INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA

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EFEITO DA ESTRUTURA DO HABITAT NA DISTRIBUIÇÃO ESPACIAL DE DUAS ESPÉCIES DE TINAMÍDEOS (AVES: TINAMIDAE) NA FLORESTA DE TERRA-FIRME NA AMAZÔNIA CENTRAL.

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Manaus - Amazonas

Março, 2014

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Efeito da estrutura do habitat na distribuição espacial de duas espécies de tinamídeos (Aves: Tinamidae) na floresta de terra-firme na Amazônia Central.

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Sinopse

Investigou-se a influencia da estrutura da floresta na distribuição espacial e no uso do habitat para duas espécies de aves terrestres da família Tinamidae, *Tinamus major* e *Crypturellus variegatus*. Como método de amostragem utilizou-se ponto de escuta e uso das técnicas de escuta passiva e playback. Relacionou-se a frequência de registros das espécies de aves com características da estrutura e paisagem de uma floresta de terra-firme, na região da Amazônia Central.

Palavras-chave: Ecologia de populações, heterogeneidade ambiental, tinamídeos, *Tinamus major*, *Crypturellus variegatus*, uso do habitat, aves, floresta tropical, Brasil.

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Resumo

A influência da heterogeneidade ambiental na distribuição de aves arbóreas tem sido intensamente investigada, mas seus efeitos na distribuição de aves terrestres é pouco conhecido em florestas tropicais. Aqui, nós investigamos como os padrões espaciais de duas espécies de aves terrestres da família Tinamidae são modulados pela variação natural na estrutura de uma floresta de terra-firme, na Amazônia Central. Nós testamos como cinco descritores da estrutura da floresta (troncos mortos caídos no chão, abertura de dossel, abundância de árvores, profundidade da serapilheira e distância de corpo d'água) explicaram a variação na distribuição espacial de Inhambu-de-cabeça-vermelha (*Tinamus major*) e Inhambu-anhangá (*Crypturellus variegatus*). Entre outubro de 2012 e abril de 2013, utilizamos trinta pontos de escuta para estimar a frequência de registros das espécies dentro de uma área de 25 km^2. As amostragens foram realizadas entre 5:30 e 10:00 h da manhã com uso das técnicas de escuta passiva e playback. Nos mesmos pontos em que registramos as aves, nós utilizamos parcelas de 250 m x 40 m para mensurar os componentes de estrutura da floresta. Modelos lineares múltiplos indicaram que a variação na frequência de registros de *Tinamus major* não foi explicado por nenhum componente de estrutura da floresta. Entretanto, a frequência de registros de *Crypturellus variegatus* aumentou significativamente com o aumento na abertura de dossel da floresta e o aumento da abundância de troncos mortos no chão, e diminuiu com o aumento na profundidade de serapilheira. Os resultados apoiam as evidências que sugerem a heterogeneidade da floresta como um fator importante na distribuição espacial de aves. Além disso, esse estudo contribui para o conhecimento sobre como aves terrestres respondem de maneiras diferentes à variação espacial dos mesmos componentes da estrutura de uma floresta Amazônica de terra-firme.

Palavras-chave: Heterogeneidade ambiental, tinamídeos, *Tinamus major*, *Crypturellus variegatus*, componentes de estrutura da floresta, uso do habitat, frequência de encontros, aves.

Abstract

The influence of environmental heterogeneity on the distribution of arboreal birds has been studied intensively, but such effects are little studied in terrestrial birds in tropical forests. Here we investigate how the spatial distribution of two terrestrial bird species from the family Tinamidae is modulated by the variation in the natural structure of central Amazonian terra-firme forest. We test five descriptors of forest structure (dead fallen trunks, canopy openness, tree abundance, leaf-litter depth and distance to water bodies) as explanations for the variation in the spatial distribution of Great (*Tinamus major*) and Variegated (*Crypturellus variegatus*) Tinamou. Between October 2012 and April 2013, we used 30 listening points to estimate the frequency of occurrence of these species within a 25 km² area. Studies were conducted between 05:30 and 10:00 h using passive listening and playback. In the same area we used 250 x 40 m plots to measure the forest structure components. Multiple linear models indicated that the frequency of occurrence of *Tinamus major* was not explained by any tested component of the forest structure. However, the number of *Crypturellus variegatus* encounters increased significantly in areas beneath more open canopy and where there were more fallen dead trunks. It diminished in areas where leaf litter was deeper. The results provide additional evidence that forest heterogeneity can be an important factor influencing the spatial distribution of terrestrial birds. In addition, this study contributes to the knowledge of how terrestrial birds respond in different ways to the spatial variation in the same components of structure of Amazonian terra-firme forest.

Keywords: Environmental heterogeneity, tinamous, *Tinamus major*, *Crypturellus variegatus*, structural forest components, habitat use, encounter frequency, birds.

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Apresentação

Capitulo 1

Apresentação

A separação espacial no uso do ambiente ou a repartição de recursos em um mesmo ambiente pelas espécies em geral representam padrões de ocupação do espaço o qual é parte das dimensões do nicho ecológico das espécies (e.g. Pianka, 1969; Schoener, 1974). Nesse estudo, nicho ecológico é interpretado como a representação teórica dos limites de atividades de uma espécie que são descritos por todas as dimensões do ambiente que, por sua vez, incluem fatores físicos, químicos e biológicos (Hutchinson, 1957; Pulliam 2000, Holt, 2009). É esperado que entre espécies que compartilham um mesmo espaço devem existir mecanismos para minimizar a competição intra e interespecífica e a sobreposição de nicho (Cody, 1974; Pianka, 1974; Begon et al. 2007; Di Bitetti et al., 2010). Em aves, diferenças na morfologia, modo de alimentação e composição da dieta, separação no uso do habitat e na distribuição espacial e temporal são considerados mecanismos ecológicos que permitem a coexistência de espécies (Ricklefs & Cox, 1977; Ricklefs & Travis, 1980; Cintra, 1997).

A estrutura ou heterogeneidade do ambiente é também um importante fator para explicar os padrões de uso e seleção de habitat pelas espécies (e.g. MacArthur & MacArthur, 1961; August, 1983; Karr & Freemark, 1983; Khanaposhtani et al., 2012). As florestas tropicais apresentam componentes de estrutura da floresta os quais são características bióticas ou abióticas que descrevem a organização de uma comunidade vegetal e da paisagem como, por exemplo, densidade de árvores, profundidade da serapilheira ou topografia do terreno. A variação espacial de componentes de estrutura da floresta promove o aumento de micro-habitats disponíveis e, consequentemente, maior segregação na utilização de recursos (Sousa, 1984; Tews et al., 2004; Oliveira et al., 2011; Bagchi et al., 2011) e tem sido empregado para explicar a distribuição e interação entre espécies de diversos grupos de vertebrados (August, 1983; Bernard, 2001; Tews et al., 2004; Watling, 2005; Lambert et al., 2006; Menin et at., 2007; Espírito-Santo et al., 2013) inclusive aves (Aleixo, 1999; Bersier & Meyer, 1994; Díaz et al., 2005; Miranda et al., 2010; Bueno et al. 2012; Poindexter et al., 2012).

Em florestas tropicais de terra firme na Amazônia brasileira estudos compararam o uso do ambiente por aves e demonstraram que a variação espacial em alguns desses componentes de estrutura influência as distribuições de espécies de pássaros congenéricas diurnas como arapaçus (Cintra el al., 2006), aves predadoras noturnas como corujas (Barros & Cintra, 2009), e até em mudanças na composição de comunidades (Cintra & Naka, 2012). Porém, a maioria desses estudos foram feitos com espécies de aves arbóreas.

Inambús (família Tinamidae) são aves terrestres e habitam áreas abertas ou florestais, tanto em regiões tropicais como subtropicais (Cabot, 1992). Devido ao seu comportamento de caminhar lentamente no solo, ser frequentemente silencioso, ter coloração críptica, além da quase completa falta de métodos padronizados para a coleta de dados, a ecologia do grupo é pouco conhecida (Brennan, 2004). O conhecimento da história natural é escasso e para cerca de 40% das espécies (Schelsky, 2004).

Os inambús, incluem na dieta frutos, sementes, folhas, raízes ou tubérculos, e pequenos animais, principalmente invertebrados (Schubart et al., 1965; Cabot, 1992; Mosa, 1993; Garitano-Zavala et al., 2003). A alta sobreposição na dieta, hábitos de forrageamento similares e baixa capacidade seletiva em itens alimentares sugerem que tinamídeos tenham estratégias generalistas e oportunistas de uso do habitat (Mosa, 1993,1997, 2004; Garitano-Zavala et al., 2003). Espécies florestais, que incluem os gêneros *Tinamus*, *Crypturellus* e *Nothocercus*, tem dieta principalmente de frutos disponíveis no chão ou ocasionalmente saltam ou utilizam algum substrato para alcançar frutos ou insetos (Cabot, 1992). Além disso, tendem a remexer serapilheira com o bico à procura de insetos, pequenos moluscos ou anelídeos (Cabot, 1992; Sick, 1997). Tinamídeos florestais nidificam no solo e perto de troncos caídos no chão ou entre raízes tabulares de grandes árvores e o ninho é apenas uma leve depressão no solo coberta por uma fina camada de folhas (MacKay, 1980; Brennan, 2010; Cabot, 1992; Sick, 1997, obs. pess.).

Por ocuparem somente um estrato vegetal do gradiente vegetacional (sub-bosque), presume-se que mecanismos de segregação ecológica são muito importantes para a coexistência das espécies de tinamídeos em um mesmo ambiente (Cabot, 1992). A segregação espacial investigada em uma comunidade de aves de caça, que incluíram tinamídeos, em floresta tropical na Amazônia Peruana, evidenciou a separação espacial no uso de diferentes tipos e estratos florestais, bem como separação temporal na atividade vocal das espécies (Brooks et al., 2001, Brooks et al., 2004). Entender as diferenças entre o uso de micro-hábitats ou parte dos nichos das espécies e suas habilidades competitivas é, portanto, um importante passo para compreender os mecanismos determinantes da coexistência das mesmas (Adler et al., 2007; Levine & HilleRisLambers, 2009; Mayfield & Levine, 2010).

Nesse estudo foi investigado como diferenças na estrutura do habitat, aqui determinada pela variação espacial de componentes da estrutura da floresta, influencia a distribuição espacial e a frequência de uso de micro-hábitat por duas espécies de aves de solo, *Tinamus major* (Figura 1) e *Crypturellus variegatus* (Figura 2).

Figura 1: Foto de um indivíduo adulto de *Tinamus major* em seu habitat natural registrado pelo método de câmera trap, na área de estudo. Foto cedida pelo Projeto TEAM/INPA.

Figura 2: Foto de um indivíduo adulto de *Crypturellus variegatus* em seu habitat natural registrado pelo método de câmera trap, na área de estudo. Foto cedida pelo Projeto TEAM/INPA.

Selecionou-se um conjunto de seis componentes de estrutura da floresta que incluem, elevação do terreno, abundância de troncos mortos caídos no chão, abertura de dossel, abundância de árvores, profundidade da serapilheira e distância do igarapé mais próximo. Esses componentes foram escolhidos com base em informações sobre a história natural do grupo (e.g. Montes, 1977; Cabot, 1992; Sick, 1997) e que podem ser importantes na descrição do uso do habitat das espécies porque estas aves dependem do substrato mais baixo da floresta para forragear em busca de invertebrados e frutos caídos no chão. Na floresta Amazônica, espécies arbóreas raras são predominantes (Hubble 2013), portanto, o esperado é que áreas com mais árvores tenham maior riqueza de espécies, sendo potencialmente ambientes mais favoráveis com maior oferta de alimentos do que áreas com menor riqueza; áreas com maior abundância de troncos mortos no chão podem fornecer mais locais e substrato de forrageamento, abrigo e nidificação (Cabot, 1992; Brennan, 2009) do que outras com menos troncos; o aumento na abundância de pequenos invertebrados, presas potenciais para tinamídeos, está diretamente relacionado ao aumento na quantidade de serapilheira (Adis, 1988); locais com mais abertura de dossel ou com maior quantidade de luz no sub-bosque podem atrair pequenos vertebrados ectotérmicos, aumentar a produção local de frutos atraindo mais artrópodes, aumentando a disponibilidade de presas para as espécies (Banks & Cintra, 2008); corpos d'água são importantes componentes da estrutura da floresta e constituem micro-hábitats para muitas espécies. Esses corpos d'água delimitam zonas ripárias que são distintas e percebidas por aves de sub-bosque, determinando mudanças na composição das comunidades (Bueno et al. 2012; Cintra & Naka, 2012).

Fundamentado na abordagem teórica de que espécies parecidas têm menores tendências de sobreporem o uso do espaço no habitat do que o esperado pelo acaso (e.g. Graves & Gotelli, 1993; Webb et al., 2002), nesse estudo foi testada a hipótese geral de que a variação espacial em componentes de estrutura da floresta influenciam de maneira distinta a distribuição espacial e o uso do micro-hábitat pelas espécies de tinamídeos. As previsões foram que o aumento na frequência de ocorrência das espécies está relacionado à elevação do terreno, ao aumento na densidade da vegetação, na profundidade da serapilheira, na abundância de troncos mortos no chão, na abertura do dossel e com a proximidade de corpos d'água.

Objetivo Geral

Estudar a ocorrência de duas espécies simpátricas e sintópicas de tinamídeos, *Tinamus major* e *Crypturellus variegatus,* e sua relação a variação espacial no micro-hábitat.

Objetivos específicos

1- Determinar como as ocorrências de *Tinamus major* e *Crypturellus variegatus* são influenciadas pela variação espacial em componentes de estrutura da floresta representada por elevação do terreno, abundância de troncos mortos caídos no chão, abertura do dossel, abundância de árvores, profundidade da serapilheira e proximidade de corpos d'água;

2- Determinar as diferenças nos efeitos dos componentes de estrutura da floresta sobre cada uma das duas espécies estudadas.

Capítulo 1

Guerta, R. S.; Cintra, R. Effects of habitat structure on the spatial distribution of two species of tinamou (Aves: Tinamidae) in a central Amazon terra-firme forest.
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Effects of habitat structure on the spatial distribution of two species of tinamou (Aves: Tinamidae) in a central Amazon terra-firme forest.

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RESUMO

A influência da heterogeneidade ambiental na distribuição de aves arbóreas tem sido intensamente estudada, mas seus efeitos na distribuição de aves terrestres é pouco conhecido em florestas tropicais. Aqui, nós investigamos como a distribuição espacial de duas espécies de aves terrestres da família Tinamidae é modulada pela variação natural na estrutura de uma floresta de terra-firme, na Amazônia Central. Nós testamos como cinco descritores da estrutura da floresta (troncos mortos caídos no chão, abertura de dossel, abundância de árvores, profundidade da serapilheira e distância de corpo d'água) explicaram a variação na distribuição espacial de Inhambu-de-cabeça-vermelha (*Tinamus major*) e Inhambu-anhangá (*Crypturellus variegatus*). Entre outubro de 2012 e abril de 2013, utilizamos trinta pontos de escuta para estimar a frequência de registros das espécies dentro de uma área de 25 km^2. As amostragens foram realizadas entre 5:30 e 10:00 h da manhã com uso das técnicas de escuta passiva e playback. Nos mesmos pontos em que registramos as aves, nós utilizamos parcelas de 250 m x 40 m para mensurar os componentes de estrutura da floresta. Modelos lineares múltiplos indicaram que a variação na frequência de registros de Inhambu-de-cabeça-vermelha não foi explicado por nenhum componente de estrutura da floresta. Entretanto, a frequência de registros de Inhambu-anhangá aumentou significativamente com o aumento na abertura de dossel da floresta e o aumento da abundância de troncos mortos no chão, e diminuiu com o aumento na profundidade de serapilheira. Os resultados apoiam as evidências que sugerem a heterogeneidade da floresta como um fator importante na distribuição espacial de aves. Além disso, esse estudo contribui para o conhecimento sobre como aves terrestres respondem de maneiras diferentes à variação espacial nos mesmos componentes da estrutura de uma floresta Amazônica de terra-firme.

Palavras-chave: Heterogeneidade ambiental, tinamídeos, *Tinamus major*, *Crypturellus variegatus*, componentes de estrutura da floresta, uso do habitat, frequência de encontros, aves.

ABSTRACT

Does habitat structure modulate the spatial distribution of two terrestrial birds (Aves: Tinamidae) in a central Amazon terra-firme forest ? The influence of environmental heterogeneity on the distribution of arboreal birds has been studied intensively. But such effects are little studied in terrestrial birds in tropical forests. Here we investigate how the spatial distribution of two terrestrial bird species from the family Tinamidae is modulated by the variation in the natural structure of central Amazonian terra-firme forest. We test five descriptors of forest structure (dead fallen trunks, canopy openness, tree abundance, leaf-litter depth and distance to water bodies) as explanations for the variation in the spatial distribution of Great (*Tinamus major*) and Variegated (*Crypturellus variegatus*) Tinamou. Between October 2012 and April 2013, we used 30 listening points to estimate the frequency of occurrence of these species within a 25 km^2 area. Studies were conducted between 05:30 and 10:00 h using passive listening and playback. In the same area we used 250 x 40 m plots to measure the forest structure components. Multiple linear models indicated that the frequency of occurrence of

Greater Tinamou was not explained by any tested component of the forest structure. However, the number of Variegated Tinamou encounters increased significantly in areas beneath more open canopy and where there were more fallen dead trunks. It diminished in areas where leaf litter was deeper. The results provide additional evidence that forest heterogeneity can be an important factor influencing the spatial distribution of terrestrial birds. In addition, this study contributes to the knowledge of how terrestrial birds respond in different ways to the spatial variation in the same components of structure of Amazonian terra-firme forest.

Keywords: Environmental heterogeneity, tinamous, *Tinamus major*, *Crypturellus variegatus,* structural forest components, habitat use, encounter frequency, birds.

INTRODUCTION

Environmental heterogeneity is an important element in the patterns of habitat use and selection by species (e.g., MacArthur & MacArthur 1961, August 1983, Karr & Freemark 1983, Khanaposhtani *et al.* 2012). Heterogeneity within forests, a result in part of spatial variation of the components of forest structure (*sensu* McCoy & Bell 1991 and references cited therein), promotes and augments the volume and types of available micro-habitats and, in consequence, can potentially heighten the segregation of resource utilization (Tews *et al.* 2004, Bagchi *et al.* 2011, Oliveira *et al.* 2011). This segregation in resource use has been recognized as one of the mechanisms by which the spatial distributions of species may be explained and has been applied to a variety of taxons (invertebrates: Tews *et al.* 2004; amphibians and reptiles: Watling 2005, Menin *et at.* 2007; fish: Espírito-Santo *et al.* 2013; mammals: August 1983, Lambert *et al.* 2006, bats: Bernard 2001). In this respect, birds are one of the best-studied groups (Bersier & Meyer 1994, Marra & Remsen 1997, Aleixo 1999, Díaz *et al.* 2005, Miranda *et al.* 2010, Bueno *et al.* 2012, Poindexter *et al.* 2012). The majority of such studies have been of arboreal species, and gap remains for terrestrial birds.

Tinamous (Family Tinamidae) are a strictly Neotropical group, which are characterized by their terrestrial habits, conservative morphological characteristics and a life style that has led to their being widely considered as one of the most basal of living bird groups (Cabot 1992, Bertelli *et al.* 2002, Bertelli & Porzecanski 2004). There are Tinamidae in closed or open habitats in all major areas of tropical and sub-tropical Central and South America (Cabot 1992), however, the greatest diversity both in terms of species and life styles occur in the Amazon Basin, where tinamids occupy a variety of forest habitats (Cabot 1992, Sick 1997). However, many tinamid species are in decline (Lees & Peres 2006, Parry *et al.* 2007), and, as with many other of the region's larger bird species, this is largely due to hunting and habitat loss to conversion of natural cover for human activities (Terborgh & Winter 1980, Gaston & Blackburn 1995, Thiollay 2005). In fact, Peres (2000) estimated that at least 455.000 tinamous (*Tinamus* spp. and *Crypturellus* spp.) were eaten annually by rural low-income families in Amazonia, Brazil. This level of impact was considered unsustainable for the majority of populations. Improved knowledge of the ecology and behavior of these species will be useful for conservation strategies for the group.

Species in this group have similar foraging habits, and appear to be generalists with very little selectivity for items included in the diet (Cabot 1992, Mosa 1993, 2004; Garitano-Zavala *et al.* 2003). Forest species, such as those in the genera *Tinamus*, *Crypturellus* and *Nothocercus* forage mainly on the ground, occasionally accessing insects or hanging fruit by direct jumping or accessing elevated substrates such as logs (Cabot 1992). They also often use the beak to fossick in leaf-litter for insects, small mollusks and annelids (Cabot 1992, Sick 1997). Forest-living tinamous use fallen tree trunks as locals for foraging and shelter, and will nest in-between the buttress roots of large standing trees though the nest itself is but a shallow depression in the soil, covered with a thin layer of leaves (McKay 1980, Cabot 1992, Sick 1997, Brennan 2009, 2010). Differences in the frequency with which different micro-habitats are used open the possibility of distributions without spatial overlap for sympatric congeneric species. This has been suggested for the Undulated Tinamou (*Crypturellus undulatus*) and Brazilian Tinamou (*C. strigulosus*) by Sick (1997). Due to their cryptic coloration, slow quiet movements, infrequent vocalizations and predilection or crepuscular and nocturnal activity, the ecology of the group is little known (Brennan 2004, Schelsky 2004), with basic natural history poorly known for some 40% (Schelsky 2004) of the 47 described species (Cabot 1992).

Studies investigating habitat use in bird communities that include hunted species, such as tinamous, encounter differences in how the species use the various forest strata, as well as temporal separations in the vocal activity of the species involved (Brooks *et al.* 2001). Nevertheless, an analysis of the spatial distribution of tinamou communities in a series of environments with different forest structures (Brooks *et al.* 2004, Schelsky 2004) found partial superimposition for the areas used by Great Tinamou (*Tinamus major)* and Variegated Tinamou (*Crypturellus variegatus*). Situations in which species with similar behaviours and physical characteristics overlap in their use of a heterogeneous environment, such as the understory of a terra-firme forest, would advance understanding of which of those characteristics of the exploited habitats are related to the observed patterns of use and occupation.

The current study investigated how the spatial variation in micro-habitats, here characterized by components of the forest structure, influence the spatial distribution and frequency of habitat use in two species of ground-living bird, the Great and the Variegated Tinamou. The inter-specific differences in the influence of the these components were also evaluated. We selected two components of landscape structure: local elevation and distance to water bodies; and four components of forest structure: abundance of fallen dead trunks, canopy openness, tree abundance and leaf-litter depth. Choice of components was informed by knowledge of the natural history of these birds (e.g., Montes 1977, Cabot 1992, Sick 1997, Davies 2002).

We tested the hypotheses that spatial variation in structural components of the forest will influence the spatial distribution and micro-habitat use by the tinamou study species. We predicted that the frequency of occurrence of the species would be greater in areas that were flatter with denser vegetation, where there was thicker leaf-litter and a higher number of fallen dead trunks, in areas where the canopy was more open and in more humid areas, close to bodies of water.

METHODS

Study area

The study was conducted in the Adolfo Ducke Forest Reserve (ADFR), situated in the municipality of Manaus, Amazonas state, Brazil (2º53’S, 59º58’W). The reserve has an area of 10.000 ha, and is composed of primary lowland Amazonian rainforest (terra-firme) (Ribeiro *et al.* 1999, Oliveira *et al.* 2008). In the region the annual median temperature is 26ºC, and annual precipitation varies between 1750 mm and 2500 mm, with the heaviest rain between November and May, and the least between June and October (Oliveira *et al.* 2008). The dominant vegetation is mature evergreen lowland forest with a canopy of 30–40 m, with emergent to 55 m (Ribeiro *et al.* 1999). The topography is changes gently, and is dominated by plateaus with closed canopy and a poorly-lit understory (Oliveira *et al.* 2008).

Experimental designg

Sampling of forest structure components and the recording of the study species occurred in 30 pre-established plots located systematically along six trails, each 5 km in length (for further details, see Oliveira *et al*. 2008). All plots are separated by at least 1km. The plots are non-linear 250 x 40m in dimensions and follow an undulation in the level of the terrain (additional details are present in Magnusson *et al.* 2005).

Bird surveys

Species occurrence was surveyed at listening points (Gregory *et al.* 2004), situated at the center (position meter-125) of each of the 30 permanent plots. Species recording occurred during a series of five extended field visits for bird surveys made between October 2012 and March 2013. During these visits, bird surveys were conducted between 05:30 and 10:00 daily.

Preliminary field tests, using a digital recorder and a portable loudspeaker, indicated that the maximum distance at which the two tinamou species could be identified by ear by R. S. G. was approximately 100 m. Assuming that the distance of one kilometer between sample plots was sufficient to minimize the risk of spatial pseudoreplication, and considering the small home ranges of the species involved, it is therefore considered unlikely that the same individual bird will have been recorded at more than one listening station (see Vispo 1995, Johnson *et al.* 2011 for details of home range estimation).

Auditory sampling began with 10 minutes of passive listening at each listening point. This was followed by two sequences of one minute of call broadcasting followed by two minutes of passive listening a sample regimen totaling 6 minutes. This was done for each species independently. In total 22 minutes of such sampling occurred in each of the 30 plots in total and the same effort was done in each one of the five visits for bird surveys. The sequence of call presentation was randomized to minimize the potential effects of inter-species dominance hierarchies on vocalization likelihood. The duration of playback and passive observation were the result of a series of pilot field studies in which the field methodology was progressively refined.

The recordings of calls used in the playback experiments (Naka *et al.* 2008), were made in areas close to the study area. While playback occurred the loudspeaker was positioned 30 cm above the forest floor, and pointed in four directions (north, south, east and west) and was done for 30 seconds each with the order decided randomly. Response calls were recorded with directional microphones (Seenheiser ME66) and a digital recorder (Sony ICD-PX720) for later identification, in case of any in-field doubt or difficulty. Playback volume was standardized at all points at a level similar to that of the target species' vocalizations. At all points, visual searching simultaneously supplemented auditory sampling.

Forest structural component sampling

Data on the elevation of each permanent study plot were collected in 2000 by a topographic surveyor, as part of the set-up process. Distance of the plots to water body were calculated using a detailed topographic map of the area. For both these components more details are available at the PPBio website (http://ppbio.inpa.gov.br).

In April 2013 the number of fallen dead trunks with a DBH > 20 cm were counted in a 10 m-wide sector of each 250 m study plot. With the height of a standing tinamou in mind, such trunks offer the birds refugia from predator attack and also places for nesting. In the same month, we recorded forest canopy openness using a Spherical Crown Densiometer (Concave - Mode C - Robert E. Lemon, Forest Densiometer - Bartlesville, OK, USA). Measurements were obtained from four readings (north, south, east, and west) at points at each 10 m along each plot, and median value then calculated and used as an index of canopy openness for each plot as a whole.

Tree abundance was recorded in February 2007 and March 2009. Within the permanent plots a hierarchical sampling design based on tree DBH was established using the methods of Castilho *et al.* (2006), with the total number of trees used as an index of abundance.

For each plot mean leaf-litter depth was calculated using data collected six-times a year between 2007 and 2013 (months: March, April, May, August, October, November). All samples followed the same protocol, measuring with a ruler the maximum depth of leaf-litter. Depth measurements were made every five meters down the central line of each plot, and a median per plot value calculated. This value then formed an index of leaf-litter density. More details are available at the PPBio database (http://ppbio.inpa.gov.br).

Data analysis

A Spearman correlation matrix was constructed to establish if significant correlations existed between the forest structure components (independent variables). When a significant correlation was found between two variables (see Results), the one included in the model was that which was considered to provide the best description of the micro-habitat for the tinamou species concerned. Testes for normality and distribution of residuals were made for all variables. Multiple linear models were used to evaluate the effect of each structural component on plot use frequency by Great and Variegated Tinamou. All tests were performed using the statistics program R 2.15.2 (R Development Core Team 2013).

RESULTADOS

Forest structural components

The elevation of the plots varied between 46 and 105 m (mean ± SD = 75.67 ± 20.56 m, n = 30). The abundance of dead fallen trunks varied between 8 and 40 (22.83 ± 7.54, n = 30). The mean percentage of canopy openness varied between 1.4 and 4.52% (2.86 ± 0.74%, n = 30). The abundance of trees varied between 565 and 1184 per plot (775.60 ± 134.62, n = 30). Mean leaf-litter depth varied between 1.77 and 2.88 cm (2.38 ± 0.29 cm, n = 30). Distance from plot to nearest water body varied between 18 and 579m (214.10 ± 160.98 m, n = 30). There was a significant correlation between terrain elevation and distance to water body (Table 1). In this instance, we selected the variable distance to water body as the preferred micro-habitat descriptor to be included in the multiple linear model analysis.

Effects of forest structure components on the frequency of records of *Tinamus major* and *Crypturellus variegatus*

Tinamus major occurred in 60% (18) of the listening posts and the frequency of encounter per post varied between 0 and 3 encounters during the entire sample time. Variation in the frequency of encounters was not correlated with any of the forest structure components (Table 2; $F = 0.98$, r^2 (adjusted) = –0.002, $DF = 24$, $P = 0.447$). The frequency of encounter was not significantly influenced by variation in the abundance of fallen dead trunks, canopy openness, tree abundance, leaf-litter depth or distance to water body (Table 2, Fig. 2).

Crypturellus variegatus had a greater spatial distribution than the *Tinamus major*, and were recorded in 29 of the 30 (97%) listening posts, with encounter rates varying between 0 and 5 encounters per post during the whole sampling time (Fig. 1). The frequency of encounters was influenced by the variation in some of the forest structure components (Table2; $F = 3.56$, r^2 (adjusted) = 0.306, $DF = 24$, $P = 0.015$). The frequency of occurrence of *Crypturellus variegatus* increased significantly with the increase in canopy openness and with the increase in the abundance of dead fallen trunks, and diminished with the increase in the depth of leaf-litter (Table 2, Fig. 3).

DISCUSSION

This study has added new evidence to the existing body of knowledge that suggests that heterogeneity in tropical forests can influence the spatial distribution of bird species (e.g., Karr & Freemark 1983, Terborgh 1985, 1990; Pearman 2002, Cintra & Naka 2012).This is the first study to investigate, with the simultaneous use of observation and call playback, the effect of this heterogeneity on the spatial distribution of species of tinamous. We found that spatial variation in the same of structural components of terra-firme forest influenced the frequency with which two species of the same family used the studied microhabitats.

The frequency of use by the *Tinamus major* which we recorded was similar in all the localities within the terra-firme forest. In this forest type, the spatial variation in the measured forest structural components, which act as proxies for the spatial variation between microhabitats and its extent, had no effect on the spatial distribution of *Tinamus major*, nor in the frequency with which it used these microhabitats. There is a direct relationship between body size between and size of area used by individuals of a species (Schoener 1968, Holling 1992) as well as in the manner in which they perceive differences in habitat patch size or the availability of those resources required for basic survival (Ziv 2000, Haskell *et al.* 2002).

Previous studies have demonstrated differences in habitat use by *Tinamus major*, when occupancy was compared between different vegetation forms (secondary forest, terra-firme and seasonally-flooded forest, várzea), each one structurally distinct (Brooks 2004, Schelsky 2004). This suggests that the species perceives the differences in the characteristics of the habitat at a level greater than the fine-scale special variation measured by the structural components of a terra-firme forest (e.g., Wiens 1976, Kotliar & Wiens 1990, Tews *et al.* 2004). The fact that the *Tinamus major* is larger than the *Crypturellus variegatus* implies greater energetic requirements, reflected in the greater home range (Kelt & Vuren 1999, Brown 2007). This difference in size could explain the need of each *Tinamus major* to explore a larger area overall and so encompass a greater range of microhabitats, leading to both lower frequency within the forest and less microhabitat selectivity.

The frequency of habitat use by the *Crypturellus variegatus* is related to the spatial variation in the number of fallen dead trunks, canopy openness and leaf-litter depth. This suggests that the species uses some sub-sets of the available micro-habitat array more frequently than others. In addition, some structural forest components had distinct effects on the *Crypturellus variegatus* use frequency.

Our prediction that use frequency by the Variegated Tinamou would be greater in areas with a more open canopy is corroborated. Such areas have a forest understory that receives more light, permitting greater and more constant growth of under-story vegetation in comparison to less well-lit areas (Nicotra *et al.* 1999, Montgomery & Chazdon 2002, Richards & Coley 2007), and this attracts more herbivorous arthropods (Moore *et al.* 1988, Basset *et al.* 2001). Thus, the use of better illuminated areas of the understory by *Crypturellus variegatus* is probably related to the greater availability of food items, such as invertebrates, fruits, seeds, buds and young leaves (Schubart *et al.* 1965, Cabot 1992, Sick 1997). On the other hand, use of such areas of dense cover may expose foraging individuals to increased risk of predation by hawk, bush dog, jaguarundi and spoted cats (Murray & Gardner 1997, Zuercher *et al.* 2005, Calleia *et al.* 2009, Tófoli *et al.* 2009, Melnyk *et al.* 2013). It is possible that there exists a balance between time spent foraging in such areas and the frequency of such foraging visits, to reduce vulnerability to predators and at the same time visit areas with the most favorable conditions for foraging (e.g., Lima & Dill 1990, Masse *et al.* 2013).

The prediction that variation in spatial abundance of logs influenced the use frequency by *Crypturellus variegatus* was confirmed. Areas with greater abundance of dead trunks appear to be places of refuge and nesting sites for tinamous. In addition they are probably places in which foraging tinamous are more likely to encounter such potential prey items as invertebrates living within decomposing wood (McKay 1980, Cabot 1992). Furthermore, such locals tend to be more humid, especially in the dry season, when the majority of terrestrial birds in the Ducke Reserve are nesting (see appendix in Cintra & Naka 2012).

We had imagined that the occurrence of the *Crypturellus variegatus* would be positively associated with areas of greater leaf-litter depth, since arthropod abundance in leaf-litter increase with deposit depth (Lieberman & Dock 1982, Adis 1988, Sayer *et al.* 2010). A relation between the spatial variation in leaf-litter layer depth has been shown to influence the distribution of a wide variety of understory birds in the Ducke Reserve (Cintra & Cancelli 2008, Cintra & Naka 2012), and in other tropical forests elsewhere (Pearson 1977, Pearson & Derr 1986). However, our results suggest that the *Crypturellus variegatus* preferentially uses those parts of the forest with the lowest depth of leaf-litter. In general, tinamous are opportunistic foragers with a generalized diet (Schubart *et al.* 1965, Cabot 1992, Sick 1997). Their more frequent use of areas with thin leaf-litter cover might be explained by the formation of prey search images individuals (e.g., Pietrewicz & Kamil 1979, Gendron 1986, Bond & Riley 1991). Such behavior increases individual capacity to recognize and capture food items (such as small fruits, seeds and invertebrates) and these would be more evident in where a shallow leaf-litter layer makes such items more swiftly detectable on the forest floor. In addition, tinamous walk very slowly on the forest floor without calling, using the beak to sweep the layers of leaf-litter (Cabot 1992). Such actions produce rustling noises which could alert predators to the tinamous presence. Hence, areas with shallow layers of leaf-litter may be preferred less noise will be generated during foraging, reducing the risk of predation, especially during the dry season.

Overall, this study has shown that tinamous respond in distinct ways to natural variation in microhabitat, suggesting that the heterogeneity of the central Amazonian terra-firme forest has an important role, perhaps species specific, in determining the spacial distribution of bird species (Terborgh 1985, Aleixo 1999, Cintra *et al.* 2006). The lack of correlation between the frequency of microhabitat use by the species and the variation in some structural forest components suggests that only some of the variables in forest structure determine the species' microhabitat use. In addition, the number of records for *Tinamus major* and *Crypturellus variegatus* made during the current study appear proportional to the natural densities of the species calculated by previous studies at Ducke (Soto 2013), and in an area nearby (Johnson *et al.* 2011). The lower numbers of *Tinamus major* compared to *Crypturellus variegatus* could reflect their lower natural density in the forest. However, we assume that at least some portion of the forest structure is important for the understanding of the partitioning of the spatial niche between the two species.

Some of the same structural forest components studied here also influence habitat use and spatial distribution in other species of diurnal and nocturnal birds at the Ducke Reserve (Cintra *et al.* 2006, Cintra & Cancelli 2008, Barros & Cintra 2009). Despite the interspecific differences in habitat use and the spatial scale at which species discriminate microhabitat patches, there exists a clear superimposition of home ranges and habit patches used by sympatric bird species even when these are from very different families (Okland 1996, Rauset *et al.* 2013). Certainly, spatial variation in the microhabitat components are important elements in the distribution of species and will therefore contribute to the maintenance of local (alpha) diversity and the coexistence of bird species (e.g., Karr 1976, Terborgh *et al.* 1990, Cohn-Haft *et al.* 1997, Marra &

Remsen 1997). In addition to this, the effects of other components, as such including food availability, predator density and distribution of nesting locations, on the use of space by tinamou also need to be evaluated for a better understanding to be achieved of the ecology of this interesting and little-understood group of birds.

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APÊNDICE

TABLE 1. Spearman correlation coefficients (ρ) and associated probability (p) for the forest structural components recorded in 30 permanent plots in the Adolpho Ducke Forest Reserve, Central Amazonia, Brazil.

Structural components	Abundance of fallen dead trunks	Canopy openness	Leaf-litter depth	Elevation	Distance to water body	Tree abundance
Abundance of fallen dead trunks	1					
Canopy openness	-0.22	1				
Leaf-litter depth	0.19	0.07	1			
Elevation	-0.21	-0.06	-0.24	1		
Distance to water body	-0.06	0.05	-0.32	0.80**	1	
Tree abundance	-0.04	0.10	0.001	0.24	0.21	1

Significance levels: ** $P < 0.001$

TABLE 2. Correlation coefficients (standard error values and significance (*p)* for each structural forest component recorded in 30 permanent plots in the Adolpho Ducke Forest Reserve, Central Amazonia, including multiple linear models for the *Tinamus major* and *Crypturellus variegatus*.

Forest structure components	*Tinamus major*		*Crypturellus variegatus*	
	Estimated	*p*-value	Estimated	*p*-value
Distance to water body	-0.002	0.21	0.0001	0.99
Abundance of fallen dead trunks	-0.044	0.10	0.055	**0.04**
Canopy openness	-0.041	0.88	0.7708	**0.008**
Tree abundance	0.0003	0.86	-0.0002	0.87
Leaf-litter depth	2.918	0.67	-2.1	**0.006**

FIG. 1 Frequency of encounter rates for the *Tinamus major* and *Crypturellus variegatus* in 30 sample plots, in relation to elevation gradients in the Adolpho Ducke Forest Reserve, Manaus, Brazil.

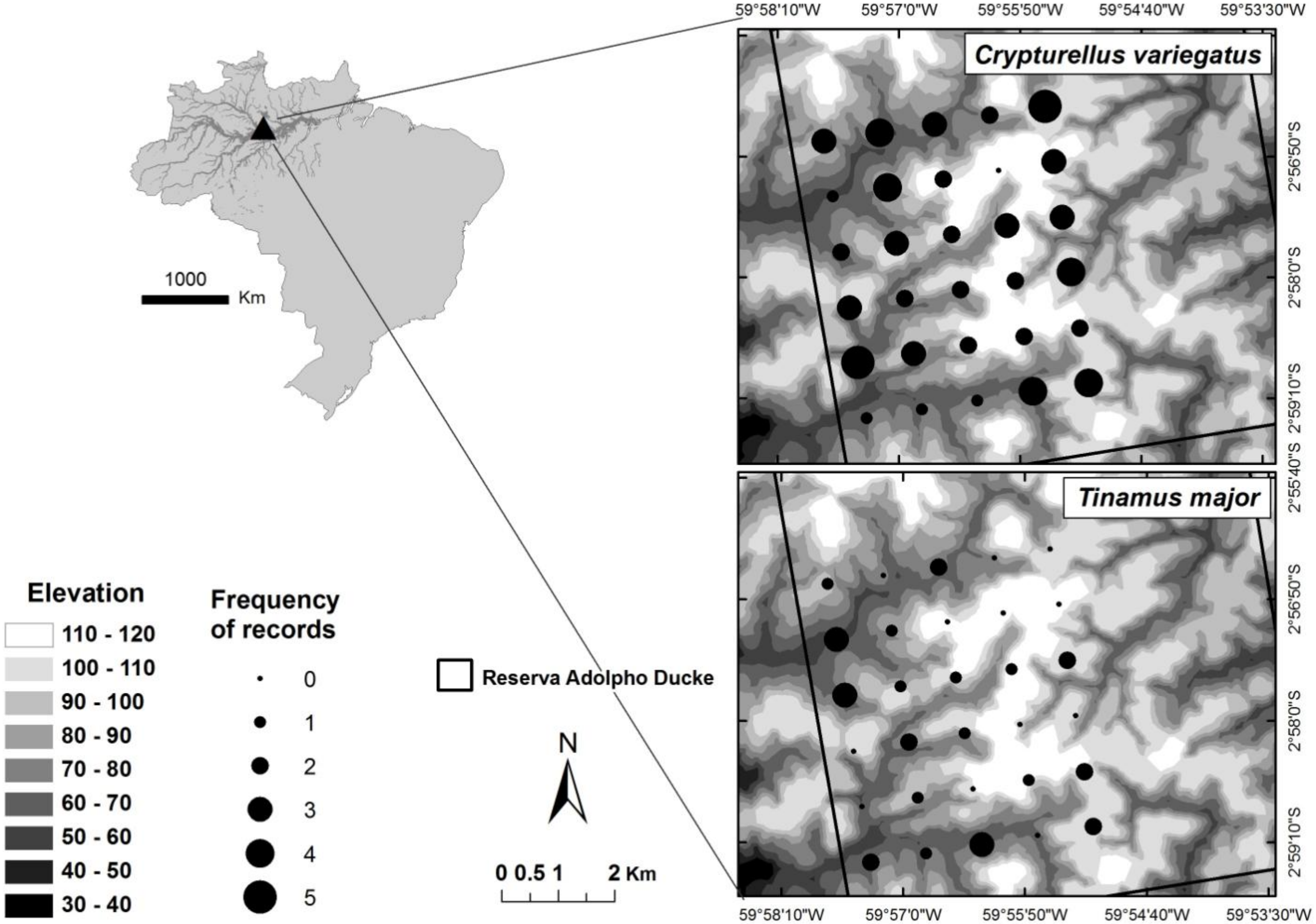
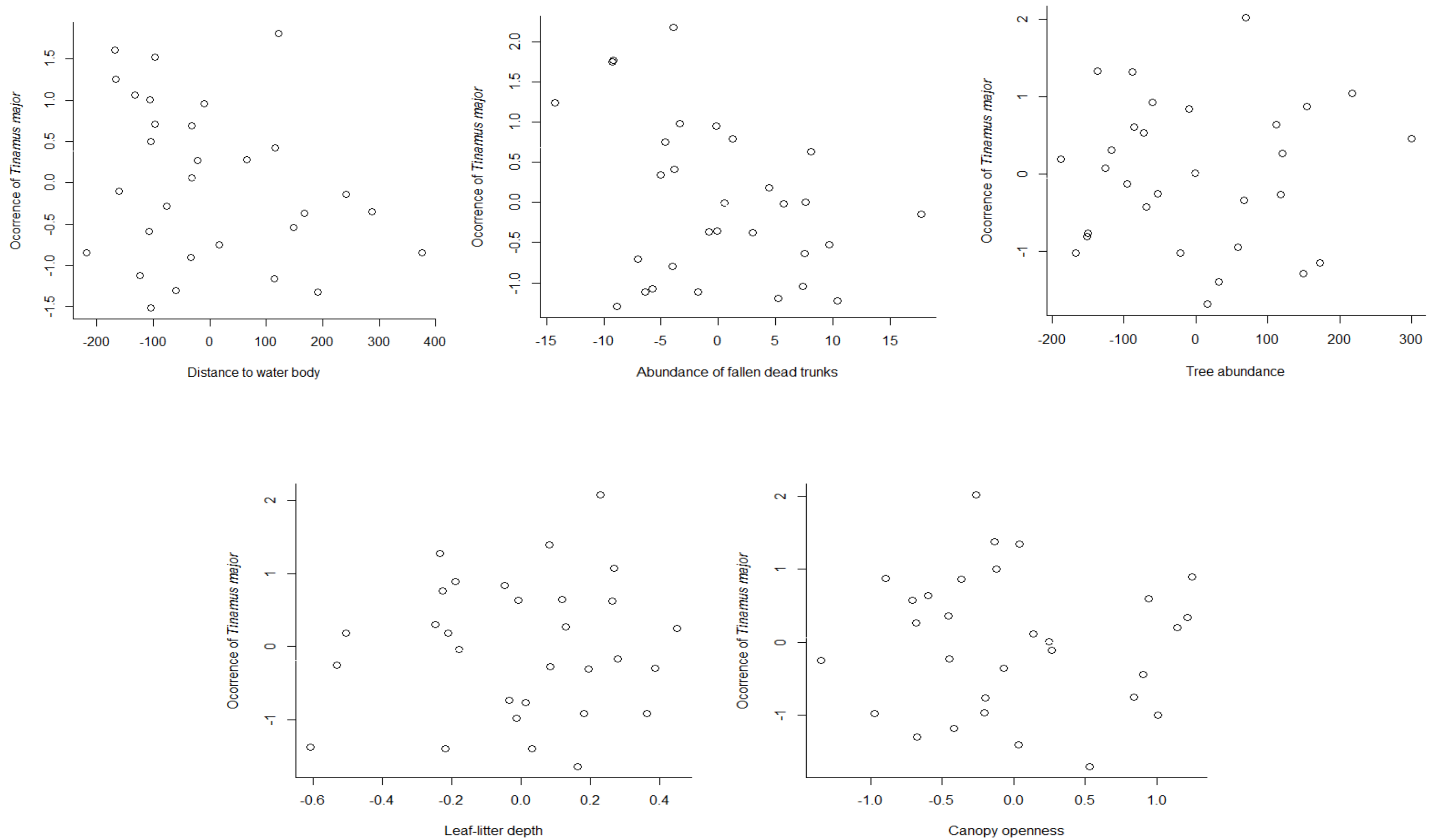
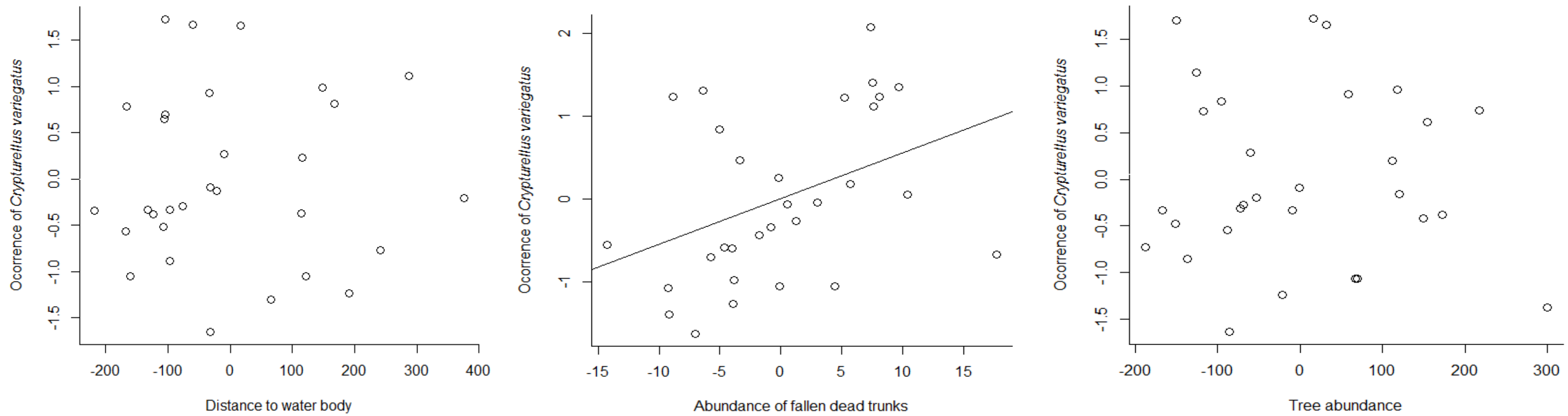


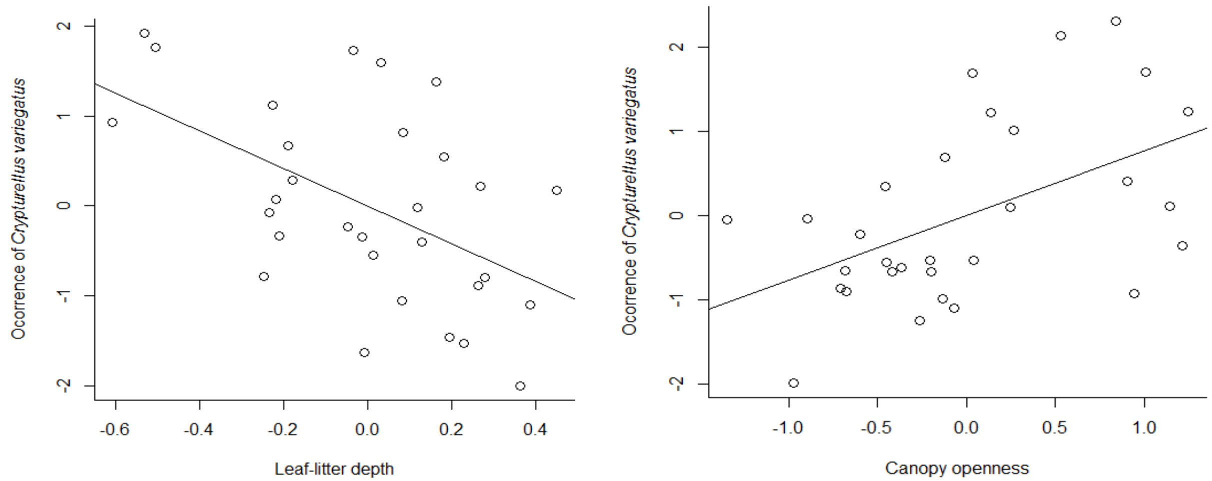
FIG. 2 Multiple linear model for the frequency of *Tinamus major* encounters and the components of forest structure: distance from water body, abundance of fallen dead trunks, abundance of trees, leaf- litter depth, and canopy openness. Some numbers on the axes are negative because they represent the deviations from the expected results when the other variables are held constant at their observed means.



Ocorrence of Tinamus major
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5
-200 -100 0 100 200 300 400
Distance to water body
Ocorrence of Tinamus major
-1.0 -0.5 0.0 0.5 1.0 1.5 2.0
-15 -10 -5 0 5 10 15
Abundance of fallen dead trunks
Ocorrence of Tinamus major
-1 0 1 2
-200 -100 0 100 200 300
Tree abundance
Ocorrence of Tinamus major
-1 0 1 2
-0.6 -0.4 -0.2 0.0 0.2 0.4
Leaf-litter depth
Ocorrence of Tinamus major
-1 0 1 2
-1.0 -0.5 0.0 0.5 1.0
Canopy openness

FIG. 3 Multiple linear model for the frequency of *Crypturellus variegatus* encounters and the components of forest structure: distance from water body, abundance of fallen dead trunks, abundance of trees, leaf-litter depth, and canopy openness. Some numbers on the axes are negative because they represent the deviations from the expected results when the other variables are held constant at their observed means.


Ocorrence of Crypturellus variegatus
Distance to water body
Ocorrence of Crypturellus variegatus
Abundance of fallen dead trunks
Ocorrence of Crypturellus variegatus
Tree abundance


Ocorrence of Crypturellus variegatus
Leaf-litter depth
Ocorrence of Crypturellus variegatus
Canopy openness

Conclusões

A importância da característica heterogênea do ambiente para explicar os padrões de distribuição das espécies tem sido evidenciada por estudos para diferentes grupos taxonômicos. O presente estudo contribui com novas evidência sobre o efeito da heterogeneidade da floresta, descrita pelos componentes de estrutura, na separação no uso do habitat e distribuição espacial de duas espécies de aves terrestres que apresentam hábitos e comportamentos semelhantes e pertencem a mesma família. Além disso, ficou evidente os efeitos distintos de um mesmo componente de estrutura no modo como as espécies usam os diferentes micro-hábitats, dentro de uma floresta de terra-firme, na região da Amazônia Central.

ANEXOS

Ata da aula de qualificação

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AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): RAFAEL SOAVE GUERTA
Curso: ECOLOGIA
Nível: MESTRADO
Orientador(a): RENATO CINTRA

Título:

"Efeitos da heterogeneidade da floresta sobre a co-ocorrência e distribuição espacial de duas espécies de tinamídeos (AVES:Tinamidae) em floresta de terra-firme, na Amazônia Central, Brasil"

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Ata da defesa pública

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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 25 dias do mês de março do ano de 2014, às 14:00 horas, no Auditório do PPG-CLIAMB, prédio LBA, Campus II, INPA/Aleixo, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Marcelo Gordo** da Universidade Federal do Amazonas - UFAM, o(a) Prof(a). Dr(a). **Wilson Roberto Spironello** do Instituto Nacional de Pesquisas da Amazônia - INPA e o(a) Prof(a). Dr(a). **Thierry Ray Jehlen Gasnier,** da Universidade Federal do Amazonas - UFAM, tendo como suplentes o(a) Prof(a). Dr(a). Albertina Pimentel Lima, do Instituto Nacional de Pesquisas da Amazônia - INPA, e o(a) Prof(a). Dr(a). José Luís Campana Camargo do Instituto Nacional de Pesquisas da Amazônia – INPA, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **RAFAEL SOAVE GUERTA,** intitulado "**Estrutura do habitat modula a distribuição espacial de duas espécies de aves terrestres (Aves: Tinamidae) na floresta de terra-firme na Amazônia Central ?",** orientado pelo(a) Prof(a). Dr(a). Renato Cintra Soares do Instituto Nacional de Pesquisas da Amazônia – INPA.

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

[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 Gordo** ____________

Prof(a).Dr(a). **Wilson Roberto Spironello** ____________

Prof(a).Dr(a). **Thierry Ray Jehlen Gasnier** ____________

____

Coordenação PPG-ECO/INPA