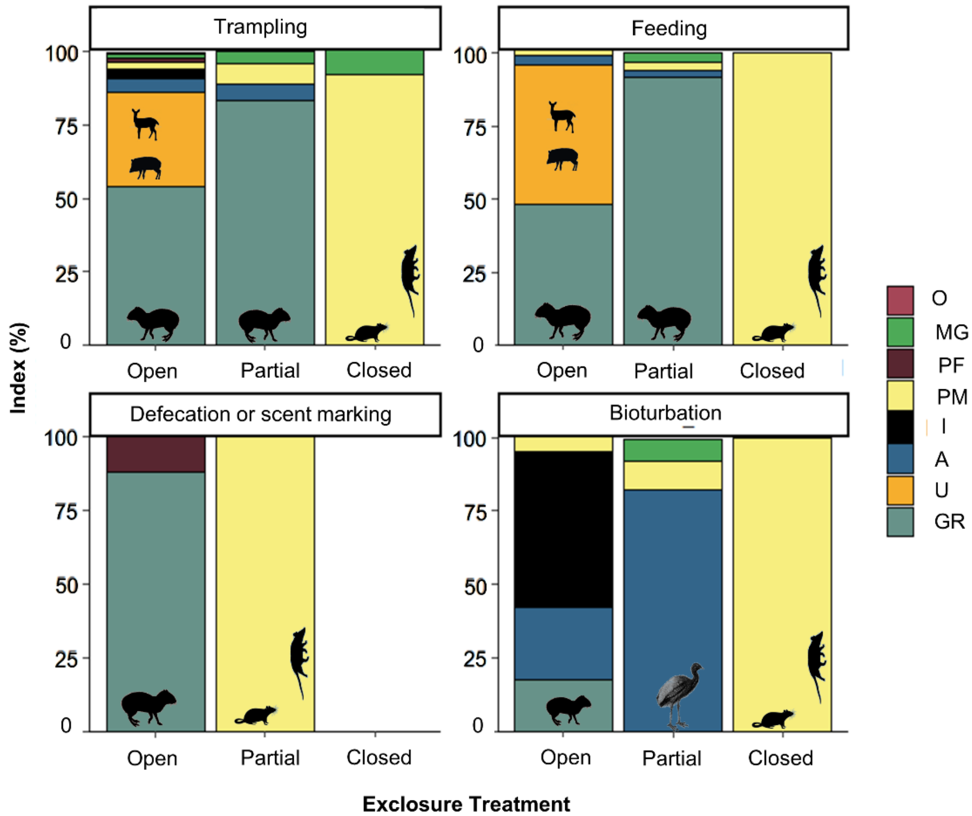


Figure 3: Percentage of behavior indices by functional group in each of the experimental treatments (n=11), simulating different levels of defaunation (see Materials and Methods). Functional groups: birds (A) (guans, tinamous, curassows, and similar species), large rodents (GR) (agoutis and pacas), insectivores (I) (armadillos and anteaters), large marsupials (MG) (opossums >1kg), omnivores (O) (tayras, bush dogs, and coatis), small felines (PF), small mammals (PM) (rodents and cuicas ≤400g), and ungulates (U) (deer, tapirs, collared peccaries, and white-lipped peccaries). Analyses were performed with the mean values per plot.

Seasonality of Behaviors under Defaunation Conditions

Four types of behaviors were recorded during the dry season (trampling, feeding, defecation or scent marking, and bioturbation), and three during the rainy season (trampling, feeding, and bioturbation). There was no variation in behaviors (bioturbation, defecation or scent marking, and feeding) in the total exclusion treatment with respect to functional groups; small mammals were the only group that contributed to the indices in both seasonal periods (Figure 4). On average, the indices for trampling, feeding and bioturbation behaviors were six, forty, and twenty-three times higher, respectively during the dry season compared to the rainy season. For all types of behavior and experimental treatments, the indices were consistently higher on average during the dry season than during the rainy season, with significant differences in all cases (Table 4).

Table 4: Results of significant 'emmeans' post hoc analyses between the interactions of the experimental treatments: control, partial exclusion, total exclusion (n=5 for each) with seasonal variation.

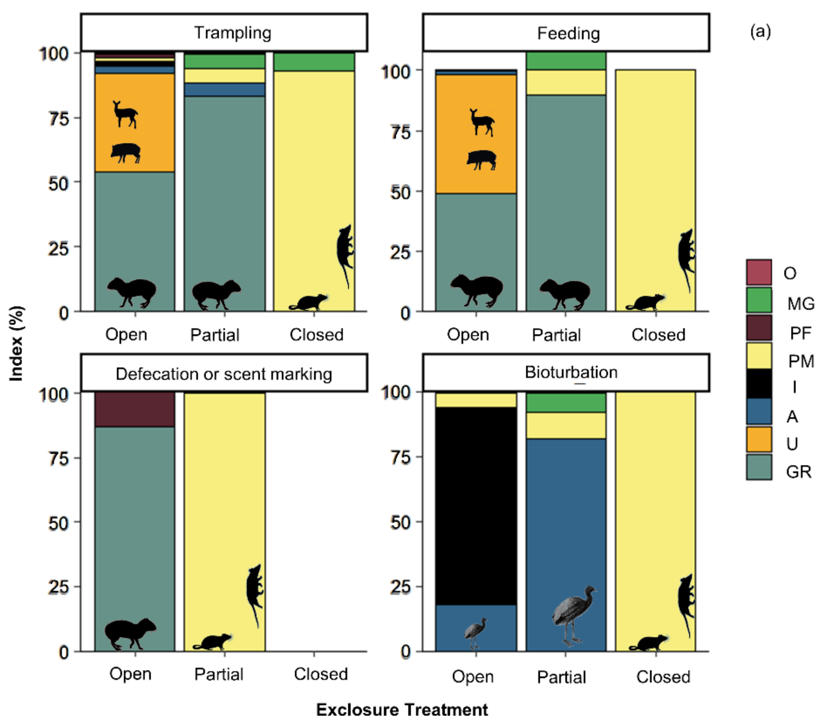
Interactions between plot and season time	estimate	p.value
Trampling		
control rain - control dry	-2.29	0.0001
partial exclusion rain - partial exclusion dry	-2.29	0.0001
total exclusion rain - total exclusion dry	-2.29	0.0001
Feeding		
control rain - control dry	-2.96	0.0002
partial exclusion rain - partial exclusion dry	-2.96	0.0002
total exclusion rain - total exclusion dry	-2.96	0.0002
Bioturbation		
control rain - control dry	-1.89	0.0002
partial exclusion rain - partial exclusion dry	-1.89	0.0002
total exclusion rain - total exclusion dry	-1.89	0.0002

During the dry season, trampling was six times higher in the control treatment, nine times higher in the partial exclusion treatment, and 20 times higher in the total exclusion treatment compared to the treatments during the rainy season. In the dry season, ungulates (38%) and large rodents (54%) contributed the most to trampling in the control treatment, large rodents (83%) and large marsupials (6%) in the partial exclusion treatment, and small mammals (92%) and large marsupials (7%) in the total exclusion treatment. During the rainy season, birds (36%) and ungulates (52%) were responsible for the highest indices in the control treatment, large rodents (36%) and birds (35%) in the partial exclusion treatment, while only small mammals contributed to the index in the total exclusion treatment (100%) (Figure 4a, b).

Feeding during the dry season was 46 times higher in the control treatment, 20 times higher in the partial exclusion treatment, and 67 times higher in the total exclusion treatment compared to the rainy season. Ungulates (49%) and large rodents (49%) contributed the most to this behavior in the control treatment, while in the partial exclusion treatment, large rodents accounted for 90% of the index during the dry season. In the control treatment during the rainy season, birds represented 55% of this behavior, and large rodents contributed 40%, while in the partial exclusion treatment during the rainy season, large rodents (81%) made the most significant contribution.

Defecation or scent marking behavior were not recorded in the treatments during the rainy season, only in the control and partial exclusion treatments during the dry season. The functional groups that contributed the most to this behavior during the dry season were large rodents (87%) and small felids (13%) in the control treatment, and in the partial exclusion treatment, 100% of the small mammals contributed.

During the dry season, bioturbation was 125 times higher in the control treatment, eight times higher in the partial exclusion treatment, and three times higher in the total exclusion treatment compared to the treatments during the rainy season. In the control treatment, insectivores (76%) and birds (18%) contributed the most to this behavior, while in the partial exclusion treatment during the dry season, birds were responsible for 82% of the index. During the rainy season, in the control treatment, birds represented 100% of this behavior, and in the partial exclusion treatment, birds (90%) also made the most significant contribution.



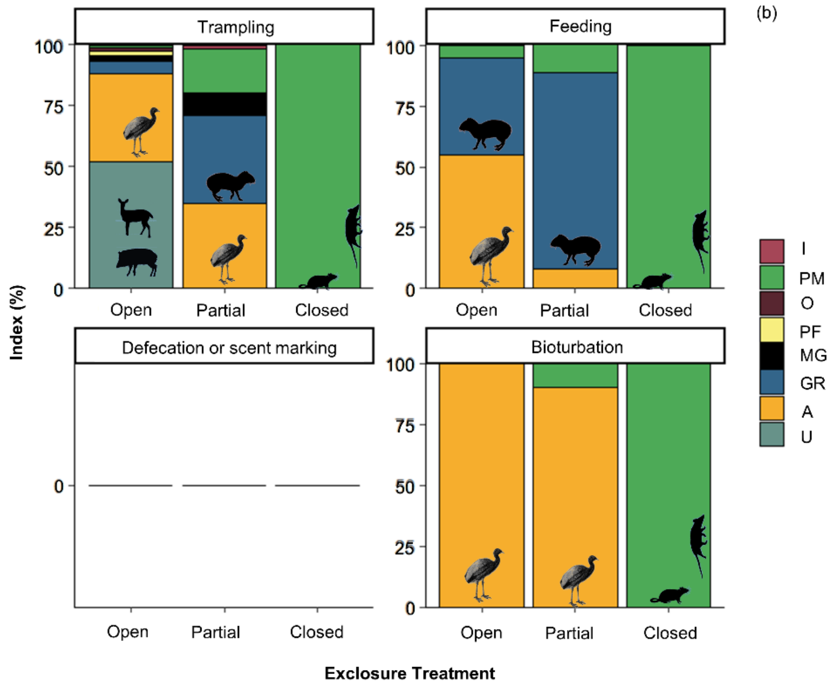


Figure 4: Sum of the indices for behaviors by functional group in each experimental treatment (n=5), simulating different levels of defaunation (see Materials and Methods). (a) - DRY SEASON, (b) - RAINY SEASON. Functional groups: birds (A) (guans, trumpeters, tinamous, and related species), large rodents (GR) (agoutis and pacas), insectivores (I) (armadillos and anteaters), large marsupials (MG) (opossums ≥1 kg), omnivores (O) (tayras, bush dogs, and coatis), small felines (PF), small mammals (PM) (rodents and opossums ≤400g), and ungulates (U) (deer, tapirs, peccaries, and collared peccaries).

DISCUSSION

Camera traps have been recently used to study vertebrate behaviors (Caravaggi et al., 2017), but their application in on species behaviour evaluating the consequences of defaunation in exclusion experiments is non-existent. Our approach allowed us to quantify the loss of behaviors in experimentally defaunated areas, using camera traps in front of exclusion treatment. We demonstrated that the ecological functions performed by various species of mammals and birds, represented by behaviors as a proxy in this study, were severely disrupted under conditions of severe defaunation, implying potential changes in ecological services caused by the absence of several species and functional groups, especially large ones (such as *Mazama* spp., *Pecari tajacu* and *Tapirus terrestris)*.

Our results indicate that large rodents (agoutis and pacas) did not compensate functionally for the absence of ungulates in the treatment simulating intermediate defaunation. On average, the feeding index for the few ungulate records was twice as high for large rodents in plots with intermediate defaunation. Despite large rodents are important seed dispersers (Galetti et al., 2010; Mittelman et al., 2021;) and act as seed hoarders and affecting seed dormancy (Jansen et al., 2006) in tropical forests, they have lower biomass and process less food than ungulates. Small rodents can also act as secondary dispersers of large seeds(Vieira et al., 2003; Wall et al., 2005), as well as medium-sized marsupials (Didelphis sp.), which are generalists in habitat and diet, occurring abundantly in disturbed areas (Amador & Giannini, 2016; Cáceres & Monteiro-Filho, 2007; Lessa & Geise, 2010). However, ungulates play pivotal roles as dispersers and seed predators of large trees, consume more plant biomass, and disperse seeds over longer distances through defecation compared to rodents (Bodmer, 1991; Doughty et al., 2013; Kerley & Landman, 2006; Poulsen et al., 2013), favoring large-scale forest heterogeneity.

Further, our results also show that large rodents had high index values in several behavior categories in comparison to other functional groups, even in the control plots. This process of "rodentization" in forests, more evident in fragmented, and disturbed ones (Galetti et al., 2015), but also in continuous forest areas (Rosa et al., 2021; Peres & Palacios, 2007; this study), seem to be widespread in the Neotropics. The causes of rodentization may be related to a defaunation process that is in course in several Amazon areas (Peres & Palacios, 2007). For example, the increase in the density of agoutis (and of other species such as collared peccaries and deer) may be related to the absence (or the low density) of White-lipped peccaries in our study site, as this should be the case in other Amazonian sites (Whitworth et al., 2022). Therefore, it is worrying that large tracts of apparently pristine Amazonian forests have been dominated by agoutis, especially because they cannot substitute the ecological functions of large herbivores accordingly.

As expected, the behaviors in the treatment simulating severe defaunation did not vary seasonally, with only small mammals exhibiting behaviors. In non-defaunated area we recorded only the trampling behavior for ungulates and insectivores during the rainy season. In the dry season, we observed additional behaviors such as feeding (ungulates) and bioturbation (insectivores). Furthermore, large rodents showed higher rates of feeding, trampling, and defecation or scent marking in all experimental treatments during the dry season. This finding may be related to food availability, in response to a peak ripe fruit conditions in *terra firme* forests during the dry season (Hawes & Peres 2016). This could lead to these functional groups (medium and large species) spending more time in the study area and being recorded more frequently while exhibiting all the behaviors analyzed in this research.

The rainy season resulted in more frequent records of birds feeding in areas with intermediate defaunation compared to the dry season. Some species of the recorded species (*Psophia* and *Tinamus* genus) recorded in this study have been abundantly detected in various seasons in inventories in the Amazon (e.g., Carvalho et al., 2023; Michalski et al., 2015). This finding may be related to hypotheses regarding the absence of predators (Brodie et al., 2014) and reduced competition (Herrmann et al., 2021) in the plot area, leading to an increase of their records. In our case, we suggest that terrestrial birds in forests with intermediate defaunation might benefit from the lower occurrence of large rodents, which act as (competitors).

Our research provides experimental support for predicting the future of dysfunctional defaunated Amazonian forests. Quantifying and grouping the functional traits of animals and linking them to the loss of ecological functions and consequently changes in ecosystem services is an expanding area of research (Forbes et al., 2019; Gong et al., 2015). Although we found evidence that behaviors (and potentially ecological functions) are affected by experimental defaunation, more samplings at various times of the year increase the chances of recording other behaviors, less conspicuous ones. We faced challenges in identifying certain species' movements to categorize them into specific behaviors due to video quality and camera range limitations. Additionally, conducting behavioral studies on focal animals, and measuring the consequences of behavior (i.e., plant survivorship, soil composition and compaction, etc.) could complement and improve the quality of our findings.

We emphasize that manipulative exclusion experiments do not exclude aerial birds and primates, which play important ecological roles in the dispersal of large-seeded species. For example, some primate species (genera *Ateles*, *Lagothrix*, and *Alouatta*) are the only known arboreal seed dispersers, in the Neotropics for seeds measuring 25 to 46 mm in length (Peres & Roosmalen, 2002), in addition to tapirs (O'Farrill et al., 2013). Therefore, manipulative experiments simulating defaunated areas should take this bias into account, and if possible, monitor the presence of these species in the experimental plots continuously. Seedling recruitment, growth, and mortality, as well as soil chemical characteristics, are being monitored in the plots as part of a broader project developed in the area. It is expected that the reduction in behaviors shown here, associated with wildlife activity, will have an impact on various ecological functions, reducing the range of services provided by large mammals in tropical forests

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AUTHOR CONTRIBUTIONS

Batista, GS: Conception, data collection, analysis and writing of the article.

Fadini, RF: Conception, data analysis and writing of the article.

Brocardo, C: Data analysis and writing of the article.

Pires, M: Data analysis and writing of the article.

Arlison, C: Data collection.

Fogliatti, E: Writing of the article (ethogram).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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TABLES

Table S1: Body mass and number of records of each species and functional group present in exclusion treatment of the following experimental treatments: control, partial exclusion, total exclusion, and landscape (n=11 for each). Experiment conducted in the Tapajós National Forest, Pará, Brazil.

Functional group	**Species**	**Body (kg)**	**Control**	**Partial exclusion**	**Total exclusion**
Birds	*Crypturellus sp*	0.4	9	-	-
Birds	*Crypturellus variegatus*	0.37	7	6	-
Birds	*Penelope sp*	1.25	1	-	-
Birds	*Psophia dextralis*	1.07	35	6	-
Birds	*Tinamus guttatus*	0.68	8	-	-
Birds	*Tinamus sp*	1.2	1	2	-
Birds	*Tinamus tao*	1.6	12	5	-
Large rodents	*Cuniculus paca*	8.17	15	14	-
Large rodents	*Dasyprocta croconota*	2.5	138	50	-
Insectivores	*Coendou logicaudatis*	4.39	1	-	-
Insectivores	*Dasypus sp*	36	9	1	-
Insectivores	*Myrmecophaga tridactyla*	22.3	1	-	-
Large marsupials	*Didelphis marsupialis*	1.09	23	21	3
Large marsupials	*Didelphis sp*	1.09	-	2	1
Omnivores	*Eira barbara*	3.9	2	1	-
Small felines	*Leopardus wiedii*	3.2	7	-	-
Small felines	*Herpailurus*	6.8	1	-	-

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Small felines	*Leopardus pardalis*	11.9	1	-	-
Ungulates	*Mazama nemorivaga*	16.6	1	-	-
Ungulates	*Mazama sp*	19	6	-	-
Ungulates	*Pecari tajacu*	21.26	15	-	-
Small mammals	*Gracilinanus emiliae*	0.0076	6	12	5
Small mammals	*Guerlinguetus sp.*	0.18	8	12	7
Small mammals	*Metachirus sp.*	0.37	50	42	43
Small mammals	*Proechimys sp.*	0.26	52	48	77
Small mammals	Rodentia	0.26	2	3	2

Table S2: Ethogram used in the identification of study target behaviors. Developed through ad libitum observation and adjusted with ethograms or behavior descriptions from the references cited for each taxon.

Species/Functional Group and Behavioral Category	**Feeding**	**Defecation or scent marking**	**Bioturbation**	**Locomotion, and Other Behaviors (trampling)**
Terrestrial Birds (Cracidae e Tinamidae) *Psophia dextralis* *Penelope sp* *Crypturellus variegatus* *Crypturellus sp* *Tinamus guttatus* *Tinamus tao* *Tinamus sp* (Lancaster 1964, de Magalhães 1994,	Introduces items, such as fruits, seeds, insects, and other potential prey, into its beak and do not release them..	Elimination of excreta from the posterior part of its body or a slight lowering of the posterior part of the body prior to elimination	Repetitive movement of the beak or legs contacting the ground, moving from front to back or to the sides, causing displacement of leaf litter or soil	Whole-body movement, moving from one point to another on the ground (locomotion). Also included are all behaviors on the ground that do not fall into the other categories, such as

Brennan 2004)				resting, social behaviors, among others
Terrestrial large rodents *Cuniculus paca* *Dasyprocta croconota* (Paranhos & da Costa 2001, Kaiser et al. 2011)	Introduction of fruits, seeds, or plant parts into its mouth, with no observation of releasing them	Performing potential movements of defecation or urination: staying in a quadruped position for a few seconds, lowering the hind part of the body without touching the ground, keeping the hind legs squatted.	Movement of one or both front limbs contacting the ground, with a repetitive front-to-back motion that causes the displacement of litter or soil. The snout may also be used.	Whole-body movement, moving from one point to another on the ground (locomotion). Also included are all behaviors on the ground that do not fall into the other categories, such as resting, social behaviors, among others
Omnivores *Eira barbara* (Pereira & Oliveira 2010)	Introduction of fruits, seeds, plant parts, or small animals into its mouth, with no observation of releasing them	Potential movements of defecation or urination: remaining in a quadruped position for a few seconds, lowering the posterior part of the body without touching the ground, and keeping the hind legs crouched	Movement of one or both front limbs contacting the ground, with a repetitive front-to-back motion that causes the displacement of litter or soil. The snout may also be used.	Whole-body movement, moving from one point to another on the ground (locomotion). Also included are all behaviors on the ground that do not fall into the other categories, such as resting, social behaviors, among others
Insectivores *Coendou prehensilis* (Passamani 2010)	Introduction of fruits, seeds, or plant parts into its mouth, with no observation of releasing them.	Potential movements of defecation or urination: remaining in a quadruped position for a few seconds, lowering the posterior part of the body without touching the ground, and keeping the hind legs crouched	Movement of one or both front limbs contacting the ground, with a repetitive front-to-back motion that causes the displacement of litter or soil. The snout may also be used.	Whole-body movement, moving from one point to another on the ground (locomotion). Also included are all behaviors on the ground that do not fall into the other categories, such as resting, social behaviors, among others
Insectivores *Myrmecophaga tridactyla* (Schmidt 2012)	Repetitive introduction and retraction of the tongue into the prey source.	Elimination of excreta from the posterior part of its body or lowering the posterior part	Movement, in a quadruped position, of one or both front limbs contacting the	Whole-body movement, moving from one point to another on the ground

		of the body slightly prior to elimination.	ground with claws. It involves a repetitive front-to-back motion that causes the displacement of litter or soil. The snout may also be used.	(locomotion). Also included are all behaviors on the ground that do not fall into the other categories, such as resting, social behaviors, among others
Insectivores *Dasypus sp* (Cortés-Duarte 2015)	Introduction of fruits, seeds, or plant parts into its mouth, with no observation of releasing them.	Elimination of excreta from the posterior part of its body or lowering the posterior part of the body slightly prior to elimination.	Movement of one or both front limbs, and/or the snout or tail, contacting the ground, involving a repetitive front-to-back or lateral motion that causes the displacement of litter or soil	Whole-body movement, moving from one point to another on the ground (locomotion). Also included are all behaviors on the ground that do not fall into the other categories, such as resting, social behaviors, among others
Large marsupials *Didelphis sp* *Didelphis marsupialis* (Kimble 1997)	Introduction of fruits, seeds, or plant parts into its mouth, with no observation of releasing them.	Elimination of excreta from the posterior part of its body or lowering the posterior part of the body slightly prior to elimination.	Movement of one or both front limbs, and/or the snout or tail, contacting the ground, involving a repetitive front-to-back or lateral motion that causes the displacement of litter or soil. This category also includes the use of the tail to capture litter for nest construction.	Whole-body movement, moving from one point to another on the ground (locomotion). Also included are all behaviors on the ground that do not fall into the other categories, such as resting, social behaviors, among others
Small felids *Leopardus wiedii* *Herpailurus yagouaroundi* *Leopardus pardalis* (Stanton et al. 2015, Edwards 2018)	Introduction into its mouth, animals, and it was not observed to release them.	Performing potential movements of defecation or urination: remaining in a quadrupedal position for a few seconds, lowering the posterior part	Movement of one or both front limbs contacting the ground, with a repetitive front-to-back motion that causes the displacement of litter or soil. The snout may also be	Whole-body movement, moving from one point to another on the ground (locomotion). Also included are all behaviors on the ground that do not fall into the other

		of the body without touching the ground, keeping the hind legs crouched. Also included was marking behavior, where the individual places its posterior part of the body near a structure (usually a tree), and, with the tail perpendicular to the body, eliminates excreta towards that structure.	used	categories, such as resting, social behaviors, among others
<u>*Ungulates*</u> *Pecari tajacu* (Edwards 2018, da Silva et al. 2020)	Introduction of fruits, seeds, plant parts, or small animals into its mouth, with no observation of releasing them	Performing potential movements of defecation or urination: remaining in a quadrupedal position for a few seconds, lowering the posterior part of the body without touching the ground, keeping the hind legs crouched.	Movement of one or both front limbs, and/or the snout, contacting the ground, involving a repetitive front-to-back or lateral motion that causes the displacement of litter or soil.	Whole-body movement, moving from one point to another on the ground (locomotion). Also included are all behaviors on the ground that do not fall into the other categories, such as resting, social behaviors, among others
<u>*Ungulates*</u> Veados *Mazama nemorivaga* *Mazama sp* (Mamone 2001, Edwards 2018)	Introduction of fruits, seeds, plant parts, or small animals into its mouth, with no observation of releasing them.	Performing potential movements of defecation or urination: remaining in a quadrupedal position for a few seconds, lowering the posterior part of the body without touching the ground, keeping the hind legs crouched.	Movement of one or both front limbs, and/or the snout, contacting the ground, involving a repetitive front-to-back or lateral motion that causes the displacement of litter or soil.	Whole-body movement, moving from one point to another on the ground (locomotion). Also included are all behaviors on the ground that do not fall into the other categories, such as resting, social behaviors, among others

Small mammals *Gracilinanus emiliae* *Guerlinguetus sp* *Metachirus sp* *Proechimys sp* *Rodentia* (Mendes & Cândido-Jr 2014, Cantano et al. 2021)	Introduction of fruits, seeds, plant parts, or small animals into its mouth, with no observation of releasing them.	Performing potential movements of defecation or urination: remaining in a quadrupedal position for a few seconds, lowering the posterior part of the body without touching the ground, keeping the hind legs crouched.	Movement of one or both front limbs, and/or the snout, contacting the ground, involving a repetitive front-to-back or lateral motion that causes the displacement of litter or soil. This includes capturing litter with the tail for nest construction.	Whole-body movement, moving from one point to another on the ground (locomotion). Also included are all behaviors on the ground that do not fall into the other categories, such as resting, social behaviors, among others

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Table S3: Description of behaviors and their relationship with potential ecological functions and ecosystem services, according to the Common International Classification of Ecosystem Services (CICES) v5.1. (Haines-Young & Potschin, 2018).

Behavior	**Ecological functions**	**Provisioning ecosystem services**	**Regulating ecosystem services**
Feeding	Predation of seeds, fruits, and other animals, Consumption of any plant part (Herbivory)	Seed quality Organic matter for the soil (regurgitation) Reduction in plant biomass (herbivory)	Animal population control Forest heterogeneity Forest fire control
Defecation or scent marking	Seed dispersal and soil nutrients	Organic matter for soil	Forest heterogeneity and

		Nutrient cycling in the soil Germination of genetically favored trees/plants	regeneration. Climate regulation. Soil quality regulation.
Bioturbation	Litter mixing, dispersing seeds, and fruits	Germination of genetically favored trees/plants Nutrient cycling in the soil	Forest heterogeneity Soil Quality Regulation
Trampling	Soil or litter compaction and gap creation	Organic matter for soil (seedling and sapling mortality) and Soil nutrient cycling	Heterogeneity and Forest Maintenance, Soil Quality Regulation

Haines-Young, R. and M.B. Potschin (2018). Common International Classification of Ecosystem Services (CICES) V5.1 and Guidance on the Application of the Revised Structure. Available from www.cices.eu