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

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Manaus, Amazonas

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Sinopse:

Foram estudadas mudanças na composição de morcegos em uma floresta de terra-firme, no interflúvio Purus-Madeira. A contribuição relativa de morcegos frugívoros e morcegos animalívoros catadores foi relacionada com a densidade da vegetação no sub-bosque

Palavras-chave: Morcegos, Ecologia de Comunidades, Estrutura da Vegmetação, Floresta de terra firme - Amazônia, BR-319

Aos meus pais, Rosemeire e Reinaldo;

minha esposa Ignês e

à Maria Clara, minha semente para o futuro!

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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 relacionei a densidade da vegetação do sub-bosque, como uma medida de obstrução do espaço, e a composição de espécies em assembléias de morcegos Phyllostomidae. Em florestas primárias, nos sítios com sub-bosque mais denso, eu esparava 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 (Emballunoridae, 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. Diferenças na disponibilidade e distribuição de frutos e presas animais em sítios com diferentes graus de obstrução podem afetar a proporção de espécies de diferentes guildas alimentares que usam sítios com vegetação densa na floresta.

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

Cluttered vegetation structure demands maneuverable fight for bats. Based on wing morphology, it has been suggested that animalivorous bats have better flight performance in cluttered areas than others trophic guilds. I related density of understory vegetation as a measure of clutter to species composition of Phyllostomidae bats assemblages. I expected find a great contribution of animalivores bats to species composition in mature-forest sites with denser understory. The study was carried out in Purus-Madeira interfluves, along BR-319 highway where eight sample units at least 40 km apart and constituted for ten permanents plots were sampled. I employed ordination techniques and generalized linear models to make inferences about habitat use by phyllostomid bats along a clutter gradient. With a capture effort of 3,840 nets-hour, 511 bats of 4 families (Emballunoridae, Phyllostomidae, Vespertilionidae and Thyropteridae) and 27 species were captured, of which 12 were frugivores (n=414 captures) and 10 animalivores (n=70 capturas). The number of species was reduced from 16 to 7 along a gradient of vegetation obstruction among 53% to 73%. This negative effect occurred for both trophic guilds. Assemblages showed a nested pattern along the clutter gradient, with animalivorous bats tending to occur in sites with denser vegetation. The filter effect on body size alone was not sufficient to explain the structure of bat assemblages in relation to clutter. The effect of clutter differed between foraging guilds. Differences in availability and distribution of food resources in forest sites with different degrees of clutter may affect the proportion of different guilds that use cluttered sites.

Key words: Neotropical Bats, Vegetation Structure, Clutter; Trophic Structture

SUMÁRIO

APRESENTAÇÃO

Morcegos representam cerca de um quarto da diversidade dos mamíferos viventes (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).

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.

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

ARTIGO

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

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ABSTRACT

We related density of understory vegetation as a measure of clutter to species composition of phyllostomid bat assemblages, theirs 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 permanents 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 distintive of preivous 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.

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

Based on wing morphology, Norberg and Rayner (1987) suggests that animalivorous bats have better flight performance than other trophic guilds in cluttered locations. However, field examples show contradictory evidence. In sites with more open understory, such as flooded forests (Haugaasen & Peres 2006), Pereira *et al.* (2009) captured few animalivorous species in comparison with the dense understory of *terra firme* unflooded forests. In contrast, sites with dense vegetation, such as regrowth (Mesquita *et al.* 2001, Gehring *et al.* 2005), also have few animalivorous species (Peters *et al.* 2006b, Bobrowiec & Gribel 2010). Animalivores bats are more sensitive to habitat disturbances than frugivous species (Fenton *et al.* 1992, Ochoa 2000, Gorresen *et al.* 2005, Willig *et al.* 2007, Presley *et al.* 2008, Klingbeil & Willig 2009, Bobrowiec & Gribel 2010), so apparent associations between bat trophic guilds and clutter are confounded by other aspects related to human disturbance.

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

METHODS

SITE DESCRIPTION.—The study was carried out along 520 km of the BR-319 highway, in the State of Amazonas, Brazil. The highway is located between the Purus and Madeira Rivers, linking Manaus to the southwest region of Amazonas (Figure 1). Forest structure varies from dense lowland tropical forest in the north, to open lowland tropical forest near the municiaplity of Humaitá in the southwest (IBGE 1997). Mean annual preciptation 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 preciptation < 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 topograhy 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. Nomencalture follows

(Simmons 2005), except for recognizing *Artibeus planirsotris* 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 aereal 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 parallell 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-phyllostomid 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 obstrution 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 deriveded from the direct ordination analysis, with species as columns and sample units as rows.

We evalueted 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 overdispertion 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 ± 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 acounted 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 PATERN.—The direct-gradient analysis between bat captures and vegetation obstruction (Figure 4) showed that species occupancy of modules had a true nestedness pattern (NODFc, *Fill* = 51%, *nestedness degree* = 66,80, *Z* = 2,21, *p* = 0,011). Species assemblagess 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 relatioin to understory obstruction (GLM, *pseudo-*R^2 = 0,46, *g.l* = 18). Foraging guilds were strongly related to assemblage structure (*t-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 promissing 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 strutucture 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 diveristy 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 afected 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 habitity and maneuverabilty of flight, these conflicting demands are associated with foraging niches and determine flight performance of bats in cluttered sites (Norberg & Rayner 1987). The filter effect over body size of bats was not suficient to explain occurence of species for obstructed sites, and our results shown that species feeding habits has a strong influence in the use of sites with denser vegetation understory.

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

Meyer and Kalko (2008) also demonstrated nestedness patern (Patterson & Atmar 1986) in bats assemblages structure based on dispersal abitlity of bat species, and frugivores bats (with greater dispersal hability) were more frequent on isolated islands in Lake Gatún, 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 hability 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 ocurrence 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 abscent. However, animalivorous bats are considered sensitive to habitat disturbances, whereas frugivorous bats are favored by sencondary 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 evidance available indicates that patterns of assemblage structures may be different in primary forests.

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

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

	Phyllostomidae			FR			GA			NE			Vegetation obstruction	
Modules	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

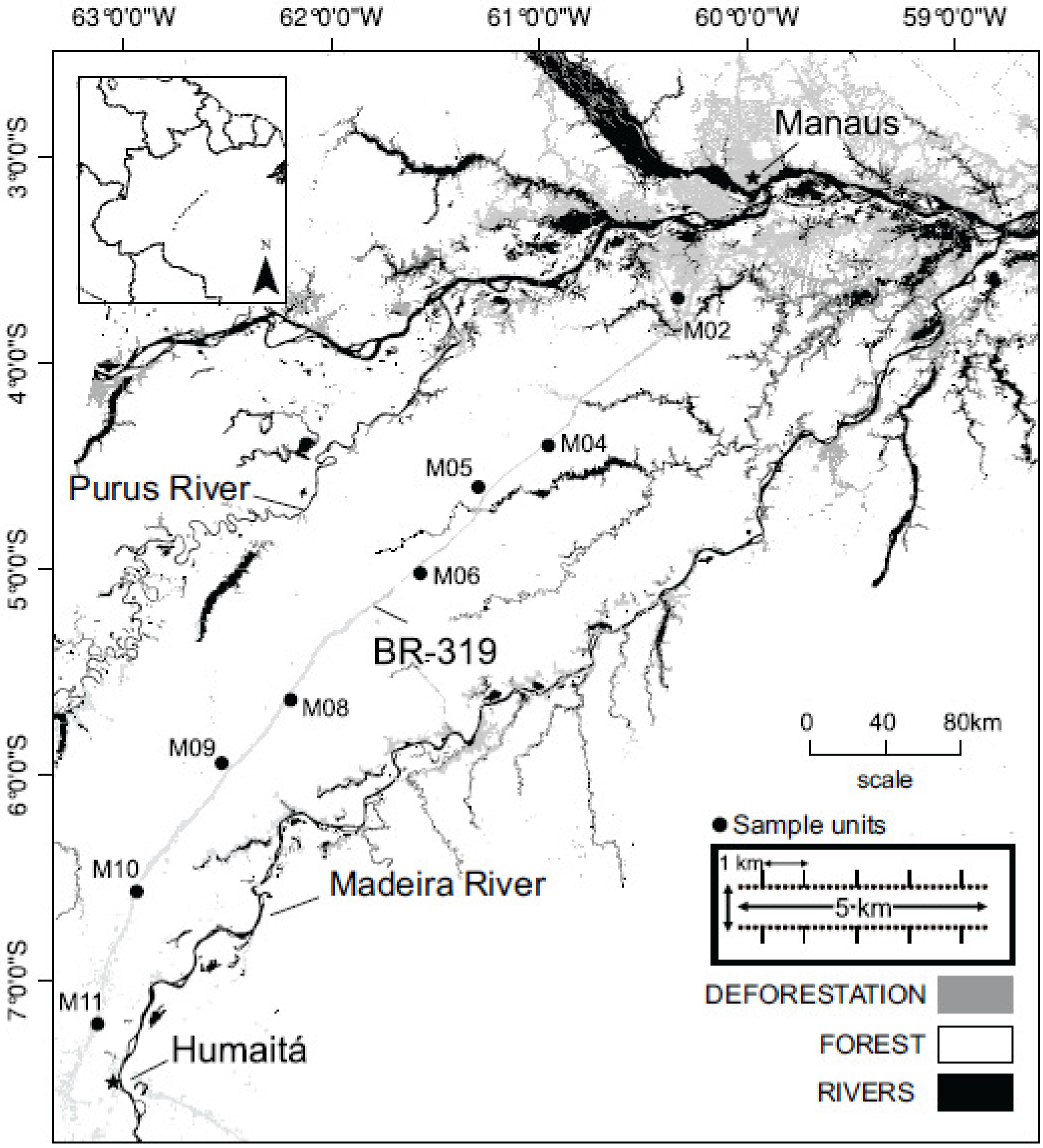
FIGURE 1. Localition of modules sampled along BR-319 highway, Central Amazonia, Brazil, and spatial distribution of plots in each module sampled in the study.

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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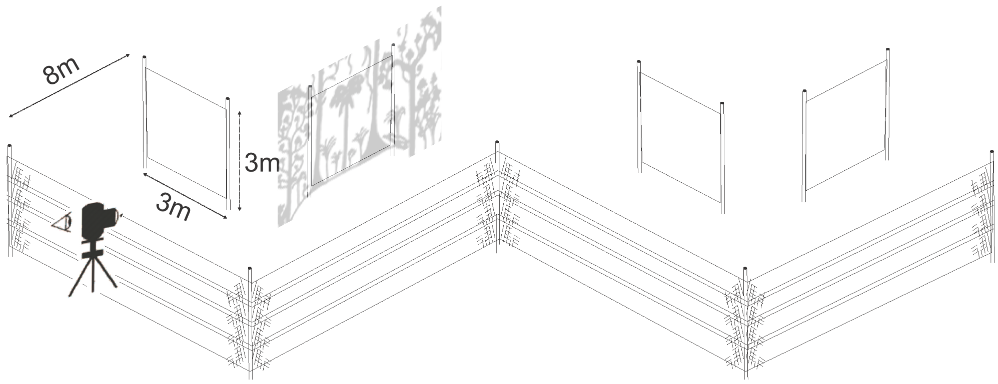
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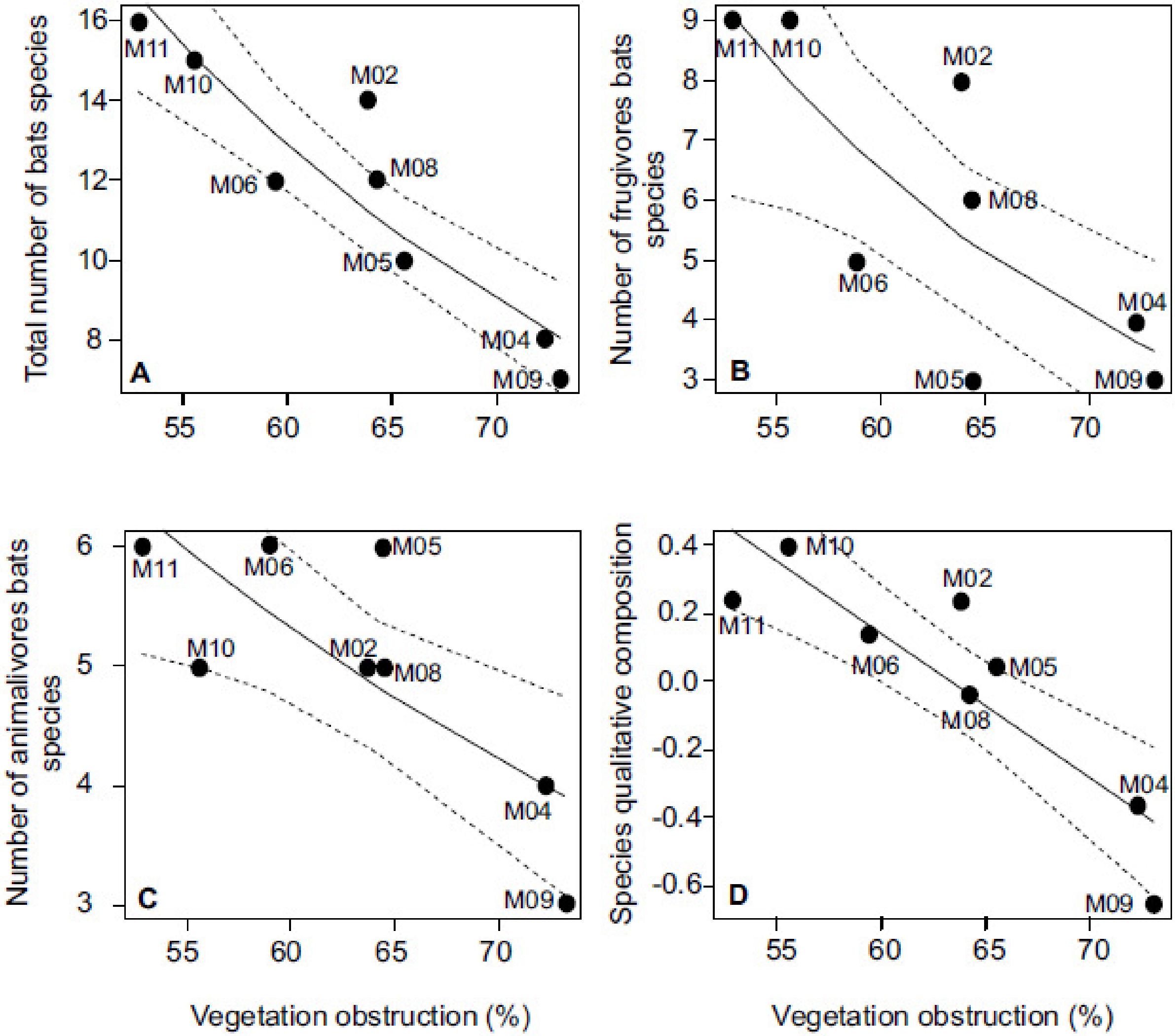
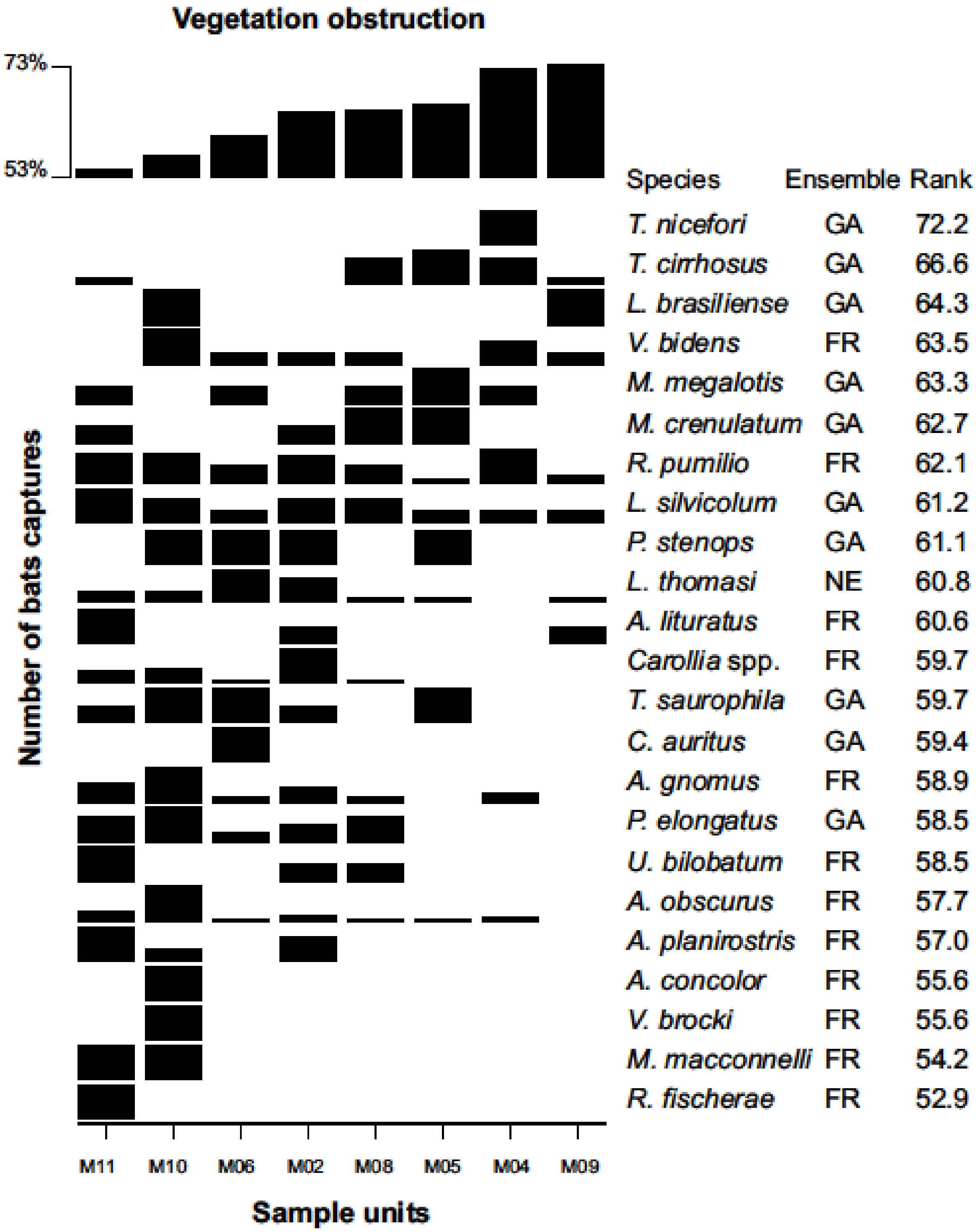
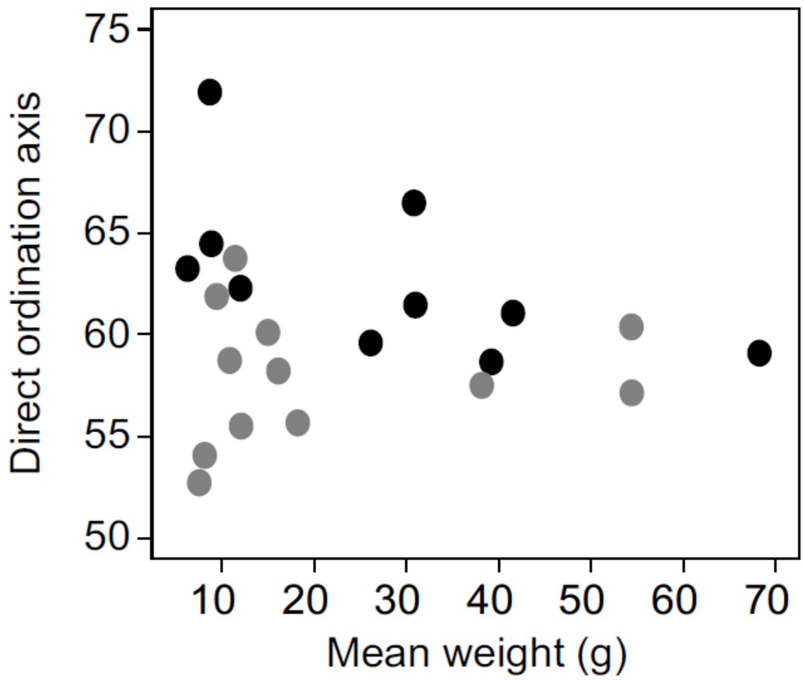


Total number of bats species
Number of frugivores bats species
Number of animalivores bats species
Species qualitative composition
Vegetation obstruction (%)
Vegetation obstruction (%)
A
B
C
D
M02
M04
M05
M06
M08
M09
M10
M11


Vegetation obstruction
73%
53%
Number of bats captures
M11
M10
M06
M02
M08
M05
M04
M09
Sample units
Species Ensemble Rank
T. nicefori GA 72.2
T. cirrhosus GA 66.6
L. brasiliense GA 64.3
V. bidens FR 63.5
M. megalotis GA 63.3
M. crenulatum GA 62.7
R. pumilio FR 62.1
L. silvicolum GA 61.2
P. stenops GA 61.1
L. thomasi NE 60.8
A. lituratus FR 60.6
Carollia spp. FR 59.7
T. saurophila GA 59.7
C. auritus GA 59.4
A. gnomus FR 58.9
P. elongatus GA 58.5
U. bilobatum FR 58.5
A. obscurus FR 57.7
A. planirostris FR 57.0
A. concolor FR 55.6
V. brocki FR 55.6
M. macconnelli FR 54.2
R. fischerae FR 52.9



Direct ordination axis
75
70
65
60
55
50
10
20
30
40
50
60
70
Mean weight (g)

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

PG-ECO-INPA
PÓS-GRADUAÇÃO EM ECOLOGIA

INPA
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): RODRIGO MARCIENTE 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)

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

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

Manaus(AM), 26 de abril de 2011

OBS: A banca encoraja o aluno a fazer previsões biológicas na distribuição dos morcegos ao longo da área de estudo. O aluno mostrou ter conhecimento da história natural do grupo suficiente para formular previsões informativas.

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Instituto Nacional de Pesquisas da Amazônia - INPA
Programa de Pós-graduação em Ecologia

Avaliação de dissertação de mestrado

Título: **Resposta de morcegos frugivoros e animalivoros 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 ítem 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)	( )	( )	( )

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

London, 06/06/2012, [signature]
Local, Data, Assinatura

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Endereço para envio de correspondência:

Claudia Keller
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Brazil

Avaliação de dissertação de mestrado

Título: **Resposta de morcegos frugivoros e animalivoros 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: **Erich Fischer**

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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,

Instituto Nacional de Pesquisas da Amazônia - INPA
Programa de Pós-graduação em Ecologia

Avaliação de dissertação de mestrado

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

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Avaliador:

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____________________, __________________, ________________________
Local Data Assinatura

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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 argüição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **RODRIGO MARCIENTE 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 Estefano 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:

[X] APROVADO(A) [ ] REPROVADO(A)

[X] 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