PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA
UNIVERSIDADE FEDERAL DO PARÁ
MUSEU PARAENSE EMÍLIO GOELDI

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Fatores determinantes para a abundância de espécies de mamíferos ameaçados em área de alta pressão antrópica na Amazônia oriental

Belém, 2019

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Dissertação apresentada ao Programa de Pós-Graduação em Zoologia, do convênio da Universidade Federal do Pará e Museu Paraense Emílio Goeldi, como requisito parcial para obtenção do título de Mestre em Zoologia.
Área de concentração: Biodiversidade e Conservação
Linha de pesquisa: Ecologia animal

Orientadora: Profa. Dra. Ana Cristina Mendes de Oliveira.
Coorientador: Prof. Dr. Oystein Wiig.

Belém, 2019

Dados Internacionais de Catalogação na Publicação (CIP)
Sistema de Bibliotecas da Universidade Federal do Pará
Gerada automaticamente pelo módulo Ficat, mediante os dados
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T266f Teixeira Santos, Juliana
Fatores determinantes para a abundância de espécies de mamíferos ameaçados em área de alta pressão antrópica na Amazônia oriental / Juliana Teixeira Santos. — 2018
55 f. : il. color

Orientara: Profa. Dra. Ana Cristina Mendes-Oliveira
Coorientador: Prof. Dr. Oystein Wiig
Dissertação (Mestrado) - Programa de Pós-graduação em Zoologia (PPGZOOL), Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, 2018.

1. Floresta Degradada. 2. Espécies ameaçadas. 3. Amazônia.
II. Título

CDD 574.5264

FOLHA DE APROVAÇÃO

JULIANA JANUÁRIA TEIXEIRA SANTOS

FATORES DETERMINANTES PARA A ABUNDÂNCIA DE ESPÉCIES DE MAMÍFEROS AMEAÇADOS EM ÁREA DE ALTA PRESSÃO ANTRÓPICA NA AMAZÔNIA ORIENTAL

Dissertação apresentada ao Programa de Pós-graduação em Zoologia, do convênio da Universidade Federal do Pará e Museu Paraense Emílio Goeldi, como requisito parcial para obtenção do título de Mestre, sendo a COMISSÃO JULGADORA composta pelos seguintes membros:

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Aprovada em: 17 de abril de 2018

Local de defesa: Belém, PA

Dedico a meu Deus, meu
marido, minhas mães e
irmãos.

Porque, de muitos trabalhos vêm os sonhos...
(Eclesiastes 5:3)

AGRADECIMENTOS

Tão bom poder agradecer a Deus por ter sido meu porto seguro em meio a este período tão desafiador! Tudo vem de Ti, e das Tuas próprias mãos eu te devolvo! Obrigada meu Deus!

Não sei nem o que dizer para expressar minha gratidão a meu Emerson, marido, amigo, companheiro, suporte, por todo o apoio, paciência e amor que sempre foram constantes. Obrigada por estar comigo. Sem você eu não teria conseguido!

Agradeço as minhas mães, Ilma e Dalva, que mesmo sem entender nada do que faço ou o porquê, sempre me apoiaram e morrem de felicidade junto comigo! Agradeço a minha Tia Ione por sempre demonstrar interesse no mestrado.

À Dona Dileia e Lu que cuidaram da minha casa e dos meus cachorros enquanto eu ficava longe, sem precisar preocupar.

À minha orientadora Cris, pela oportunidade, pelo ensinamento e orientação que agregaram tanto valor a minha carreira.

Ao meu coorientador Oystein, que em 2013 teve a coragem de me aceitar como parte do seu time, sem falar quase nada em inglês, e parecendo uma doida tentando. Obrigada por todo incentivo, por todo suporte e por acreditar! Este momento é nosso como equipe! Equipe Cameras Trap! Obrigada pela amizade!

À minha amiga e Parceira Carulina. Lembro da gente morta de feliz instalando a primeira câmera em 2013! Lembro da gente morta de cansada do nosso trabalho e ainda assim empolgada revisando câmera, na época uma atividade paralela. Lembro da gente cheia de carrapato, fugindo de abelhas, cortando cipó, sofrendo para estudar para entrar no mestrado, felizes porque fomos aprovadas, doidas perdidas quando entramos, achando o caminho, perdendo o caminho, achando o caminho de novo, sofrendo com uma análise, sofrendo por mudar de análise, brigando as vezes, ajudando uma a outra. Sempre juntas! E conquistando este momento juntas!

Obrigada Leonardo Sena, por ter nos ajudado tanto na parte burocrática do desenvolvimento do projeto!

À galera do Laboratório de Ecologia e Zoologia de Vertebrados, vocês são demais! Todos buscando juntos crescer ajudando uns aos outros.

Phyna Flor da Pesquisa!!! Melhor grupo! Uma galera doida pra caramba, mas é em resumo amizade e apoio! Vi isso em poucos lugares na vida! Pessoal que compartilha conhecimento com vontade, que fica feliz com o outro, sofre junto. Espero estar neste grupo para sempre! Obrigada por fazer meus dias longe de casa mais leves!

À Suzanne, que foi a primeira a me incentivar de verdade a tentar e correr atrás do mestrado! Suzie, lindona! Obrigada!

Agradeço aos presentes que Belém me deu. Paulinha e Gabi. Meninas, vocês são MARAVILHOSAS! Quero ser como vocês! Este trabalho não seria possível sem o apoio e principalmente sem a amizade de vocês.

Gaiola das Loucas! Obrigada! Sou tão grata a Deus por vocês meninas! A melhor república do mundo! Lorreynhy, caçula, minha Young Sheldon, obrigada por sempre me ajudar, por fazer meus slides ficarem lindos, por ser minha rainha da formatação, por fazer parte deste trabalho, por ser minha amiga e por me ensinar o idioma maranhense! Carulina (de novo), obrigada várias vezes pelo apoio e amizade! Amo vocês.

Ao meu querido amigo Fernando Carvalho Filho, que me incentivou, deu altas dicas e me forneceu gentilmente as ilustrações das espécies. Seus desenhos são lindos!

Ao Professor Dr. Leandro Juen por sempre me atender, ajudar nas ideias, discutir meu tema e me apresentar uma pessoa para me ajudar nas análises (abaixo, segue ele, Nelson).

Obrigada Nelson, GLMM em pessoa! Ai de mim se não fosse você! Obrigada por me ensinar sobre esta análise, obrigada pelo empenho e paciência e por nunca desmerecer meu conhecimento até aquele momento.

À galera do campo! Ehhhhhhhh galera bacana! Tanta gente nos ajudou! Agradeço especialmente ao Maranhão (melhor GPS vivo do mundo), Fabrício e Francisco. Agradeço também ao Rildo, Daldi, Tião, Alberani, Elísio (*in memorian*) e ao Lélio! Pessoal, vocês são os melhores!

Ao Dr. Paulo de Marco Júnior, à Dra. Luciana Signorelli e à Dra. Lilian Sales, todos da UFG. Agraço a Me. Tatiane, que descobri no Google e ainda assim ela respondeu aos meus e-mails, permitiu que eu lesse sua dissertação, e me deu muitas dicas sobre análises.

À banca que aceitou avaliar e colaborar com a minha dissertação, dando contribuições muito valiosas: Dr. Leandro Juen, Dra. Marcela Lima, Dr. Raphael Ligeiro (desde a qualificação colaborando), Dr. Carlos Peres e Dra. Renata Pardini.

Agradeço ao Consórcio de Pesquisa em Biodiversidade Brasil-Noruega *(*BRC) pela oportunidade de fazer parte deste time maravilhoso e fazer ciência, convivendo com pesquisadores tão competentes.

À Hydro Paragominas por nos permitir trabalhar em sua área, por todo apoio logístico e todo suporte. A Gerência de Meio Ambiente por sempre se apresentarem disponíveis a auxiliar.

Ao Programa de Pós-Graduação em Zoologia (PPGZOOL), a Universidade Federal do Pará (UFPA) e o Museu Paraense Emílio Goeldi (MPEG), que representados pelos professores me ajudaram a construir, entender e melhorar a construção deste trabalho.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela concessão da bolsa.

Este texto é cheio de !!!! mesmo, para representar o quão importante vocês foram para esta conquista. A todos que fizeram parte da construção deste conhecimento, mesmo os que não citei, mas não menos importantes! Obrigada!

SUMÁRIO

Fatores determinantes para a abundância de espécies de mamíferos ameaçados em área de alta pressão antrópica na Amazônia oriental

RESUMO

Nos últimos 60 anos, a degradação e fragmentação de habitats nativos modificaram a paisagem na Amazônia oriental brasileira. A plasticidade adaptativa de um organismo tem sido crucial para sua sobrevivência e sucesso a longo prazo nesses novos ecossistemas. Neste estudo, investigamos a resposta de quatro espécies ameaçadas de grandes mamíferos terrestres às variações na qualidade de seus habitats originais, em um contexto de alta pressão antrópica. A distribuição dos *Myrmecophaga tridactyla*, *Priodontes maximus*, *Tapirus terrestris* e *Tayassu pecari* em todos os habitats amostrados sugere sua tolerância à degradação. No entanto, a capacidade de sobrevivência de cada espécie nos diferentes habitats não foi a mesma. Entre as quatro espécies, *T. pecari* parece ser a que possui menor capacidade de sobrevivência em ambientes mais alterados. A influência positiva dos habitats alterados antropogenicamente nas abundâncias de três das quatro espécies estudadas, como observado nas áreas de regeneração, pode ser considerada como uma possível indicação do fenômeno das armadilhas ecológicas. Este estudo reforça a importância dos remanescentes florestais para a sobrevivência de espécies de mamíferos ameaçadas, em regiões de alta pressão antropogênica, como na Amazônia oriental brasileira.

Palavras-chave: *Myrmecophaga tridactyla*; *Priodontes maximus*; *Tapirus terrestres; Tayassu Pecari;* Floresta degradada; espécies vulneráveis.

Environmental factors influencing the abundance of four species of threatened mammals in degraded habitats in eastern Amazon

ABSTRACT

On the latest 60 years the degradation and fragmentation of native habitats have been modifying the landscape in the eastern Brazilian Amazon. The adaptive plasticity of an organism has been crucial for its long-term survival and success in these novel ecosystems. In this study, we investigated the response of four endangered species of large terrestrial mammals to the variations in the quality of their original habitats, in a context of high anthropogenic pressure. The distribution of the *Myrmecophaga tridactyla* (Giant anteater), *Priodontes maximus* (Giant armadillo), *Tapirus terrestris* (Lowland tapir) and *Tayassu pecari* (White-lipped peccary) in all sampled habitats suggests their tolerance to degradation. However, the survival ability of each species in the different habitats was not the same. Among the four species, *T. pecari* seems to be the one with the least ability to survive in more altered environments. The positive influence of the anthropogenically altered habitats on abundances of three of the four species studied, as observed at the regeneration areas, can be considered as a potential indication of the ecological trap phenomenon. This study reinforces the importance of the forest remnants for the survival of endangered mammal species, in regions of high anthropogenic pressure, as in the eastern Brazilian Amazon.

Keywords: *Myrmecophaga tridactyla*; *Priodontes maximus*; *Tapirus terrestres; Tayassu Pecari*; Degraded forest; vulnerable species.

Capítulo Único

Fatores determinantes para a abundância de espécies de mamíferos ameaçados em área de alta pressão antrópica na Amazônia oriental

O capítulo único desta dissertação foi elaborado e formatado conforme as normas da publicação científica *Plos One,* as quais se encontram em Material Suplementar (S4)

Environmental factors influencing the abundance of four species of threatened mammals in degraded habitats in eastern Amazon

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Abstract

On the latest 60 years the degradation and fragmentation of native habitats have been modifying the landscape in the eastern Brazilian Amazon. The adaptive plasticity of an organism has been crucial for its long-term survival and success in these novel ecosystems. In this study, we investigated the response of four endangered species of large terrestrial mammals to the variations in the quality of their original habitats, in a context of high anthropogenic pressure. The distribution of the *Myrmecophaga tridactyla* (Giant anteater), *Priodontes maximus* (Giant armadillo), *Tapirus terrestris* (Lowland tapir) and *Tayassu pecari* (White-lipped peccary) in all sampled habitats suggests their tolerance to degradation. However, the survival ability of each species in the different habitats was not the same. Among the four species, *T. pecari* seems to be the one with the least ability to survive in more altered environments. The positive influence of the anthropogenically

altered habitats on abundances of three of the four species studied, as observed at the regeneration areas, can be considered as a potential indication of the ecological trap phenomenon. This study reinforces the importance of the forest remnants for the survival of endangered mammal species, in regions of high anthropogenic pressure, as in the eastern Brazilian Amazon.

Introduction

Since the 1960s the Brazilian Amazon rainforest has been degraded at a fast pace. Land use changes have led to an accumulated deforestation of 20% of this Biome by 2017 [1]. About 90% of this deforestation is concentrated in the "Deforestation Arc" [2], located in the eastern and southern portion of the area, which encompass the agricultural and cattle frontier of the Amazon rainforest in Brazil. In addition to the substitution of the forest for agriculture and pasture [3], there is also a removal of forest and soil for mining activities [4], and degradation of the forest through logging x. All these anthropogenic processes lead to an expansion of urban and industrial infrastructure areas. The consequences are changes in the dynamics of the Amazon ecosystem, reducing environmental complexity, modifying ecosystem functions and drastically impacting the region's biodiversity [5-8].

The response of the fauna to the new environmental conditions may vary according to the taxon and the intensity of the anthropogenic impact. The adaptive fitness of a species is closely related to its evolutionary history. The organisms evolved based on environmental factors that shaped preferences and ecological demands over a sufficient evolutionary time to allow genotypic and phenotypic adaptations that favored and increased the fitness of the species [9]. However, rapid human-induced environmental changes (HIREC) [10] has resulted in a new reality in tropical forests, with the emergence of "novel ecosystems" that differ in composition, function and/or appearance from the past systems [11]. The response of the fauna to this phenomenon, usually associated with climate changes or invasive species, has been referred to as the "Ecological

Trap"[11]. This term defines the choice or preference of an organism for a resource or habitat different from the original, even if this means reducing its fitness [11,12].

Currently, the Amazon rainforest is not exempt from the phenomena of ecological novelties or ecological traps [11]. The fragmentation and degradation of native habitats have modified the landscape in the eastern Amazon, with the formation of remnants of primary forests at different levels of degradation, mixed with secondary forests at different levels of regeneration and economically productive open areas [13]. The adaptive Plasticity of an organism, which is its ability to suit these new environments, will be crucial for its long-term survival and success [9]. However, the survival ability of a species may be more efficient when the taxon has already been exposed to similar situations in its evolutionary past [11]. In addition, the intensity and time scale of environmental and structural changes may also interfere with these responses [14].

Mammals represent a group which is greatly threatened by environmental changes in the Amazon [6, 8]. Thirty-five species of Amazon mammals are listed in the Brazilian Red List of threatened species [15]. In this study, we selected four of these threatened species to study and understand factors that have influenced their abundance in a context of high anthropogenic pressure: *Myrmecophaga tridactyla* (Giant anteater), *Priodontes maximus* (Giant armadillo), *Tapirus terrestris* (Lowland tapir) and *Tayassu pecari* (White-lipped peccary). All are large neotropical mammals, which originally had a wide distribution in South America but are now considered threatened mainly by hunting and degradation of their natural habitats [15,16].

All four target species of this study represent ancient evolutionary histories in the American continent [17-19]. Molecular analyses indicate for example that the order Xenarthra, which includes the species *M. tridactyla* and *P. maximus*, had a common origin to the order Afrotheria at the end of the Cretaceous (106 million years ago), when Africa, South America, Antarctica, and Australia still formed the Gondwana supercontinent [19]. As Xenarthrans, other representatives of terrestrial mammals, including Arctidactyla and Perisssodactyla ancestors, developed up to the Pliocene in total isolation from the rest of the placentarians [19]. During this geological period, the mastofauna of this continent developed morphological, physiological and behavioral adaptations making them capable of colonizing the niches developing in this region [17,18]. These animals are therefore genuinely neotropical and, although they are widely distributed in South America, the way they use native habitats today is closely related to their evolutionary history [11].

In this study, we investigated the response of *M. tridactyla*, *P. maximus*, *T. terrestris* and *T. pecari* to variations in the quality of their original habitats, in the Eastern Amazon. Our hypothesis is that environmental differences caused by anthropogenic factors alter the ability of species to tolerate and remain in particular habitat. Finally, we discuss the implications of these results for species conservation on the theoretical view of "Ecological Novelty" and "Ecological Trap"[11].

Material and Methods

Study Area

The study was carried out in the area of the Hydro Paragominas Bauxite Mine (MPSA) located in the municipality of Paragominas, state of Pará, in the Eastern Amazon (Fig 1). According to the Köppen-Geiger classification, the climate in the area is moist tropical [20]. The original vegetation of the area was composed mostly by typical Dense Amazon Rainforest [21], with a continuous canopy ranging from 25-30 m in height, with a low dense understory and an average basal area of 20-30 m^2/ha [22].

However, the study area region has been undergoing an intense process of forest degradation and deforestation, mainly between the 1970s and 2000s [2]. Illegal and predatory logging impoverished the region's forests, and later agro-industry and livestock farming have caused high rates of deforestation. According to the Brazilian National Institute of Space Research (INPE), in 2015 about 45% of the forest area of Paragominas had already been deforested [23] and about 60% of the forest remnants had already suffered some kind of anthropogenic impact [24,25].

The region of Paragominas also presents a high concentration of bauxite (sedimentary rock with high aluminum content), which covers about 58% of the district's soil [24]. Bauxite is the basis for the production of aluminum. The environmental consequences of this activity are changes in the landscape due to the total withdrawal of vegetation as well as the removal of the fertile soil and its content of seeds, causing a decrease in local biodiversity [26-29]. In the study area, the bauxite mined areas are later reforested with native species, through the Degraded Area Recovery Programs (PRAD) implemented by the MPSA [30,31].

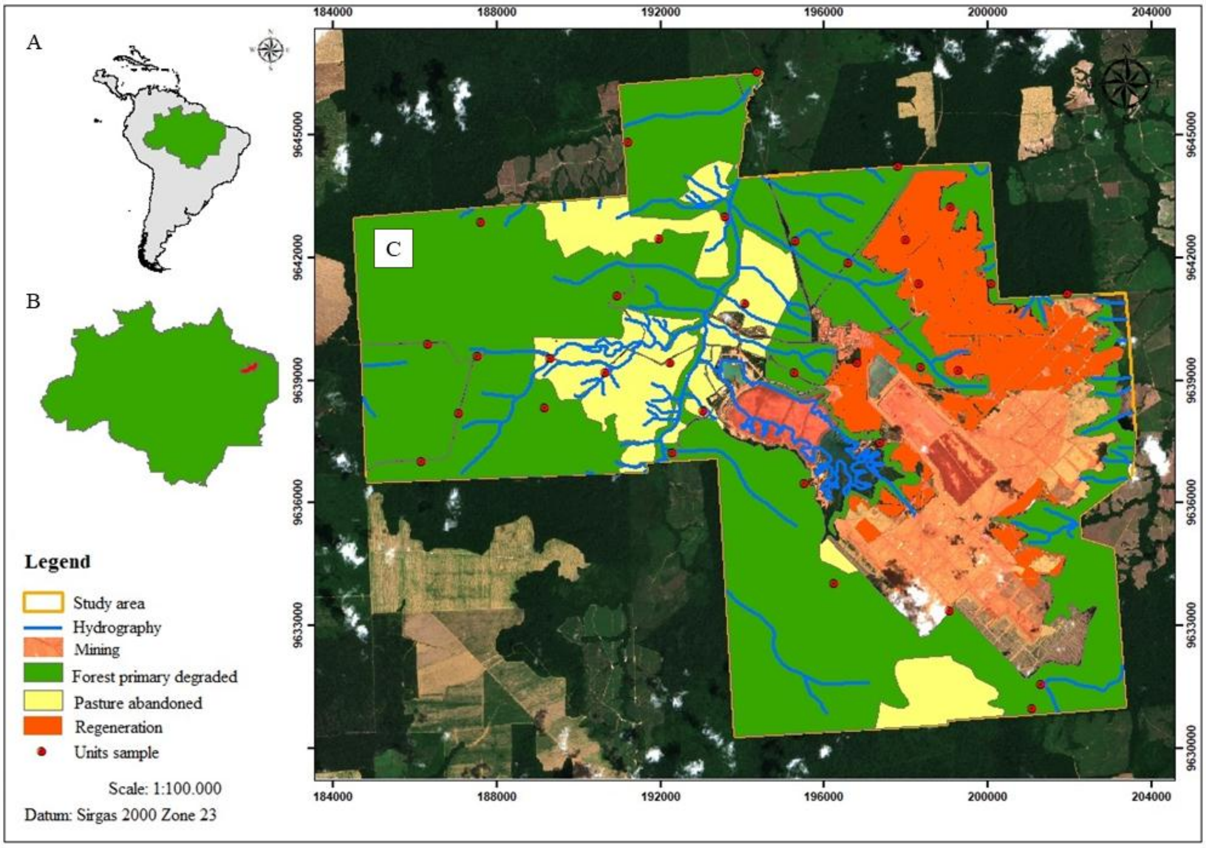

Figure 1: **Location of the study area.** (A) South America highlighting the Brazilian Amazon; (B) District of Paragominas; (C) Limits of the study area and the spatial distribution of the 35 sampling points (camera traps) in the different habitats.

Anthropogenic activities have transformed the landscape of the study region into a mosaic of emerging habitats at different levels of degradation. The area has a total of 18,764 ha, which includes: degraded primary forests, where high-impact logging cycles occurred; bauxite mining areas, where vegetation and soil were completely removed; areas of abandoned pasture; and post-mining forest regeneration areas that are part of the PRAD (Fig 1) [32]. In this study, we sampled three habitats: 1) degraded primary forests, 2) abandoned pasture, and 3) post-mining forest regeneration sites implemented from 2009 to 2012. The area is also surrounded by productive areas, including livestock and monoculture of soybeans and corn, as well as burnt forest patches [32]. There are no areas of primary forest preserved in the study region [33]. The hunting activity is discouraged by the MPSA, however, it is possible to see hunter records in the area. This activity seems to be developed as recreation, with the use of dogs and has only a few target species, especially deer, paca and minor armadillos (Mendes-Oliveira, personal observation). In this work, hunting activity is considered to be a constant variable in all studied habitats.

Data collection

Field trips for data collection occurred between June 2014 and July 2016. We used 35 camera traps [34] to record the four target species of this study. We spread the traps throughout the study area to sample the maximum of its environmental variability (Fig 1). We consider a grid of 3 x 3 km implemented on a satellite image of the area and installed the cameras as close as possible to the coordinates of the vertices of this grid. Some vertices were too difficult to reach and we placed the cameras as close as possible.

We installed all the traps at a height of approximately 40 cm from the ground and left them running uninterrupted throughout the duration of the study. We checked the traps every 90 to 120 days, to change SD-cards with photos, to exchange batteries or replace cameras when necessary. We programmed the traps to take 3 photos every 30 seconds, recording the date and time of each record, as well as the geographical coordinates of the place. We consider each trap as a sampling unit. The camera traps photographs were defined as an independent event if consecutive photos recorded (i) one or more individuals of different species; or (ii) one or more individuals of the same species over a minimum time interval greater than 60 min [35-37]. Using these criteria, all photos defined as non-independent were excluded from subsequent analyses. We used the program Camera Base version 1.7 (http://www.atrium-biodiversity.org/tools/camerabase/) to process and store the photo records.

Sampling of environmental variables

We measured environmental and anthropogenic variables to verify their influence on the abundance of mammalian species. We used a protocol adapted [38] and based on the work of [39], which evaluates habitat characteristics and human influence. At all camera traps we placed two plots of 50 m x 10 m, located at each side of the camera trap. In each plot we recorded 21 variables that could be related to the species occurrences: 1) Proportion of the area covered by water, 2) Proportion of deforestation area, 3) Proportion of degraded primary forest, 4) Proportion of riparian area, 5) Proportion of regeneration area, 6) Estimated number of seedlings in plot, 7) Distance from degraded primary forest (m), 8) Depth of litter, 9) Number of standing dead trees, 10) Number of fallen dead trees, 11) Proportion of trees with DAP < 55 cm, 12) Proportion of trees with DAP > 55 cm, 13) Canopy height, 14) Proportion of trees with lianas, 15) Average canopy opening, 16) Distance to permanent watercourse, 17) Distance to productive area, 18) Distance to burned area, 19) Sub-surface opening ratio, 20) Distance to mining area, and 21) Minimum distance to trail /road (See S1 Table for definitions. The variables 8, 9, 10, 11, 12, 13, 14, 15 and 19 were collected at the site by us, while the other variables were collected through the use of satellite images available from Instituto do Homem e Meio Ambiente da Amazônia (IMAZON) (S1 Table).

Using the PCA analysis we selected 5 environmental variables: proportion of degraded primary forest (PF), canopy opening (CO), distance from the degraded primary forest (DF), distance from permanent watercourse (DW), and distance to the mining area (DM).

To characterize the habitat structure, we calculated the percentage of canopy opening (CO) in each camera trap sampling point. We took five photos for sampling point, one at each 50 m x 10 m sampling plot and one right where the camera trap was positioned. We used a camera with a fisheye lens, positioned 1.20 meters from the ground, fully directed to the canopy. The photos were analyzed in the software ENVI 5.3, where we calculated the average percentage of canopy opening (AD) for each sampling point similar to that proposed by [40] for sub-forest complexity analysis [40].

We used *Arc Gis* software version 10.2 and shapefile of the study area (IMAZON) to extract vegetation and land use variables. We draw circular 1 km radius buffers from each photographic trap in each sampling unit. We used the buffers as the basis for calculating the values of the variable proportion of degraded primary forest (PF) [41]. We also measured the *Arc Gis* program the perpendicular distance of each sample unit to the nearest forested area (DF), to the nearest permanent water body (DW), and to the nearest mining area (DM).

Data Analysis

We used Principal Component Analysis (PCA) to select some of the correlated environmental variables and avoid multicollinearity. This analysis provided the most important information axes to represent the 21 variables sampled (S1 Table) using the broken stick criterion [42]. We use the R platform through the Vegan, Permute, lattice and MASS packets to perform the analyzes.

We used Generalized Linear Mixed Models (GLMM) [43] to evaluate the influence of the predictive variables, selected by the PCA, on the abundance of the species. In this case, we used the numbers of days of exposure of each camera trap as a random effect and the 5 selected environmental variables as fixed effects. We used the Poisson distribution family (log binding function) since the data residues did not fit to the Gaussian distribution family. To analyze all the possible effects of the predictive variables isolated and the combinations of these variables, we built different models considering all possible combinations between the predictor variables. We used the BOBYQA optimizer to obtain the best performance in the convergence analysis [44]. To select the best model, we used the Akaike Information Criterion adjusted for small samples (AICc) [45]. For these analyses, we used the AICcmodavg package [46], which makes the selection of the most parsimonious model. The model with the lowest AICc value was considered the model with the best fit [45]. To generate the GLMMs we use the glmer function, present in the lme4 package [47]. All analyses were done in Software R [48].

For more descriptive analyses between habitats, we used the Abundance Rate, calculated considering individual species records as independent photographic records per 100 functioning camera-trap night (FCTNs). The mean FCTNs per camera trap deployment was572.34 ± 161.42. We compared the abundance between habitats observing the overlap of the confidence interval of the averages. To understand the relationship between the habitats and the environmental variables, we used the Principal Component Analysis (PCA) [49].

Results

We obtained 2059 independent records of the four endangered species evaluated in this study, of which 263 were of *M. tridactyla*, 50 of *P. maximus*, 1585 of *T. terrestris* and 161 of *T. pecari*. All four species were widely distributed in the study area.

For the species, *M. tridactyla*, the global model considering all the predictive variables (Δ AICc = 0.00), was the most adequate to explain the variation of the abundance of this species (S2 Table). When assessing the relative importance of each variable alone, only PF does not affect the abundance rate of this species (Fig 2, Table 1). The DF, CO, and DM have a negative influence on the abundance rate of *M. tridactyla* (Table 1), indicating that they prefer areas not distant from the mining but also not distant from the forest. On the other hand, the greater the DW, the higher the abundance rate of *M. tridactyla*.

Table 1: Results for predictor variables selected by the GLM Models for *M. tridactyla* (Giant anteater), *P. maximus* (Giant armadillo), *T. terrestris* (Lowland tapir) and *T. pecari* (White-lipped peccary). Bold values indicate interactions at the level of significance of P < 0.05.

Species	Predictor variables	*β*	SE	z-test	P
M. tridactyla	Proportion of degraded primary forest (PF)	-1.729	1.119	-1.545	0.122
	Distance from the degraded primary forest (DF)	**-3.178**	**0.953**	**-3.334**	**< 0.001**
	Average canopy opening (CO)	**-5.453**	**2.053**	**-2.657**	**0.008**
	Distance from watercourse (DW)	**1.862**	**0.932**	**1.999**	**0.046**
	Distance from the mining (DM)	**-2.460**	**0.927**	**-2.654**	**0.008**
P. maximus	Average canopy opening (CO)	-3.070	1.865	-1.646	0.100
T. terrestris	Proportion of degraded primary forest (PF)	**2.326**	**0.8445**	**2.754**	**< 0.001**
	Distance from the degraded primary forest (DF)	**3.731**	**0.644**	**5.793**	**< 0.001**
	Average canopy opening (CO)	2.198	1.265	1.738	0.082
	Distance from watercourse (DW)	-1.119	0.656	-1.707	0.088
	Distance from the mining (DM)	**2.452**	**0.486**	**5.045**	**< 0.001**
T. pecari	Proportion of degraded primary forest (PF)	3.207	0.766	4.188	**< 0.001**

For *P. maximus* the most suitable model to explain the variation in abundance included only CO (Δ AICc = 0.00). However, this variable had no significant effect (Table 1 and S2 Table). For *T. terrestris*, the global model considering all the predictive variables (Δ AICc = 0.00), was the most adequate model to explain the variation in abundance rate for this species (S2 Table). We observed that PF, DF, CO and DM increase the abundance, while DW decreases the abundance of this species (Table 1, Fig 2). The CO and the DW were not individually significant but, together with the others variables influenced the abundance of *T. terrestris* (Table 1, Fig 2). For *T. pecari* only the model including the PF (Δ AICc = 0.00), was the most adequate to explain the variation of the abundance (S2 Table). In this model, the PF was significant and had a positive influence on the abundance of *T. pecari* (Table 1, Fig 2).

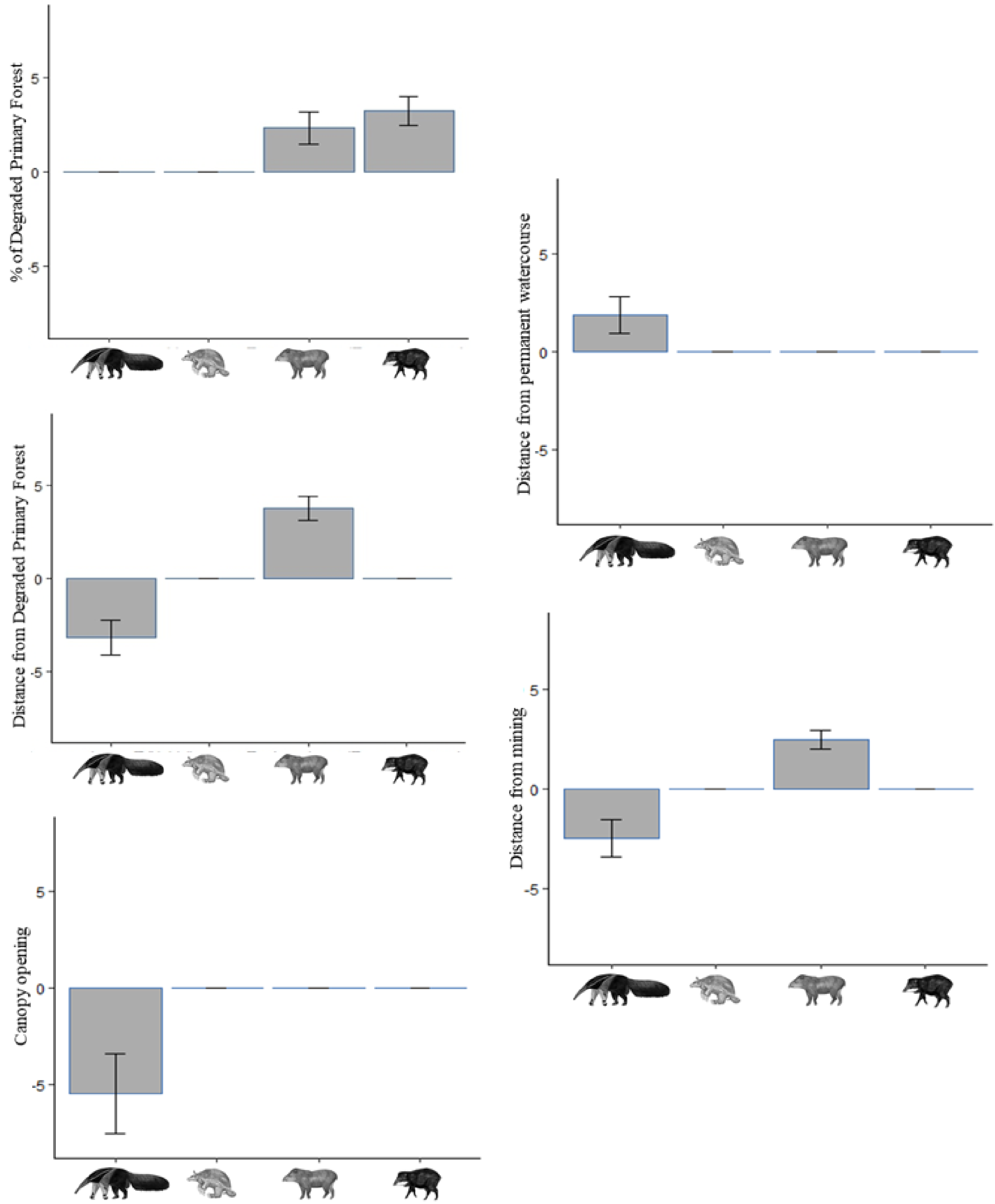

Figure 2: Predictor variables selected by the Mixed Generalized Linear Models and the size of the effect for each species. Detail of the effect size and the influence, positive or negative, of each variable for each species. Variables analyzed: (A) Proportion of degraded primary forest (PF), (B) Distance from the degraded primary forest (DF), (C) Average canopy opening (CO), (D) Distance from permanent watercourses (DW), (E) Distance from the mining (DM). Species analyzed from left to right in the X axes of each plot: *M. tridactyla* (Giant anteater); *P. maximus* (Giant armadillo); *T. terrestris* (Lowland tapir); *T. pecari* (White-lipped peccary).

The PCA results showed that the environmental variables PF, DW and DM are positively related to the habitat of Degraded Primary Forest, while the samples of abandoned pasture and regeneration are more related to the CO and DF (S4 Fig).

Considering the three sampled habitats, in general the species had similar preference for the forested environments and for the regeneration areas, with the exception of *T. pecari*, that was scarcely recorded outside the forested areas (Fig 3 and 4). The species *M. tridactyla* and *P. maximus* seems to avoid the abandoned pasture (Fig 3 and 4), but this is more evident in *M. tridactyla* (Fig 3). However, the place where the abundance of *P. maximus* was highest in the PRAD areas is positioned at the edge of a plateau, where the area presents a large slope (Fig 4). In the case of *T. terrestres*, we recorded a high abundance of this species in the whole area, especially in the regeneration areas, but also at the degraded primary forest (Fig 4). There is no difference on abundance rate of *T. terrestres* between habitats (Fig 3). The abandoned pasture seems to be the less used habitat by the four species studied.

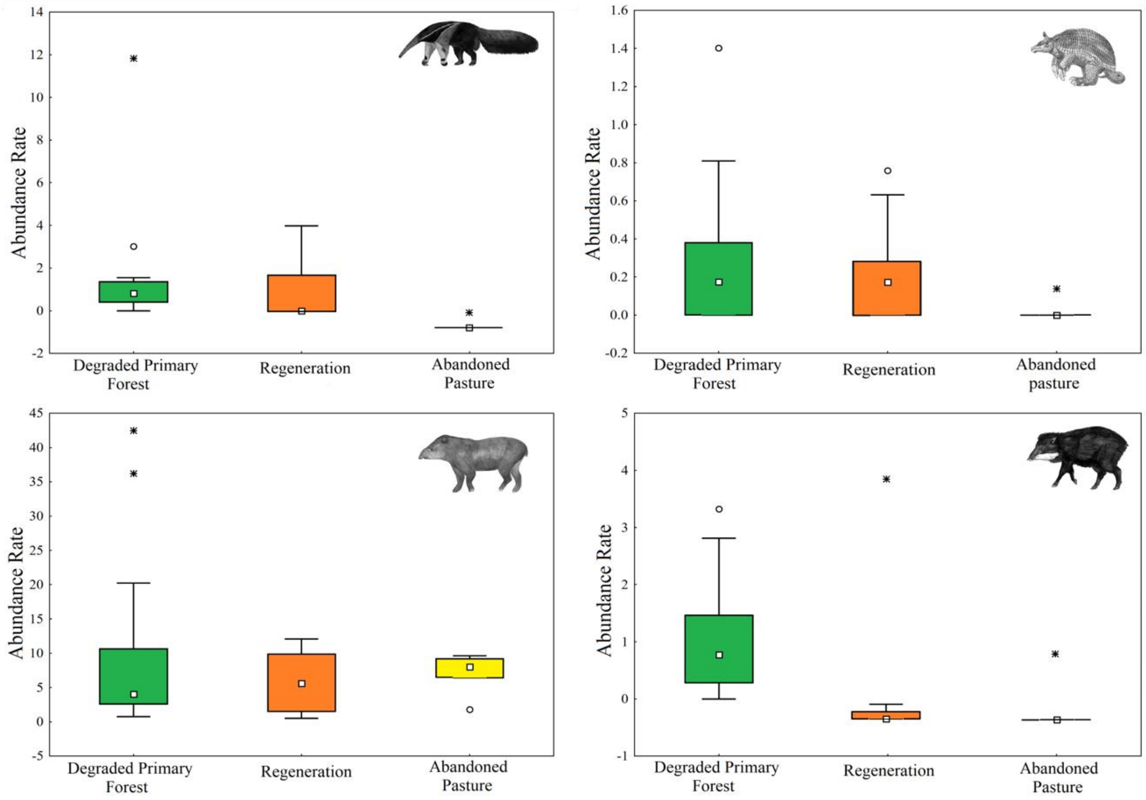

Figure 3: Comparison of the Abundance Rate averages between habitats and its confidence intervals (95% of confidence).

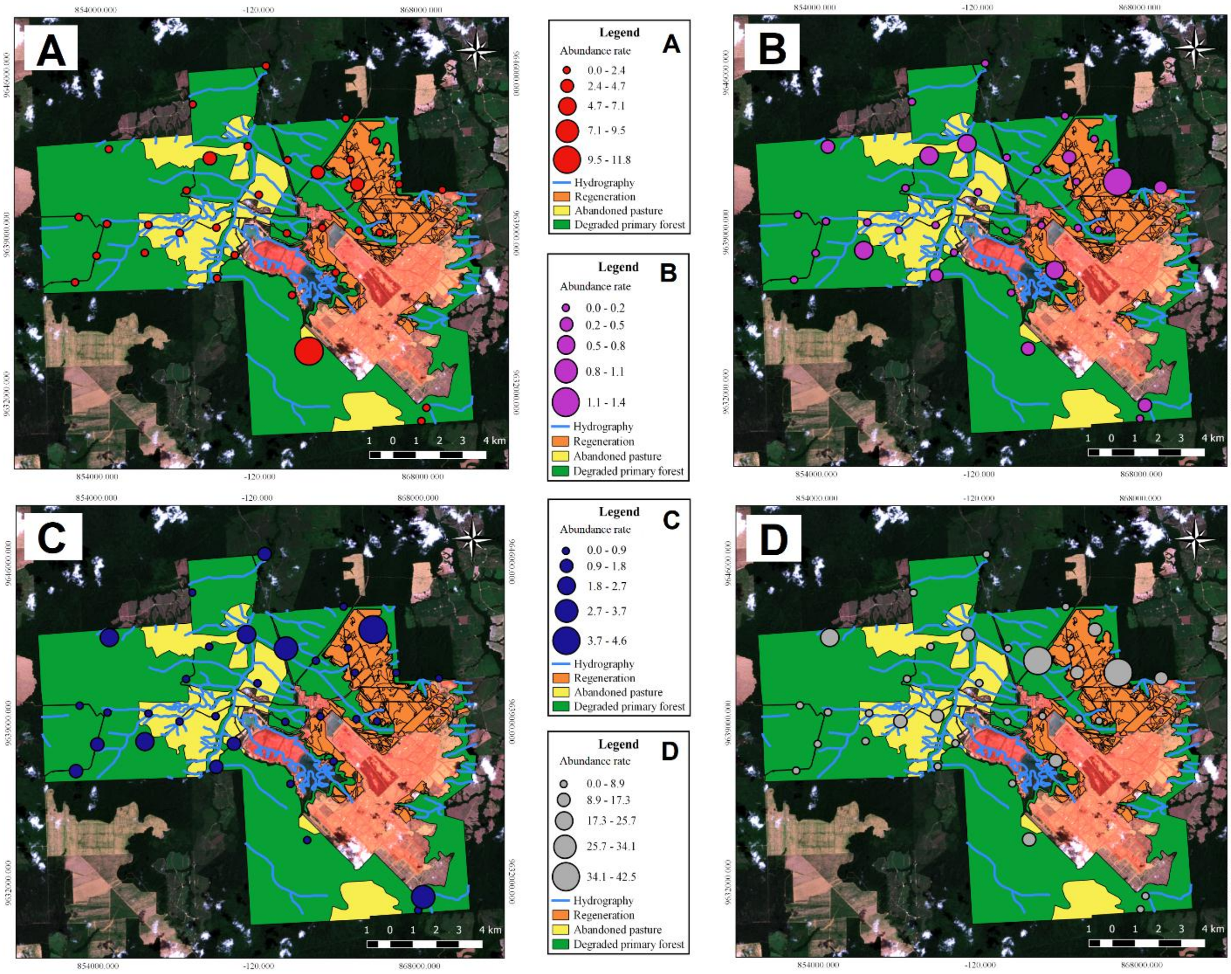

Figure 4: Distribution of each species in the sampled habitat types. (A) *M. tridactyla* (Giant anteater), (B) *P. maximus* (Giant armadillo), (C) *T. terrestris* (Lowland tapir) and (D) *T. pecari* (White-lipped peccary).

Discussion

All four species studied were distributed in all three sampled habitats which suggest that they have some level of tolerance to degradation. However, we observed that the abundance rate of each species in the various habitats was not the same, and the environment variables act in distinct ways on them. This probably will influence the adaptive plasticity of each one different in the long term [9,11].

The *M. tridactyla* was influenced negatively by the DF, DM and CO. This suggests the preference of this species for the edge habitats, that can be defined in this study as open areas, not distant from the mining, but also not distant from the forest. These characteristics reflect the regeneration habitat. This species is often found in forested environments with low density of understory, probably due to its locomotion patterns [50,51]. In addition, *M. tridactyla* is one of the largest ant and termite eaters in the world [52] and because of its restricted and low-calorie diet the species has a slow metabolism with a preference for warm environments [53]. In this study, *M. tridactyla* had preference both for forest environments, as well as by more open areas, represented by the regeneration areas. However, it seemed to avoid the more open areas of abandoned pasture.

In our study the distribution of *P. maximus* was not influenced by any of the measured environmental variables. However, it had a greater abundance in regeneration areas as in degraded primary forest, and less abundance in open areas as abandoned pasture. The *P. maximus* seems to avoid areas with dense understory, as a strategy to facilitate its movement [54, 55]. The *P. maximus* has a diet of ants and termites similar to *M. tridactyla*, but can also feed on other arthropods, carrion and plant material [56, 57]. The sites with the highest number of records of *P. maximus* coincide with the boundary of the bauxite mine plateau area, where the slope of the terrain increases considerably. This species digs burrows in the ground to protect itself from predators and destroys termite and ant mounds to feed [58]. In order to decrease the energy cost of digging they prefer to make burrows in sloped terrain [55]. The species is considered naturally rare in nature [50,59] and in our study was the species with the lowest number of records.

The *T. terrestris* was the species with the highest abundance in all three habitats sampled, indicating that probably has greater ecological plasticity between all four species studied. The large felids *Panthera onca* and *Puma concolor* are distributed in the study area but the tapir seems not to be the preferred prey of these species, due to the high cost of hunting [60,61]. In general, hunting by humans may be the greatest threat to tapirs in the Amazon [62,63]. The hunting activity in the study area seems to be more sportive, practiced with the use of dogs to select some target species, especially deers (*Mazama americana* and *Mazama nemorivaga*) and pacas (*Cuniculus paca*). The lack of predation and hunting and a high abundance of food resources, especially in the regeneration areas, may be the main causes of the high rate of tapirs recorded in the study area [64,65].

The *T. terrestris* was positively influenced by the environmental variables tested, except the DW, which had a negative influence. This species is known to be highly dependent on aquatic environments for regulation of the intestinal tract, thermoregulation, elimination of ectoparasites, and as shelter against predators [66]. In this study we observed a preference for regeneration areas, probably due to high abundance of food resources in these areas. *T. terrestris* is the largest herbivore in South America and feed daily on huge quantities of fallen fruits, leaves, stems and sprouts. Due to the low efficiency of its digestive system for cellulose fermentation, this animal spends a great part of its day feeding [50,67].

Among the four species studied, *T. pecari* seems to be the one with the least preference for degraded environments. The only variable that positively influenced the relative abundance of this species was the PF. Although *T. pecari* is considered omnivorous, feeding on seeds, invertebrates, small vertebrates and larger carcasses, this species has a preference for a frugivorous diet [68]. This type of diet normally is dependent on a high quality habitat [69]. *T. pecari* usually lives in large social groups, ranging from 10 to 300 individuals, but depending on the environmental conditions [70]. Due to a great bite force, these animals are able to feed on hard fruits and beans with medium seeds, about 1-3 cm, which are more common in mature forests than in regeneration areas [71,72].

The environmental changes occurring in the study area due to the bauxite mining fit the concept of HIREC suggested by [10]. HIREC may alter interspecific and intraspecific interactions, leading to reduced species richness, behavioral changes, or spatiotemporal conditions [10,73-75] These changes may favor new evolutionary responses to HIREC in the long term [76,77]. The study area has been undergoing profound changes in its vegetation cover, with several economic cycles occurring in the last 60 years [24]. These changes can be considered to have led to "novel" or "emerging" ecosystems [10,11], to which the terrestrial Amazonian mastofauna is adapting.

However, taking our results as examples of the "ecological trap" phenomenon [11,12] may be premature since we did not measure the fitness changes of the species over time. But the positive influence of anthropogenically altered habitats on species abundances in this study can be considered as a potential indication of this phenomenon. In this case, regeneration areas could be considered "ecological trap" [11,12] for at least three of the four species studied, *M. tridactyla*, *P. maximus, and T. terrestris*.

In spite of the tolerance of the species studied to the degraded habitats and the ability to occupy regeneration areas, with the exception of *P. maximus*, the distribution of the other species *M. tridactyla*, *T. terrestris* and *T. pecari* were all positively influenced by forested environments. We observed that the occurrence of the species in the degraded areas depends on the presence of the forested areas. This study reinforces that, in regions of high anthropogenic pressure, as is the case in the northeastern Brazilian Amazon, all forest remnants, whether degraded or secondary, at different levels of degradation, are important for the survival of endangered mammal species [8,78,79].

Acknowledgments

We are thankful to the Biodiversity Research Consortium Brazil-Norway (BRC) for logistic and technical support to this Research Project. To Hydro Paragominas Company for its economic, logistic support and for the construction of the location map of the area. We thank MPEG Dr. Fernando Carvalho Filho for the illustrations of the animals in the graphics. IMAZON by the shapes provided for extraction of environmental variables.

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Supporting Information

S1 Table. Variables Collected in Field or through Satellite Image. Environmental and anthropogenic variables measured at sampling points.

	Variables		Unalised	Minimum	Maximum
1	Proportion of the area covered by water		No	0	0.19
2	Proportion of deforestation area		No	0	3.0
3	Proportion of degraded primary forest	(FD)	Yes	0	3.14
4	Proportion of riparian area		No	0	0.06
5	Proportion of riparian area		No	0	2.36
6	Proportion of riparian area		No	0	62
7	Distance from degraded primary forest (m)	(DF)	Yes	0	1695
8	Depth of litter (cm)		No	0.2	7.8
9	Number of standing dead trees		No	1	49
10	Number of fallen dead trees		No	0	42
11	Proportion of trees with DAP < 55 cm		No	86.2	100
12	Proportion of trees with DAP > 55 cm		No	0	13.8
13	Canopy height (m)		No	3	34.2
14	Proportion of trees with lianas		No	18.03	96.2
15	Average canopy opening	(AD)	Yes	24.1	82.3

16	Distance to permanent watercourse (m)	(DA)	Yes	8	3770
17	Distance to productive area (m)	(DP)	No	10	4050
18	Distance to burned area (m)		No	335	11850
19	Sub-surface opening ratio		No	41.7	71.5
20	Distance to mining area (m)		Yes	231	8045
21	Minimum distance to trail /road (m)		No	13	1500

S2 Table. Models Created for Analysis and Selection of Models by AICc. Models used in GLMM Analysis.

Models	**Predictor variables**
Modelo 1	PF+DF+CO+DW+DM
Modelo 2	PF+DF+CO+DW
Modelo 3	PF+DF+CO
Modelo 4	PF+DF
Modelo 5	PF
Modelo 6	DF
Modelo 7	CO
Modelo 8	DW
Modelo 9	DM

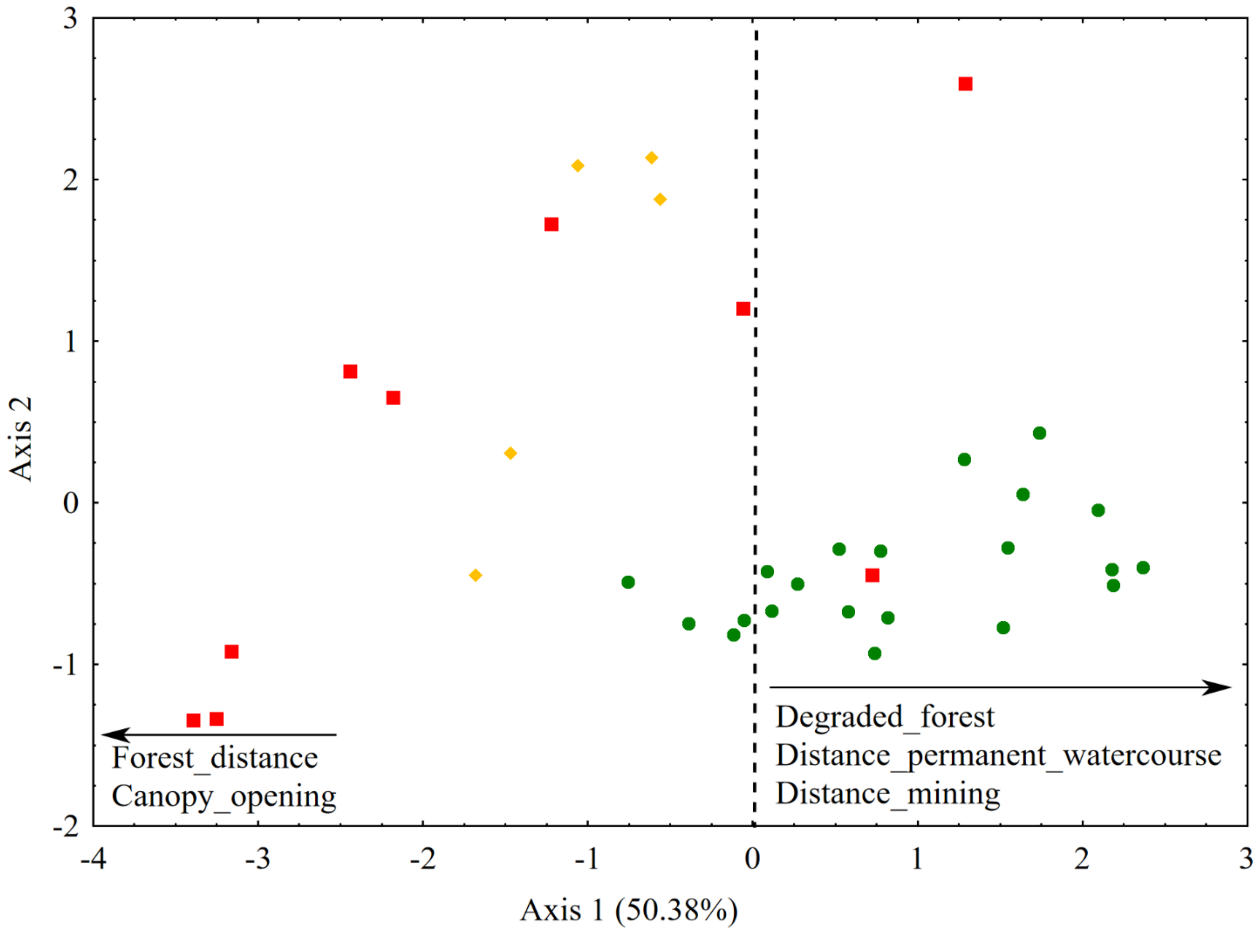
S3 Table. Selection of models through the AICc.

Model	*M. tridactyla*		
	AICc	dAICc	df
Model 1	211.4	0.0	7
Model 2	215.8	4.4	6
Model 3	220.2	8.9	5
Model 8	221.1	9.7	3
Model 4	227.0	15.6	4
Model 7	227.3	15.9	3
Model 6	228.4	17.0	3
Model 0	228.7	17.4	2
Model 9	230.0	18.7	3
Model 5	230.6	19.2	3
Model	*P. maximus*		
	AICc	dAICc	df
Model 7	107.9	0.0	3
Model 0	108.6	0.7	2
Model 9	110.1	2.2	3
Model 8	110.8	2.9	3
Model 5	110.9	3.0	3
Model 6	110.9	3.0	3
Model 3	112.7	4.8	5
Model 4	113.5	5.6	4
Model 1	115.2	7.3	7

Model 2	115.4	7.5	6
Modelo	*T. terrestris*		
	AICc	dAICc	df
Model 1	352.6	0.0	7
Model 2	379.5	26.9	6
Model 3	394.1	41.5	5
Model 4	400.0	47.4	4
Model 9	435.3	82.7	3
Model 8	449.9	97.3	3
Model 5	465.2	112.6	3
Model 0	468.4	115.8	2
Model 7	470.2	117.6	3
Model 6	470.8	118.2	3
Model	*T. pecari*		
	AICc	dAICc	df
Model 5	180.4	0.0	3
Model 2	180.5	0.1	6
Model 4	182.8	2.4	4
Model 1	183.7	3.3	7
Model 3	185.0	4.6	5
Model 9	191.1	10.7	3
Model 6	191.3	10.9	3
Model 0	207.7	27.2	2

Model 7	209.0	28.6	3
Model 8	209.8	29.4	3

S4 Fig. PCA results showed that the environmental variables PF, DW and DM are positively related to the habitat of Degraded Primary Forest, while the samples of abandoned pasture and regeneration are more related to the CO and DF.



S4 Rules for publication in the journal Plos One

Related information for authors

- Submission system
- Journal scope and publication criteria
- Getting started guide
- Guidelines for revisions
- Publication fees

- Chinese translation of PLOS policies: PLOS

Style and Format

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Manuscript files can be in the following formats: DOC, DOCX, or RTF. Microsoft Word documents should not be locked or protected.

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Define abbreviations upon first appearance in the text.

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Avoid using MathType, Equation Editor, or the Insert→Equation function to insert single variables (e.g., “$a^2 + b^2= c^2$”), Greek or other symbols (e.g., β, Δ, or ′ [prime]), or mathematical operators (e.g., x, ≥, or ±) in running text. Wherever possible, insert single symbols as normal text with the correct Unicode (hex) values.

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Use correct and established nomenclature wherever possible.

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These sections may all be separate, or may be combined to create a mixed Results/Discussion section (commonly labeled “Results and Discussion”) or a mixed Discussion/Conclusions section (commonly labeled “Discussion”). These sections may be further divided into subsections, each with a concise subheading, as appropriate. These sections have no word limit, but the language should be clear and concise.

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Source	**Format**
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Accepted, unpublished articles	Same as published articles, but substitute "Forthcoming" for page numbers or DOI.
Online articles	Huynen MMTE, Martens P, Hilderlink HBM. The health impacts of globalisation: a conceptual framework. Global Health. 2005;1: 14. Available from: http://www.globalizationandhealth.com/content/1/1/14
Books	Bates B. Bargaining for life: A social history of tuberculosis. 1st ed. Philadelphia: University of Pennsylvania Press; 1992.

Book chapters	Hansen B. New York City epidemics and history for the public. In: Harden VA, Risse GB, editors. AIDS and the historian. Bethesda: National Institutes of Health; 1991. pp. 21-28.
Deposited articles (preprints, e-prints, or arXiv)	Krick T, Shub DA, Verstraete N, Ferreiro DU, Alonso LG, Shub M, et al. Amino acid metabolism conflicts with protein diversity; 1991. Preprint. Available from: arXiv:1403.3301v1. Cited 17 March 2014.
Published media (print or online newspapers and magazine articles)	Fountain H. For Already Vulnerable Penguins, Study Finds Climate Change Is Another Danger. The New York Times. 29 Jan 2014. Available from: http://www.nytimes.com/2014/01/30/science/earth/climate-change-taking-toll-on-penguins-study-finds.html Cited 17 March 2014.
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Databases and repositories (Figshare, arXiv)	Roberts SB. QPX Genome Browser Feature Tracks; 2013 [cited 2013 Oct 5]. Database: figshare [Internet]. Available from: http://figshare.com/articles/QPX_Genome_Browser_Feature_Tracks/701214
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- Entrez Gene
- FlyBase
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- Mouse Genome Database (MGD)
- Online Mendelian Inheritance in Man (OMIM)
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