

Abundance of two *Dendrocincla* woodcreepers (Aves: Dendrocolaptidae) in relation to forest structure in Central Amazonia

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ABSTRACT

Few studies have been conducted to verify how the structure of the forest affects the occurrence and abundance of neotropical birds. Our research was undertaken between January 2002 and July 2004 at the Reserva Ducke, near Manaus (02°55',03°01'S; 59°53',59°59'W) in central Amazonia, to verify how the forest structure affects the occurrence and abundance of two bird species: the Plain-brown Woodcreeper *Dendrocincla fuliginosa* and the White-chinned Woodcreeper *Dendrocincla merula*. Bird species occurrence was recorded using lines of 20 mist-nets (one sample unit), along 51 1-km transects distributed along 9 parallel 8 km trails covering an area of 6400 ha. Along these transects, we placed 50 x 50m plots where we recorded forest structure components (tree abundance, canopy openness, leaf litter, standing dead trees, logs, proximity to streams, and altitude). We then related these variables to bird occurrence and abundance using multiple logistic and multiple linear regression models, respectively. We found that *D. fuliginosa* frequently used plateau areas; being more abundant in areas with more trees. On the other hand, *D. merula* occurred more frequently and was more abundant in areas with low tree abundance. Our results suggest that although both species overlap in the reserve (both were recorded in at least 68% of the sampled sites), they differ in the way they use the forest microhabitats. Therefore, local variation in the forest structure may contribute to the coexistence of congeneric species and may help to maintain local alpha diversity.

KEY WORDS

Abundance, distribution, birds, Dendrocolaptidae, *Dendrocincla*, Amazon forest.

O uso do habitat por duas espécies de arapaçus *Dendrocincla* (Aves: Dendrocolaptidae) em relação a estrutura da floresta na Amazônia Central

RESUMO

Em florestas neotropicais, poucos estudos tem sido conduzidos para verificar como a estrutura da floresta afeta o uso desse ambiente por aves. Este estudo foi realizado entre Janeiro de 2002 e Julho de 2004 na Reserva Ducke próximo a Manaus (02°55',03°01'S; 59°53',59°59'W), para verificar como a estrutura da floresta afeta a ocorrência e abundância de duas espécies de aves: o Arapaçu-pardo, *Dendrocincla fuliginosa* e o Arapaçu-da-taoca, *Dendrocincla merula*. A ocorrência das espécies de aves foi registrada com 20 redes ornitológicas (unidade amostral), dispostas em linha contínua ao longo de cada um dos 51 transectos de 1 km distribuídos ao longo de nove trilhas paralelas de 8 km em uma área de 6400 ha. Em cada transecto foram demarcadas parcelas de 50 x 50 m, para registrar alguns componentes da estrutura da floresta (abundância de árvores, abertura do dossel, folhicho, troncos mortos em pé, troncos mortos no chão, proximidade de igarapés e altitude) os quais foram então relacionados com a ocorrência e a abundância das aves através de modelos de regressão múltipla logística e múltipla linear, respectivamente. *D. fuliginosa* utiliza mais frequentemente áreas de platô, e a sua abundância foi maior em áreas com maior abundância de árvores. *D. merula* ocorreu mais frequentemente e em maiores abundâncias em áreas com baixa abundância de árvores. Os resultados sugerem que as duas espécies sobrepõem suas áreas de uso (ambas foram registradas em pelo menos 68,6% dos locais amostrados), mas elas separaram-se no modo de uso do microhabitat. Portanto, a variação local na estrutura da floresta pode contribuir para a co-ocorrência de espécies congênicas e deve ajudar a manter a diversidade alfa local.

PALAVRAS-CHAVE

Abundância, distribuição, aves, Dendrocolaptidae, *Dendrocincla*, Floresta Amazônica.

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INTRODUCTION

Habitat structure and forest heterogeneity are believed to play a key role in organizing and structuring avian communities (MacArthur *et al.*, 1966; Karr & Roth, 1971; Roth, 1976; Martin, 1985). Features of habitat structure or floristic composition can determine, among other things, availability of food, nesting sites, or refuge from predators. Due to its importance, ecologists have considered habitat features to be crucial components of birds' niches (Wiens *et al.*, 1987).

The effects of habitat heterogeneity on bird populations and communities, however, have received far more attention in temperate regions than in the tropics (MacArthur & MacArthur, 1961; Karr & Roth, 1971; Wiens, 1974; Roth, 1976; Rey, 1995), and the mechanisms that determine habitat use by bird populations in tropical rain forests are not well known.

Understanding how the structure of tropical forests vary is important to describe the bird community associated with them, and to recognize the mechanisms that allow the high species coexistence seen in these forests (Pearson, 1977; Manasse & Howe, 1983; Martin, 1985; Levey, 1988; Loisselle, 1988; Terborgh *et al.*, 1990; Naranjo, 1992). Tropical forests, however, are complex environments, and detecting exactly what components of the vegetation affect the distribution, occurrence, and abundance of birds is difficult.

Human-disturbed forests present a clear example of the importance of forest structure on the occurrence of birds. It is known that selective logging has drastic effects on the vegetation structure, by reducing or increasing tree density, tree abundance, number of dead trees, canopy opening, etc. Therefore, it is very likely that changes in bird species richness and abundance in disturbed forests are mainly due to changes in some vegetation components, which could affect the availability of food resource and microclimatic conditions (Johns, 1991).

Primary or undisturbed forests also show a relatively high degree of environmental heterogeneity. The role of this heterogeneity is mostly unexplored, but can also affect the abundance and occurrence of birds. Woodcreepers are believed to be sensitive to changes in forest structure principally when the abundance of trees is reduced (Thioly, 1992; Guilherme & Cintra 2001). Therefore, we believe that they represent a good study group to evaluate the effects of the forest environment on their distribution and abundance.

We selected two species of congeneric woodcreepers: the Plain-brown Woodcreeper (*Dendrocincla fuliginosa*) and the White-chinned Woodcreeper (*Dendrocincla merula*), which live in the middle and lower levels of lowland neotropical forests in similar types of forest, but differ in their ecology, the first being a solitary tree dweller that sometimes joins mixed-species flocks, and the second an obligate army-ant follower (Willis, 1979). We studied their abundance and occurrence in a 10,000 ha reserve in Central Amazonia, and related their distribution with

some variables of the forests, including the number of trees, number of logs, number of standing dead trees, leaf litter depth, percentage of canopy opening, the distance to the nearest stream (igarapé), and altitude.

We tested the null hypothesis of no differences between the variation on forest structure components where birds were captured, and randomly selected locations within the reserve. We believe that the variables selected may be important because i) woodcreepers depend on vertical support or tree trunks for foraging, therefore areas with more trees could be more attractive to woodcreepers; ii) the abundance of logs and snags may provide more area for foraging and nesting; iii) although woodcreepers are essentially arboreal, areas with more leaf litter may have higher arthropod abundance; iv) canopy opening allowing higher light incidence may increase plant production and attract more insects than shaded sites; v) sites near streams (igarapé) are more humid and may have higher abundance of arthropods than sites away from igarapés; and vi) altitude is directly related to soil components, which affect the whole vegetation in the area.

STUDY SITE

The study was conducted between January 2002 and July 2004 at Reserva Florestal Ducke (02° 55', 03° 01' S; 59° 53', 59° 59' W), a 10,000-ha reserve, located 30 km north of Manaus. Mean annual precipitation is 2,286 mm. The rainy season is mostly between November and May and the dry season between June and October.

In the reserve there are two drainage water-basins divided by a central ridge. Larger streams at the eastern side of the reserve run into the Amazon River tributaries, whereas streams on the western side drain into the Negro River tributaries (Ribeiro *et al.*, 1999).

The dominant vegetation is primary Terra Firme forest, which is never seasonally inundated by river fluctuations. Soils are composed of oxisols, and small streams are abundant in the area, which is highly irregular and undulated with plateaus reaching altitudes of 140 m (Ribeiro *et al.*, 1999).

METHODS

In order to record the occurrence and local abundance of *Dendrocincla fuliginosa* and *D. merula*, we sampled the forest understory using mist-nets, which we complemented with acoustic surveys in part of the reserve. Birds were captured using 20 mist-nets (12 m length, 2.5 m height, and 2.5 m mesh) positioned in a continuous line covering 240 m. The reserve has a grid of trails formed by two perpendicular sets of trails that creates 72 1-km transects, one km apart from one another, covering 6400 ha. We placed fifty-one lines of nets systematically located in the median point of these transects. Trails are numbered and marked every 100 m.

Mist-nets were opened between 6:00 am and 01:00 pm, during two consecutive days. Captured birds were identified and marked with numbered aluminum bands (CEMAVE – Center of Bird Migration, IBAMA, Brazil). Recaptured birds were not included in the analyses. Standardized bird measurements (total body length, culmen, wing, tail, tarsus, and mass) were taken using a caliper (1 mm precision) and Pesola spring scales (0.1 g precision). To standardize sampling effort, we consider each mist net line as our sample unity.

One of us (LNN) performed acoustic surveys to complement mist-netting data, sampling 22 transects already sampled with mist-nets. LNN did general surveys, where bird vocalizations were tape-recorded, and the exact location of each species was recorded. These transects were surveyed by walking through the trails slowly, and covering 1 km twice from 5:30 to 10 AM. Data obtained from these transects were later used to verify the occurrence of the bird species in question in areas already sampled with mist-nets. No playback was used during the surveys, and to avoid double counting, birds of the same species were recorded only once in the same general spot.

RECORDING THE FOREST STRUCTURE COMPONENTS

We established 50 x 50 m plots at the same sites where mist-nets were located. Within these plots, we quantified the following forest structure components and features of the landscape, including: 1) number of trees (diameter at breast height - DBH > 10cm); 2) number of logs; 3) number of snags; 4) leaf litter depth; 5) percentage of canopy opening; 6) distance to the nearest stream (igarapé); and 7) altitude.

We used the number of trees (DBH > 10 cm), logs (diameter > 20 cm), and snags, as a measurement of their abundance in the analyses. Litter depth was recorded by inserting a knife blade in the forest floor and counting the number of impaled dead leaves. We recorded the leaf litter depth on the four corners and at the center of 21 subplots of 1 m², 10 m equidistant one from another, with 20 sub-plots distributed along the sides and one at the center of each 50 x 50 m plot. The mean value of the sub-plots was used in the analyses. We recorded forest canopy openness using a Spherical Crown Densiometer (Concave – Mode C – Robert E. Lemonn, Forest Densiometer, 5733 SE Cornell Dr. – Bartlesville, OK, USA). We make four readings (north, south, east, and west) at the corners and center the plots. According to the instrument recommendations we multiplied each reading by 1.04, and the mean value of the measurements was used in the analyses. Distance to the nearest stream and altitude were collected from a topographic map already available.

STATISTICAL ANALYSES

Pearson correlation matrix was constructed to verify correlation significance among forest structure components (independent variables). In those cases where independent

variables were significantly correlated, these were used in different statistical models. We used multiple logistic regression analyses to investigate the effects of forest structure components on bird occurrence for each species (presence/absence). The effects of forest structure components on abundance of each bird species were evaluated using models of multiple linear regressions, where the dependent variable was the abundance of each bird species. These analyses were all performed using the Systat statistical package software (Wilkinson, 1998).

RESULTS

CORRELATIONS AMONG FOREST STRUCTURE COMPONENTS

To avoid using correlated variables in the same model, we included abundance of trees, logs, and snags, leaf litter depth, and distance to the nearest stream in one model, and percentage of canopy opening and altitude, in another one (Table 1).

The abundance of trees in the plots (N = 51) ranged from 64 to 228 (mean = 131.8 trees), where that of logs ranged from 5 to 38 (mean = 11.3), and of snags varied from 0 to 11 (mean = 4.9). Mean leaf litter depth in the plots varied from 1.4 to 4.6 leaves, with an overall plot mean of 3.4 leaves. The mean percentage of canopy opening varied from 2.6 to 19.4 (mean = 9.5). The altitude varied from 38.7 to 114.7 m (mean = 76.5), and the distance to the nearest stream (igarapé) varied from 0 m to 571 m (mean = 207.3 m).

OCCURENCE OF *Dendrocincla fuliginosa* AND *D. merula*

Overall, we captured 74 individuals of *Dendrocincla fuliginosa* and 53 individuals of *D. merula* along the mist-nets. *D. fuliginosa* was present in 68.6% of the mist-netting transects (ranging from 0 to 8 individuals/transect), and *D. merula* was present in 51.9% (ranging from 0 to 6 individuals/transect). In the acoustic censuses *D. fuliginosa* occurred in 11 transects, whereas *D. merula* was not recorded in any of them (Figure 1).

Sexual dimorphism is not apparent in either species, and at least 93% of *D. fuliginosa* and 91% of *D. merula* individuals were adults. In general body length measurements were similar between both species, but they differed in body mass (*D. merula* being notably larger than *D. fuliginosa*), (Table 2).

EFFECTS OF FOREST STRUCTURE COMPONENTS IN THE OCCURENCE AND ABUNDANCE OF *Dendrocincla fuliginosa*

Variations in altitude were significantly related to the occurrence of *Dendrocincla fuliginosa* (Multiple logistic regression analyses, McFadden's Rho-Squared (MRS) = 0.071, N = 51, T = 2.029, p = 0.042), indicating that *D. fuliginosa* prefers plateaus to lowland and flooded areas. The occurrence of individuals of this species was not significantly affected by the other forest structure components, such as abundance of trees (MRS = 0.077; N = 51; T = 1.300; p = 0.193), abundance of logs (MRS = 0.077; N = 51; T = 1.153; p = 0.249), abundance of snags (MRS =

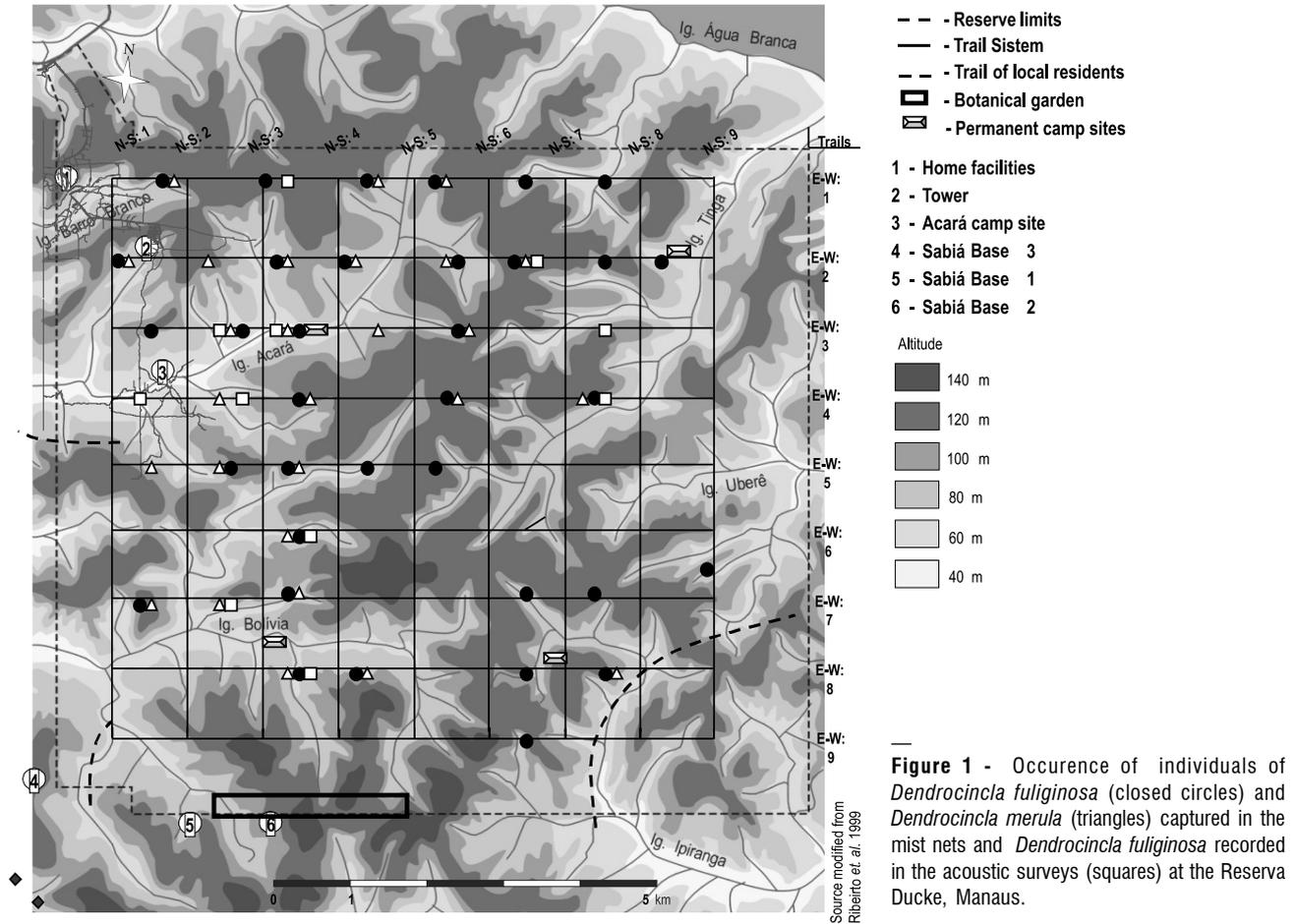


Figure 1 - Occurrence of individuals of *Dendrocincla fuliginosa* (closed circles) and *Dendrocincla merula* (triangles) captured in the mist nets and *Dendrocincla fuliginosa* recorded in the acoustic surveys (squares) at the Reserva Ducke, Manaus.

Table 1 - Pearson correlation matrix for the forest structure components, tree abundance (TA), snags abundance (SA), forest logs abundance (LA), proximity to streams (PS), leaf litter depth (LD), altitude (ALT), canopy opening (CO) recorded in areas with and without the occurrence of the two woodcreepers *Dendrocincla fuliginosa* and *Dendrocincla merula*, in Reserva Ducke, Manaus

	TA	SA	LA	LD	ALT (m)	PS (m)	CO (%)
TA	1.000						
SA	-0.093	1.000					
LA	0.128	-0.323	1.000				
LD	0.151	0.294	-0.338	1.000			
ALT (m)	0.162	-0.117	0.136	-0.388	1000		
PS (m)	-0.062	0.097	0.048	-0.136	0.534*	1.000	
CO (%)	0.245	0.520*	-0.432*	0.535*	-0.314	-0.189	1.000

* The asterisks corresponds to the statistical significance of $p < 0.05$ resulting from the Bonferroni probability matrix used to evaluate how strong and significant were the correlations among the independent variables (forest structure components).

Table 2 - Body linear dimensions and weight of *Dendrocincla fuliginosa* and *Dendrocincla merula* in Reserva Ducke, Manaus.

Species	<i>D. fuliginosa</i>	<i>D. merula</i>
	Mean ± Standard deviation	Mean ± Standard deviation
Body length (cm)	23.6 ± 2.55 (66)	21.3 ± 3.6 (43)
Culmen (cm)	3.2 ± 3.42 (69)	2.5 ± 0.4 (45)
Wing length (cm)	10.9 ± 0.9 (69)	10.3 ± 1.6 (45)
Tail length (cm)	9.2 ± 1.3 (67)	7.5 ± 1.4 (42)
Tarsus length (cm)	2.6 ± 0.4 (61)	2.7 ± 0.4 (45)
Weight (g)	38.4 ± 8.6 (69)	51.5 ± 6.3 (45)

*Number in parenthesis is sample size (N). These N values are different, because some birds escaped before we had finished the measurements of their dimensions.

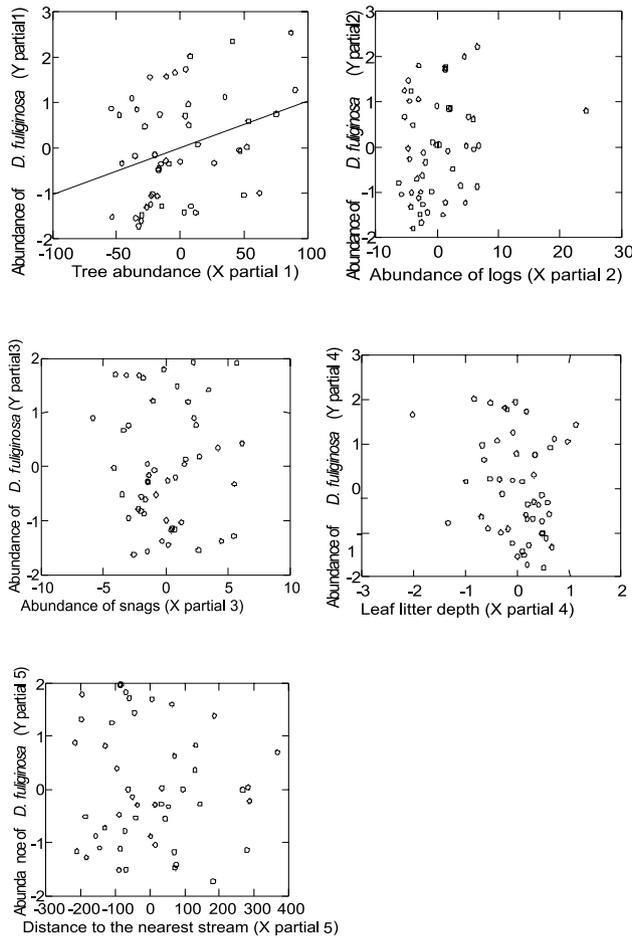


Figure 2 - Partials of multiple linear regression on abundance of *Dendrocincla fuliginosa* variation in relation to forest structure components: tree abundance, abundance of logs, abundance of snags, leaf litter depth and the distance to the nearest stream. Some numbers in the axis are negative because the partial regression represents the deviation of the expected results, if all the other independent variables are kept in their observed means.

0.077; $N = 51$; $T = -0.232$; $p = 0.816$), leaf litter depth (MRS = 0.077; $N = 51$; $T = -0.185$; $p = 0.853$), distance to the nearest stream (MRS = 0.077; $N = 51$; $T = 0.969$; $p = 0.333$) or mean percentage of canopy opening (MRS = 0.071; $N = 51$; $T = 0.536$; $p = 0.592$).

D. fuliginosa was more abundant in areas with higher abundance of trees (Multiple linear regression analysis, $R^2 = 0.151$, $N = 51$, $T = 2.303$, $p = 0.026$, Figure 2), but was not significantly affected by other forest structure components (Figures 2 and 3), such as abundance of logs ($R^2 = 0.151$, $N = 51$, $T = 1.413$, $p = 0.165$), abundance of snags ($R^2 = 0.151$, $N = 51$, $T = -0.016$, $p = 0.987$), leaf litter depth ($R^2 = 0.151$, $N = 51$, $T = -1.589$, $p = 0.119$), distance to the nearest stream ($R^2 = 0.151$, $N = 51$, $T = -0.464$, $p = 0.645$), mean canopy opening ($R^2 = 0.036$, $N = 51$, $T = -0.935$, $p = 0.354$), or altitude ($R^2 = 0.036$, $N = 51$, $T = 0.608$, $p = 0.546$).

EFFECTS OF FOREST STRUCTURE COMPONENTS IN THE OCCURENCE AND ABUNDANCE OF *Dendrocincla merula*

Dendrocincla merula occurred significantly more often in areas with lower forest tree abundance (Multiple logistic regression analysis, MRS = 0.214, $N = 51$, $T = -2.555$, $p = 0.011$). There was also an inverse relationship between mean percentage of canopy opening and bird occurrence (MRS = 0.057, $N = 51$, $T = -1.904$, $p = 0.057$), suggesting that this bird species is more frequent in more shaded areas. The occurrence of *D. merula* was not significantly affected by other forest structure components, such as abundance of logs (MRS = 0.214; $N = 51$; $T = 1.350$; $p = 0.177$), abundance of snags (MRS = 0.214; $N = 51$; $T = 0.556$, $p = 0.578$), leaf litter depth (MRS = 0.214; $N = 51$; $T = -1.188$; $p = 0.235$), distance to the nearest stream (MRS = 0.214; $N = 51$; $T = 1.003$; $p = 0.316$), or altitude (MRS = 0.057; $N = 51$; $T = -0.785$; $p = 0.433$).

We found a significant inverse relationship between the abundance of *D. merula*, and the abundance of trees (Multiple linear regression analysis, $R^2 = 0.231$, $N = 51$, $T = -2.754$, $p = 0.009$, Figure 4) and the mean percentage of canopy opening ($R^2 = 0.179$, $N = 51$, $T = -3.090$, $p = 0.003$, Figure 5).

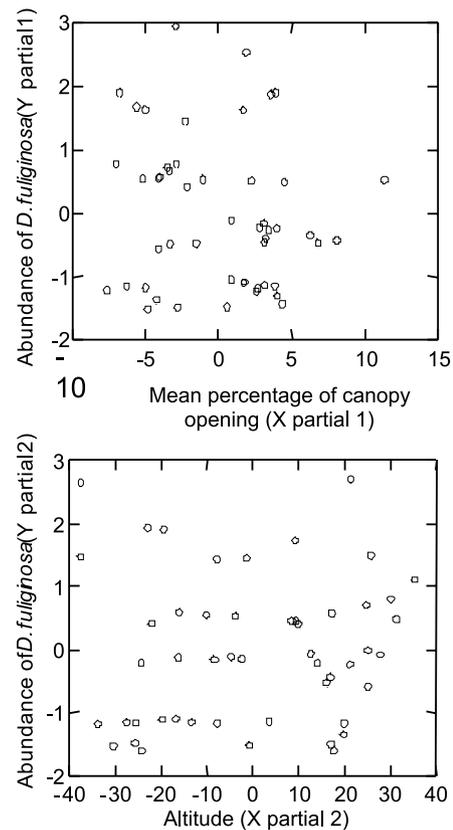


Figure 3 - Partials of multiple linear regression on abundance of *Dendrocincla fuliginosa* variation in relation to forest structure components: mean percentage of canopy opening and altitude.

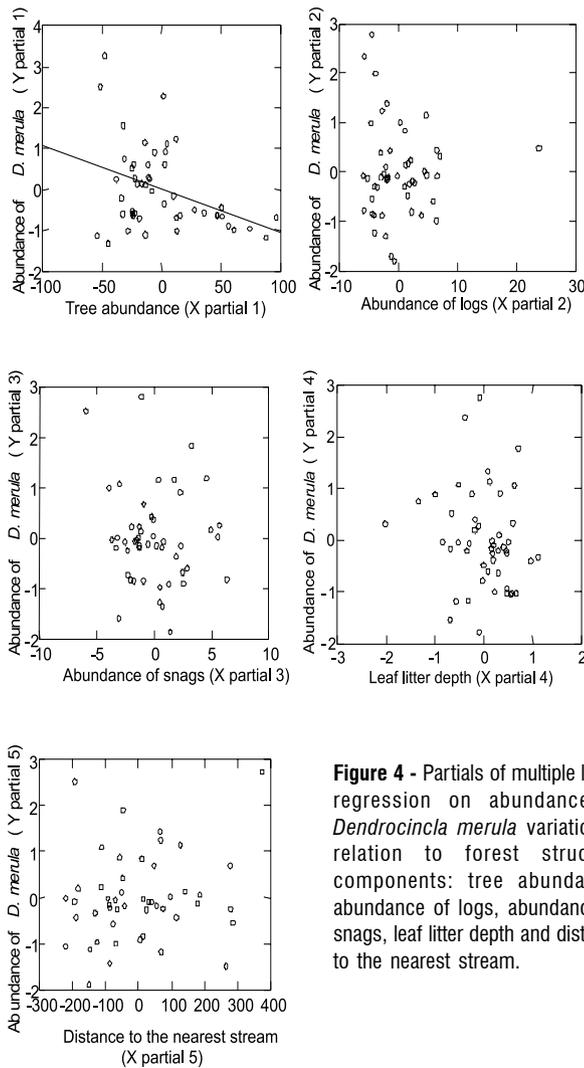


Figure 4 - Partial regression of multiple linear regression on abundance of *Dendrocincla merula* variation in relation to forest structure components: tree abundance, abundance of logs, abundance of snags, leaf litter depth and distance to the nearest stream.

The abundance of *D. merula* was not significantly affected by other forest structure components (Figures 4 and 5), such as abundance of logs ($R^2 = 0.231$, $N = 51$, $T = -0.245$, $p = 0.807$), abundance of snags ($R^2 = 0.231$, $N = 51$, $T = -0.760$, $p = 0.452$), leaf litter depth ($R^2 = 0.231$, $N = 51$, $T = -1.030$, $p = 0.309$), distance to the nearest stream ($R^2 = 0.231$, $N = 51$, $T = 1.209$, $p = 0.233$), or altitude ($R^2 = 0.179$, $N = 51$, $T = -0.313$, $p = 0.756$).

DISCUSSION

Until recently, studies have focused on bird species distribution and richness in relation to the number of forest vertical vegetation layers; the more vegetation layers, the more bird species the forest can accommodate (MacArthur & MacArthur, 1961). Although this seems to be valid for many bird communities in temperate regions, it may not apply to the tropics (Terborgh, 1985; Pearson, 1977; Bierregaard, 1990).

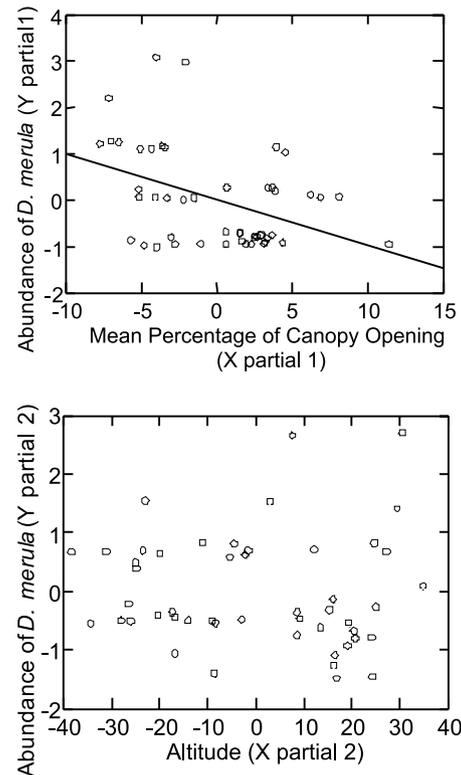


Figure 5 - Partial regression of multiple linear regression on abundance of *Dendrocincla fuliginosa* variation in relation to forest structure components: mean percentage of canopy opening and altitude.

In general, studies in neotropical forests have concentrated in analyzing factors affecting bird species richness and their distribution in relation to the various habitats (Remsen & Parker, 1983; Terborgh, 1985), and the effects of vegetation structure on bird guilds or communities (Pearson, 1975; Howe & Smallwood, 1982; Terborgh *et al.*, 1990; Loiselle & Blake, 1991). However, few studies have investigated how the natural variation in the components of habitat structure affects the distribution and abundance of individual bird species (but see Aleixo, 1999; Cintra, 1997; Guilherme & Cintra, 2001).

According to our results, the two species of *Dendrocincla* appear to concentrate their activities in the western part of the Reserve (Figure 1). The two bird species were recorded in at least 68% of the sampled sites, overlapping significantly in terms of areas used; both being recorded in at least 50% of the sampled sites (Figure 1).

Willis (1977) found that *D. fuliginosa* and *D. merula* occurred mainly in plateaus. Woodcreepers are known to be relatively sedentary, however, these two species may perform local movements and visit other areas in the reserve. Females of both species can move over areas of 2-3 km across, and even settled females raising juveniles can overlap widely on their territories and distribution, whereas non-breeding males may overlap in their home ranges (Willis 1972b, 1979).

Our results support the conclusion that some components of the landscape and the forest structure are determinants of the occurrence and abundance of the two woodcreepers species we studied. The spatial variation in topographic conditions and tree density have influenced the occurrence and abundance of *Dendrocincla fuliginosa*; and spatial variation in tree density and forest canopy opening affected *Dendrocincla merula*. This may be expected since insectivorous birds can be very selective in the type of landscapes, habitats, trees, perch positions and foraging techniques (Stouffer & Bierregaard, 1995; Cintra, 1997). Other woodcreeper species that we studied in the same area were also affected by the structure of the forest. For instance, *Glyphorhynchus spirurus* was more abundant in areas with lower density of trees, lower abundance of logs, and higher canopy opening. Similarly, *Xiphorhynchus pardalotus* was more abundant in plateaus away from streams (unpubl. data). Additionally, data from the Atlantic forest suggests that *Sittasomus griseicapillus* (a species also present in our study area) is more abundant at higher elevations (Aleixo, 1999).

The abundance of woodcreepers and other insectivorous birds such as tyrant flycatchers and antbirds has also been found to be affected by the spatial variation in the leaf litter and by the abundance of arthropods (Pearson, 1977; Pearson & Derr 1986), tree height (Cintra, 1997), species differences in diet (Chapman & Rosenberg, 1991), and competition for food and spots to forage (Pierpoint, 1986).

We found that the abundance of *D. fuliginosa* was higher in areas with more trees, suggesting that this species, by being essentially arboreal, as most woodcreepers, depends on vertical support for foraging (Orians, 1969). Areas with higher abundance of trees may be more intensively used for nesting, foraging or even looking for shelter.

D. merula occurrence was inversely related to the abundance of trees. This species has a larger body mass than *D. fuliginosa* (Table 2) and might be less efficient in flight maneuvers. This could help to partially explain why we found *D. merula* using areas with open understory in the forest. In these areas less flight maneuvers are needed during the relatively long and local movements. In addition *D. merula* is "less adept at arboreal foraging, with less stiffened rectrices than other woodcreepers and more "clumsy", sallying to substrates above the ground" (Willis, 1979; Chapman & Rosenberg, 1991).

Banks Leite (2004) studying bird community dynamics in our study area found that the composition of insectivorous bird assemblages was significantly correlated with tree-fall gaps, which may be due to the availability of illuminated spots with roosts and perches there (which probably are used for better detection of insects flying by) than in the continuous forest understory. We do not know how often woodcreepers visit gaps, and it

seems that they do not like areas with high tree density. In fact, our results suggest that *D. merula* prefers areas with lower abundance of trees and a continuous shaded understory. At Reserva Ducke, Willis (1979) observed that *D. merula* preferred the open forest undergrowth of upland woods and mention that individuals of this species concentrate in these areas to follow large ant swarms. Our results suggest that variations in altitude can also affect the occurrence of *D. fuliginosa*, indicating that this species may be using plateaus more often than the bottom of the valleys.

The lack of correlation between the occurrence and abundance of the two species of *Dendrocincla* here analyzed and other forest structure components suggest that the factors governing microhabitat use and habitat selection are complex and still need to be determined.

Our results indicate that each species of woodcreeper use the forest differently. This could be due to competition for good spots to forage or simply due to interspecific differences in microhabitat preferences (Pierpoint, 1986). At Reserva Ducke, *D. fuliginosa* forages on arthropods on the ground, leaf litter, and tree trunks (RC pers.obs), whereas *D. merula*, being an obligatory army ant follower, concentrates its foraging on catching arthropods in the leaf litter on the forest floor (Willis, 1979).

In Panama, Willis (1979) found that *D. fuliginosa* forages on the ground, but also on tree trunks, roots, stems, lianas, the surface of leaves, twigs, dead leaves, on the air, and also following army ants to catch prey. In Bolivia and Peru, *D. fuliginosa* was seen mostly from 5 to 8 m above ground (Chapman & Rosenberg, 1991). *D. merula* perches within 1 m of the ground, and 90% of its foraging consists of sallies to the ground in pursuit of arthropods fleeing ants (Willis, 1979; Chapman & Rosenberg, 1991). Interspecific aggressive behaviors have been seen between both species when following army ants; *D. merula* being dominant and displacing *D. fuliginosa* to higher perches when the availability of prey escaping from the army ants is lower (Willis, 1979).

Chapman & Rosenberg (1991) suggested that the segregation, both in foraging height and substrate use may have resulted in a shift in the proportions of main prey items, with more spiders and roaches in the diet of *D. merula* (associated with ground-foraging) and more beetles associated with foraging on trunks and vines in *D. fuliginosa*. Additionally, woodcreepers are territorial and aggressive birds, and direct interactions are frequently reported (John Terborgh, pers. com.; Willis, 1966, 1972b, 1978, 1979; RC, pers. obs.).

Dendrocincla woodcreepers are relatively long-lived species (individuals over 10 years old have been found); therefore, it is possible that they learn how to maximize the use of the forest (Snow & Lill, 1974). Although these two woodcreepers differ

in their use of substrates, foraging space and diet, their overlap in diet may represent a case of complementarity of niches (Chapman & Rosenberg, 1991).

We recorded individuals of *Dendrocincla fuliginosa* joining mixed-species flocks and flying close to 1 m above the ground, which may have facilitated their capture in the mist nets. This suggests that mist-nets represent an appropriate method for studying the occurrence of understory woodcreepers in the forest. During the study period, at least nine other woodcreeper species were captured by mist-nets, representing about two thirds of the 14 species present in the reserve (Willis, 1977).

Habitat disturbances due to deforestation may affect negatively woodcreeper populations. Thirty kilometers from our study area, Harper (1989) noticed a population decline of *D. fuliginosa* and *D. merula*, in forest fragments. In fact, woodcreepers seem to be very sensitive to changes in the forest structure, principally when tree abundance is reduced. In French Guiana, Thiolay (1992) reported that even 8-12 years after logging, the abundance of *D. fuliginosa* and *D. merula* was 7.7 times lower in logged areas than in undisturbed forest. In the Brazilian Atlantic Forest, Olivaceous Woodcreeper (*Sittasomus griseicapillus*) showed significantly higher abundance in primary forest than in areas of selective logging (Aleixo, 1999). The results of this study indicate that these three species can be affected by the forest structure when forest management is not adequate or is too intense (Thiolay, 1992; Aleixo, 1999; Guilherme & Cintra, 2001).

On the other hand, some years after fragmentation Stouffer & Bierregaard (1995) found that *D. fuliginosa* occurrence was stable in forest fragments and this probably reflects its mode of foraging at the fragment's edges and secondary vegetation (Willis, 1972a,b, 1977). Although *Dendrocincla* species are reluctant to invade areas of secondary vegetation or to cross open areas (Terborgh & Weske, 1969), they have been seen visiting the forest edge and even tree crop plantations (Willis 1972a, 1979). This behavioral flexibility may allow this species to occur where other woodcreepers were extirpated; *D. merula*, being an obligate ant-follower may be more vulnerable. Therefore, local variation in the forest structure may contribute to the coexistence of congeneric species and may help to maintain local alpha diversity.

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Appendix I - Raw data on the occurrence and abundance of *Dendrocincla fuliginosa* and *Dendrocincla merula* and the forest structure components recorded in the study.

LOCAL	DATE	A	B	C	D	E	F	G	H	I	J	K
E-W1/1/0-250	January	0	0	0	0	115	5	7	2.7	5.1	285	99.9
E-W1/950-1300	March	3	1	1	1	141	9	5	1.4	5.0	142	108.8
E-W1/2000-2300	March	1	1	0	0	82	10	7	2.8	3.1	500	110.8
E-W1/3100-3400	March	2	1	2	1	110	8	6	3.9	6.2	71	71.2
E-W1/5500-5750	August	1	1	0	0	188	6	2	3.9	13.0	71	63.4
E-W1/6600-6850	August	1	1	0	0	187	10	4	4.1	13.2	214	69.1
E-W1/7250-7500	August	0	0	0	0	115	7	2	4.0	13.1	35	44.2
E-W2/0-250	February	2	1	4	1	83	6	4	3.2	4.3	0	92.5
E-W2/1000-1250	February	0	0	2	1	151	5	11	3.0	4.7	285	82.8
E-W2/2100-2350	February	2	1	4	1	121	9	0	3.0	4.8	571	114.7
E-W2/3000-3300	March	2	1	2	1	122	11	7	3.5	5.8	339	78.1
E-W2/4500-4750	November	1	1	1	1	111	21	1	4.0	16.5	228	92.0
E-W2/5250-5500	August	1	1	1	1	119	18	4	3.9	14.9	357	96.8
E-W2/6500-6800	May	1	1	0	0	151	9	4	3.9	11.9	464	87.4
E-W2/7250-7500	August	1	1	0	0	162	15	2	4.1	13.8	0	54.4
E-W3/550-800	March	3	1	0	0	161	9	6	4.6	3.7	71	77.1
E-W3/1600-1900	March	3	1	2	1	117	15	0	3.5	4.5	214	46.3
E-W3/2250-2500	October	2	1	3	1	92	6	8	3.7	3.1	142	63.7
E-W3/3250-3500	December	0	0	0	0	64	10	2	2.7	13.2	71	58.1
E-W3/3500-3750	November	0	0	1	1	111	8	11	2.9	5.6	17	56.6
E-W3/4500-4750	November	2	1	1	1	105	8	5	4.1	4.2	357	93.6
E-W3/5500-5800	May	0	0	0	0	192	10	3	4.3	12.7	71	64.5
E-W3/6500-6800	May	0	0	0	0	118	11	2	4.1	12.6	178	38.7
E-W3/7500-7800	May	0	0	0	0	113	9	2	4.0	14.1	100	50.5
E-W4/500-800	March	0	0	0	0	98	19	3	3.9	13.0	71	46.4
E-W4/1600-1900	March	0	0	2	1	103	8	6	2.8	2.6	500	62.3
E-W4/3500-3750	October	0	0	0	0	97	6	7	2.5	2.8	142	103.8
E-W4/4300-4550	November	1	1	1	1	120	8	6	2.9	4.5	250	99.8
E-W4/5250-5500	November	0	0	0	0	196	9	3	3.8	12.7	357	92.1
E-W4/6500-6850	May	1	1	1	1	122	15	2	4.0	11.9	142	49.0
E-W5/4250-4500	October	1	1	0	0	185	9	3	4.0	11.3	128	95.3
E-W5/3250-3500	November	2	1	0	0	201	9	2	3.3	19.3	128	98.1
E-W6/1500-1800	August	0	0	0	0	113	17	4	4.2	14.7	214	52.6
E-W6/2500-2800	August	1	1	1	1	130	16	9	3.9	14.0	178	65.6
E-W7/500-800	April	3	1	1	1	117	13	2	3.5	15.1	9	45.9
E-W7/1500-1800	July	0	0	2	1	135	17	4	3.7	13.5	286	74.7
E-W7/2500-2800	August	1	1	1	1	113	14	2	4.0	15.3	285	81.2
E-W7/5500-5800	July	2	1	0	0	151	14	11	3.4	10.1	357	100.6
E-W7/6500-6800	July	3	1	0	0	228	12	11	2.8	10.5	142	84.5
E-W8/2500-2750	April	8	1	5	1	87	22	4	3.8	15.3	285	56.2
E-W8/3500-3750	April	3	1	1	1	108	17	3	3.8	14.6	142	50.2
E-W8/5500-5800	July	4	1	0	0	211	11	5	2.8	9.9	285	97.5
E-W8/6500-6800	July	4	1	6	1	185	14	11	3.3	8.6	142	40.5
E-W9/6500-6800	July	2	1	0	0	188	9	8	3.0	6.9	250	97.5
E-W9/7350-7600	September	0	0	0	0	151	10	8	3.3	8.6	142	97.8
E-W9/5250-5500	September	2	1	0	0	109	11	7	3.3	7.2	0	63.9
E-W4/2500-2750	January	2	1	2	1	107	38	0	3.2	12.2	357	103.0
E-W5/1500-1750	January	2	1	1	1	123	7	3	2.7	2.9	286	95.9

Appendix I - Continuation

LOCAL	DATE	A	B	C	D	E	F	G	H	I	J	K
E-W5/500-750	January	0	0	2	1	84	5	7	1.7	4.5	71	53.5
E-W5/2500-2750	January	3	1	2	1	128	6	3	2.9	3.9	143	83.3
E-W1/4000-4250	January	1	1	1	1	99	5	9	2.8	6.5	500	97.8

A = Abundance of *Dendrocincla fuliginosa*; B = Occurrence of *Dendrocincla fuliginosa*; C = Abundance of *Dendrocincla merula*; D = Occurrence of *Dendrocincla merula*; E = Abundance of tree; F = Abundance of forest logs; G = Abundance of snags; H = Mean leaf litter depth; I = Mean percentage of canopy opening; J = Distance to the nearest stream (m); K = Altitude (m)

