Local-scale spatial variation in diversity of social wasps in an Amazonian rain forest in Caxiuanã, Pará, Brazil (Hymenoptera, Vespidae, Polistinae)

Orlando Tobias Silveira[1], Suzanna de Sousa Silva[1], Jorge Luis Gavina Pereira[1] & Ingrid da Silva Tavares[2]

[1]Museu Paraense Emílio Goeldi, Coordenação de Zoologia, Av. Perimetral 1901, 66077–830 Belém-PA, Brazil. orlando@museu-goeldi.br
[2]Coordenação de Botânica.

ABSTRACT. Local-scale spatial variation in diversity of social wasps in an Amazonian rain forest in Caxiuanã, Pará, Brazil (Hymenoptera, Vespidae, Polistinae). Polistine wasps are important in Neotropical ecosystems due to their ubiquity and diversity. Inventories have not adequately considered spatial attributes of collected specimens. Spatial data on biodiversity are important for study and mitigation of anthropogenic impacts over natural ecosystems and for protecting species. We described and analyzed local-scale spatial patterns of collecting records of wasp species, as well as spatial variation of diversity descriptors in a 2500-hectare area of an Amazon forest in Brazil. Rare species comprised the largest fraction of the fauna. Close range spatial effects were detected for most of the more common species, with clustering of presence-data at short distances. Larger spatial lag effects could also be identified in some species, constituting probably cases of exogenous autocorrelation and candidates for explanations based on environmental factors. In a few cases, significant or near significant correlations were found between five species (of *Agelaia*, *Angiopolybia,* and *Mischocyttarus*) and three studied environmental variables: distance to nearest stream, terrain altitude, and the type of forest canopy. However, association between these factors and biodiversity variables were generally low. When used as predictors of polistine richness in a linear multiple regression, only the coefficient for the forest canopy variable resulted significant. Some level of prediction of wasp diversity variables can be attained based on environmental variables, especially vegetation structure. Large-scale landscape and regional studies should be scheduled to address this issue.

KEYWORDS. Neotropical wasps; polistine faunas; spatial analysis; biodiversity; forest habitats.

RESUMO. Variação na diversidade de vespas sociais em escala local numa floresta pluvial amazônica em Caxiuanã, Pará, Brasil (Hymenoptera, Vespidae, Polistinae). Vespas sociais são importantes nos ecossistemas neotropicais pela abundância e diversidade. A maioria dos inventários recentes não têm dedicado atenção aos atributos espaciais dos espécimes coletados. Dados espaciais são importantes para estudar e mitigar impactos sobre ecossistemas naturais e proteger espécies. Este artigo descreve e analisa em escala local padrões espaciais de registros de coleta, investigando também a variação espacial de descritores de diversidade numa área de 2.500 hectares de floresta amazônica no Brasil. Espécies raras constituíram a maior parte da fauna. Efeitos espaciais de curta distância foram detectados para a maioria das espécies mais comuns, com agregação de registros em distâncias até ca. 800 metros. Hiatos espaciais maiores foram identificados para algumas espécies, constituindo provavelmente autocorrelação exógena e candidatos a explicação por fatores ambientais. Nalguns casos, foram encontradas correlações significativas (ou quase) entre cinco espécies (de *Agelaia*, *Angiopolybia* e *Mischocyttarus*) e três variáveis ambientais estudadas: distância ao riacho mais próximo, altitude topográfica e tipo de copa da floresta. A associação desses fatores com variáveis de biodiversidade foi geralmente baixa. Quando utilizados como preditores de riqueza de Polistinae numa regressão linear múltipla, apenas o coeficiente para tipo de dossel florestal resultou significativo. Alguma predição mostra-se possível sobre variáveis de biodiversidade com base no conhecimento de condições ambientais, especialmente estrutura da vegetação. Estudos devem ser agendados para tratar do assunto em escalas espaciais mais amplas.

PALAVRAS-CHAVE. Vespas neotropicais; faunas de polistíneos; análise espacial; biodiversidade; habitats florestais.

Polistine social wasps are important components of Neotropical ecosystems due to their ubiquity and diversity, as well as by the complex interactions with other organisms. They are mainly predators of other insects, especially Lepidoptera caterpillars, but also collect various natural materials including wood fibers and nectar (Gobbi *et al.* 1984; O'Donnell 1995; Raveret-Richter 2000; Richards 1971, 1978). Some studies have also shown them to be important as flower visitors and potential pollinators of plant species (Granja e Barros 1998; Heithaus 1979; Hermes & Köhler 2006; Sühs *et al.* 2009). Social wasps are among the better studied groups of insects in Brazil. However, until recently, most survey work has been conducted as qualitative museum inventories, without special concern for the controlling of benchmark aspects as collecting effort or area explored. The work of Adolpho Ducke (1904, 1905, 1907) represents a landmark pioneering initiative of a resident scientist in the Amazon region in surveying one of world's richest wasp faunas. The wasp fauna of the Brazilian Amazon is currently known to comprise 20 genera and about 200 species, representing nearly two-thirds of the total Brazilian wasp fauna (Carpenter & Marques 2001; Silveira 2002, Silveira *et al.* 2008).

Several authors have recently published wasp inventories based on protocols amenable to replication in different areas so that more comparable information is expected to result from these studies (Corbara *et al.* 2009; Elpino-Campos *et* *al.* 2007; Gomes & Noll 2009; Kumar *et al.* 2009; Morato *et al.* 2008; Santos *et al.* 2007a; Santos *et al.* 2007b; Santos *et al.* 2009a; Santos *et al.* 2009b; Silva & Silveira 2009; Silva-Pereira & Santos 2006; Silveira 2002; Tanaka Jr. & Noll 2011; Togni 2009). The collecting methods usually employed active searches for colonies and individuals, Malaise traps, automatic traps with some attractive material, or a combination of baits with active netting of attracted individuals. Besides being able to compare sites, another advantage of using protocols based on replicate samples has been the possibility of estimating upper limits for local species richness (Cowell & Coddington 1994). With few exceptions, however, these studies have not dedicated attention to the spatial attributes of the collected specimens or the spatial dimension of the data. Most studies have been carried out at landscape scales, sometimes involving comparisons between habitats in adjacent patches or along transects – while more explicit spatial designs and methods have generally been underutilized.

Spatial data on biodiversity are important components of the information needed to study and mitigate anthropogenic impacts on natural ecosystems and protect species (Williams *et al.* 2002). Many basic questions of conservation planning depend on information about biodiversity distribution: where certain species occur or are more abundant, where there are more species or endemic taxa, where certain taxa are more vulnerable to extinction, and how intrinsic population and environmental factors interact in time and space to affect species distributions (Boakes *et al.* 2010; Diniz-Filho *et al.* 2009; Elith & Leathwick 2009; Fritz *et al.* 2009; Guisan & Thuiller 2005). Modern techniques for mapping biodiversity or for modeling species distributions have been developed through advances in the past few decades in remote data acquisition, computational technologies, and analytical methods that can elucidate spatial relationships of biological processes and patterns at various scales (Fortin & Dale 2005; Philips *et al.* 2006; Rangel *et al.* 2006; Rosenberg & Anderson 2011; Storch & Gaston 2004). Of particular importance are methods for studying different kinds of spatial autocorrelations in species distributions and identifying possible associations with environmental and/or geographic variables (Diniz-Filho *et al.* 2003; Fortin *et al.* 2002; Legendre 1993).

The present paper describes and analyzes local-scale spatial patterns in the collecting records of social wasps, as well as the spatial variation in diversity descriptors in a 2500 hectare area of Amazon rain forest in Brazil.

MATERIAL AND METHODS

The study was supported by PPBio (Program of Research on Biodiversity), an inter-institutional scientific program for the study of Amazonian biodiversity sponsored by the Brazilian government. A major goal of the program is creation of a research network to assess biological diversity at different scales, and understanding the processes that influence species distribution in the Amazon rainforest. This is pursued by adoption of a unified spatial design and structured inventory protocols (see below).

Study area. The Caxiuanã PPBio plot is a 25 km^2 forest area located in the "Floresta Nacional de Caxiuanã" (FLONA Caxiuanã; Fig. 1), a large conservation reserve with 300.000 hectare distant 400 km from Belém, Pará state, Brazil (Silva & Silveira 2009). The climate is Köppen's tropical humid type (Ami) (Costa & Morais 2002; see also figure 5). The studied site is covered mainly by undisturbed high "terra firme" forest (Fig. 2). However, variably sized clearings exist resulting from the falling of large branches and trees (Fig. 3 B), often with subsequent proliferation of vines. The forest is seasonally flooded at some places by the overflow of small forest streams (Fig. 3 C).

Field collecting procedures. Three expeditions were made to the study area along the year 2006: March-April (16 days; rainy season), July-August (18 days; beginning of dry season) and October-November (10 days; peak of dry season), adding to a total of 44 days of fieldwork. Samples were collected in a square plot of 5x5 km, traversed by a system of two perpendicular sets of six 5-km trails intercrossing at intervals of one kilometer in grid-like fashion, resulting in a total of sixty 1-km trail segments which were treated as sampling units (Fig. 4). Each 1-km trail section in the plot was marked every 100 m, thus allowing the recording of the approximate point in the trail system where wasp individuals or colonies were found. All sixty trail segments were surveyed for wasps by three to four collectors who explored the vegetation up to five meters on each side of the trail (and to a similar height above it, by visual inspection of the lower tree branches). The entire PPBio plot was explored in a progressive manner, with 12 trail samples being surveyed during the first expedition (the northeastern sector of the 5x5 km plot) 28 trail sections during the second expedition (mainly the northwestern sector), and 20 trail sections during the third expedition (southern sector) (Fig. 4).

During the first expedition (training phase), the collectors spent up to four or five hours on each trail section; trail sections were covered in about two hours during the other two expeditions. Malaise traps (Townes model) were placed at 26 points (for 10-day periods), with 22 of them being located at trail intersections separated by 1000 m (Fig. 4). Four traps were set up at internal points along two trails in the southern sector of the plot. Three of these were relatively close (200 m) to previously sampled intersections, while the fourth was near an unsampled intersection. Ten traps were set in the northern sector of the plot during the first expedition (rainy season); 10 and 6 traps were set in the western and southern sectors of the plot, respectively, during the second and third expeditions (at the beginning and peak of the dry season).

Altitudinal data. Topographic data were made available by the project PPBio. Terrain elevations in the 5x5 km plot ranged from 19 to 47 meters. The mean altitude values for each of the sixty 1-km sampling trail sections are represented by the environmental variable ALTITUD.

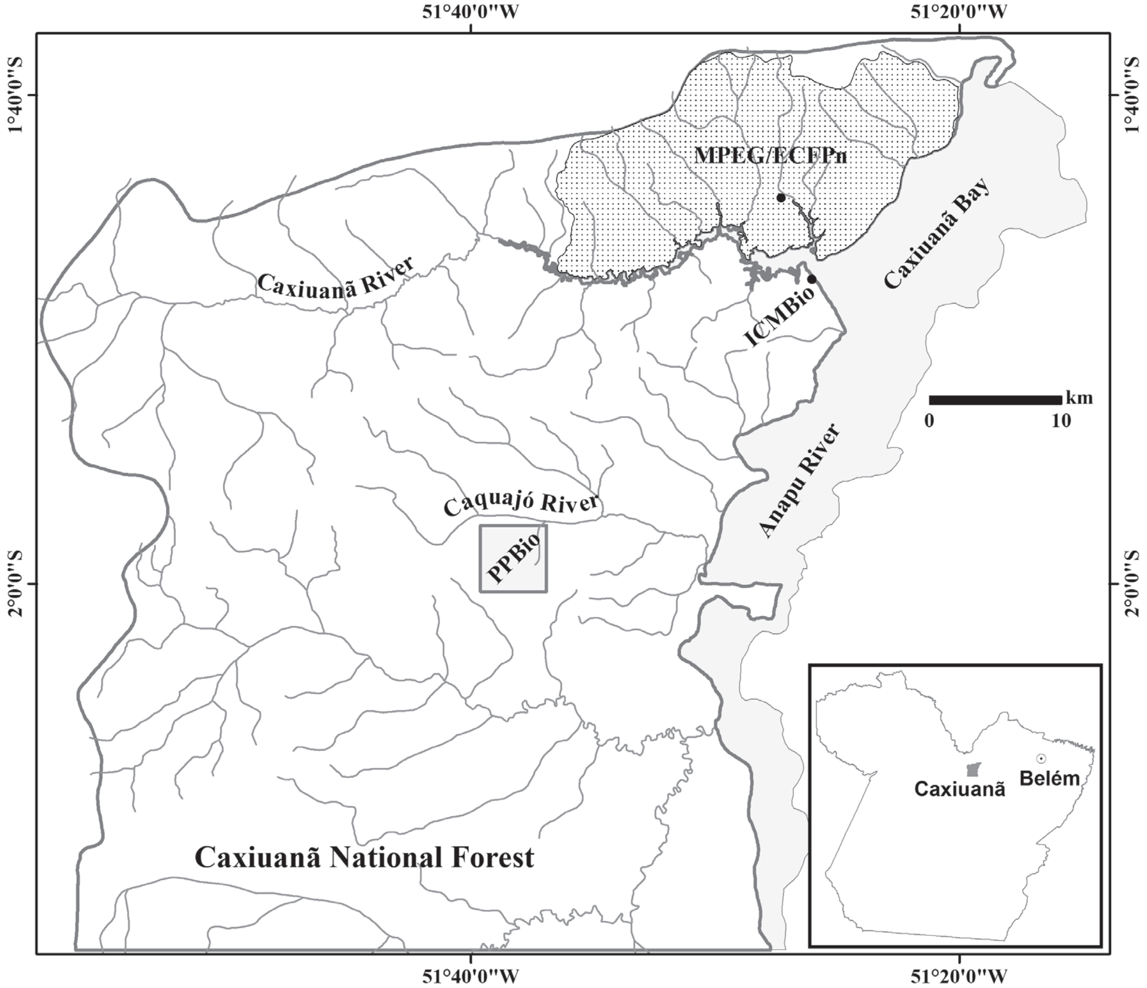


Fig. 1. Maps showing localization of the studied area (PPBio plot) within the Caxiuanã National Forest (FLONA Caxiaunã), in Pará state, Brazil. The larger drainage element to the right of the figure is the Anapu River, which forms the Caxiuanã Bay. The PPBio plot is located about 30 km south of the "Estação Científica Ferreira Penna" – ECFPn station studied by Silveira (2002).

Drainage. The drainage data of the PPBio plot were collected from "TOPODATA – Geomorphometric Database of Brazil", available at <http://www.dsr.inpe.br/topodata/>, based on data generated by the Shuttle Radar Topography Mission (SRTM). The SRTM data, originally with 90 m resolution, were interpolated to produce information on terrain altitude with a 30 m resolution. Based on field observations, the 35 m quota was defined as the upper limit of altitudes indicating the occurrence of streams. Polygons of areas below the 35 m quota were superimposed onto horizontal curvature data from TOPODATA and the lines digitalized following the lowest values – which then theoretically represented courses of water flow (Fig. 4). The least distance between the center of a sampling trail and the nearest stream was found with the ArcGIS tool "Near" (ESRI 2004). Values indicating the proximity of samples to forest streams represent the environmental variable NEARHYDR.

Land Cover. A land cover classification was produced for part of the area of the FLONA Caxiuanã, including the PPBio plot, based on Landsat satellite imagery and using a supervised approach by regions (Fig. 2). The study area is dominated by Upland Forest – Heterogeneous Canopy (67.6%) that, together with the Homogeneous Canopy type (8.3%), occupies the highest areas (~46 m). Areas with Slope Forests (8.0%) and Secondary Regrowth (1.6%) occupy intermediate topographic altitudes (~42 m). Water-associated vegetation (12.0%) occupies the lower topographic levels (~39 m). In the PPBio plot itself, where the collecting activities were undertaken, Upland Forest – Heterogeneous Canopy (61.7%) and Homogeneous Canopy (26.2%) predominated. In addition to differences in spectral responses, there were also differences in terrain elevation and slope. The environmental variable HETCAN% describes the proportional area (of a 1000 x 200 m^2 rectangle centered along the trail) of each sampling trail with the spectral properties of a heterogeneous canopy.

Phytosociological studies are in progress in the area and are expected to confirm the satellite data classifications. Preliminary field observations revealed that the PPBio plot has a forest canopy approximately 25 to 30 meters tall, with

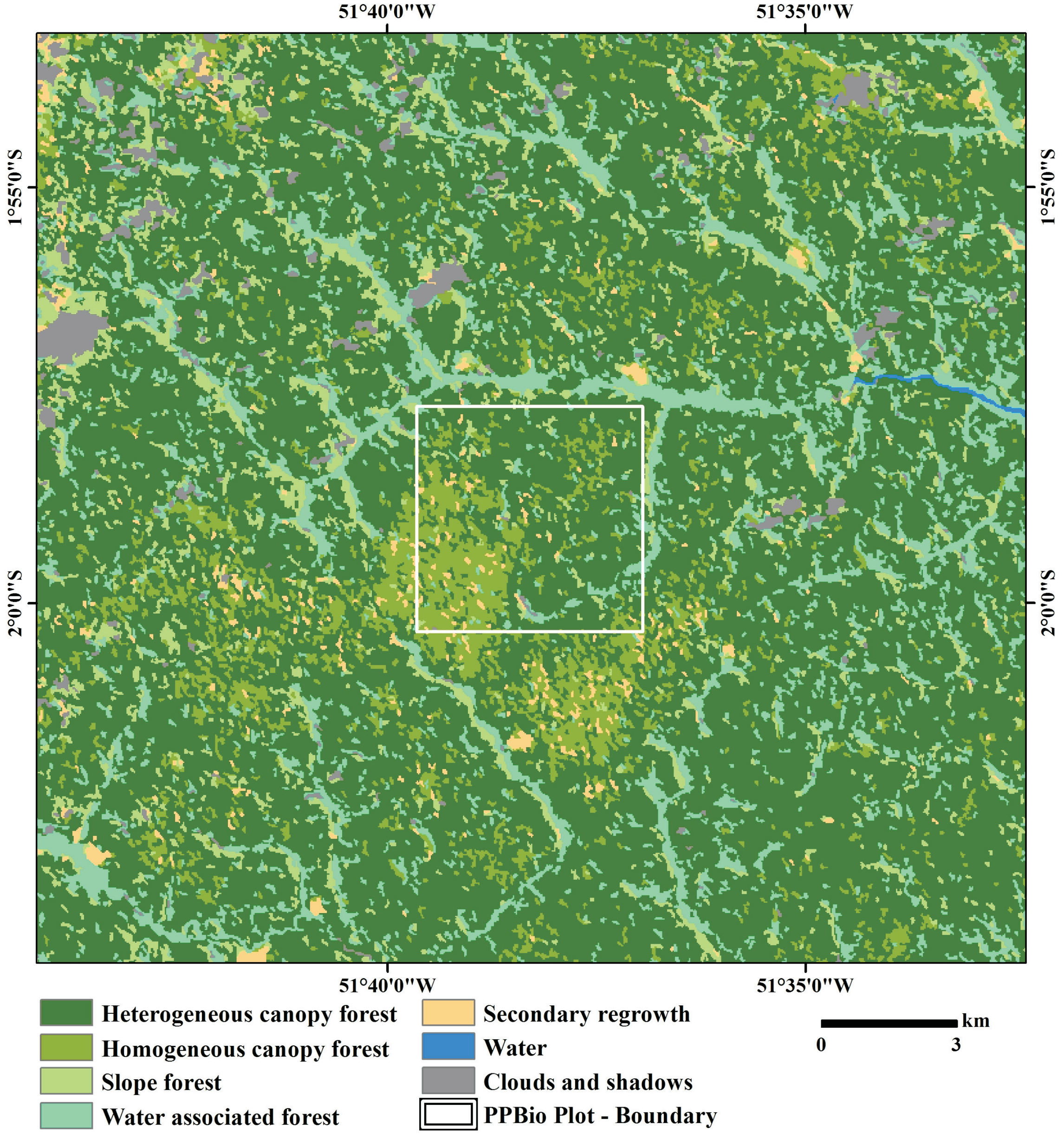


Fig. 2. Land cover classification at the studied 5x5 km Caxiaunã PPBio plot (small quadrate area) and surrounding areas. Two principal spectral classes of land cover prevail within the plot: Heterogeneous canopy and Homogeneous canopy. The drainage element running parallel to the northern border of the plot is the Caquajó River.

emergent individuals with heights varying from 35 to 45 meters, such as *Eschweilera* sp., *Manilkara huberi* (Ducke) A.Chev., *Couratari guianensis* Aubl., *Swartzia polyphylla* D.C., *Hymenolobium petraeum* Ducke. The understory is generally open with some palm trees, principally *Astrocaryum gynacanthum* Mart. and *Bactris* sp. The most abundant vines are *Doliocarpus dentatus* (Aubl.) Standl., *Bauhinia guianensis* Aubl., and *Derris* sp. Phytophysiognomies resembling open areas (secondary regrowth with abundant vines) cover relatively large areas, with great abundances of vines, especially in the southern sector of the plot. Recruitment of resident species appears to be intense, and these plants form an intermediate stratum from 15 to 25 meters tall.

Spatial distributions of wasp records. Metric coordinates of the collecting locations of individual wasps and colonies within the grid system are expressed as either UTM coordinates (for input in the ARCGis program (ESRI 2004) and map preparation), or as Cartesian coordinates (in other programs).

Data analysis. The distributions of species records were treated either as primary maps for visual inspection, or grouped by sample in the various analyses performed and thus organized as the biodiversity variables: ABUND: numbers of polistine records per sample; RICHNESS: total polistine species per sample; RAgAn: number of species of the epiponine clade (*Agelaia*+*Angiopolybia*); RMischo: number of species of the genus *Mischocyttarus*; RPolybia num-

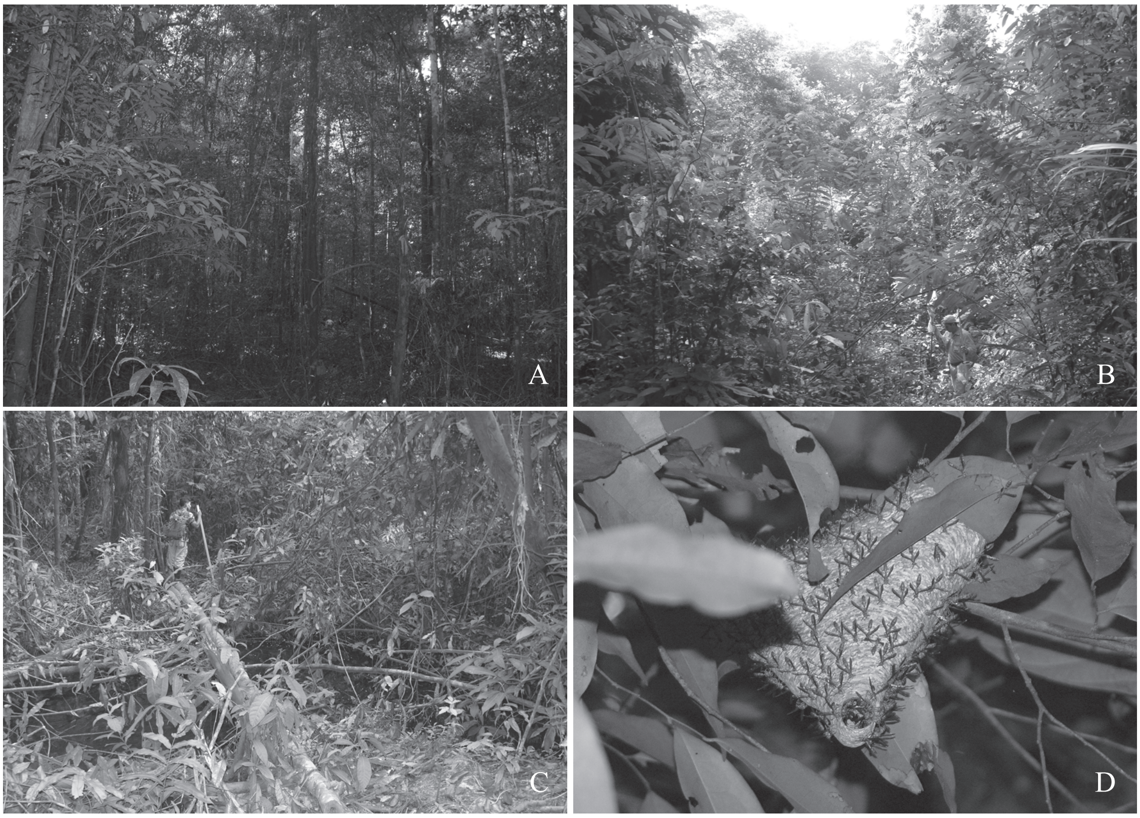


Fig. 3. Photographs showing different aspects of forest vegetation in the studied area in the FLONA Caxiuanã. A- undisturbed high forest; B- open forest with natural clearings; C- vegetation around a small seasonal forest stream (igarapé), with a fallen tree serving as bridge for collectors; D- detail of tree branch with nest of *Angiopolybia pallens*.

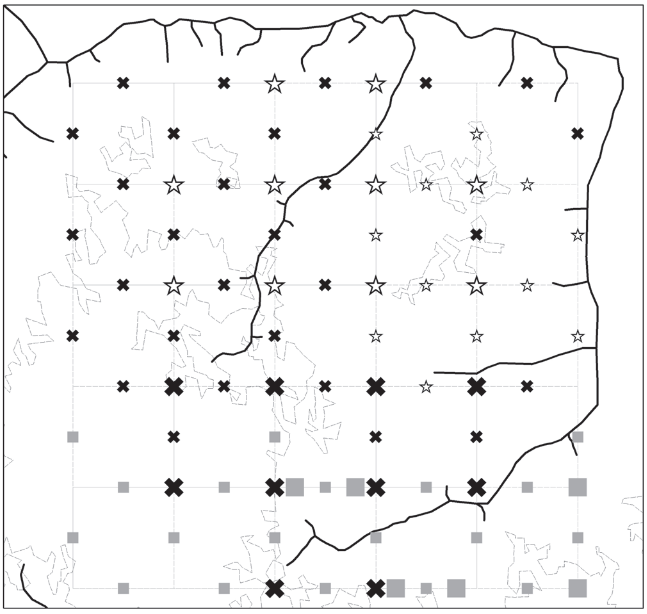


Fig. 4. Scheme of the grid system at the 5x5 km PPBio plot with indication of drainage and major spectral types of forest canopy; different symbols indicate the epoch of the year a given 1000m trail was sampled in 2006 (first expedition: March-April, rainy season; second expedition: July-August, beginning of dry season; third expedition: October-November, dry season). All 60 trails were actively searched for wasps; larger symbols refer to 26 Malaise traps, most installed at intersections of the grid. Expedion: ☆ 1 ✖ 2 ■ 3.

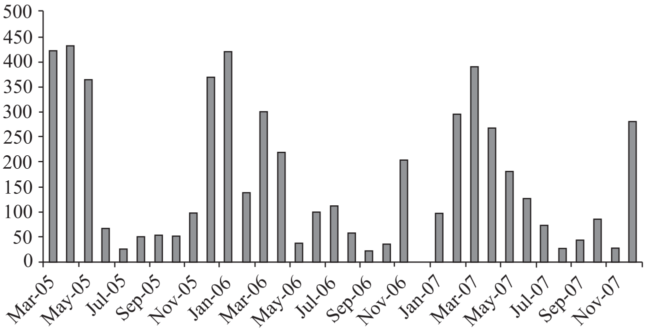


Fig. 5. Monthly precipitation (mm) in Caxiuanã for the years 2005, 2006 and 2007 (data from the LBA Project; provided by W.J.S Souza).

ber of species of the genus *Polybia*. Two subsets of 25 sampling trails in the PPBio plot with maximum richness (63 species; excluding two species captured only in Malaise traps; Silva & Silveira 2009) were considered in the analyses as richness shortcuts. These sample subsets were iteratively identified using computer software (DIVA-GIS; Hijmans *et al.* 2005) as containing the largest numbers of species in as few samples as possible, and eventually the total number of species found in the studied area.

Sample rarity scores. Rarity analysis as described by Lobo *et al* (2008) was used to calculate a synthetic rarity score (RI) for each sample in the PPBio plot. This variable is a linear combination of three rarity indexes: Rarity value (R; the sum, by sample, of the reciprocals of the absolute frequencies of each of the constituent species); Mean Rarity (RM; R divided by the number of species in a given sample); Numbers of rare species in a given sample (RS). The synthetic scores for each of the sixty samples were calculated using principal component analysis of the correlation matrix of the three rarity indexes cited above, and are expressed as the variable RARITY.

Join Count Analysis. Spatial patterns for binary data (presence/absence) in redefined sampling units were assessed by join count statistics (Fortin & Dale 2005). Join counts can be computed for different classes of distances between pairs of points; i.e. two points are considered "connected" and included in the test if the distance separating them falls within the limits of a specified distance class. Join count analyses (only 1x1 matches) were made with the program PASSAGE (Pattern Analysis, Spatial Statistics and Geographic Exegesis; Rosenberg & Anderson 2011; see also Durães *et al.* 2005 for another study of insect ecology using this program) to investigate the occurrence of spatial autocorrelations in intraspecific data grouped as presence/absence in 100 m trail segments.

The distances between these smaller trail segments (as measured from their centers) were used as the criterion to include pairs of samples into each of five distance classes. This finer-scale grouping of the recorded data (100 m; within the resolution limits of the spatial measurements made in the plot) permits the detection of autocorrelations at short distances that may be related to colony territorial effects or migratory processes.

Autocorrelation Analysis. Spatial autocorrelation is a measure of the lack of randomness of a variable due to spatial structuring (Fortin *et al.* 2002; Rosenberg & Anderson 2011). Moran's I coefficient computes the degree of correlation between the values of a variable as a function of spatial lags. Plotting Moran's I against distance classes results in a spatial correlogram. In the present study, spatial correlograms were used to investigate spatial structuring among biodiversity variables and environmental factors (considering the original 1-km samples), with Moran's coefficients being computed for five distance classes using the program SAM (Spatial Analysis in Macroecology; Rangel *et al.* 2006; see also Sabu *et al.* 2008 for another study of insect ecology using this program). The centers of the trails were considered reference points for measuring the distances between samples (i.e. data obtained from linear trail segments were treated as referring to points).

Association between biodiversity variables and environmental factors. In these analyses, samples were always 1 km trail segments. Intraspecific variables describing species occurrences refer simply to their presence/absence in samples, and the calculated correlations in these cases are point biserial coefficients (computed only for species recorded in at least three samples). In relations involving continuous and count variables, computed correlations are Pearson's product-moment coefficients and significance tests used Dutilleul's correction for spatial autocorrelation as implemented by the program SAM (Rangel *et al.* 2006). Data obtained in Malaise traps were also included in some analyses as a type of true point-sample information.

Linear multiple regression analyses were performed using environmental factors as predictor variables and the general abundances of polistines (ABUND) and the numbers of species (RICHNESS) as response variables; Principal component analysis was used to reduce the dimensions of the correlation matrices.

RESULTS

Intraspecific patterns. Species names cited here can be found in their complete form in Appendix 1. A taxonomic list and other information concerning the wasp fauna collected in the Caxiuanã PPBio plot can be encountered in Silva & Silveira (2009); voucher specimens were deposited in the Museu Goeldi, Belém (MPEG). Sixty-five species of social wasps were encountered in the PPBio plot, raising to one hundred the number of known polistines in the region around the FLONA Caxiuanã. The spatial distributions of wasp records collected by active searches and Malaise traps are presented in Figures 6-8, including species with different levels of abundance, ranging from very abundant species such as *Agelaia fulvofasciata* (Fig. 6A) and *Angiopolybia pallens* (Fig. 6B) to uncommon species such as *Polybia platycephala* (Fig. 8F).

Uncommon and rare species comprised far greater proportions of the wasp fauna, with forty species (62%) being recorded in only one to three places in the entire 5x5 km plot. The two collecting methods agreed fairly well with regards to the distribution patterns of the most common species of the genera *Agelaia* and *Angiopolybia*, but disagreed markedly with respect to species of *Mischocyttarus* and *Polybia,* the two most speciose genera of local Amazonian faunas. While reasonable numbers of *Mischocyttarus* species were found with certain regularity along the trails, most were absent from Malaise traps. Some species of *Polybia*, such as *P. liliacea* (Fig. 8A) and *P. emaciata* (Fig. 8D), demonstrated inverse tendencies, being rarely found or even absent during active searches but better represented in Malaise captures. Figures 8G and H present general summaries of these two genera from active searches – yielding two different and rather surprising data sets given the fact that *Polybia* colonies are generally of much larger sizes.

Some degree of clustering of the records obtained by active search in trails is immediately apparent in many cases, especially among species with intermediate numbers of records. Table I displaying the results of join count analysis shows significant evidence of positive short-distance autocorrelation (in the first distance class up to 791 meters) for most of the more abundant species.

For some species, test results with alternating positive and negative sign in the near and far distance classes respec-

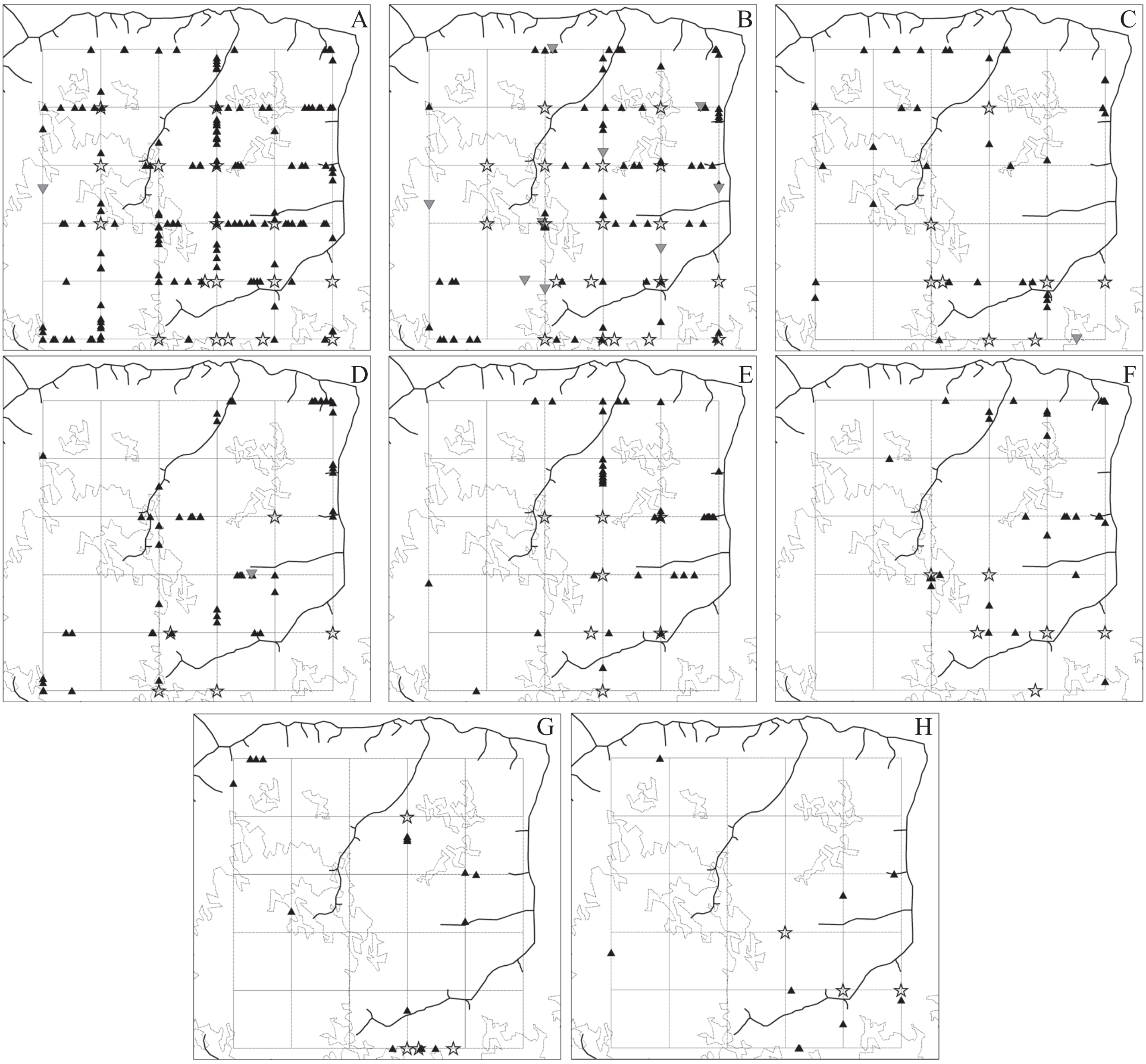


Fig. 6. Distribution of wasp occurrences in the PPBio plot, with indication of drainage and spectral types of canopy; A- *A. fulvofasciata*, B. *An. pallens*, C- *A. pallipes*, D- *A. angulata*, E- *An. paraensis*, F- *A. centralis*, G- *A. testacea*, H- *A. myrmecophila*; colonies are larger inverted grey triangles; stars are captures in Malaise traps. Figure 11. Biplot with two first axes of principal component analysis (above; PC1, horizontal; PC2, vertical) performed on correlation matrix of five environmental/biodiversity variables (NEARHYDR, ALTITUD, HETCAN%, RICHNESS, ABUND). Graph at bottom-right for analysis (pc1', pc2') substituting partial richnesses of clades (*Agelaia*+*Angiopolybia*), *Mischocyttarus*, and *Polybia* (RAgAn; RMischo; RPolybia); 60 samples represented according to their scores; correlations between variables and principal axes as directions indicated by lines; eigenvalues and loadings in associated table; filled squares are samples on southwestern quadrant of the plot; open squares on northwestern quadrant; crosses on eastern side; open circles are samples along the central meridian crossing the plot.

tively suggest a clinal pattern, as in *Agelaia fulvofasciata* (Fig. 6A), *Angiopolybia pallens* (Fig. 6B), *Angiopolybia paraensis* (Fig. 6E) and *Agelaia centralis* (Fig. 6F). In other cases, significant positive effects detected at both near and far distances appear to be in agreement with the visual aspects of some distributions, with several small clusters spread over the plot as in *Agelaia angulata* (Fig. 6D), *Agelaia testacea* (Fig. 6G), *Agelaia angulicollis* (Fig. 7C) and *Mischocyttarus carbonarius* (Fig. 7D).

Two additional impressions emerge from the inspection of intraspecific data in figures 6-8. The first one is that there were generally more wasp records on the eastern side of the plot. The second refers to eventual associations of small clusters of records with forest streams, which seem more evident in species like *Agelaia angulata*, *Agelai testacea* and *Agelaia angulicollis* (Figs. 6 D, G; 7C). The eastern side of the plot has a prevalence of vegetation with spectral properties suggesting a slightly higher and more heterogeneous canopy, while the western side corresponds to a watershed region where the forest canopy is more homogeneous. Correlation analyses of intraspecific data with environmental variables, however, resulted in significant or near significant coefficients for only five species (Table II and Appendix 1). *Agelaia angulata*, *Angiopolybia pallens,* and *Mischocyttarus duckei* showed significant or near significant negative correlation with the variable expressing the distance to the nearest forest stream (NEARHYDR). Some of these species showed similar results in respect to the variable expressing mean topographic altitude (ALTITUD), in this case being also included the species *Agelaia centralis*. *Agelaia angulicollis* demonstrated a similar negative relationship with distance to the nearest stream, but only if information from Malaise traps was added to the dataset (see Fig. 7C). Only three species (*Angiopolybia pallens*, *Agelaia centralis* and *Agelaia cajennensis*) presented significant or near significant correlation with the variable expressing canopy spectral properties (HETCAN%). The addition of Malaise data, however, altered the correlation probabilities for some of these species.

Interspecific patterns. The spatial distributions of species richness and general abundance of polistines along the sampling trails in the PPBio plot are presented in Figures 9A

Fig. 7. Distribution of wasp occurrences in the PPBio plot, with indication of drainage and spectral types of canopy; A- *L. dorsata*, B. *M. lecointei*, C- *A. angullicollis*, D- *M. carbonarius*, E- *P. dimidiata*, F- *P. cattillifex*, G- *M. sylvestris*, H- *M. oecothrix*; colonies are larger inverted grey triangles; stars are captures in Malaise traps.

Table I. Results of Join Count analysis (1x1 matches) of occurrence data (active search only) of thirteen wasp species amongst the most frequent in the PPBio plot, with records resumed as presence/absence in 100 m trail segments. Column headings show the upper limits of distance classes in meters. Symbols + and – indicate respectively significant positive and negative departures (at 0.05 level) from the expected join count for a given distance class.

Species	Distance classes																			
	791	1077	1300	1570	1851	2036	2193	2393	2609	2847	3027	3185	3395	3640	3904	4100	4362	4719	5120	7001
A. fulvofasciata	+	+			+	+						–					–		–	
A. pallens		+			+						–	–	–			–				
A. pallipes				–								–				+				
A. angulata	+		–								–		+					–		+
A. paraensis	+	+	+	+			+		–					–	–				–	
A. centralis	+					+			+							–		–		
A. testacea	+					–	–					+								+
A. myrmecophila		+																		
A. angullicollis	+														+					
M. carbonarius	+																	+	+	
A. cajennensis		+											+							
M. nr. mallaris	+													+						
P. gorytoides																+				

Table II. correlations of environmental factors with variables representing diversity aspects of polistine wasps, and with presence/absence descriptors for five species, along 1–km sampling trails in the PPBio plot (active search only). Symbols * and # indicate respectively significance and near significance (at 0.05 level); Dutilleul's correction for spatial autocorrelation was used, except with the intraspecific variables and "diversity shortcuts".

	NEARHYDR	ALTITUD	HETCAN%	RICHNESS	ABUND	RARITY
NEARHYDR	–	–	–	–	–	–0.03
ALTITUD	0.78*	–	–	–	–	0.07
HETCAN%	–0.50*	–0.50*	–	–	–	0.09
RICHNESS	–0.28#	–0.23	0.42#	–	–	**0.52***
ABUND	–0.17	–0.20	0.33	0.72*	–	0.19
RAgAn	–0.35*	–0.34*	0.38#			0.02
RMischo	–0.06	–0.06	0.36*			0.63*
RPolybia	0.001	0.07	–0.02			0.45*
An. pallens	–0.31*	–0.30*	0.24#	–	–	–
A. angulata	–0.26*	–0.30*	0.02	–	–	–
A. centralis	–0.17	–0.33*	0.36*	–	–	–
A. cajennensis	0.01	–0.08	0.24#	–	–	–
M. duckei	–0.25#	–0.06	0.16	–	–	–
Shortcut1	–0.08	0.07	–0.01	0.37*	0.22#	**0.75***
Shortcut2	–0.02	0.08	0.03	0.37*	0.22#	**0.74***

NEARHYDR: least distance between the center of a sampling trail and the nearest stream; ALTITUD: mean topographic altitude along a sampling trail; HETCAN%: area proportion (of a 1000 x 200 m^2 rectangle centered along a trail segment) with spectral properties indicating heterogeneous canopy; RICHNESS: number of species; ABUND: number of wasp records; RAgAn; RMischo, RPolybia: respectively the number of species for the clade *Agelaia*+*Angiopolybia*, and genera *Mischocyttarus* and *Polybia*; RARITY: rarity score of a sampling trail, computed as the "synthetic rarity index" (RI) of Lobo *et al.* (2008); shortcut (1 and 2): approximate optimum subset of 25 trails with total species numbers equaling that of the entire plot.

and C. The visual aspects point to larger numbers in the eastern sector of the plot in both cases; the Malaise data appear to indicate much the same type of distribution in this respect (Fig. 9B). The fact that richness and abundance data are not randomly distributed over the plot was also confirmed by autocorrelation analyses. In the correlograms of figures 10A and B, both variables show clear signs of spatial structuring, with rather low but significant Moran's coefficients for most of the distance classes.. The pattern of positive autocorrelation within near distances classes and negative autocorrelation at far distances is consistent with the clinal aspect (east-west) observed in figures 9A and C. A similar correlogram (but with a much stronger signal) resulted for the variable measuring the spectral properties of forest canopy (Fig. 10C). The correlograms for the variables describing distance to the nearest stream and mean topographic altitude were similar to each other (Figs. 10D and E), with alternating low positive and negative coefficients that probably reflect the distribution of hydrographic elements in the plot (larger streams are rather regularly separated by distances of about 3000m).

The results of the correlation analyses of the biodiversity variables and environmental factors are summarized in Table II (Pearson coefficients). The interpretations of the probability tests may have been affected by the lack of normal distri-

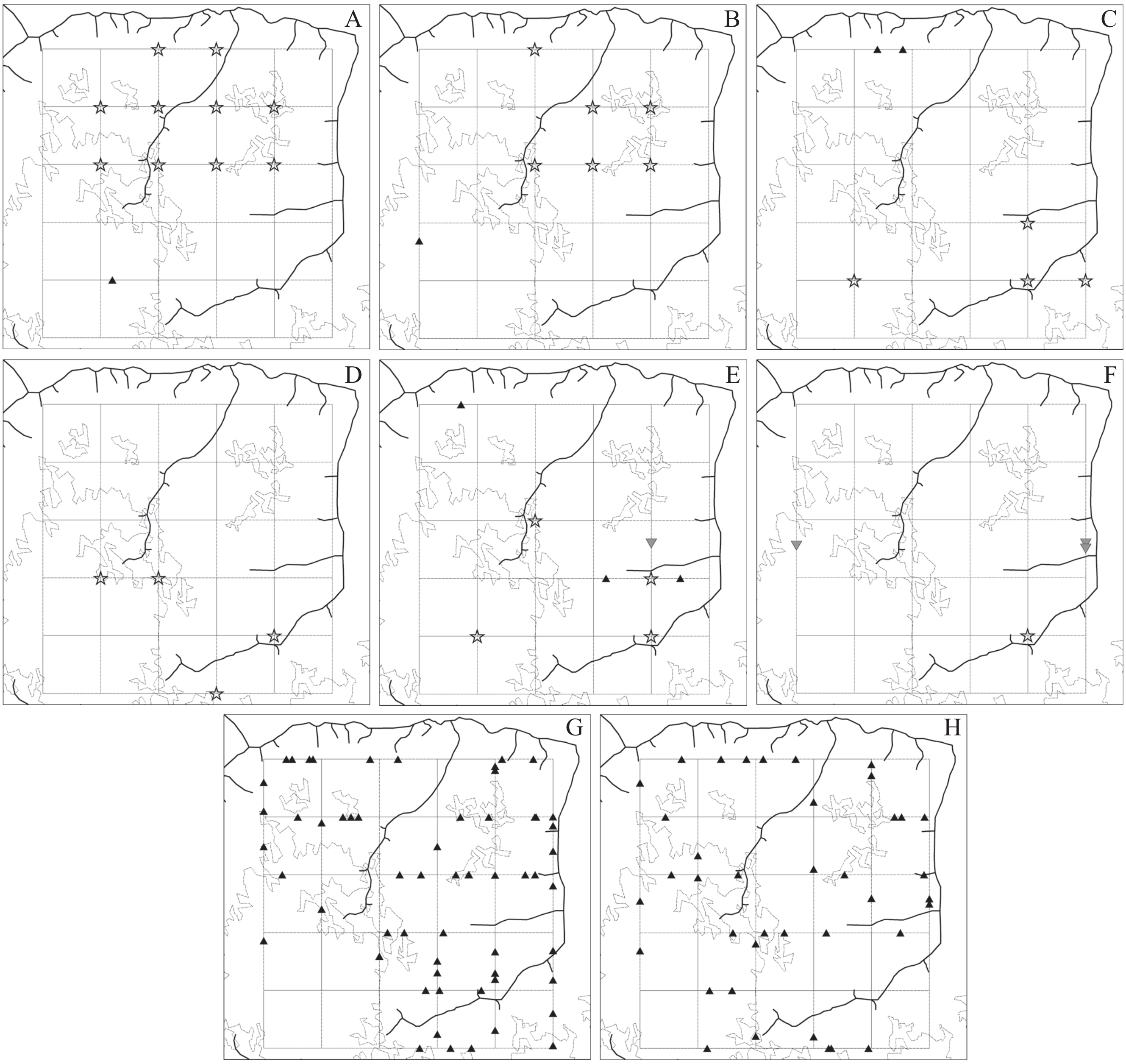


Fig. 8. Distribution of wasp occurrences in the PPBio plot, with indication of drainage and spectral types of canopy; A- *P. liliacea*, B. *P. striata*, C- *P. singularis*, D- *P.emaciata*, E- *P. gorytoides*, F- *P. platycephala*; colonies are larger inverted grey triangles; stars are captures in Malaise traps; G and H – total records (active search only) of *Mischocyttarus* and *Polybia* species respectively.

butions. Only the variable for mean topographic altitude passed the Shapiro-Wilk normality test, while the richness variables for polistines (RICHNESS) and for the *Agelaia*-*Angiopolybia* clade (RAgAn) showed near normality. The remaining variables showed right skewed distributions in most cases. However, Spearman coefficients resulted quite similar in values and in significance tests. The richness of polistines showed generally rather low correlations with the environmental factors (but slightly higher with respect to the canopy spectral properties variable HETCAN%), and often with losses of statistical significance after using Dutilleul's correction for spatial autocorrelation. The general abundance of wasp records (ABUND) gave similar results, but with the correlation coefficients being even lower. As would be expected, richness and general abundance were highly correlated with each other. When species richness was split and investigated from the perspectives of the three major clades (*Agelaia*+*Angiopolybia*, *Mischoyttarus*, and *Polybia*; comprising together about 80% of the species found in the plot), the results were remarkably different. Only the *Agelaia*-*Angiopolybia* clade (RAgAn) demonstrated a pattern of correlations similar to that found for total polistine richness, with even a slightly higher signal with respect to the variables related to streams and terrain elevation. On the other hand, *Mischocyttarus* richness (RMischo)

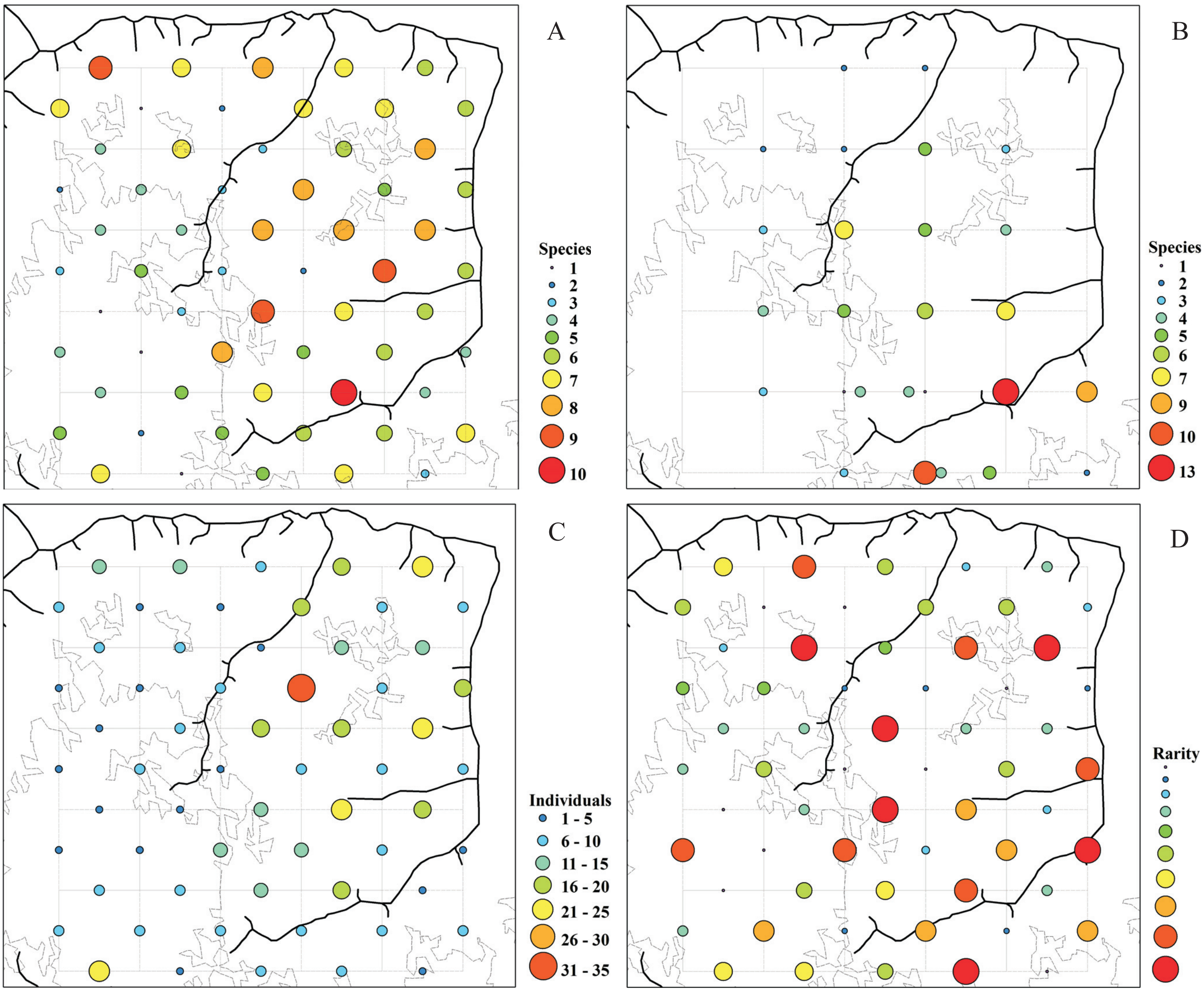


Fig. 9. Spatial distribution of biodiversity variables for the social wasp fauna in the PPBio plot, with indication of drainage and major spectral types of forest canopy. A- species richness in 60 sampling trails; B- richness in 26 Malaise traps; C- numbers of wasp records in 60 sampling trails; D- samples' synthetic rarity scores.

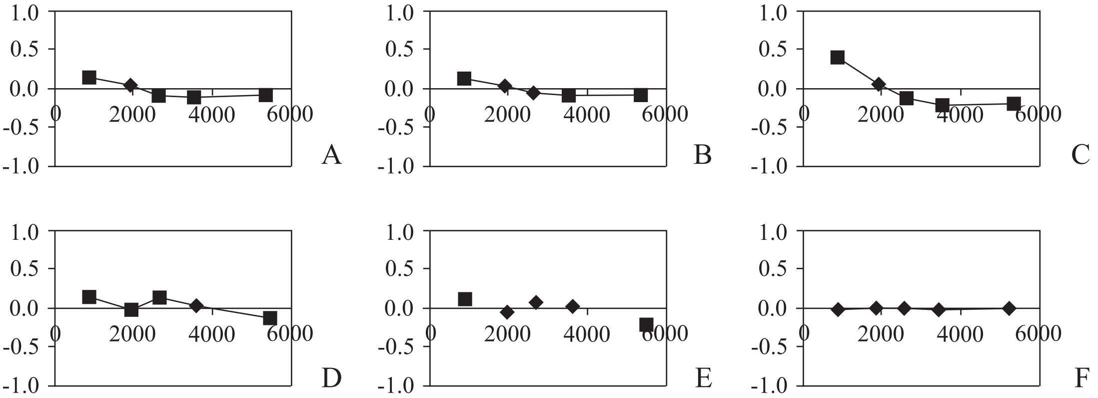


Fig. 10. Spatial correlograms with Moran's autocorrelation coefficients (I) for five distance classes, indicating spatial structuring of variation in biodiversity variables and environmental factors in the PPBio plot; A- ABUND: number of wasp records; B- RICHNESS: number of polistine species; C- HETCAN%: area proportion (of a 1000 x 200 m^2 rectangle centered along a trail segment) with spectral properties indicating heterogeneous canopy; D- NEARHYDR: least distance between the centre of a sampling trail and the nearest stream; E- ALTITUD: mean topographic altitude; F- RARITY: sample's score of rarity; coefficients marked with a "x" are significant at 0.05 level.

showed near zero correlations with these variables, although it had a firm significant correlation with the forest canopy variable. Quite remarkably, the richness of the genus *Polybia* (RPolybia) showed no evidence of correlations with any of the environmental factors, with all coefficients having near zero values.

The relationships between biodiversity variables and environmental factors can also be visualized in Figure 11, which presents plots of principal component analyses performed on the correlation matrices of the variables examined. The subspace encompassed by the first two axes includes approximately 80% of the total variation, so that the angles between the lines representing the variables reasonably indicate their bivariate relations. The relational positions between the samples and the variables in the biplot show notable agreement with their actual physical-spatial relationships. Of particular interest is the graphical representation of the decomposition of polistine RICHNESS into the three variables for the less inclusive clades *Mischocyttarus*, *Agelaia*-*Angiopolybia*, and *Polybia*. In agreement with the bivariate correlations, the variable RMischo is nearly orthogonal to NEARHYDR and ALTITUD while showing some relationship to HETCAN%. In contrast, RPolybia is almost orthogonal to HETCAN%, although some level of association with the other two environmental variables is apparent in this subspace (all bivariate correlations involving RPolybia are near zero). The relationships with RAgAn are in good agreement with bivariate correlations.

The distribution of the variable expressing the synthetic rarity score of the sample (RARITY) is presented in Figure 9D. A distinct pattern cannot immediately be perceived and, in fact, no evidence of spatial effects could be detected by autocorrelation analysis (Fig. 10F). The correlogram for this variable has low non-significant Moran's coefficients for all of the distance classes. The rarity variable showed moderately significant correlations only with the richness variables (except for the *Agelaia*-*Angiopolybia* clade, which had a near-zero correlation coefficient). Remarkably, rarity scores showed high point biserial correlations (around 0.75) with the two 25-sample richness shortcuts found by Silva & Silveira (2009) for the wasp fauna of the Caxiuanã PPBio plot.

Mean numbers of species and records per sample are presented in table III. Differences are larger and significant when the first expedition is compared to the other collecting periods, but only for samples obtained by active search. No significant differences were observed between the three periods in the means of Malaise samples. Data collected previously with the same methods in nearby locations at the "Estação Científica Ferreira Penna" (ECFPn; see Fig. 1), as published by Silveira (2002), showed no significant seasonal differences in the mean numbers of of polistine species and individuals collected either along forest trails or in Malaise traps (Table IV). Differences in mean richness and abundance along trails of the first expedition relative to the other two expeditions in the PPBio plot were further investigated by linear multiple regression (Table V). These analyses tested the effects of two additional variables, one referring to the quantity of precipitation during months with collecting activities (based on data from the LBA project for the year 2006; see figure 4), and the other referring to approximate differences in collecting effort between expeditions as given by the number of hours spent per sample (EFFORT; Table V). The results shown in table V demonstrate that the greater

Table III. Means and standard deviations of wasp diversity variables for each collecting period and season during the year 2006 in the PPBio plot in the FLONA Caxiuanã; MLRICHNESS and MLABUND are respectively the number of species and individuals in Malaise traps; other variables as in table II; symbol * refers to significant differences between means across periods (rainy period: March-April; transition period: July-August; dry period: October-November).

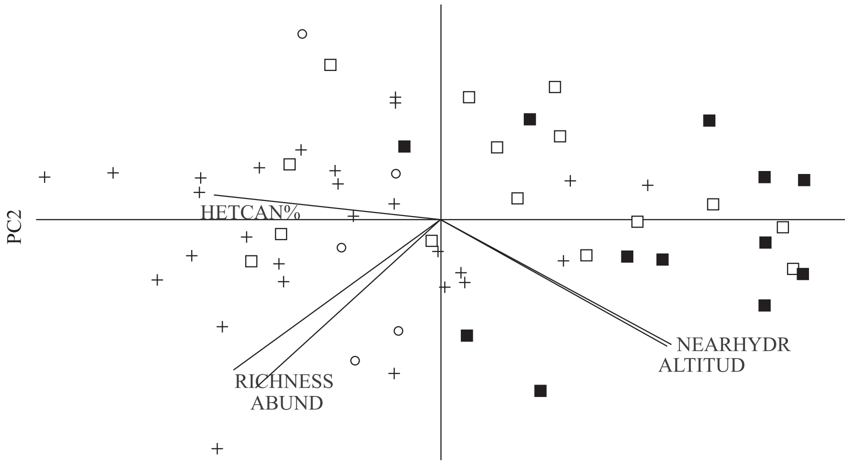
Period	rainy	transition	dry	All periods
Active Search	(n = 12)	(n = 29)	(n = 19)	(n = 60)
Richness *	6.8 (1.80)	4.8 (2.38)	5.3 (2.16)	5.3 (2.31)
RAgAn	4.2 (1.53)	3.0 (1.55)	3.4 (1.68)	3.4 (1.62)
RMischo	1.2 (0.72)	1.0 (1.20)	0.7 (0.75)	0.9 (0.99)
RPolybia	1.1 (0.90)	0.5 (0.63)	0.6 (0.90)	0.6 (0.80)
remaining spp	0.4 (0.69)	0.2 (0.49)	0.6 (0.61)	0.4 (0.58)
Abund *	16.4 (8.07)	8.0 (5.58)	8.3 (5.11)	9.8 (6.79)
Malaise	(n = 10)	(n = 10)	(n = 6)	(n = 26)
MLRICHNESS	3.6 (1.78)	5.2 (4.32)	5.0 (2.37)	4.5 (3.09)
MLABUND	8.6 (5.12)	9.4 (6.10)	11 (5.22)	9.5 (5.40)

Table IV. Means and standard deviations of wasp diversity variables for different seasons in the ECFPn, in the FLONA Caxiuanã, during the years 1998 and1999; MLRICHNESS and MLABUND are the species richness and number of individuals in Malaise traps; other variables as in table II; differences between means across periods are non-significant (rainy period: March/1998 and April-May/1999; transition period: June-July/1998; dry period: November/1998) (see also Silveira 2002).

Period	rainy	transition	dry	All periods
Active Search	(n = 8)	(n = 9)	(n = 6)	(n = 23)
Richness	4.6 (2.55)	3.3 (2.50)	5.3 (1.75)	4.3 (2.40)
Malaise	(n = 20)	(n = 10)	(n = 10)	(n = 40)
MLRICHNESS	4.3 (3.77)	5.7 (4.92)	4.2 (2.25)	4.6 (3.75)
MLABUND	2.0 (1.30)	2.7 (1.64)	2.3 (1.42)	2.25 (1.41)

Table V. Statistical results of linear multiple regression analyses using respectively the general abundance of polistines (number of records; ABUND) and the number of species along trail samples (RICHNESS) as the response variables; as predictor variables, HETCAN% refers to differences in spectral properties of forest canopy in the PPBio plot, and EFFORT refers to the approximate difference in hours spent by collectors per sample between different expeditions.

Variable	Standardized Coefficient	Std. Error	t	P Value
ABUND				
Constant	0	2.677	-1.021	0.311
HETCAN%	0.235	0.029	2.058	0.044
EFFORT	0.44	1.921	3.855	<0.001
RICHNESS				
Constant	0	0.956	1.945	0.057
HETCAN%	0.352	0.01	2.931	0.005
EFFORT	0.242	0.686	2.014	0.049



	PC1	PC2
eigenvalue (%)	53.1	26.3
NEARHYDR	0.77	-0.50
ALTITUD	0.77	-0.50
HETCAN%	-0.77	0.09
RICHNESS	-0.70	-0.60
ABUND	-0.63	-0.67

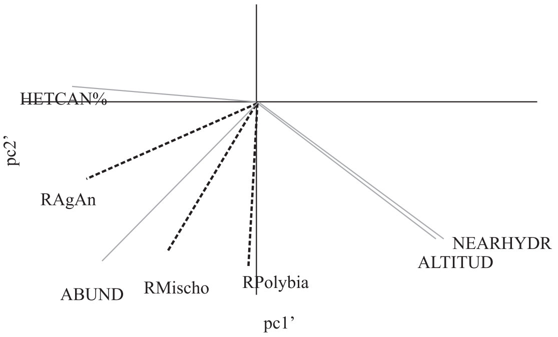


Figure 11. Biplot with two first axes of principal component analysis (above; PC1, horizontal; PC2, vertical) performed on correlation matrix of five environmental/biodiversity variables (NEARHYDR, ALTITUD, HETCAN%, RICHNESS, ABUND). Graph at bottom-right for analysis (pc1', pc2') substituting partial richnesses of clades (*Agelaia+Angiopolybia*), *Mischocyttarus*, and *Polybia* (RAgAn; RMischo; RPolybia); 60 samples represented according to their scores; correlations between variables and principal axes as directions indicated by lines; eigenvalues and loadings in associated table; filled squares are samples on southwestern quadrant of the plot; open squares on northwestern quadrant; crosses on eastern side; open circles are samples along the central meridian crossing the plot.

(doubled) time dedicated by collectors per sample in the first expedition (and not the quantity of rainfall) was responsible for the mean number of wasp records being about twice as large during this period, with a corresponding slightly larger richness. The kind of forest canopy (HETCAN%) is the other variable that significantly accounts for variation in wasp diversity between expeditions, and across the PPBio plot. Residuals of these regressions showed low non-significant Moran's autocorrelation coefficients for all distance classes.

DISCUSSION

Kind and limitation of the spatial data. Populations of Neotropical polistine social wasps occupy the space by way of three kinds of socially integrated agents and their constructs. Colonies are formed by highly mobile flying adult individuals (1) that perform a series of tasks in their home range to sustain and care for immature colony mates that are practically immobile in stationary nests that serve as homes/nurseries (2). Additionally, in the tribe Epiponini, at times of colony division or in response to predators or other kinds of disturbance, a mobile colonial group or swarm (3) can travel a variable distance across the area until a new nesting site is found (Jeanne 1991). In independent founding Polistini and Mischocyttarini, new colonies are founded by solitary females or by (comparatively) very small groups formed mostly of sisters (Reeve 1991; Gadagkar 1991).

While individual foraging wasps are commonly seen while in flight, epiponine swarms are comparatively infrequent, and the wasp nests themselves are usually cryptic and difficult to find, especially in the rain forest interior, so that foraging individuals are more easily recorded by wasp collectors (see figures 6–8). Maps showing colonies would be an ideal type of representation of a species' occupation of an area at small scales (informing the spatial variation in colony abundances). On the other hand, the occurrence of a foraging wasp individual is an indisputable indication of the presence of a nearby mother-colony, and maps of individual records may be considered partial instantaneous representations of a species' distribution in a given locality. However, because of the spatially clumped structure of social groups, these maps would only provide a distorted picture of the spatial variations of species abundance. Variation in the number of detected individuals along a transect will be greatly affected by the pattern of proximities of colonies to each location on the transect line, more specifically by the distance to the nearest colony or cluster of colonies. Large numbers of individuals detected at a given point may simply indicate closer proximity to one or quite a few mother-colonies. For points separated by small distances, this results in spatial autocorrelation caused by colonial territoriality (as in figures 6A, B, D, E, etc.; see also table I).

The above situation seems to be even less certain in the case of epiponine species that have very large colonies with many foraging individuals utilizing the space around the nest (see Zucchi *et al.* 1995 about extremely large colonies of *Agelaia vicina* (de Saussure, 1854) in southeastern Brazil). While this situation might not be a complicating factor in respect to the question of "which species are locally more abundant?" (or which species cause larger ecological impacts), it could often lead to false impressions in regard to the question "where is a given species more abundant?". Another problem with mapping foraging individuals is that the different location records will not be simultaneous, and if the temporal lag becomes more accentuated in virtue of the normal logistic limitations encountered during field expeditions (especially in large areas like the Caxiuanã PPBio plot) it may result in the distributional data being scattered over time (if sampling progress is spatially unordered) and more susceptible to the effects of colony migration/extinction, or being clustered (if sampling is spatially ordered) and thus susceptible to complicating seasonal effects (and to the effects of colony migration/extinction) (*e.g.* Fig. 4).

Rarity. An outstanding feature of the wasp fauna present in the Caxiuanã PPBio plot is the local rarity of most species. Histograms of either species frequency or abundance showed quite abrupt transitions from the most abundant to uncommon and rare species (see Silva & Silveira 2009). Silveira (2002) surveyed a larger area (ECFPn) some 30 km north of the PPBio plot finding similar results with respect to the number of rare species. Skewed rank-abundance distributions are the norm in biological communities (Magurran & Henderson 2003), but is the extensive rarity in these forest wasp faunas a reasonable approximation of their real abundance profiles, or an artifact of inefficient collecting methods?

The method of active searches along trails used in this survey can be characterized as a line-census method (Ohgushi *et al.* 1998; Silveira 2002), in which searching activity is undertaken during a single pass through the environment at relatively low speed (under daylight conditions), even though the target objects are of limited visibility, especially if they sit at great heights above the ground. This method is not expected to be highly efficient in surveying wasp species that nest or forage in the forest canopy, or that make highly cryptic nests, or that are nocturnal. Malaise traps, on the other hand, are passive capture devices typically set to operate at ground level at a single point for relatively long periods of time. If stationarity can to some extent be compensated for its prolonged operation time, capture efficiency would be expected to be dependent to a large extent on the target species' behavior. For example, in figures 6–8, data from Malaise traps are in most cases concurrent with results of active search, but for some species they can otherwise significantly change one's ideas on distribution/abundance, as for *Agelaia angulicollis* (Fig. 7C), and principally *Polybia liliacea*, *P. striata*, *P. singularis*, *P. emaciata*, and *P. gorytoides* (respectively Figs. 8A, B, C, D, E). Extended trapping time and/or baiting could possibly compensate for the low detectability of some taxa, but the available results are not yet conclusive as to the cost/benefit aspects of these methods. While taking into account the great difference in size of regional faunas, it is interesting to note that the numbers of species (per sample) collected along several months along baited transects of variable lengths (sugar solution, Gomes & Noll 2009; Tanaka Jr. & Noll 2011; fruit juice, processed fish meat, Togni 2009) in semideciduous forests and "Mata Atlântica" (considering only core transects representing the typical habitats) in southeastern Brazil were not very different from the sample richness values obtained in this study, or from those presented by Silveira (2002). Baiting for social polistines is probably effective at small ranges (actually increasing the continuous or discontinuous permanency of an individual at a given point). It is not yet known if the kinds of wasp baits currently used are sufficiently attractive to bring in individuals from more distantly located colonies, or even bringing them down from the forest canopy. Baits are expected to reduce problems related to estimating abundance variation between sampling points for a single species, i.e. helping to respond to the question "where is a given species more abundant". However, its utility in studies of the spatial distribution of species occurrences will be dependent on implementation costs that would allow its regular application over the entire study area.

Techniques designed to account for low detectability in wildlife surveys depend on sampling repetitions to estimate the parameters to be used in models calculating unbiased species occupancy values (Gillera-Arroita *et al.* 2010; Royle *et al.* 2005). Because of the relatively large area covered by the present inventory (and its primary objectives) only very limited efforts were spent on repeated sampling. Two trail sections were chosen for an additional round of active search and complementary Malaise trap efforts. However, the objective there was not to assess the detectability of particular species, but the related one of knowing about additional species that could be discovered. No extra species were added to the ones found in the first programmed pass of the collecting team on these trails. Additionally, the generally greater times (ca. 4 hours) dedicated to sampling during the first expedition resulted in only a modest average increase (of two species) as compared to the other expeditions (Table III), and this was not independent on the effects of an environmental variable related to forest canopy (Table V). Given the low levels of the required information, it is difficult to gain a precise idea of how many wasp species will go unnoticed along a 1-km trail section in a typical undisturbed Amazon forest using the survey methods employed in this study.

As an aspect or condition related to population size or density, rarity is assumed to have an important role (as parameter or variable) in models of ecological and evolutionary processes (Kunin & Gaston 1993; Holt 1996). As such, it is also a factor of great concern within the context of biological conservation (Hartley & Kunin 2003; Rabinowitz *et al.* 1986). While local rarity seems to be a real condition for many species of the Caxiuanã wasp fauna, these species are also generally known to have relatively wide distributions in the Amazon basin (Richards 1978), except for the unidentified and possibly new species, about which little information is available (mostly of *Mischocyttarus*). On the other hand, many of these species are probably dependent on relatively undisturbed forest habitats, presenting a situation of great concern that involves a combination of wide geographical ranges with small or rarified local populations, and dependence on a yet widespread but highly threatened forest habitat.

Collecting record distributions and possible causal factors. The spatial patterning of intraspecific distributions could only be properly investigated in the cases of relatively common and abundant species for which reasonable amounts of data had been collected. Close-range spatial effects were detected for most of these species, with presence data being clustered at distances below ca. 800 meters (Table I). These are most probably cases of endogenous autocorrelation related to colony home ranges and/or short range migratory processes. Larger spatial lag effects could also be identified in the distributions of certain species, constituting probably cases of exogenous autocorrelation, and candidates for explanations based on environmental factors. In some species, the autocorrelated patterns suggest clinal variation of the causal factors, while the patterns of other species suggest the role of factors with clustered distributions. Autocorrelation analyses of the studied environmental variables indicated that forest canopy (HETCAN%) conforms to a clinal variation pattern, while distance to forest streams (NEARHYDR) and mean ground altitude (ALTITUD) conform to clustered factors (Fig. 10).

In just a few cases, significant or near significant correlations were found among only five species and environmental variables (Table II). In spite of the general low magnitude of correlations involving species presence/absence descriptors, however, when viewed by groups some coherence is apparent in sign and values of the coefficients (Appendix 1). This can be seen for species of the *Agelaia*-*Angiopolybia* clade with respect to all three environmental variables, as well as for species of *Mischocyttarus* with respect to the variable of canopy type (HETCAN%). Too few *Polybia* species had enough data to compute correlations. Such weak but coherent patterns are apparently reflected in the correlations between two of the clades richness variables (RMischo, RAgAn) and environmental variables (Table III). Interpretation is not for instance that *Mischocyttarus* species did not correlate in general to the variables related to forest streams (NEARHYDR) or mean terrain altitude (ALTITUD), but that as for this group, the species tendencies were too different or incongruous. Species of the *Agelaia*-*Angiopolybia* clade, in contrast, showed generally more similar correlations with these variables. However, both of the clades mentioned above demonstrated concordant patterns of correlations between species richness and the forest canopy variable (HETCAN%). On the other hand, no level of richness prediction could be determined based on correlations with any of the studied environmental variables for *Polybia*.

Environmental variables were highly intercorrelated as was expected, and certainly subsume information on the resources/habitat conditions required in different contexts by theses insects, as free water availability, wind and shading conditions at nesting sites, and possibly other aspects related to vegetation structure. However, the observed ranges of these factors in the Caxiuanã plot are comparatively narrow, and the variable describing spectral properties of forest canopy (HETCAN%) can only be taken as a proxy for yet poorly understood aspects of that vegetation. Furthermore, the observed levels of association of such factors with the biodiversity variables must be considered low. When used as predictors of polistine richness in a linear multiple regression, only the coefficient for variable HETCAN% resulted significant at a 0.05 probability level, and the associated coefficient of determination (R^2) was only about 17%, indicating a poor fit. Additionally, the different responses of the richness variables of the three less inclusive clades (*Agelaia*+*Angiopolybia*; *Mischocyttarus*; *Polybia*) in regard to association with the environmental variables serve as a call for caution about generalizations made for large and heterogeneous taxa, and to emphasize the importance of considering peculiarities of the faunal composition in a given region.

Apparent association between some species frequencies and the margins of large water bodies has been observed by Silveira (2002) in Caxiuanã, typically for species such as *Mischocyttarus injucundus* (cited as *juruanus*; see Silveira 2006), *Apoica pallida*, *Polybia rejecta*, *Protopolybia emortualis* and *Chatergus metanotalis*. However, such environments should be better considered as edge habitats, and most of these species were indeed absent from the PPBio plot (except for *P. rejecta*, which had a very low frequency). The observed weak association between collecting records of some species and their spatial proximity to small streams in a core high forest habitat (as in most of the PPBio plot) certainly represents a distinct phenomenon that will require additional investigation.

CONCLUSIONS

The types of spatial information presented in this study are important for understanding ecological processes influencing wasp populations and communities. Spatial analyses of collecting records at local scales in tropical rainforests may give us an idea of the variation in spatial occupation mediated by ecological factors, and also provide indirect indications of inter-colony distance patterns. Evidence was seen of the relative importance of some aspects of habitat structure (hydrography and vegetation) on spatial occupation for at least some species in Caxiuanã. Strong relationships between wasp species and environmental variables are hardly expected in such a within-habitat context and at the scale that was used, as for example in the case of nest-substrate specialists like *Mischocyttarus adolphi*, which nests on myrmecophilous plants (and all three colonies in the plot were found on the same individual of *Cordia* sp. [Boraginaceae]). Less extreme associations between wasp, plant, and arboreal ant species were recently discussed by Corbara *et al.* (2009). However, if it becomes well established that species like *Angiopolybia pallens* or *Agelaia centralis* are sensible to rather subtle habitat alterations, it will have important implications for conservation planning and could be used as an indicator of the health/stress levels of forest habitats.

The results of the present work also demonstrated that modest levels of predictability of interspecific variables (such as sample's species richness) can be based on one's knowledge of environmental variables, especially vegetation structure. This will be important to wasp conservation, and studies at larger landscape and regional scales should be undertaken. The benefits of studying spatial phenomena at different geographical scales were noted by Storch & Gaston (2004) when they pointed out the influence of large-scale constraints on small-scale patterns and processes and the importance of dissecting macroecological phenomena in order to understand how these large-scale regularities emerge and how they are connected to one another.

In a direction opposite to that of the results for sample richness, another notable finding of this study refers to the poor capacity of predicting sample rarity scores from environmental variables. Because these quantities are related to compositional complementarity between samples, a practical but undesirable consequence is that wasp inventories cannot benefit from earlier environmental information beyond the possibility of anticipating some variations in species richness among different sites. Matters of scale must be considered here, however, as well as taxonomic specificities. In a study of dung beetles covering the entire territory of France, Lobo *et al.* (2008) found that they relationships of rarity with species richness (or with environmental factors) varied among different taxa. Species turnover between samples across the PPBio plot were considerable, as judged by a mean richness of only 5.4 species per sample and a total richness of 65 species for the entire PPBio plot; i.e. the samples capture only a very small proportion of the locally occurring species (Koleff *et al.* 2003). Species turnover is probably several times smaller at a regional scale if one roughly considers the Amazon's regional pool of ca. 250 species and a mean richness for local faunas of ca. 100 species (see Silveira 2002). As already pointed out above in regards to the lack of spatial patterns in rarity scores, such high local species turnover seem to be random relative to the spatial and environmental factors studied. However, as noted earlier, the relatively low mean numbers of species per sample may be a result of sampling biases and the low detectability of rare species.

ACKNOWLEDGMENTS

We are grateful to Alexandre Felizola Diniz Filho and Edilberto Giannotti for reading and commenting upon an earlier version of the manuscript. We also thank "Programa de Pós-Graduação em Zoologia (MPEG/UFPA)" and the Brazilian "Conselho Nacional de Desenvolvimento Científico e Tecnológico" (CNPq) for a grant conceded to S. S. Silva (132617/2005-6). Support given by the Moore Foundation is also greatly recognized (BECA Program – B/2005/02/BMP/16). The study was supported in many ways by the Brazilian government "Programa de Pesquisa em Biodiversidade da Amazônia" (PPBio).

REFERENCES

Boakes, E. H.; P. J. K. McGowan; R. A. Fuller; D. Chang-qing; N. E. Clark; K. O'Connor & G. M. Mace. 2010. Distorted views of biodiversity: spatial and temporal bias in species occurrence data. **PLoS Biology 8**: e1000385.

Carpenter, J. M. & O. M. Marques. 2001. **Contribuição ao estudo dos vespídeos do Brasil (Insecta, Hymenoptera, Vespoidea, Vespidae)**. Cruz das Almas, Universidade Federal da Bahia. Publicações digitais. Vol. 2.

Corbara, B.; J. M. Carpenter; R. Céréghino; M. Leponce; M. Gibernau & A. Dejean. 2009. Diversity and nest site selection of social wasps along Guianese forest edges: assessing the influence of arboreal ants. **Comptes rendus Biologies 332**: 470–479.

Colwell, R. K. & J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. **Philosophical Transactions of the Royal Society (Series B) 345**: 101–118.

Costa, J. de P. R. da & J. C. de Morais. 2002. Médias mensais de variáveis meteorológicas (1996-1999), p. 225-232. *In*: P. L. B. Lisboa (org). **Caxiuanã: Populações tradicionais, meio físico e diversidade biológica**. Belém, Museu Paraense Emílio Goeldi, 734 p.

Diniz-Filho, J. A. F.; L. M. Bini & B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. **Global Ecology & Biogeography 12**: 53–64.

Diniz-Filho, J. A. F.; L. C. Terribile; G. de Oliveira & T. F. L. V. B. Rangel. 2009. Padrões e processos ecológicos e evolutivos em escala regional. **Megadiversidade 5**: 5–16.

Ducke, A. 1904. Sobre as Vespidas sociaes do Pará. **Boletim do Museu Paraense Emílio Goeldi de História Natural e Etnografia 4**: 317–374.

Ducke, A. 1905. Nouvelles contributions à la connaissance des Vespides sociales de l'Amérique du Sud. **Revue Entomologique 24**: 5–24.

Ducke, A. 1907. Novas contribuições para o conhecimento das Vespas (Vespidae sociales) da Região Neotropical. **Boletim do Museu Paraense Emílio Goeldi 5**: 152–199.

Durães, R.; P. W. Martins & F. Z. Vaz-de-Mellos. 2005. Dung beetle (Coleoptera: Scarabaeidae) assemblages across a natural forest-cerrado ecotone in Minas Gerais, Brazil. **Neotropical Entomology 34**: 721–731.

Elith, J. & J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. **Annual Review of Ecology, Evolution, and Systematics 40**: 677–697.

Elpino-Campos, Á.; K. Del-Claro & F. Prezoto. 2007. Diversity of social wasps (Hymenoptera: Vespidae) in Cerrado fragments of Uberlândia, Minas Gerais State, Brazil. **Neotropical Entomology 36**: 685–692.

ESRI. 2004. **ArcGIS 9. What is ArcGIS?** Redlands, 119 p.

Fortin, M. -J. & M. R. T. Dale. 2005. **Spatial Analysis: a guide for ecologists**. Cambridge, Cambridge University Press, 365 p.

Fortin, M. -J.; M. R. T. Dale & J. ver Hoef. 2002. Spatial analysis in ecology, p. 2051–2058. *In*: A. El-Shaarawi & W.W. Piegorsch (eds.). **Encyclopedia of Environmetrics**, vol. 4, Chichester, Wiley.

Fritz, S. A.; O. R. P. Bininda-Emonds & A. Purvis. 2009 Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. **Ecology Letters 12**: 538–549.

Gadagkar, R. 1991. *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and independent founding *Ropalidia*, p. 149–190. *In*: K. G. Ross & R. W. Matthews (eds). **The social biology of wasps**. Ithaca, Cornell University Press, xvii+678 p.

Guillera-Arroita, G.; M. S. Ridout & B. J. T. Morgan. 2010. Design of occupancy studies with imperfect detection. **Methods in Ecology & Evolution 1**: 131–139.

Gobbi, N.; V. L. L. Machado & J. A. Tavares Filho. 1984. Sazonalidade das presas utilizadas na alimentação de *Polybia occidentalis occidentalis*

(Olivier, 1791) (Hym., Vespidae). **Anais da Sociedade Entomológica do Brasil 13**: 63–69.

Gomes, B. & F. B. Noll. 2009. Diversity of social wasps (Hymenoptera, Vespidae, Polistinae) in three fragments of semideciduous seasonal forest in the northwest of São Paulo State, Brazil. **Revista Brasileira de Entomologia 53**: 428–431

Granja e Barros, M. 1998. Sistemas reprodutivos e polinização em espécies simpátricas de *Erythroxylum* P. Br. (Erythroxylaceae) do Brasil. **Revista Brasileira de Botânica 21**: 159–166.

Guisan, A. & W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. **Ecology Letters 8**: 993–1009.

Hartley, S. & W. E. Kunin. 2003. The scale-dependency of rarity, extinction risk and conservation priority. **Conservation Biology 17**: 1559–1570

Heithaus, E.R. 1979a. Community structure of Neotropical flower visiting bees and wasps: Diversity and phenology. **Ecology 60**: 190–202.

Hermes, M. G. & A. Köhler. 2006. The flower-visiting social wasps (Hymenoptera, Vespidae, Polistinae) in two areas of Rio Grande do Sul state, southern Brazil. **Revista Brasileira de Entomologia 50**: 268–274

Hijmans, R. J.; L. Guarino; A. Jarvis; R. O'Brien; P. Mathur; C. Bussink; M. Cruz; I. Barrantes & E. Rojas. 2005. **DIVA-GIS version 5.2**. http://www.diva-gis.org/docs/DIVA-GIS5_manual.pdf.

Holt, R. D. 1996. Rarity and evolution: some theoretical considerations, p.[intervalo do capítulo]. *In*: W. E. Kunin, & K. J. Gaston (eds.). **The Biology of Rarity: causes and consequences of rare-common differences**. London, Chapman & Hall, 300 p.

Jeanne, R. L. 1991. The swarm-founding Polistinae, p. 191–231. *In*: K. G. Ross & R. W. Matthews (eds). **The social biology of wasps**. Ithaca, Cornell University Press, xvii+678 p.

Koleff, P.; K. J. Gaston & J. J. Lennon. 2003. Measuring beta diversity for presence–absence data. **Journal of Animal Ecology 72**: 367–382.

Kumar, A.; J. T. Longino; R. K. Colwell & S. O'Donnell. 2009. Elevational patterns of diversity and abundance of eusocial paper wasps (Vespidae) in Costa Rica. **Biotropica 41**: 338–346.

Kunin, W. E. & K. J. Gaston. 1993. The Biology of Rarity: Patterns, Causes and Consequences. **Trends in Ecology and Evolution 8**: 298–301.

Legendre, P. 1993. Spatial Autocorrelation: Trouble or New paradigm? **Ecology 74**: 1659–1673.

Lobo, J. M.; P. Jay-Robert & J. P. Lumaret. 2008. The relationship between forecasted rarity and species richness values for Scarabaeidae and Aphodiinae species in France (Coleoptera, Scarabaeoidea). **Insect Ecology and Conservation**: 299–317.

Magurran, A. E. & P. A. Henderson. 2003. Explaining the excess of rare species in natural species abundance distributions. **Nature 422**: 714–716.

Morato, E. F.; S. T. Amarante & O. T. Silveira. 2008. Avaliação ecológica rápida da fauna de vespas (Hymenoptera: Aculeata) do Parque Nacional da Serra do Divisor, Acre, Brasil. **Acta Amazonica 38**: 789–798.

O'Donnell, S. 1995. Necrophagy by Neotropical Swarm-Founding Wasps (Hymenoptera: Vespidae, Epiponini). **Biotropica 27**: 133–136.

Ohgushi, R.-i; S. Yamane & S. F. Sakagami. 1988. Ecological distribution and habitat-linked density of colonies of Stenogastrine wasps in tropical S. E. Asia. **Zoological Science 5**: 869–874.

Phillips, S. J.; R. P. Anderson & R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. **Ecological Modelling 190**: 231–259.

Rabinowitz, D.; S. Cairns & T. Dillon. 1986. Seven forms of rarity and their frequency in the flora of the British Isles, p. 182–204. *In*: M. E. Soulé (ed) **Conservation Biology: The Science of Scarcity and Diversity**. Sunderland, Sinauer Associates, 584 p.

Rangel, T. F. L. V. B; J. A. F. Diniz-Filho & L. M. Bini. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. **Global Ecology & Biogeography 15**: 321–327.

Raveret Richter, M. 2000. Social wasp (Hymenoptera: Vespidae) foraging behavior. **Annual Review of Entomology 45**: 121–150.

Reeve, H. K. 1991. *Polistes*, p. 99–148. *In*: K. G. Ross & R. W. Mathews (eds.). **The social biology of wasps**. Ithaca, Cornell University Press, xvii+678 p.

Richards, O. W. 1971. The biology of the social wasps (Hymenoptera: Vespidae). **Biological Review 46**: 483–528.

Richards, O. W. 1978. **The social wasps of the Americas: Excluding the Vespinae**. London, British Museum, 580 p.

Rosenberg, M. S. & C. D. Anderson. 2011. PASSaGE: Pattern Analysis, Spatial Statistics and Geographic Exegesis. Version 2. **Methods in Ecology & Evolution 2**: 229–232.

Royle, J. A.; J. D. Nichols & M. Kéry. 2005. Modelling occurrence and abundance of species when detection is imperfect. **Oikos 110**: 353–359.

Sabu, T. K.; P. J. Vineesh & K.V. Vinod. 2008. Diversity of forest litter-inhabiting ants along elevations in the Wayanad region of the Western Ghats. **Journal of Insect Science 8**: 1–14.

Santos. G. M. M.; J. D. da Cruz; C. C. Bichara Filho; O. M. Marques & C. M. L. Aguiar. 2007a. Utilização de frutos de cactos (Cactaceae) como recurso alimentar por vespas sociais (Hymenoptera, Vespidae, Polistinae) em uma área de caatinga (Ipirá, Bahia, Brasil). **Revista Brasileira de Zoologia 24**: 1052–1056.

Santos. G. M. de M.; C. C. Bichara Filho; J. J. Resende; J. D. da Cruz & O. M. Marques. 2007b. Diversity and Community Structure of Social Wasps (Hymenoptera: Vespidae) in Three Ecosystems in Itaparica Island, Bahia State, Brazil. **Neotropical Entomology 36**: 180–185.

Santos, G. M. de M.; P. C. Bispo & C. M. L. Aguiar. 2009a. Fluctuations in Richness and Abundance of Social Wasps During the Dry and Wet Seasons in Three Phyto-Physiognomies at the Tropical Dry Forest of Brazil. **Environmental Entomology 38**: 1613–1617.

Santos. G. M. de M.; J. D. da Cruz; O. M. Marques & N. Gobbi. 2009b. Diversidade de Vespas Sociais (Hymenoptera: Vespidae) em Áreas de Cerrado na Bahia. **Neotropical Entomology 38**: 317–320.

Silva, S. de S. & O. T. Silveira. 2009. Vespas sociais (Hymenoptera, Vespidae, Polistinae) de floresta pluvial Amazônica de terra firme em Caxiuanã, Melgaço, Pará. **Iheringia Série Zoologia 99**: 317–323.

Silva-Pereira, V. da & G. M. de Santos. 2006. Diversity in bee (Hymenoptera, Apoidea) and social wasps (Hymenoptera, Vespidae) comumnity in "Campos Rupestres", Bahia, Brazil. **Neotropical Entomology 35**: 165–174.

Silveira, O. T. 2002. Surveying Neotropical social wasps. An evaluation of methods in the "Ferreira Penna" Research station (ECFPn), in Caxiuanã, PA, Brazil (Hym., Vespidae, Polistinae). **Papéis Avulsos de Zoologia 42**: 299–323.

Silveira, O. T. 2006. Revision of the subgenus *Kappa* de Saussure of *Mischocyttarus* de Saussure (Hym.; Vespidae, Polistinae, Mischocyttarini). **Zootaxa 1321**: 3–108.

Silveira, O. T.; S. V. da Costa Neto & O. F. M. da Silveira. 2008. Social wasps of two wetland ecosystems in brazilian Amazonia (Hymenoptera, Vespidae, Polistinae). **Acta Amazonica 38**: 333–344.

Storch, D. & K. J. Gaston. 2004. Untangling ecological complexity on different scales of space and time. **Basic and Applied Ecology 5**: 389–400.

Sühs, R. B.; A. Somavilla; A. Köhler & J. Putzke. 2009. Vespídeos (Hymenoptera, Vespidae) vetores de pólen de Schinus terebinthifolius Raddi (Anacardiaceae), Santa Cruz do Sul, RS, Brasil. **Revista Brasileira de Biociências 7**: 138–143.

Tanaka Junior, G. M. & F. B. Noll. 2011. Diversity of SocialWasps on Semideciduous Seasonal Forest Fragments with Different Surrounding Matrix in Brazil. **Psyche**: 1–8.

Togni, O. C. 2009. Diversidade de vespas sociais (Hymenoptera, Vespidae) na Mata Atlântica do litoral norte do estado de São Paulo. Dissertação de mestrado. Universidade Estadual Paulista Júlio de Mesquita Filho. 98 p.

Williams, P. H.; C. R. Margules & D. W. Hilbert. 2002. Data requirements and data sources for biodiversity priority area selection. **Journal of Biosciences 27**: 327–338.

Zucchi, R.; S. F. Sakagami; F. B. Noll; M. R. Mechi; S. Mateus; M. V. Baio & S. N. Shima. 1995. *Agelaia vicina*, a swarm-founding polistine with the largest colony size among wasps and bees (Hymenoptera: Vespidae). **Journal of the New York Entomological Society 103**: 129–137.

Appendix 1. Wasp species mentioned in this article and correlations between species presence/absence variables and environmental factors in the Caxiuanã PPBio plot (computed only for species occurring in at least three samples); point biserial coefficients (above) and respective probabilities (below) are shown in each case.

Agelaia angulata (Fabricius 1804)	-0.259	-0.303	0.023
	0.044	0.018	0.858
Agelaia angulicollis (Spinola 1851)	-0.091	-0.007	-0.022
	0.486	0.957	0.864
Agelaia cajennensis (Fabricius 1798)	0.011	-0.084	0.243
	0.934	0.522	0.059
Agelaia centralis (Cameron 1907)	-0.173	-0.328	0.358
	0.182	0.010	0.005
Agelaia fulvofasciata (Degeer 1773)	-0.011	0.102	0.199
	0.932	0.435	0.125
Agelaia myrmecophila (Ducke 1905)	-0.036	0.048	0.086
	0.783	0.715	0.512
Agelaia pallipes (Olivier 1791)	-0.104	-0.107	0.053
	0.426	0.414	0.685
Agelaia testacea (Fabricius 1804)	-0.117	0.003	0.188
	0.369	0.979	0.148
Angiopolybia pallens (Lepeletier 1836)	-0.311	-0.300	0.243
	0.015	0.019	0.059
Angiopolybia paraensis (Spinola 1851)	-0.169	-0.179	0.133
	0.194	0.168	0.306
Apoica pallens (Fabricius 1804)	0.058	0.128	-0.045
	0.658	0.324	0.732
Leipomeles dorsata (Fabricius 1804)	-0.040	0.019	0.178
	0.760	0.885	0.171
Mischocyttarus carbonarius (de Saussure 1854)	-0.106	-0.131	0.193
	0.417	0.315	0.137
Mischocyttarus collarellus Richards 1940	0.164	0.092	-0.092
	0.206	0.479	0.482
Mischocyttarus duckei (Buysson 1908)	-0.250	-0.055	0.162
	0.052	0.673	0.212
Mischocyttarus lecointei (Ducke 1904)	-0.089	-0.204	0.185
	0.496	0.115	0.154
Mischocyttarus nr. *mallaris*	0.028	0.069	0.139
	0.829	0.600	0.286
Mischocyttarus nr. *synoecus*	-0.086	-0.08	0.186
	0.511	0.540	0.152
Mischocyttarus oecothrix Richards 1940	0.037	0.034	0.079
	0.780	0.792	0.543
Mischocyttarus sylvestris Richards 1945	0.132	0.019	0.053
	0.310	0.883	0.686
Polybia (*Alpha*) sp.	-0.132	-0.166	0.030
	0.309	0.202	0.816
Polybia cattillifex Moebius 1856	0.160	0.138	-0.048
	0.218	0.290	0.714
Polybia dimidiata (Olivier 1791)	0.198	0.053	-0.032
	0.126	0.687	0.809
Polybia gorytoides Fox 1898	-0.212	-0.092	0.211
	0.101	0.480	0.102
Polybia platycephala Richards 1951	–	–	–
Polybia liliacea (Fabricius 1804)	–	–	–
Polybia emaciate Lucas 1879	–	–	–
Polybia striata (Fabricius 1787)	–	–	–
Polybia singularis Ducke 1909	–	–	–
Mischocyttarus adolphi Zikán 1935	–	–	–

Received 14/3/2012; accepted 17/7/2012
Editor: Eduardo A. B. Almeida