

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

**EFEITO DA OBSTRUÇÃO GERADA PELA DENSIDADE DA VEGETAÇÃO DO
SUB-BOSQUE SOBRE MORCEGOS FRUGÍVOROS E ANIMALÍVOROS
CATADORES (CHIROPTERA: PHYLLOSTOMIDAE) NA AMAZÔNIA CENTRAL,
BRASIL**

RODRIGO MARCIENTE TEIXEIRA DA SILVA

Manaus, Amazonas

Novembro 2012

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BRASIL**

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Dissertação apresentada ao
Instituto Nacional de Pesquisas da
Amazônia como parte dos
requisitos para obtenção do título
de Mestre em Biologia (Ecologia).

Manaus, Amazonas

Novembro 2012

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Aos meus pais, Rosemeire e Reinaldo;
minha esposa Ignês e
à Maria Clara, minha semente para o futuro!

AGRADECIMENTOS

Este trabalho não seria realizado sem importantes financiadores e colaboradores que de alguma forma contribuíram para sua conclusão. Dentre os quais, agradeço ao Instituto Nacional de Pesquisas da Amazônia (INPA) que, por intermédio do Programa de Pós-Graduação em Ecologia, possibilitou a realização de meu Mestrado; ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) por viabilizar minha bolsa de estudos durante todo o processo de capacitação.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) através dos recursos do PNPD do Paulo Bobrowiec (co-orientador), Bat Conservation International (BCI), Centro de Estudos Integrados da Biodiversidade Amazônica (INCT-CENBAM), e Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) pelo financiamento do projeto.

Aos companheiros de campo, em especial Ocírio de Souza Pereira (Juruna) que carregou este fardo ombro a ombro durante as longas campanhas de campo.

Por fim, e não menos importante, agradeço a minha família pelo incentivo e motivação necessária para seguir sempre em frente.

RESUMO

Locais onde a vegetação florestal é fechada demandam dos morcegos maior capacidade de manobrar durante o voo. Baseado na morfologia das asas sugere-se que morcegos animalívoros catadores apresentam melhor desempenho de voo em ambientes obstruídos do que outras guildas tróficas. Eu relatei a densidade da vegetação do sub-bosque, como uma medida de obstrução do espaço, e a composição de espécies em assembleias de morcegos Phyllostomidae. Em florestas primárias, nos sítios com sub-bosque mais denso, eu esperava encontrar uma maior contribuição de morcegos animalívoros na composição de espécies. Realizei o estudo no Interflúvio dos Rios Purus e Madeira, ao longo da rodovia BR-319 onde oito unidades amostrais distantes no mínimo 40 km e compostas por dez parcelas permanentes foram amostradas. Empreguei técnicas de ordenação e modelos lineares generalizados, para realizar inferências sobre o uso de ambientes com diferentes níveis de obstrução por morcegos Phyllostomidae. Após 3.840 horas-rede, 511 morcegos de 4 famílias (Emballonuridae, Phyllostomidae, Vespertilionidae e Thyropteridae) e 27 espécies foram capturadas, dos quais 12 espécies foram frugívoras (n=414 capturas) e 10 espécies foram animalívoras (n=70 capturas). Ao longo de um gradiente de obstrução cuja amplitude variou de 53% a 73%, o número de espécies foi reduzido de 16 para 7 sete espécies registradas, respectivamente. O efeito negativo da obstrução ocorreu em ambos os morcegos animalívoros e frugívoros. A ocorrência das espécies nos sítios apresentou estrutura aninhada e morcegos animalívoros contribuíram mais para a composição de espécies em sítios com sub-bosque mais denso. O efeito de filtro sobre o tamanho corporal não foi suficiente para explicar a estrutura de comunidades de morcegos em função da obstrução do espaço. A relação das espécies com a obstrução foi dependente do hábito alimentar, com morcegos animalívoros ocorrendo em locais com vegetação mais densa. Nossos resultados sugerem que em florestas primárias os efeitos da estrutura da vegetação sobre assembleias de morcegos são diferentes dos reportados para florestas secundárias e muitas inferências sobre a ecologia de morcegos podem estar enviesadas para locais perturbados.

Palavras chave: Morcegos, Estrutura da vegetação, Obstrução, Estrutura trófica.

ABSTRACT

Effect of understory vegetation clutter on frugivorous and animalivorous bats (Chiroptera: Phyllostomidae) in Central Amazonia, Brazil

We related density of understory vegetation as a measure of clutter to species composition of phyllostomid bat assemblages, their trophic structure and body-size of species. We expected to find a great contribution of animalivorous bats to species composition in mature-forest sites with denser understory associated with a negative effect on large-bodied species. The study was carried out between the Purus and Madeira Rivers, along the BR-319 highway, Central Amazonia. We sampled 80 permanent plots grouped into eight sample units at least 40 km apart. We employed ordination techniques and generalized linear models to make inferences about habitat use by phyllostomid bats along the clutter gradient. After 3,840 net-hours, 511 bats of 4 families (Emballonuridae, Phyllostomidae, Vespertilionidae and Thyropteridae) and 27 species were captured, of which 12 were frugivores (n=414 captures) and 10 animalivores (n=70 captures). The number of species was reduced from 16 to 7 along a gradient of vegetation obstruction ranging from 53% to 73%. This negative effect occurred for both trophic guilds. Assemblages showed a nested pattern along the clutter gradient. The filter effect on body size alone was not sufficient to explain the bat assemblage structure. The effect of clutter differed between foraging guilds, with animalivorous bats tending to occur in sites with denser vegetation. Our results suggest that, in primary forests the effects of vegetation structure on bat assemblages are distinctive of previous results reported from secondary forests and that most inferences of bat ecology can be biased for anthropogenic disturbances.

Key words: Brazil; BR-319 highway; chiroptera, neotropical bats; phyllostomid bats; species composition; species diversity; trophic structure; understory vegetation clutter.

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APRESENTAÇÃO

Morcegos representam cerca de um quarto da diversidade dos mamíferos vivos (Simmons 2005). Até 90 espécies de morcegos podem ser capturadas na mesma localidade nos neotrópicos (Simmons & Voss 1998) e a família Phyllostomidae integra o maior contingente de espécies registradas no Bioma Amazônico (Sampaio et al. 2003, Bernard et al. 2011). Geralmente, morcegos Phyllostomidae são reconhecidos por usar ambientes com vegetação densa, que gera obstrução do espaço (Kalko et al. 1996). As subfamílias Carolliinae e Stenodermatinae são categorizadas dentro da guilda trófica frugívora, e morcegos Phyllostominae são animalívoros (Giannini & Kalko 2004). Juntas, estas três subfamílias englobam a maioria das espécies da família Phyllostomidae. Ambas as linhagens de frugívoros e animalívoros apresentam voo lento e com capacidade para manobrar em meio à vegetação (Norberg & Rayner 1987). Considerando a diversidade de hábitos alimentares vistas em morcegos Phyllostomidae, é possível que a utilização de ambientes por ambas as guildas tróficas seja diferente. Assim, este manuscrito apresentará como estes dois grandes agrupamentos tróficos respondem a um mesmo parâmetro da estrutura da vegetação no sub-bosque, sua densidade, aqui chamada de obstrução. Os dados foram coletados no interflúvio dos rios Purus e Madeira, na Amazônia brasileira, em uma extensão aproximada de 500 km. Este trabalho é parte integrante do esforço de inúmeros pesquisadores para descrever, compreender e monitorar a biota ao longo da BR-319, que corta o interflúvio e liga as capitais Porto Velho (RO) e Manaus (AM).

HIPÓTESES

I - Se o hábito alimentar determinar o desempenho de voo em sítios obstruídos, então morcegos animalívoros e morcegos frugívoros serão afetados diferencialmente pela densidade da vegetação no sub-bosque.

II - Em florestas contínuas e maduras morcegos animalívoros devem ser menos afetados pelo aumento da obstrução em sítios com sub-bosque mais denso.

OBJETIVO

O presente estudo investigou a relação entre densidade da vegetação do sub-bosque, como uma medida de obstrução do espaço, e a composição de espécies em assembléias de morcegos *Phyllostomidae*.

ARTIGO

Marciente, R.; Bobrowiec P. E. D.; William E. Magnusson. **Understory vegetation clutter effect on frugivorous and animalivorous bats in Central Amazonia**

Formatado para submissão na revista Biotropica.

LRH: Marciente, Bobrowiec, and Magnusson

RRH: **Understory clutter effect on neotropical bats**

Understory vegetation clutter effect on frugivorous and animalivorous bats in Central Amazonia

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Received ____; revision accepted ____

ABSTRACT

We related density of understory vegetation as a measure of clutter to species composition of phyllostomid bat assemblages, their trophic structure and body-size of species. We expected to find a great contribution of animalivorous bats to species composition in mature-forest sites with denser understory associated with a negative effect on large-bodied species. The study was carried out between the Purus and Madeira Rivers, along the BR-319 highway, Central Amazonia. We sampled 80 permanent plots grouped into eight sample units at least 40 km apart. We employed ordination techniques and generalized linear models to make inferences about habitat use by phyllostomid bats along the clutter gradient. After 3,840 net-hours, 511 bats of 4 families (Emballonuridae, Phyllostomidae, Vespertilionidae and Thyropteridae) and 27 species were captured, of which 12 were frugivores (n=414 captures) and 10 animalivores (n=70 captures). The number of species was reduced from 16 to 7 along a gradient of vegetation obstruction ranging from 53% to 73%. This negative effect occurred for both trophic guilds. Assemblages showed a nested pattern along the clutter gradient. The filter effect on body size alone was not sufficient to explain the bat assemblage structure. The effect of clutter differed between foraging guilds, with animalivorous bats tending to occur in sites with denser vegetation. Our results suggest that, in primary forests the effects of vegetation structure on bat assemblages are distinctive of previous results reported from secondary forests and that most inferences of bat ecology can be biased for anthropogenic disturbances.

Key words: Brazil; BR-319 highway; chiroptera, neotropical bats; phyllostomid bats; species composition; species diversity; trophic structure; understory vegetation clutter.

1 VEGETATION STRUCTURE PLAYS AN IMPORTANT ROLE ON SPATIAL DISTRIBUTION OF ANIMAL SPECIES,
 2 SPECIES-ASSEMBLAGE ORGANIZATION AND HABITAT SELECTION (MacArthur & MacArthur 1961,
 3 Rotenberry & Wiens 1980, Hurlbert 2004). Mosaics of structurally distinctive habitats provide
 4 many ways to exploit the environment, and individual species are partitioned on breeding sites,
 5 refuges, and foraging niches. Studies with Amazonian flying vertebrates show that vegetation
 6 structure affects patterns of species composition and organization of assemblages (Borges and
 7 Carvalhaes 2000, Haugaasen and Peres 2005, Peters *et al.* 2006, Beja *et al.* 2009, Pereira *et al.* 2009,
 8 Bobrowiec and Gribel 2010). Understory-vegetation density influences the occurrence of some
 9 species in avian (Borges & Carvalhaes 2000, Pereira *et al.* 2009) and bat assemblages (Peters *et al.*
 10 2006, Pereira *et al.* 2009), especially for species that use this stratum for roosting and foraging, or
 11 limits access due to physical clutter. Vegetation clutter is an important factor on selection of
 12 foraging sites for bats ensembles (Kalko *et al.* 1996). Besides restricting flight performance
 13 (Stockwell 2001), the clutter noise negatively affects echolocation (Schnitzler & Kalko 2001).
 14 Frugivorous and animalivorous phyllostomid bats are commonly captured in the understory in
 15 Central Amazonia ((Sampaio *et al.* 2003, Bernard *et al.* 2011). Phyllostomid bats feed very close
 16 to, or within, vegetation clutter and are categorized as highly-cluttered-space gleaners (Kalko *et*
 17 *al.* 1996). Phyllostomid bats use alternative sensorial clues, such as passive listening (Neuweiler
 18 1990, Arlettaz *et al.* 2001), olfaction (Thies *et al.* 1998, Bianconi *et al.* 2007) and vision. Thus,
 19 clutter-noise constraints do not necessarily reduce the accessibility of thick habitats for phyllostomid
 20 bats, and the mechanical constraints associated with flight maneuverability seem to be a more
 21 important in cluttered vegetation.

22 Based on wing morphology, Norberg and Rayner (1987) suggests that animalivorous bats
 23 have better flight performance than other trophic guilds in cluttered locations. However, field
 24 examples show contradictory evidence. In sites with more open understory, such as flooded forests
 25 (Haugaasen & Peres 2006), Pereira *et al.* (2009) captured few animalivorous species in comparison

1 with the dense understory of *terra firme* unflooded forests. In contrast, sites with dense vegetation,
2 such as regrowth (Mesquita *et al.* 2001, Gehring *et al.* 2005), also have few animalivorous species
3 (Peters *et al.* 2006b, Bobrowiec & Gribel 2010). Animalivores bats are more sensitive to habitat
4 disturbances than frugivorous species (Fenton *et al.* 1992, Ochoa 2000, Gorresen *et al.* 2005, Willig *et*
5 *al.* 2007, Presley *et al.* 2008, Klingbeil & Willig 2009, Bobrowiec & Gribel 2010), so apparent
6 associations between bat trophic guilds and clutter are confounded by other aspects related to human
7 disturbance.

8 In this study, we investigated the relationship between vegetation density, as a measure of
9 physical clutter, and species composition of phyllostomid-bat assemblages in *terra firme* forests in
10 Central Amazonia, Brazil. We hypothesized that understory cluttered by vegetation would affect
11 frugivorous and animalivorous bats differently, with animalivorous species being more tolerant to
12 increasing understory density. Additionally, we expected that large-bodied species would be less
13 frequent in cluttered sites, due to restrictions on flight performance (Stockwell 2001). We also
14 expected to find a nested assemblage structure (Patterson & Atmar 1986), with sites with more
15 cluttered vegetation used by subsets of the species recorded in more open vegetation sites. To avoid
16 confusion between edge-effects and other characteristics of secondary vegetation, with those of
17 vegetation clutter, we only sampled continuous mature forests.

19 **METHODS**

20
21 **SITE DESCRIPTION.**—The study was carried out along 520 km of the BR-319 highway, in the
22 State of Amazonas, Brazil. The highway is located between the Purus and Madeira Rivers,
23 linking Manaus to the southwest region of Amazonas (Figure 1). Forest structure varies from
24 dense lowland tropical forest in the north, to open lowland tropical forest near the
25 municipality of Humaitá in the southwest (IBGE 1997). Mean annual precipitation is

irregularly distributed in the region, and varies from about 2400 mm, near Manus and Humaitá, to around 2800 mm in the middle of the highway. The number of dry months, with mean precipitation < 100 mm, varies from two to four from south to north along the highway (Sombroek 2001).

DATA COLLECTION: SAMPLING DESIGN.—The sampling desing was based on RAPELD methodology (Magnusson *et al.* 2005, Costa & Magnusson 2010), as part of the Brazilian Biodiversity Research Program (PPBio) network (<http://ppbio.inpa.gov.br/en/home>). We sampled 80 plots hierarchically grouped into 8 sample units called modules. These modules were located at intervals of about 60 km along the BR-319 (Figure 1). Each module comprises two paralell 5 km long trails, 1 km apart, with permanent plots at 1 km intervals, totaling five plots per trail and ten plots per module (Figure 1). The permanent plots are 250 m long, and follow the topographic contours to minimize variation due to topograhly on environmental and biological variables (Magnusson *et al.* 2005).

DATA COLLECTION: BAT CAPTURES.—The bat fauna was sampled between October 2010 and November 2011 in two dry seasons using eigth ground-level mist nets (12x3 m, 6 shelves, and 19 mm mesh, Ecotone[®]) in each plot. Nets were opened between 1800 h and 2400 h and checked at intervals of 30-45 min. Each plot was sampled one night, totaling 10 nights of captures in each module or 480 nets-hour per sample unit. Nights with rain and full moon were not sampled. Captured bats were placed in individual cotton bags, measured and identified following Charles-Dominique *et al.* (2001), Lim and Engstrom (2001), Simmons *et al.* (2002), and Gardner (2008). We chose to be conservative, grouping captures of *C. perspicillata* and *C. brevicauda* into *Carollia* spp. for all analyses, as we could not distiguish between these two species using external measures in the field. Nomenclature follows

(Simmons 2005), except for recognizing *Artibeus planirostris* rather *Artibeus jamaicensis* (Lim *et al.* 2004), *Vampyriscus bidens* and *Vampyriscus brocki* rather than *Vampyressa bidens* and *Vampyressa brocki* (Baker *et al.* 2003), and for recognizing Lonchohyllinae as a subfamily (Baker *et al.* 2003). Bats were classified into broad foraging guilds (frugivores, gleaning animalivores, nectarivores and aerial insectivores; Table 1) based on published feeding habits (Willig 1986, Giannini & Kalko 2004). Local representatives of these guilds compose ensembles, sensu Fauth *et al.* (1996). Voucher specimens of each species were collected, preserved in 70 percent ethanol, and deposited in the INPA Mammal Collection in Manaus.

DATA COLLECTION: UNDERSTORY VEGETATION CLUTTER.—As a measure of vegetation clutter, we estimated understory density vegetation obstruction) using digital images. The method was an adaption of the method proposed for Marsden *et al.* (2002) and used by (Baumgarten 2009). We took digital photographs of a white target (3 x 3m) positioned parallel to, and 8 m distant from, the nets (Figure 2). The target height corresponded to the maximum height of opened mist nets. One digital image was obtained from each net, giving eight images for each plot and 80 images for each module. Images were processed using the software SideLook 1.1.01 (Zehm *et al.* 2003). Vegetation obstruction in each module was estimated as the mean percentage of area covered by vegetation (trunks, branches and leafs) in the 80 images.

DATA ANALYSES.—We excluded all non-phylostomid species, since they are not be adequately sampled with mist nets (Kalko 1998). We used a non-metric multidimensional scaling analysis (NMDS) to reduce the dimensionality of species composition data (presence-absence) to one axis of a indirect multivariate ordination (Legendre & Legendre 1998). Dissimilarity in species composition between plots was calculated based on the Sørensen

measure (Magurran 2004). We use direct gradient analysis (McCune & Grace 2002) to illustrate graphically the distribution of species in relation to vegetation obstruction of modules (Figure 4). For this analysis, modules were ordered following the gradient of vegetation obstruction. Species were ordered using the mean of vegetation obstruction in the capture plot for individuals of each species. The scores of each species on the direct ordination axis were calculated using the equation $(\sum [n_{ij} \times obstruction_j]) / N_i$, where n_{ij} is the number of captures of species i in the module j , $obstruction_j$ is the mean percentage of area covered for vegetation in the module j , and N_i is the total of captures of species i in all sample units. We employed a null model to evaluate if the structure of bat assemblage was more related to vegetation obstruction than expected by chance (Gotelli & Graves 1996). The metric NODF (Almeida-Neto *et al.* 2008) was used to test the nestedness of assemblages, using the algorithm Random 1, fixed incidence proportional (Gotelli 2000, Ulrich *et al.* 2009), and 10,000 permutations for the null model. The data matrix used for this model was derived from the direct ordination analysis, with species as columns and sample units as rows.

We evaluated effects of vegetation obstruction on number of species for assemblages and ensembles, as well as on species composition and trophic structure of assemblage. Generalised linear modelling (GLM) was used to test for relationships between total number of species, number of frugivorous species, and number of animalivorous species. Because data were counts, they were modelled using Poisson distributions with goodness of fit considering overdispersion of residuals based on quasi-GLM models (Zuur *et al.* 2009). We used the NMDS indirect ordination axis, and the direct ordination axis of species in relation to vegetation obstruction as response variables to test effects of vegetation clutter on species composition of assemblages using two GLM models. Because data from multivariate ordinations were not counts, they were modelled using Gaussian distributions. To evaluate if bat assemblage structure captured by the direct ordination analysis can be explained for filters

on body sized and/or feeding habits of species, we incorporate an interaction between the variables body mass (g) and foraging guild (frugivores and animalivores). We excluded nectarivores, since they were represented only by *Lonchophylla thomasi* and the analysis was based on species as units. All analyses were undertaken in the R 2.14.1 computing environment (R Development Core Team 2012), using the vegan package for ordinations (Oksanen *et al.* 2011) and the oecosimu function for nestedness analysis and null model. All original data can be found in the PPBio public data repository (<http://ppbio.inpa.gov.br/knb/style/skins/ppbio/>) using “marciente” as a key word.

RESULTS

BATS CAPTURES.—A total of 3840 mist-h resulted in the capture of 511 bats, in 4 families (Emballonuridae, Phyllostomidae, Vespertilionidae, and Thyropteridae), 19 genera and 27 species (Table 1). Phyllostomids contributed 502 captures, of 17 genera and 23 species, which 12 species of frugivores (n = 413 captures), 10 animalivores (n = 70) and 1 nectarivore (n = 19) (Table 2). The total number of species in each module ranged from 8 to 16 (11.8 ± 3.2 [mean $\pm$ standard deviation]), and the number of bats captures ranged from 13 to 137 (62.9 ± 46.3). The nine species with more than 10 captures accounted for 89 percent of total captures for phyllostomid bats. *Lophostoma silvicolum* and *Rhinophylla pumilio* were captured in all modules, *Artibeus concolor*, *Chrotopterus auritus*, *Rhinophylla fischerae*, *Trinycteris nicefori*, and *Vampyriscus brocki* were each captured only in one module. *Carollia* spp. and *Rhinophylla pumilio* accounted 34 and 33 percent of all captures respectively.

EFFECTS OF VEGETATION CLUTTER OVER BAT ASSEMBLAGES.—Mean vegetation obstruction of modules ranged from 53 to 73 percent (Table 2). Fewer bat species (GLM, $pseudo-R^2 = 0.84$,

g.l. = 6 $p = 0,001$), fewer frugivores (GLM, $pseudo-R^2 = 0,64$, g.l = 6 $p = 0,017$) and fewer animalivorous species (GLM, $pseudo-R^2 = 0,52$, g.l = 6, $p = 0,04$) were captured in modules with more obstructed vegetation (Figures 3A, 3B e 3C, respectively). The NMDS axis with presence-absence data explained 75 % of the variation of original dissimilarities between bat species assemblages in modules, and was related (Figure 3D) to understory vegetation obstruction (GLM, $pseudo-R^2 = 0,77$, g.l = 6, $p = 0,003$).

NESTEDNESS PATTERN.—The direct-gradient analysis between bat captures and vegetation obstruction (Figure 4) showed that species occupancy of modules had a true nestedness pattern (NODF_c, $Fill = 51\%$, $nestedness\ degree = 66,80$, $Z = 2,21$, $p = 0,011$). Species assemblages in modules with more obstructed understory were a subset of assemblages in modules with more open vegetation. The module with opened understory (53% cluttered) had double the number of species captured in the two modules with more obstructed vegetation (> 70% cluttered). Only three species (*Trinycteris nicefori*, *Lophostoma brasiliense*, and *Vampyriscus bidens*) captured in more obstructed modules were not captured in modules with more open vegetation, with no evidence of species turnover along the vegetation obstruction gradient. As understory obstruction decreases, more species were added to the bat assemblages, mainly with species from the subfamily Stenodermatinae subfamily, such as *Mesophylla. macconelli*, *Vampyriscus brocki*, *Artibeus concolor*, *A. gnomus*, *A. obscurus*, and *A. planirostris*.

EXPLAINING ASSEMBLAGES STRUCTURE: BODY SIZE OR FEEDING HABITS?—The GLM model that included foraging guilds and body size of species explained 46 percent of the variance in the direct ordination scores for species in relation to understory obstruction (GLM, $pseudo-R^2 = 0,46$, g.l = 18). Foraging guilds were strongly related to assemblage structure ($t\text{-value} =$

3,471; $p = 0,002$). We did not detect a filter effect on body size for the total species pool (t -value = 0,380; $p = 0,70$). Animalivorous bats were associated with obstructed understory (Figure 5), and for this ensemble there was some evidence of decreasing of body size in more obstructed modules ($t = -1,736$; $p = 0,09$).

DISCUSSION

The use of digital images proved to be a promising tool to quantifying elements of vegetation structure and understanding ecological requirements of species, ensembles and assemblages of bats. Benefits of this method include reducing time expended in data collection in field, the use of low cost devices, easy replication for quantifying vegetation obstruction and the possibility for comparisons of results among studies.

Vegetation obstruction of understory had a strong influence on bat assemblage structure in terms of observed number of richness, species composition and occurrence of ensembles. Total number of species in more dense sites was half that in more sites with more open vegetation, a pattern also seen in studies of bat activity realized in a great diversity of habitats (Law & Chidel 2002, Hodgkison *et al.* 2004, Peters *et al.* 2006c, Adams *et al.* 2009, Caras & Korine 2009). The number of animalivorous species and number of frugivorous species were both negatively affected by increasing vegetation obstruction. However, the species distribution along the vegetation-obstruction gradient suggests that animalivorous bats are more tolerant of high understory obstruction. Some trying. The simplest hypothesis to explain the effects of space obstruction on bat flight is the filter effect on body-size (Stockwell 2001, Hodgkison *et al.* 2004), where small-bodied species have a better flight performance among obstacles. Another hypothesis suggests a trade-off between dispersal habituity and maneuverability of flight, these conflicting demands are associated with foraging

1 niches and determine flight performance of bats in cluttered sites (Norberg & Rayner 1987).
2 The filter effect over body size of bats was not sufficient to explain occurrence of species for
3 obstructed sites, and our results shown that species feeding habits has a strong influence in the
4 use of sites with denser vegetation understory.

5 Foraging guilds of phyllostomid bats are representatives of filogenetic clades
6 (Wetterer *et al.* 2000, Cruz-Neto *et al.* 2001) and it may be that sensorial and morphological
7 characteristics of these clades are responsible for the relationship between species
8 composition and degree of obstruction by understory vegetation. Feeding habits and
9 behaviour have been suggested as important factors associated with habitat selection
10 (Rosenzweig 1981, Krausman 1997), and these are dependent on distribution, predictability
11 and accessibility of food resources. Spatial distribution of food resources and their association
12 with flight behaviour of bats define a greater or lesser flight performance of species within
13 vegetation clutter. The abundance of arthropds is greater in dense vegetation, and more
14 homegeneously distributed (Müller *et al.* 2012), and animalivorous species have short
15 commuting flights in small foraging areas (Kalko *et al.* 1999). In contrast, fruits eaten by bats
16 are patchily distributed, forcing frugivorous bats to fly long distances in commuting flitghts
17 and spend most of their flight time searching for food (Fleming *et al.* 1977, Heithaus and
18 Fleming 1978, Morrison 1978, 1980, Kalko and Condon 1998, Henry and Kalko 2007). Thus,
19 whereas a high maneuverability is required for animalivorous bats during flight, high
20 dispersal hability may be more important for frugivores bats commuting among foraging
21 patches.

22 Meyer and Kalko (2008) also demonstrated nestedness patern (Patterson & Atmar
23 1986) in bats assemblages structure based on dispersal abitlity of bat species, and frugivores
24 bats (with greater dispersal hability) were more frequent on isolated islands in Lake Gatún,
25 Panamá; while occurrence of animalivorous bats was negatively affected by isolation.

Inverting the logic used by (Meyer & Kalko 2008), we suggest that the nestedness structure of bats assemblages demonstrated in our results is a result of the trade-off between dispersal ability and maneuverability suggested by (Norberg & Rayner 1987). In our study, frugivorous bats were more frequent in sites with open understory vegetation, while animalivores (presumably with more maneuverable flight) tended to occur in sites with obstructed vegetation.

We conclude that vegetation obstruction acts as a filter, limiting the use of sites with denser vegetation to clutter-tolerant species. Primary feeding habits (animalivory or frugivory) influenced the occurrence of bats, and animalivorous bats were less affected for the vegetation obstruction. Peters *et al.* (2006) showed that there are fewer frugivorous bats in logged sites in Brazilian Amazonia, where understory is denser due to regrowth and animalivores bats are virtually absent. However, animalivorous bats are considered sensitive to habitat disturbances, whereas frugivorous bats are favored by secondary forests (Fenton *et al.* 1992, Ochoa 2000, Gorresen *et al.* 2005, Willig *et al.* 2007, Presley *et al.* 2008, Klingbeil & Willig 2009, Bobrowiec & Gribel 2010). In that case, we can not distinguish between vegetation-obstruction effects and disturbance effects (Laurance *et al.* 2011). Our results suggest that, in primary forests, both frugivorous and animalivorous bats are negatively affected for vegetation obstruction, even though animalivorous bats seem to tolerate increase in vegetation obstruction better than frugivorous species when the increase in obstruction is not due human disturbance.

In conclusion, we consider that few studies with bats have been conducted in mature Neotropical forests, where captures rates tend to be lower than in sites in secondary vegetation or forest fragments (Sampaio *et al.* 2003). However, the benefit of distinguish effects of habitat features and habitat disturbances may be compensate for the extra sample effort required. Our conceptions about Amazonian bats are biased toward disturbed areas, even

though most of the area is still covered by mature forest. The limited evidence available indicates that patterns of assemblage structures may be different in primary forests.

ACKNOWLEDGMENTS

This study was financed by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq grant no 132573/2010-5 to RM), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES grant no 23038.006422/2012-17 to PEDB), Bat Conservation International (2011 Student Research Scholarships to RM), Centro de Estudos Integrados da Biodiversidade Amazônica (INCT-CENBAM) and Fundação de Amparo à Pesquisa do Amazonas (FAPEAM). CENBAM and the Programa de Pesquisa em Biodiversidade (PPBio) maintained the data repositories. We thank the logistic support provided by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) of Humaitá. We are grateful to Ocírio de Souza Pereira (Juruna) by the field assistance and Vitor L. Landeiro by the original version of script used in the direct gradient. This study was authorized by Instituto Chico Mendes de Conservação da Biodiversidade (Sisbio licences no. 25781-1 and 25799-2).

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TABLE 1. *Bats captured in modules sampled along the BR-319 highway, Central Amazonia, Brazil. For ensembles: AI = aerial insectivore, FR = frugivore, GA = gleaning animalivore, NE = nectarivore. Rank represents the scores of species based on direct ordination analysis for phyllostomids bats.*

Taxon	Captures	Range	Rank	Ensemble
Emballonuridae				
<i>Saccopteryx bilineata</i>	1	0-1		AI
Phyllostomidae				
Carollinae				
<i>Carollia spp</i>	167	0-86	59,7	FR
<i>Rhinophylla fischerae</i>	1	0-1	52,9	FR
<i>Rhinophylla pumilio</i>	160	3-33	62,1	FR
Lonchophyllinae				
<i>Lonchophylla thomasi</i>	19	0-7	60,5	NE
Phyllostominae				
<i>Chrotopterus auritus</i>	1	0-1	59,4	GA
<i>Lophostoma brasiliense</i>	2	0-1	64,3	GA
<i>Lophostoma silvicolum</i>	13	1-3	61,2	GA
<i>Micronycteris megalotis</i>	6	0-2	63,3	GA
<i>Mimon crenulatum</i>	6	0-2	62,7	GA
<i>Phylloderma stenops</i>	4	0-1	61,1	GA
<i>Phyllostomus elongatus</i>	13	0-4	58,5	GA
<i>Tonatia saurophilla</i>	8	0-2	59,7	GA
<i>Trachops cirrhosus</i>	15	0-5	66,6	GA

<i>Trinycteris nicefori</i>	2	0-2	72,2	GA
<i>Stenodermatinae</i>				
<i>Artibeus concolor</i>	1	0-1	55,6	FR
<i>Artibeus gnomus</i>	18	0-7	58,9	FR
<i>Artibeus lituratus</i>	4	0-2	60,6	FR
<i>Artibeus obscurus</i>	31	0-18	57,7	FR
<i>Artibeus planirostris</i>	12	0-6	57,0	FR
<i>Mesophylla macconnelli</i>	6	0-3	54,2	FR
<i>Uroderma bilobatum</i>	4	0-2	58,5	FR
<i>Vampyriscus bidens</i>	9	0-3	63,5	FR
<i>Vampyriscus brocki</i>	1	0-1	55,6	FR
<i>Vespertilionidae</i>				
<i>Myotis</i> sp.	3	0-2		AI
<i>Thyropteridae</i>				
<i>Thyroptera discifera</i>	1	0-1		AI
<i>Thyroptera tricolor</i>	4	0-2		AI

TABLE 2. *Number of bats captures (N), number of species captured (S), relative abundance for individuals and ensembles (%), and understory vegetation obstruction (mean $\pm$ standard deviation) of each module sampled along the BR-319 highway, Central Amazonia, Brazil. Locations of modules are shown in Figure 1. FR = frugivores, GA = gleaning animalivores, and NE = nectarivores.*

Modules	Phyllostomidae			FR			GA			NE			Vegetation obstruction	
	N	%	S	N	%	S	N	%	S	N	%	S	Mean	SD
M02	137	27	14	125	25	8	7	1.4	5	5	1	1	63.8	12.66
M04	47	9.3	8	41	8.2	4	8	1.6	4	0	0	0	71.2	14.76
M05	19	3.8	10	5	1	3	13	2.6	6	1	0.2	1	65.5	8.39
M06	38	7.6	12	24	4.8	5	7	1.4	6	7	1.4	1	59.4	11.17
M08	39	7.8	12	26	5.2	6	12	2.4	5	1	0.2	1	64.2	13.65
M09	13	2.6	7	9	1.8	3	3	0.6	3	1	0.2	1	73	12.77
M10	113	22	15	103	20	9	10	2	5	2	0.4	1	55.6	15.54
M11	97	19	16	85	17	9	10	2	6	2	0.4	1	52.9	14.35

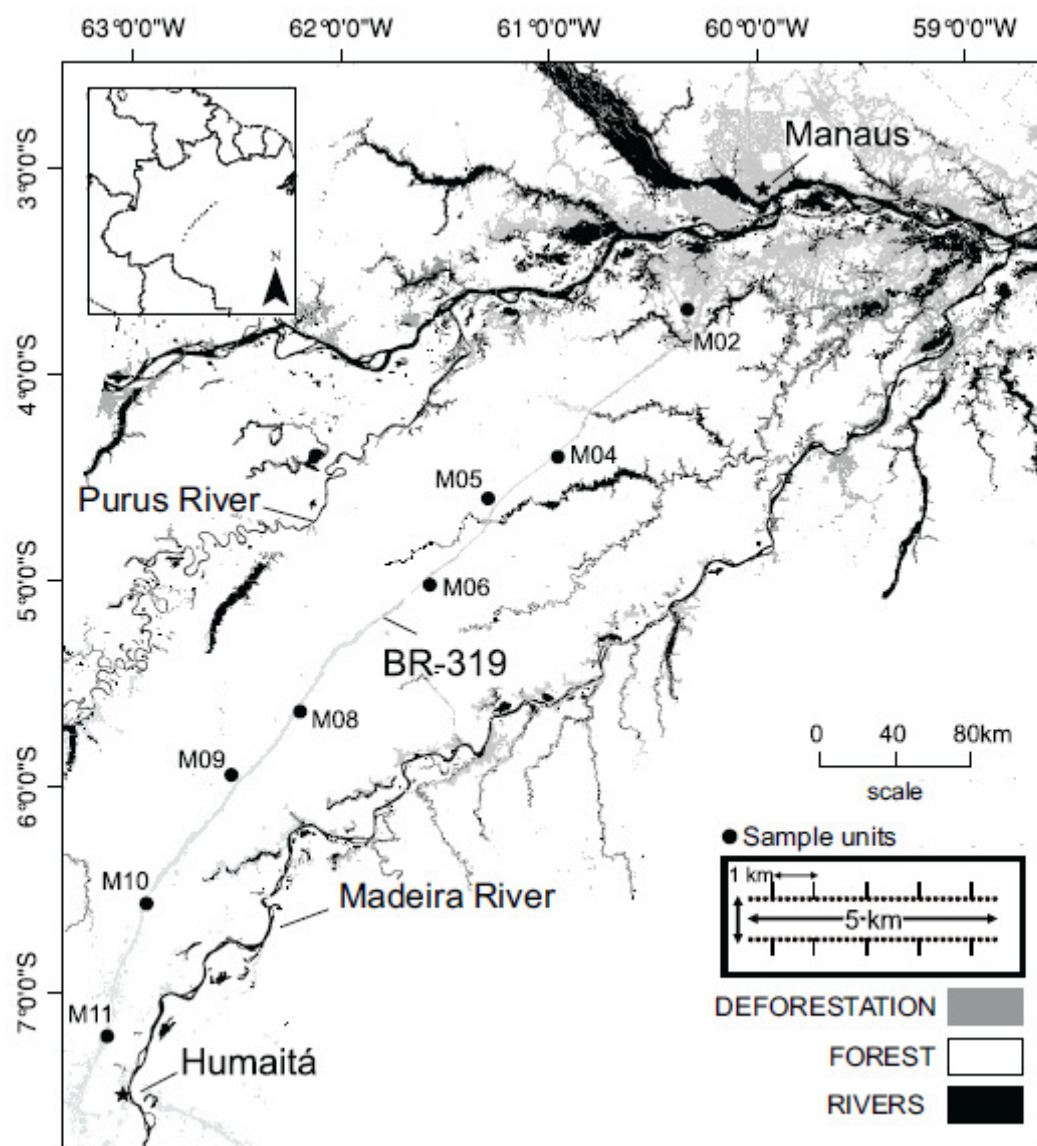
FIGURE 1. Localition of modules sampled along BR-319 highway, Central Amazonia, Brazil, and spatial distribution of plots in each module sampled in the study.

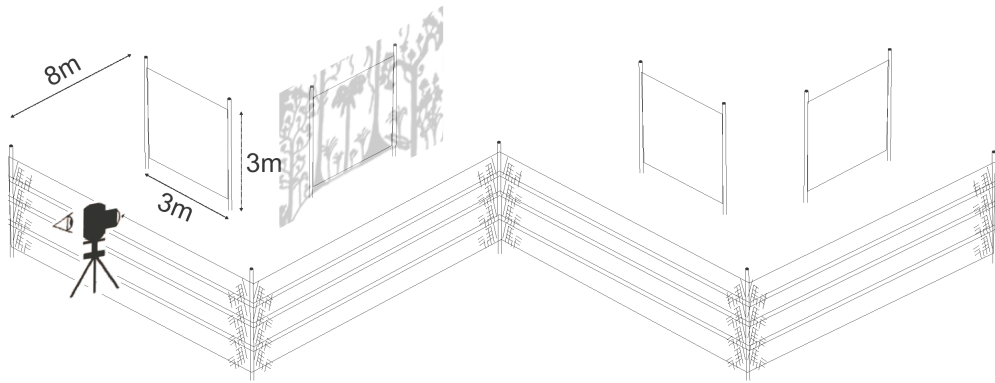
FIGURE 2. Schematic ilustration of digital photographs used to describe the understory vegetation obstruction in each sample plot.

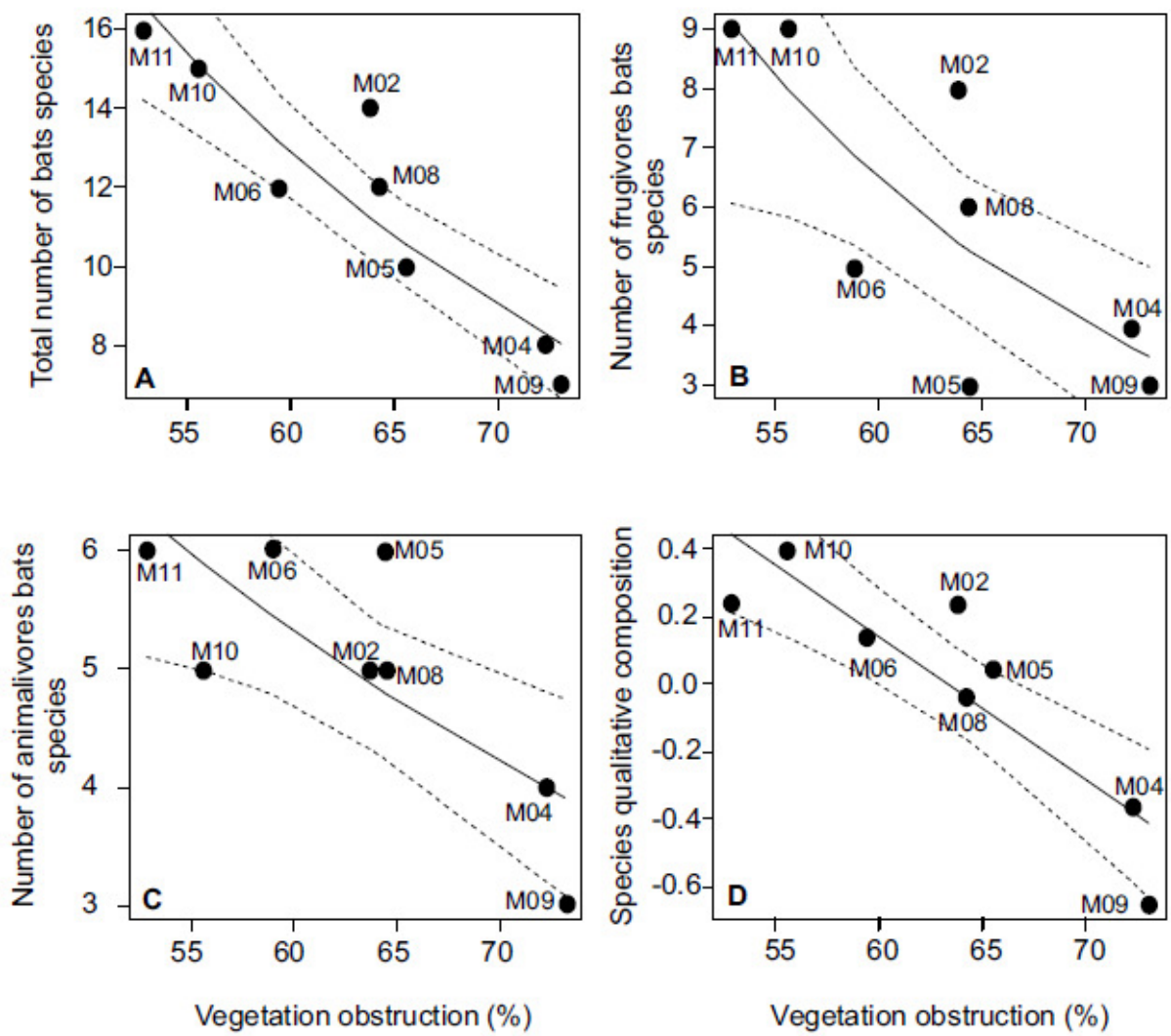
FIGURE 3. Relations between total number of bat species (a), number of frugivores species (b), number of animalivores species (c), and the axis of NMDS ordination (d) of Phyllostomidae bats against understory vegetation obstruction along the BR-319 highway, Central.Amazonia, Brazil.

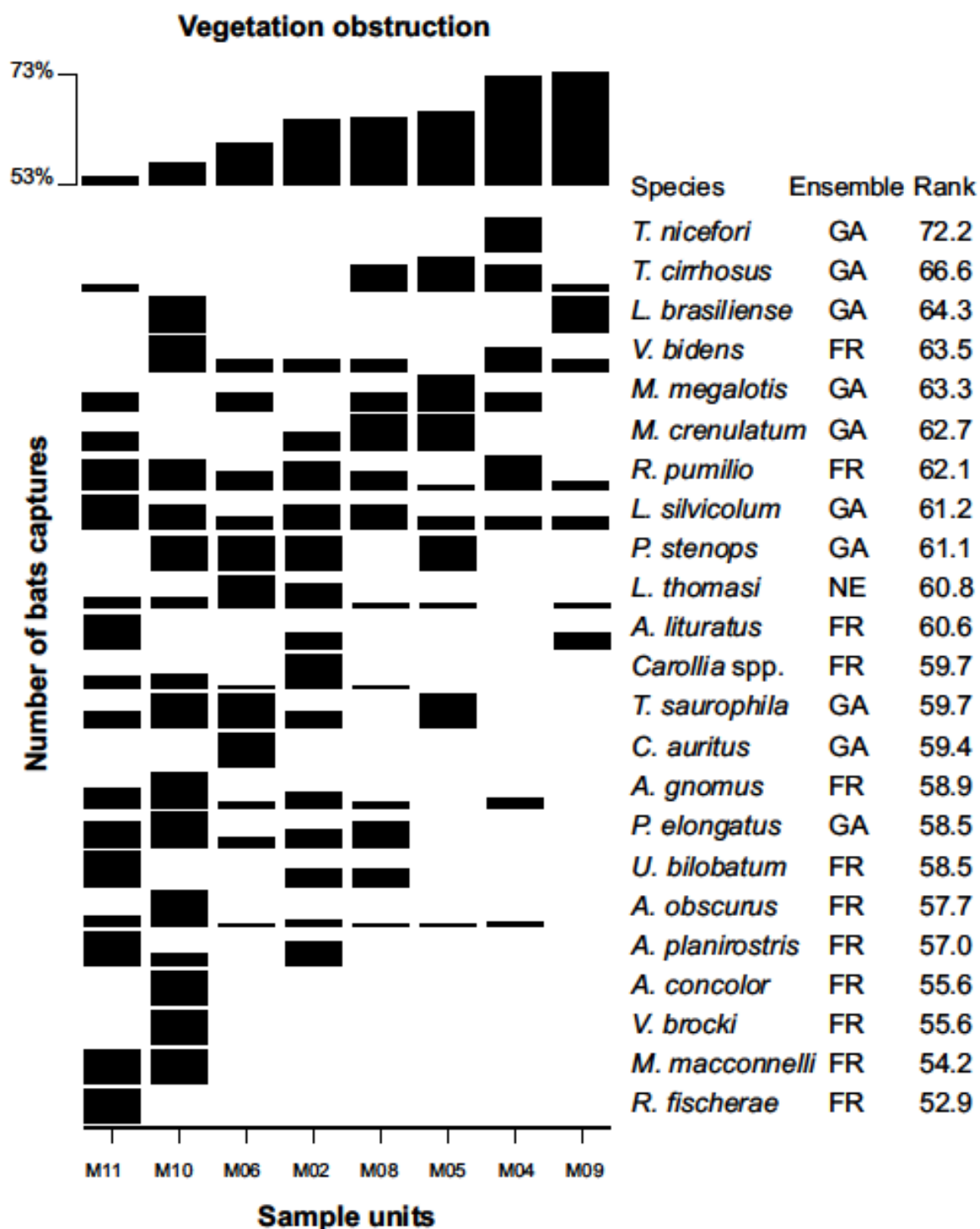
FIGURE 4. Ordination of bat assemblages using direct-gradient analysis. Rank values represents scores of species and describe the association between the number of captures for each species and the understory-vegetation obstruction.

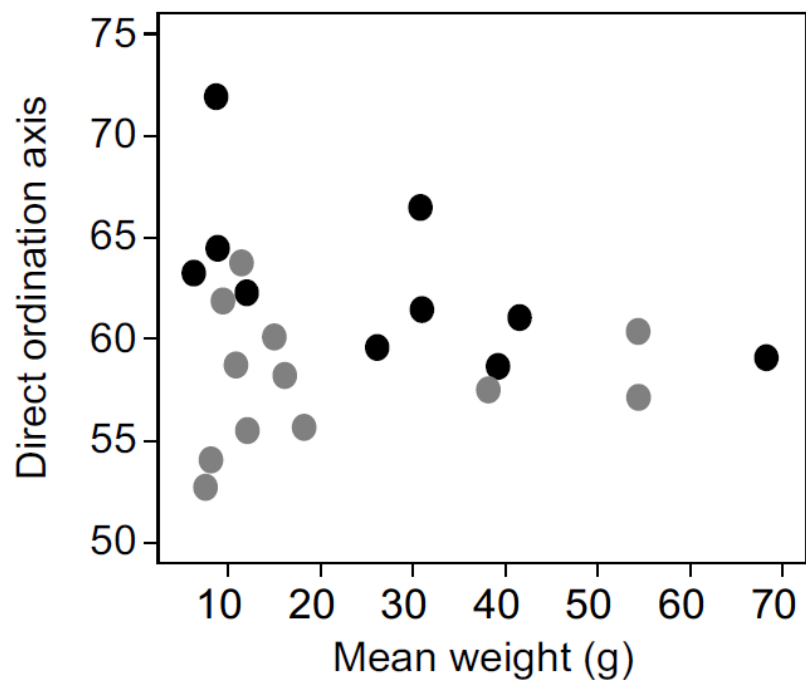
FIGURE 5. Relation of mean weight of species, feeding habits and species scores of direct-gradient analysis between species and understory-vegetation obstruction. Black dots represents animalivores, and gray dots represent frugivorous bats species











CONCLUSÕES

A obstrução da vegetação no sub-bosque é relacionada com a estrutura de assembleias de morcegos na área estudada. O número de espécies nas assembleias de morcegos diminuiu com o aumento da densidade da vegetação. As previsões de uso do ambiente baseadas no desempenho do voo de morcegos estão de acordo com os o uso de locais com diferentes graus de obstrução. Morcegos animalívoros, considerados por terem maior desempenho de voo em áreas obstruídas foram mais frequentes em ambientes com sub-bosque mais denso.

APÊNDICES



AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): RODRIGO MARCIANTE TEIXEIRA DA SILVA
 Curso: ECOLOGIA
 Nível: MESTRADO
 Orientador(a): WILLIAM ERNEST MAGNUSSON
 Co-orientador(a): PAULO ESTEFANO DINELLI BOBROWIEC

Título:

"Efeito da estrutura e heterogeneidade da vegetação do sub-bosque sobre uma assembléia de morcegos no interflúvio Purus-Madeira, Amazônia Ocidental".

BANCA JULGADORA:

TITULARES:

Gonçalo Ferraz (INPA/PDBFF)
 Marcelo Menin (UFAM)
 Pedro Ivo Simões (INPA/CPEC)

SUPLENTE:

Bruce Walker Nelson (INPA/CPEC)
 Jansen A. Zuanon (INPA/CPBA)

	PARECER	ASSINATURA
Gonçalo Ferraz (INPA/PDBFF)	☐ Aprovado ☒ Reprovado	<i>Gonçalo Ferraz</i>
Marcelo Menin (UFAM)	☒ Aprovado ☐ Reprovado	<i>Marcelo Menin</i>
Pedro Ivo Simões (INPA/CPEC)	☒ Aprovado ☐ Reprovado	<i>Pedro Ivo Simões</i>
Bruce W. Nelson (INPA/CPEC)	☐ Aprovado ☐ Reprovado	
Jansen A. Zuanon (INPA)	☐ Aprovado ☐ Reprovado	

Manaus(AM), 26 de abril de 2011

OBS: A banca julgadora e o aluno a partir dos dados biológicos em
 determinadas áreas de morcegos no longo da aula de estudo.
 O aluno mostrou ter conhecimento da literatura acadêmica
 do grupo suficiente para promover pesquisas em áreas relacionadas.

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA INPA
 PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA (PPG-ECO/INPA)

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Avaliação de dissertação de mestrado

Título: Resposta de morcegos frugívoros e animalívoros catadores (Chiroptera: Phyllostomidae) a obstrução da vegetação no sub-bosque na Amazonia central, Brasil

Aluno: RODRIGO MARCIENTE TEIXEIRA DA SILVA

Orientador: William E. Magnusson

Co-orientador: Paulo E. D. Bobrowiec

Avaliador: Cristina Banks Leite (Imperial College, London)

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	()	(x)	()	()
Revisão bibliográfica	(x)	()	()	()
Desenho amostral/experimental	(x)	()	()	()
Metodologia	(x)	()	()	()
Resultados	(x)	()	()	()
Discussão e conclusões	()	(x)	()	()
Formatação e estilo texto	(x)	()	()	()
Potencial para publicação em periódico(s) indexado(s)	(x)	()	()	()

PARECER FINAL

(X) **Aprovada** (Indica que o avaliador aprova o trabalho sem correções ou com correções mínimas)

() **Aprovada com correções** (Indica que o avaliador aprova o trabalho com correções extensas, mas que não precisa retornar ao avaliador para reavaliação)

() **Necessita revisão** (Indica que há necessidade de reformulação do trabalho e que o avaliador quer reavaliar a nova versão antes de emitir uma decisão final)

() **Reprovada** (Indica que o trabalho não é adequado, nem com modificações substanciais)

London

Local

06/06/2012

Data

C.B. Leite

Assinatura

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgeecologia@gmail.com e claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

Endereço para envio de correspondência:

Claudia Keller
DCEC/CPEC/INPA
CP 478
69011-970 Manaus AM
Brazil

Avaliação de dissertação de mestrado

Título: Resposta de morcegos frugívoros e animalívoros catadores (Chiroptera: Phyllostomidae) a obstrução da vegetação no sub-bosque na Amazonia central, Brasil

Aluno: RODRIGO MARCIENTE TEIXEIRA DA SILVA

Orientador: William E. Magnusson

Co-orientador: Paulo E. D. Bobrowiec

Avaliador: Erich Fischer

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

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Parecer

O trabalho de dissertação foi bem delineado, a coleta de dados e análises foram feitas adequadamente, e com foco sobre os objetivos conforme apresentado. A questão abordada – efeito da densidade de subosque (como fator de obstrução física) sobre comunidades de filostomídeos – é interessante e acrescenta novas idéias às teorias sobre fatores que determinam a composição de comunidades de filostomídeos. Considerando esses aspectos avalio que o Rodrigo merece aprovação do trabalho de dissertação. Entretanto, é possível melhorar a redação e apresentação de conteúdos, conforme comentários que fiz diretamente sobre a dissertação (encaminhada em anexo).

Campo Grande, 4 de junho de 2012,



Avaliação de dissertação de mestrado

Título: Resposta de morcegos frugívoros e animalívoros catadores (Chiroptera: Phyllostomidae) a obstrução da vegetação no sub-bosque na Amazonia central, Brasil

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Orientador: William E. Magnusson

Co-orientador: Paulo E. D. Bobrowiec

Avaliador:

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69011-970 Manaus AM
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ATA DA DEFESA PÚBLICA DA
DISSERTAÇÃO DE MESTRADO DO
PROGRAMA DE PÓS-GRADUAÇÃO EM
ECOLOGIA DO INSTITUTO NACIONAL
DE PESQUISAS DA AMAZÔNIA.

Aos 17 dias do mês de setembro do ano de 2012, às 09:00 horas, no auditório do Programa de Pós Graduação em Biologia de Água Doce e Pesca Interior - PPG BADPI/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Marcelo Menin**, da Universidade Federal do Amazonas - UFAM, o(a) Prof(a). Dr(a). **Pedro Ivo Simões**, do Instituto Nacional de Pesquisas da Amazônia - INPA e o(a) Prof(a). Dr(a). **Flávia Regina Capellotto Costa**, do Instituto Nacional de Pesquisas da Amazônia - INPA, tendo como suplentes o(a) Prof(a). Dr(a). Marina Anciães, do Instituto Nacional de Pesquisas da Amazônia e o(a) Prof(a). Dr(a). Thierry Ray Jehlen Gasnier, da Universidade Federal do Amazonas - UFAM, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **RODRIGO MARCIANTE TEIXEIRA DA SILVA**, intitulado "Resposta de morcegos frugívoros e animalívoros catadores (Chiroptera: Phyllostomidae) a obstrução da vegetação no sub-bosque na Amazônia Central, Brasil", orientado pelo(a) Prof(a). Dr(a). William Ernest Magnusson, do Instituto Nacional de Pesquisas da Amazônia - INPA e co-orientado pelo(a) Prof(a). Dr(a). Paulo Estevão Dineli Bobrowiec, do Instituto Nacional de Pesquisas da Amazônia - INPA/CENBAM/PDBFF.

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

☒ APROVADO(A)

☐ REPROVADO(A)

☒ POR UNANIMIDADE

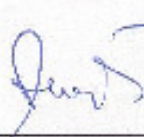
☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Marcelo Menin

Prof(a).Dr(a). Pedro Ivo Simões

Prof(a).Dr(a). Flávia Regina Capellotto Costa


Coordenação PPG-ECO/INPA