EFFECTS OF TERRA FIRME-FOREST STRUCTURE ON HABITAT USE BY OWLS (AVES: STRIGIFORMES) IN CENTRAL BRAZILIAN AMAZONIA

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Resumo. – Efeitos da estrutura da Floresta de Terra-Firme no uso de hábitat por corujas (Aves: Strigiformes) na Amazônia central brasileira. – As corujas, apesar de atuarem na regulação de presas e controle biológico, é um grupo ainda pouco estudado quanto à distribuição e abundância, principalmente as espécies neotropicais. Os componentes da estrutura da floresta têm sido usados para explicar padrões de uso de habitat e a estrutura de comunidades de aves, porém, os estudos relacionando tais componentes às corujas concentram-se em espécies do hemisfério norte. O presente estudo analisou se os componentes de estrutura da floresta influenciam o uso de habitat (ocorrência e abundância) por seis espécies de corujas em uma floresta de terra-firme na Amazônia central do Brasil. Para amostrar ocorrência e abundância foi usado o método playback, em 30 pontos distantes entre si em 1 km, nos meses de outubro e novembro de 2012. Em análise de regressão linear múltipla obtivemos relação entre a variação na abundância de quatro espécies de corujas e componentes da estrutura da floresta associados à disponibilidade de alimento; caburé-da-amazônia *(Glaucidium hardyi)* e distância do igarapé (*p* = 0,023), corujinha-orelhuda *(Megascops watsonii)* e profundidade da serrapilheira (*p* = 0,045), coruja-de-crista *(Lophostrix cristata)* e troncos mortos no chão (*p* = 0,042), murucututu (*Pulsatrix perspicillata)* e troncos mortos no chão (*p* = 0,009). Em relação a ocorrência, e usando regressão logística múltipla, obtivemos relação somente entre a presença de murucututu e troncos mortos no chão (*p* = 0,050). Assim, a influência dos componentes da estrutura da floresta difere de acordo com a espécie de coruja, demonstrando as diferenças interespecíficas no uso de micro-habitats, porém reflete a importância da disponibilidade de recurso alimentar na percepção de habitat pelas corujas.

Abstract. – Owls are a poorly-studied avian group, despite their well-established role in prey regulation and biological control. For Neotropical species, distribution and abundance are especially poorly known. Structural components of forests have been used to explain patterns of owl habitat use and community structure, but such analyses have largely focused on species in the northern hemisphere. The present study examines whether components of forest structure influence habitat use (occurrence and abundance) for six species of owls in an upland forest in central Amazonian Brazil. Between October and November 2012, a playback method was used to sample occurrence and abundance in 30 points, each separated from the next by 1 km. Multiple linear regression analysis revealed relationships between four owl species and components of forest structure associated with food availability: Amazonian Pygmy Owl (*Glaucidium hardyi*) and distance to nearest stream (*p* = 0.023), Northern Tawny-bellied Screech Owl *(Megascops watsonii)* and leaf-litter depth (*p* = 0.045), Crested Owl (*Lophostrix cristata)* and dead fallen trunks on forest floor (*p* = 0.042), and Spectacled Owl *(Pulsatrix perspicillata)* and dead fallen trunks on forest floor (*p* = 0.009). A multiple logistic regression also revealed a significant association (*p* = 0.050) between the Spectacled Owl and dead fallen trunks on forest floor. The influence of the components of

forest structure differs between the species, demonstrating interspecific differences in micro-habitat use, and reflecting the importance of food resource availability in habitat choice. *Accepted 12 December 2014.*

INTRODUCTION

In terms of habitat ecology, heterogeneity is defined as the degree of discontinuity within the environmental conditions of a landscape (Morrison 1998). These conditions may vary according to the composition and structure of vegetation or according to the flow of energy and other resources essential for a given organism. In recent years, based on the concepts of habitat and niche, environmental heterogeneity has been widely used to explain patterns of habitat use and community structure (Day 2000, Gaston 2000, Allen & Gillooly 2006). In the sense adopted in this paper, *habitat* includes where the organism lives, as well as the conditions for the survival of the organism, while *niche* is a description of the habitat conditions that meet the minimum requirements of a given species, so that the reproduction rate is equal to or greater than the mortality rate under the impact of environmental conditions on the population (Chase & Leibold 2003).

Knowledge of how organisms are distributed is an essential prerequisite for effective inference of which evolutionary and ecological factors determine patterns of habitat occupation and residence (Gayne & Balda 1994, Ricklefs 2004, Graham *et al.* 2006). The ability to use different features of the environment varies greatly between organisms, but most are able to track changes in the features of suitable habitat (Enfjäll & Leimar 2009). The perception of ideal habitat depends on a variety of factors, including morphological characteristics of the species (Srugley & Chai

1990, Hughes *et al.* 2007), social structure (Yaber & Rabenold 2002, Le Galliard *et al.* 2005), and life history (Levin 1984) as well as environmental factors, such as climate (Best *et al.* 2007, Hughes *et al.* 2007), landscape structure (Kuch & Idelberger 2005), and abundance of conspecific individuals at a specific site (Fletcher 2006, 2007).

Environmental heterogeneity influences directly or indirectly the spatial distribution, richness, and composition of an area's avifauna, since individual choices will be influenced by such factors as forest composition and species diversity, vegetation density and structure, and the status of local ecological succession (Hildén 1965, Orians 1969, Wiens 1969, Whitacre *et al.* 1990, Robinson 1994, Thiollay 1996, Amaral 2007).

The loss of habitat elements also has a direct effect on birds. Some structural components of the forest, such as tree density or the abundance of fallen logs, furnish localized micro-habitats for foraging and are known to be prime factors for site selection by nesting birds (Rodewald & Yahner 2000, Slaght *et al.* 2013). Despite this, the effect of spatial variation in forest-structure components on habitat choice by birds has been little studied (Enfjäll & Leimar 2009), even though such factors are important for an improved understanding of how interactions between organisms operate, and for the organization and structure of populations and ecological communities (Begon *et al.* 1986). Such changes may impact both the survival of individual birds and the maintenance of community structure. However, because of species-spe-

cific effects neither cause nor effect will be uniform within such a community (Orians 1969, Wiens 1969, Cintra & Naka 2012).

Several studies in central Amazonia have related forest-structure components to avian occurrence and abundance (e.g., Borges *et al.* 2004, Barros & Cintra 2009, Cintra *et al.* 2006). Rice *et al.* (1983) suggested that habitat selection by birds may vary seasonally according to the availability of food, and that the leaf-litter layer may also be sufficiently important in habitat choice as to influence the density of ground-foraging by birds-of-prey.

Patterns of distribution and abundance of nocturnal birds are generally related to environmental components, such as forest age, availability of cavities, edge distance, and the spatial and temporal abundance of food. According to Kavanagh *et al.* (1995), environmental generalists were more specific towards their prey while environmental specialists were more general in relation to their prey. According to Martin (1998) birds have "preferences for micro-habitats," which reflects the selection of a place to stay and use. Such variation can be highly species-specific so that, even when the same substrate is chosen for nesting, the characteristics of the adjacent vegetation may well be different for each bird species.

Because tropical bird communities are rich, complex, and heterogeneous, factors determining community structure are likely to be diffuse in the way they operate (Cintra & Naka 2012). Consequently, for many species of rainforest birds, little is known about their biology, including key factors in determining presence and abundance, such as habitat requirements and social structure, among others (Thiollay 2002).

The ecology of Neotropical raptors is little known, especially concerning aspects of forest structure used for the selection of habitats or territories (Throstom 2000). In some diurnal predators, such as Eurasian Spar-rowhawk (*Accipiter nisus*) and Osprey *(Pandion haliaetus)*, population density is regulated by the availability of prey and of favorable sites for nesting (Newton *et al.* 1977, Van Daele & Van Daele 1982). The situation is currently less certain for nocturnal raptors, especially in the tropics, where species' biology is often poorly known, especially in relation to habitat use and to the question which components of forest structure most directly influence occupation and residence (Amaral 2007, Motta-Junior & Braga 2012).

Most studies relating components of forest structure to the occurrence of owls have been conducted in the northern hemisphere. Several authors have suggested that a general preference among owls exists for habitats in mature forests, and that differences in the structure of the preferred habitat may vary with species' body size (Zwank *et al.* 1994, Gayne & Balda 1994, Hunter *et al.* 1995, Manzur *et al.* 1998, Peery *et al.* 1999, La Haye & Gutiérrez 1999). Evidence suggests that smaller species often use more open areas and choose shrubs as nesting sites (McCallum & Gehlbach 1988), while larger species prefer denser canopy and cavities in trunks for nesting (Bull *et al.* 1989, Belthoff & Ritchinson 1990).

Dead, broken, but still-standing trunks are often used by nesting owls (Hershey *et al.* 1998), and areas with a greater number of these will support a higher abundance of owls. Food-resource availability has also been related to the occurrence and abundance of owls, and indeed some species form pairs according to the abundance cycles of main prey (McInvaille & Keith 1974, Ellinson 1980, Smith *et al.* 1981, Village 1982, Smith & Gilbert 1984, Sparks *et al.* 1994). In addition, both the presence of fallen logs and great depths of leaf litter have been shown to provide shelter for owls' prey species, such as rodents, lizards, crickets, spiders, and beetles, which use leaf litter for concealment (Kiltie

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1981). Such sites can both attract and support more owls, and so increase their local abundance (Smith & Gilbert 1984).

Sometimes, similar features combine to influence both food and nest sites. For example, this is true for the Blakiston's Fish Owl (*Bubo blakistoni*), perhaps one of the best-studied owl species, which has been found to nest in valleys and near to water bodies (Spangenberg 1965, Pukinski 1973, Surmach 1998, Slaght 2011). Nest occurrence is also related to tree-trunk diameter, the availability of still-standing, but dead trees, and fallen logs clogging waterways (the latter being associated with abundance of salmon, an important food: Slaght *et al.* 2013).

Survival and area-size usage in the Spotted Owl (*Strix occidentalis caurina*) increase with the proportion of available habitat in late successional stages and with the amount of edge habitat, but decrease with the distance from the closest neighbor (Schilling *et al.* 2013), while the area used and breeding period expand in more fragmented habitats. This accords with the suggestion by Filloy & Bellocq (2013) that spatial variation in the abundance of forest birds is mainly due to structural components of the forest.

In the Amazon rainforest, there are few studies that relate the habitat structure with the distribution, abundance, and behavior of owls (see Willis 1977, Enriquéz-Rocha & Rangel-Salazar 2001, Borges *et al.* 2004, Sberze *et al.* 2010). A recent study of nocturnal birds in the Brazilian Amazon analyzed habitat use in primary and secondary forest (Sberze *et al.* 2010), but among the species analyzed only two were owls – Crested Owl and Amazonian Pygmy Owl. However, their levels of occurrence did not differ significantly between the two forest types.

A more recent study in the Reserva Florestal Adolpho Ducke (RFAD) evaluated the effects of forest-structure components on habitat use by six owl species (Barros & Cin-tra 2009), describing their general spatial distribution from records in 72 plots spaced from each other for 1 km and distributed in a large spatial scale of 64 km². The study showed very clear patterns of spatial distribution and influence of environmental heterogeneity in different species of owls (Barros & Cintra 2009). The abundance of still-standing dead trunks was used to explain the variation in density of Crested Owl and Northern Tawny-bellied Screech Owl, with the latter showing more frequent use of areas with higher tree abundance. The Amazonian Pygmy Owl preferred forest areas near streams. In this study, playback was not used as a complimentary technique to listening records at point counts (Granzinolli & Motta-Junior 2010), even though combining both methods can increase detections, thus minimizing false absence records (Mackenzie *et al.* 2002). So, even when underestimating the records by using this technique the study showed very clear patterns of spatial distribution and influence of environmental heterogeneity in different species of owls (Barros & Cintra 2009). As the species included in that study have different body sizes, probably differ in the size of areas used, and occur at different densities, it seemed interesting to evaluate whether at smaller spatial scales these patterns are similar to the spatial pattern found by Barros & Cintra (2009). Hence the aim of the current study was to describe the spatial distribution of six owl species (*Glaucidium hardyi, Lophostrix cristata, Megascops watsonii, Pulsatrix perspicillata, Strix virgata, Strix huhula*) in the RFAD at a smaller spatial scale (25 km²) than applied by Barros & Cintra (2009) while using the same sample design and the same 1-km spacing between plots, but with twice as many samples in plots and using additional detection techniques.

Specifically, this study examined how seven forest-structure components influenced habitat use (occurrence and abun-

dance) by owls in a central Amazonian upland forest. The forest-structure components were: 1) leaf-litter depth, 2) density of living trees, 3) standing dead-trunk density, 4) fallen dead-trunk density, 5) canopy opening, 6) terrain elevation, and 7) distance to nearest stream. The presence and density of the species was estimated using playback, a method barely used for owls in Neotropical forest environments.

Our hypothesis is that the spatial variation in the components of forest structure influences the spatial distribution and use of microhabitat by owls (verified on a species-by-species basis). We predict that the abundance and frequency of species occurrence will increase with the presence of flatter areas in the forest and with increases in vegetation density, leaf-litter depth, fallen-log abundance, the extent of canopy opening, and proximity to more humid areas, such as water bodies.

Considering some possibly important aspects for our focal species, e.g., known feeding habits and local preference for shelter and nest building, our hypothesis predicts: 1) increase in the density of the Amazonian Pygmy Owl (*G. hardyi*) with increase in canopy opening; 2) increase in the density of the Northern Tawny-bellied Screech Owl (*M. watsonii*) with the decrease in the canopy opening and increase in live-tree density, standing dead-trunk density, fallen dead-trunk density, and leaf-litter depth; 3) increase in the density of the Mottled Owl (*S. virgata*) with decrease in the canopy opening and increase in live-tree density, standing dead-trunk density, fallen dead-trunk density, and leaf-litter depth; and 4) increase in the density of the Black-banded Owl (*S. huhula*) with decrease in the canopy opening, together with an increase in standing dead-trunk density and fallen dead-trunk density, respectively. For the two largest species, our hypothesis predicts for the Crested Owl (*L. cristata*) an increase in density with an increase in canopy opening, live-tree density, standing dead-trunk density, and fallen dead-trunk density, and for the Spectacled Owl (*P. perspicillata*) a decrease in density with an increase in distance to nearest stream and in canopy opening, and an increase in density with the increase in standing/fallen dead-trunk density (Gwynne *et al.* 2010, König & Weick 2008).

METHODS

Study area. The study was conducted in the Reserva Florestal Adolfo Ducke (RFAD), located near Manaus, Amazonas State, Brazil (02°55'–03°01'S, 59°53'–59°59'W). Administered by the National Institute of Amazonian Research (INPA), the RFAD covers some 10,000 ha of primary *terra firme* forest, and is one of the best-studied areas of the Brazilian Amazon (Ribeiro *et al.* 1999, Oliveira *et al.* 2008).

Within the RFAD, average annual temperature is 26°C, and annual rainfall ranges from 1750 to 2500 mm, with a rainy season (November to May) and a dry season (June to October) (Oliveira *et al.* 2008). The dominant vegetation is mature evergreen forest with a canopy between 30–40 m, with emergent trees reaching up to 55 m (Ribeiro *et al.* 1999). The local topography consists of undulating plateaus, with predominantly a closed forest canopy and poorly-lit understory (Oliveira *et al.* 2008), incised by stream-bearing valley bottoms. In the central sector, an elevated plateau area divides the local stream system into two distinct basins. The clear-water streams of the eastern region flow into the Amazon River, while the black-water creeks on the western side flow into tributaries of the Rio Negro (Fig. 1).

Sample design. This study involved six common species of Strigiformes in the study area: Amazonian Pygmy Owl, Northern Tawny-bellied Screech Owl, Mottled Owl, Black-
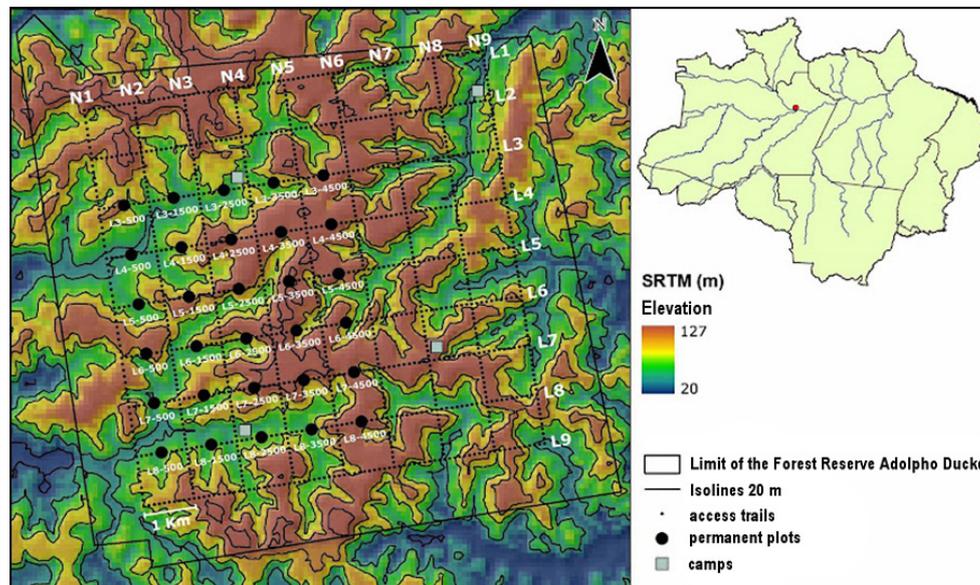
FIG. 1. Reserva Ducke **(**RFAD), Central Amazon, Brazil – trail grid and plots used during the study (source: http://ppbio.inpa. gov.br/repositorio/imagens).

banded Owl*,* Crested Owl, and Spectacled Owl. Sampling occurred on clear nights with little wind, between 18:00 and 23:00 h. During the breeding season, the owls are more sedentary, which guarded against possible double-counting of the same individual in more than one point. Additionally, observers' movements between sampling points were made as quickly as possible to minimize effects of individual bird movements between sampling locations.

The PPBio grid used had 30 plots with 250 m in length and each is separated from the next by 1000 m, and to minimize within-plot variation, each follows the local topographic curve. Each plot in this study was considered as a sampling unit. Playback (broadcasting recordings of the spontaneous vocalizations of each species, so that animals respond to these calls: Motta-Junior *et al.* 2004, Braga & Motta-Junior 2009) was used to test species' presence. The center of each plot was used as the listening point, and

meant the center of the radius of detection (125 m around the observer). The radius of detection of the observer was previously determined by experimental simulations evaluating the detection capability of the observer in the field.

Initially, each sampling sequence started with a listening session of five minutes, which was directed to identify and estimate whether the target owl species was vocalizing spontaneously. Following an initial 5-minutes interval, the listener began the sequence of playbacks for the five remaining species, each vocalization being played for three minutes with an interval of another three minutes until the playback changed to the next species, following from the smallest-sized (*G. hardyi*) to the largest owl (*P. perspicillata*), in order to minimize the potential effects of dominance rank (Motta-Junior *et al.* 2004). A full sampling sequence lasted 35 minutes at each listening point, including the initial playback-free minutes and the playback times. Some 25

minutes were spent commuting between listening points, so that 3–4 plots were sampled per night. Each plot was visited twice.

The methods were combined in order to minimize the effects of false absences. The following information was recorded for each individual point counts: date and time of registration, species and number of individuals vocalizing. To estimate the number of owls, we considered simultaneous vocalizations, assuming vocalizations in different directions not to be simultaneous, as a result of displacement of same individual. We also noted whether there were spontaneous vocalizations or response to playback, the length of response times, and responses of species vs playback. A digital recorder (Panasonic RR-XS4410) with microphone (Yoga EM-9600) and a portable speaker (MaxPrint 2W R.M.S.) were used to broadcast owl calls, always played using the same setting for volume (20) in the four directions (north, south, east, west) from the center point. In case of difficulties in species' identification, vocalizations were recorded for later laboratory analysis.

Within each sampling plot from which playback occurred, the following forest-structure variables were measured: 1) leaf-litter depth, 2) fallen dead-log density, 3) standing dead-log density, 4) live-tree density (DBH > 10 cm), 5) canopy opening, 6) terrain elevation, and 7) distance to nearest stream. All these variables were shown by a previous study (Barros & Cintra 2009) in the same area to impact the owls' micro-habitat use.

Leaf-litter depth, fallen dead-log, standing dead-trunk densities, and canopy opening were measured during the same period of field work to avoid any seasonal variation (Luizão & Schubart 1987, Luizão 1989, Rodrigues *et al.* 2000, Vital *et al.* 2004, Nascimento *et al.* 2006). Five records of leaf-litter depth were taken every 5 m within each plot, using a ruler graduated in millimeters. The resulting 51 per-plot records were then averaged. Fallen logs

and standing dead trunks were counted by direct observation for an area within 20 m from both sides of the plot's center line, and along the entire plot length. Canopy cover was measured with a densiospherometer, via four records (north, south, east, and west) every 10 m along the plot's central line, and a total of 26 measures averaged for each plot. For the other variables, we used the existing information available in the LTER database (http//peld.inpa.gov.br).

The correlation between the independent variables (forest-structure components) was tested with a Pearson correlation matrix.

To test whether forest-structure components influence habitat use by owl species, we performed an analysis using a multiple linear model for the density of each species, and a multiple logistic model analysis for occurrence (using as dependent variables the categorical variables presence = 1, absence = 0) with Systat 13.0. Multiple linear models were assessed with a quantitative response variable and continuous Y for explanatory variables (forest-structure components). The general logistic equation is $p = 1/ 1+e^{-z}$.

A qualitative array was generated with presence/absence, and analyses conducted separately for each owl species.

Raw densities were converted to a density index by multiplying the maximum number of individuals recorded per species by the time spent on each plot (35 minutes/plot), so that species' density ranged from 0–0.11. To estimate the total density per species for the entire study area, we used the density given by the number of plots where the species occurred divided by the total number of plots studied, multiplied by the value obtained for the density index per sample unit.

RESULTS

Across all plots, forest-structure variables showed the following patterns of variation:

TABLE 1. Densities of owl species in the 25 km^2 PPBio grid at Reserva Ducke, Central Amazon.

Species	Density per plot	Density by grid
Glaucidium hardyi	0–0,11	0,102
Megascops watsonii	0–0,08	0,048
Strix huhula	0–0,02	0,002
Strix virgata	0–0,02	0,004
Lophostrix cristata	0–0,11	0,102
Pulsatrix perspicillata	0–0,05	0,021

1) Fallen dead-trunk number ranged from 9–40, and standing dead-trunk number from 0–16; 2) leaf-litter depth varied from 2.94–5.84 cm; 3) distance to nearest stream ranged from 20–493.33 m; 4) canopy opening varied from 1.29–3.94%; 5) density of trees with DBH > 10 cm ranged from 293–393 individuals; and 6) overall terrain elevation ranged from 46–105 m a.s.l..

Of the six owl species that responded to playback, Amazonian Pygmy Owl and Crested Owl were recorded in 28 of the 30 plots (93.4 % of the sampled area), and were the most abundant species. The Northern Tawny-bellied Screech Owl was recorded in 18 plots (60 %) and the Spectacled Owl in 13 plots (43.4 %). The Mottled Owl occurred in 7 plots (23.4 %) and the Black-banded Owl in only 3 plots (10 %). The latter two species were excluded from the statistical analysis because of low numbers of records. Three species were not considered by a previous study (Barros & Cintra 2009) for a similar reason (*Strix virgata*, *S. huhula*, *Pulsatrix perspicillata*). However, the playback method used here allowed the inclusion of the Spectacled Owl, which Barros & Cintra (2009) excluded because of low detectability.

All owl species were detected in at least three sampling plots (10%) in each field visit. In seven plots of the PPBio grid, the Mottled Owl, a species not included in the study, responded to playbacks of the other owl species.

Densities of the owl species in the PPBio grid ranged from 0.002 to 0.102 (Table 1). However, the species distribution maps within RFAD were made for the six species (Fig. 2).

From a correlation test (Table 2), we separate the environmental variables in two models, keeping the variables most strongly and significantly correlated separated in different models. Thus, for each species, the models were constructed as following, Model 1: dead logs on the ground, standing dead trunks, distance from stream, and canopy opening, and Model 2: litter depth, abundance of trees with DBH greater than 10 cm, and terrain elevation (Tables 3–6).

The results of multiple linear models show that the 1) density of *G. hardyi* increases with increasing distance from stream and increase in terrain elevation (Fig. 3); 2) density of *M. watsonii* increases with decreasing depth of leaf litter (Fig. 4); 3) density of *L. cristata* increases with the increase in the abundance of standing dead trunks (Fig. 5); and 4) density and occurrence of *P. perspicillata* increase with the increase in the abundance of fallen dead trunks (Figs 6, 7).

DISCUSSION

This is probably the first study that used two simultaneous methods minimizing false absences (direct observation by counting points, and playback) to demonstrate how the spatial variation in the structural components of a terra firme upland forest influences the use of micro-habitats by nocturnal predatory birds. The key interest from the ecological perspective is that they are of various sizes and in the same family, thus representing a potentially competing array (Marshal 1939). The results of this study support existing evidence (e.g., Terborgh 1985, Barros & Cintra 2009, Cintra & Naka 2012) that, by variation in forest-structure components, the hetero-
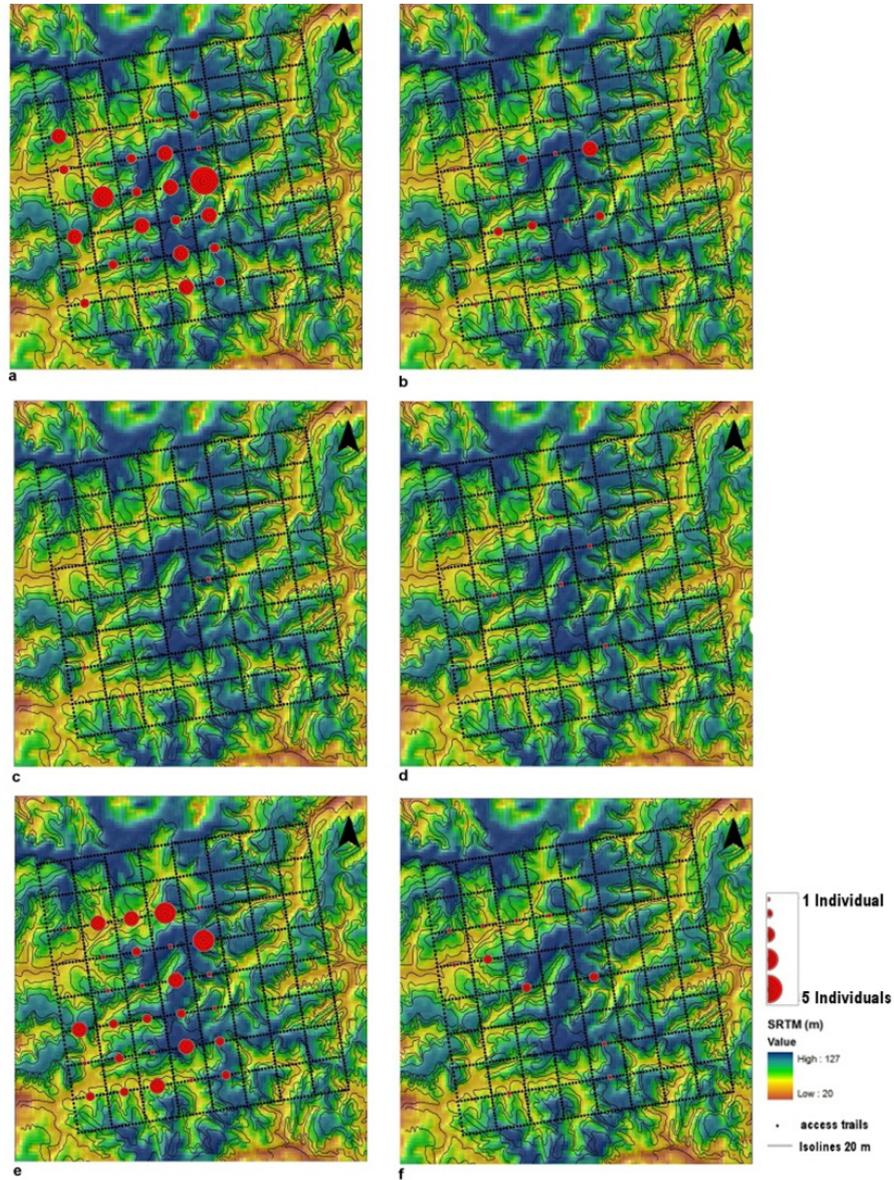
FIG. 2. Species distributions in the PPBio plots at Reserva Ducke, Central Amazon: a) *Glaucidium hardyi*, b) *Megascops watsonii*, c) *Strix huhula,* d) *Strix virgata*, e) *Lophostrix cristata*, f) *Pulsatrix perspicillata*.

geneity of tropical forests can influence the spatial distribution of bird species, indicating that such effects have broad impacts throughout bird communities, irrespective of their diet and time of activity.

Owls, like other predatory birds, select territories according to their potential for breeding and nesting areas (Motta-Junior *et al.* 2004). Cavities for nesting and shelter are rarely constructed by owls, with existing cavi-

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TABLE 2. Pearson Correlation Matrix for the forest-structure components recorded in 30 PPBio plots at Reserva Ducke, Central Amazon.

	Logs	Litter	Snags	Distance to stream	Canopy opening	Tree abundance	Terrain elevation
Logs	1,000						
Litter	0,172	1,000					
Snags	0,061	0,029	1,000				
Distance to stream	-0,030	-0,253	0,089	1,000			
Canopy opening	-0,208	0,339	0,092	0,017	1,000		
Tree abundance	-0,243	-0,369	0,118	0,359	0,246	1,000	
Terrain elevation	-0,135	-0,381	0,180	0,757	-0,087	0,410	1,000

ties (natural rot holes; holes made by woodpeckers, armadillos, and others) exploited opportunistically, sometimes being slightly enlarged or otherwise modified (Glinski & Ohmart 1983).

The use of dead and/or broken trunks are common among owls, and several studies have demonstrated their importance in habitat selection by owls (La Haye 1988, Hershey *et al.* 1988, Carrey 1990, Thorstrom 2011, Barros & Cintra 2009, Slaght *et al.* 2013). However, the current study found no relationship between the abundance of standing dead trunks and density of owls at the micro-habitat level, suggesting that owls may use other forest-structure components in the studied habitat and probably depend on the availability of food resources.

Food availability is one of the many factors limiting habitat use. In owls, low food availability may interfere with reproduction, both extending inter-breeding intervals and reducing clutch size. Additionally, pair formation may be tied to cycles of prey abundance (McInvaille & Keith 1974, Ellinson 1980, Smith *et al.* 1981, Village 1982, Rice *et al.* 1983, Smith & Gilbert 1984, Sparks *et al.* 1994, Motta-Junior *et al.* 2004). In the present study, we used two proxies for food availability - depth of litter and number of fallen dead trunks - and found that these variables were significantly influencing the presence of three owl species (*Megascops watsonii, Lophostrix cristata, Pulsatrix perspicillata*).

For the Crested Owl, the frequency of micro-habitat use varied between different areas within the study site. Though studies were conducted in the same location, this result differs from the study of Barros & Cintra (2009) conducted at a higher spatial scale (covering almost the entire area of RFAD). In our study, the species were also widely distributed in the grid and not influenced by the central plateau areas as in the aforementioned study.

It is commonly accepted that body size is directly related to the species' home-range size (Schoener 1968, Holling 1992), which, in turn, reflects differences in how individuals fulfill their basic survival requirements and perceive differences in the distribution of micro-habitat patches (Ziv 2000, Haskell *et al.* 2002). An earlier study in the Central Amazon comparing occupancy in owls discriminated different species assemblages in secondary and primary terra firme and in seasonally flooded forest, and proposed that habitat-structure differences might be influential (Borges *et al.* 2004). This suggests that the way in which the species involved perceive differences in habitat characteristics may not occur at the level of simple spatial variation, but at a finer scale related to the structural components of forest (e.g., Wiens 1976,

TABLE 3. Results of Multiple Linear Models and Multiple Logistic Models of variation of *Glaucidium hardyi* density in relation to forest-structure components (Model 1 and 2) recorded in 30 plots at Reserva Ducke, Central Amazon.

Effect	Multiple linear models						Multiple logistic models					
	Coefficient	Standard error	Standard coefficient	Tolerance	t	*p*-value	Estimate	Standard error	Z	*p*-value	95% Confidence Interval	
											Lower	Upper
Model 1												
Constant	2,254	1,004	0,000	-	2,246	0,034	-340,279	1,23E+010	0,000	1,000	2,412E+010	2,41E+010
Logs	-0,032	0,023	-0,248	0,949	1,402	0,173	18,217	5,150E+008	0,000	1,000	1,009E+009	1,009E+009
Snags	-0,033	0,052	-0,110	0,977	0,631	0,534	-27,408	8,119E+008	0,000	1,000	1,591E+009	1,591E+009
Distance to stream	0,003	0,001	0,420	0,991	2,424	0,023	-7,672	1,660E+008	0,000	1,000	3,254E+008	3,254E+008
Canopy opening	0,049	0,258	0,034	0,946	0,191	0,850	112,312	3,103E+009	0,000	1,000	6,082E+009	6,082E+009
Model 2												
Constant	0,854	2,588	0,000	-	0,330	0,744	395,751	9,124E+011	0,000	1,000	1,788E+012	1,788E+012
Litter	-0,335	0,238	-0,252	0,800	1,404	0,172	114,462	3,159E+010	0,000	1,000	6,192E+010	6,192E+010
Tree abundance	0,003	0,006	0,100	0,779	0,552	0,586	1,566	2,384E+009	0,000	1,000	4,673E+009	4,673E+009
Terrain elevation	0,018	0,009	0,370	0,771	2,024	0,053	-13,524	1,160E+009	0,000	1,000	2,274E+009	2,274E+009

TABLE 4. Results of Multiple Linear Models and Multiple Logistic Models of variation of *Megascops watsonii* density in relation to forest-structure components (Model 1 and 2) recorded in 30 plots at Reserva Ducke, Central Amazon.

Effect	Multiple linear models						Multiple logistic models					
	Coefficient	Standard error	Standard coefficient	Tolerance	t	*p*-value	Estimate	Standard error	Z	*p*-value	95% Confidence Interval	
											Lower	Upper
Model 1												
Constant	1,648	0,954	0,000	-	1,728	0,096	-4,308	2,515	-1,713	0,087	-9,237	0,620
Logs	-0,001	0,022	-0,012	0,949	-0,060	0,953	0,054	0,056	0,976	0,329	-0,055	0,163
Snags	-0,054	0,049	-0,211	0,977	-1,097	0,283	0,132	0,128	1,032	0,302	-0,119	0,383
Distance to stream	0,001	0,001	0,118	0,991	0,618	0,542	0,000	0,003	-0,149	0,882	-0,005	0,005
Canopy opening	-0,235	0,246	-0,187	0,946	-0,956	0,348	0,717	0,611	1,173	0,241	-0,481	1,915
Model 2												
Constant	5,328	2,488	0,000	-	2,141	0,042	-12,687	7,340	-1,728	0,084	-27,074	1,699
Litter	-0,482	0,229	-0,421	0,800	-2,103	0,045	0,667	0,611	1,092	0,275	-0,530	1,865
Tree abundance	-0,007	0,006	-0,254	0,779	-1,253	0,221	0,029	0,018	1,622	0,105	-0,006	0,064
Terrain elevation	0,001	0,008	0,029	0,771	0,142	0,888	-0,010	0,023	-0,430	0,667	-0,056	0,036

TABLE 5. Results of Multiple Linear Models and Multiple Logistic Models of variation of *Lophostrix cristata* density in relation to forest-structure components (Model 1 and 2) recorded in 30 plots at Reserva Ducke, Central Amazon.

| | Multiple linear models | | | | | | Multiple logistic models | | | | 95% Confidence Interval | |
Effect	Coefficient	Standard error	Standard coefficient	Tolerance	t	p-value	Estimate	Standard error	Z	p-value	Lower	Upper
Model 1												
Constant	1,437	1,102	0,000	-	1,305	0,204	592,839	6,142E+010	0,000	1,000	-1,204E+011	1,204E+011
Logs	0,054	0,025	0,389	0,949	2,146	0,042	-26,981	2,227E+009	0,000	1,000	-4,366E+009	4,366E+009
Snags	-0,042	0,057	-0,131	0,977	-0,731	0,471	-18,768	5,505E+009	0,000	1,000	-1,079E+010	1,079E+010
Distance to stream	0,000	0,001	0,058	0,991	0,327	0,746	-0,425	74,595,600	0,000	1,000	-1,462E+008	1,462E+008
Canopy opening	-0,254	0,284	-0,162	0,946	-0,894	0,380	-20,149	2,967E+010	0,000	1,000	-5,816E+010	5,816E+010
Model 2												
Constant	0,276	3,329	0,000	-	0,083	0,935	1.000,619	8,193E+010	0,000	1,000	-1,606E+011	1,606E+011
Litter	0,272	0,307	0,191	0,800	0,887	0,383	-144,626	1,157E+010	0,000	1,000	-2,268E+010	2,268E+010
Tree abundance	0,000	0,008	-0,008	0,779	-0,035	0,972	2,330	1,495E+008	0,000	1,000	-2,930E+008	2,930E+008
Terrain elevation	0,007	0,011	0,135	0,771	0,617	0,542	-22,375	1,091E+009	0,000	1,000	-2,137E+009	2,137E+009

TABLE 6. Results of Multiple Linear Models and Multiple Logistic Models of variation of *Pulsatrix perspicillata* density in relation to forest-structure components (Model 1 and 2) recorded in 30 plots at Reserva Ducke, Central Amazon.

Effect	Multiple linear models						Multiple logistic models					
	Coefficient	Standard error	Standard coefficient	Tolerance	t	*p*-value	Estimate	Standard error	Z	*p*-value	95% Confidence Interval	
											Lower	Upper
Model 1												
Constant	-0,883	0,616	0,000	-	-1,433	0,164	6,656	3,385	1,967	0,049	0,023	13,290
Logs	0,040	0,014	0,479	0,949	2,822	0,009	-0,151	0,077	-1,963	0,050	-0,302	0,0001
Snags	0,049	0,032	0,260	0,977	1,554	0,133	-0,348	0,204	-1,706	0,088	-0,747	0,052
Distance to stream	0,000	0,001	-0,111	0,991	-0,669	0,509	0,001	0,003	0,345	0,730	-0,005	0,007
Canopy opening	0,099	0,159	0,107	0,946	0,627	0,536	-0,433	0,640	-0,677	0,499	-1,687	0,821
Model 2												
Constant	-0,754	1,952	0,000	-	-0,386	0,702	8,668	6,711	1,292	0,196	-4,485	21,820
Litter	0,219	0,180	0,257	0,800	1,216	0,235	-0,920	0,625	-1,472	0,141	-2,145	0,305
Tree abundance	0,001	0,005	0,066	0,779	0,306	0,762	-0,014	0,016	-0,900	0,368	-0,045	0,017
Terrain elevation	-0,002	0,007	-0,068	0,771	-0,314	0,756	0,006	0,022	0,271	0,787	-0,037	0,048

Model 1
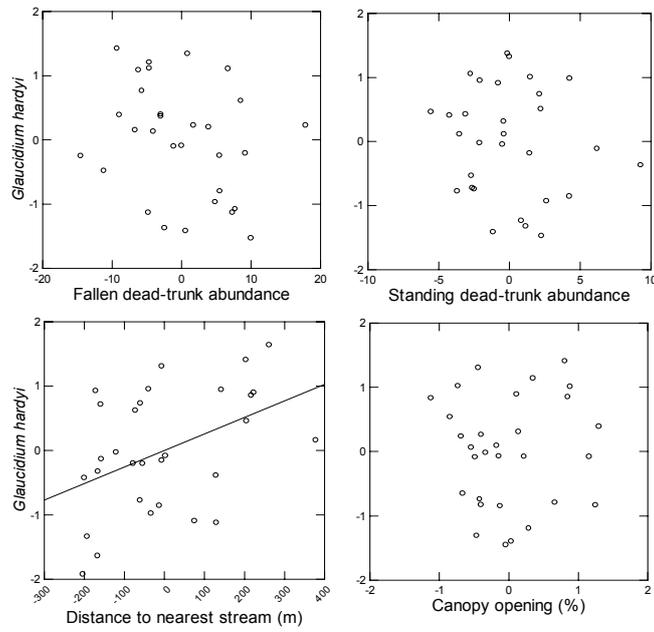
Model 2
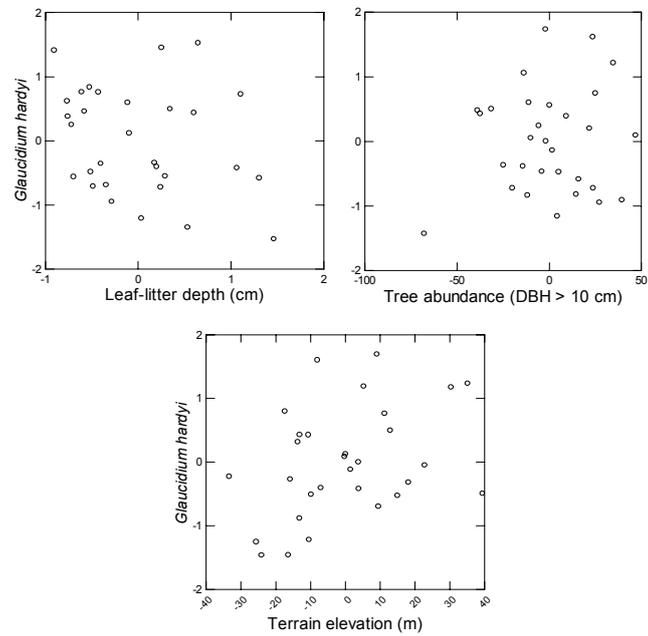
FIG. 3. Results of multiple linear models of *Glaucidium hardyi* density in relation to forest-structure components (Model 1 and 2). Some numbers of the axes are negative because the partial relationships deviations of the expected results as all the other variables are maintained constant with their observed means.

Model 1
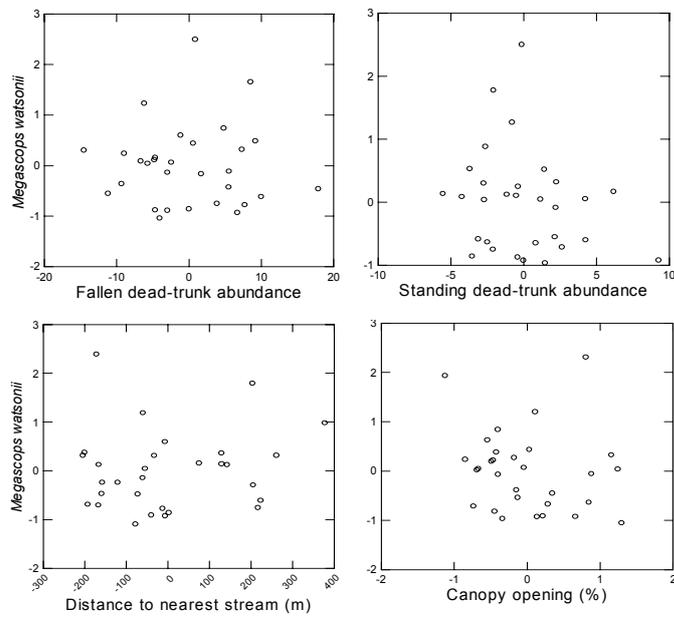
Model 2
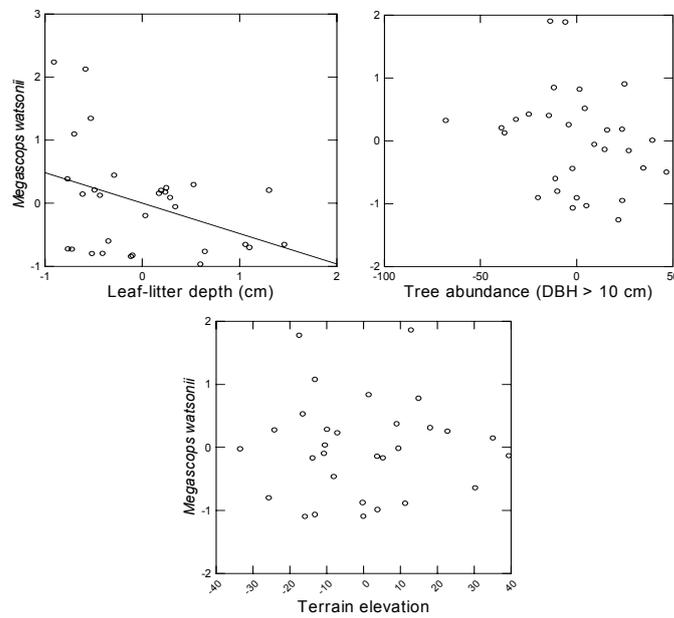
FIG. 4. Results of multiple linear models of *Megascops watsonii* density in relation to forest-structure components (Model 1 and 2).
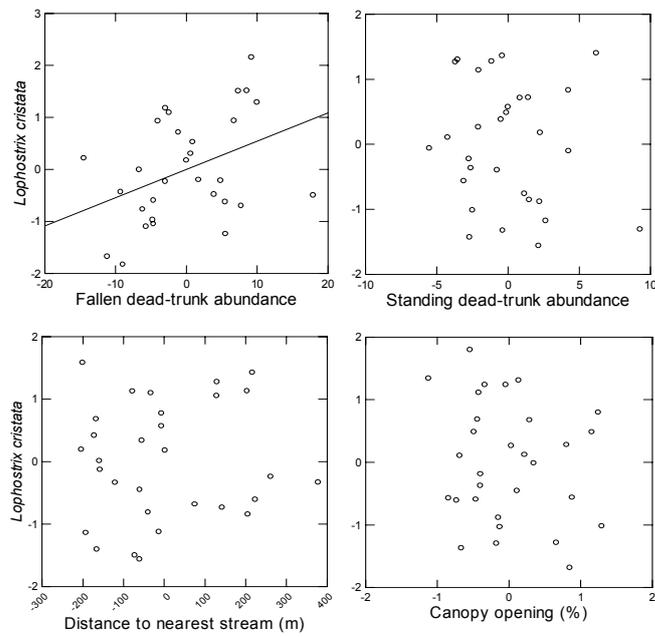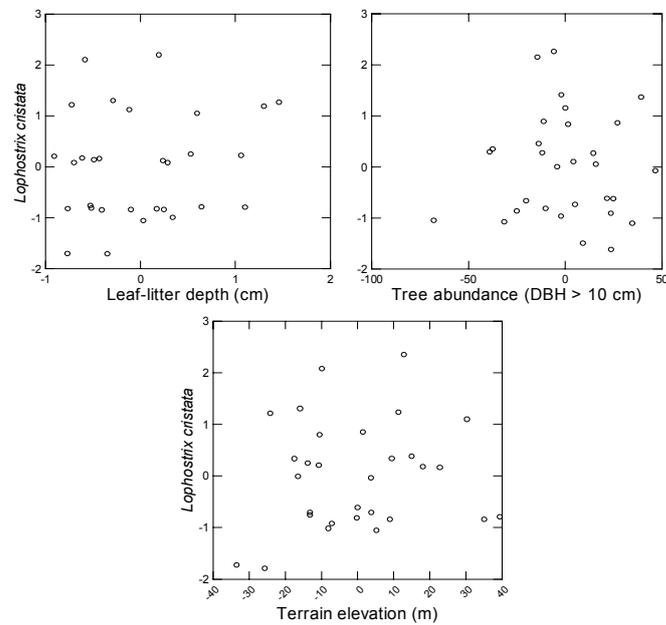
Model 1

Model 2

FIG. 5. Results of multiple linear models of *Lophostrix cristata* density in relation to forest-structure components (Model 1 and 2).
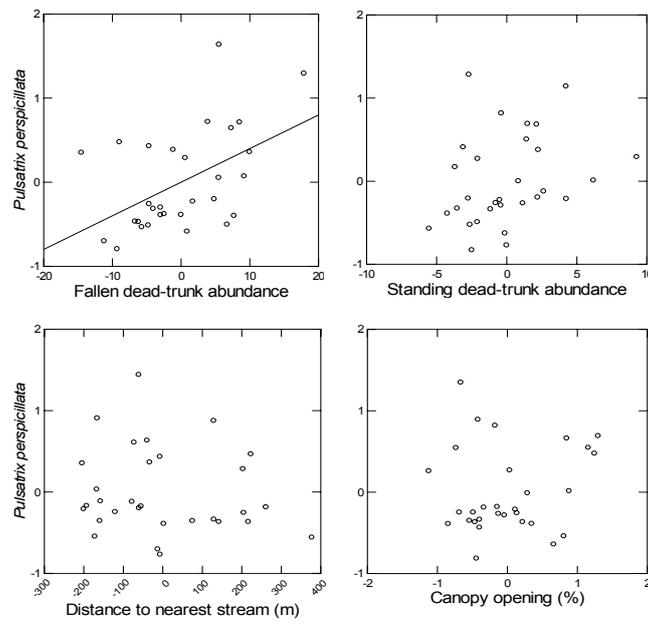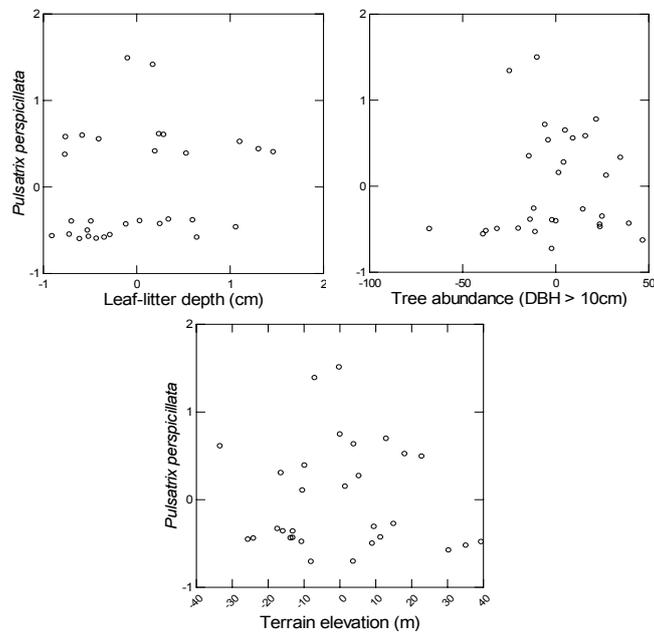
Model 1

Model 2

FIG. 6. Results of multiple linear models of *Pulsathrix perspicillata* density in relation to forest-structure components (Model 1 and 2).

FIG. 7. Results of multiple linear models of *Pulsatrix perspicillata* density in relation to abundance of fallen logs.

Kotliar & Wiens 1990, Tews *et al.* 2004). For example, *Lophostrix* and *Pulsatrix* are larger than *Glaucidium* and *Megascops*, which implies higher energy demands in the former ones and hence more extensive home ranges (Kelt & Vuren 1999, Brown 2007). These size differences may explain why *Lophostrix* and *Pulsatrix* exploit larger areas, which likely include a greater variety of micro-habitats than those embraced by the smaller home ranges of smaller-sized owl species.

Unlike the study by Barros & Cintra (2009), where Crested Owl density was found to be related to the abundance of standing dead trunks, the current study found habitat use by Spectacled Owl and Crested Owl correlated with an increase in fallen-log abundance. As forest-floor logs attract potential owl-prey items, such as invertebrates and small mammals (Kiltie, 1981), a general positive relationship between forest logs and owl abundance is indicated even when habitat, prey type, and owl size are very different (see Smith & Gilbert 1984). This suggests that the studied owl species preferably use particular areas within the available habitat. In addition, the different components of forest structure

had different effects on use frequency by such smaller species as Amazonian Pygmy Owl and Northern Tawny-bellied Screech Owl.

Obviously, use frequency by Crested Owl and Spectacled Owl is increased in areas with a greater abundance of fallen logs. Forest-floor areas with increased log abundance are widely considered as places important to forage and find potential prey, such as rodents as well as invertebrates within decaying trunks (del Hoyo 1999). Moreover, the understory environment near such trunks tends to be more humid, and this may be important in the dry season, which at RFAD coincides with the nesting season of most species of ground-breeding birds (see appendix Cintra & Naka 2012). Owls at RFAD are likely to find food items more promptly when visiting areas with higher than those with lower abundance of fallen logs. However, areas with these characteristics can increase the risk of exposure of individuals to potential predators, like snakes that use such locations as refuges and for breeding, and hunting wild cats (ocelots, jaguars) that use them for concealment. Therefore, owls visiting such profitable foraging sites must balance visit length and frequency

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in order to reduce their vulnerability to predators (e.g., Lima & Dill 1990, Masse *et al.* 2013). We had expected that the Crested Owl occurrence would be positively related to elevation, since a previous study (Barros & Cintra 2009) had demonstrated a strong association of this large owl with higher altitude, probably because in such areas the forest tends to be more open. However, the current study found that the Crested Owl also uses low-lying and sloped areas, a novelty for the biology of this species, previously believed to use only flat forested areas in the plateaus.

Arthropod abundance increases with litter depth, which, in turn, influences the occurrence of understory-living species of insectivorous birds (for the tropics: Pearson 1977, Pearson & Derr 1986; for RFAD: Cintra & Cancelli 2008, Cintra & Naka 2012). Confirming results from a study conducted within the reserve but at a larger spatial scale (Barros & Cintra 2009), our results show that the Northern Tawny-bellied Screech Owl prefers forest environments with shallow leaf-litter layers. Though specialists exist, many owl species are opportunistic and have a generalist diet (Schubart *et al.* 1965, Sick 1997). The Northern Tawny-bellied Screech Owl eats small rodents, birds, and invertebrates, so the fact that it most frequently uses areas with shallow leaf-litter may be due to the ease with which such prey is both recognized and captured in these places. Such foraging may be energetically effective since the use of sites with less litter increases predation-success rates, hence economizing the predator's time and energy budgets (Amaral 2007).

In our study, the Amazonian Pygmy Owl had a higher density in areas closer to creeks. This was also found by Barros & Cintra (2009), who believe this may be explained by the more open canopy and understory close to streams, which increase visibility as well as the frequency of small animals (lizards, frogs, small mammals) in such areas. In a study of Eastern Screech Owls (*Megascops asio*), Smith & Gilberd (1984) found that they used different habitats during the breeding and non-breeding season, preferring more open areas, which increased successful predation.

The Amazonian Pygmy Owl responded promptly and aggressively to playback vocalizations, even to those of three-times larger species (i.e., Spectacled Owl). This suggests that *G. hardyi*, being the smallest representative of owls at RFAD, is highly territorial and invests more energy to defend its resources than other (i.e., larger) species. Alternatively, this aggressive behavior could be interpreted as reaction towards the presence of similar-sized or larger, physically more dominant owls that may represent both competitors and/or potential predators. Generally, in the context of signaling theory aggressive calling can indicate towards an intruder defense capability and readiness for the next level of aggression, respectively, which could help to avoid further, e.g., more costly interactions (Georgiev *et al.* 2013; cf. Gill 2007), including the risk of being predated (Jakobsson *et al.* 1995).

Crested Owl and Amazonian Pygmy Owl were the commonest owl species at RFAD, being absent from only two sampled plots but abundant in the remaining 28 plots. Given their spatial overlaps, these species probably are likely not competitors and thus can coexist in the same habitat. The current study found the Crested Owl to be uniformly distributed within the study area. This contradicts the results of Barros & Cintra (2009), who indicated that its abundance is clumped on the RFAD central plateau.

The current study found that the Northern Tawny-bellied Screech Owl was abundant and widely distributed across the study grid. This is also in contrast to the findings of Barros & Cintra (2009), who found it to be restricted to one area, Ipiranga, in the southwestern part of the RFAD (not included in

this study). Thus, the currently observed pattern might be linked to methodological differences or to a recent expansion and colonization of new areas by this owl.

According to maps generated by the study, the Spectacled Owl occurs in areas close to streams below 100 m a.s.l.. This may be related to its diet that includes small mammals, birds, large spiders, insects, and freshwater crabs (Sick 1997, Sigrist 2009). Similar results have been recorded for other owl species; e.g., a study of the diet of the Ural Owl (*Strix uralensis*), Korpimaki & Sulkava (1987) found a positive correlation between the proportion of water bodies and an increased predation on rodents, possibly because prey animals are more vulnerable to the predation at such localities. The frequency, with which the Spectacled Owl was recorded in the sampled area, corroborates the view of Stotz *et al.* (1997) that this species is common in areas of central Amazonian terra firme, a fact that is still is no consensus among researchers. Our results also confirm hitherto untested occasional observations that the species prefers areas closer to water bodies (Sick 1997).

The Black-banded Owl was recorded in only three plots, all in a single hydrological micro-basin, while the Mottled Owl was present only in plots with minimal canopy opening.

Although the current study covered only one breeding season, our results demonstrate that six species of owls at RFAD, being dissimilar in body size as well as in their habitat requirements, food, and reproductive behaviors, use different micro-habitats. According to the relationships between the components of forest structure and its importance to the species, the components related to the availability of food resources were significantly associated with the occurrence and density of species of owls. This was possibly founded in the fact that they already had chicks in the nest, which also contributes to the increase in the density of species in the sampling points, as well as parents seeking food for themselves have to seek to feed their offspring. Comparing our results with those from Barros & Cintra (2009) it is indicated that the differences in study results mentioned before might be due to the use of different sampling methods, but there may be also substantial inter-annual variation in habitat preferences. Consequently, we would recommend a multi-seasonal monitoring program that includes habitat use and movement of individuals in order to determine whether the presence of individuals of various species in a given area is related to the influence of vegetation structure or might be a result of population dispersal events, with expansion of the species and occupation of territories across consecutive breeding seasons (Ritchison *et al.* 1988).

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