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DEPARTAMENTO DE ZOOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL
NÍVEL: DOUTORADO

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DETERMINANTES AMBIENTAIS DA VARIAÇÃO DA DIVERSIDADE DE MAMÍFEROS AO LONGO DA PAISAGEM DA BACIA DO RIO NEGRO: UMA ANÁLISE COM AUXÍLIO DE SENSORIAMENTO REMOTO.

Recife

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Tese apresentada como requisito parcial para a obtenção do grau de doutor em Biologia Animal, pelo Programa de Pós-graduação em Biologia Animal da Universidade Federal de Pernambuco.

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Co-orientador: Prof^a. Dr^a Josiclêda Domiciano Galvíncio

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RESUMO

Introdução: O presente estudo tem por objetivos testar a influência de fatores ambientais, da produtividade do ambiente e da heterogeneidade ambiental, sobre a diversidade e abundância de mamíferos, bem como testar a relação massa corpórea x abundância, verificando os fatores que a influencia na região da bacia do Rio Negro.

Métodos: Avaliamos a comunidade de mamíferos de médio e grande em porte em cinco áreas na bacia do Rio Negro, utilizando o método de transecto linear, através do qual obtivemos variáveis dependentes, as quais: (1) densidade de grupo, (2) densidade individual, (3) biomassa, (4) tamanho médio de grupo e (5) índices de diversidade. Através de técnicas de sensoriamento remoto obtivemos índices de vegetação de diferença normalizada (NDVI), índice de área foliar (LAI), Declividade do ambiente e heterogeneidade. Utilizamos o Modelo Linear Generalizado (GLM), baseado no Critério de informação de Akaike (AIC), para determinar quais das variáveis preditivas explicariam essa relação para os primatas das áreas estudadas. Para isso, utilizamos o modelo de regressão linear simples para relacionar massa corpórea com os diversos parâmetros de abundância de toda comunidade de mamíferos. Utilizamos a correlação produto-momento Pearson, para testar a influência da diversidade e NDVI sobre o coeficiente de regressão.

Resultados: Houve uma correlação entre NDVI e tamanho médio de grupo (R= -0,65; p=0,015), LAI e tamanho médio de grupo de primatas (R= -0,64; p=0,017), declividade e tamanho médio de grupo (R= -0,67; p=0,008) e heterogeneidade e tamanho médio de grupo (R= -0,67; p=0,008). O GLM baseado no AIC, mostrou NDVI e declividade como a melhor variável explicativa para tamanho médio de grupo. Para toda a comunidade de mamíferos as relações significativas entre massa corpórea e abundância variaram consideravelmente, com valores entre -0,76 a 0,75, o que dependeu do parâmetro de abundância avaliado, da categoria trófica e do hábito das espécies. As correlações apontaram para uma influência da diversidade de mamíferos sobre as inclinações das retas.

Discussão: Os índices de vegetação, declividade do terreno e heterogeneidade não explicaram a diversidade de primatas. A relação inversa entre tamanho médio de grupo e NDVI, LAI e declividade mostrou que nos ambientes menos produtivos os primatas tendem a formar grupos maiores como uma estratégia para aumentar a defesa contra predadores e a eficiência de forrageamento. As relações massa corpórea x abundância mostraram que em ambientes mais equilibrados os recursos estariam melhor partilhados e a inclinação da reta seria mais negativa, o que estaria mais de acordo com a regra da equivalência energética. Análises de acordo com o hábito terrestre mostraram correlação com a produtividade das florestas e, de acordo com a dieta, verificamos relações significativas para a categoria dos frugívoros, a qual possui maior amplitude de massa corpórea.

Palavras-chaves: NDVI, Sensoriamento remoto, Regra da equivalência energética.

ABSTRACT

Introduction: This present study aimed at testing the influence of environmental parameters, productivity and heterogeneity on mammalian diversity and abundance, as well as testing the relationship between body mass and abundance, verifying which factors contribute to this relationship in the Rio Negro basin region, northernmost Brazilian Amazonia.

Methods: We assessed the medium-large sized mammalian community in five areas in the Rio Negro basin by linear transect method, wherewith we obtained dependent variables, as follows: (1) group density, (2) individual density, (3) biomass, (4) mean group size and (5) diversity indexes. Through remote sensing techniques, we gathered the predicted variables Normalized Differential Vegetation Index (NDVI), Leaf Area Index (LAI), slope and environmental heterogeneity. Moreover, we performed a Generalized Linear Module (GLM), based in an Akaike Information Criterion (AIC), in order to determine which predictive variables explained this relationship for primates at the studied areas. Thereunto, we accomplished a simple linear regression model, in order to relate species body mass with all abundance parameters of the whole mammalian community, in addition, we use Pearson product-moment correlation in order to test the influence of diversity and NDVI on regression coefficient.

Results: There was a significative negative correlation between NDVI and mean group size (R= -0.65; p=0.015), LAI and mean group size (R= -0.64; p=0.017), Slope and mean group size (R= -0.67; p=0.008) and heterogeneity and mean group size (R= -0.67; p=0.008). The GLM based in the AIC, however, showed NDVI and Slope as the best explanatory variables for mean group size. The significative relationships for the whole mammalian community between body mass and abundance varied considerably, ranging from -0.76 to 0.75, which depended on the abundance parameter assessed, trophic category and species habit. The correlations indicated an influence of mammalian diversity on the slopes of the regression lines.

Discussion: Vegetation indexes, slope and heterogeneity did not explain primate diversity. An inverse relationship between mean group size and NDVI, LAI and slope showed that in less productive environments, primates tend to have larger groups as a strategy to increase the defence against predators and foraging efficiency. The relationships between body mass and abundance showed that in more balanced environment, resources would be better distributed and the line slope would be negative, which agrees with the energetic equivalence rule. Analysis performed according to terrestrial habit indicated correlation with forest productivity and, according to diet, we verified significative relationships to frugivorous category, which encompasses a greater body mass extent.

Keywords: NDVI, Remote sensing, Energetic equivalence rule.

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Anexo B – Normas para a submissão do artigo ao periódico: *Journal of zoology*

1.0 INTRODUÇÃO GERAL

O estudo da diversidade pode ser explicado através de duas linhas de raciocínio diferentes, que considera fatores relacionados à dispersão (HUBBELL, 2001) ou fatores relacionados à heterogeneidade ambiental (JONES *et al.* 2006). Os padrões de diversidade podem variar nas mais diversas escalas (GASTON, 2000; HILLEBRAND, 2004), em maiores escalas o padrão mais comum é o gradiente latitudinal de diversidade, o qual prevê que a diversidade aumenta em direção aos trópicos (PIANKA, 1966). Em menores escalas, umidade se mostrou importante para aves (JANKOWSKI *et al*, 2009), a distância geográfica para árvores na Amazônia (CONDIT *et al*, 2002), produtividade para a flora (HARRISON *et al*, 2006), heterogeneidade ambiental para mamíferos (KERR; PACKER, 1997). A produtividade primária vem sendo apontada como o mais importante fator para determinar a estrutura das comunidades (STEVENSON, 2001; HE; ZHANG, 2009; HE, ZHANG e ZHANG, 2009). Diversos estudos sobre o relacionamento produtividade-diversidade têm sido realizados, mas os resultados permanecem inconclusivos.

A abundância de mamíferos decresce com o aumento da massa corpórea dos mesmos (PETERS; WASSENBERG, 1983; PETERS; RAELSON, 1984; CHIARELLO, 1999). No entanto o fator dieta influencia nesse tipo de relação, fazendo com que carnívoros sejam menos abundantes do que os herbívoros (PETERS; WASSENBERG, 1983; MENDES PONTES, 2004). Biedermann (2003), mostrou que existe uma relação positiva entre o tamanho do corpo de animais terrestres e o tamanho de seus habitats. Outros estudos, no entanto, mostram a importância da dieta como determinante da abundância de populações de mamíferos, ou seja, espécies que possuem dieta muito específica ou ocupam altos níveis tróficos, tendem a ocorrer em menor densidade, devido a menor disponibilidade de alimento. (KINNAIRD; EISENBERG, 1989). Certas espécies generalistas, as quais se adaptam melhor a áreas degradadas, possuem suas densidades aumentadas em seus habitats (FONSECA; ROBINSON, 1990).

Com relação à abundância de primatas, tem sido evidenciado que o seu fator determinante é a disponibilidade de alimento (PERES, 1997; MENDES PONTES, 1999), a fertilidade do solo também tem sido relatada como determinante de abundância, visto que estaria diretamente ligada à produtividade da floresta, assim como a complexidade estrutural da floresta (EMMONS, 1984). Para primatas frugívoros, a disponibilidade de frutos tem sido apontada como o principal fator que afeta a abundância de primatas (JANSON; CHAPMAN, 1999; STEVENSON, 2001). A forma como os primatas usam o ambiente, preferindo um tipo vegetacional em detrimento de outro, poderia ser reflexo da produtividade de alimentos e competição interespecífica (MENDES PONTES, PAULA e MAGNUSSON, 2012).

O presente trabalho objetiva avaliar diversidade e abundância de mamíferos, trazendo à tona o uso de ferramentas do sensoriamento remoto para obtenção de variáveis explicativas. A tecnologia de sensoriamento remoto tem possibilitado estudar a dinâmica dos ecossistemas e monitorar mudanças na diversidade de espécies, baseados na reflectância espectral da vegetação, bem como prover dados precisos em nível de paisagem (NAGENDRA, 2001; PETTORELLI *et al*, 2005). Isto pode fornecer a ecólogos uma completa ferramenta que explicaria como o ambiente varia e quais outras variações estariam associadas. Índices de vegetação obtidos por imagens de satélite têm sido utilizados por ecólogos para verificar a relação entre produtividade, biodiversidade e heterogeneidade ambiental (NAGENDRA, 2001; TURNER *et al*, 2003; PETTORELLI *et al*, 2005; LASSAU; HOCHULI, 2008; HE; ZHANG, 2009; HE *et al*, 2009).

No primeiro capítulo procurou-se investigar a influência da vegetação e do relevo sobre a diversidade e abundância de primatas. Os dados de vegetação e relevo foram obtidos com índices gerados por técnicas de sensoriamento remoto: Índice de Vegetação de Diferença Normalizada (NDVI), Índice de Área Foliar (IAF) e Módulo de Elevação Digital (MED). No segundo capítulo testamos a relação Abundância vs. Massa corpórea, em diferentes áreas nas proximidades do escudo das Guianas. Procurou-se testar o efeito da diversidade de espécies e da vegetação sobre as relações.

2.0 METODOLOGIA GERAL

2.1 Áreas de estudo

Com o objetivo de determinar quais variáveis ambientais definem a diversidade e abundância no extremo norte da Amazônia brasileira, selecionou-se um conjunto de áreas com vegetação típica da bacia do Rio Negro, as quais variaram de floresta tropical densa até florestas abertas, incluindo campinas e campinaranas, classificadas de acordo com IBGE (1992) e (RADAMBRASIL, 1975). Estudos prévios neste mesmo conjunto de áreas, mostraram que a caça nas regiões não protegidas, abrangidas nesse conjunto, não apresentam níveis que interferem na diversidade ou abundância de mamíferos (ALVES, 2012; MELO, 2012). As áreas incluídas nesse estudo são:

2.1.1 Assentamento humano de Entre Rios

Entre Rios é um assentamento humano que se apresenta em forma de espinha de peixe, imerso na floresta amazônica, ao longo de 90 km de uma Estrada principal não pavimentada, estabelecido desde 1970, localizado à uma latitude de 0°48'N and longitude 59°25'W, formado por floresta tropical ombrófila, com argissolo vermelho e amarelo, à uma altitude entre 80 e 160 metros (IBGE, 2010). A temperatura média anual é em torno de 28ºC e a precipitação é em torno de 3000 mm (SOMBROEK, 2001).

2.1.2 Reserva Biológica de Uatumã

Uatumã é uma área protegida com 942.786 ha, localizada à latitude 1°55'S e longitude 58°50'W, é formada por floresta tropical densa e aberta, com argissolo vermelho e amarelo, a uma altitude entre 80 e 160 m (IBGE, 2010). A temperatura média anual é em torno de 28ºC e a pluviosidade é de 2376 mm (FEARNSIDE, 2005).

2.1.3 Assentamento Humano de Novo Paraíso

Novo Paraíso é um assentamento humano estabelecido ao longo de uma rodovia principal, não pavimentada, de 70 km cortando a floresta. É localizada à latitude 2°14'N e longitude 60°31'W, e formada por floresta tropical densa e aberta, campinaranas e campinas. O solo é latossolo vermelho e amarelo, e localiza-se à uma altitude entre 80 e 160 m (IBGE, 2010). A temperatura média anual fica em torno de 26ºC e a pluviosidade em torno de 1500 mm (SOMBROEK, 2001).

2.1.4 Parque Nacional do Viruá

Viruá é uma área protegida de 229.100 ha localizada à latitude 01º42'N e longitude 61º10'W, é formada por floresta tropical densa e aberta, campinaranas e campinas. O solo é espodossolo ferrilúvico. A região situa-se à uma altitude de entre 80 and 160 m (IBGE, 2010). A temperature média anual é em torno de 26ºC e a precipitação é em torno de 1500 mm (SOMBROEK, 2001).

2.1.5 Estação Ecológica de Maracá

Maracá é uma ilha fluvial com 103.976,48 ha, localizada à latitude 3°24'N e longitude 61°40'O, formada por floresta tropical densa e aberta, campinaranas e campinas. O solo é argissolo vermelho e amarelo, e a altitude varia entre 80 e 160 m (IBGE, 2010). A temperatura media é em torno de 31.6ºC, e a pluviosidade é em torno de 1577 mm, com forte declínio na estação seca (MENDES PONTES, 2004).

2.1.6 Amostragem de mamíferos de mamíferos

As amostragens de mamíferos foram realizadas usando o método de Amostragem por Transecto Linear (BURNHAM *et al*, 1980; BUCKLAND *et al*, 1993). Nos assentamentos foram abertas 3 trilhas paralelas de 5 km, em cada uma das localidades, com o auxílio de bússola e aparelho de GPS, tomando o cuidado de mantê-las retas.

Na Reserva Biológica de Uatumã e no Parque Nacional de Viruá, usamos três trilhas do Programa de Pesquisa em Biodiversidade (PPBio) (www.ppbio.inpa.gov.br), que pertencem à grades padrão de 25-km², que consiste em 5 trilhas paralelas de 5 km, marcadas alfanumericamente a cada 100 m.

As amostragens diurnas foram realizadas entre 07:00 e 17:30h. Foram percorridos 10 km por dia com velocidade média de 1 km/h. As amostragens noturnas foram realizadas entre 18:30 e 04:30 h, percorrendo em torno de 8 km por noite, em uma velocidade média de 1.25 km/h. Utilizamos lanternas de mão, de baixa intensidade luminosa para enxergar o caminho e lanternas de longo alcance que foram acesas sempre haviam indícios da presença de algum animal.

A matriz de dados de amostragens de mamíferos usadas nesse trabalho, compreenderam: (1) Estação Ecológica de Maracá (Jan. 1997/ Jan. 98); (2) Assentamento de Novo Paraíso (Dez. e Jan. 2010); (3) Assentamento de Entre Rios (Jan. e Fev. 2012); (4) Parque Nacional de Viruá (Março de 2011) e (5) Reserva Biológica de Uatumã (Set. 2011). O esforço amostral de cada área foi de 450 km andados, totalizando 2250 km.

Para cada animal ou grupo de animais visualizados durante as amostragens, as seguintes informações foram anotadas: tamanho do grupo, distância perpendicular, horário e localização ao longo da trilha.

A amostragem de mamíferos foi conduzida pelos mesmos observadores e assistentes de campo treinados, que andaram em pares e alternando-se entre as trilhas. A velocidade da caminhada foi controlada observando o tempo de chegada a cada marco de 100 m.

2.2 Sensoriamento remoto

2.2.1 Obtenção de imagens

Os dados de índices de vegetação foram obtidos através do sensor TM (Thematic Mapper), um instrumento a bordo do satélite LANDSAT 5, Lançado em 01/03/84 e desativado em 11/10/11. O sensor TM faz o imageamento da superfície terrestre produzindo imagens com 185 Km de largura no terreno, resolução espacial de 30 metros e 7 bandas espectrais. O tempo de revisita do satélite para imagear uma mesma porção do terreno é de 16 dias.

Foram coletadas imagens de satélites, disponíveis no endereço eletrônico http://www.inpe.br/ das 5 áreas em períodos próximos ao período da coleta de dados biológicos, dando preferência às imagens com menor percentual de nuvens.

Os dados de topografia foram obtidos através de imagens geradas por um radar à bordo do ônibus espacial Endeavour na missão SRTM (Shuttle Radar Topography Mission) disponíveis no endereço eletrônico: http://www.relevobr.cnpm.embrapa.br/download/index.htm.

2.2.2 Tratamento das imagens

O software utilizado foi o Erdas Imagine 9.1 (licença do Departamento de Ciências Geográficas da UFPE) utilizando as funções de registro, empilhamento das bandas espectrais, recortes e uso de modelos matemáticos entre as bandas espectrais, entre elas a banda 3 do visível e banda 4 do infravermelho próximo que possibilita a determinação de índices de vegetação (NDVI e IAF). A primeira etapa é chamada de Radiância, ou seja, é a conversão do número digital, ND, de cada pixel da imagem em

Radiância espectral monocromática de acordo com a equação de Markham e Baker (1987).

$$L\lambda i = ai + \frac{bi + ai}{255} \text{ ND}$$

onde a e b são as radiâncias espectrais mínima e máxima, respectivamente $(\mathrm{W\,m^{-2}}sr^{-1}\mu m^{-1})$ND é a intensidade do pixel (valor inteiro entre 0 e 255) e i corresponde às bandas do TM –Landsat 5. Os coeficientes de calibração utilizados são os propostos por Chander *et al*, (2007).

A segunda etapa consiste no cômputo da reflectância que é a razão entre o fluxo de radiação refletida e o fluxo de radiação incidente de acordo com a equação de Allen *et al*, (2002):

$$\rho\lambda i = \frac{\pi . L\lambda i}{ESUN\lambda . \cos Z . dr}$$

Onde $L\lambda i$ é a radiância espectral de cada banda, ESUN é a irradiância solar espectral de cada banda no topo da atmosfera $(\mathrm{W\,m^{-2}}\mu m^{-1})$, Z é o ângulo zenital solar e d é o inverso do quadrado da distância relativa Terra-Sol.

As etapas finais do processamento das imagens do LANDSAT 5, é o processamento dos índices de vegetação através da ferramenta “modele maker”. O índice de vegetação de diferença normalizada (NDVI) é calculado a partir da equação de Tucker (1979).

$$NDVI = \frac{\rho_{iv} - \rho_v}{\rho_{iv} + \rho_v}$$

O índice de área foliar (LAI) é descrito de acordo com a seguinte equação:

$$LAI = -\frac{\ln\left(\frac{0,69 - SAVI}{0,59}\right)}{0,91}$$

O cômputo da declividade média foi obtido através da ferramenta “interpreter” e “topographic analysis” sobre a imagem de radar do recorte de cada área.

2.2.3 Classificação

Análise de heterogeneidade de habitat foi realizada utilizando o processo de classificação de imagens não supervisionada, onde de maneira automática dividiu-se o recorte da imagem processada no modelo de NDVI, em 10 classes, quantificamos o número de pixels de cada classe e submetemos a análise de índice de equitabilidade de Pielou, mais utilizada para indicar equitabilidade de espécies no ambiente. Através dos resultados obtidos pela classificação não supervisionada das imagens, a vegetação das áreas estudadas foi caracterizada de acordo com a variação do NDVI.

2.3 Análise de dados

Para o primeiro capítulo os parâmetros de abundância avaliados foram: taxa de avistamento (avistamentos/10 km andados) (GALETTI, 2009), abundância relativa (indivíduos/10 km andados), e tamanho médio de grupo (número total de indivíduos pelo número total de avistamentos). Para esses cálculos, foram utilizados o número total de kilômetros andados correspondentes ao período de atividade de cada espécie. Esses períodos de atividades (diurno, noturno ou catemeral) foram obtidos da literatura (EISENBERG; REDFORD, 1999; EMMONS e FEER, 1997). A biomassa relativa (kg/10 km andados) de cada espécie por unidade de área, foi calculada multiplicando a massa corpórea por sua abundância relativa, como em Galetti *et al*. (2009). A massa corpórea de cada espécie foi considerada como a media aritimética dos valores constantes na literatura em: Eisenberg e Redford (1999), Emmons e Feer (1997), e Reis *et al* (2003).

No segundo capítulo, para cada área amostrada, cálculos de densidade de grupo foram realizados de acordo com o método King's (ROBINETTE, LOVELOSS E JONES, 1974), cuja fórmula é: D = n / 2 x L x S, onde n = é o número de registros, L = comprimento total do transecto e S = distância média animal-observador. Para a obtenção da densidade individual, multiplicamos a densidade de grupo pelo tamanho médio de grupo de cada espécie.

O tamanho de grupo foi calculado como a média aritmética do número de indivíduos de uma determinada espécie e a biomassa foi obtida multiplicando a densidade individual de cada espécie por sua massa corpórea. A massa corpórea de cada espécie foi considerada como a média aritmética de valores registrados por Emmons e Feer (1997), Eisenberg e Redford (1999), Mendes Pontes (2004) e Reis *et al* (2011). A diversidade de espécies foi calculada através do PRIME 6.0 (CLARKE; GORLEY, 2006), utilizando-se o exponencial do índice de Shannon, por pesar todas as variáveis sem favorecer espécies raras ou comuns (JOST, 2006; 2007).

As relações entre massa corpórea e densidade de grupo, densidade individual, biomassa e tamanho de grupo e foram analisadas com o modelo de regressão linear simples com transformação logarítmica de ambos os eixos, o que equivalente a função $D = aW^2$ (SOKAL; ROHLF, 1981). Utilizamos as seguintes categorias, separadamente: (1) toda a comunidade de mamíferos de médio e grande porte, (2) mamíferos terrestres (3) mamíferos arborícolas/escansoreais, e (4) categorias de dieta.

3.0 FUNDAMENTAÇÃO TEÓRICA

3.1 Bioma Amazônia

Amazônia compreende o maior sistema de floresta e rio do mundo. É o palco para uma diversidade impressionante de vida. Com uma estimativa de dois a três mil espécies, a fauna de peixes da Amazônia representa mais de 20% das espécies de peixe de água doce do mundo (LUNDBERG *et al*, 2000; REIS *et al*, 2003). Diversidade florística é enorme, com até 473 espécies de árvores que ocorrem em um único hectare de floresta tropical equatoriana várzea (VALENCIA *et al*, 1994). Não são apenas os números de espécies altas em amazônica ecossistemas notáveis, mas também as interações ecológicas e evolutivas entre as espécies As florestas da Amazônia e rios estão repletos de tais expressões extraordinárias da vida.

A bacia Amazônica cobre mais de 8 milhões de quilômetros quadrados e inclui uma variedade de paisagens, como os tepuis enigmáticas no norte, as encostas florestadas ao pé da Cordilheira dos Andes, no a oeste, e as amplas áreas de floresta na parte central da bacia. Possui a maior floresta tropical da Terra (SIOLI, 1984), que é responsável por 10% da produtividade primária líquida de toda a biosfera terrestre. O rio Amazonas possui 6400 km de comprimento, a partir de sua origem na Cordilheira dos Andes até a sua foz no Atlântico. Os nutrientes entregues pelo rio Amazonas ajuda a promover a vida oceânica que sequestra globalmente quantidades relevantes de carbono (SUBRAMANIAM, 2008).

A região é conhecida por sua grande biodiversidade. Dados que precisem a quantificação desta diversidade ainda não existem, pois as estimativas de números de espécies continuam aumentando. Até o momento sabe-se que a região abriga 7.500

espécies de borboletas (possivelmente cerca de 40% das espécies de borboleta mundo), 1500 espécies de aves, 399 espécies de mamíferos e uma estimativa de 11.200 árvore espécies (Hubbell *et al*, 2008).

3.2 Vegetação da Amazônia

A classificação da vegetação adotada é segundo o Instituto Brasileiro de Geografia e Estatítica (IBGE), que utiliza o sistema fisionômico-ecológico de classificação de vegetação brasileira (IBGE, 1992) que é subdividido em classes, subclasses, grupos, subgrupos, formações e subformações, assim, como exemplos de Classes (Estruturas/Formas de vida) temos: Floresta, Campinarana, Savana; exemplos de Subclasses (Clima/Déficit hídrico) temos: Ombrófila e Estacional; como exemplos de Grupos (Fisiologia/Transpiração e fertilidade) temos: higrófita e xerófita; como exemplos de Subgrupos (Fisionomia/Hábitos) temos: Densa, Aberta, Semidecidual, Decidual, etc.; como exemplos de Formações (Ambiente, Relevo) temos: aluvial, terras baixas, submontana, montana, etc. e como exemplo de subformações temos: dossel uniforme, dossel emergente, com palmeiras, etc.

Na floresta amazônica se destaca a Floresta Ombrófila. No bioma, também ocorrem Savanas, Savanas-Estépicas, Campinaranas, Florestas Estacionais, dentre outros tipos de vegetação primária. Dentre os diferentes tipos vegetacionais da Amazônia, a Floresta Ombrófila Densa é o tipo mais expressivo, que representa 38,2% do bioma, já as Florestas Estacionais Semidecidual e Decidual são os tipos florestais que ocupam menor superfície do bioma Amazônia, com o valor de 5,4% da região e sua ocupação predominante é em posições periféricas, em contato com áreas de Savana.

As Campinaranas estão concentradas nas calhas dos rios Branco e Negro e em pequenas manchas espalhadas por toda a região. As Savanas se concentram no limite sul da Amazônia e no nordeste de Roraima.

3.3 Áreas de endemismo na Amazônia

A maioria das espécies de vertebrados na Amazônia não se apresenta amplamente distribuída, ocorrendo em regiões delimitadas chamadas “áreas de endemismo”, as quais foram delimitadas em estudos clássicos como, Ayres e Clutton-Brock (1992), Carnaval *et al* (2008), Goldani *et al* (2002). Essas áreas são consideradas as menores unidades geográficas para análise de biogeografia histórica (CRACRAFT, 1985; MORRONE, 1994).

Wallace (1852) dividiu a Amazônia em quatro áreas de endemismos: Guiana, Equador, Peru e Brasil, tendo como limites os rios Amazonas-Solimões, Negro e Madeira e desde então sua hipótese vem sendo apoiada por outros autores como, Haffer (2008) e Cracraft (1985), que identificaram sete áreas de endemismo para aves nas áreas de endemismo propostas por Wallace, com algumas subdivisões geradas em algumas áreas e modificação de nomes. Ficando assim: Guiana, Imeri, Napo, Inambari, Rondônia, Pará e Belém. Silva *et al* (2002) sugeriram, baseados em informações filogenéticas de algumas aves, que a área do Pará é composta por duas áreas: Tapajós e Xingu. Dessa forma, de acordo estudos com vertebrados são reconhecidas na Amazônia oito áreas de endemismo

3.4 Diversidade

Duas maneiras extremas de interpretar os fatores que estruturam comunidades têm sido recorrentes na literatura. A escola neutralista enfatiza a importância do acaso e da chance de colonização dos indivíduos (HUBBELL; FOSTER, 1986), e, portanto, comunidades seriam estruturadas por dispersão. A escola determinista considera que a heterogeneidade ambiental é a principal causa para a substituição gradual de espécies em escala regional, logo comunidades seriam estruturadas por nichos (JONES *et al,* 2006).

A Teoria Neutra de Hubbell (2001), pressupõe que a composição local da comunidade não está relacionada às características ecológicas do local, mas da composição da metacomunidade do entorno e da taxa de migração das espécies desta. A mesma teoria considera que todos os indivíduos têm a mesma capacidade de colonizar um determinado local. Portanto, a abundância das espécies dependeria do acaso e da chance, excluindo a ideia de que comunidades são estruturadas de acordo com características individuais, que tornam um indivíduo superior competitivamente em um determinado ambiente. A importância da variabilidade espacial nas condições ambientais, as limitações de dispersão das espécies e as interações interespecíficas como determinantes de diversidade, são pouco conhecidas, principalmente em animais. Estudos com plantas têm sugerido que o ambiente pode ser mais determinante do que efeitos relacionados às limitações na dispersão (TUOMISTO *et al,* 2003; JONES *et al,* 2006) em direção oposta a Teoria de Neutra de Hubbel (2001), contudo Tuomisto *et al* (2003) demonstrou que em ampla escala (até 1400 Km de distância entre os pontos amostrados). Condit *et al*, (2002), comparando áreas de florestas do Panamá, Peru e Equador, observaram um decréscimo na similaridade de árvores com a distância geográfica e atribuiu essas diferenças à maior pluviosidade no Panamá. Esses estudos mostram que distribuição poderia estar sofrendo efeitos da variação ambiental e de fatores relacionados à dispersão agindo em sinergia.

Em relação à escola determinista, a diversidade poderia ser explicada por inúmeros fatores relacionados à heterogeneidade ambiental (JONES *et al*, 2006). Esses padrões de diversidade mudariam de acordo com as diferentes escalas (GASTON, 2000; HILLEBRAND, 2004).

Em escala global e continental (2000 a 10000 km) (PETERSON *et al*, 2011), as variáveis ambientais que mais influenciam na diversidade são: clima, latitude, topografia e heterogeneidade, produtividade (medida através do Índice de Vegetação de Diferença Normalizada-NDVI) e fatores históricos (KERR; PACKER, 1997; KAUFMAN, WILLIG, 1998; HAWKINS, PORTER e DINIZ-FILHO, 2003; HE, ZHANG e ZHANG, 2009; MELO, RANGEL e DINIZ-FILHO, 2009; HOORN *et al*, 2010; SVENNING, FLØJGAARD e BASELGA, 2011; QIAN; XIAO, 2012). Assim, de acordo com esses autores, a diversidade aumentaria em direção aos trópicos, alcançando os mais altos níveis nas regiões mais úmidas, com maiores heterogeneidades topográficas e vegetais. De fato, essas variáveis se apresentam como determinantes da diversidade de mamíferos, pássaros, répteis, anfíbios e invertebrados.

Em escalas regionais (200 até 2000 km) (PETERSON *et al*, 2011) diversidade é positivamente correlacionada com altitude, sazonalidade, pluviosidade, humidade, complexidade topográfica, heterogeneidade ambiental, energia (medida através da Rede de Produtividade Primária) e disponibilidade de recursos. Essas variáveis tem sido apresentadas como determinantes da diversidade de mamíferos, pássaros, répteis, anfíbios e artrópodes em regiões como mediterrâneo, lhanos venezuelanos, florestas tropicais mexicanas e savanas africanas (TEWS *et al*, 2004; ROMPRÉ *et al*, 2007; JANKOWSKI *et al*, 2009; TELLO e STEVENS, 2010; JONSSON, ENGLUND e WARDLE, 2011; RICKART *et al*, 2011). De acordo com esses autores, essas regiões com maior humidade, elevação, produtividade primária e mosaicos vegetacionais mais complexos, irão comportar maiores diversidades.

Em escala de paisagem (de 10 até 200 km) (PETERSON *et al,* 2011), diversidade tem sido determinada pela pluviosidade, topografia, heterogeneidade do habitat e produtividade primária medida à partir do Índice de Vegetação de Diferença Normalizada (NDVI) (ABRAMSKY, 1988; CUETO e CASENAVE, 1999; ROMPRÉ *et al*, 2007; LASSAU e HOCHULI, 2008). Essas variáveis foram determinantes da diversidade de besouros, pássaros e também de mamíferos, em diferentes ambientes, como dunas do mediterrâneo, florestas temperadas e tropicais.

Em escala local (1-10 km) (PETERSON *et al*, 2011) as mais importantes variáveis que determinam diversidade são, heterogeneidade espacial do habitat, altura da floresta, continuidade do dossel, humidade e produtividade, todos apresentando uma relação positiva com a diversidade em várias regiões da terra (KAY *et al,* 1997; PERES, 1997; STEVENSON, 2001; WILLIAMS, MARSH e WINTER, 2002; HAUGAASEN; PERES, 2005; LOUYS et al, 2011; MENDES PONTES, PAULA e MAGNUSSON, 2012). Esses foram os determinantes da diversidade de mamíferos e primatas na Amazônia central e setentrional, bem como Floresta Atlântica, Caatinga e Pantanal, no Brasil.

A produtividade primária vem sendo apontada como o mais importante fator para determinar a estrutura das comunidades (HE; ZHANG, 2009; He *et al*, 2009; STEVENSON, 2001). Diversos estudos sobre o relacionamento produtividade-diversidade têm sido realizados, mas os resultados permanecem inconclusivos. Alguns estudos esclarecem que deve haver cuidado quanto à escala a ser observada nessa relação (SAFFORD, REJMANEK e HADAČ, 2001) e possivelmente a escala estaria mostrando discrepâncias entre diferentes estudos que observam a relação diversidade-produtividade. (WAIDE *et al*, 1999; MITTELBACH *et al*, 2001). Em grandes escalas, como biomas ou grandes regiões geográficas a produtividade dos ambientes é positivamente correlacionada com a diversidade. (FRANCIS e CURRIE, 1998; HAWKINS, PORTER e DINIZ-FILHO, 2003), já em menores escalas essa relação não se mostra tão robusta. (SAFFORD *et al*, 2001).

Estudar diversidade entre comunidades de diversos organismos é um problema quando existe pouco conhecimento taxonômico de um determinado grupo. No caso dos vertebrados, mesmo sendo um grupo taxonomicamente bem conhecido e bem estudado, os estudos se concentram em padrões biogeográficos, análise regional de espécies e distribuição geográfica, enquanto estudos sobre variação regional de diversidade permanecem raros. Entender como as comunidades de organismos se complementam em diferentes localidades é de fundamental importância para objetivos conservacionistas, como um bom planejamento de estabelecimento de reservas e ações de defesa do meio ambiente (MARGULES *et al*, 2002).

3.4.1 Diversidade de primatas

A diversidade de primatas na Amazônia vem sendo estudada primordialmente através do parâmetro riqueza, essa riqueza se apresenta bastante variável, com registros de regiões com até 16 espécies simpátricas ao longo do Rio Madeira (MESSIAS *et al*, 2005; OLIVEIRA *et al*, 2005), ou entre 13 e 14 espécies simpátricas no centro-oeste da Amazônia (PERES, 1988, 1990, 1997; HAUGAASEN; PERES, 2005), enquanto que em áreas com menor diversidade, no escudo das Guianas, se observa entre 5 e 7 espécies (NUNES, 1995; LEHMAN, 2000, 2004; MENDES PONTES/, 2004). Esta variação de riqueza em diferentes regiões da Amazônia pode ser atribuída a variações na fertilidade do solo (EMMONS, 1984), diversidade de habitats (HAUGAASEN; PERES, 2005), produtividade de frutos (STEVENSON, 2001; HANYA *et al*, 2011), produtividade primária (medida através da serapilheira) (KAY *et al*, 1997) e altitude (MELO *et al*, 2009), isolamento de populações por barreiras fluviais (KAY *et al*, 1997; STEVENSON, 2001; BEAUDROT; MARSHAL, 2011), ou ainda de acordo com um padrão longitudinal, com um aumento da diversidade no sentido leste a oeste (PERES; JANSON, 1999). Aumento na produtividade primária pode gerar diferentes resultados: (i) aumento na diversidade e biomassa de consumidores primários (BEGON, 2006), (ii) aumento na biomassa mas decréscimo na diversidade (ROZENWEIG, 1992), (iii) aumento na diversidade e manutenção da biomassa por espécies (BEGON, 2006).

3.5 Abundância de mamíferos

A abundância de mamíferos decresce com o aumento da massa corporal dos mesmos (PETERS; WASSENBERG, 1983; PETERS; RAELSON, 1984; CHIARELLO, 1999). No entanto o fator dieta influencia nesse tipo de relação, fazendo com que carnívoros sejam menos abundantes do que os herbívoros (PETERS; WASSENBERG, 1983; MENDES PONTES, 2003). Biedermann (2003), mostrou que existe uma relação positiva entre o tamanho do corpo de animais terrestres e o tamanho de seus habitats. Outros estudos, no entanto, mostram a importância da dieta como determinante da abundância de populações de mamíferos, ou seja, espécies que possuem dieta muito específica ou ocupam altos níveis tróficos, tendem a ocorrer em menor densidade, devido a menor disponibilidade de alimento. (KINNAIRD; EISENBERG, 1989). Certas espécies generalistas, as quais se adaptam melhor a áreas degradadas, possuem suas densidades aumentadas em seus habitats (FONSECA; ROBINSON, 1990).

Com relação à abundância de primatas, tem sido evidenciado que o seu fator determinante é a disponibilidade de alimento (PERES, 1997; MENDES PONTES, 1999), a fertilidade do solo também tem sido relatada como determinante de abundância, visto que estaria diretamente ligada à produtividade da floresta, assim como a complexidade estrutural da floresta (EMMONS, 1984). Para primatas frugívoros, a disponibilidade de frutos tem sido apontada como o principal fator que afeta a abundância de primatas (JANSON; CHAPMAN, 1999; STEVENSON, 2001). A forma como os primatas usam o ambiente, preferindo um tipo vegetacional em detrimento de outro, poderia ser reflexo da produtividade de alimentos e competição interespecífica (MENDES PONTES, PAULA e MAGNUSSON, 2012).

Para primatas, a vida em grandes grupos pode ser benéfica por uma série de fatores, como aumentar a defesa contra predadores, aumentar a eficiência de forrageio e ataques conspecíficos. No entanto, grupos maiores necessitariam viajar maiores distâncias para busca de alimento e o gasto energético poderia não ser viável (CHAPMAN; CHAPMAN, 2000). Dados empíricos mostram que em ambientes muito produtivos, os grupos de primatas folívoros tendem a ser mais numerosos (SNAITH; CHAPMAN, 2007). Para *Cebus apela*, análise em uma área da Caatinga demonstrou que a média de grupo não se altera mesmo nos ambientes menos produtivos, o que poderia ser atribuído à sua extrema plasticidade alimentar e capacidade cognitiva (MOURA, 2007).

3.6 A relação Densidade vs. Massa Corpórea

A relação entre densidade (D) e massa corpórea (M) tem sido fonte de inúmeros debates ao longo de mais de 25 anos (HAYWARD, 2010), contudo, controvérsias têm surgido a respeito da forma dessa relação e parte dessas controvérsias surgem do fato de que as relações são influenciadas por uma série de fatores, entre eles, a origem dos dados, que podem provir de compilações ou comunidades reais e a escala de observação (WHITE *et al*, 2007).

Os primeiros estudos sobre o tema, realizados em escala global com mamíferos, surgiram de compilações de dados, as quais resultaram em inclinações da reta em torno de -0.75, o que levou Damuth (1981) a defender a ideia de que as populações de espécies de diferentes tamanhos usariam a mesma quantidade de energia do ambiente em iguais proporções, baseado no fato de que a taxa metabólica individual aumenta linearmente com a massa corpórea e com uma inclinação em torno de 0.75 (KLEIBER, 1975). Este conceito se tornou posteriormente conhecido como Regra da Equivalência Energética (REE) (NEE *et al*, 1991). Em estudos posteriores, em escala global, abrangendo principalmente o grupo mamíferos, Damuth (1987, 1993) reafirmou sua teoria negando a influência de fatores como competição e dieta, continuou demonstrando uma inclinação com poder de -0.75.

Estudos em outras escalas como Robinson e Redford (1986) em comunidades reais de mamíferos em escala continental, corroboraram a REE, analisando toda a comunidade de mamíferos. Nessa mesma escala, discordando da REE, Ernest (2005), através da análise do uso da energia pelas populações, concluiu que esse uso não é uniforme.

Em escala regional, Juanes (1986), cujos resultados não corroboram a REE, argumenta que o padrão seria diferente para aves, devido ao uso do habitat em três dimensões. Peters e Wassenberg (1983), estudando mamíferos em escala regional e também local, encontraram variações no padrão de acordo com a dieta e táxon, demonstrando diferenças entre os grupos quanto à inclinação da reta. Em um outro estudo em nível regional, Russo *et al*, (2003), estudando aves, sugeriu que estudos em nível de comunidade reduz a amplitude das massas corpóreas, tornando a relação mais fraca.

Em escala local apenas três estudos defendem a REE. Nee *et al*, (1991) num estudo com aves, corroborou a REE, no entanto, separando as análises por diferentes grupos não encontrou consistência. Bohlin *et al* (1994) num estudo com peixes em escala local, encontraram uma relação próxima de -1, o que enfraquece a REE, mesmo que o autor tenha defendido a mesma.

A maioria dos estudos em comunidades reais, com as escalas variando de continental a local, mostrou resultados inconsistentes com a REE. Pagel *et al* (1991) estudando dados de relações de 72 comunidades naturais, encontraram que as relações D-M foram fracas na maioria das comunidades. Schmid *et al* (2000) obteve resultados consistentes com a REE, contudo analisando as diferenças entre táxons, concluiu que apenas a REE não explicaria toda a relação. Stork e Blackburn (1993), num estudo com artrópodes, encontraram relações negativas com inclinações em torno de -3.25, mostrando extrema discrepância com a REE. Blackburn e Lawton (1994) estudando comunidades terrestres, aquáticas e marinhas, encontraram relações negativas, altamente variáveis, mas com baixo poder de explicação (r^2), apesar das inclinações serem mais negativas do que -0.75.

Também discordando do ponto de vista da REE, Marquet *et al* (1995), em um estudo com organismos intertidais, em seu estudo relacionando o uso da energia com a massa corpórea das espécies concluiu que a REE não tem consistência empírica, visto que o uso da energia pelas populações variou de acordo com a dieta e tamanho do corpo. Brown e Maurer (1986), estudando peixes, aves e mamíferos encontrou uma relação fraca (b= -0.30) entre D-M. Morse *et al* (1988), num estudo local com artrópodes, também encontrou uma fraca relação.

Desta forma, dos modelos que já surgiram para explicar essa relação, apenas Damuth (2007) reafirma a REE, ressaltando que em relações com inclinações mais negativas que -0.75 indicam mais baixo uso de energia pelas espécies de maior porte no ambiente, fazendo das mesmas mais susceptíveis à extinção. Adicionalmente, os estudos de modelagens posteriores refutaram esta teoria. Currie (1993), Loeuille e Loreau (2006) e Hayward *et al* (2010) propuseram modelos e não chegaram a corroborar a REE.

3.6.1 Determinantes das relações D-M

3.6.1.1 Dieta e metabolismo das espécies

Damuth (1987, 1993) negou a influência da dieta nas relações D-M, afirmando que mesmo dentro de um nível trófico em particular ou categoria de dieta, o uso da energia permaneceria relacionado com o tamanho do corpo com inclinação de 0.75, contudo, a dieta tem sido apontada como um dos principais determinantes da relação D-M. Robinson e Redford (1986) ressaltaram a importância da dieta nas relações D-M, concluindo que a abundância das populações de mamíferos é limitada pela disponibilidade de recursos do ambiente. Marquet *et al* (1995), mostraram em seu estudo relacionando o uso da energia com a massa corpórea das espécies e mostraram que a REE não tem consistência empírica porque o uso da energia pelas populações varia de acordo com a dieta e tamanho do corpo.

Assim como Robinson e Redford (1986) trouxeram à tona a ideia de que os recursos de uma forma geral influenciariam nas relações D-M, Ernest (2005) relacionando o uso da energia por espécies de diferentes classes de tamanho, concluiu que seus resultados não apoiam a ideia de que o uso da energia é uniforme ao longo de diferentes classes de tamanho. Ernest (2005) também não suportou a ideia de que picos de energia resultariam em agregação de espécies de tamanhos similares nas comunidades e que nesse caso, o uso uniforme da energia não ocorreria em comunidades de pequenos mamíferos. No entanto, de acordo com Meehan *et al* (2004), não apenas a dieta e a disponibilidade de recursos exerceriam efeitos sobre a relação densidade vs. massa corpórea, mas o metabolismo individual aumenta com a produtividade com o poder de 0.61 e decresce com a massa corpórea e temperatura do ambiente, Desta forma, pequenas espécies são menos abundantes em locais frios. Esses resultados enfatizam a importância do metabolismo em nível individual para entender padrões ecológicos em grandes escalas.

3.6.1.2 Metodologias aplicadas

As escalas de estudo mais amplas, podem aumentar a amplitude das massas corpóreas, o que pode levar a inclinações mais próximas de -0,75. Em menores escalas, a baixa amplitude das massas corpóreas, tem sido sugerida também como determinante de uma fraca relação D-M. Juanes (1986) e Cotgreave (1992) estudando aves, mostraram que a relação fraca poderia ser explicada, além das peculiaridades do grupo em questão, por uma baixa amplitude de massas corpóreas (e.g. amplitude entre 112.0-4536 para raptores). Russo *et al* (2003), também em seu estudo com aves, ratificaram que estudos em nível de comunidade reduz a amplitude das massas corpóreas, tornando a relação mais fraca. Ainda relacionando com os métodos de estudo, Blackburn *et al* (1993), testou dois modelos de regressão linear e encontrou diferenças entre o Método dos Mínimos Quadrados (MMQ) e Eixo Maior Reduzido (EMR), percebendo que o modelo de regressão baseado no MMQ produz retas com menores inclinações, próximas de zero. Blackburn *et al* (1993) mostrou que o modelo de regressão linear adotado teria grande influência nos resultados. Hayward *et al* (2010) em seu modelo, mostrou que a relação D-M pode ser resultado de mecanismos biológicos e revisando explicações de trabalhos prévios pôde perceber que os mecanismos usados para explicar a variação nas relações, invocam mecanismos associados à massa corpórea e sugere que a amplitude de massa corpórea seria o principal fator explicativo. Hayward *et al* (2010) conclui em seu modelo que a REE seria corroborada, mas se limitando em maiores escalas de observação.

Blackburn *et al* (1993), estudando comunidades reais de aves e insetos, encontrou fracas relações entre D-M, argumentando que as comunidades do seu estudo não seriam limitadas por energia, exceto as espécies mais abundantes. De acordo com o mesmo autor, as espécies raras estariam atuando enfraquecendo a inclinação da reta, sendo sua relação fraca ou negativa. Essa relação se mostraria mais forte em menores escalas (regional e local), refutando a REE.

3.6.1.3 Porte das espécies

Pagel *et al*, (1991) estudando dados de relações de 72 comunidades naturais, encontraram que as relações D-M foram fracas na maioria das comunidades, podendo ter sido afetadas pela baixa densidade de pequenas espécies, o que é explicado pela distribuição desigual dos recursos, pela maior flutuação populacional e pelo fato de serem mais susceptíveis à extinção.

No tocante às vantagens das espécies de maior porte no ambiente, Brown e Maurer (1986), estudando peixes, aves e mamíferos, encontraram uma relação fraca (b= -0.30) e argumentaram que o seu estudo diferia do estabelecido pela REE devido ao fato das espécies de maior porte dominarem o ambiente alterando as relações D-M.

3.6.1.4 Alta mobilidade, migrações e táxon

Juanes (1986) Em seu estudo mostrou que a relação D-M para aves é mais fraca do que para mamíferos devido à ampla variedade de recursos nas três dimensões de seus nichos. Morse *et al* (1988), num estudo local com artrópodes, também encontraram uma fraca relação, a qual foi atribuída a alta mobilidade das espécies e capacidade do uso do ambiente em várias dimensões. Cotgreave (1992) também justificou a fraca relação D-M encontrada no seu estudo com aves, pela migração e uso das três dimensões de habitat, o que afirmou ser uma peculiaridade do seu grupo.

3.6.1.5 Relações filogenéticas

Nee *et al* (1991), num estudo com aves, corroboraram a REE. Entretanto, separando as análises por diferentes grupos percebeu a importância das relações filogenéticas entre os táxons. Nee *et al* (1991) mostrou que quanto menos relacionados são os grupos estudados (e.g. pica-paus e passeriformes), há maior possibilidade de uma relação positiva. O estudo aponta para a possibilidade de que diferentes localidades com diferentes histórias evolutivas (e.g Inglaterra e Suécia) possam mostrar diferenças na relação D-M devido ao relacionamento filogenético dos espécimes.

3.6.1.6 Estabilidade do ambiente

Notando uma ausência de padrão entre consumo de energia e tamanho das espécies em diferentes ambientes com diferentes níveis de estabilidade, Jennings e Mackinson (2003), resolveram testar os efeitos da estabilidade do ambiente nas relações D-M em uma teia trófica marinha. Chegaram à conclusão de que retas mais íngremes seriam encontradas em ecossistemas mais estáveis, mostrando que menores oscilações na disponibilidade de recursos, tornaria a relação D-M mais de acordo com a REE.

Makarieva *et al* (2004), em seu modelo com inúmeras comunidades naturais mostraram que em ecossistemas instáveis, onde o ambiente é moldado por processos abióticos (e.g. fluxos de matéria orgânica), nenhuma restrição ecológica pode ser imposta nas flutuações bióticas do ambiente, como mudanças promovidas por grandes heterótrofos. Como consequência disso, em ecossistemas instáveis o fluxo de energia pode ser distribuído irregularmente em diferentes classes de tamanho, não mostrando dependência do tamanho do corpo.

3.6.1.7 Distribuição dos recursos no ambiente

Pagel *et al* (1991) estudando as relações D-M em 72 comunidades naturais, encontraram que as relações foram fracas na maioria das comunidades, podendo ter sido afetadas pela baixa densidade de espécies de pequeno porte. Isto seria explicado pela distribuição desigual dos recursos e pela maior flutuação populacional, concluindo que características individuais, relacionadas à massa corpórea e dieta, devem ser levadas em conta nessa relação. As espécies de menor porte possuem altas taxas metabólicas, o que as forçaria a viver em áreas concentradas de recursos energéticos. Se esses recursos são distribuídos de forma desigual no ambiente, elas estariam confinadas em agrupamentos nas comunidades.

Ernest (2005) mostrou que a relação foi afetada pela baixa densidade de espécies de menor porte, o que parece ser uma função da distribuição dos recursos no ambiente, pela maior flutuação populacional e por sofrerem mais predação. Ernest (2005) mostrou ainda que características individuais devem ser levadas em conta nessa relação. Loeuille e Loreau (2006), em seu modelo com variados grupos biológicos, encontraram uma fraca relação D-M, mostrando que os recursos não são igualmente distribuídos entre as diferentes massas corpórea, ressaltando a importância da interação entre as espécies como uma variável explicativa das variações encontradas.

3.6.1.8 Conclusões sobre relações Massa corpórea vs. Abundância

Após décadas de estudos, pode-se concluir que a REE é inconsistente, exceto em compilações de estudos de amplas escalas, onde muitos fatores, como vantagens competitivas, amplitude das massas corpóreas, presença de espécies raras, exerceriam pouca influência na inclinação da reta (HAYWARD, 2010). Até o momento, nenhum estudo considerou a importância da diversidade de espécies sobre a relação tamanho do corpo e abundância. Apesar de Hayward (2010) ter percebido que em comunidades com maior riqueza de espécies a relação massa corpórea densidade se torna mais clara, pois força os indivíduos a dividirem os recursos de forma mais equilibrada, nenhum estudo considerou índices de diversidade correlacionados com o coeficiente de regressão. A diversidade de espécies em um ambiente é influenciada pelo balanço entre imigração e extinção, assim como inúmeros outros fatores relacionados ao nicho ou capacidade de dispersão, os mesmos fatores poderiam ser influenciados pela massa corpórea das espécies (PETERS, 1983). Assim, a maneira como as comunidades se estruturam nos mais diversos tipos de habitat, poderiam influenciar a forma da relação tamanho do corpo abundância.

3.7 Sensoriamento remoto

Tradicionalmente, a maioria dos estudos relacionando diversidade e variáveis ambientais é baseada em dados de campo de biomassa e cobertura vegetal ou dados climáticos como temperatura e evapotranspiração. Avanços na tecnologia de sensoriamento remoto têm possibilitado estudar a dinâmica dos ecossistemas e monitorar mudanças na diversidade de espécies, baseados na refletância espectral da vegetação (NAGENDRA, 2001; PETTORELLI *et al*, 2005).

Índices de vegetação obtidos por imagens de satélite têm sido amplamente utilizados por ecólogos para verificar a relação entre produtividade, biodiversidade e heterogeneidade ambiental (HE & ZHANG, 2009). O índice de vegetação de diferença normalizada (NDVI) tem sido amplamente usado para correlacionar observações de sensoriamento remoto com características da vegetação (MYNENI; WILLIAMS, 1994; TOTTRUP; RASMUSSEN, 2004). O mesmo índice revelou-se quantitativamente e funcionalmente relacionado à vários parâmetros vegetacionais, como índice de área foliar (IAF), percentual de cobertura vegetal, radiação fotossinteticamente ativa interceptada (IPAR) e biomassa verde (MYNENI; WILLIAMS, 1994; ELVIDGE; CHEN, 1995).

A relação entre o Índice de Vegetação de Diferença Normalizada (NDVI) tem sido estudada por um longo período de tempo e tem sido bem documentada (PETTORELLI *et al*, 2005; TURNER *et al*, 2003). Estes índices de vegetação nada mais são do que a razão entre medidas de reflectância de bandas, principalmente na faixa do vermelho e do infravermelho próximo, e entre eles, um dos mais usados é o Índice de Vegetação por Diferença Normalizada (NDVI). Este índice é considerado por muitos pesquisadores como um bom indicador do crescimento e do vigor da vegetação.

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4.0 Capítulo 1

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Silva Júnior, A.P., Galvíncio, J.D., Mendes Pontes, A.R. Environmental determinants of primate diversity and abundance in the Rio Negro basin, northern Brazilian Amazonia

Environmental determinants of primate diversity and abundance in the Rio Negro basin, northern Brazilian Amazonia

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Summary: ***Purpose:*** Since species diversity and abundances in tropical forests follow some widely-accepted patterns, in which habitat diversity leads to species diversity because of habitat heterogeneity (or forest diversity), we aimed at testing if increasing habitat diversity (or heterogeneity) would lead to an increase in species diversity and, additionally, to test if biomass and group size would follow the same pattern in the Rio Negro basin, northernmost Brazilian Amazonia.

Methods: In a regional scale that encompassed five study sites we carried out diurnal and nocturnal line transect surveys, from which we obtained the dependent variables primate diversity indexes, relative abundance and biomass, and the predictive variables Normalized Differential Vegetation Index – NDVI, Leaf Area Index - LAI, and Digital Elevation Module (DEM - also known as slope), and run a Generalized Linear Module, based in an Akaike Information Criterion (AIC), in order to determine which of these predictive variables explained this relationship and to which extent.

Results: There was a significative negative correlation between NDVI and mean group size (R=-0.65, p=0.015), LAI and mean group size (R=-0.64, p=0.017), Slope and mean group size (R=-0.67, p=0.008) and heterogeneity and mean group size (R=-0.67, p=0.008). The GLM, however, based in the AIC, showed NDVI and Slope as the best explanatory variables for mean group size.

Discussion: Vegetation indexes, slope and heterogeneity did not explain primate diversity. Primate abundances in the Rio Negro basin can be explained by three different scenarios, which consists of: (1) sites of ombrophilous dense tropical rainforests with absence of campinaranas and campinas, in which the abundance of some species and mean group sizes were reduced; (2) sites with terra firme forests mixed with campinas and campinaranas, with relative biomass and mean group sizes

comparatively higher; and (3) the hypothetical scenario, involving the entire Rio Negro basin, where large areas of campinas and campinaranas would consist of poorly suited environments for primates.

Key-words Primate Diversity, Remote sensing, Diversity Index

Introduction

Species diversity and abundances in tropical forests follow some widely-accepted patterns, in which larger areas tend to have more species (MacArthur & Wilson 1967), (Peres & Janson 1999) and habitat diversity leads to species diversity (Rosenzweig 1995). This seems to be possible because of habitat heterogeneity, which enhances opportunities for different, but closely-related, species, or even competitors, to co-exist (Chesson & Rozenzweig, 1991).

Diversity can vary at multiple scales (Gaston 2000; Hillebrand 2004), from global (linear distance between sites from 10000 km) to site (10 to 1000 m), or even in a micro scale within single sites (<10 m) (see Figure 6.2 from Peterson *et al.* 2011). Thus, it depends on the spatial extension of the biogeographical and ecological processes that govern it (Cornell & Lawton 1992). Climatic fluctuations may, for instance, impel competition, or interference competition, and lead to competitive exclusion of the out-competed, and to a decrease in diversity (Chesson & Huntly 1988; Post & Stenseth 1998).

At the regional scale (200 and 2000 km) (Peterson *et al.* 2011) diversity and abundance appears to be positively correlated to altitude, seasonality, rainfall, and therefore, humidity, topography complexity, habitat heterogeneity, energy (as a measure of Net Primary Productivity (NPP), and resource availability. This has equally been shown to influence mammals, birds, reptiles, amphibians, and arthropods in regions as diverse as

Mediterranean, Venezuelan lhanos, Mexican tropical rainforests and African savannas (August 2003; Tews *et al*. 2004; Romprè *et al*. 2007; Jankowski *et al*. 2009; Tello & Stevens 2010; Jonsson, Englund & Wardle 2011; Rickart *et al*. 2011). According to these authors, those regions with higher humidity, elevation, and primary productivity, and more complex vegetation mosaics, would hold the highest diversities and abundances.

At the landscape level (10 to 200 km) (Peterson *et al*. 2011), diversity and abundance hasbeen shown to be a function of rainfall, topography and habitat heterogeneity, and productivity of the environment measured from Normalized Differential Vegetation indexes (NDVI) (Abramsky 1988; Bohning-Gaese 1997; Cueto & Casenave 1999; Rompré *et al* 2007; Lassau & Hochuli 2008). These variables were the determinants of the diversity of beetles, birds and mammals, in different environments, such as Mediterranean dunes, temperate and tropical forests.

At the local scale (1-10 km) (Peterson *et al*. 2011) the most important variable determining diversity and abundance appears to be habitat spatial heterogeneity, forest height, canopy continuity, humidity, productivity and soil fertility, all presenting a positive relationship with diversity and abundance in various regions of the earth (Kay *et al*. 1997; Peres 1997; Stevenson 2001; Williams *et al*. 2002; Haugaasen & Peres 2005; Louys *et al*. 2011; Mendes Pontes, Paula & Magnusson 2012). These were the determinants of mammal, and primate diversity abundance, in central and northern Amazonia, tropical rainforests of Central America, as well as Atlantic forest, dry scrub Caatinga and Pantanal, in Brazil.

Primate diversity and abundance in the Amazonia seems to be highly variable in different regions, but show a general trend in which it decreases from the richest edaphic mosaics of the Andean substrates in the western and northwestern basin, towards the Guyana shield, where, despite the much older history of geological stability, has considerably poorer soils, and drier and more seasonal climates (Hoorn *et al*. 2010). Thus, the richest communities are along the Madeira river in the western Amazonia where up to 18 species may occur sympatrically (Iwanaga 2004), which is followed by Central Amazonia, where between 13 and 16 species may occur (Peres 1997; Haugaasen & Peres 2005), and the poorest is the northern Amazonia, where a maximum of 9 and a minimum of 2 species may co-exist (Lehman 2000, 2004; Mendes Pontes, Paula & Magnusson 2012).

This richness gradient has been hypothesized to be a result of soil quality, habitat diversity, primary productivity, altitude, or interfluvial barriers (Emmons 1984; Ayres & Clutton-Brock 1992; Kay *et al*. 1997; Stevenson 2001; Melo, Rangel & Diniz-Filho 2009; Hanya *et al*. 2011). No studies to date, nevertheless, have quantified and tested the effects of productivity, leaf cover, or slope, all related to the above mentioned hypothesis, as genuinely explaining primates diversity and abundance in Amazonia. Even more, diversity and abundance are frequently measured without taking into account species group size, which narrows the informative power of the analysis (Koleff, Gaston & Lennon 2003; Jankowski *et al*. 2009), since they are also significantly affected by those scenopoetic and bionomic variables, such as the availability and divisibility of food resources in the environment (Hutchinson & MacArthur 1959; Brown 1981; Schoener 1983; Brown & Maurer 1986; Juanes 1986; Robinson & Redford 1986; Maurer & Brown 1988; Nee *et al*. 1991; Mendes Pontes *et al*. 1997).

Primate biomass, nevertheless, varies widely according to the region (Rudran 1979; Emmons 1984; Peres 1997; Janson & Chapman 1999; Mendes Pontes 1999; Stevenson 2001; Haugaasen & Peres 2005; Mendes Pontes, Paula & Magnusson 2012). It increases with increasing body weight and is shaped mainly by diet (Eisenberg, O'Connell & August 1979; Peters & Wassenberg 1983; Robinson & Redford 1986). Equally variable are group sizes (Mittermeier & van Roosmalen 1981; Defler & Pintor 1985; Johns 1985; Peres 1993; Mendes Pontes 1997; Chapman & Chapman 2000), which are also related to food acquisition, protection against predation, and is balanced by body weight (Terborgh & Janson 1986), albeit their dynamics in relation to diversity is unknown.

The use of remote sensing techniques based in the vegetation spectral reflectance to assess and monitor species diversity has become increasingly disseminated (Nagendra 2001; Pettorelli *et al.* 2005), due to providing a comparatively more robust, standardized and comparable tool to assess how species assemblages change along the landscape and at different scales (Nagendra 2001; Turner *et al.* 2004; Pettorelli *et al.* 2005; Lassau & Hochuli 2008; He, Zhang & Zhang 2009).

Since most of the variables previously used to explain primate diversity in the region, such as soil quality, habitat diversity, primary productivity, and altitude (Emmons 1984; Ayres & Clutton-Brock 1992; Kay *et al.* 1997; Stevenson 2001; Melo, Rangel & Diniz-Filho 2009; Hanya *et al.* 2011), may indeed be part of the scenopoetic variables that govern them at larger scales, we aimed at determining the contribution of productivity, leaf cover, slope and heterogeneity to primate diversity and abundance, and consequently, biomass and group size at the regional level in the Rio Negro basin, Northern Brazilian Amazonia.

Materials and methods

Study areas

Design

Aiming at detecting changes in primate diversity at the regional scale (linear distances between sites from 200 to 2000 km (Peterson *et al*. 2011) in the Rio Negro basin, northernmost Brazilian Amazonia, we selected five study sites located in different latitudes and encompassing the major regional phytophysiognomies, which spam from mostly ombrophilous dense tropical rainforests (characterized by tall trees (40 m-60 m) with massive trunks and sometimes large buttresses or stilt roots) to mostly dry forests, including also the intermediate, shorter, thinner Campinaranas, and the highly discontinuous, short campina (IBGE 2010; RADAMBRASIL 1975), recognizable from satellite images (Table 1). Since hunting did not present any statistically significant impact on the primate communities of the two human settlements of the chosen scenario (Alves 2012; Melo 2012), they were also included in this study.

Surveys of medium- and large-sized mammals

The surveys of medium- and large-sized mammals were performed using the line transect method (Burnham, Anderson & Laake 1980; Buckland *et al*. 1993). Three parallel 5-km trails were used in each of the study areas, with the exception of Maracá Ecological Station, which had only two non-parallel trails. In the case of Uatumã Biological Reserve and Viruá National Park, we used three trails from the Long-Term

Ecological Research Project (RAPELD) 25-km^2 standard grid system of the Biodiversity Research Program (PPBio) (www.ppbio.inpa.gov.br). They were all alphanumerically marked every 100 m with metal tags and were totally cleared of debris to minimize disturbance when walking.

The diurnal surveys were conducted between 07:00 and 17:30h. On average, 10 km was covered per day at an average speed of 1 km/h. The nocturnal surveys were conducted between 18:30 and 04:30 h, traveling on average 8 km per night at an average speed of 1.25 km/h. During the nocturnal surveys, headlamps were used to illuminate the trail, and long-range flashlights were used to view the animals.

The mammal surveys here used comprise the data matrix from the Rio Negro basin, as follows: (1) Maracá Ecological Station (Jan. 1997/ Jan. 98); (2) Novo Paraíso human settlement (Dec. and Jan. 2010); (3) Entre Rios human settlement (Jan. and Feb. 2012); (4) Viruá National Park (March 2011), and (5) Uatumã Biological Reserve (Sept. 2011). For each animal or group of animals seen during the surveys the following data were recorded: group size, perpendicular distance, time and location along the trail.

Mammal surveys were carried out by the same experienced observers and trained field assistants who walked in pairs and alternately in the different transects. Walking speed was controlled through time of arrival in each 100 m alphanumerical transect marking.

Remote sensing

For the five studied areas vegetation indexes were obtained from images from the sensor TM (Thematic Mapper) of Landsat 5 considering the least cloud cover and those periods closest to the collection of the bionomic variables (see Table 1). Subsequently, we determined the Normalized Differential Vegetation Indexes (NDVI) and Leaf Area Index (LAI) of each area, according to Tucker (1979), using Erdas Imagine 9.3 (Licenced to the Department of Geographic Sciences, Federal University of Pernambuco, Brazil). Topography images were obtained from Digital Elevation Modules (DEM) generated from the mission SRTM (Shuttle Radar Topography Mission) of Endeavour, re-sampled in order to equalize them with the images from landsat 5.

In order to determine habitat heterogeneity we divided the NDVI of each of the study areas into 10 classes (unsupervised classification), and quantified the number of pixels in each of them to subsequently determine their eveness.

Data analysis

We calculated for each species in each area: relative abundance (individuals/10 km walked), which is encounter rate multiplied by mean group size, and relative biomass (kg/10 km walked), which is body weight multiplied by their relative abundance (Galetti *et al*. 2009). For these calculations, only the total number of kilometers walked that corresponded to the activity period of each species was considered (diurnal, nocturnal, or cathemeral), obtained from literature (Emmons & Feer 1997; Mendes Pontes 2004; Reis *et al*. 2011).

Body mass of each species was considered as the arithmetic mean of the values reported by Emmons and Feer (1997) and Mendes Pontes (2004). Species diversity was calculated through the Shannon index exponential, chosen due to weighting all variables for their frequencies without favoring rare or common species, ‘the true diversity’ (Jost, 2006; 2007). Subsequently, we compared the diversity indexes among the five studied areas by a Kruskall Wallis test. Habitat heterogeneity was calculated through the Eveness Pielou's index (Brower & Zar 1984), with PRIME 6.0 (Clarke & Gorley 2006).

A Kruskal Wallis test was used to test if there was any statistically significant difference in species relative biomass, mean group size, and diversity indexes (H'), among the five studied areas. A subsequent Mann-Whitney test was used to identify which of those areas differed among them. In order to determine which of the predictive variables (NDVI, LAI, Slope, Heterogeneity) were correlated to the dependent variables diversity, relative abundance and group size we run a Spearman Correlation, and subsequently run a Generalized Linear Module, based in an Akaike Information Criterion (AIC), with the only correlated dependent variable group size.

Results

Primate abundance and diversity in the five study sites

During this study we recorded 10 primate species in the five study sites (Table 2), which were: *Alouatta macconnelli* (Linnaeus 1766), *Aotus trivirgatus* (Humboldt 1812), *Ateles belzebuth* (Geoffroy 1806)*, Ateles paniscus* (Linnaeus 1758), *Cebus apella* (Linnaeus 1758), *Cebus olivaceus* (Schomburgk 1848), *Chiropotes satanas* (Hoffmannsegg 1807)*, Pithecia pithecia* (Linnaeus 1766), *Saguinus midas* (Linnaeus 1758)*, Saimiri sciureus* (Linnaeus 1758).

Only two species showed significative diferences on their relative biomass in relation to the five studied areas, namely: *Cebus apella* (H=10.45, p=0.033) and *Pithecia pithecia* (H=8.51, p=0.036) (Table 2). The relative biomass of *Cebus apella* was higher in Viruá

(55.65 kg/10km), followed by Novo Paraíso (25.57 kg/10km). *Pithecia pithecia* showed higher relative biomass in Novo Paraíso (2.76 kg/10 km), followed by Viruá (0.96 kg/10 km).

In relation to the mean group size, two species presented significant difference among the five different areas, wich where: *Pithecia pithecia* (H=9.6, p=0.022) and *Saguinus midas* (H=8.71, p=0.033) (Table 3). For species that presented significative difference relation to mean group size, *Pithecia pithecia* reached the highest mean group size (3.14 ind./group), followed by Viruá (2.44 ind./group). *Saguinus midas* presented highest mean group size in Viruá (5.75 ind./group) followed by Novo Paraíso (5.56 ind./group) (Table 3).

The Mann Whitney test showed a significative difference for the relative biomass of *Cebus apella* between the areas of Entre Rios X Uatumã (U=0, p=0.050), Entre Rios X Maracá (U=0, p=0.046), Uatumã X Novo Paraíso (U=0, p=0.050), Uatumã X Viruá (U=0, p=0.050), Viruá X Maracá (U=0, p=0.046). For *Pithecia pithecia* the relative biomass showed significative difference between Uatumã X Novo Paraíso (U=0, p=0.037) and Uatumã X Viruá (U=0, p=0.037).

Mean group size presented significative differences between Entre Rios X Novo Paraíso (U=0, p=0.050), Entre Rios X Viruá (U=0, p=0.050), Uatumã X Novo Paraíso (U=0 p=0.050), Uatumã X Viruá (U=0, p=0.037). For *Saguinus midas,* mean group size showed significative diferences for: Entre Rios X Novo Paraíso, Entre Rios X Viruá, Uatumã X Novo Paraíso, Uatumã X Viruá, all presenting values of U=0 and p=0.037 (Table 4).

The diversity indexes also did not differ significantly among the different areas (H= 1.03, p=0.905), although the highest diversity index was recorded in Entre Rios (EXP H' = 4.72), followed by Novo Paraíso (EXP H' = 4.22), and the lowest was recorded Maracá (EXP H' = 3.36).

Spectral characterization of the vegetation in the study sites

There were no statistically significant differences between the predictive variables (NDVI, LAI, Slope and Heterogeneity) among the different localities (H =1.05; p =0.901). However, the highest vegetation biomass was recorded in Entre Rios (NDVI=0.781), followed by Uatumã (NDVI=0.715), and the lowest, was recorded in Maracá (NDVI=0.566). The highest vegetation cover was recorded in Uatumã (LAI=2.13), followed by Entre Rios (LAI=2.02), and the lowest, in Maracá (LAI=1.50) (Table 3). Forest terrain slope was highest in Uatumã (6.278), followed by Novo Paraíso (3.857), and lowest, in Viruá (1.858) (Table 3). Vegetation heterogeneity was highest in Entre Rios (0.960), followed by Uatumã (0.959), and lowest, in Novo Paraíso (0.846).

A Spearman correlation has shown that the predictive variables NDVI, LAI, Slope and Heterogeneity were all correlated with the dependent variable group size, a GLM with an AIC as a criterion of variables selection, showed that only NDVI and Slope explain the dependent variable (Table 6).

Discussion

Overall primate diversity and abundance in the Rio Negro basin

The Rio Negro basin is covered by continuous tracts of tropical forests characterized by highly heterogeneous mosaics of ombrophilous terra firme forests (with its variations from dense to open), campinaranas and campinas, with little human disturbance and high conservation potential (Mendes Pontes, Paula & Magnusson 2012). As in other studies in the region (Nunes *et al.* 1988; Lehman 2000, 2004; Hoorn *et al.* 2011; Mendes Pontes, Paula & Magnusson 2012), however, we found between five and nine primate species, confirming that this is one of the poorest primate assemblages in Amazonia, the poorest of all being recorded in Maracá, one of the poorest mammal assemblages in the Guyana shield.

According to what has been postulated in the literature, we should expect that the highest diversity would be found in those sites with the highest heterogeneity of forest types, because of the possibility of the competing species to segregate to the different forest types (Chesson & Huntly 1988; Chesson & Rozenzweig 1991; Messier 1991; Post & Stenseth 1998). Additionally, we hypothesize that where primate diversity is the highest, overall biomass and group sizes should be the lowest, because of the even contribution of the species for the abundance indexes independently of their body sizes.

But, although many studies have confirmed that Amazonian primate species show habitat segregation within broad classes of forest (Peres 1988; Schwarzkopf & Rylands 1989; Peres 1993; Mendes Pontes 2004), Mendes Pontes, Paula & Magnusson (2012), in a 25 km^2 grid system, showed that these widely accepted patterns of species distributions are in fact a function of the scale at which the study is carried out as well as of the quality and percentage of each of the forest types in the mosaic.

Primate diversity and abundance in mosaics of terra firme forests: an ideal scenario

The sites that comprised forest mosaics formed exclusively by ombrophilous forests, Uatumã and Entre Rios, presented the highest habitat heterogeneity (highest NDVI and LAI, highest habitat diversity, consequently, highest productivity), or, in other words, the most evenly distributed forest types in the region. These highly heterogeneous and diverse mosaics, however, comprised exclusively those forest types most appropriate for primates – namely Terra Firme forests (from the densest, most humid, taller, closed-canopy, to the less humid, discontinuous, more open types). No campinaranas or campinas occured, not even in small pockets within terra firme. In this scenario, higher habitat heterogeneity (habitat diversity) should lead to higher primate diversity, most probably due to allowing species segregation (MacArthur & Levins 1967; Mendes Pontes, Paula & Magnusson 2012) at a small temporal and spatial scale.

In such an ideal scenario, primate species can be more evenly distributed, temporally or spatially segregate to maximize their survival by exploiting different habitat types and food resources (avoid competition) (Chesson & Rozenzweig 1991; Eeley & Lawes 2004; Fleagle *et al.* 2004; Ganzhorn 2004), but essentially use all forest types, which would not result in an allopatric distribution. In these scenarios, with these fine-grained variations, habitat segregation was behavioural rather than adaptation (or compulsory exclusion) to totally different environments, and consequently would not result in lowered diversity (Mendes Pontes, Paula & Magnusson 2012).

The same trend was observed in group sizes, which also correlated negatively with NDVI, LAI, Slope, Heterogeneity, being lowest in these forests, and should also be related to the contribution of the other species and forest structure. Group sizes are generally highly variable, and related to food acquisition, protection against predation, and balanced by body weight (Izawa 1976; Mittermeier & van Roosmalen 1981; Defler & Pintor 1985; Johns 1985; Terborgh & Janson 1986; Peres 1993; Mendes Pontes 1997;

Chapman & Chapman 2000). Thus, in these rich forests primate species can maximize food acquisition without investing much in group sizes, at the same time that in these ombrophilous forests predator avoidance should be most efficient due to the denser forest cover.

Primate diversity and abundance in mosaics dominated by the drier and more open scrub forests campinaranas and campinas: the misleading scenario

In the study sites where the ombrophilous terra firme forests are much less extensive and interspersed with campinaranas and campinas, Novo Paraíso, Viruá and Maracá, we recorded the highest biomass and group sizes. This suggests that the occurrence of these less favorable forest types benefits only a few species (that reach the highest biomasses and group sizes), in detriment of most of the others. Habitat heterogeneity (habitat diversity) and the resulting primate habitat partitioning did not promote primate diversity, but rather impelled them to aggregate in the terra firme forests (as shown by Mendes Pontes, Paula & Magnussom 2012).

Still, campinaranas and campinas that occur in these sites as small pockets within the terra firme forests, have little detrimental effect on primates, and may even be beneficial because primates can exploit them when appropriate and quickly return to other formations (in the realm of the study transect). For instance, *Alouatta* and *Ateles*, large primates that favour tall ombrophilous terra firme forests (Thoisy, Renoux & Julliot 2005; Alves 2012) can enter the campinaranas or even campinas in the vicinity of terra firme for a few minutes to exploit a short *Spondias lutea* tree that is fruiting and quickly return to safety (Mendes Pontes unpubl. data). These sightings in campinaranas and campinas nevertheless can be misleading for they do not necessarily indicate that viable populations could be maintained only in those habitats.

Primate diversity and abundance in the Rio Negro basin: ecological implications of such a limiting scenario

This study showed that although habitat heterogeneity may promote primate species diversity, and that high diversity may lead to an equally distributed contribution of the species biomasses and group sizes, it depends on the quality of the forest types studied and on the scale of the study. For instance, primate diversity in this study was not explained by any of the predictive variables, but, in turn, the latter revealed a significant negative relationship with group sizes, showing that the least productive environments hold larger primate groups. This suggests that larger groups should be necessary in poor environments in order to maximize food acquisition.

If we consider a much larger scale, realizing that the Rio Negro basin has extensive areas of campinaranas and campinas (IBGE 2009), which are dozens of kilometers from any type of terra firme forest (as shown by Mendes Pontes, Paula & Magnussom (2012) in Viruá), it is unlikely that most of the primate species in this study could maintain viable populations exclusively in those habitats. In this much larger scale, therefore, the predominant forest types will be virtually empty of primates. Those primates that will survive and maintain long-term viable populations will be those that are able to form stable large groups.

Finally, the predictive variables analyzed in this study, which are forest productivity, leaf cover, slope and habitat heterogeneity, althout did not explain primate diversity, were the main environment determinants of the primate communities in the form of mean group size.

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Figure legends

Figure 1. Location of the studied scenario, detailing the studied sites and their vegetation, in the Rio Negro basin, northern Brazilian Amazonia.

Table 1. Characterization of the study areas in the Rio Negro basin, northern Brazilian Amazonia.

	Location, area and data from images	Mean annual temperature and rainfall	Soil, slope	Phytophysiognomy
Entre Rios Human Settlement	Latitude 0°48'N Longitude 59°25'W 52 km (main road); Orbit 231, point 60, date 2007/02/09	28^{o}C 3000 mm (Sombroek 2001)	Red yellow argisoils. Between 80 and 160 m (IBGE 2010)	Ombrophilous tropical rainforests
Uatumã Biological Reserve	Latitude 1°55'S Longitude 58°50'W 942.786 ha; Orbit 230, point 61, date 2011/08/08	28^{o}C 2376 mm (Sombroek 2001).	Red yellow argisoils. Between 80 and 160 m (IBGE, 2010)	Ombrophilous tropical rainforests
Novo Paraíso Human Settlement	Latitude 2°14'N Longitude 60°31'W 100 km (main road); Orbit 231, point 59, date 2007/02/09	26^{o}C 1500 mm (Sombroek 2001).	Red yellow latosoil. Between 80 and 160 m (IBGE, 2010)	Mosaic of ombrophilous tropical rainforests, campinaranas and campinas
Viruá National Park	Latitude 01º42’N Longitude 61º10’W 229.100 ha; Orbit 232, point 59, date 2007/04/07	26^{o}C 1500 mm (Sombroek 2001).	Ferriluvic espodossoil. Between 80 and 160 m (IBGE 2010)	Mosaic of ombrophilous tropical rainforests, campinaranas and campinas
Maracá Ecological Station	Latitude 3°24'N Longitude 61°40'W 103.976 ha; Orbit 58, point 58, date 1997/09/16	31.6^{o}C 1577 mm (Mendes Pontes 2004).	Red–yellow argisoil Between 80 and 160 m (IBGE 2010)	Mosaic of ombrophilous tropical rainforests, campinaranas and campinas, presenting also dry forests in the abrupt ecotonal eastern limit

Table 2. Primate relative biomass in the studied sites in the Rio Negro basin, northern Brazilian Amazonia. Significant relationships in bold.

Species	Entre Rios	Uatumã	Novo Paraíso	Viruá	Maracá	Kruskall-Wallis test
	Mean ± Std deviation	Mean ± Std deviation	Mean ± Std deviation	Mean ± Std deviation	Mean ± Std deviation	
Alouatta macconnelli	12,23 ± 4,97	3,21 ± 1,97	8,81 ± 1,99	4,29 ± 3,04	12,34 ± 8,84	H=6.69, df=4, p=0.153
Aotus trivirgatus	0	0,2 ± 0,21	0,73 ± 0,20	0,23 ± 0,12	0,22 ± 0,16	H=9.41, df=4, p=0.052
Ateles belzebuth	X	X	X	X	26,76 ± 20,27	
Ateles paniscus	23,4 ± 9,49	9,25 ± 3,92	6,17 ± 4,43	10,18 ± 9,82	X	H=4.72, df=3, p=0.193
Cebus apella	16,03 ± 3,29	4,52 ± 1,14	25,57 ± 20,17	55,65 ± 50,57	3,44 ± 4,87	**H=10.45, df=4, p=0.033**
Cebus olivaceus	X	X	X	X	9,27 ± 6,57	
Chiropotes chiropotes	3,00 ± 4,24	2,4 ± 1,77	2,70 ± 2,00	21,01 ± 21,04	X	H=4.38, df=3, p=0.222
Pithecia pithecia	0,52 ± 0,59	0	2,76 ± 1,27	0,96 ± 0,42	X	**H=8.51, df=3, p=0,036**
Saguinus midas	1,77 ± 0,38	0,31 ± 0,31	2,40 ± 1,17	1,47 ± 0,72	X	H=6.01, df=3, p=0.111
Saimiri sciureus	0,81 ± 0,09	0,35 ± 0,42	0,66 ± 0,93	8,27 ± 9,11	2,16 ± 1,53	H=5.68, df=4, p=0.224

Legend: X: Species not occurring in the area

Table 3. Primate mean group size in the studied sites in the Rio Negro basin, northern Brazilian Amazonia.

Species	Entre Rios	Uatumã	Novo Paraíso	Viruá	Maracá	Kruskall-Wallis test
	Mean ± Std deviation	Mean ± Std deviation	Mean ± Std deviation	Mean ± Std deviation	Mean ± Std deviation	
Alouatta macconnelli	2.78 ± 0.41	1.80 ± 0.70	2.97 ± 0.37	2.11 ± 1.50	2.02 ± 1.44	H=2.35, df=4, p=0.671
Aotus trivirgatus	0	0.67 ± 0.47	1.28 ± 0.21	1.67 ± 0.47	1.33 ± 0.94	H=7.67, df=4, p=0.104
Ateles belzebuth	X	X	X	X	2.92 ± 2.22	
Ateles paniscus	3.83 ± 1.11	2.98 ± 0.99	2.58 ± 2.26	3.20 ± 0.59	X	H=1.48, df=3, p=0.686
Cebus apella	3.78 ± 0.24	3.51 ± 0.21	4.62 ± 1.33	6.05 ± 1.56	1.67 ± 2.36	H=6.78, df=4, p=0.148
Cebus olivaceus	X	X	X	X	2.78 ± 1.97	
Chiropotes chiropotes	3.33 ± 4.71	5.67 ± 4.19	3.61 ± 2.55	14.76 ± 7.37	X	H=5.16, df=3, p=0.161
Pithecia pithecia	0.92 ± 0.72	0	3.14 ± 0.62	2.44 ± 0.42	X	**H=9.6, df=3, p=0.022**
Saguinus midas	3.71 ± 0.15	1.92 ± 1.53	5.56 ± 1.24	5.75 ± 0.59	X	**H=8.71, df=3, p=0.033**
Saimiri sciureus	5.67 ± 1.7	2.00 ± 2.16	3.50 ± 4.95	7.81 ± 3.02	7.77 ± 5.70	H=3.47, df=4, p=0.481

Legend: X: Species not occurring in the area

Table 4. A Mann-Whitney test used to identify those areas which differed among them in the Rio Negro basin, northern Brazilian Amazonia.

	Cebus apella	*Pithecia pithecia*	*Pithecia pithecia*	*Saguinus midas*
	Relative Biomass	Relative Biomass	Mean group size	Mean group size
Entre Rios X Uatumã	**U=0, p=0.050**	U=1.5, p=0.121	U=1.5, p=0.121	U=2, p=0.275
Entre Rios X Novo Paraíso	U=4, p=1.000	U=0.5 p=0.077	**U=0, p=0.050**	**U=0, p=0.037**
Entre Rios X Viruá	U=1, p=0.200	U=2.5, p=0.376	**U=0, p=0.050**	**U=0, p=0.037**
Entre Rios X Maracá	**U=0, p=0.046**			
Uatumã X Novo Paraíso	**U=0, p=0.050**	**U=0, p=0.037**	**U=0, p=0.050**	**U=0, p=0.037**
Uatumã X Viruá	**U=0, p=0.050**	**U=0, p=0.037**	**U=0, p=0.037**	**U=0, p=0.037**
Uatumã X Maracá	U=3, p=0.507			
Novo Paraíso X Viruá	U=2, p=0.275	U=0.5, p=0.077	U=1.5, p=0.184	U=3.5, p=0.658
Novo Paraíso X Maracá	U=1, p=0.121			
Viruá X Maracá	**U=0, p=0.046**			

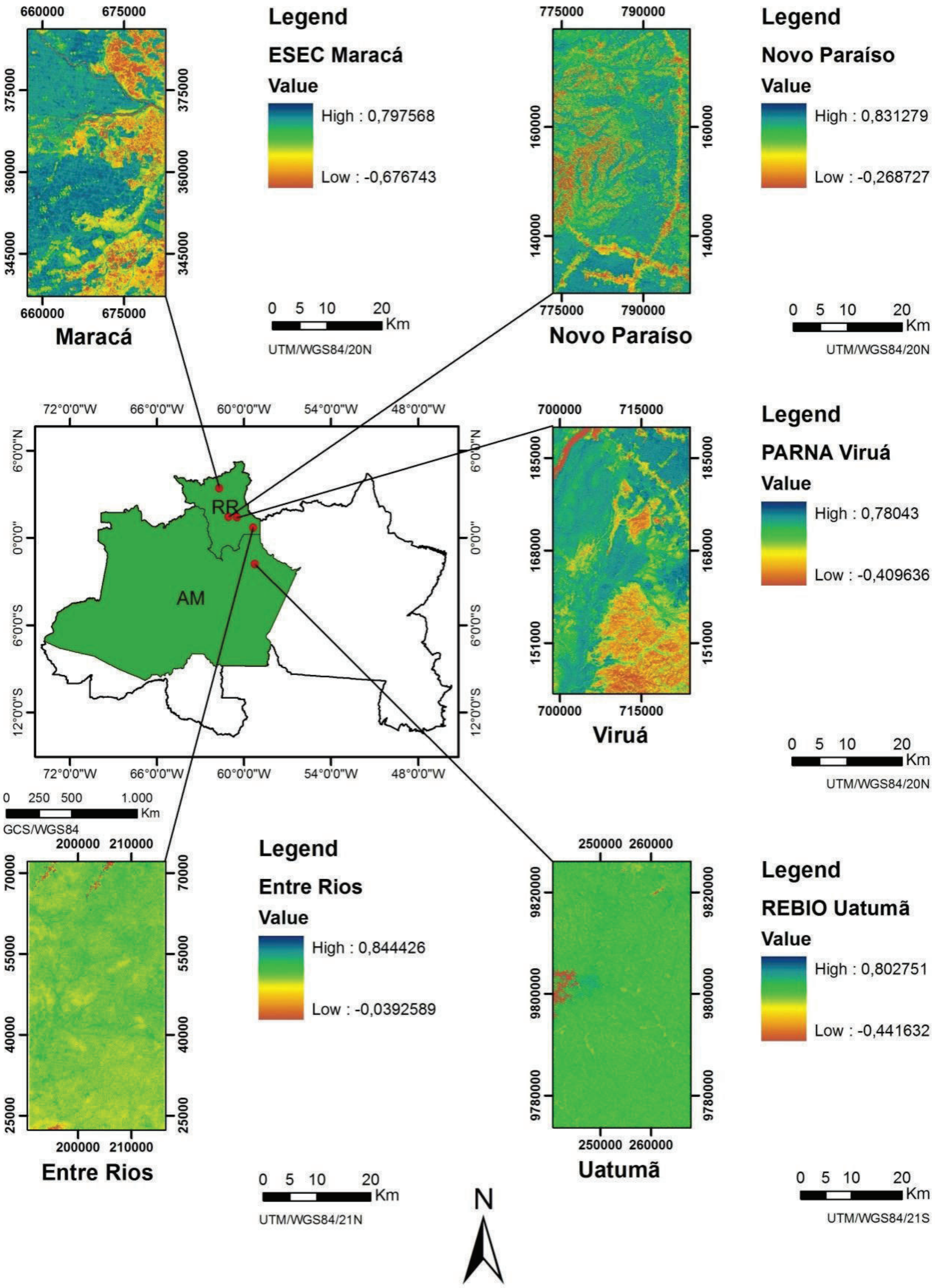
Table 5. A Spearman correlation used to identify the relationship between predictive and dependent variables from the study areas in the Rio Negro basin, northern Brazilian Amazonia.

	NDVI	LAI	Slope	Heterogeneity
H’	R= -0.14, p=0.638	R= -0.10, p=0.773	R= 0.25, p=0.391	R= -0.10, p=0.740
Relative biomass	R= -0.28, p=0.341	R= -0.15, p=0.616	R= -0.43, p=0.124	R= -0.42, p=0.131
Mean group size	**R= -0.65, p=0.015**	**R= -0.64, p=0.017**	**R= -0.60, p=0.022**	**R= -0.67, p=0.008**

Table 6. A Generalized Linear Model (GLM) used to determine which predictive variables explained group sizes in the study areas in the Rio Negro basin, northern Brazilian Amazonia.

	Estimate	Std. Error	t value	p
Intercept	-0.39090	0.18939	-2.064	0.06343
NDVI	**0.72900**	**0.30045**	**2.426**	**0.03362**
Slope	**0.05567**	**0.01727**	**3.223**	**0.00812**
AIC: 42.879				

Fig 1.


660000
675000
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360000
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Maracá
Legend
ESEC Maracá
Value
High : 0,797568
Low : -0,676743
0 5 10 20 Km
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High : 0,831279
Low : -0,268727
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54°0'0"W
48°0'0"W
6°0'0"N
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6°0'0"S
12°0'0"S
RR
AM
0 250 500 1.000 Km
GCS/WGS84
700000
715000
185000
168000
151000
Viruá
Legend
PARNA Viruá
Value
High : 0,78043
Low : -0,409636
0 5 10 20 Km
UTM/WGS84/20N
200000
210000
70000
55000
40000
25000
Entre Rios
Legend
Entre Rios
Value
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Low : -0,0392589
0 5 10 20 Km
UTM/WGS84/21N
N
250000
260000
9820000
9800000
9780000
Uatumã
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REBIO Uatumã
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Low : -0,441632
0 5 10 20 Km
UTM/WGS84/21S

5.0 Capítulo 2

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Silva Júnior, A.P., Galvíncio, J.D., Mendes Pontes, A.R. Variação na relação massa corpórea X abundância de mamíferos na região da bacia do Rio Negro

Variation in the relationship body mass *vs.* abundance of mammals in Rio Negro basin

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Abstract

The relationship body mass *vs*. abundance has been broadly studied. Nevertheless, it has been found that intrinsic and different ecological processes can lead to inconsistent results. In order to understand the role of the environmental and taxa features on the relationship between body mass and abundance, we assessed the large and medium-sized mammal community in five areas from the Rio Negro basin. Thereunto, we use the line transect method whereby we obtained group density, individual density, biomass, average group size and diversity indexes. Furthermore, we obtained Normalized Difference Vegetation Indexes

(NDVI) through the remote sensing technique. We performed simple linear regression model in order to relate body mass to the several parameters of abundance under logarithmic form. The significant relationship between abundance and body mass varied considerably, ranging from -0.76 to 0.75, depending on the abundance parameter assessed, on the trophic category and species' habit. The correlations indicated an influence of mammalian diversity on the lines slope, in other words, the more balanced the environment is, the resources are better shared and the line slope would be negative, which comply with the Energy Equivalence Rule. Analysis related to terrestrial habits were correlated with forests productivity, and, according to species diet, we found significant relationships with the frugivorous species. Overall, the relationship body mass *vs.* abundance found in the Rio Negro basin is a product of diversity and productivity.

Key-words:

Mammals; Amazonia Forest; abundance *vs.* body mass

Introduction

The relationship body mass *vs.* abundance has been one of the most studied patterns in ecology (Cotgreave, 1993), however, controversies have arisen regarding the shape of this relationship, and some of these controversies stem from the fact that relationships are generated by different combinations of different processes (White et al., 2007). One of these cases concerns an analysis on a global scale, in which the data come from a large compilation of the literature gathered in many parts of the globe, and presents a linear exponent near -0.75, a relationship called "Global Size-Density Relation" (GSDR) by White et al. (2007).

Damuth (1981) concluded that values of the relationship body mass *vs.* abundance which are about -0.75 (GSDR), found for both terrestrial species and aquatic animals in general, would be an evidence that all species in communities resort the same amount of energy, which we call the Energy Equivalence Rule (EER). Studies on different scales showed that the EER may not be adequate to describe the community, and thereafter controversies began to emerge. On a continental scale, Robinson & Redford (1986) supported the EER, by analysing the entire community of mammals, however, in this same scale, Ernest (2005), through the analysis of energy use by populations, concluded that this usage is not uniform.

Some authors conducting studies on a regional scale justify the discrepancies in EER due to differences amongst taxa which would lead to a differential habitat use (Juanes, 1986), moreover, studies on smaller scales would lead to a reduction in the amplitude of corporeal masses, which makes that relationship weaker (Russo et al. 2003).

In studies in which the abundances of species would be gathered at a single site ("Local Size-Density Relation" - LSDR) (White *et al*, 2007), altogether, the linear exponent is quite below -0.75, being about -0.25 (Blackburn *et al*, 1993; Blackburn & Gaston, 1997), or else presents triangular patterns, in which the relative body mass and abundance have higher peaks due to the great concentration of medium-sized species (Lawton 1990; Cotgreave, 1993, Marquet *et al*. 1995).

The polygonal relationship has a higher peak for the species of intermediate sizes, decreasing to both sides, which would suggest that models with strong linear relationship could be suffering from biased sampling with absence of rare species and smaller species (Brown & Maurer, 1987). Species with restrict diet or those which are at the top of the trophic levels, which consequently have less energy available in the habitat, occur at lower densities.

Additional explanations for the pattern at the local level suggest that diet could play a key role in the body mass *vs.* abundance relationship (Robinson & Redford, 1986; Kinnaird & Eisenberg, 1989, Lawton, 1990; Marquet, 2002); competition for food would lead to variations in this relationship amongst communities, which does not comply the pattern proposed by Damuth (1981), and that would weaken the Energy Equivalence Rule on a local level (Russo *et al*., 2003 Mendes Pontes *et al*., 2007). Hayward *et al*. (2010), however, showed that density *vs.* body mass relationship (D-M) could be a result of biological mechanisms. Reviewing explanations from previous studies, we found that mechanisms used to explain the relationships variations invoke mechanisms associated to body mass index, and suggests that the amplitude of body mass would be the main explanatory factor. Hayward *et al*. (2010) concludes in his model that the EER would be supported, but limited at larger scales of observation.

The diversity of species in an environment is affected by the balance between immigration and extinction, as well as numerous others features related to the niche or dispersal ability, which could be influenced by the body mass of the species (Peters, 1983). Thus, the way communities are structured in several habitat types could influence the shape of the relationship body size *vs.* abundance. Hayward *et al*. (2010) noticed that in communities with higher species richness, the relationship body mass *vs.* density becomes clearer since it forces the individuals share resources more evenly. As the diversity of environments is related to its productivity (He & Zhang, 2009), this relationship could be stronger in more productive and/or more diverse environments.

Thus, we aim to assess, on a local scale, how the relationship between body mass and abundance performs at the Rio Negro basin and identify the factors that influence it. We attempt to answer the following questions: (1) what is the form of the relationship body mass *vs.* abundance, on a local scale, in different areas of the Rio Negro basin? (2) how species habit and diet could influence this relationship? and (3) what the role of the environment biomass (NDVI) and/or the diversity of species on this relationship?

Materials and methods

Studied areas

The mammalian sampling used in this work comprises the following array of data: (1) Maracá Ecological Station (Jan. 1997 / Jan. 98); (2) Novo Paraíso Settlement (Dec. and Jan., 2010); (3) Entre Rios Settlement (Jan. and Feb. 2012) (4) Uatumã Biological Reserve (Sept. 2011) and Viruá National Park (March 2012) (Figure 1). For each individual or animal group viewed during the sampling, the following data were collected: group size, perpendicular distance, time and position along the trail (see Table 1 for detailed description of the areas). The standard effort was 420 km walked each area, totalling 2100 km sampling in all areas.

Sampling of medium and large sized mammals

The sampling were performed by using transect line method (Buckland *et al*., 1993). Three parallel tracks, measuring 5 km, were used in each study area, excepting Maracá Ecological Station, which had two non-parallel tracks (Mendes Pontes, 1999). In the case of Uatumã Biological Reserve and Viruá National Park, we used three tracks from the standard grid of the Biodiversity Research Program (PPBio) (www.ppbio.inpa.gov.br), which consists of six north-south tracks and six east-west tracks measuring 5 km each one, totalling 25 km². In other cases we opened three trails, 5 km each one. The trails were marked alphanumerically every 100 m with metal labels and were cleaned of debris to minimize noise while walking.

Diurnal samplings were carried out from 07:00 to 17:30 h every day. Each day, were travelled 10 km at a speed of 1 km/h. The nocturnal samplings were carried out from 18:30

to 04:30 h, walking 10 km per night as well, at an average speed of 1.25 km / h. During the night sampling, headlamps were used to illuminate the trail and long-range lanterns were used in order to seek the animals.

The mammalian sampling was performed by the same observers and trained field workers, who walked in pairs and alternating amongst tracks. The walking speed was controlled by observing the arrival time at each landmark of 100 m.

Remote sensing

In the studied areas, vegetation indexes were obtained from images of the sensor TM (Thematic Mapper) aboard the satellite Landsat 5, considering the images with less cloud cover and dated to the period close to the field sampling period. The images were processed using ERDAS Imagine 9.3 (license from the Department of Geographical Sciences, Federal University of Pernambuco, Brazil) software. The vegetation index (NDVI) was calculated according to Tucker (1979).

Data analysis

For each sampled area, group density calculations were performed in agreement with King's method (Robinette *et al*, 1974), whose formula is: D = n / 2 x L x S, in which, n = number of records, L = total length of the transect and S = average animal-observer distance. In order to obtain the individual density, we multiply the group density by the average group size of each species. The group size was calculated as the arithmetic mean of the number of individuals per specie record, and, biomass was obtained by multiplying the individual density of each species by its body mass. The body mass of each species was considered as the arithmetic mean of values recorded by Emmons & Feer (1997), Eisenberg & Redford (1999), Mendes Pontes (2004) and Reis *et al*. (2011). The species diversity was calculated using the PRIME 6.0 (Clarke & Gorley, 2006) using the exponential index Shannon, by weighing all variables without favouring common or rare species (Jost, 2006; 2007).

The relationships between body mass and group density, individual density, biomass and group size, were analysed with simple linear regression model, with logarithmic transformation of both axes. We used the following categories, separately: (1) the whole medium and large sized mammalian community, (2) terrestrial mammals, (3) arboreal/escansorial mammals, and (4) dietary categories.

For diet categories we followed Mendes Pontes et al. (2007), as follows: (1) Fauni-frugivorous (*Aotus trivirgatus* Humboldt, 1811; *Cebus apella* Linnaeus, 1758; *Cebus olivaceus* Schomburgk, 1848; *Chiropotes chiropotes* Humboldt, 1811; *Pecari tajacu* Linnaeus, 1758; *Saguinus midas* Linnaeus, 1758, *Saimiri sciureus* Linnaeus, 1758; *Tayassu pecari* Link, 1795); (2) Foli-frugivorous (*Mazama americana* Erxleben, 1777; *Mazama gouzoubira* G. Fischer [von Waldheim], 1814; *Tapirus terrestris* Linnaeus, 1758); (3) Frugi-folivorous (*Alouatta macoconelli* Linnaeus, 1766; *Ateles belzebuth* E. Geoffroy,1806; *Ateles paniscus* Linnaeus, 1758; *Coendou prehensilis* Linnaeus, 1758; *Cuniculus paca* Linnaeus, 1766); (4) Grani-frugivorous (*Dasyprocta fuliginosa* Wagler, 1832; *Dasyprocta leporina* Linnaeus, 1758; *Myoprocta acouchy* Erxleben, 1777; *Sciurus (Guerlinguetus) aestuans* Linnaeus, 1766; *Sciurus igniventris* Wagner, 1842); (5) Frugi-faunivorous (invertebrates; *Dasypus kappleri* Krauss,1862; *Dasypus novemcinctus* Linnaeus, 1758; *Priodontes maximus* Kerr, 1792); (6) Faunivorous (invertebrates; *Myrmecophaga tridactyla* Linnaeus, 1758; *Tamandua tetradactyla* Linnaeus, 1758); (7) Frugi-faunivorous (*Bassaricyon beddardi* Pocock, 1921; *Cerdocyon thous* Linnaeus, 1766; *Eira barbara* Linnaeus, 1758; *Nasua nasua* Linnaeus, 1766; *Potos flavus* Schreber, 1774); (8) Faunivorous (*Leopardus wiedii* Schinz, 1821; *Lontra longicaudis* Olfers, 1818; *Panthera onca* Linnaeus, 1758; *Puma concolor* Linnaeus, 1771; *Pteronura brasiliensis* Gmelin, 1788; *Speothos venaticus* Lund, 1842).

Species such as *Bradypus stridactylus* and *Choelopus didactylus* were not used in the analysis of trophic category for being the only exclusively folivorous. The following food categories, however, were grouped so that it had a more robust sample: (1) Frugivores: Foli-frugivorous, Frugi-folivorous and Grani-frugivorous; (2) Insectivorous: Frugi-faunivorous (invertebrates), Faunivorous (invertebrates); (3) Carnivorous: Frugi-faunivorous and Faunivorous. In order to test the correlation between the values of the regression coefficient with species diversity and NDVI, we performed a Pearson product-moment correlation, using the "software" SPSS version 20.

Results

Body mass *vs.* abundance relationship for all mammals

Group density showed significant negative correlation with body mass index in the five areas studied (Figure 2a-e, Table 2), showing highest values in Uatumã (r^2=0.21; P= 0.04) and lowest in Maracá (r^2=0.19; P=0.04). Individual density presented a significant negative relationship with body mass in Entre Rios (r^2=0.2; P=0.02), and Novo Paraíso (r^2=0.23; P=0.01) (Figure 3a-b, Table 2). Biomass showed a significant positive relationship with body mass in all areas except Maracá, with a line slope ranging from 0.35 in Viruá to 0.51 in Entre Rios (Table 2, Figure 4a-d).

Body mass *vs.* abundance relationship from habit

Analysing the relationship according to the specie habit, we found that group density of terrestrial mammals from Entre Rios showed a significant negative relationship with body mass index ($r^2=0.4$; $P=0.02$) (Table 3, Figure 5a). The group density of arboreal mammals from Viruá also showed a significant negative relationship with body mass index ($r^2=0.46$; $P=0.01$) (Table 3, Figure 5b).

Individual density of terrestrial mammals from Entre Rios presented a significant negative relationship with body mass index, ($r^2=0.35$; $P=0.03$), as well as the arboreal from Viruá ($r^2=0.37$; $P=0.04$) (Table 3, Figure 6a-b). The relationships biomass *vs.* body mass of terrestrial mammals were significant and positive in all areas, except Maracá, with the highest values recorded in Viruá ($r^2=0.46$; $P=0.04$) (Table 3, Figure 7a-d).

Body mass *vs.* abundance relationship from diet

The available data were not sufficient to test the relationship in the classes of insectivorous and carnivorous diet. There was a significant negative relationship between group density and body mass of frugivorous in Uatumã ($r^2=0.47$; $P=0.003$) and in Viruá ($r^2=0.28$; $P=0.05$) (Table 4, Figure 8a-b), as well as between biomass and body mass in all areas, having been more significant in Maracá ($r^2=0.77$; $P=0.0001$) and less significant in Entre Rios ($r^2=0.41$; $P=0.002$) (Table 4, and Figure 9a). Group size presented a significant positive relationship with body mass only for frugivorous in Uatumã ($r^2=0.38$; $P=0.01$) (Table 4, Figure 10).

Influence of species diversity and forest productivity on the relationship abundance *vs.* density

The regression coefficient between body mass and individual density showed a significant negative relationship with the diversity index ($r=-0.93$; $P\leq0.05$) (Table 6). The NDVI values showed no significant positive correlation with the values of the regressions between body mass and individual density ($r=0.87$) (Table 6). The diversity of arboreal mammals was positively correlated with NDVI ($r=0.92$; $P<0.05$).

Discussion

At all scales, would be expected that the relationship body mass *vs*. abundance were negative, but this value can vary mainly on smaller scales even reaching a positive trend. The D-M ratio on smaller scales can be masked by other factors (Hayward *et al*., 2010). Assessing data at local level (each area separately) our results pointed to a variable mammal community structure related to vegetation cover and mammalian diversity. Areas with higher diversity indexes showed line slope with more accordance to the EER, tending to be more negative.

Individual and group density *vs.* body mass relationship

Density group analysis showed significant negative relationships for all mammals in all areas, reaching high negative values in Viruá and Uatumã, which reveals a pattern similar to that found in global gradient analysis (White *et al*., 2007). For this abundance parameter, the results showed a less negative line slope than the expected for an analysis of abundance at the local scale, which would be about -0.25.

Regarding the individual density, the relationship showed a negative trend, except for the region of Uatumã. Only for Entre Rios and Novo Paraíso the line slope was significant (-0.45 and -0.46, respectively); this can be explained by the expression of mammalian diversity in these two regions, which is a reflection of its forest cover, expressed by the NDVI, which would be an indicator of the environment productivity. The remaining areas had values about -0.30, except Uatumã, a result that complies with that found by Pagel *et al*., (1991), which he attributed to an unequal distribution of resources.

Line slopes near to -0.30 were found by Brown & Maurer (1987), which is attributed to the fact that the larger species dominate the environment by changing the D-M relations. The same could be happening at the studied areas, since, taking as an example, the region of Viruá and Maracá we perceive a greater abundance of larger species, which would be taking competitive advantage in an environment where the NDVI were the lowest recorded from the five areas. This reflects in areas with lower resources availability that would be dominated by species better adapted, furthermore, individuals would compete for food or space, as we can see in some generalist primates (eg. *Cebus apella*) and large terrestrial species (eg. *Tayassu peccary*).

Body mass *vs.* biomass relationship

The relationship body mass *vs*. biomass for all mammals have always been positive, with line slope values higher than 0.30. Studies on mammals in different Neotropical regions show that biomass is positively related to body mass (Peters & Wassenberg, 1983; Raelson & Peters, 1984; Robinson & Redford, 1986).

Mendes Pontes *et al*., (2007), testing density *vs*. body mass relationship, suggested that the positive relation between biomass and body mass would be a result of diet and competition that would shape the community structure, thus, peccaries (*Pecari tajacu*, *Tayassu pecari*), deer (*Mazama americana*, *Mazama gouzoubira*) and tapirs (*Tapirus terrestris*) were the most frequent, making positive the relationship density *vs*. body mass.

Body mass *vs.* group size relationship

There was no significant relationship between body mass and average group size, when tested all mammals species, which agrees with Mendes Pontes *et al*. (2007), when testing the same relationship in Maracá. For the frugivorous from Uatumã, however, there was a significant positive relationship, which demonstrates to the finding of previous studies (Silva Júnior *et al*. *in prep.*), showing that the higher the NDVI the greater the forest productivity, the greater the primate groups, even those larger species, because the maintenance of their groups can be guaranteed by the availability of food

Increasing the size of groups is a strategy widely recognized in primates, which the formation of large groups could be beneficial to increase defence against predators and foraging efficiency (Chapman & Chapman, 2000), and at these denser forests, the animals would be more protected from the predators, besides, they would have more food available.

Body mass *vs*. abundance relationships according to habit

As regards the habit, we noticed significant results for terrestrial mammals from Entre Rios, where the ratio reached -0.75 for the group density parameter. However, the correlation showed that for terrestrial mammals, the biomass parameter would be explained by the NDVI, thus, the more productive the forest the more positive the relationship for the biomass parameters. The great productivity would make the environment more conducive to support larger species, since, according to the literature the biomass is positively related to body mass (Peters & Wassenberg, 1983; Peters & Raelson, 1984; Robinson & Redford, 1986), as discussed before.

Some studies show that in Neotropical forests the highest concentration of mammals' biomass is limited to the tree canopies, however, in forests subject to extreme seasonal droughts, biomass of arboreal mammals is suggested to be lower than that of terrestrial mammals (Eisenberg *et al*., 1979), which explains the more balanced relationship for terrestrial mammals.

For arboreal mammals from Viruá, the correlations showed, just for a moment, a positive correlation with NDVI, taking into account the mammals' biomass parameter. Regarding arboreal species, there was a negative correlation with species diversity for medium sized group parameter, which refers to the idea that the most diverse environments would agree with the EER. Looking from the point of view of EER, it is expected that the energy partition amongst mammals should be considered as the division between arboreal and terrestrial, since the entire community shares the energy of the environment in a way that each species would occupy a different niche avoiding competition. Thus, the habit of the species would not be a good determinant for body mass *vs.* abundance relationships, which could vary depending on the community structure.

Body mass *vs.* abundance relationship according to the diet

The first studies related to body mass *vs.* abundance relationship showed that the EER would be applied even within a particular trophic level (Damuth, 1987, 1993), yet our results point to relations with more negative slopes than -0.30, following the trend of analyses on a local scale, since the slopes were statistically significant only for frugivorous. These results show that the group of frugivorous would probably be the most representative for Neotropical mammals adapted to life in dense forests, and the partition of resources would be more balanced amongst the members of this particular group, by having greater range of body mass classes, approaching, thus, the EER.

Differences in body mass *vs.* abundance relationship according to the diet would be expected, since the availability of resources determines population abundance, and diet specialist species would be rarer due to limited resources (Robinson & Redford, 1986). Other studies also emphasize the importance of diet in these relationships, as Peters & Wassenberg (1983), who found variations in the pattern according to the diet and showed differences between the groups regarding the slope of the line. Following the same trend, Marquet *et al*. (1995) concluded that EER would not have empirical consistency, since the energy use by populations varied according to the diet and body size.

Influence of mammalian diversity on body mass *vs.* abundance relationship

The most robust negative relationships (body mass *vs.* abundance) were found at the areas with the highest diversity of mammals, where the line slopes were about -0.40; this pattern is above from expected for local analysis. This result shows that in more balanced areas, resource availability is more accessible to a greater range of size classes (Hill, 1973), which would make the relationship closer to the Energy Equivalence Rule. Considering the individual density parameter, the mammalian diversity was explained by environments productivity (NDVI) for arboreal and frugivorous mammals.

Since the environmental conditions favour some species over others, it is expected that the distribution of biomass among species are not even; at Viruá, for instance, which is a mosaic of terra firme, campina and campinaranas (Mendes Pontes, *pers. comm.*), occurred a predominance of only two species. The low mammals' diversity index made the relationship between the body mass and individual density less robust compared to Entre Rios, Novo Paraíso and Maracá. Similar results, as in Makarieva *et al*. (2004), showed that the instability of the environment makes the allocation of resources among different size classes occur more evenly.

Finally, we conclude that the relationship abundance *vs.* body mass in the Rio Negro basin would be mainly explained by diversity, which would be related to environments productivity. Overall, the lines slopes reached more negative values than expected for analysis at the local level in those areas with greater diversity of mammals. Furthermore, this relationship had considerable influence on frugivorous, which have greater range of body mass classes, approaching, thus, the EER.

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Table 1. Characterization of the study areas in the Rio Negro basin, northern Brazilian Amazonia.

	Location, area and data from images	**Mean annual temperature and rainfall**	**Soil, slope**	**Phytophysiognomy**
Entre Rios Human Settlement	Latitude 0°48'N Longitude 59°25'W 52 km (main road); Orbit 231, point 60, date 2007/02/09	28ºC 3000 mm (Sombroek 2001)	Red yellow argisoils. Between 80 and 160 m (IBGE 2010)	Ombrophilous tropical rainforests
Uatumã Biological Reserve	Latitude 1°55'S Longitude 58°50'W 942.786 ha; Orbit 230, point 61, date 2011/08/08	28ºC 2376 mm (Sombroek 2001).	Red yellow argisoils. Between 80 and 160 m (IBGE, 2010)	Ombrophilous tropical rainforests
Novo Paraíso Human Settlement	Latitude 2°14'N Longitude 60°31'W 100 km (main road); Orbit 231, point 59, date 2007/02/09	26ºC 1500 mm (Sombroek 2001).	Red yellow latosoil. Between 80 and 160 m (IBGE, 2010)	Mosaic of ombrophilous tropical rainforests, campinaranas and campinas
Viruá National Park	Latitude 01º42'N Longitude 61º10'W 229.100 ha; Orbit 232, point 59, date 2007/04/07	26ºC 1500 mm (Sombroek 2001).	Ferriluvic espodossoil. Between 80 and 160 m (IBGE 2010)	Mosaic of ombrophilous tropical rainforests, campinaranas and campinas
Maracá Ecological Station	Latitude 3°24'N Longitude 61°40'W 103.976 ha; Orbit 58, point 58, date 1997/09/16	31.6ºC 1577 mm (Mendes Pontes 2004).	Red–yellow argisoil Between 80 and 160 m (IBGE 2010)	Mosaic of ombrophilous tropical rainforests, campinaranas and campinas, presenting also dry forests in the abrupt ecotonal eastern limit

Table 2. Body mass x abundance relationships for all mammals in the Rio Negro basin.

Área	Relationship	b	r²	p
Uatumã	Body mass vs Group density	-0.73	0.21	0.04
Uatumã	Body mass vs Individual density	0.04	0.00	0.84
Uatumã	Body mass vs Biomass	0.46	0.48	0.00
Uatumã	Body mass vs Group size	0.40	0.14	0.10
Entre Rios	Body mass vs Group density	-0.60	0.21	0.01
Entre Rios	Body mass vs Individual density	-0.46	0.20	0.02
Entre Rios	Body mass vs Biomass	0.51	0.28	0.00
Entre Rios	Body mass vs Group size	0.60	0.06	0.22
Novo Paraíso	Body mass vs Group density	-0.55	0.20	0.03
Novo Paraíso	Body mass vs Individual density	-0.45	0.23	0.01
Novo Paraíso	Body mass vs Biomass	0.43	0.21	0.02
Novo Paraíso	Body mass vs Group size	-0.81	0.13	0.08
Viruá	Body mass vs Group density	-0.67	0.28	0.01
Viruá	Body mass vs Individual density	-0.32	0.15	0.08
Viruá	Body mass vs Biomass	0.35	0.19	0.05
Viruá	Body mass vs Group size	-0.01	0.01	0.77
Maracá	Body mass vs Group density	-0.46	0.19	0.04
Maracá	Body mass vs Individual density	-0.34	0.14	0.08
Maracá	Body mass vs Biomass	0.40	0.16	0.06
Maracá	Body mass vs Group size	0.74	0.11	0.13

Tabela 3. Body mass x abundance relationships according to habit mammals in the Rio Negro basin.

Área	Habit	Relationship	b	r²	p
Uatumã	Terrestrial	Body mass vs Group density	0.13	0.007	0.79
Uatumã	Terrestrial	Body mass vs Individual density	0.28	0.11	0.26
Uatumã	Terrestrial	Body mass vs Biomass	0.65	0.31	0.04
Uatumã	Terrestrial	Body mass vs Group size	0.39	0.18	0.14
Uatumã	Arboreal	Body mass vs Group density	0.77	0.25	0.2
Uatumã	Arboreal	Body mass vs Individual density	0.26	0.13	0.38
Uatumã	Arboreal	Body mass vs Biomass	0.31	0.27	0.06
Uatumã	Arboreal	Body mass vs Group size	0.57	0.48	0.06
Entre Rios	Terrestrial	Body mass vs Group density	-0.74	0.4	0.02
Entre Rios	Terrestrial	Body mass vs Individual density	-0.67	0.35	0.03
Entre Rios	Terrestrial	Body mass vs Biomass	0.65	0.31	0.04
Entre Rios	Terrestrial	Body mass vs Group size	0.71	0	0.76
Entre Rios	Arboreal	Body mass vs Group density	0.21	0.05	0.46
Entre Rios	Arboreal	Body mass vs Individual density	0.07	0.009	0.75
Entre Rios	Arboreal	Body mass vs Biomass	0.31	0.27	0.06
Entre Rios	Arboreal	Body mass vs Group size	0.21	0.02	0.65
Novo Paraíso	Terrestrial	Body mass vs Group density	-0.2	0.04	0.55
Novo Paraíso	Terrestrial	Body mass vs Individual density	0.15	0.03	0.62
Novo Paraíso	Terrestrial	Body mass vs Biomass	0.47	0.39	0.03
Novo Paraíso	Terrestrial	Body mass vs Group size	0.36	0.005	0.83
Novo Paraíso	Arboreal	Body mass vs Group density	0.64	0.25	0.08
Novo Paraíso	Arboreal	Body mass vs Individual density	0.36	0.17	0.17
Novo Paraíso	Arboreal	Body mass vs Biomass	0.4	0.22	0.11
Novo Paraíso	Arboreal	Body mass vs Group size	0.17	0.01	0.71
Maracá	Terrestrial	Body mass vs Group density	0.19	0.05	0.47
Maracá	Terrestrial	Body mass vs Individual density	0.18	0.06	0.44
Maracá	Terrestrial	Body mass vs Biomass	0.3	0.2	0.15

Maracá	Terrestrial	Body mass vs Group size	0.29	0.01	0.71
Maracá	Arboreal	Body mass vs Group density	0.26	0.09	0.37
Maracá	Arboreal	Body mass vs Individual density	0.21	0.01	0.35
Maracá	Arboreal	Body mass vs Biomass	0.25	0.13	0.27
Maracá	Arboreal	Body mass vs Group size	0.02	0.016	0.71
Viruá	Terrestrial	Body mass vs Group density	0.23	0.03	0.67
Viruá	Terrestrial	Body mass vs Individual density	0.11	0.02	0.71
Viruá	Terrestrial	Body mass vs Biomass	0.39	0.46	0.04
Viruá	Terrestrial	Body mass vs Group size	0.43	0.13	0.33
Viruá	Arboreal	Body mass vs Group density	-0.76	0.46	0.01
Viruá	Arboreal	Body mass vs Individual density	-0.5	0.37	0.04
Viruá	Arboreal	Body mass vs Biomass	0.4	0.22	0.11
Viruá	Arboreal	Body mass vs Group size	0.34	0.046	0.51

Table 4. Body mass x abundance relationship according to the diet in the Rio Negro basin.

Area	Category	Relationship	b	r²	p
Uatumã	Frugivores	Body mass vs Group density	-1.25	0.47	0.003
Uatumã	Frugivores	Body mass vs Individual density	0.13	0.02	0.63
Uatumã	Frugivores	Body mass vs Biomass	0.49	0.56	0.0009
Uatumã	Frugivores	Body mass vs Group size	0.75	0.38	0.01
Entre Rios	Frugivores	Body mass vs Group density	-0.39	0.08	0.24
Entre Rios	Frugivores	Body mass vs Individual density	-0.31	0.08	0.22
Entre Rios	Frugivores	Body mass vs Biomass	0.56	0.41	0.002
Entre Rios	Frugivores	Body mass vs Group size	-0.5	0.04	0.43
Entre Rios	Carnivorous	Body mass vs Group density	-1.03	0.55	0.15
Entre Rios	Carnivorous	Body mass vs Individual density	-0.46	0.37	0.27
Entre Rios	Carnivorous	Body mass vs Biomass	0.18	0.04	0.76
Entre Rios	Carnivorous	Body mass vs Group size	-0.66	0.18	0.48
Novo Paraíso	Frugivores	Body mass vs Group density	-0.66	0.12	0.18
Novo Paraíso	Frugivores	Body mass vs Individual density	-0.58	0.19	0.09
Novo Paraíso	Frugivores	Body mass vs Biomass	0.74	0.49	0.002
Novo Paraíso	Frugivores	Body mass vs Group size	-0.74	0.1	0.23
Novo Paraíso	Carnivorous	Body mass vs Group density	-0.3	0.21	0.36
Novo Paraíso	Carnivorous	Body mass vs Individual density	-0.34	0.2	0.37
Novo Paraíso	Carnivorous	Body mass vs Biomass	0.47	0.29	0.27
Novo Paraíso	Carnivorous	Body mass vs Group size	0.9	0.07	0.62
Viruá	Frugivores	Body mass vs Group density	-1.04	0.27	0.05
Viruá	Frugivores	Body mass vs Individual density	-0.29	0.07	0.3
Viruá	Frugivores	Body mass vs Biomass	0.57	0.44	0.007
Viruá	Frugivores	Body mass vs Group size	0.08	0.003	0.86
Maracá	Frugivores	Body mass vs Group density	-0.34	0.02	0.65
Maracá	Frugivores	Body mass vs Individual density	-0.72	0.12	0.27
Maracá	Frugivores	Body mass vs Biomass	0.93	0.77	0.0001

Maracá	Frugivores	Body mass vs Group size	-0.66	0.07	0.41
Maracá	Insectivorous	Body mass vs Group density	-0.68	0.3	0.21
Maracá	Insectivorous	Body mass vs Individual density	-0.68	0.3	0.21
Maracá	Insectivorous	Body mass vs Biomass	0.73	0.42	0.12

Table 5. Pearson correlation between the regression coefficients of the relationship Density vs Body mass, mammalian diversity index, NDVI, and between NDVI and diversity in the Rio Negro basin.

		Diversity vs. b	NDVI vs. b	Diversity vs. NDVI
B vs I.D	All Mammals	-0.93	0.87	-0.26; NS
	Arboreals	-0.2; NS	0.42; NS	0.92
	Terrestrials	0.43; NS	-0.11; NS	0.65; NS
	Frugivores	-0.57; NS	-0.82	0.9
B vs. G.D	All mammals	0.86	-0.66; NS	-0.27; NS
	Arboreals	-0.69; NS	0.26; NS	-0.26; NS
	Terrestrials	-0.52; NS	-0.59; NS	-0.26; NS
	Frugivores	0.91	-0.37; NS	-0.26; NS
B vs. Bio	All mammals	-0.26; NS	0.69; NS	-0.26; NS
	Arboreals	-0.06; NS	0.32; NS	0.16; NS
	Terrestrials	-0.32; NS	0.95	-0.26; NS
	Frugivores	0.67; NS	-0.82; NS	-0.26; NS
B vs. G.S	All mammals	-0.35; NS	-0.23; NS	-0.26; NS
	Arboreals	-0.91	0.63; NS	-0.26; NS
	Terrestrials	0.13; NS	0.62; NS	-0.26; NS
	Frugivores	-0.99	0.38; NS	-0.26; NS

Legends: b Coefficient of linear regression between body mass and abundance parameters. B.M. Body mass; I.D. Individual Density; G.D. Group density; Bio Biomass; G.S Group size.

Figure 1. Location of the studied scenario, detailing the studied sites and their vegetation, in the Rio Negro basin, northern Brazilian Amazonia.

Figure 2. Body mass vs. Group density relationship, in the Rio Negro basin. (a)Uatumã; (b)Entre Rios; (c)Novo Paraíso; (d)Viruá; e (e)Maracá.

Figure 3. Body mass vs. Individual density relationship, in the Rio Negro basin. (a)Entre Rios e (b) Novo Paraíso.

Figure 4. Body mass vs. Biomass relationship, in the Rio Negro basin. (a)Uatumã; (b)Entre Rios; (c)Novo Paraíso e (d)Viruá.

Figure 5. Body mass vs. Group density relationship according to habit (terrestrials and arboreals) in the Rio Negro basin. (a)Entre Rios e (b) Viruá.

Figure 6. Body mass vs. Individual density relationship according to habit (terrestrials and arboreals) in the Rio Negro basin. (a)Entre Rios e (b) Viruá.

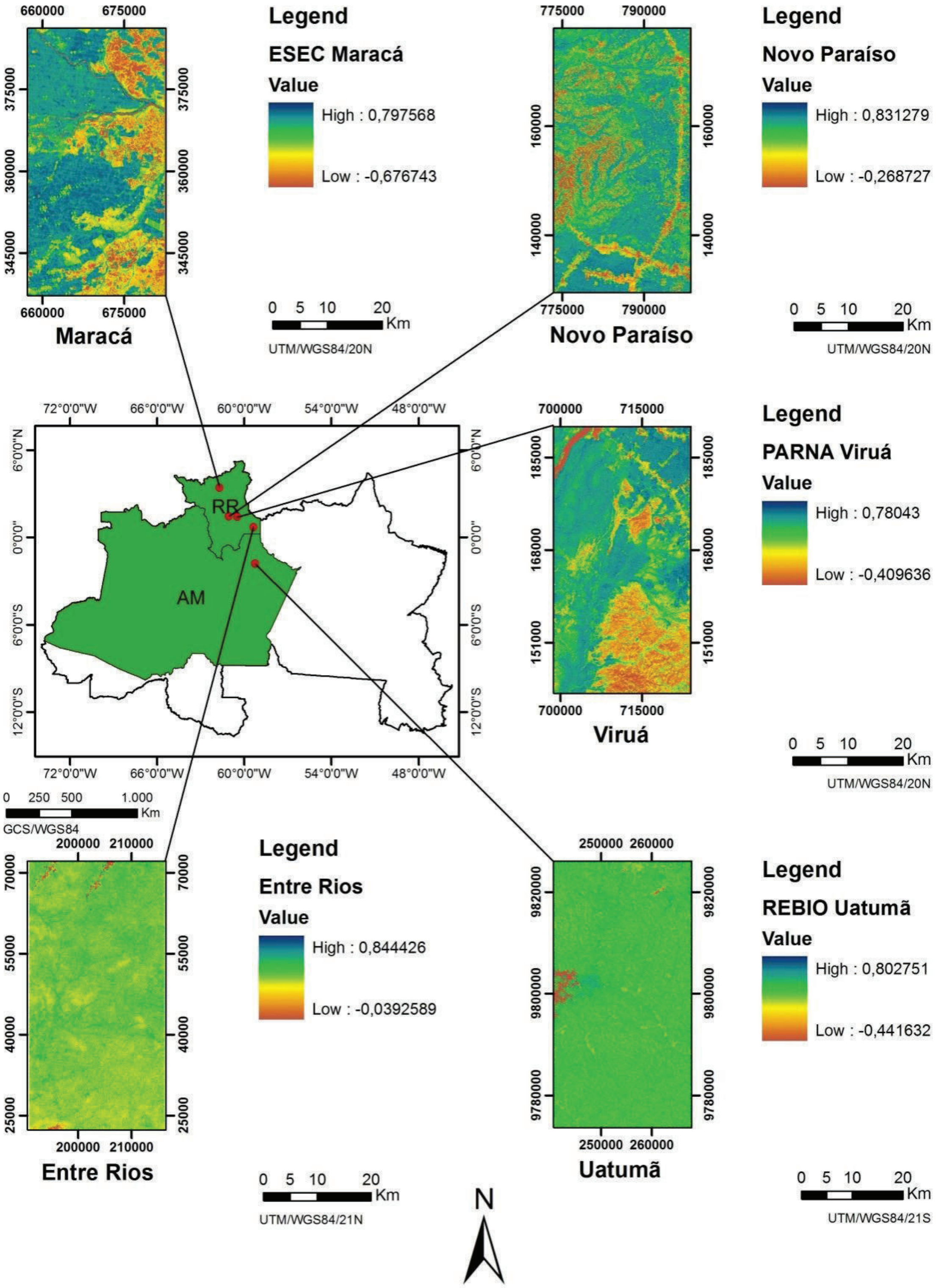
Figure 7. Body mass vs. Biomass relationship according to habit (terrestrial and arboreals) in the Rio Negro basin. (a)Uatumã; (b)Entre Rios (c)Novo Paraíso; (d)Viruá.

Figure 8. Body mass vs. Group density relationship according to diet (frugivores) in the Rio Negro basin. (a)Uatumã e (b)Viruá.

Figure 9. Body mass vs. Biomass relationship according to diet (frugivores) in the Rio Negro basin. (a)Uatumã; (b)Entre Rios; (c)Novo Paraíso; (d) Viruá; e (e)Maracá.

Figure 10. Body mass vs. Group size according to diet (frugivores) in the Rio Negro basin. (a)Uatumã

Figure 1.


660000
675000
375000
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Maracá
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Value
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775000
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Low : -0,268727
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60°0'0"W
54°0'0"W
48°0'0"W
6°0'0"N
0°0'0"
6°0'0"S
12°0'0"S
RR
AM
0 250 500 1.000 Km
GCS/WGS84
700000
715000
185000
168000
151000
Viruá
Legend
PARNA Viruá
Value
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Low : -0,409636
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210000
70000
55000
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25000
Entre Rios
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Entre Rios
Value
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Figure 2.

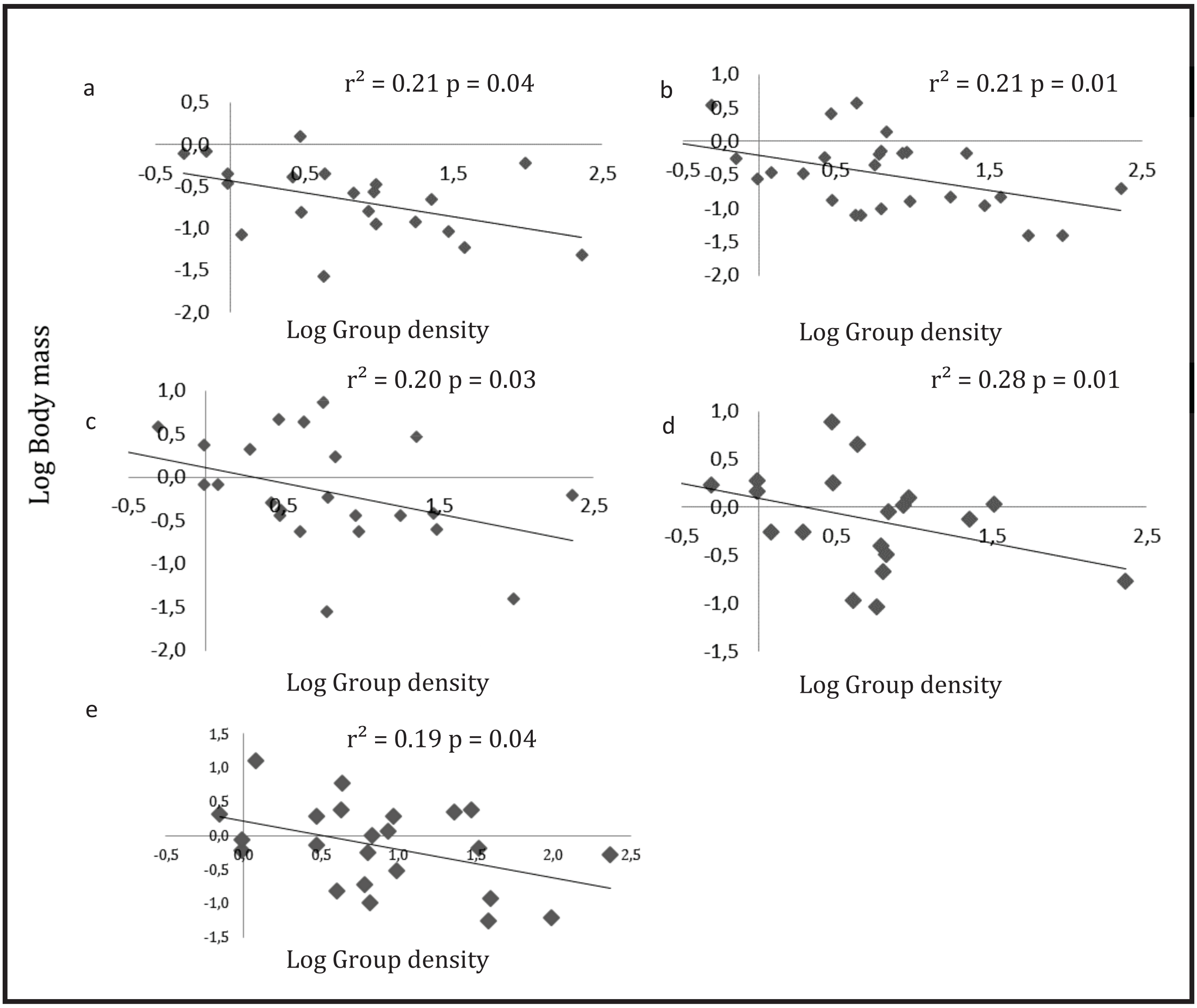

Log Body mass
a
r² = 0.21 p = 0.04
0,5
0,0
-0,5
-1,0
-1,5
-2,0
-0,5
0,5
1,5
2,5
Log Group density
b
r² = 0.21 p = 0.01
1,0
0,5
0,0
-0,5
-1,0
-1,5
-2,0
-0,5
0,5
1,5
2,5
Log Group density
c
r² = 0.20 p = 0.03
1,0
0,5
0,0
-0,5
-1,0
-1,5
-2,0
-0,5
0,5
1,5
2,5
Log Group density
d
r² = 0.28 p = 0.01
1,0
0,5
0,0
-0,5
-1,0
-1,5
-0,5
0,5
1,5
2,5
Log Group density
e
r² = 0.19 p = 0.04
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
Log Group density

Figure 3

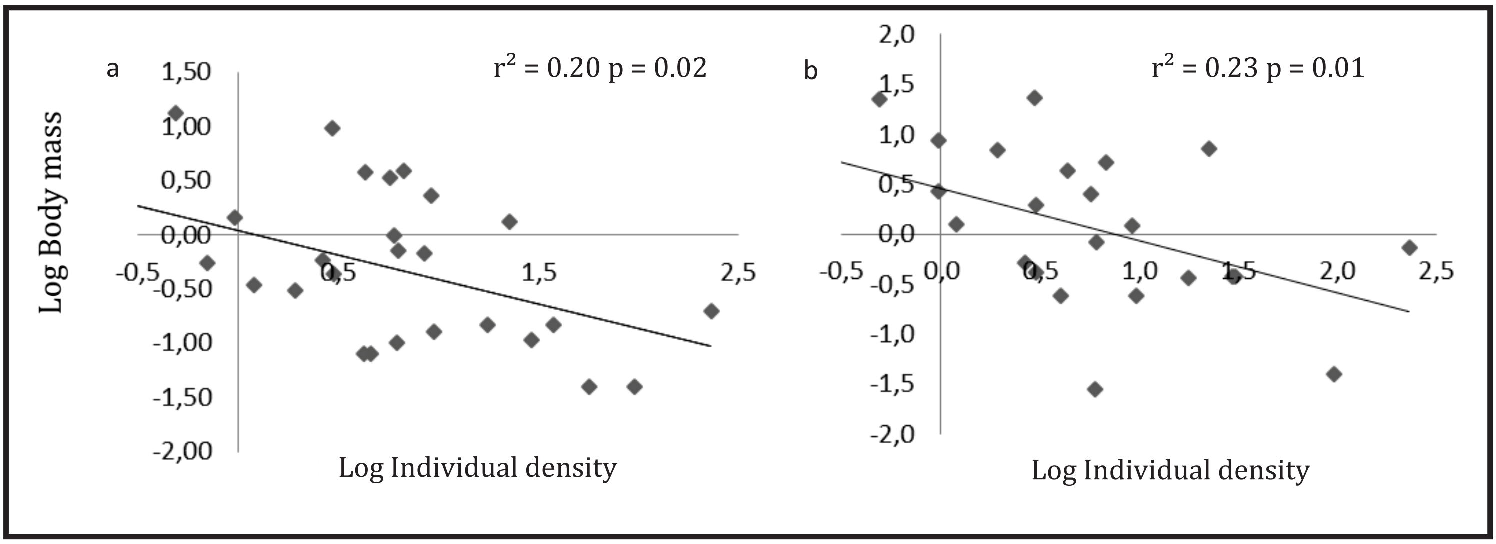

a
Log Body mass
1,50
1,00
0,50
0,00
-0,50
-1,00
-1,50
-2,00
-0,5
0,5
1,5
2,5
r^2 = 0.20 p = 0.02
Log Individual density
b
2,0
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-2,0
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
r^2 = 0.23 p = 0.01
Log Individual density

Figure 4

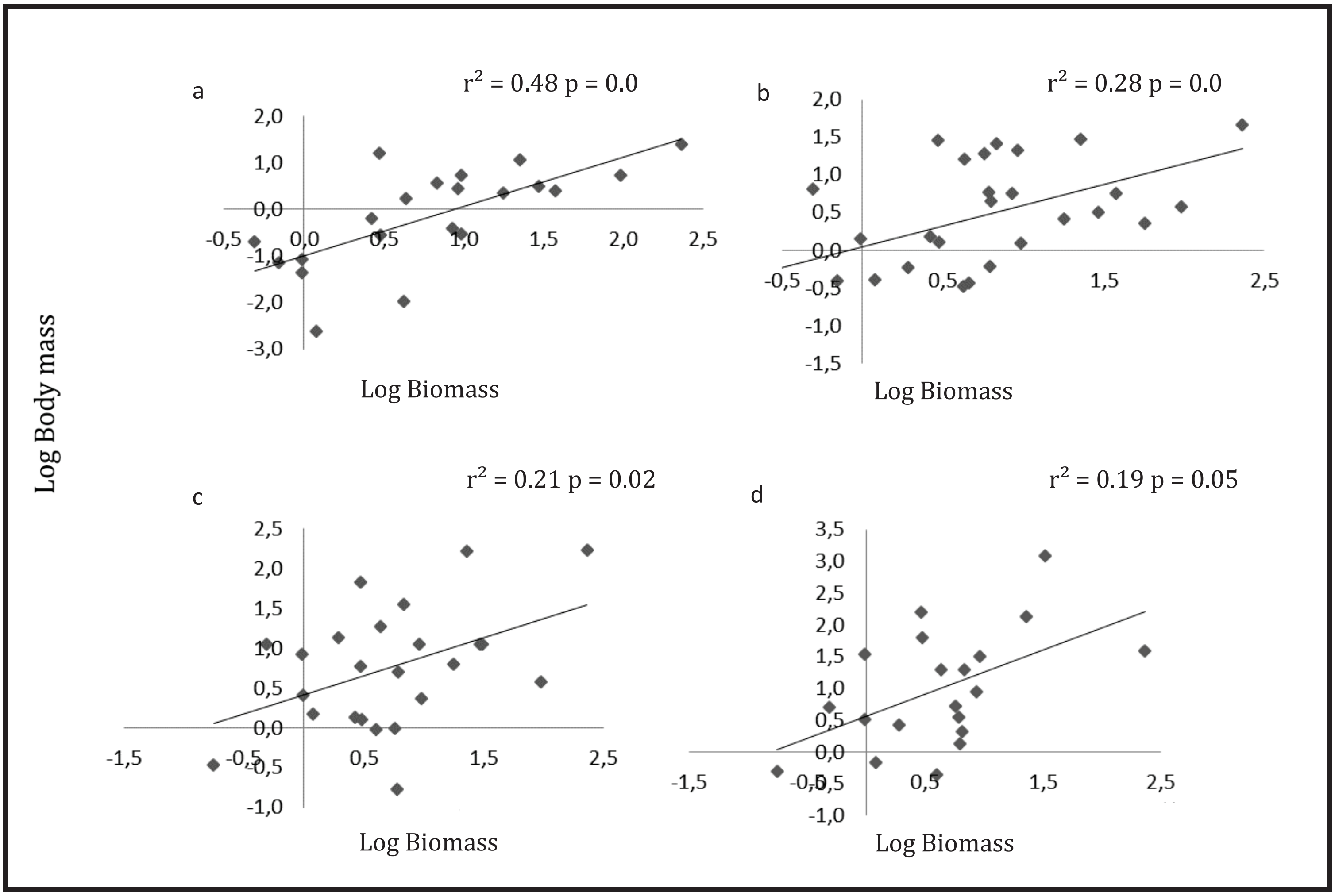

Log Body mass
a
r² = 0.48 p = 0.0
2,0
1,0
0,0
-1,0
-2,0
-3,0
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
Log Biomass
b
r² = 0.28 p = 0.0
2,0
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-0,5
0,5
1,5
2,5
Log Biomass
c
r² = 0.21 p = 0.02
2,5
2,0
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-0,5
0,5
1,5
2,5
Log Biomass
d
r² = 0.19 p = 0.05
3,5
3,0
2,5
2,0
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-0,5
0,5
1,5
2,5
Log Biomass

Figure 5

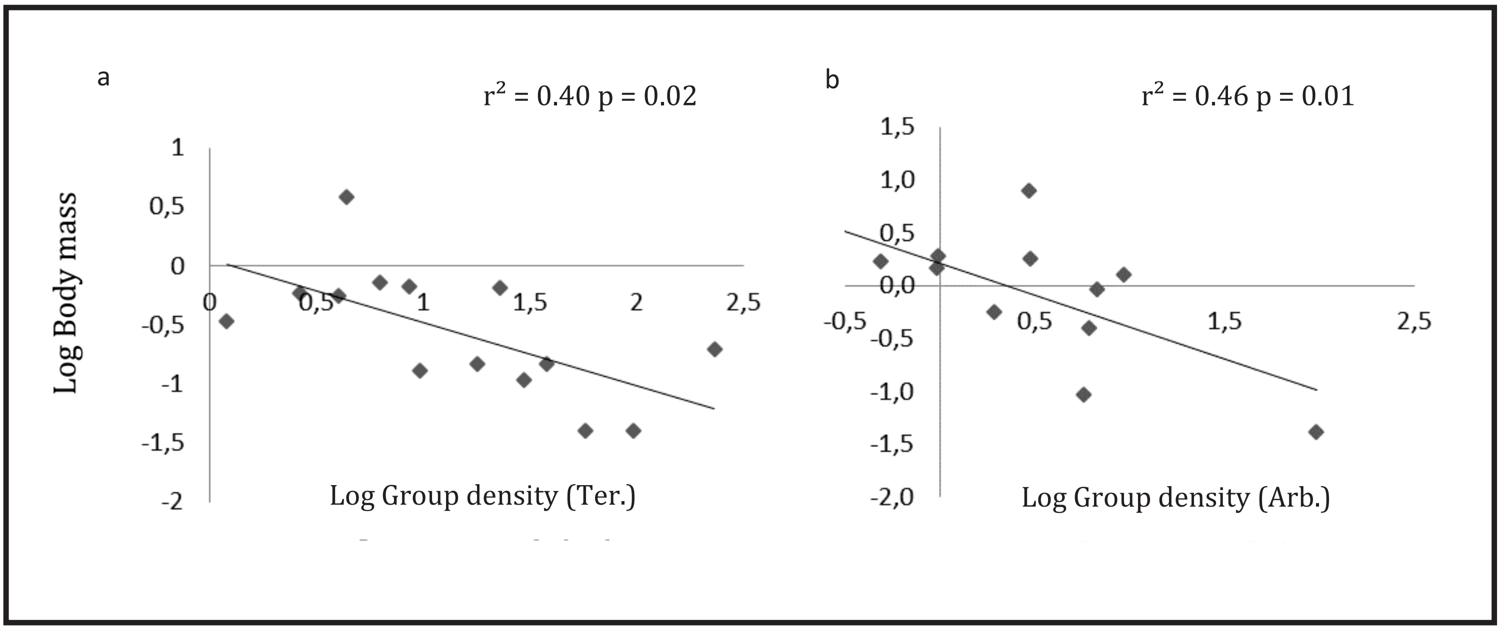

a
$r^2 = 0.40$ p = 0.02
Log Body mass
1
0,5
0
-0,5
-1
-1,5
-2
0
0,5
1
1,5
2
2,5
Log Group density (Ter.)
b
$r^2 = 0.46$ p = 0.01
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-2,0
-0,5
0,5
1,5
2,5
Log Group density (Arb.)

Figure 6

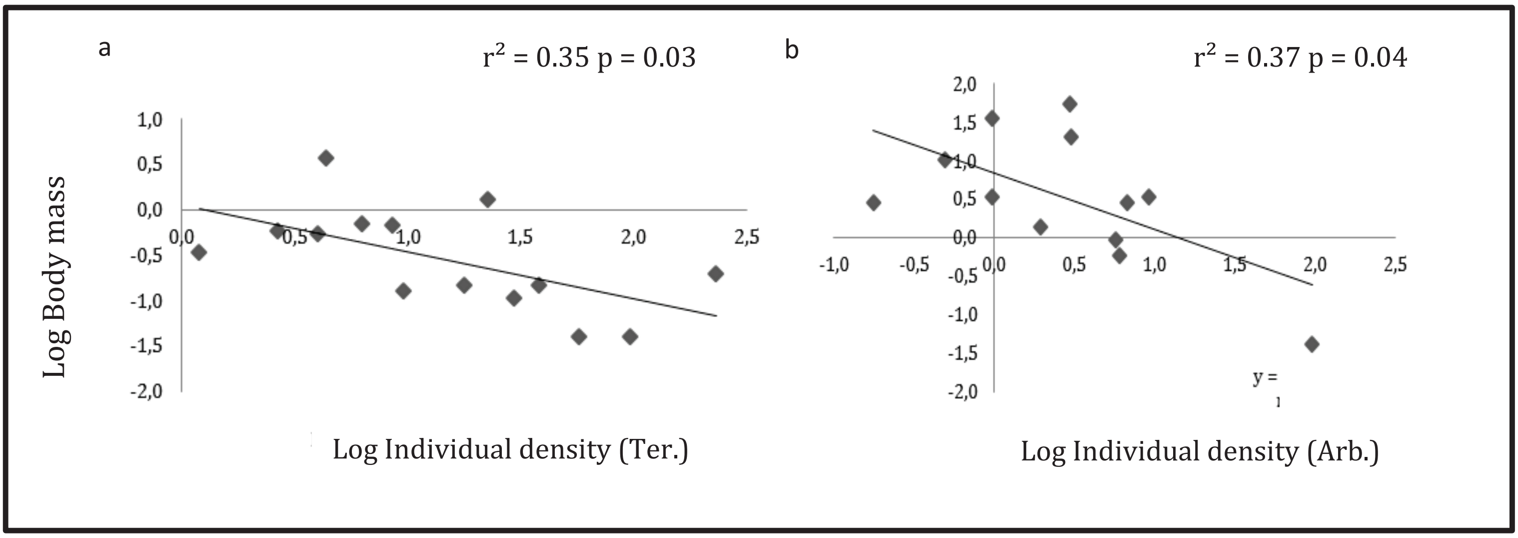

a
r² = 0.35 p = 0.03
1,0
0,5
0,0
-0,5
-1,0
-1,5
-2,0
0,0
0,5
1,0
1,5
2,0
2,5
Log Body mass
Log Individual density (Ter.)
b
r² = 0.37 p = 0.04
2,0
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-2,0
-1,0
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
y =
Log Individual density (Arb.)

Figure 7

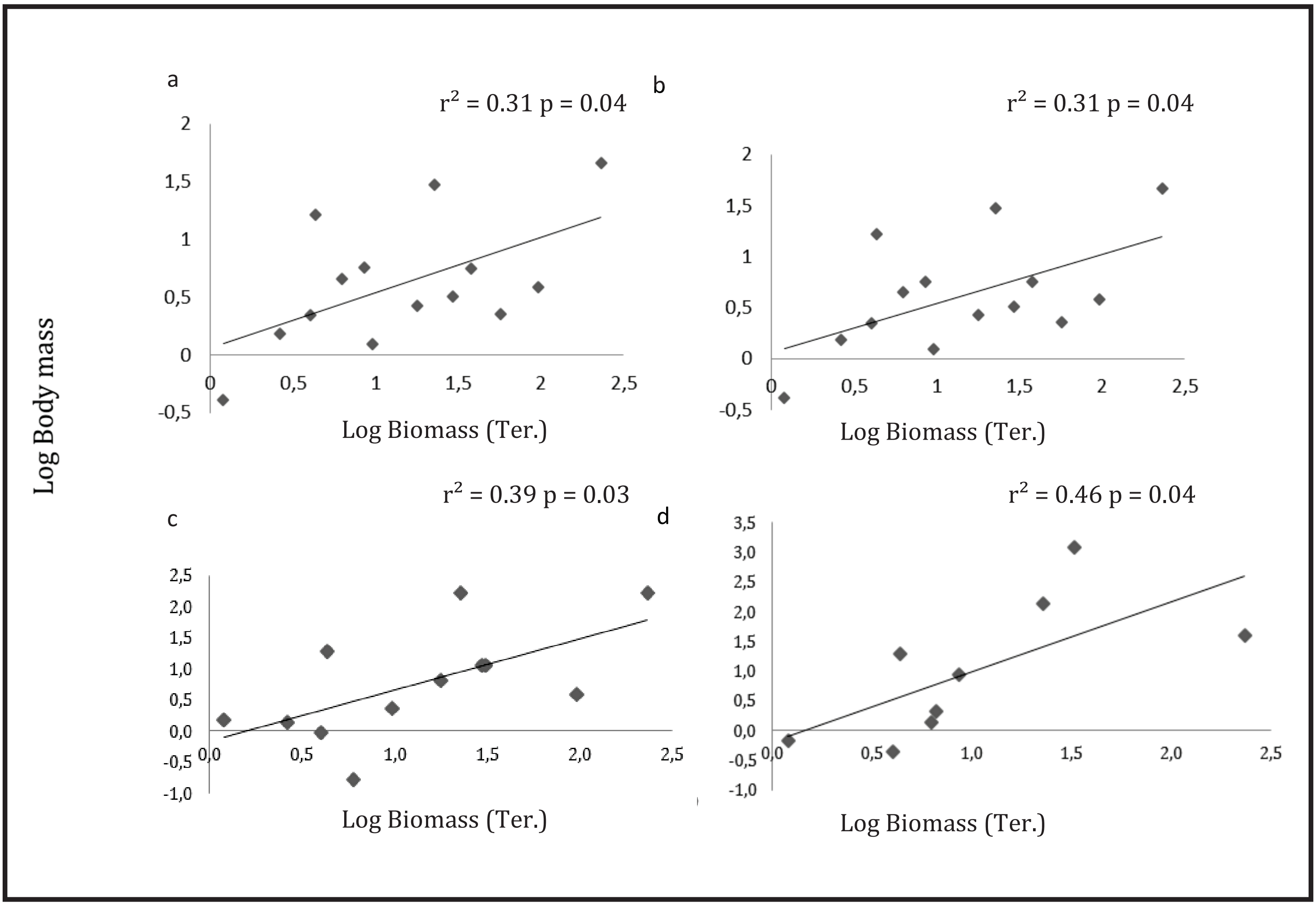

Log Body mass
a
r² = 0.31 p = 0.04
2
1,5
1
0,5
0
-0,5
0
0,5
1
1,5
2
2,5
Log Biomass (Ter.)
b
r² = 0.31 p = 0.04
2
1,5
1
0,5
0
-0,5
0
0,5
1
1,5
2
2,5
Log Biomass (Ter.)
c
r² = 0.39 p = 0.03
2,5
2,0
1,5
1,0
0,5
0,0
-0,5
-1,0
0,0
0,5
1,0
1,5
2,0
2,5
Log Biomass (Ter.)
d
r² = 0.46 p = 0.04
3,5
3,0
2,5
2,0
1,5
1,0
0,5
0,0
-0,5
-1,0
0,0
0,5
1,0
1,5
2,0
2,5
Log Biomass (Ter.)

Figure 8

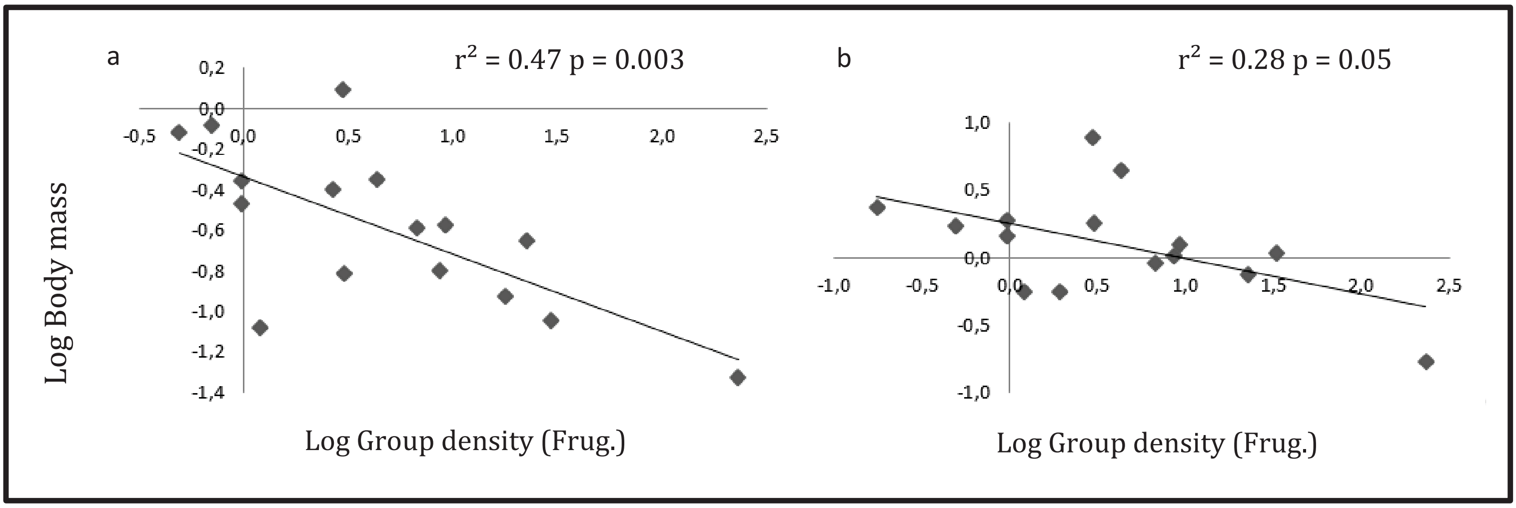

a
r² = 0.47 p = 0.003
0,2
0,0
-0,2
-0,4
-0,6
-0,8
-1,0
-1,2
-1,4
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
Log Body mass
Log Group density (Frug.)
b
r² = 0.28 p = 0.05
1,0
0,5
0,0
-0,5
-1,0
-1,0
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
Log Group density (Frug.)

Figure 9

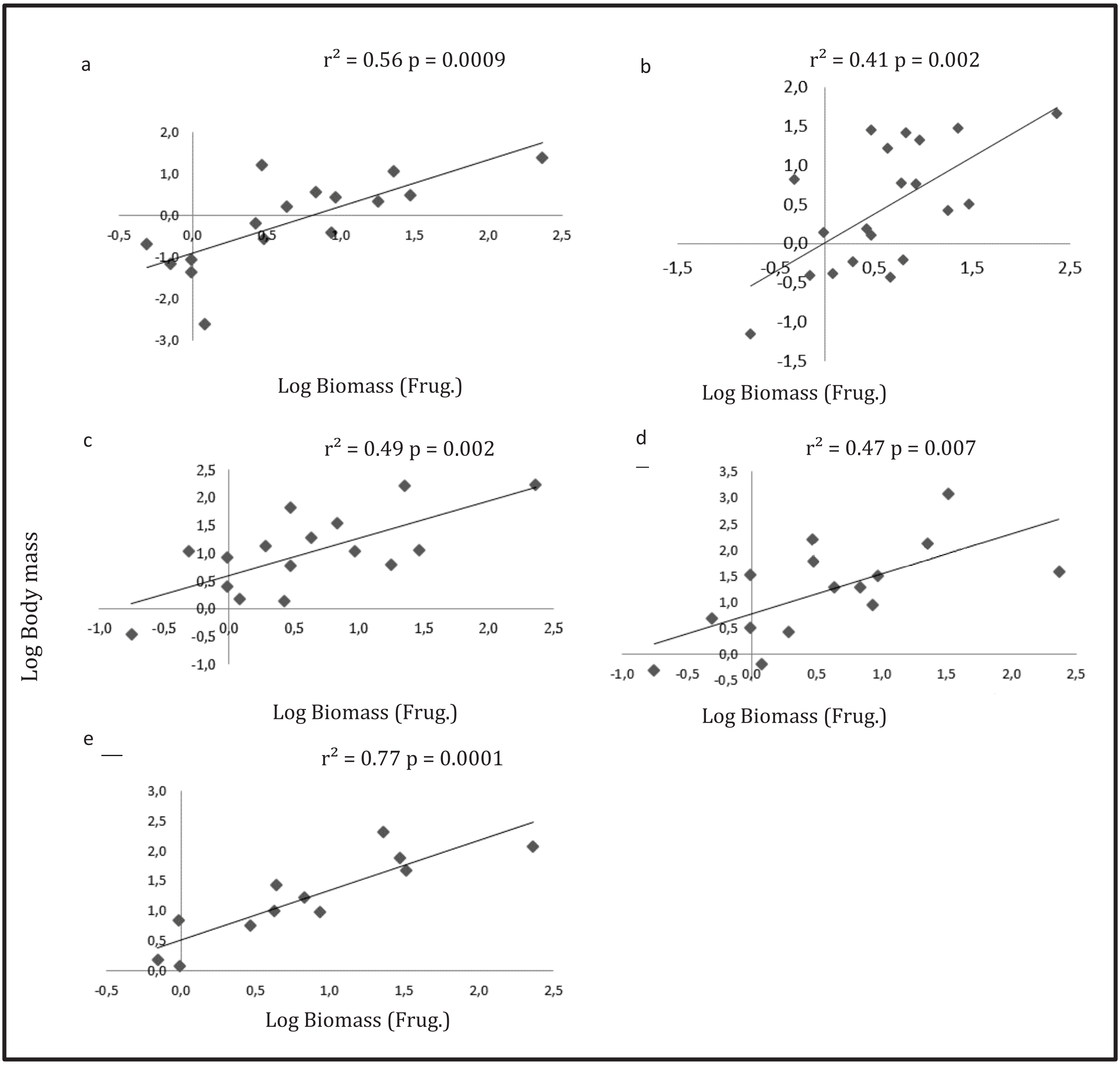
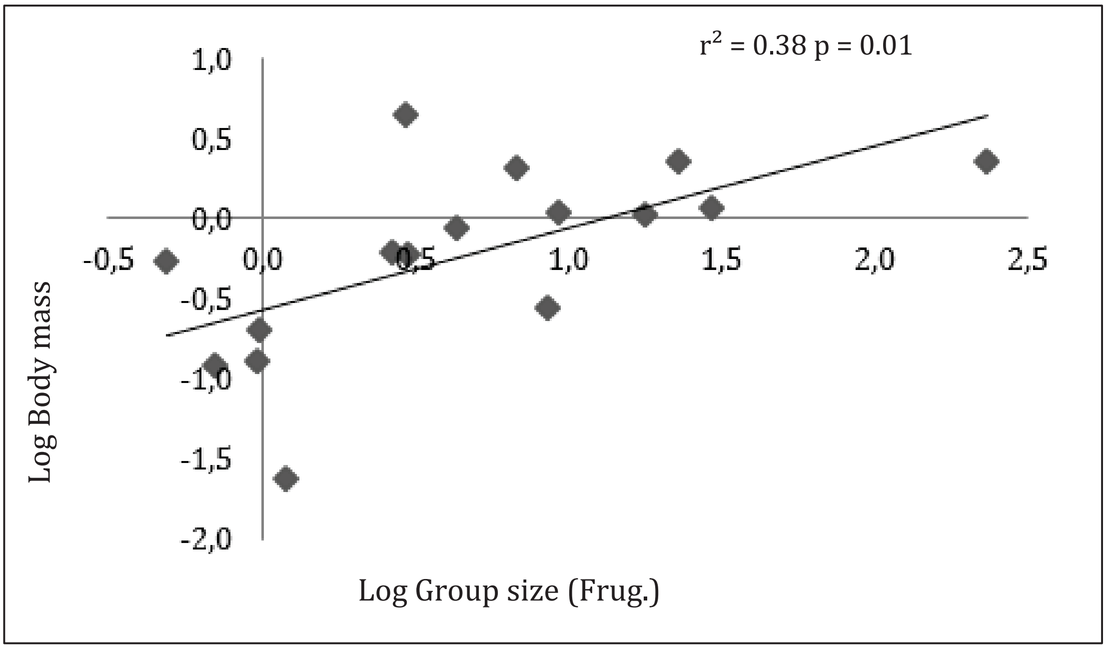

Log Body mass
a
$r^2 = 0.56$ $p = 0.0009$
2,0
1,0
0,0
-1,0
-2,0
-3,0
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
Log Biomass (Frug.)
b
$r^2 = 0.41$ $p = 0.002$
2,0
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-1,5
-0,5
0,5
1,5
2,5
Log Biomass (Frug.)
c
$r^2 = 0.49$ $p = 0.002$
2,5
2,0
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,0
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
Log Biomass (Frug.)
d
$r^2 = 0.47$ $p = 0.007$
3,5
3,0
2,5
2,0
1,5
1,0
0,5
0,0
-0,5
-1,0
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
Log Biomass (Frug.)
e
$r^2 = 0.77$ $p = 0.0001$
3,0
2,5
2,0
1,5
1,0
0,5
0,0
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
Log Biomass (Frug.)

Figure 10


r² = 0.38 p = 0.01
1,0
0,5
0,0
-0,5
-1,0
-1,5
-2,0
-0,5
0,0
0,5
1,0
1,5
2,0
2,5
Log Body mass
Log Group size (Frug.)

Anexos

Anexo A

Normas para submissão para o periódico: *Journal of animal ecology*

Journal of Animal Ecology Author Guidelines:

Manuscript Style and Formatting for Standard Papers

A. Author[*] [a], B. Author [b], C. Author [c], … and X. Author [x]

[a] Department of Life Sciences, University of Somewhere, City, Country

[b] Department of Life Sciences, University of Somewhere, City, Country

[c] Department of Life Sciences, University of Somewhere, City, Country

[x] Department of Life Sciences, University of Somewhere, City, Country

[*] Corresponding author: a.author@email.com

Summary

1. This should summarise the main results and conclusions of the paper using simple, factual, numbered statements. **It must not exceed 350 words**.

2. Summaries/abstracts are key to getting people to read your article.

3. Summaries should be understandable in isolation from your article.

4. Summaries should only have 5 points, ideally, listing; (1) what the question is, (2) why it is interesting, (3) what was done in the study, (4) what was found and (5) what this means.

5. Advice for optimising your *Summary/Abstract* (and Title) so that your paper is more likely to be found in online searches is provided at http://www.blackwellpublishing.com/bauthor/seo.asp

Key-words Listed in alphabetical order, the key-words should not exceed 10 words or short phrases. Please pay attention to the keywords you select: they should not already appear in the title or abstract. Rather, they should be selected to draw in readers from wider areas that might not otherwise pick up your paper when they are using search engines.

Introduction

This should state the reason for doing the work, the nature of the hypothesis or hypotheses under consideration, and should outline the essential background.

Materials and methods

This should provide sufficient details of the techniques to enable the work to be repeated. Do not describe or refer to commonplace statistical tests in Methods but allude to them briefly in Results.

Results

This should state the results, drawing attention in the text to important details shown in tables and figures.

Discussion

This should point out the significance of the results in relation to the reasons for doing the work, and place them in the context of other work.

Acknowledgements

In addition to acknowledging collaborators and research assistants, include relevant permit numbers (including institutional animal use permits), acknowledgment of funding sources, and give recognition to nature reserves or other organizations that made this work possible. Do not acknowledge Editors by name.

Specifications

Manuscripts should be typed in double spacing with a generous margin. ***The paper must include sequential line numbering throughout, and pages should be numbered consecutively, including those containing acknowledgements, references, tables and figure legends.*** Authors should submit the main document as a RTF or Word file. Figures can be embedded or uploaded as separate files. The RTF and Word will be converted to PDF (portable document format) upon upload. Reviewers will review the PDF version while the Word file will remain accessible by the Editorial Office. Manuscripts must be in English, and spelling should conform to the *Concise Oxford Dictionary of Current English*.

References

References in the text to work by up to three authors should be in full, e.g. (Johnson, Myers & James 2006). If there are more than three authors, they should always be abbreviated thus: (Nilsen et al. 2009). When different groups of authors with the same first author and date occur, they should be cited thus: (Jonsen, Myers & James 2006a; Jonsen, James & Myers 2006b), then subsequently abbreviated to (Jonsen *et al*. 2006a, b). The references in the list should be in alphabetical order with the journal name in full. The format for papers, entire books, chapters in books, and PhD theses is as follows.

Underwood, N. (2009) Effect of genetic variance in plant quality on the population dynamics of a herbivorous insect. *Journal of Animal Ecology*, 78, 839–847.

Jonsen, I.D., Myers, R.A. & James, M.C. (2006) Robust hierarchical state–space models reveal diel variation in travel rates of migrating leatherback turtles. Journal of Animal Ecology, 75, 1046–1057.

Nilsen, E.B., Linnell, J.D.C., Odden, J. & Anderson, R. (2009) Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. *Journal of Animal Ecology*, 78, 741–751.

Otto, S.P. & Day, T. (2007) *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*. Princeton University Press, Princeton, New Jersey, USA.

Conway. G. (2007) A Doubly Green Revolution: ecology and food production. *Theoretical Ecology: Principles and Applications*, 3rd edn (eds R. May & A. McLean), pp. 158–171. Oxford University Press, Oxford.

Stevenson, I.R. (1994) *Male-biased mortality in Soay sheep*. PhD thesis, University of Cambridge, Cambridge.

References should only be cited as 'in press' if the paper has been accepted for publication. Other references should be cited as 'unpublished' and not included in the list. Work not yet accepted for publication may be cited in the text and attributed to its author as: author name (including initials), unpublished data. In press articles should be uploaded with the manuscript as ‘supplementary files’.

We recommend the use of a tool such as EndNote or Reference Manager for reference management and formatting. EndNote reference styles can be searched for here:

http://www.endnote.com/support/enstyles.asp

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Citations from the world-wide-web are only allowed when alternative hard literature sources do not exist for the cited information. Authors are asked to ensure that:

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- The sites or information sources have sufficient longevity and ease of access for others to follow up the citation.
- The information is of a scientific quality at least equal to that of peer reviewed information available in learned scientific journals.

Units, symbols and abbreviations

Authors are requested to use the International System of Units (SI, Système International d'Unités) where possible for all measurements (see *Quantities, Units and Symbols*, 2nd edn (1975) The Royal Society, London). Note that mathematical expressions should contain symbols not abbreviations. If the paper contains many symbols, it is recommended that they should be defined as early in the text as possible, or within a subsection of the Materials and methods section.

Scientific names

Give the Latin names of each species in full, together with the authority for its name, at first mention in the main text. If they appear in the Summary/Abstract, use the common and Latin name only in the first instance, then the Latin or common name thereafter. If there are many species, cite a Flora or checklist which may be consulted for authorities instead of listing them in the text. Do not give authorities for species cited from published references. Give priority to scientific names in the text (with colloquial names in parentheses, if desired).

Makers' names

When a special piece of equipment has been used it should be described so that the reader can trace its specifications by writing to the manufacturer; thus: 'Data were collected using a solid-state data logger (CR21X, Campbell Scientific, Utah, USA)'.

Mathematical material

Mathematical expressions should be carefully represented. Suffixes and operators such as d, log, ln and exp will be set in Roman type; matrices and vectors will be set in bold type; other algebraic symbols will be set in italic. Make sure that there is no confusion between similar characters like 'l' (ell) and '1' (one). Also make sure that expressions are spaced as you would like them to appear, and if there are several equations they should be identified by eqn 1, etc.

Numbers in tables

Do not use an excessive number of digits when writing a decimal number to represent the mean of a set of measurements (the number of digits should reflect the precision of the measurement).

Numbers in text

Numbers from one to nine should be spelled out except when used with units; e.g. two eyes but 10 stomata and 5°C.

Figures

The publishers would like to receive your artwork in electronic form. Please save vector graphics (e.g. line artwork) in Encapsulated Postscript Format (EPS), and bitmap files (e.g. half-tones) in Tagged Image File Format (TIFF). *Ideally, vector graphics that have been saved in a metafile (.WMF) or pict (.PCT) format should be embedded within the body of the text file*. Detailed information on the Wiley-Blackwell digital illustration standards is available at:

http://www.blackwellpublishing.com/bauthor/illustration.asp

Figures should not be boxed (superfluous bounding axes) and tick marks must be on the inside of the axes. Where possible, figures should fit on a single page in the submitted paper. In a final version they will generally be reduced in size by about 50% during production. Wherever possible, they should be sized to fit into a single column width (*c*. 70mm final size). To make best use of space, you may need to rearrange parts of figures (e.g. so that they appear side by side). Please ensure that symbols, labels, etc. are large enough to allow reduction to a final size of *c*. 8

point, i.e. capital letters will be about 2 mm tall. Lettering should use a sans serif font (e.g. Helvetica and Arial) with **capitals used for the initial letter of the first word only. Bold lettering should not be used**. Units of axes should appear in parentheses after the axis name. Please note that line figures should be at least 600 dpi and half-tones (photos) should be at least 300 dpi.

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Tables

These should be referred to in the text as Table 1, etc. Do not present the same data in both figure and table form. Each table should be on a separate page, numbered and accompanied by a title at the top.

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For the printed version, any Appendices should be listed under 'Supporting Information', and added after the References, with the opening statement: 'The following Supporting Information is available for this article online' followed by brief captions for the Appendices/Figs/Tables to be included. These should be numbered Appendix S1, Fig. S1, Table S1, etc.

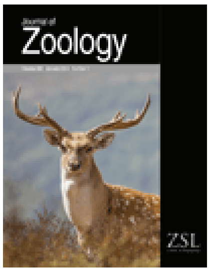
Any literature referred to in the Appendix or online Supporting Information should also be referenced in the Appendix or online Supporting Information so that it is a self-contained piece of work. This may mean duplicating references if any literature is cited in both the main text and the Supporting Information.

All Supporting Information should be submitted online as part of the main manuscript. Please name your online supporting files as ‘online supporting information' and upload them with the main document. This allows the submission web site to combine all the relevant files together but keep them separate when it comes to publication stage.

Anexo B

Normas para submissão para o periódico: *Journal of zoology*

Journal of Zoology



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Online ISSN: 1469-7998

Associated Title(s): Animal Conservation, International Zoo Yearbook

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Presentation

Papers should not exceed 5000 words including references (excluding the abstract and figure and table legends). Typescripts must be typed in double spacing, and pages should be numbered consecutively, including those containing acknowledgements, references, tables and figures. Lines must be numbered, preferably within pages.

Manuscripts for review must consist of a single text file with figure and table legends included at the end of this file on separate pages and with figure files uploaded separately. Please note that separate high resolution figure files will be required upon acceptance (see below). Typescripts must be in English (both English and American English are acceptable). The Editors reserve the right to modify accepted manuscripts that do not conform to scientific, technical, stylistic or grammatical standards, and these minor alterations may not be seen by the authors until the proof stage.

Conventions

The Metric system must be used and SI units where appropriate. For further details see Baron, D.N. (1988). *Units, symbols and abbreviations*. 5th edition. London: Royal Society of Medicine Series. Whole numbers one to nine should be spelled out and number

10 onwards given in numerals. If a new taxon is described, the institution in which the type material is deposited must be given, together with details of the registration assigned to it. Full binomial names should be given on the first occasion an organism is mentioned (and abbreviated thereafter), except at the beginning of a sentence. Avoid footnotes except to add information below the body of a table. Do not use initial capitals for the common names of animals unless derived from a proper noun.

Typescript

The typescript should follow the conventional form and must include:
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(3) ***Keywords***. A maximum of eight keywords may be suggested.
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(7) ***Discussion***. This should point out the significance of the results in relation to the reasons for undertaking the research.

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Accuracy of references is the responsibility of the author(s). References must be checked against the text to ensure (a) that the spelling of authors' names and the dates given are consistent and (b) that all authors quoted in the text (in date order if more than one) are given in the reference list and vice versa. The full title of the paper must be given together with the first and last pages.

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Examples
Lemelin, P. (1996a). Relationships between hand morphology and feeding strategies in small-bodied prosimians. *Am. J. phys. Anthrop* ` (Suppl.) 22, 148.
Lemelin, P. (1996*b*). *The evolution of manual prehensility in primates: a comparative study of prosimians and didelphid marsupials*. PhD thesis, State University of New York at Stony Brook.
Pianka, E. R. (1978). *Evolutionary ecology*.2nd edn. New York: Harper & Row.
Whitear, M. (1992). Solitary chemosensory cells. In *Fish chemoreception*: 103-125. Hara, T. J. (Ed.). London: Chapman & Hall.

References in Articles

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