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**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA**

**Fertilidade do solo como principal preditor da abundância de  
mamíferos herbívoros em ilhas fluviais do Rio Negro, Amazônia**

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**Banca examinadora da defesa oral pública**

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**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA**

**ATA DA DEFESA PÚBLICA DA  
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Aos 28 dias do mês de junho do ano de 2018, às 09h00min, na Sala de aula do LBA, Campus II, INPA/ALEIXO. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Orlando Ferreira Cruz Junior**, do Instituto Nacional de Pesquisas da Amazônia – INPA, o(a) Prof(a). Dr(a). **Mario Eric Cohn Haft**, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). **Sonia Sena Alfaia**, do Instituto Nacional de Pesquisas da Amazônia – INPA, tendo como suplentes o(a) Prof(a). Dr(a). Newton Paulo de Souza Falcão, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). Juliana Schietti de Almeida, do Instituto Nacional de Pesquisas da Amazônia – INPA, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO de GILSON DE SOUZA FERREIRA NETO**, intitulado: **“FERTILIDADE DO SOLO COMO PRINCIPAL PROPULSOR DA ABUNDÂNCIA DE MAMÍFEROS HERBÍVOROS EM ILHAS FLUVIAIS DO RIO NEGRO, AMAZÔNIA”**, orientado(a) pelo(a) Prof(a) Adrian Paul Ashton Barnett, do Instituto Nacional de Pesquisas da Amazônia - INPA e Coorientado(a) pelo(a) Prof(a). Dr(a). Wilson Roberto Spironelo, do Instituto Nacional de Pesquisas da Amazônia – INPA.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

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### Sinopse:

Avaliamos como variáveis ambientais e antrópicas influenciaram a abundância de mamíferos não voadores em ilhas fluviais. Esperávamos que solos mais férteis comportariam maior abundância de mamíferos e também que a distância do ponto amostral a comunidade humana mais próxima, área basal de árvores e área florestada da ilha tivessem um efeito positivo sobre a abundância, enquanto que corte de madeira e distância do ponto amostral a terra firme mais próxima, tivessem um efeito negativo. Nossos registros foram dominados pela espécie onívora *Didelphis marsupialis* a qual esteve presente em 60% dos registros totais de mamíferos. Logo, para a abundância total e proporção de generalistas onívoros na assembléia, não houve efeito das variáveis ambientais e antrópicas. No entanto, ao considerar somente os mamíferos herbívoros, a fertilidade do solo tem o efeito mais forte e positivo.

**Palavras-chave:** variáveis ambientais, variáveis antrópicas, *Didelphis marsupialis*.

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## Resumo

Os principais mecanismos que regulam a distribuição das espécies em ilhas fluviais são pouco conhecidos. Entender como os ciclos biogeoquímicos afetam a biosfera é um fator-chave para a compreensão do funcionamento dos ecossistemas. Na Amazônia, em uma escala regional, poucos estudos investigaram como a fertilidade do solo pode influenciar a abundância de mamíferos. Estudos prévios têm demonstrado que os mamíferos herbívoros podem ser indiretamente influenciados pela fertilidade do solo por meio de maior investimento das plantas em frutos e maior qualidade nutricional de folhas e frutos. A maioria desses estudos compararam extremos de gradientes ambientais (terra-firme e várzea e Amazônia sentido leste-oeste). Neste trabalho objetivamos investigar como a variação pequena de nutrientes encontrada nos solos, e adicionalmente outros aspectos da paisagem e fatores antrópicos, em ilhas fluviais, podem afetar as assembleias de mamíferos. A nossa expectativa era de que a fertilidade do solo, área basal de árvores, área florestada e distância do ponto de amostragem para a comunidade humana mais próxima influenciassem positivamente, enquanto que a exploração madeireira nestes ambientes e distância do ponto de amostragem a áreas de terra firme influenciassem negativamente a abundância total de mamíferos e proporção de herbívoros. Ainda, para espécies generalistas e onívoras estas relações seriam nulas. Os dados de abundância relativa das espécies de mamíferos foram estimados utilizando 49 armadilhas fotográficas espaçadas cerca de 2km umas das outras no arquipélago, as quais operaram 24 horas durante 60 dias de amostragem. As relações entre as variáveis preditoras e a abundância relativa foram investigadas por uma série de modelos lineares generalizados (GLM). A espécie onívora *Didelphis marsupialis* contabilizou 60% dos registros totais de mamíferos. Nenhuma das variáveis preditoras, tanto ambientais quanto antrópicas foram capazes de explicar a abundância total de indivíduos e a proporção de *Didelphis marsupialis* na assembleia. Por outro lado, ao considerar somente as espécies herbívoras nas análises, a fertilidade do solo foi a variável explicativa com o maior poder preditivo e influenciou positivamente a proporção de mamíferos herbívoros. Os resultados deste trabalho indicam que a fertilidade do solo, em ilhas fluviais que recebem diferentes aportes de nutrientes, afeta de forma diferencial a proporção de indivíduos dentro de grandes agrupamentos taxonômicos, como os mamíferos terrestres.

## Abstract

The key factors driving species distribution within fluvial island systems worldwide are poorly known. Previous studies have shown that herbivore abundance and proportion in the mammal assemblage can be indirectly influenced by soil fertility via production of nutritious fruits and leaves and higher ecosystem dynamics linked to vegetation growth on more productive soils. The goal of this study was to investigate which environmental (soil fertility, tree basal area, forest cover and distance from sampling point to nearest mainland) and anthropogenic factors (logging, distance from the sampling point to nearest human community) were most closely-linked to observed patterns of mammalian abundance and proportions of omnivorous and herbivorous mammals on fluvial islands of the Rio Negro, Amazonas State, Brazil. Several of these islands are located on the left bank of the river, and so receive nutrient-rich sediments from the Rio Branco. We expected that our chosen environmental and anthropogenic factors could predict island mammalian abundance patterns. We used camera traps to examine this, surveying 49 sampling sites across 60 days when water levels were seasonally low. We calculated the proportion of herbivorous and omnivorous mammals per site, and assayed their relationships to predictor variables with a series of generalized linear models (GLM). As expected, the number of records was low on all studied fluvial islands, compared with upland terra-firme studies. In 70,560 sampling hours we obtained 126 independent camera trap records, for a total of 11 mammal species. Total mammal abundance and proportion of the generalist omnivore *Didelphis marsupialis* was not affected by our chosen environmental and anthropic variables. However, soil fertility played a central role in determining the proportion of herbivorous species. Thus, gradients of soil fertility can help to explain herbivore distributions on riverine islands, and define crucial areas for conservation and future restoration. Additionally, logging, distance to the nearest human community and to the mainland had a positive effect, and forest cover a negative effect, on the proportion of herbivorous mammals, but did not affect generalist omnivorous species. Therefore, results suggest that island soil fertility can differentially impact proportions of mammals from the same feeding guild.

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## **Introdução geral**

A fertilidade do solo é considerada um fator chave que regula a produtividade primária e a qualidade de recursos disponíveis [1]. Os nutrientes do solo se movem através da cadeia trófica provendo recursos para as plantas e, conseqüentemente, para os demais organismos, dentre estes os mamíferos [2]. A fertilidade do solo afeta a biosfera, e esta os ciclos biogeoquímicos e o funcionamento do ecossistema [2]. Por exemplo, a diminuição da diversidade de mamíferos pode influenciar o ciclo de nutrientes no ecossistema modificando processos como decomposição, dispersão de sementes e deposição de fezes [3,4]. Logo, algumas florestas defaunadas são incapazes de retomar a ciclagem de nutrientes, devido à ausência ou diminuição desses processos ecológicos [5]. Apesar que fatores ecossistêmicos sejam considerados métricas úteis para estimar a capacidade de suporte, através da produtividade primária [6], os mecanismos que relacionam a fertilidade do solo com a assembleia de mamíferos continuam pouco investigados em regiões neotropicais.

A disponibilidade de recursos pode ter um efeito diferenciado em espécies da mesma ordem, por apresentarem diferentes demandas de dieta [7]. Por exemplo, na Polônia, florestas mais produtivas em solos mais férteis mostraram um aumento acentuado da proporção de espécies e indivíduos de pequenos mamíferos herbívoros, enquanto insetívoros responderam menos intensamente a produtividade florestal [7]. Isso porque, recursos da planta são mais abundantes e diversos em florestas mais produtivas afetando mais diretamente os mamíferos herbívoros do que os insetívoros [7]. Em uma escala continental, estes padrões também são observados em relação a influência da fertilidade do solo sobre a distribuição de mamíferos [8]. A variação na distribuição biogeográfica entre mamíferos com diferentes histórias de vida e ecologia está relacionada com estratégias de forrageamento, competição, área de vida e dieta [8]. Plantas sob solos mais férteis tem em média menos compostos secundários [15]. Por isso, é sugerido que mamíferos herbívoros de menor porte são geralmente mais abundantes em solos mais férteis por serem menos resistentes a altos níveis de compostos secundários [8]. O contrário sendo verdadeiro para as espécies de maior porte, que por serem melhores

competidores e mais resistentes a estes compostos, são mais comumente encontrados em solos mais pobres [8]. Alguns outros trabalhos também corroboram esta relação entre a fertilidade do solo com a abundância e composição de diferentes grupos de mamíferos em outros continentes, eg: marsupiais folívoros na Austrália [9]; elefantes na África[10] e ungulados na América do Norte[11] e África[12].

Na Amazônia, existe um gradiente de fertilidade, com solos mais férteis na parte oeste e mais pobres na direção leste devido aos diferentes processos pedogênicos responsáveis pela formação da bacia [13,14]. Isto se reflete nos organismos, como as plantas que nestas áreas mais férteis investem mais em reprodução do que em fotossíntese ou produção de raízes, e conseqüentemente terão menor área basal de árvores [13]. Todavia, folhas mais nutritivas [15] e com maior investimento em frutos [16]. Esse processo implica em variação na disponibilidade de alimento para diferentes grupos de mamíferos [2,18]. Isso porque solos mais férteis são geralmente associados com maior capacidade do ecossistema [19]. Por tais motivos, a fertilidade do solo pode ser considerada então um excelente preditor para a resiliência e densidade populacional de diversos grupos de mamíferos na Amazônia como ungulados [19], pequenos mamíferos [20] e primatas [21]. Apesar de vários estudos terem investigado os mecanismos que controlam a abundância de mamíferos na Amazônia [2,20,21], poucos tiveram como foco ilhas fluviais [22]. A distribuição das espécies em ambientes fluviais é regulada também não somente pela fertilidade do solo, tornando-se importante desta forma avalia-láem conjunto com variáveis locais ou de paisagem, a exemplo da distância da terra firme e área florestada, que são importantes preditores da ocorrência de mamíferos [26].

O solo das ilhas fluviais recebem um constante suprimento de materiais suspensos no solo que são completamente alagados pela maior parte do ano. As características dos vários rios amazônicos é um dos fatores que explicam a diferença regional em termos de fertilidade do solo e produtividade [27]. Florestas inundadas recebem muitos sedimentos advindos de água branca e são denominados várzeas, enquanto as florestas alagadas por água preta e clara são chamados de igapós [23]. O Rio Branco é um importante contribuinte de íons em solução dissolvidos nas águas do Baixo Rio Negro [23]. Anavilhanas e Jaú estão localizados na Amazônia Central e são hidroquimicamente influenciados

pelo Rio Branco, em sua maioria na margem esquerda contrastando com a quantidade de nutrientes do Rio Negro e do Rio Branco [30]. Apesar de ser considerado um rio de água branca, o Rio Branco tem uma quantidade intermediária de íons orgânicos, maior do que o presente em rios de água preta, mas menor do que rios com origem andina, como o Madeira, Purus e Amazonas [23]. Logo, um grande número de espécies de plantas em Anavilhanas também ocorrem em áreas de várzea [27]. Como resultado, a produtividade diferencial de regiões alagadas pode favorecer a colonização de algumas espécies devido à diferença de espécies de plantas nas florestas alagadas e suprimento de alimento [24].

Além dos fatores ambientais, a ação antrópica também pode ser determinante para a distribuição espacial e abundância de mamíferos [24]. Alguns grupos de mamíferos como primatas, ungulados e felinos evitam lugares próximos de comunidades humanas [34] devido a atividades como caça, extração de madeira e desmatamento [35]. Mesmo com tais impactos, há indícios de que a assembleia de mamíferos é mais resiliente em solos mais férteis devido à maior produtividade florestal [19]. No entanto, espécies onívoras como o *Didelphis marsupialis*, parecem ser indiferentes a tais distúrbios [36]. Os mamíferos onívoros podem mudar a dieta, e se alimentar inclusive de recursos antropogênicos em áreas degradadas porque eles podem forragear em diferentes habitats, e por isso podem ocorrer mesmo em áreas com baixa produtividade primária [37]. Portanto, devido aos requerimentos ecológicos básicos de cada espécie, o distúrbio humano afeta as espécies de modo diferencial [33].

Neste estudo avaliamos o efeito da fertilidade do solo, área basal, cobertura florestal, distância do ponto amostral a terra firme mais próxima, exploração madeireira e distância do ponto amostral a comunidade mais próxima sobre a abundância e proporção de mamíferos, em ilhas fluviais localizadas na Amazônia Central. Os resultados esperados são apresentados por meio de um fluxograma, onde as setas azuis e vermelhas representam relações positivas e negativas, respectivamente. (Fig. 1).

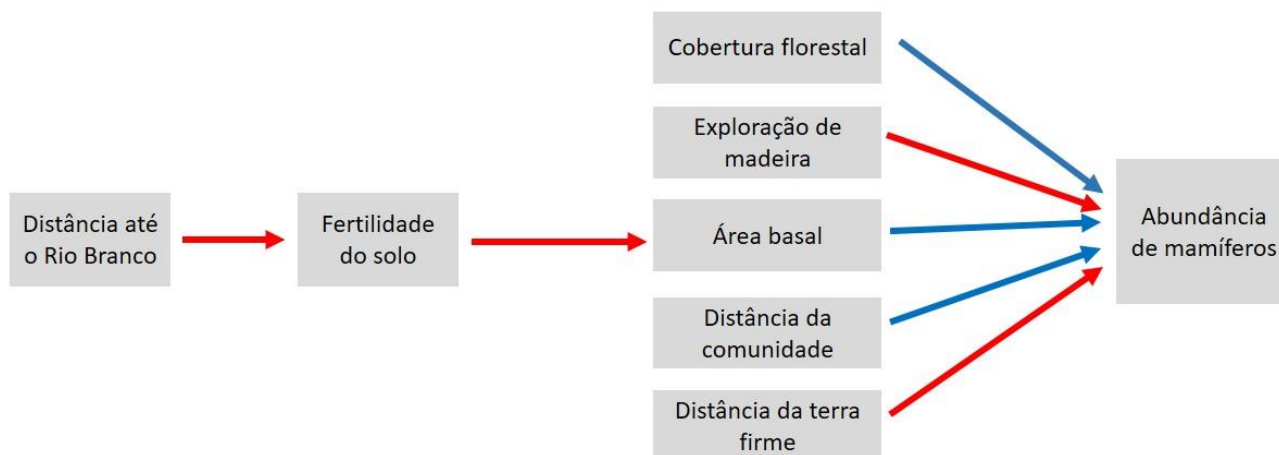


Figura 1. Fluxograma do efeito esperado de cada variável explicativa sobre a abundância relativa de mamíferos.

## Objetivo geral

1. Avaliar como a abundância relativa e a proporção de mamíferos onívoros e herbívoros varia em relação às variáveis ambientais e antrópicas.

Especificamente, nós testamos duas hipóteses:

- i. A abundância de mamíferos varia de acordo com as variáveis ambientais e antrópicas. Espera-se que a fertilidade do solo, área florestada, área basal e distância do ponto amostral à comunidade ribeirinha mais próxima tenham um efeito positivo na abundância de mamíferos, enquanto exploração madeireira e distância do ponto amostral à terra firme tenham um efeito negativo.
- ii. A proporção das espécies de mamíferos onívoros e herbívoros varia em relação a variáveis ambientais e antrópicas. Espera-se que a fertilidade do solo, área florestada, área basal e distância do ponto amostral à comunidade mais próxima apresentem uma relação positiva na proporção de herbívoros, enquanto distância do ponto amostral a terra firme mais próxima e exploração madeireira tenham uma relação negativa. Ademais, espera-se que a proporção de espécies onívoros seja indiferente as variáveis mensuradas.

**Soil fertility as the key driver of herbivorous mammal abundance on Amazonian fluvial islands. Manuscrito submetido ao periódico PLoSOne**

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## Abstract

When inundated, seasonally-flooded forests in Amazonia receive constant nutrient-input from water-deposited sediments, so that different areas will receive different levels of nutrients. Previous studies have shown that mammals can be indirectly affected by soil fertility via food source nutritional quality. To follow-up such studies, we investigated the effect of soil fertility, tree basal area, forest cover, distance of sampling points to nearest mainland, distance of sampling points to nearest human community and logging, on the mammalian assemblage on central Amazonian fluvial islands of varying soil fertility. Relationships between predictor variables and mammalian abundance and proportions were investigated with a series of generalized linear models (GLM). We collected species data using 49 camera traps which were operated 24 hours a day for 60 days. A total of 11 species of mammals were recorded and their relative abundance could not be predicted by any of the variables considered. However, our records were dominated by the omnivorous generalist species *Didelphis marsupialis*, which accounted for 60% of all mammal records. The proportion of generalist omnivorous appeared not to be affected by the predictive factors. However, when considering only records for proportion of herbivorous mammals, soil fertility was the measured variable with the strongest positive effect on their proportional representation in the mammalian assemblage. The proportion of herbivorous mammals also responded positively to sampling point distance to nearest human community, logging and sampling point distance to nearest mainland, while forest cover responded negatively. Therefore, results suggest that island soil fertility can differentially impact proportions of mammals from the same feeding guild.

**Key words:** environmental and anthropogenic factors, camera trap, *Didelphis marsupialis*, proportion of herbivorous and omnivores.

## Introduction

Soil fertility is considered a key control of primary productivity and quality of food sources[1]. The higher concentration of nutrients in more fertile soils provide resources for plants and consequently for other organisms, such as mammals[2]. Not only do soil factors play an important role in the mammalian assemblage, but the mammalian assemblage can also affect the biogeochemical cycles and forest functioning [3]. Edaphic factors control forest functioning and dynamics, in turn affecting the assemblage and abundance of fauna species. This relationship is bidirectional, so that changes in mammalian abundance have been observed to alter the forest's nutrient cycles, through reduction of processes such as frugivory, herbivory and deposition of feces [3,4]. Some defaunated forests degrade in soil fertility through time due to the lack of faeces and decomposing bodies pulsing nutrients into their systems[5]. Despite primary productivity providing a useful metric for estimating the ecosystem carrying capacity, such as the number of individuals [6], the ecological and biogeochemical implications of soil fertility on mammal assemblage structure remains poorly investigated.

Resource availability may have different impacts on species in same taxonomic group, but differing diets [7]. Forest productivity has been observed to directly affect herbivorous rodents diversity while insectivores (shrews) responded weakly to changes in forest productivity [7]. Soil fertility has also been reported as influencing mammalian distributions at the continental scale [8]. The explanation for this lies with nutritional status and plant abundance which can, in turn, impact competition, home range and diet of herbivorous mammals. It is widely considered that plants growing on poorer soils have higher levels of

secondary compounds, and larger mammals are more likely to deal better with toxins and therefore be more tolerant of poorer soils, while small mammals are more commonly abundant in areas with lower species plant abundance, but only if plants have higher nutritive quality [8]. Studies have corroborated the relationship between soil fertility and both assemblage composition and individual abundance of mammals on several continents, including marsupials in Australia [9]; elephants in Africa [10] and ungulate mammals in Africa [11] and North America [12].

In the Amazon Basin, there is a soil fertility gradient from southwestern (more fertile) to Central Amazonia (poorer soils) as a result of a variety of pedogenic processes [13,14]. On more fertile soils plants invest more in reproduction than in secondary compounds or root production [13]. Individually, this results in leaves with higher nutrient content [15], greater investment in fruit yields [16], and lower tree basal area. High fertility soils are younger and these soils are not as well developed physically, so that is why there is more disturbance (mortality) since the trees cannot hold themselves (physically bad soils). The trees there are usually fast growing (high productivity) since there are ample nutrients but they grow with lower biomass. On the poor fertile soils it's the opposite. They grow slow (little nutrients, low nutrient release) but with high biomass and there is less disturbance (mortality) since the soils has a good physical structure [13, 17]. This has consequences for consumer communities, such as mammals [2,18]. As a result, soil fertility is a powerful predictor of density of different groups of mammals in the Amazon, including ungulates [19] and small mammals [20]. Primate biomass is also affected [21], since more fertile soils are usually associated with higher ecosystem carrying capacity [19], so that soil

fertility is an important factor when considering conservation actions. However, while several studies have investigated the regulators of mammalian abundance in the Amazon [2,20,21], very few have focused on fluvial islands [22]. These vary in soil fertility as a result of difference in sediment loading from the rivers that inundate them [23].

Flooded forest contain few habitat-specific mammal species, and the species compositions are essentially simplified versions of those in the adjacent terra firme, which do not receive nutrients via seasonal floods [24]. For riverine islands, annual flooding means that their terrestrial mammalian assemblages are recreated every year, so that there are far fewer residents mammals compared to terra firme [25]. For example, in Amanã and Mamirauá, Central Amazonia, terra firme has nearly twice the number of mammal species than várzea [25]. In Amazonia mammalian colonization of riverine islands is greatly assisted by the widespread ability of the fauna to swim [26].

Amazon fluvial islands receive a near-constant supply of fluvially-suspended material as their soils are entirely flooded for most of the year. The geological and geomorphological processes control the characteristics of the various rivers in the Amazonian Basin explaining the differences in regional soil fertility and productivity which in turn affect the ecosystems and they flood [27]. As a result of their Andean origins, sediment loads can be 90 times higher on whitewater rivers than on nutrient-poor black water systems, which are derived from the ancient cratons of the Guyana and Brazilian shields [28]. As a consequence of variation in the amount of received organic ions and sediments, flooded forests inundated by sediment-rich white water (termed várzeas) grow on fertile soils, while those inundated by sediment-poor black and clear-water rivers

(called igapós) have poorer soils[29]. For example, the Rio Branco has an intermediate amount of organic ions, greater than present in black-water rivers such as the Rio Negro, but less than those in rivers of Andean origin like Madeira, Purus, Juruá and Solimões [23]. Where such systems meet, there may be substantial nutrient transfer from the more sediment rich systems to the poorer. For example, the Rio Branco, though less nutrient-rich than the Solimoes and other Andean-derived rivers, is, nevertheless a major contributor to the soluble ion load of the lower Rio Negro [23].

Anavilhanas Archipelago and Jaú national parks are both located in the Rio Negro Basin, central Amazonia. Here they are hydrochemically influenced by the Rio Branco, especially the islands on the northern side of the river, where the nutrient input from the Rio Branco is greatest [30]. As a result, the Rio Branco creates a natural gradient on soil fertility and differential productivity of flooded regions can favour the colonization of some species due to different tree species in the flooded forest and supply of food sources [24]. This is illustrated by the number of riverine plant species at Anavilhanas that otherwise only occur in areas of várzea, as such species require higher nutrient inputs than occur in neighboring areas under the influence of nutrient-poor black-waters [23].

Successful dispersion depends not only on the ability of individuals of a species to move between sites, but also on landscape attributes, such as matrix quality, which may impede locomotion or increase mortality [31]. Consequently, soil fertility, together with local or landscape variables, such as distance to nearest mainland and land mass area, should be important predictors of mammalian assemblage on inland islands, affecting both mammalian dispersal and habitat use on fluvial islands [26].

In addition to edaphic controls, anthropogenic actions may also influence the spatial distribution and abundance of some mammal species [33]. In Central Amazonia, some groups of mammals such as primates, felids and ungulates avoid locations close to human communities [34] due to activities such as hunting and logging [35]. Even with such impacts, there are indicators that mammalian assemblages are more likely to be able to withstand human hunting pressures on more fertile soils than lower fertility ones due to higher forest productivity [19]. For instance, even with increase of anthropogenic activities, the recovery of some groups of mammals can be more rapid on more fertile soils than on less fertile ones, which allow both larger populations and quicker population recovery, likely due to greater availability of more nutritious foods [19]. Additionally, human disturbance does not impact all species equally, with some generalist omnivorous species, such as *Didelphis marsupialis*, being either resilient to anthropogenic disturbances [18], or able to exploit anthropic environments [36]. Omnivorous mammals can switch to other diet items such as anthropogenic food and trash. Additionally, because omnivorous mammals can forage in many habitats, they can occur even in extreme environments with low primary productivity [37].

We investigated the relationships between soil fertility and mammalian assemblage composition on fluvial islands in the Rio Negro. We also analysed other environmental (forest cover, tree basal area, sampling point to the nearest mainland site) and anthropogenic (distance from the human community and logging) variables in order to test their effect on observed mammalian assemblage. We hypothesized that the variation in soil fertility would be the main factor moderating the proportion and abundance of non-volant mammals through the availability of food sources. Specifically, we expected that: (i) soil fertility,

forest cover, tree basal area and distance from the nearest human community increase the abundance of mammals, while distance from the sampling point to the nearest mainland site and logging would decrease the relative abundance of mammals; (ii) Herbivorous species will respond positively to soil fertility, human community distance, forest cover, tree basal area and negatively to distance from the sampling point to the nearest mainland and logging, while generalist omnivorous species will not be influenced (in terms of proportion in the assemblage) by such factors.

## **Methods**

### **Ethics Statement**

The study was conducted with permits IBAMA/ SISBIO 55180-1 and 59367-1 issued to Gilson de Souza Ferreira Neto by the Chico Mendes Institute for Biodiversity Conservation (ICMBio). The study was non-invasive and involved no direct contact or sampling of living animals.

### **Study area**

The study was carried out on 28 fluvial islands in the Rio Negro within two protected areas in central Amazonian Brazil — Anavilhanas National Park and Jaú National Park. Both conservation units are part of the Lower Rio Negro Mosaic and are administered by the Chico Mendes Institute (ICMBio-MMA, Brazil) (Figure 1). The total area investigated covers approximately 60,000 hectares (02.454089° S, 060.961982° W). Area of individual islands investigated ranged from 50 to 11,000 hectares, and the proximity of the camera location to the nearest mainland ranged from 0.24 to 8.74 km.

Some 100 traditional human communities occur in Anavilhanas, Jaú National Park and other immediately adjacent areas [38]. Although both areas are conservation units, illegal extraction of high value commercial timber occurs frequently [39]. Even though the human communities occur at low densities, there is a long history of hunting in the area now gazetted as Anavilhanas and Jaú national parks[38].

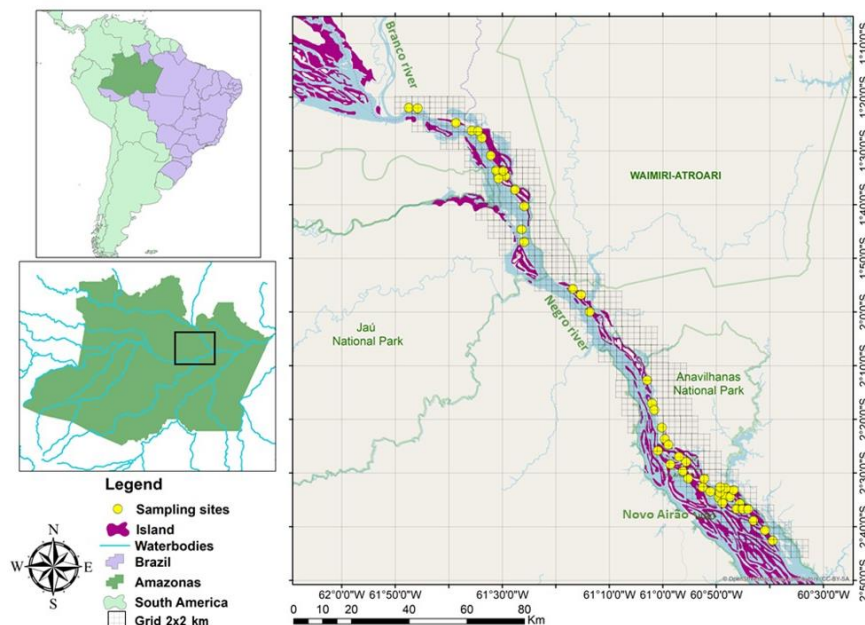


Figure 1. Location of study sites (Anavilhanas and Jaú national parks) in the lower Rio Negro Basin, Amazonian Brazil. Yellow points indicate locations of camera traps sampling points. Data for predictive variables were also collected at these locations.

At the study sites, the annual flood pulse (the rise and fall of the water level on the rivers) is both seasonal and gradual [40]. The floodwaters reach their peak in May, and the forest floor is generally dry between June and October [38]. Thus flooding is off-set from local seasonal rainfall patterns which include a short dry season from June to October, and a rainy season from November to May [38].



During peak flooding, all local fluvial islands are completely inundated, often to a depth of several meters [40], so temporarily transforming terrestrial environments into aquatic ones [41]. Annual regional average precipitation is 3000 mm, with average monthly temperature of 25°C [38].

The sampled fluvial islands are alluvial, and were created by increased sediment load, as a result of both precipitation and sediment supply in the Rio Branco basin having increased over the last 15,000 years [42]. As a result, while both Anavilhanas and Jaú overlay the Cretaceous Alter do Chão Formation [43], they have contrasting geomorphological characteristics: while fluvial islands of Jaú National Park is characterized by a narrow alluvial plain with small and elongated islands, Anavilhanas National Park has much wider channels [43].

The variation in soil fertility is not only associated with the temporal-spatial transport of sediments from the Rio Branco River, but also to island age [44] and elevation. The age of the islands in Anavilhanas may differ from centuries to more than 18,000 years, so that there are soils with varied and distinct degrees of leaching (loss of water-soluble plant nutrients from the soil), origin of the sediment (substrate age, degree of weathering) and therefore differences in soil fertility [44]. Elevation, determine flood duration and hence the degree of leaching and new inputs river sediments [42]. The geological characteristics of poor black water systems in central Amazonia can also greatly affect plants diversity, so that, older geological formations (usually less fertile soils) are associated with lower alpha-diversity of woody plants [45]. The combination of age and substrate elevation of the islands can influence soil characteristics, since older soils may be more leached and impoverished [42].

## **Sampling design**

Following QGIS development methodology [47], we created a virtual grid with 2 x 2 km spacing to layout sampling locations (Fig.1). In the current study we placed single camera traps at 49 points, which also served as the reference point for subsequent collection of predictive variables. All camera traps were installed when islands were not flooded. To avoid bias in the species capture rates, camera traps were not baited [46]. To minimize spatial pseudoreplication cameras were spaced at least 1.85 km from each other, and then located camera traps as close as logistically possible to grid intercept points on non-flooded islands. We used satellite images from GeoEye in Google Earth to define which islands were generally influenced by the Rio Branco waters based on the color of the river water. As a result, the majority of the islands lay on the northern sector of the archipelago, towards the left bank of the Rio Negro [23] (Figure 1). The number of sampling points did not always correspond to the size of the island since they were not chosen a priori.

## **Mammalian data**

We surveyed for mammals with 49 camera traps operating continually for 24 hours-a-day across 60 days from August to November 2017. Terrestrial and scansorial mammal species were recorded by two digital camera traps types (35ReconyxHyperfire HC600 and 14Reconyx RM45 Rapidfire) deployed at 30 to 40 cm above the ground and operating continually for 24 hours-a-day across 60 days from August to November 2017. All photos of the same species on the same camera taken within 30 minutes of each other were considered as a single independent record or if individuals could be told-apart by natural marks[48].

Abundance was assumed to be the total number of records, per sampling point. For group-living species, we considered each individual register in a photo as one individual record. Small mammal species recorded by the camera traps were identified with the help of field guides [47,49], and confirmed by their geographical range and reinforced by experienced specialists for the region.

### **Environmental and anthropogenic variables**

We sampled the local variables (soil fertility, tree basal area) in the plot of 0.1 hectare (10 × 100m) around each camera trap. Soil sampling was carried out between August and September, 2017. Using a Dutch auger we collected soil samples from 10 sites spaced 10 m apart within the sample plot. Soil was collected to a depth of 0 to 20 cm, after leaf litter removal. In the field we combined all 10 samples to derive an average value per plot. We prevented the volatilization of inorganic nitrogen - ammonium ( $\text{NH}_4^+$ ) and nitrate ( $\text{NO}_3^-$ ) by storing the sample in a styrofoam box in the field before transferring to freezing conditions of the ICMBio base in Novo Airão (Figure 1). Time between collection and freezing was never more than 48 hours [50]. Chemical analysis was carried out at the Thematic Laboratory of Soils and Plants at the National Institute of Amazonian Research (INPA), with soils refrozen upon arrival in the laboratory to avoid volatilization.

Preparation of extracts for inorganic nitrogen analysis was done using 20 grams of soil and 40 millimeter of Potassium sulfate ( $\text{K}_2\text{SO}_4$ ) at 0.5 molar in falcon tubes, with centrifugation at 200 revolutions per minute for 15 minutes. Extracts were then decanted for 30 minutes and filtered and frozen for further analysis of N-inorganic contents.  $\text{NH}_4^+$  (ammonium) and  $\text{NO}_3^-$  (nitrate) were determined by

colorimetry, using a Shimadzu Spectrophotometer (UV mini 1240). The N analysis were not over dried. For the other soil analyses, each soil sample was oven dried at 65°C, and particles smaller than 2 millimeters were removed [51].

All soil variables are given in Appendix S1.

The following soil characteristics were obtained:

Soil pH in water: determined using 10 grams of fine soil in 25 milliliters H<sub>2</sub>O for 1 minute with a mechanical stirrer. A pH reading was taken after the mixture had settled for 1 minute rest using a pH meter [50].

Na, K, Ca, Mg, Al: determined with the Thiourea and Silver Nitrate method (Ag-TU), cationic extraction in 0.01M Ag-TU solution, stirred together with the sample, where the complete cation exchange is achieved [51].

Sum of bases: NA, K, Ca, Mg [50].

Cation exchange capacity was calculated from the equation:  $E_{cec} = (\text{Sum Of Bases} + \text{Hydrogen} + \text{Aluminum})$  [52].

Total phosphorus and total cations: soil was passed through the digestion process through sulfuric acid. Then, 0.25 grams of soil were added to 5 milliliters of distilled water and left to settle overnight. The following day, 5 milliliters of H<sub>2</sub>SO<sub>4</sub> was added until reaching the temperature of 360°C, whereupon 0.5 milliliters of hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) was added. This process was repeated 10 times. Total phosphorus reading was done by colorimetry in a Shimadzu Spectrophotometer, while total cations were read with atomic absorption via Flame Atomic Absorption Spectrometry (FAAS)[53].

Organic phosphorus (Po) and Inorganic phosphorus (Pi): were extracted with NaHCO<sub>3</sub>(Sodium Bicarbonate)[54].

Soil grain size profiling: 10 grams of fine soil pre-treated with physical and chemical dispersants was used. Then, we separated silt percentage, which was calculated from the difference between the total weight of sand and clay [55].

To provide information on standing biomass we measured tree basal area. Tree basal area was calculated by measuring the diameter at breast height (DBH) of all live trees  $> 10$  cm in the study plot, and then we summed the basal area of all trees, which was calculated using the circle area ( $\pi \cdot r^2$ ).

We considered the percentage of forest within a 1000-meter buffer around the camera trap as a measure of forest cover at landscape level which was separated into forest and non-forest areas into three class (forest, waterbodies and open areas). Previous studies have successfully used a 1000-m buffer to predict small [56] and medium-large sized mammals [57]. Furthermore, this circle size decreased overlap between the circumferences of forested areas, minimizing spatial dependencies among samples.

To quantify the extent of logging, the area in the immediate vicinity of the camera trap was surveyed on foot to identify signs of logging, with the help of field assistants who lived in the study region. We considered noises, physical signs of logging activity (such as fallen wood) and the registered passage of loggers carrying timber and timber cutting equipment in the camera trap records as evidence of logging (Figure 2). We only considered the evidence and absence of logging at each sampling point (camera trap).



Figure 2. Loggers carrying logging equipments in the left and and stumps and sawn wood (right).

The forest cover and linear geographic distance from the camera point to the nearest neighbouring mainland forest site and the nearest traditional human community were obtained using the QGIS program [47], and images from Google Earth and Landsat TM 7 and TIRS 8.

## Data analysis

We first tested for spatial correlation via the `ncf` function `correlogram` package[58]. This preliminary analysis showed no spatial correlation between the sampling units (Appendix S2). Due to low number of records, we opted for generalized linear models (GLM) for proportion and abundance of mammals. Correlation between predictor variables was tested using a Spearman multiple correlation function chart. Correlation with the Performance Analytics package [59] with a cut off of 0.5[60], retaining only weakly correlated variables. We also tested for multicollinearity between the model variables using variation inflation factors (VIF) less than 3 [60]. Since all other soil variables were found to be highly correlated with sum of bases (Appendix S3), we excluded them, and opted to use

only sum of bases as an index of soil fertility, taking into account that it is one of the main drivers of forest dynamics in terms of productivity, tree mortality, turnover rates, soil fertility and a better measure of cation availability [13] and its relation with mammals [21]. We derived seven predictor variables that were not correlated to each other (Spearman  $r < 0.50$ ) (tree basal area, distance from the sampling point to the nearest mainland, forest cover, sum of bases, distance from the sampling point to the nearest community and logging). For range, mean and standard deviation of all predictive variables see S4 Appendix, and for their values and units of measurement see S5 Appendix.

Due to overdispersion of count data, we used a generalized linear model (GLM) with the negative binomial distribution to adjust the variance independently of the mean. In order to investigate the effects of the predictive environmental and anthropogenic variables on mammalian abundance, we opted to use all the scansorial and terrestrial records (Appendix S6).

To test the second hypothesis, we considered only the relative abundance of *D. marsupialis* and five species of herbivorous (*Cuniculus paca*, *Hydrochoerus hydrochoerus*, *Mazama americana*, *Pecari tajacu* and *Proechimys* sp.) per sampling point per total of all records to account for proportion of omnivorous and herbivorous species, respectively (Appendix S6). We defined herbivorous mammals as those with a plant-based diet, including grains, nuts, seeds, legumes, leaves and fruits, while we considered as generalist omnivores, those mammals able to feed on both plant and animal matter. We obtained information on primary diet, order, common names and locomotion [61] (Appendix S6). We did not include either insectivorous, or carnivorous species, and excluded two omnivorous species (*Philander opossum* and *Nasua nasua*) due to the very low

number of records. We fitted GLM with the binomial error distribution, as the data was proportional.

To avoid overfitting, we created 10 models with three to five predictor variables per model. The same models were used both for relative abundance and proportion, first and second hypothesis, respectively. For model selection, we used the Akaike Information Criterion [62] corrected for small sample sizes [63] using the MuMIn package [64]. For model uncertainty in multimodel inference, we used a model-averaging approach as this is considered more robust than the stepwise approach that emphasizes only the best model [65]. We considered only the most plausible models (i.e. those with  $\Delta < 4$ ) [66] for model averaging. The sum of Akaike weights was considered to assure the relative importance of each variable in the model [67]. All statistical analyzes were performed in Software R version 3.4.3 [68].

## Results

We obtained 126 records of non-volant mammals encompassing 11 species, providing a total of 70,560 hours of sampling. From this total, there were 83 records from only one species, *Didelphis marsupialis*. Also, other species were target organisms for this study including herbivorous (5 species = 22 records), omnivores (3 species = 89 records), carnivores (2 species = 4 records) and insectivores (1 species = 11 records) (Appendix S6). We were unable to identify the *Proechimys* sp. to species level from obtained photographs. We obtained an average of 5.56 independent records per camera trap, with a standard deviation of 5.07.



Contrary to our first hypothesis, none of the derived predictor variables could predict total mammalian abundance better than the null model. For generalist omnivorous species (*D. marsupialis*), the null model was the most parsimonious, again the only one with a  $\Delta$ - of less than 4 (Appendix S8). However, for the proportion of herbivorous mammals in the total mammal assemblage, the sum of bases and forest cover had significant positive effects (Figure 3 and figure 4A) on the proportion of herbivorous, followed by community distance, mainland distance and logging (S1 Table). Therefore, our chosen environmental factors were more important as anthropogenic variables for predicting the proportion of herbivorous.

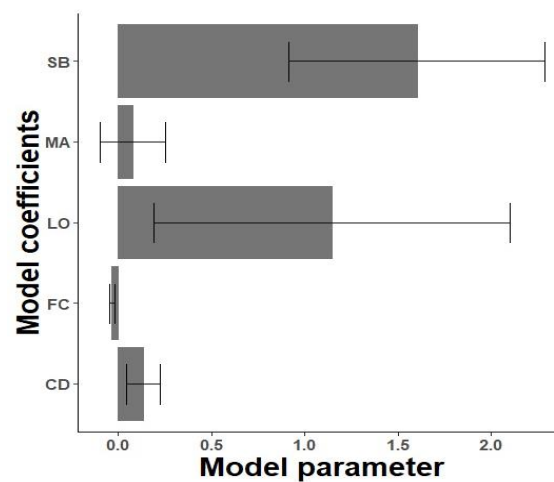


Figure 3. Mean coefficients (standard pattern) for the predictor variables of the most parsimonious models for proportion of herbivorous mammals. SB-Sum of bases; MA-Distance from the sampling point to the nearest mainland; LO-Logging; FC- Forest cover; CD- Community distance.

Table S1. Best models selected by the model selection (Akaike Criteria) with  $\Delta$ -  
 $<4$  for predicting proportions of herbivorous species. CD: Community distance;  
 Distance to nearest mainland- MA; SB: Sum of bases; LO: Logging; FC: Forest  
 cover.  $\Delta$ AIC = difference between the best model (with zero value) and the others  
 (lower numbers indicate the best model), wAIC = strength of evidence in favor of  
 each of the models (higher numbers indicate the best model).

<b>Model</b>	<b><math>\Delta</math>AIC</b>	<b>wAIC</b>
Model structure: SB + FC + CD	0.00	0.53
Model structure: SB + FC + MA	1.92	0.20
Model structure: SB + FC + MA + CD	2.47	0.15
Model structure: SB + FC + MA + LO	3.01	0.11
<b>Environmental and anthropic factors</b>	<b>Sum of Akaike weights</b>	
Soil fertility	0.99	
Forest cover	0.99	
Human community distance	0.68	
Mailanddistance	0.46	
Logging	0.11	

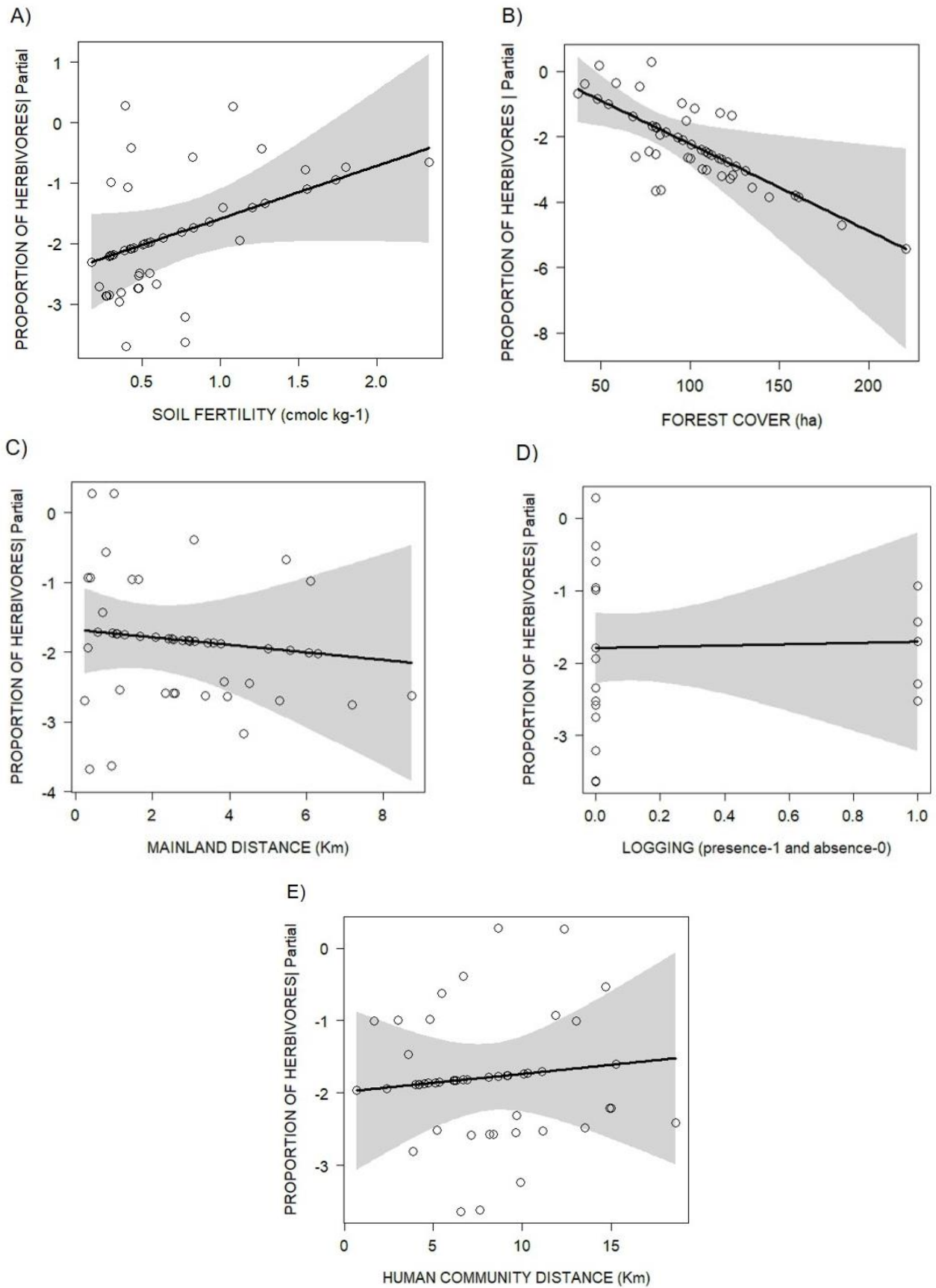


Figure 4. Graphs showing proportion of herbivorous abundance in relation by the measured environmental and anthropogenic predictors.

## Discussion

We found that different groups of mammals responded in different ways by the measured environmental and anthropogenic factors. Our results show that none of the analysed environmental and anthropogenic factors were good predictors of either mammal abundance or proportion of *D. marsupialis*. However, our results suggests that only species that are completely dependent on plant material were affected by soil fertility. Consistent with our expectation, fertile soils were characterized by a higher proportion of mammals with plant-based diets in the total community, as shown in Figure 4A. The proportion of herbivorous mammals increased linearly with soil fertility suggesting that only species which are completely dependent on plant material were affected by soil fertility. We believe that such variation in herbivorous mammals occurrence may be explained by foliar nutritional quality [69] and fruit investment [16]. One possible explanation is that plants invest less in anti-herbivory defence when nutrients are plentiful [15]. In the generally nutrient-poor study area, plants are known to invest heavily in antiherbivory-defense such as tannins and other phenolic compounds, which in turn is considered to reduce carrying capacity for different organisms [29]. In addition, our measured environmental factors were better predictors than anthropogenic factors for the proportion of the total assemblage by herbivorous mammals.

In contrast to our expectations, we found that none of the considered environmental and anthropogenic variables could explain the total mammalian abundance nor the proportion of *D. marsupialis*, the most abundant species in our list of records. This could be since our records were dominated by the generalist omnivorous species *D. marsupialis*, which accounted for 60% of all

records. The lack of predictability for this species can be explained by the fact that *D. marsupialis* is one of the most common mammal species found in the neotropics and it is extremely adaptable, with noted ability to adjust its diet to reflect local resource profiles [49]. Indeed, as has been demonstrated in a highly degraded agricultural area in Colombia, *D. marsupialis* can tolerate extremely high levels of human impact [36]. We also acknowledge the possibility that because *D. marsupialis* is considered a scansorial mammal [61] it may well ascend into the trees when the flood waters come. Thus, while most terrestrial species will be wiped out every time the island is inundated, this marsupial may not be and it could therefore breed and build up substantial populations that colonize from above every season, rather than colonize from the size as must all those species that arrive by walking or swimming. The characteristics of the Amazon mammal's species to survive such as dispersal ability, their population sizes and home range greatly affects how they manage to survive post island inundation[26].

Soil fertility can have different effects on the same taxonomic group, as mammals. Generalist omnivorous mammals can base their diet on other food sources, and not only plant material. For the generalist omnivorous species considered in this study: the diet of *D. marsupialis* is not composed mainly of plant matter, rather it is composed largely of invertebrates and vertebrates items. The species can feed even on anthropic refuse [70]. Besides this, *D. marsupialis* is also a low ranked species in terms of hunted bushmeat preference [71]. Therefore, our data suggests that this generalist omnivorous species were unlikely to be impacted by the measured environmental and anthropogenic components in this study.

Soil fertility varies greatly within the Amazon basin [13]. In the entire Amazon basin, the variation of soil fertility ranges from 1 to 90 mmolc/kg-1, from southwestern (more fertile) to east and central Amazonia (poorer soils), which greatly affects forest functioning and structure in the Amazon [17]. For the current study, we found a variation of 1.8 to 23.3 mmolc/kg-1 in terms of sum of bases (Appendix S10), being 3 to 50 times lower than values reported for the most fertile Amazonian soils [28]. The variation in soil fertility in the study area is distributed in a non-random manner so that, more fertile soils in terms of total phosphorus, sum of bases, ammonium and cation exchange capacity are closer to the mouth of the Rio Branco River (Appendix S10). Such soils would be classified as very low to medium fertility within Central Amazonas [28]. We speculate that the variation in soil fertility in the studied fluvial islands may alter the functioning of the islands.

We would expect that only species occur on the islands who would be sufficiently generalist to adapt to the prevailing conditions of poor soils and low plant diversity once they have arrived on the island. We believe that this explanation is consistent with our findings, since most records were dominated by only one species, *D. marsupialis*. In addition to being good survivors, such species often have high population densities, which also increases the chance that they will arrive on the islands (an event which must occur annually for terrestrial species). Such factors are more important because the total, or near-total, inundation of many islands each year means that the strictly terrestrial mammal species must colonize the islands every year from the mainland. Hence, high-disperser, generalist species (equivalent to the tramp species of classical

island biogeography), are those most likely to be found in such annually-perturbed systems [72].

In the Amazon, patch and landscape factors in some cases can act as barriers for mammalian colonization and ability to persist [48]. Such considerations are also consistent with our findings for proportion of herbivorous since distance from the sampling point to the nearest mainland has a small positive effect on the proportion of herbivorous mammals. In contrast to our expectations, forest cover had a negative effect on the proportion of herbivorous mammals and it was present in all the most parsimonious models. In this study, herbivorous mammals prefer non forested areas, and we speculate that this result can be attributed to the capacity of mammals to traverse the aquatic matrix by swimming, so visiting several land masses [26]. We also speculate that these results can be attributed to the fact that some mammals may prefer open areas instead of forest. For example, the spiny rat *Proechimys* sp. are known to be the only small mammal species to inhabit open areas in very arid environments such as the Caatinga in Brazil, [73], so that some species of *Proechimys* sp. prefers non forest areas (open areas, for example), instead of forest areas.

We expected that tree basal area would have a positive effect on the proportion of herbivorous. However, tree basal area had no effect on the proportion of mammals with plant-based diet, and did not appear in any of the best models for the proportion of herbivorous. Although tree basal area is widely considered as a metric of habitat quality and also an indicator of fruiting production [74], our much smaller scale and fluvial islands study area may have been not able to detect any effect on herbivorous mammals, so that we suggest in future studies that forest productivity should be assessed with other variables.

We expected that our chosen anthropogenic factors would have a negative impact on the proportion of herbivorous. Yet in contrast to our expectations, logging had a positive effect on the proportion of plant-based diet mammals. This could be because for a short period after trees are cut, the soil fertility may increase because when the canopy is open as an effect of logging, there is an increase in pionerring plant species with younger tissues that generally have fewer secondary compounds [75], but we do not think so because this variation in soil fertility usually occurs at a larger scale [28], and differs from that found here at the smaller, regional, scale; so that logging had little effect on the proportion of herbivorous mammals in the partial graph (Figure 5e). In relation to human community distance, we corroborated our expectation, since there is a small positive effect of human community distance on the proportion of herbivorous mammals. This may be due because mammals are influenced by human presence due to greater chance of hunting [34] including deer, peccaries and capybaras. Hunting may even be surprisingly high and underestimated for terrestrial frugivores such as (*C.paca*, as well as smaller terrestrial rodents [76]).

## Conclusion

We have shown in this study how soil fertility impacts species differently in the same taxonomic group, as different species of terrestrial mammals. While the most abundant species, an omnivore *D. marsupialis* seems to be unaffected as its diet and behavior allow it to persist in fluvial islands, herbivorous mammals are strongly positively related with soil fertility likely due to the direct affect of nutritional status of plants on their survival and performance. Other related variables, as human community distance and logging were less relevant for herbivorous



mammal occurrence, while forest cover and mainland distance had a negative effect.

Even though the study area is considered generally nutrient-poor, our results indicate that observed variation in soil fertility is sufficient to result in different levels of favorability for nutritional levels of foliage and therefore mammals, given that the soil fertility was the major predictor for the proportion of herbivorous in this study. Clearly, soil fertility plays an important role in the ecosystem and consequently on the proportion and distribution of mammals, but, in addition to considering the mechanisms by which this happens, more studies are required that study how effects operate at different scales.

This will allow investigations of the ecological and biogeochemical processes involved. Such links can be clarified by evaluating the forest productivity across several years in areas with different levels of soil fertility, while simultaneously monitoring different groups of mammals and/or other vertebrates. For herbivorous, the linkage between soil fertility, ecosystem and trophic composition of mammal assemblages can be investigated via the specific diet of each mammalian group. For other groups such as omnivorous, carnivorous and insectivorous mammals we suggest studies that include other sites, as “Terra-firme”, for a longer period including other methods such as linear transect and mammalian footprints, which could complement the data. Since fluvial islands are flooded for most of the year, they are a natural laboratory where new studies could advance.

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## Author Contributions

Conception and design of experiments: GSF, AAB, WRS, FBB and ALG. Implementation of experiments: GSF. Data analysis: GSF, FBB, ALG. Contributed reagents/materials/analysis tools: GSF, CAQ, WRS. Wrote the paper: GSF, AAB, FBB, WRS.

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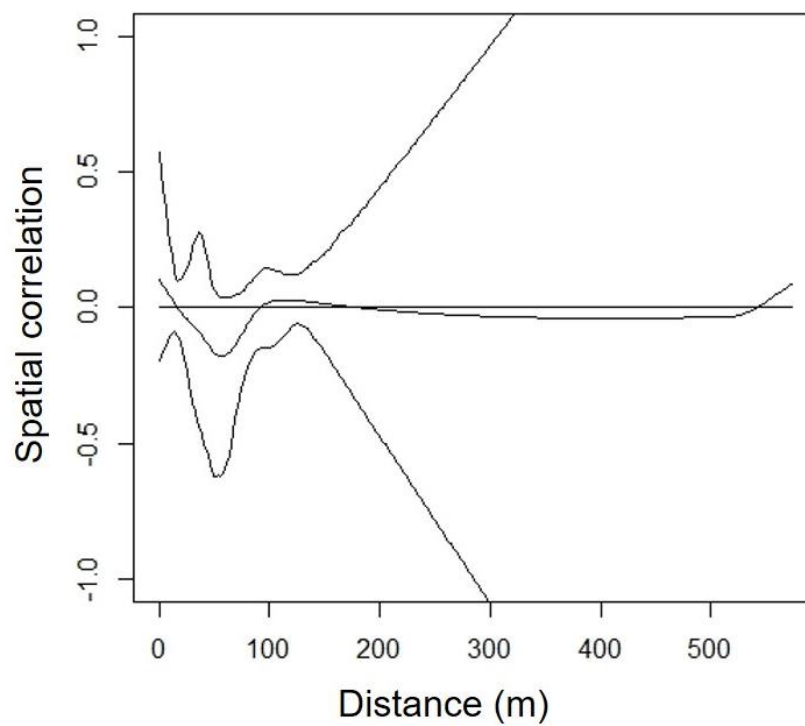
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**Appendix S1.** Descriptive statistic of chemical attributes of the soil of the fluvial islands of the Rio Negro, Amazonas State, Brazil.

		pH	Na	K	Ca	Mg	Al	O.P	I.P	T.P	Ca	Mg	K	Na	Al	TRB	NO3-	NH4+	SB	ECEC
X	Y	H2O	cmoc/kg					mg/kg			cmolc/kg						ug/g		cmolc/kg	
S 01.36634°	W 061.79113°	5.00	0.146	0.03	0.74	0.63	0.110	86.33	44.42	549.77	3.77	5.60	5.72	0.97	175.64	16.07	6.00	39.46	1.546	1.656
S 01.245660°	W 061.404618°	4.70	0.127	0.03	0.33	0.53	0.404	56.72	63.30	431.89	3.47	5.76	5.68	1.08	153.78	15.99	5.02	30.48	1.018	1.422
S.01.43701°	W061.59555°	4.60	0.092	0.01	0.15	0.29	0.368	57.02	49.59	360.97	7.74	10.53	9.52	2.16	220.62	29.95	3.63	40.08	0.540	0.908
S 01.41285	W 061.64458°	4.69	0.166	0.04	0.77	0.83	0.333	43.02	30.59	449.14	5.55	15.80	13.74	3.27	376.89	38.36	3.87	45.33	1.803	2.137
S01.45911°	W061.56334°	5.19	0.169	0.02	0.39	0.70	0.348	24.78	20.25	272.80	4.95	13.17	12.02	2.64	258.31	32.78	0.71	42.08	1.288	1.636
S 01.49382 °	W 061.54341°	5.11	0.142	0.03	0.13	0.29	0.439	42.48	25.94	221.04	3.35	7.57	8.25	3.06	159.11	22.23	7.72	87.75	0.591	1.030
S 01.51433°	W 061.53587°	5.04	0.123	0.03	0.07	0.15	0.467	44.18	54.47	333.17	2.48	6.91	6.17	1.50	129.96	17.06	2.45	39.89	0.367	0.834
S 01.57869°	W061.49066°	5.09	0.113	0.06	0.68	0.89	0.356	50.56	25.99	443.39	3.95	13.50	14.97	5.01	276.27	37.43	3.72	108.36	1.737	2.094
S 01.56088°	W 061.51875°	5.07	0.097	0.02	0.10	0.22	0.521	46.71	44.52	402.18	2.87	6.91	8.29	1.84	111.11	19.92	0.64	41.80	0.433	0.954
S 01.58602°	W 061.51136°	5.18	0.144	0.03	0.21	0.44	0.458	35.68	32.60	312.09	7.35	14.49	15.67	3.90	228.44	41.40	0.77	38.39	0.828	1.286
S.01.62100°	W 061.46025°	5.34	0.138	0.02	0.50	0.55	0.383	30.22	28.64	330.30	2.48	6.75	7.79	1.39	81.51	18.41	8.02	52.98	1.204	1.588
S 01.67150°	W 061.43144°	5.01	0.123	0.03	0.18	0.30	0.468	52.64	62.16	443.39	4.15	18.11	23.84	5.15	243.02	51.24	0.95	76.53	0.634	1.101
S 01.74363°	W 061.43983°	4.82	0.129	0.02	0.10	0.28	0.463	24.93	12.74	210.50	5.15	15.47	19.61	5.08	180.44	45.31	0.64	48.81	0.520	0.983
S 01.78268°	W 061.43177°	5.15	0.118	0.01	0.04	0.14	0.336	27.15	29.24	142.45	1.96	8.89	10.38	5.22	60.09	26.44	0.71	49.76	0.307	0.643
S 01.92844°	W 061.28011°	4.76	0.18	0.03	0.33	0.58	0.535	24.99	16.75	386.84	1.36	20.08	37.85	5.22	307.73	64.50	5.49	53.67	1.126	1.661
S 01.946 75°	W 061.25460°	4.58	0.124	0.03	0.10	0.30	0.685	35.80	18.20	313.05	1.16	18.11	38.87	4.38	271.29	62.52	4.45	47.32	0.554	1.239
S 01.99961°	W 061.22744°	5.15	0.105	0.02	0.25	0.38	0.321	34.82	25.44	238.29	5.35	16.79	21.46	5.22	132.27	48.81	3.84	62.13	0.755	1.076
S.01.43832°	W 061.57518 °	5.46	0.205	0.05	1.09	0.99	0.000	39.41	35.38	428.06	3.57	10.86	17.95	3.30	118.22	35.69	11.16	36.72	2.336	2.336
S 01.56173°	W 061.49700°	4.84	0.278	0.05	0.40	0.83	0.399	47.20	17.45	381.10	0.78	7.41	20.87	2.78	123.56	31.84	2.82	47.95	1.558	1.957
S 02.21201°	W 061.04876°	4.85	0.151	0.05	0.10	0.48	0.733	18.53	8.77	272.80	-0.32	8.72	18.46	8.45	137.69	35.32	0.58	19.70	0.776	1.510
S 02.28439°	W 061.03330°	4.80	0.125	0.03	0.07	0.27	0.458	22.68	7.67	206.67	1.18	9.38	11.75	3.27	58.84	25.58	2.42	36.44	0.485	0.943
S 02.30480°	W 061.02628°	4.77	0.057	0.02	0.08	0.24	0.310	22.38	17.02	224.87	1.58	8.23	11.79	3.48	52.36	25.08	1.63	22.40	0.400	0.711
S 02.35905°	W 061.00290°	5.03	0.104	0.02	0.26	0.54	0.218	10.52	6.71	175.03	2.08	8.89	11.55	2.82	67.73	25.33	2.08	31.25	0.934	1.151
S 02.39415°	W 060.99394°	5.21	0.112	0.04	0.31	0.62	0.213	10.76	9.77	202.83	2.28	10.86	16.56	2.96	97.69	32.66	1.43	38.77	1.082	1.295
S 02.41246°	W 060.98243°	4.70	0.079	0.03	0.07	0.22	0.513	18.44	8.18	247.88	1.58	10.21	18.21	2.99	96.53	32.98	2.06	39.42	0.396	0.909
S 02.43084°	W 061.01527°	4.68	0.054	0.02	0.06	0.16	0.443	15.83	12.18	258.42	2.57	9.22	16.31	3.20	68.44	31.30	2.20	35.60	0.298	0.740
S 02.465624°	W 060.927204°	4.77	0.112	0.03	0.12	0.29	0.296	18.82	11.34	221.04	1.68	8.56	11.51	2.92	53.51	24.67	0.71	47.32	0.550	0.846
S 0247332°	W060.97627°	4.71	0.047	0.02	0.05	0.11	0.527	13.88	9.69	280.46	0.68	10.21	18.31	3.83	83.91	33.02	2.01	18.32	0.226	0.753
S.02.44953°	W 060.94923°	4.80	0.063	0.04	0.05	0.14	0.234	9.28	48.40	172.16	1.28	8.89	10.13	2.89	34.76	23.19	1.56	34.80	0.294	0.527

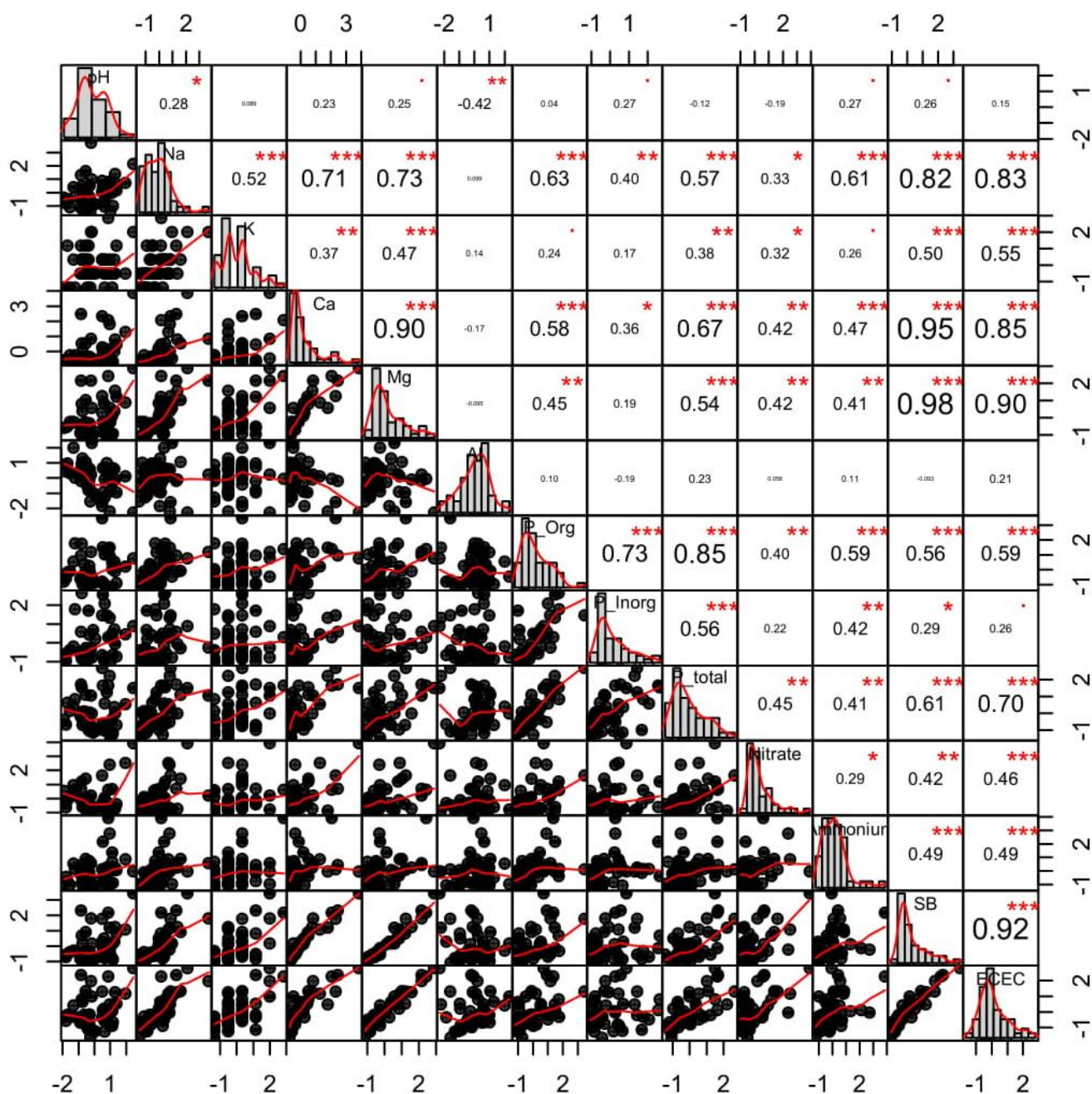
S 02.49454°	W 060.93719°	4.90	0.065	0.02	0.05	0.17	0.180	11.59	24.62	164.50	1.98	8.56	9.70	2.43	22.13	22.67	0.72	22.34	0.304	0.483
S 02.51718°	W 060.92078°	5.11	0.143	0.02	0.62	0.48	0.012	51.97	42.43	502.81	1.98	10.37	10.58	2.47	39.47	25.40	0.39	36.67	1.267	1.279
S02.518350°	W 060.871161°	5.12	0.039	0.02	0.07	0.30	0.222	5.76	4.67	125.20	0.78	8.56	9.39	2.33	33.78	21.06	1.44	19.95	0.434	0.656
S 02.54468°	W 060.87599°	5.16	0.059	0.02	0.05	0.15	0.468	6.43	11.35	153.00	1.58	9.22	9.87	2.57	32.98	23.24	0.26	21.36	0.277	0.746
S 02.55824°	W 060.85156°	5.04	0.056	0.01	0.08	0.17	0.160	8.48	8.52	168.33	1.78	9.38	9.46	2.30	27.91	22.91	0.46	33.86	0.320	0.480
S 02.57631°	W 060.82553°	4.78	0.05	0.01	0.06	0.14	0.337	12.18	6.71	206.67	1.08	10.70	10.67	2.57	53.78	25.02	0.07	21.35	0.269	0.606
S 02.57341°	W 060.80679°	4.83	0.036	0.01	0.04	0.10	0.116	14.17	14.99	163.54	1.18	8.40	7.77	2.54	9.33	19.89	1.24	14.91	0.181	0.297
S 02.57450°	W 060.78967°	4.53	0.053	0.01	0.15	0.30	0.415	24.81	15.10	288.13	1.76	22.06	19.57	4.80	114.13	48.18	2.59	18.77	0.507	0.922
S 02.55331°	W 060.77921°	4.47	0.068	0.01	0.05	0.23	0.431	16.30	6.15	205.71	1.16	20.41	22.40	6.96	98.31	50.93	0.91	29.27	0.355	0.786
S 02.59493°	W 060.76028	4.44	0.088	0.01	0.08	0.22	0.503	12.75	5.03	236.38	1.36	21.07	21.37	5.15	98.84	48.95	3.56	20.77	0.391	0.895
S 02.61151°	W 060.77030°	4.71	0.109	0.02	0.21	0.44	0.571	9.51	7.46	201.87	0.76	20.08	20.47	5.22	136.18	46.53	0.97	28.24	0.777	1.348
S 02.61236°	W 060.75213°	4.49	0.082	0.04	0.08	0.24	0.519	23.53	13.10	338.92	0.76	22.39	22.03	5.29	112.89	50.46	2.06	23.64	0.451	0.970
S 02.61238°	W 060.73413°	4.76	0.084	0.04	0.07	0.22	0.479	10.31	5.58	198.04	0.96	21.73	21.21	5.70	108.62	49.60	1.42	39.02	0.412	0.891
S 02.54789°	W 060.80404°	4.87	0.061	0.02	0.06	0.14	0.207	11.05	32.12	155.87	4.15	18.77	17.48	5.15	39.47	45.54	0.84	17.78	0.290	0.497
S 02.56110°	W 060.82261°	4.81	0.078	0.02	0.13	0.20	0.256	30.80	28.10	279.50	2.95	18.77	18.71	5.08	41.78	45.51	0.77	35.45	0.432	0.688
S 02,64803°	W 060.71751°	4.74	0.073	0.03	0.10	0.28	0.484	33.00	12.26	285.26	1.08	11.52	9.85	2.54	51.91	24.99	0.84	29.20	0.483	0.968
S 02.67837°	W 060.68189°	4.81	0.091	0.02	0.11	0.25	0.339	14.38	10.59	205.71	0.88	10.21	10.11	2.43	33.78	23.63	1.62	50.43	0.476	0.814
S 02.71006°	W 060.65781°	5.04	0.077	0.03	0.05	0.27	0.351	9.00	9.09	196.12	0.88	9.88	10.46	1.84	35.29	23.06	1.43	21.86	0.429	0.780
S 02.59359°	W 060.81361°	4.70	0.116	0.03	0.10	0.24	0.429	17.97	9.47	243.08	0.58	10.53	11.30	2.05	37.51	24.47	2.33	20.80	0.483	0.912
S 02.54438°	W 060.82154°	5.00	0.108	0.03	0.27	0.42	0.069	12.74	11.02	206.67	1.08	9.88	10.05	1.57	28.09	22.57	1.62	18.31	0.826	0.895

**Appendix S2.** Correlogram analysis of spatial data for the total mammalian abundance analyzed. Central horizontal lines represent spatial correlation values, while those on each side give 95% confidence intervals. Vertical dashed line shows the limit of autocorrelated values. Values above 1850 m (minimum distance between the camera traps in this study) were considered autocorrelated. Graph showed no spatial autocorrelation.



### Appendix S3. Correlations between soil fertility variables on fluvial islands.

Highly correlated variables are represented with Spearman greater than  $r > 0.50$ .



Legend (from right to left): pH, Na (sodium), K (potassium), Ca (calcium), Mg (magnesium), Al (aluminium), P\_Org (Organic phosphorus), P\_Inorg (Inorganic phosphorus), P\_total (Total phosphorus), Nitrate, Ammonium, SB (Sum of bases), ECEC (Cation exchange capacity).



**Appendix S4.** Local habitat, patch and landscape variables measured among 49 sites within the fluvial islands. The overall range, mean and standard deviation (SD) are provided for each variable to examine mammal relative abundance and proportion of omnivorous and herbivorous.

<b>Name (code name)</b>	<b>Range (mean <math>\pm</math> SD)</b>
<b>Local habitat scale</b>	
Basal area-BA	0.02-0.18 (0.06 $\pm$ 0.03)
Soil fertility-SB	1.8-23.4 (6.93 $\pm$ 4.79)
<b>Patch scale</b>	
Distance from the sampling point to the nearest mainland –MA	0.24-8.74 (2.81 $\pm$ 2.05)
<b>Landscape scale</b>	
Forest cover-FC	11.9-70.2 (32.28 $\pm$ 11.27)
<b>Anthropogenic</b>	
Distance from the sampling point to the nearest community-CD	0.7-18.63 (7.93 $\pm$ 3.99)
Logging-LO	0-1 (0.24 $\pm$ 0.43)

**Appendix S5.** Environmental and anthropogenic variables with their units of measurement with geographic coordinate per sampling point.

X	Y	Basal area (M <sup>2</sup> )	Community distance (Km)	Logging (presence-1 and absence-0)	Mainland distance (Km)	Sum of bases (Mmolc/Kg-1)	Forest cover (%)
S 01.36634°	W 061.79113°	0.02	4.79	0	0.38	15.5	11.87
S01.245660°	W061.404618°	0.05	3.58	1	0.70	10.2	31.19
S.01.43701°	W061.59555°	0.03	4.48	0	2.55	5.40	15.36
S 01.41285°	W 061.64458°	0.13	1.69	0	0.31	18.0	39.25
S01.45911°	W061.56334°	0.04	4.18	0	3.59	12.9	50.56
S01.49382 °	W 061.54341°	0.05	7.13	0	3.95	5.90	37.52
S 01.51433°	W 061.53587°	0.09	8.4	0	3.37	3.70	24.54
S 01.57869°	W061.49066°	0.03	4.73	0	3.09	17.4	37.08
S 01.56088°	W 061.51875°	0.04	6.2	0	6.06	4.30	34.64
S 01.58602°	W 061.51136°	0.15	6.91	0	5.57	8.30	27.58
S.01.62100°	W 061.46025°	0.03	0.70	0	1.27	12.0	51.13
S 01.67150°	W 061.43144°	0.05	6.15	1	1.68	6.30	35.74
S 01.74363°	W 061.43983°	0.06	5.11	0	2.77	5.20	30.51
S 01.78268°	W 061.43177°	0.02	8.13	0	2.51	3.10	25.72
S 01.92844°	W 061.28011°	0.10	2.37	0	0.31	11.3	26.56
S 01.946 75°	W 061.25460°	0.04	5.32	0	1.07	5.50	40.04
S 01.99961°	W 061.22744°	0.04	4.23	0	2.07	7.60	37.43
S.01.43832°	W 061.57518 °	0.06	3.0	0	1.47	23.4	37.25
S 01.56173°	W 061.49700°	0.05	4.01	0	2.94	15.6	32.00
S 02.21201°	W 061.04876°	0.07	7.62	0	0.37	7.80	25.71
S 02.28439°	W 061.03330°	0.04	5.21	0	1.15	4.80	22.16
S 02.30480°	W 061.02628°	0.07	6.53	0	0.94	4.0	26.72
S 02.35905°	W 061.00290°	0.06	9.2	0	1.08	9.3	21.64

S 02.39415°	W 060.99394°	0.14	8.63	0	0.43	10.8	25.02
S 02.41246°	W 060.98243°	0.08	12.36	0	0.99	4.0	15.65
S 02.43084°	W 061.01527°	0.06	10.3	1	5.01	3.0	33.92
S02.465624°	W060.927204°	0.07	15.02	0	4.52	5.5	31.91
S 0247332°	W060.97627°	0.06	9.69	0	8.74	2.3	39.38
S.02.44953°	W 060.94923°	0.03	13.53	1	2.54	2.9	42.84
S 02.49454°	W 060.93719°	0.04	13.05	0	6.11	3.0	30.35
S 02.51718°	W 060.92078°	0.04	14.67	0	5.47	12.7	18.64
S02.518350°	W060.871161°	0.06	10.08	0	0.57	4.3	35.13
S 02.54468°	W 060.87599°	0.05	11.14	0	2.59	2.8	58.90
S 02.55824°	W 060.85156°	0.03	9.12	0	2.93	3.2	41.64
S 02.57631°	W 060.82553°	0.04	8.14	0	5.31	2.7	33.99
S 02.57341°	W 060.80679°	0.04	6.70	1	3.78	1.8	70.20
S 02.57450°	W 060.78967°	0.03	6.26	0	3.44	5.1	25.15
S 02.55331°	W 060.77921°	0.05	3.85	0	0.24	3.6	45.96
S 02.59493°	W 060.76028	0.03	8.64	1	2.41	3.9	17.39
S 02.61151°	W 060.77030°	0.06	9.92	0	4.36	7.8	34.83
S 02.61236°	W 060.75213°	0.05	11.1	1	2.97	4.5	38.47
S 02.61238°	W 060.73413°	0.04	11.85	1	1.64	4.1	32.62
S 02.54789°	W 060.80404°	0.05	4.21	1	0.96	2.9	29.61
S 02.56110°	W 060.82261°	0.05	6.70	0	3.08	4.3	13.10
S 02,64803°	W 060.71751°	0.04	14.89	1	3.87	4.8	31.49
S 02.67837°	W 060.68189°	0.05	18.63	1	2.33	4.8	38.93
S 02.71006°	W 060.65781°	0.03	15.28	1	6.29	4.3	25.86
S 02.59359°	W 060.81361°	0.18	9.64	0	7.18	4.8	25.71
S 02.54438°	W 060.82154°	0.04	5.46	0	0.79	8.3	22.82

**Appendix S6.** Species organized by their primary diet, locomotion, number of independent records and number of camera traps where the species were registered.

Primary diet	Order	Species (Common name)	Locomotion	Number of records	Number of cameratraps
	Rodentia	<i>Cuniculus paca</i> (Spotted paca)	Terrestrial	5	3
	Rodentia	<i>Hydrochoerus hydrochoerus</i> (Capybara)	Terrestrial	3	2
<b>Herbivorous</b>	Artiodactyla	<i>Mazama americana</i> (Red brocket deer)	Terrestrial	1	1
	Artiodactyla	<i>Pecari tajacu</i> (Collared peccary)	Terrestrial	1	1
	Rodentia	<i>Proechimys</i> sp. (Spinyrat)	Terrestrial	12	8
	Didelphimorphia	<i>Didelphis marsupialis</i> (Common opossum)	Scansorial	83	19
<b>Omnivorous</b>	Carnivora	<i>Nasua nasua</i> (South American coati)	Terrestrial	2	1
	Didelphimorphia	<i>Philander opossum</i> (Gray four-eyed opossum)	Scansorial	4	2
<b>Carnivorous</b>	Carnivora	<i>Leopardus pardalis</i> (Ocelot)	Terrestrial	1	1
	Carnivora	<i>Panthera onca</i> (Jaguar)	Terrestrial	3	2
<b>Insectivorous</b>	Pilosa	<i>Tamandua tetradactyla</i> (Lesser anteater)	Scansorial	11	6



S 02.41246°	W 060.98243°	0	1	0	0	0	0	0	0	0	0	0	0	1	0.014
S 02.43084°	W 061.01527°	0	1	0	0	0	0	0	0	0	0	0	0	1	0.014
S 02.465624°	W 060.927204°	0	1	0	0	0	0	0	0	0	0	1	2	0.028	
S 0247332°	W060.97627°	0	4	0	0	0	0	0	0	2	0	0	6	0.085	
S.02.44953°	W 060.94923°	0	0	0	0	0	0	0	0	1	0	0	1	0.014	
S 02.49454°	W 060.93719°	0	0	0	0	0	0	0	0	0	0	0	0	0	
S 02.51718°	W 060.92078°	0	2	0	0	0	0	0	0	0	0	0	2	0.028	
S02.518350°	W 060.871161°	0	0	0	0	0	0	0	0	0	0	0	0	0	
S 02.54468°	W 060.87599°	0	1	0	0	0	0	0	0	0	0	1	2	0.028	
S 02.55824°	W 060.85156°	0	0	0	0	0	0	0	0	0	0	0	0	0	
S 02.57631°	W 060.82553°	0	0	0	0	0	0	0	0	0	0	0	0	0	
S 02.57341°	W 060.80679°	0	3	0	0	0	0	0	0	0	0	0	3	0.042	
S 02.57450°	W 060.78967°	0	0	0	0	0	0	0	0	0	0	0	0	0	
S 02.55331°	W 060.77921°	0	0	0	0	0	0	0	0	0	0	0	0	0	
S 02.59493°	W 060.76028°	0	1	0	0	0	0	0	0	2	0	0	3	0.042	
S 02.61151°	W 060.77030°	0	0	0	0	0	0	0	0	0	0	0	0	0	
S 02.61236°	W 060.75213°	0	0	0	0	0	0	0	0	2	0	1	3	0.042	
S 02.61238°	W 060.73413°	0	1	0	0	0	0	0	0	0	0	0	1	0.014	
S 02.54789°	W 060.80404°	0	2	0	0	0	0	0	0	0	0	0	2	0.028	
S 02.56110°	W 060.82261°	0	0	0	0	0	0	0	0	0	0	0	0	0	
S 02,64803°	W 060.71751°	0	2	0	0	0	0	0	0	0	0	0	2	0.028	
S 02.67837°	W 060.68189°	0	0	1	0	0	0	0	0	0	0	0	1	0.014	
S 02.71006°	W 060.65781°	1	22	0	0	0	0	0	3	0	0	0	26	0.368	
S 02.59359°	W 060.81361°	1	16	0	0	0	0	0	0	0	0	3	20	0.283	
S 02.54438°	W 060.82154°	3	0	0	0	0	0	0	0	0	0	0	3	0.042	

**Appendix S8.** Five best models selected by the model selection (Akaike Criteria) for total mammalian abundance and proportion of omnivorous species.

<b>Total Mammalian abundance</b>		
<b>Model structure</b>	<b><math>\Delta</math>AIC</b>	<b>wAIC</b>
Null model	0.00	0.43
Model structure: SB + FC + MA + BA	2.53	0.12
Model structure: SB + FC + MA + LO	2.68	0.11
Model structure: SB + BA + LO	2.70	0.10
Model structure: SB + FC + MA	3.54	0.07
<b>Environmental and anthropic factors</b>	<b>Sum of Akaike weights</b>	
Soil fertility	0.4	
Distance from the sampling point to the nearest mainland	0.3	
Forest cover	0.3	
Basal area	0.2	
Logging	0.2	

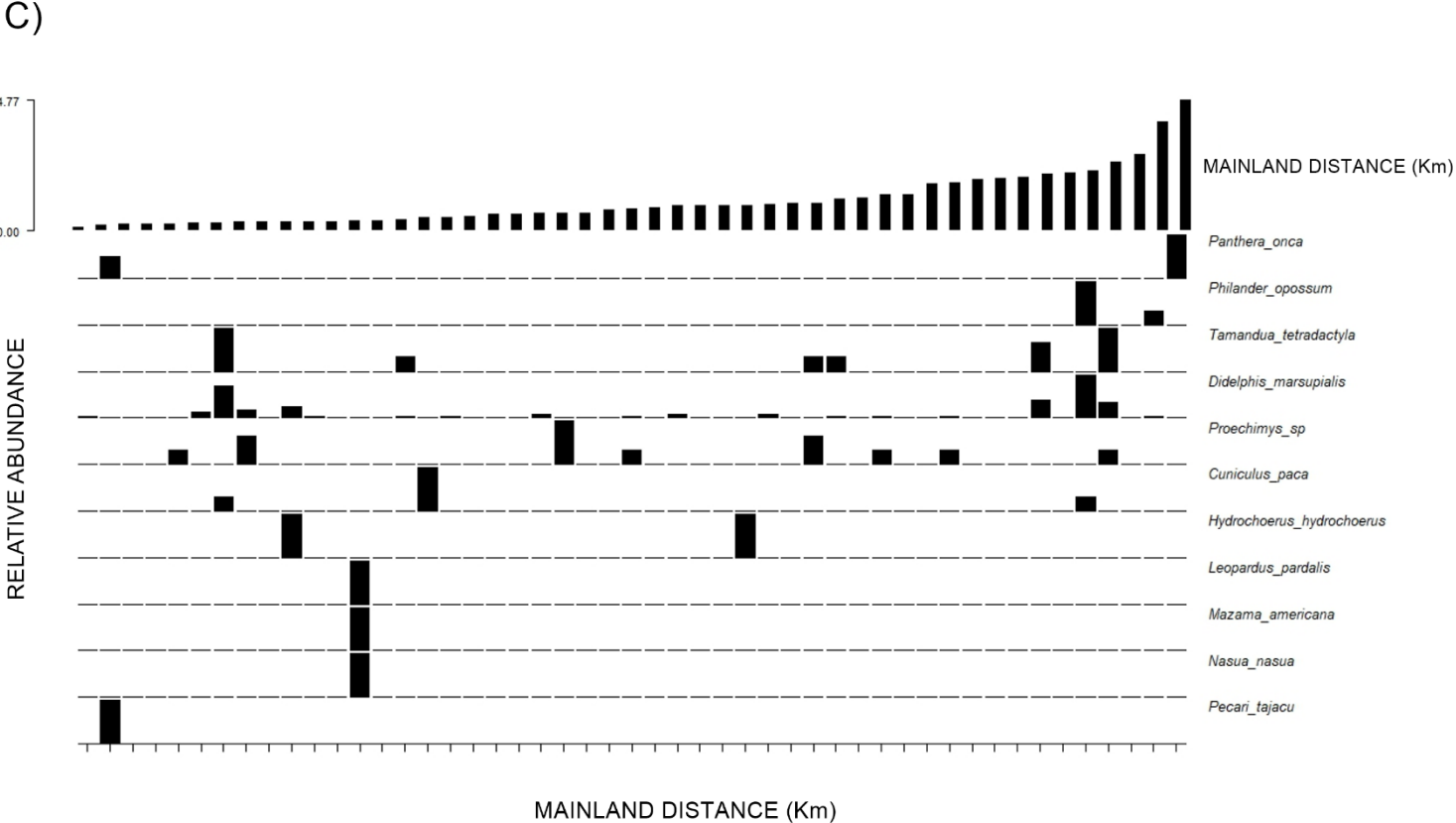
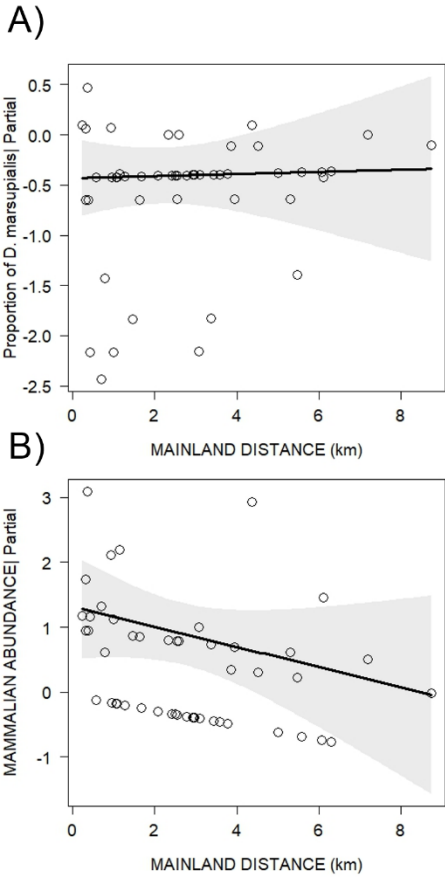
Five best models selected by the model selection (Akaike Criteria) with  $\Delta AIC < 10$  as a function for total abundance of mammals. SB: Sum of bases; Distance from the sampling point to the nearest mainland- MA; FC: Forest cover; BA: Tree Basal area; LO: Logging  
 $\Delta AIC$  = difference between the best model (with zero value) and the others where lower numbers indicate the best model,  $wAIC$  = strength of evidence in favor of each of the models where higher numbers indicate the best model.

<b>Proportion of <i>Didelphismarsupialis</i></b>		
<b>Modelstructure</b>	<b><math>\Delta AIC</math></b>	<b>wAIC</b>
Nullmodel	0.00	0.73
Model structure: SB + MA + FC	4.93	0.06
Model structure: SB + FC + CD	5.02	0.06
Model structure: SB + BA + LO	5.32	0.05
Model structure: SB + FC + MA + LO	6.13	0.03
<b>Environmental and anthropic factors</b>		
	<b>Sum of Akaike weights</b>	
Soil fertility	0.20	
Forest cover	0.15	
Distance from the sampling point to the nearest mainland	0.09	
Logging	0.08	
Distance from the sampling point to the nearest human community	0.06	
Basal area	0.05	

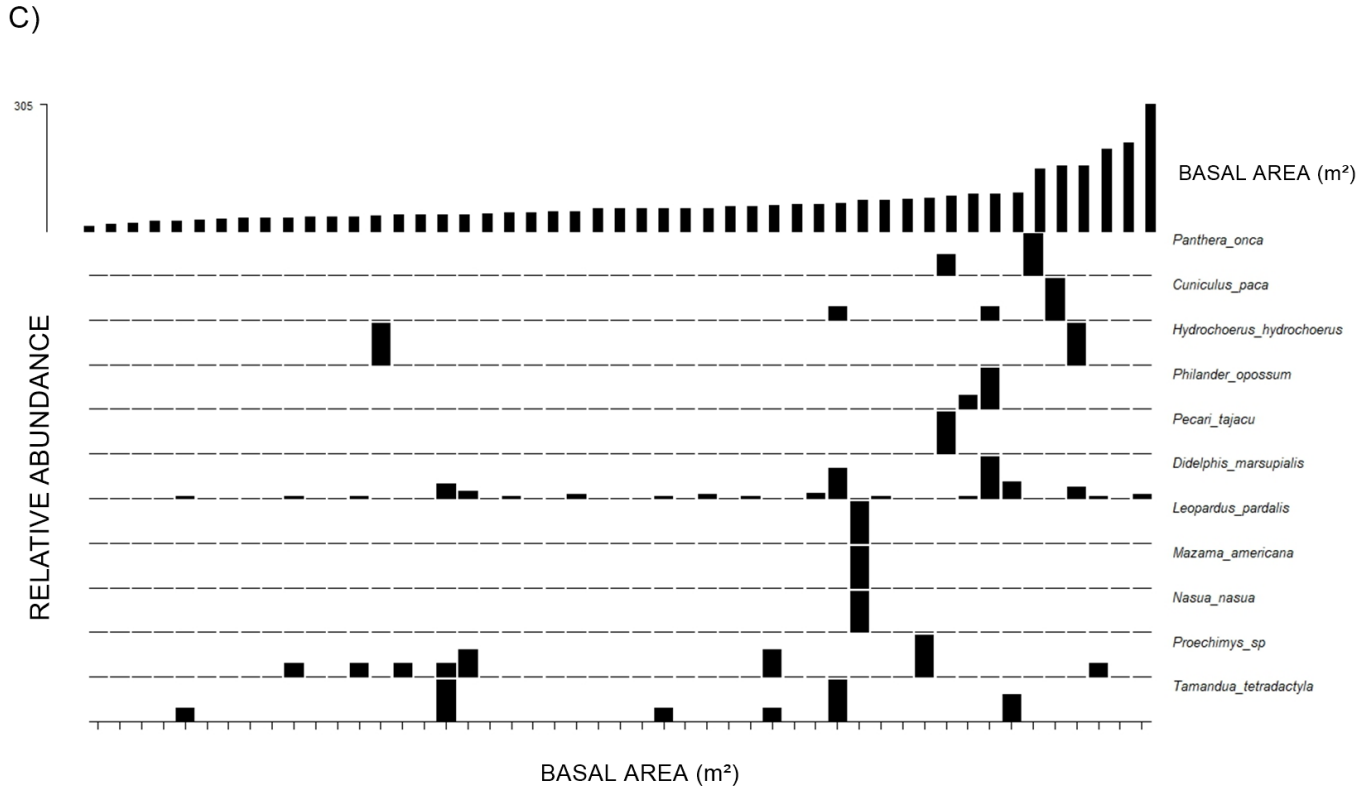
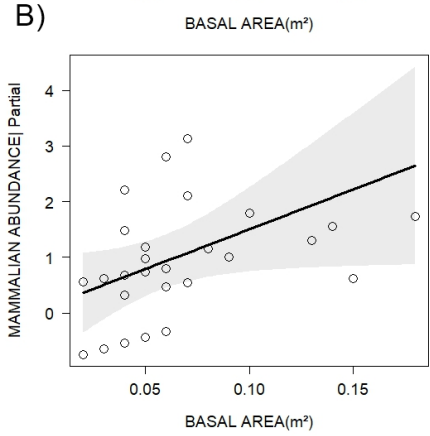
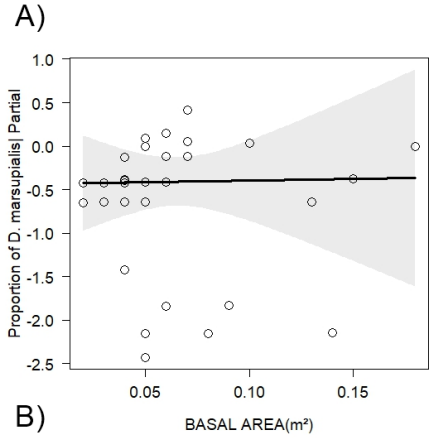


**Appendix S9.** Partial graph and generic graph for each environmental and anthropogenic variable for total abundance and proportion of omnivorous.

**DISTANCE FROM THE SAMPLING POINT TO THE NEAREST MAILAND**

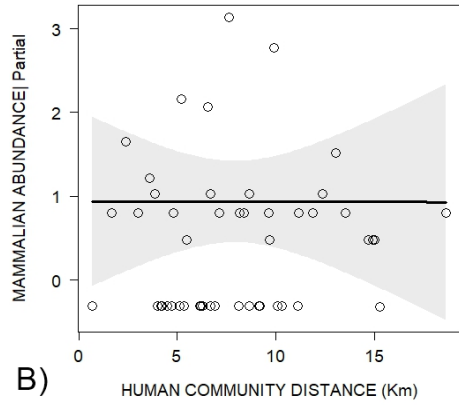


**TREE BASAL AREA**

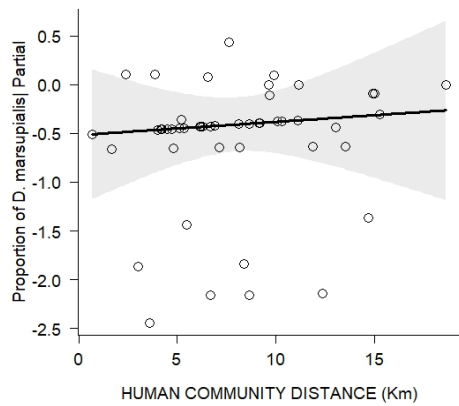


**DISTANCE FROM THE SAMPLING POINT TO THE NEAREST HUMAN COMMUNITY**

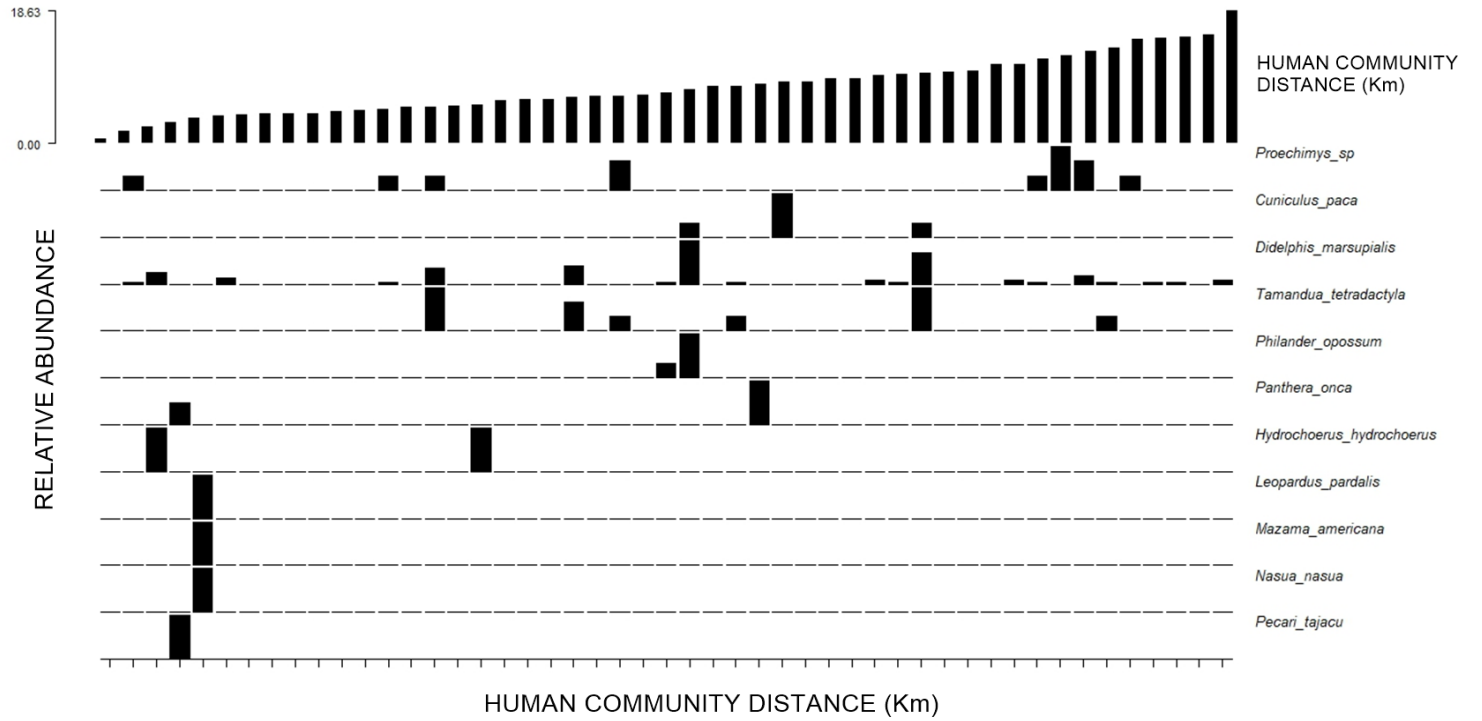
A)



B)

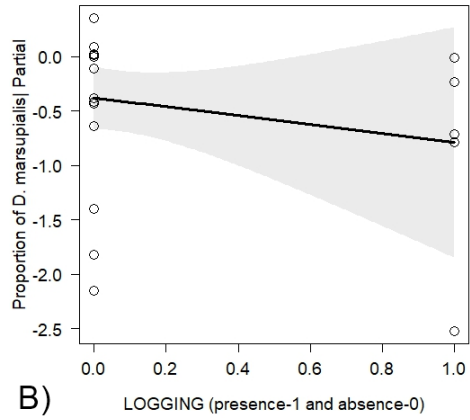


C)

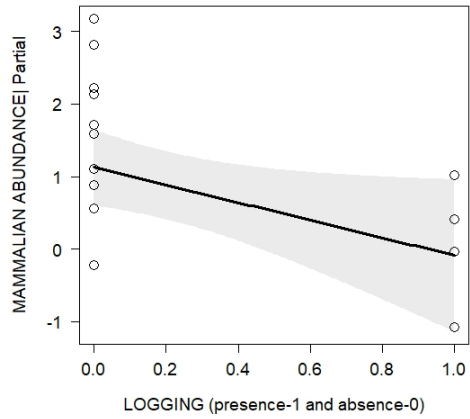


**LOGGING**

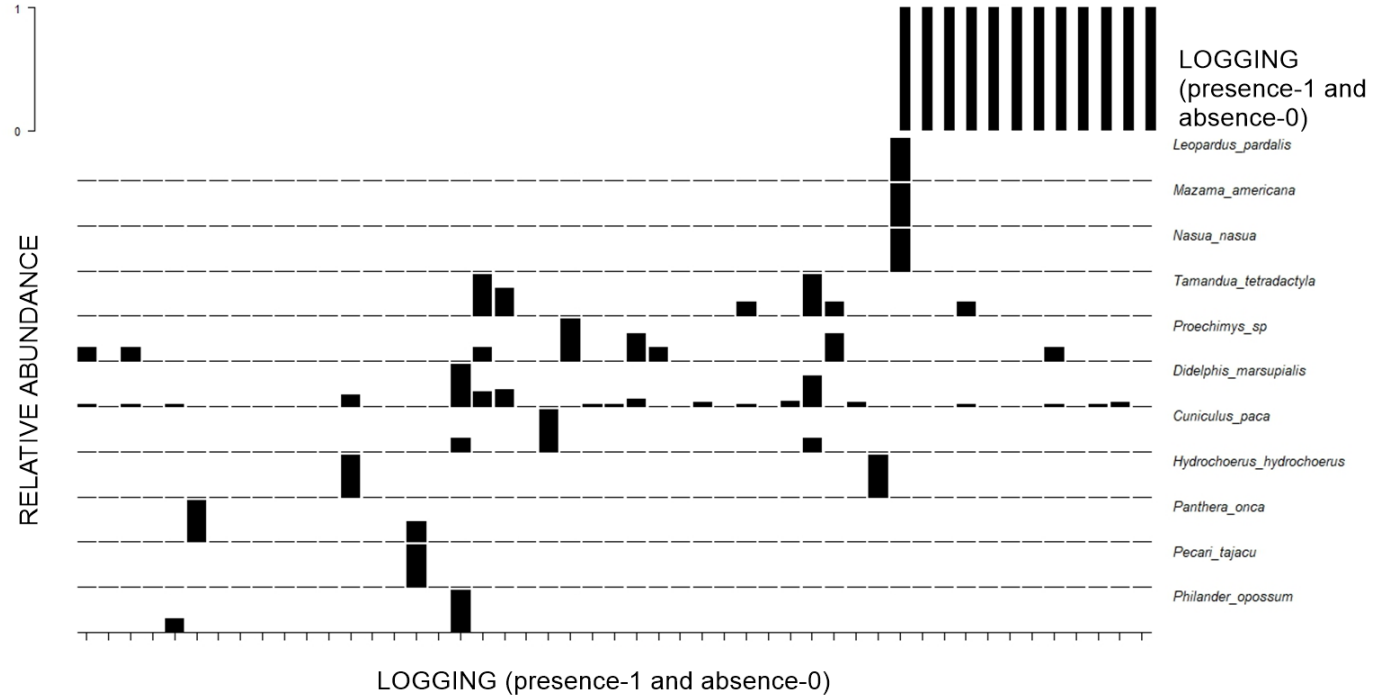
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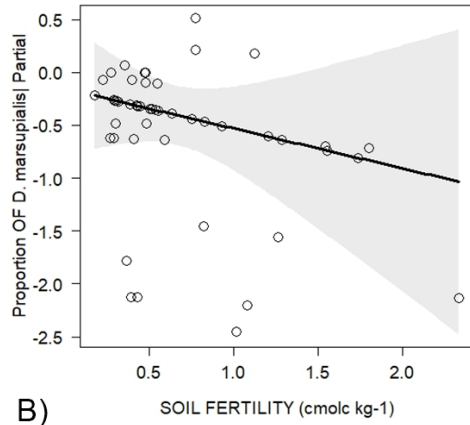


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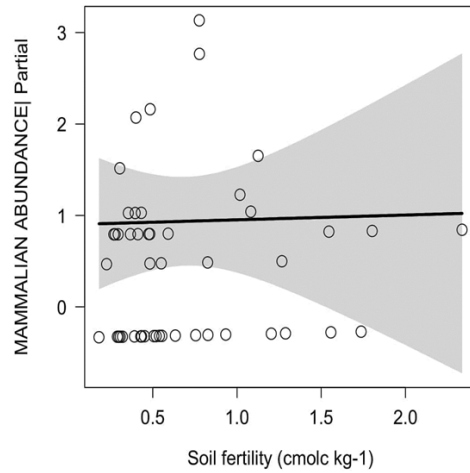


### SOIL FERTILITY

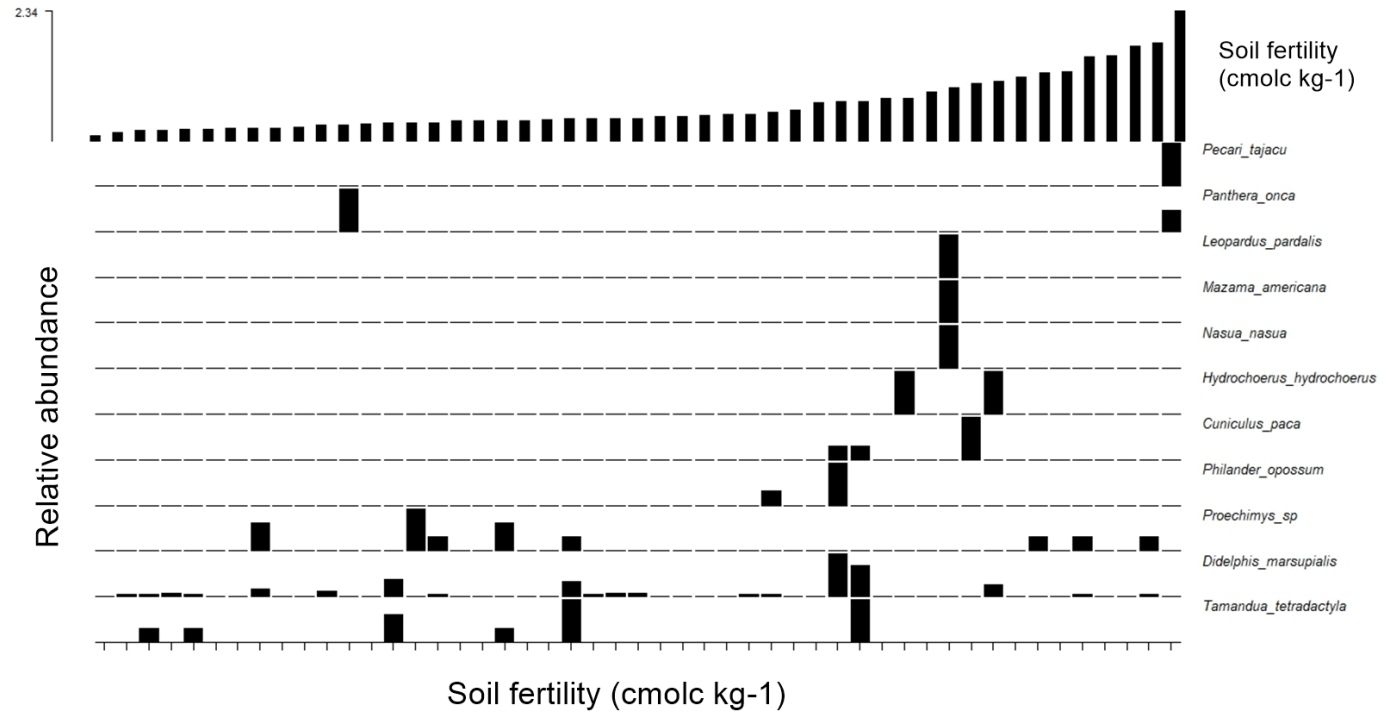
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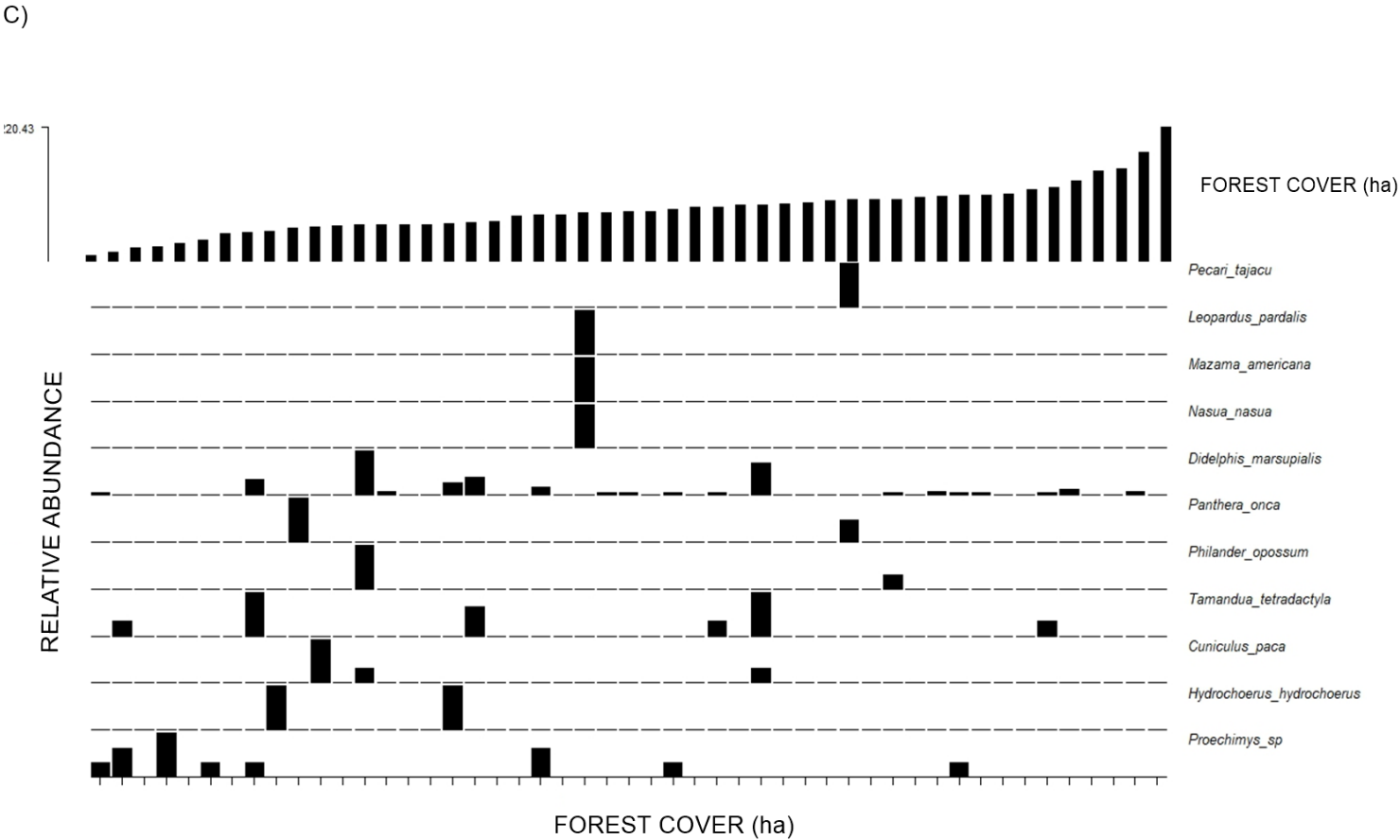
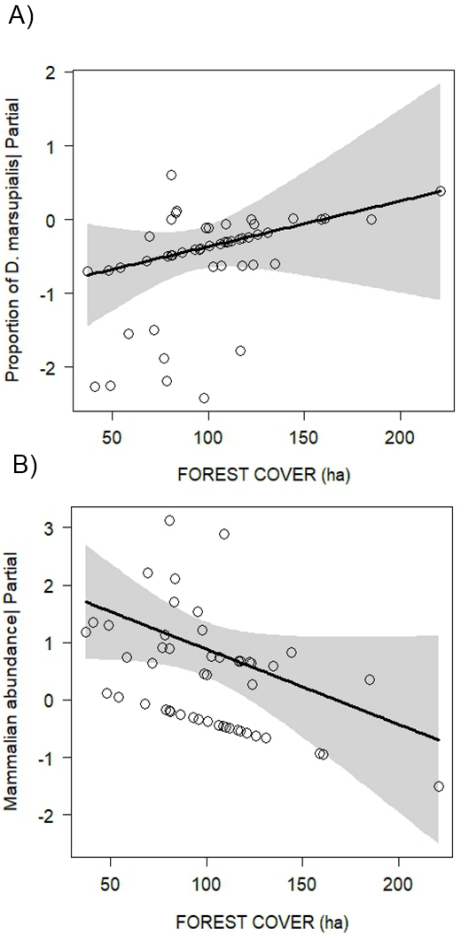
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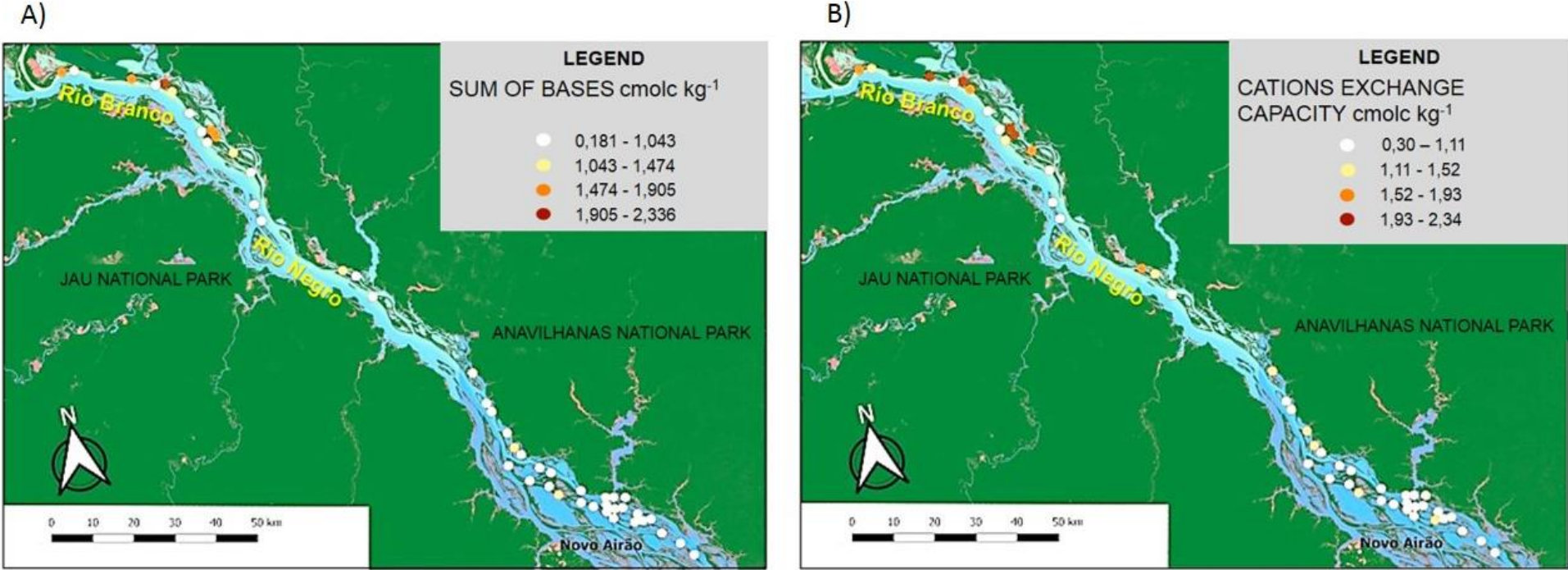
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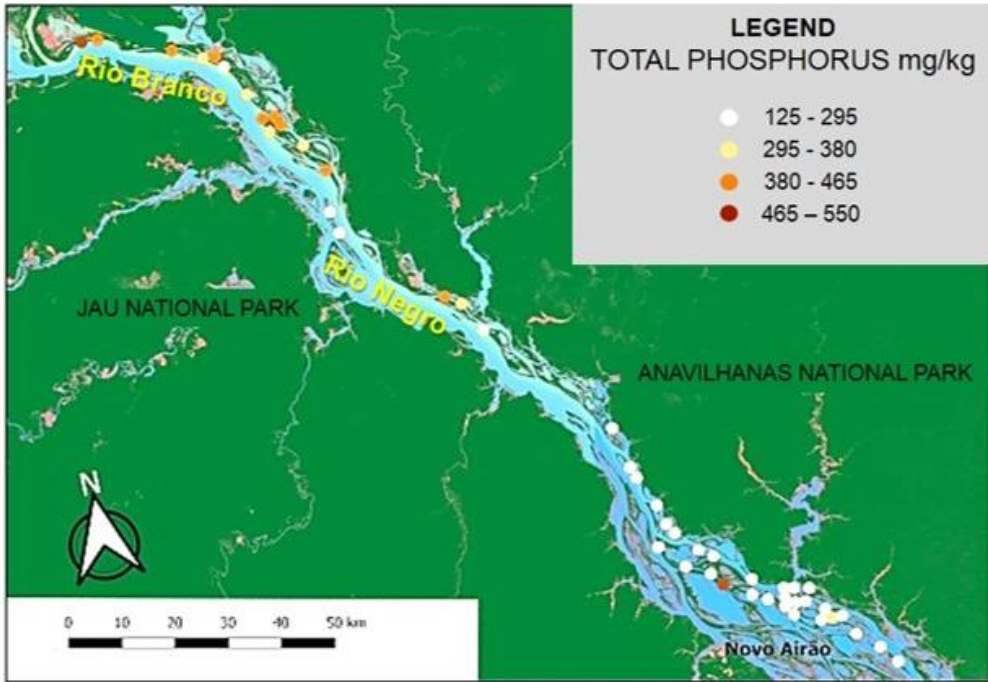
### FOREST COVER



**Appendix S10.** Observed variation in soil fertility within the fluvial islands



c)



D)

