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RESEARCH ARTICLE

Spatio-temporal variation in the diversity of social wasps (Vespidae: Polistinae) in the tropical dry forest of the Colombian Caribbean

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ABSTRACT. The temporal variation in the diversity of Polistinae was analyzed in three fragments of tropical dry forest (TDF) in the Colombian Caribbean (Reserva Campesina la Montaña = RCM, Reserva La Flecha = RCF and Finca La Clarita = FLC). Three transects, each measuring 250 × 20 m and spaced 200 m apart, were established per site. Within each transect, six collection points were marked, each separated by 50 m. The social wasps were captured using baited traps and entomological nets. A total of 2274 wasps were collected across the three TDF fragments, identified into 11 genera and 24 species. The most diverse genus was *Polybia*, followed by *Polistes* and *Agelaia*. The highest species richness among fragments was recorded at RLF (22), while the lowest was at RCM and FLC (10). Seasonally, RLF exhibited the highest richness (17) during the rainy season, whereas the lowest richness was observed at RCM during the dry season (5). According to diversity profiles, the highest value of the effective number of species (^{0}D) was recorded at RLF during the rainy season (15), and the lowest (2) during the dry season at RCM. This same pattern was observed for the other two orders of diversity (^{1}D and ^{2}D). In terms of beta diversity, a high dissimilarity was observed among the three locations, driven by both nesting and species turnover, while from a temporal perspective (dry-rainy seasons), species turnover was predominant. The diversity variation of the social wasps is associated with changes in humidity due to the onset of the rainy season, demonstrating that seasonal changes in these variables within TDF fragments are crucial in the dynamics of social wasp communities.

KEYWORDS. Communities, dissimilarity, Hill numbers, season.

INTRODUCTION

In the Colombian Caribbean, the tropical dry forest (TDF) is undergoing constant modification due to the exploitation of primary resources (e.g., timber), agricultural production, mining, human settlements, and forest fires, which have led to the loss of native fauna and flora (Janzen 1983, IAvH 1998, Pizano and García 2014). Currently, the TDF is distributed in small, isolated fragments surrounded by agricultural matrices (Rangel-Acosta and Martínez-Hernández 2017). In this region, the departments of Atlántico (5.7%), Bolívar (4.1%), and Magdalena (2.2%) have the highest percentages of TDF coverage, although most of these fragments are not within protected areas (Pizano and García 2014), despite representing the largest TDF coverage in the country.

The TDF is considered a diverse ecosystem at the local level (Amell-Caez et al. 2019), making it essential to understand the dynamics of biological communities, as they could provide crucial information for biodiversity conservation and forest reserve management (Brown 1991, Sarmiento and Saravia 1996, Lewinsohn et al. 2005). In this context, most efforts to observe the impact of forest transformation on diversity

in anthropogenic areas have focused on studying groups of invertebrates such as Coleoptera (Martínez et al. 2010a, 2010b, García-Atencia and Martínez-Hernández 2015, García-Atencia et al. 2015, Rangel-Acosta and Martínez-Hernández 2017, Rangel-Acosta et al. 2018, Amell-Caez et al. 2019, García et al. 2021, Sarmiento-Roa et al. 2024), Lepidoptera (Vargas-Zapata et al. 2011, Boom et al. 2013, Mercado et al. 2018, Ahumada et al. 2019), Mantodea (Arteaga et al. 2014), Hemiptera (Román-Garrido et al. 2016), and Hymenoptera (Formicidae) (Guerrero and Olivero 2007, Fontalvo and Domínguez-Haydar 2009, Simanca et al. 2010, Gutiérrez and Domínguez-Haydar 2017). However, few studies have focused on determining the ecological response of social insect communities to TDF transformation in the Colombian Caribbean, despite their importance within this ecosystem.

Among social insects, wasps (Vespidae: Polistinae) play crucial ecological roles such as pollination and the predation of pest insects (e.g., lepidopteran larvae) in biological pest control, making them potential bioindicators of ecosystem quality (West-Eberhard 1975, Souza et al. 2010). Additionally, some species (e.g., *Polybia paulista* Ihering, 1896) produce venom from which protein components (medicinal resources) with cancer-fighting, antimicrobial, and anticonvulsant activities have been extracted, highlighting their significance in providing important environmental services for human well-being (do Couto et al. 2012).

In the world, there are more than 1,050 species of social wasps divided into 25 genera. In Colombia, 21 genera, 224 species, and 25 subspecies of Polistinae have been recorded (*Mischocyttarus*, *Polistes*, and 19 genera of Epiponini) (Sarmiento 1997), one of the countries in the neotropical region with the greatest diversity of this taxon. However, there are few studies that estimate the diversity values of social wasps in TDF fragments in the Caribbean departments of Colombia (López et al. 2013a, 2013b), resulting in limited knowledge about the current state of Polistinae diversity in this region. Given the ecological importance of social wasps in critical ecosystems like TDF, it is relevant to understand how the diversity of these insects responds to seasonal dynamics and environmental characteristics of TDF in the Colombian Caribbean. Seasonal variation influences ecological communities through temporal changes in resource availability (e.g., food, habitats), fluctuations in environmental variables (e.g., temperature, humidity), and photoperiod (García and Cabrera-Reyes 2008). Consequently, it is expected that the composition and structure of Polistinae will differ among fragments due to the heterogeneity and seasonality of TDF between the dry and rainy seasons in the Colombian Caribbean.

Considering the above, the spatio-temporal variation in Polistinae diversity in TDF fragments of the Colombian Caribbean and its relationship with environmental variables and canopy cover was analyzed. This research is relevant due to the need to understand the diversity of social wasps in unprotected areas, given the lack of continuous species records and the rapid reduction of TDF fragments.

MATERIAL AND METHODS

Study area

Three forest fragments were selected: Reserva Campesina La Montaña (RCM), Reserva La Flecha (RLF), and Finca La Clarita (FLC), located in the departments of Atlántico, Bolívar, and Magdalena, respectively (Fig. 1, Table 1). These forest formations correspond to TDF, according to the system proposed by Holdridge (1967).

Sampling

Two sampling sessions were conducted between March and August 2017 for each fragment: one during the dry season (February to April) and another during the rainy season (May to August), to cover periods of low and high precipitation (Guzmán et al. 2014), with a temporal investment of three days (72 hours per sampling). In each TDF fragment, three transects were established, each 250 m long and 20 m wide, separated by 200 m from one another, and six points were marked 50 m apart from each other within each transect (Fig. 2). At each point, wasps were captured using an entomological net and attractive traps (Fig. 3).

Capture methods

Polistinae individuals were captured using modified attractive traps (necrotraps and fruit traps) based on the NTP-80 model (Morón and Terrón 1984, Márquez 2005), installed at each point. These traps consisted of cylindrical plastic containers 20 cm high with a 10 cm top opening, featuring two side openings with inward-facing funnels of 5 cm external diameter and 2 cm internal diameter (Fig. 3). In the case of the fruit trap (FT), the bait was a homogeneous mixture of panela honey (cane honey) and water at a ratio of 5:1 (panela: water) (Noll and Gómez 2009), with 250 mL per trap. In the necrotraps (NT), the bait consisted of 250 g of fresh marine fish, 200 mL of water, and tuna (Sarmiento and Saravia 1996). The traps were modified for an intersection-attraction model, suspended between one and eight meters above the ground, supported on tree branches, and were active for 72 hours with inspections every 24 hours.

Additionally, wasps were captured using an entomological net (EN) consisting of a 120 cm aluminum handle and a 60 cm diameter metal hoop at one end, covered by a fine mesh fabric cone 70 cm deep (Fig. 2) (Villareal et al. 2004). This technique was performed for 10 minutes per point, for a total of 60 minutes per transect, with transects being surveyed in two sessions, from 8:00 am to 12:00 pm and from 2:00 pm to 6:00 pm.

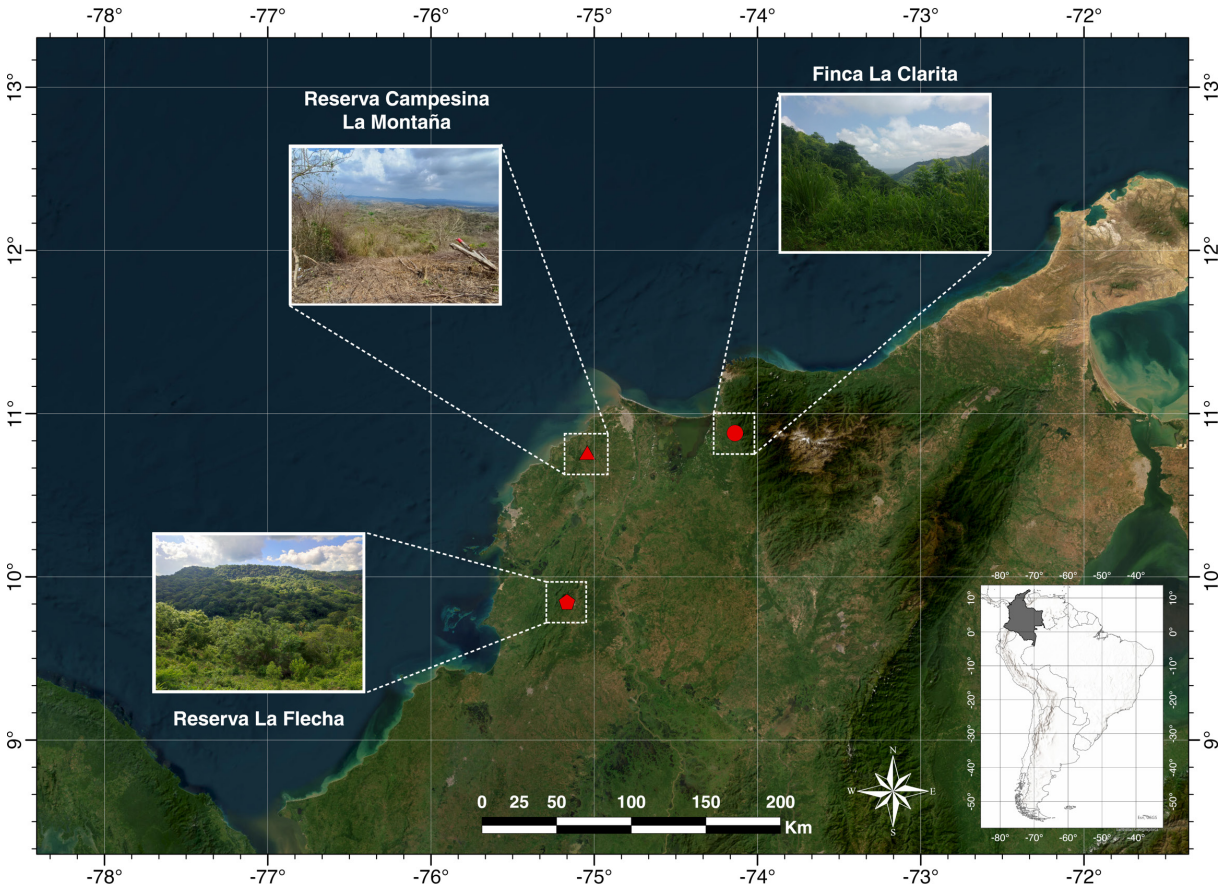
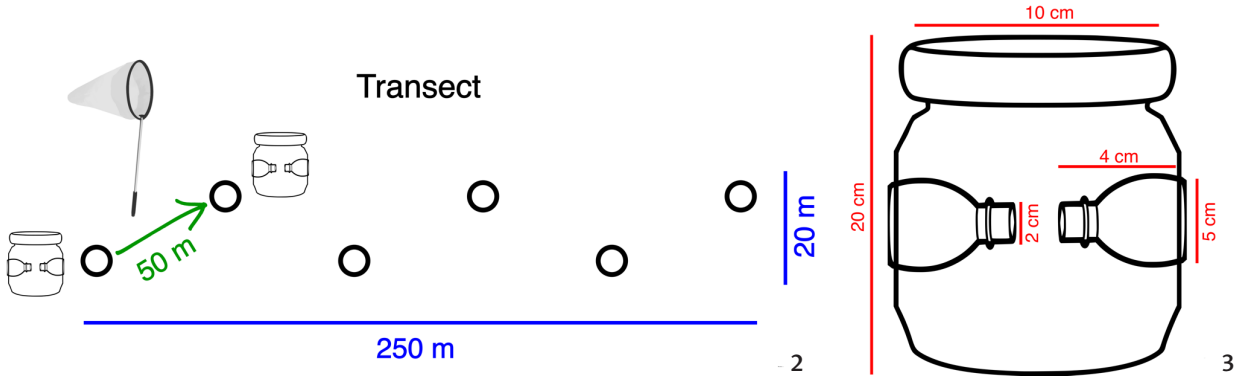


Figure 1. Location of tropical dry forest fragments in the Colombian Caribbean. The map was created using Quantum Geographic Information System (QGIS), v. 3.38.1, Grenoble (https://qgis.org/).



Figures 2–3. Distribution of capture techniques per transect (2) and description of attractive traps (3).

Table 1. Characteristics of the three forest fragments.

Locality	Coordinates and altitude	Climate Zones and Precipitation Regime	Fragment description
Finca La Clarita (FLC), San Pablo, Zona Bananera, Magdalena.	10°52'49.48" N, 78°08'14.74" W, 200 – 300 m asl	Slopes of the Sierra Nevada de Santa Marta, hygrophytic to subhygrophytic vegetation, unimodal-biestational precipitation regime.	The fragment with native vegetation covers an area of approximately 120 ha, characterized by hygrophytic and subhygrophytic vegetation, typical of the tropical alternohydric zonobiome on the slopes of the Sierra Nevada de Santa Marta, influenced by rainfall. The vegetation in this area includes representatives from the families Fabaceae, Malvaceae, Poaceae, Euphorbiaceae, Piperaceae, Araceae, Rubiaceae, Apocynaceae, and Melastomataceae. The region has areas designated for wood extraction, as well as zones allocated for agriculture and livestock.
Reserva La Flecha (RLF), Palenquito, San Jacinto, Bolívar.	09°51'26.61" N, 75°10'48.46" W, 300 – 500 m asl	Montes de María, hygrotropophytic vegetation, bimodal-tetra-seasonal precipitation regime.	The TDF fragment covers 149 ha, characterized by hygrotropophytic vegetation (a transition between dry and wet), with an average height of 25 m and emergent elements reaching up to 35 m. The dominant plant species in this area belong to the families Fabaceae, Bignoniaceae, and Malvaceae. The adjacent area is predominantly used for livestock grazing and cultivation of *Sabal mauritiiformis* (H. Karst) Griseb. and H. Wendl, *Manihot esculenta* Crantz, *Zea mays* L., *Persea americana* Mill., *Dioscorea esculenta* (Lour.) Burkill, among others (García-Atencia and Martínez-Hernández 2015). This has led to the recognition of the area as a conservation priority (Pizano and García 2014).
Reserva Campesina La Montaña (RCM), Juan de Acosta, Atlántico.	10°46'2.6" N, 75°0.2'34" W, 160 – 250 m asl	Serranía del Piojó, Pericaribbean Arid Belt, bimodal precipitation regime.	The forest fragment covers 47 ha and is characterized by a rolling terrain with a slope ranging from 12% to 25% and moderate erosion. It features three vegetation strata (shrubs, understory, and canopy), with a predominance of the families Fabaceae and Burseraceae, and adjacent areas with crops of *Manihot esculenta* Crantz, *Zea mays* L. and *Citrullus lanatus* Matsumura and Nakai in the adjacent areas (IAvH 1998).

The collected material was preserved in 70% alcohol in pre-labeled plastic containers and transported to the Ecology and Entomology Laboratory, Universidad del Atlántico. The specimens were mounted on polystyrene sheets and identified using keys proposed by Richards (1978), Cubillos and Sarmiento (1996), Sarmiento (1997), and Sarmiento and Carpenter (2006), using a Leica MC120 HD stereoscope. The species taxonomic level was determined using specialized keys (Richards 1978, Cooper 2000a, 2000b, Pickett and Wenzel 2007, Andena et al. 2009, Dos Santos et al. 2015), in addition to reviewing the collection at the Instituto de Ciencias Naturales de Colombia (ICN), Universidad Nacional de Colombia, Bogotá Campus.

Additionally, at each point, data on light intensity were recorded using a Standard ST-1308 digital lux meter, and ambient temperature and humidity were measured with an Extech RTH10 data logger. Canopy cover was also quantified using a FORE-43887 convex spherical densiometer. Precipitation data were obtained from the website of the Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM) (http://www.ideam.gov.co).

Data analysis

The species richness of Polistinae was estimated as the number of species and their abundance in terms of incidence, meaning it was calculated as the sum of the capture incidences of each species per point/transect and season in each fragment (Colwell et al. 2005).

Alpha diversity was calculated using diversity profiles (Hill numbers) (Hill 1973), expressed in units of the effective number of species (Hsieh et al. 2016, Jost 2006): ${}^0D$ (species richness), ${}^1D$ (abundant species), and ${}^2D$ (dominant species), through the interpolation and extrapolation analysis of the sample (Chao et al. 2014) with the iNEXT package (Chao et al. 2016, Hsieh et al. 2016) in RStudio (2021). The values of each diversity order were compared using 95% confidence intervals (Moreno et al. 2011). For beta diversity, the values of turnover and nestedness components were estimated (Baselga 2010, 2012, 2013) using the Jaccard dissimilarity index. This analysis was performed with the Betapart package in RStudio (Baselga and Orme 2012): $\beta_{Jac} = \beta_{Nes} + \beta_{Tur}$

On the other hand, a non-parametric multidimensional scaling (nMDS) analysis was conducted to determine the spatiotemporal variation of the social wasp community. The Bray-Curtis dissimilarity index was used for this purpose, as it determines the similar relationships between sites and the ecological distances between communities (Faith et al. 1987). To observe the differences in communities, a permutational multivariate analysis of variance (PERMANOVA) was performed using the adonis2 function from the vegan package (Oksanen et al. 2020) in RStudio.

To determine how seasonality, forest fragments, and environmental variables influenced the abundance and diversity of social wasps, a generalized linear model was applied using the glm function from the lme4 package (Bates

et al. 2015). The final models for the response variables were compared against null models, and the most parsimonious model was selected based on the Akaike Information Criterion (AIC) (Akaike 1974). High collinearity among environmental factors was ruled out using a Pearson correlation test (Pearson 1920) with the cor.test function from the stats package in RStudio.

RESULTS

Polistinae diversity

A total of 2274 wasps from Polistinae were collected, grouped into 11 genus and 24 species (Table 2). *Polybia* Lepeletier, 1836 was the most diverse with seven species, followed by *Polistes* Latreille, 1802 with four species. In contrast, *Mischocyttarus* de Saussure, 1853, *Apoica* Lepeletier, 1836, *Synoeca* de Saussure, 1852, *Brachygastra* Perty, 1833, *Charterginus* Fox, 1898, and *Protopolybia* Ducke, 1905 were represented by only one species each (Table 2).

Agelaia Lepeletier, 1836 was recorded in all three fragments during both climatic seasons (dry and rainy), while *Brachygastra*, *Mischocyttarus*, and *Synoeca* (RLF); *Apoica*, *Polistes*, *Parachartergus* Ihering, 1904 (RCM); and *Metapolybia*, *Parachartergus*, *Polistes*, and *Synoeca* (FLC) were the least frequent. In the same vein, the most frequent species was *Agelaia centralis* in all three fragments during both seasons, while the least frequent were *Polybia ignobilis*, *Polistes major colombianus*, *Polistes billardieri*, and *Metapolybia docilis* (RLF); *Polistes rufidens*, *Parachartergus colobopterus*, and *Apoica flavissima* (RCM); and *Polistes myersi* (Bequaert 1934) and *Protopolybia scutellaris* (FLC).

RLF recorded the highest species richness (22 species), followed by RCM and FLC with ten each. Richness peaked in RLF during the rainy season (17 species) and was lowest in RCM during the dry season (5 species). The highest abundance was observed in FLC during the dry season (94 individuals), and the lowest in the same fragment during the rainy season (55).

Table 2. Variation in the abundance and composition of the Polistinae community by season (dry and rainy) in three fragments of the tropical dry forest in the Colombian Caribbean. The number of individuals captured is indicated in parentheses.

Species	Reserva La Flecha		Reserva Campesina La Montaña		Finca La Clarita		Total
	Dry	Rain	Dry	Rain	Dry	Rain	
Agelaia centralis (Cameron, 1907)	49 (284)	27 (69)	39 (205)	39 (99)	49 (806)	29 (278)	232 (1741)
Agelaia panamensis (Cameron, 1906)	1 (2)	2 (2)		2 (2)			5 (6)
Agelaia pleuralis Cooper, 2000	2 (2)						2 (2)
Apoica flavissima Vecht, 1972	1 (1)	3 (13)	1 (2)		2 (5)		7 (21)
Brachygastra lecheguana (Latreille, 1824)	2 (2)			2 (2)			4 (4)
Charterginus carinatus Zavattari, 1906		2 (25)					2 (25)
Metapolybia aztecoides (Richards, 1978)	1 (8)	5 (72)			6 (6)		12 (86)
Metapolybia docilis Richards, 1978		1 (8)			0		1 (8)
Mischocyttarus sp.	2 (3)			2 (2)			4 (5)
Parachartergus colobopterus (Licht., 1796)				1 (27)	6 (25)	5 (22)	12 (74)
Parachartergus fraternus (Gribodo, 1891)		5 (5)					5 (5)
Polistes billardieri Fabricius, 1804		1 (1)					1 (1)
Polistes major colombianus Bequard, 1940	1 (1)						1 (1)
Polistes myersi Bequard, 1934	1 (1)	5 (8)		6 (13)		1 (1)	13 (23)
Polistes rufidens de Saussure, 1853		3 (3)	1 (2)				4 (5)
Polybia chrysothorax (Lichtenstein, 1796)	1 (2)	3 (3)					4 (5)
Polybia diguetana Buysson, 1905		2 (7)					2 (7)
Polybia emaciata Lucas, 1879	8 (15)	12 (18)					20 (32)
Polybia ignobilis (Haliday, 1836)	1 (1)				1 (1)	1 (3)	3 (5)
Polybia occidentalis (Olivier, 1791)	2 (3)	4 (9)	19 (30)	8 (56)	18 (31)	13 (22)	64 (151)
Polybia parvulina Richards, 1970		2 (16)					2 (16)
Polybia rejecta (Fabricius, 1798)	1 (2)	3 (3)	3 (3)	12 (2)	7(7)	4 (5)	30 (22)
Protopolybia scutellaris Bequard, 1944					1 (21)		1 (21)
Synoeca septentrionalis Richards, 1978	3 (5)	1 (1)			4 (8)	2 (2)	10 (16)
Number of species	15	17	5	8	9	7	24
Number of individuals	76 (332)	81 (254)	63 (242)	72 (203)	94 (910)	55 (333)	441 (2274)

Alpha diversity (α)

The highest sampling coverage was recorded during the rainy season in RCM (0.9872 ≈ 99%), while the lowest was observed during the dry season in RLF (0.8971 ≈ 90%). In terms of ^{0}D, the highest effective number of species (17 species) was recorded for RLF during the rainy season, while the lowest was observed in RCM during the dry season (5 species). When analyzing species' richness, no differences were found between sites during the dry season (Fig. 4), but RLF was significantly different from the other two TDF fragments during the rainy period based on confidence intervals (α = 0.05) (Fig. 4). On the other hand, in terms of common species (^{1}D), the highest diversity was observed in RLF during the rainy season (10.27), and the lowest in RCM (2.54) during the dry season; however, no differences were recorded between sites. The diversity of abundant species in the three fragments during the dry season did not show differences. The same pattern was observed for diversity based on dominant species (^{2}D) (Fig. 4).

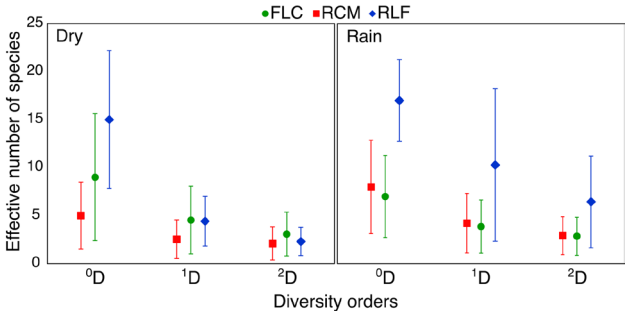


Figure 4. Variation in diversity in terms of ^{0}D, ^{1}D, and ^{2}D (Hill numbers) of the Polistinae wasp community in forest fragments during the dry and rainy seasons.

Beta diversity (β)

Considering the exclusive species, the highest value (10) was recorded in RLF, and the lowest value (1) in FLC. However, RLF and RCM shared nine species, RLF and FLC eight, and RCM and FLC six, while all three fragments shared five species each. On the other hand, high values of beta diversity (Jaccard dissimilarity) were observed. The highest dissimilarity was recorded between RLF and FLC (0.66), with similar values of nestedness and species turnover (0.33 = 33%); while the lowest dissimilarity was reported between FLC and RCM (0.57), with the net value explained by turnover (Fig. 4). Similarly, when comparing climatic periods (dry and rainy) for each fragment, the highest values were recorded in RCM (0.75 = 75%), where turnover (0.57) was greater than nestedness (0.13). On the other hand, the lowest value of beta diversity (0.40 = 40%) was reported in FLC, of which 0.25 corresponded to species turnover and 0.15 to nestedness (Fig. 5).

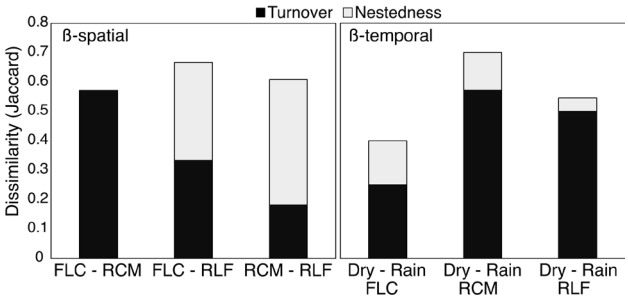


Figure 5. Spatial and temporal variation of beta diversity, based on its turnover and nestedness components, in the Polistinae community of the TDF fragments.

Spatial and temporal variation of the Polistinae community

In the non-parametric multidimensional scaling (nMDS) analysis, differences in the composition and structure of the Polistinae community were recorded in spatial and temporal terms. The wasp community was significantly distinct between the three fragments during both the dry and rainy seasons (Fig. 6). However, there was a slight overlap between RCM during the rainy period and FLC and RCM during the dry season (Fig. 6).

According to the results of the PERMANOVA, the differences observed in the nMDS in the composition and structure of the Polistinae community were confirmed for both, the seasons (Df = 1, R^2 = 0.09, F = 6.15, p = 0.001), the fragments (Df = 2, R^2 = 0.13, F = 4.43, p = 0.001), and the interaction between these two factors (Df = 2, R^2 = 0.07, F = 2.29, p = 0.005).

Relationship between Polistinae diversity and explanatory variables

The generalized linear model showed that the abundance of Polistinae responds to climatic periods (p-value < 0.001), while there are no significant differences between forest fragments (p-value = 0.118). However, the interaction between climatic periods and fragments was found to be influential in the variation of abundance (p-value = 0.023). Additionally, the abundance of Polistinae was influenced by relative humidity and its fluctuation among the three fragments (Table 3).

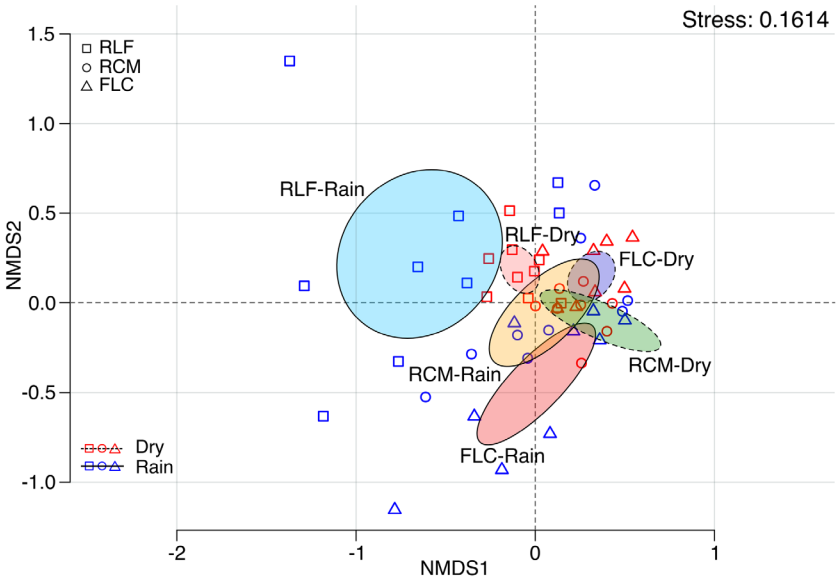


Figure 6. Spatiotemporal variation of the TDF wasp community based on a non-parametric multidimensional scaling analysis with the Bray-Curtis distance index. Abbreviations: FLC: Finca La Clarita; RCM: Reserva Campesina La Montaña; RLF: Reserva La Flecha.

Table 3. Significance level of explanatory variables on the attributes of the Polistinae community (abundance and diversity ^{0}D, ^{1}D, and ^{2}D) based on a generalized linear model. *Indicates significant level.

Response var.	Explanatory var.	LR Chisq	Df	p-value
Abundance	Season	12.3989	1	<0.001*
	Fragment	4.272	2	0.118
	Season×Fragment	7.5019	2	0.023*
	Canopy cover	0.8249	1	0.364
	Relative humidity	15.7081	1	<0.001*
	Fragment×Relative humidity	12.327	2	0.002*
^{0}D Diversity	Season	3.5743	1	0.059
	Fragment	0.2313	2	0.891
	Season×Fragment	1.9059	2	0.386
	Canopy cover	0.1037	1	0.747
	Relative humidity	6.4138	1	0.011*
	Fragment×Relative humidity	2.6371	2	0.268
^{1}D Diversity	Season	8.8362	1	0.003*
	Fragment	1.6531	2	0.438
	Season×Fragment	3.7281	2	0.155
	Canopy cover	0.1147	1	0.735
	Relative humidity	10.5703	1	0.001*
	Fragment×Relative humidity	8.6009	2	0.014*
^{2}D Diversity	Season	11.7714	1	0.001*
	Fragment	2.1086	2	0.348
	Season×Fragment	4.5347	2	0.104
	Canopy cover	0.0836	1	0.773
	Relative humidity	11.8066	1	0.001*
	Fragment×Relative humidity	9.5903	2	0.008*

On the other hand, neither climatic periods nor fragments influenced the variation in species richness (^{0}D), nor their interaction. However, ambient humidity is a factor affecting the variation of this attribute in the Polistinae community (Table 3). Additionally, the variation in the diversity of abundant species (^{1}D) and dominant species (^{2}D) is influenced by climatic periods, as well as ambient humidity and its respective changes across the three locations (Table 3). Canopy cover was not relevant to the variation of the attributes of the Polistinae community in the three fragments.

DISCUSSION

This work represents the first study on social wasps for the TDF of the Colombian Caribbean, contributing to the understanding of the ecology and biology of this group. The number of species (24) represents 9.6% of the species for Colombia (Sarmiento and Saravia 1996, Sarmiento 1997). This highlights the importance of evaluating the conservation value of forest fragments, as they may harbor a portion of the local and national Polistinae fauna. This is particularly significant given the limited number of protected areas in this ecosystem within the national system.

Considering the list of social wasp species for the Colombian Caribbean, this study presents new country records such as *Agelaia centralis*. Regionally, it reports new records

for the expansion of the distribution of *Agelaia pleuralis* in Bolívar, *Agelaia panamensis* in Atlántico and Bolívar, and *Protopolybia scutellaris* in Magdalena. Additionally, species reported for the first time in Bolívar include *Polybia parvulina*, *Polybia diguetana*, *Polistes major colombianus*, *Polistes rufidens*, *Parachartergus fraternus*, and *Metapolybia docilis*. Some species reported in the literature for Atlántico, such as *Charterginus carinatus* and *Metapolybia aztecoides*, were not found in the RCM forest fragment but were present in the RLF (Bolívar). Finally, the record of *Protopolybia scutellaris* in Magdalena expands its distribution in the country, as it had previously been reported only for Chocó. Comparing the species richness found in RLF with the list of social wasps recorded by López et al. (2013), suggests that a representative sample for this fragment was obtained, as evidenced by the high sampling coverage achieved.

The highest diversity in the genera *Polybia*, *Polistes*, and *Agelaia* respectively aligns with studies conducted on this subfamily in the Neotropical region (Sarmiento and Saravia 1996, Sarmiento 1997, Carpenter and Marques 2001, Souza and Prezoto 2006, Prezoto and Clemente 2010, López et al. 2013). For *Agelaia*, this can be attributed to the high capacity of wasps in this genus to exploit various resources and adapt to anthropogenic effects, considering them disturbance-tolerant species. Similarly, *Polybia* species are also generalists (Sarmiento and Saravia 1996, López et al. 2013a). *Polistes* species have a dietary preference for Lepidoptera larvae (Martin and Belloti 1986, Prezoto et al. 2006), which increase their abundance during the rainy season (Wolda 1988), presenting a greater availability of resources that *Polistes* wasps can exploit in the TDF in the Colombian Caribbean. In general, nests of species belonging to the tribe Epiponini can contain millions of individuals in their colonies, whereas nests of Mischocyttarini and Polistini typically have a few dozen individuals per colony (Richards 1978, Ross and Mathews 1991, Sakagami et al. 1996); a characteristic that allows their representatives to establish colonies more effectively and exploit new ecological niches. The genus-level results are similar to those described by Sarmiento (1997) in Colombia and Carpenter and Marques (2001) in Brazil, who also identify *Polybia* and *Polistes* as the most abundant.

Variability in the structure of the Polistinae community was determined by the differential contribution of species to abundance in the fragments. For example, wasps of the genus *Polistes* exhibit greater flight range (Gobbi 1978, Santos et al. 2000, Prezoto and Gobbi 2005, da Cruz et al. 2006, Ribeiro-Junior et al. 2008, Hernández et al. 2009, López et al. 2015), indicating a high likelihood of colonizing new areas and exploiting new resources for establishment, which also increases the chances of being captured. An example is the higher presence of generalist species such as *Agelaia centralis* and *Polybia occidentalis* (Sarmiento and Saravia 1996, López et al. 2013), which exhibit greater ecological tolerance, allowing them to adapt to environmental and phenological changes in the forest associated with temporal variability.

Differences in diversity may be related to the conservation status of the three forest fragments. Community ecology theory suggests that Polistinae diversity is greater in structurally complex environments; greater structural heterogeneity allows for the establishment of richer and more diverse communities due to the availability of resources, nesting sites, and protection (Giller 1984, Santos et al. 2007, 2009). Thus, both the abundance and diversity of social wasps (Polistinae) are attributes of the community determined by the relationship between the structural complexity of vegetation in the tropical dry forest and the availability of food resources (Barros-Henriques et al. 1992, Santos et al. 2009). Additionally, species tolerance to physical conditions and interactions with other organisms must be considered, as some wasps increase their abundance and interactions with other arthropod species during the rainy season, contributing to the seasonality of these social insects (Santos et al. 2007).

The lower number of species recorded in the RCM and FLC fragments can be attributed to the loss of forest cover in these areas, due to the clearing of surrounding vegetation associated with agricultural and mining activities. The higher diversity in the RLF can be attributed to the greater plant heterogeneity in this locality, as much of the primary vegetation is preserved in this fragment. This is due to local practices that prevent extensive logging of timber trees within the forest and adjacent to streams. This is consistent with the high canopy cover values, which indicate greater resource availability that supports the establishment of colonies with a high number of individuals (Richards 1978, Ross and Mathews 1991, Sakagami et al. 1996). Additionally, plant heterogeneity can enhance the coexistence of a greater number of species, such as *Angiopolybia pallens* (Lepeletier, 1836) and *Synoeca cyanea* (Fabricius, 1975), which are only recorded in environments with specific nesting conditions (Marques 1996). It is also suggested that the higher conservation status of this fragment is possibly due to its difficult access and its history as a conflict zone in Colombia. This latter factor acted as a barrier to human activities that would otherwise reduce the complexity of the tropical dry forest fragments in the area.

The higher diversity observed during the rainy season in RLF can be attributed to specific characteristics of seasonal dry forests between the dry season and the onset of the first rains, as there is a direct relationship between this variable and the phenological cycles of the forest (Berdugo and Rangel 2015). Adult Polistinae feed on nectar from flowers and fruits, as well as on the excretions of Hemiptera (Auchenorrhyncha) insects and larvae from the Lepidoptera order and other arthropods that are potential prey for these predators (West-Eberhard et al. 1995). These resources increase with the arrival of the rains in the tropical dry forest in the Colombian Caribbean, allowing the coexistence of many species at a local level.

In RCM, it was observed that much of the vegetation is surrounded by monoculture and agricultural systems, and even the presence of cattle and horses in water bodies within the forest. This indicates a degree of intervention in this fragment, which affects the reduction of understory plant species that could be used as resources by some species with specific habits. In the case of FLC, it is located in a regeneration zone of a former stone quarry; such activities directly impact the ecosystem by removing the soil's vegetation layer and affecting species interactions. Consequently, the diversity observed in this area aligns with the low species richness found in regenerating environments, likely because these phytophysiognomies have open areas with weed growth, leading to less diverse habitats, microhabitats, and food resources—conditions crucial for the establishment and success of different species of social wasps (Graham et al. 2009).

Considering beta diversity, it is evident that the composition of social wasps in the Colombian Caribbean is quite diverse. Although none of the fragments share at least 50% of the species, they showed a tendency to be occupied by very frequent and common species. The species that are shared among the fragments are the most abundant or common (e.g., *A. centralis*, *Po. occidentalis*), which have a higher likelihood of colonizing more habitats, compared to species with lower densities in the fragments (e.g., *Polistes major*, *Polybia chrysothorax*, *Po. diguetana*, *Po. parvulina*) as indicated by the data from this study. High dissimilarity values in terms of species composition of Polistinae among the three sites are due to many species being exclusive to a single fragment, likely explained by the local presence of non-generalist species or those with narrower ecological ranges, or due to past geological events, as these sites do not share the same biogeographic history. Spatial heterogeneity can also cause geographic variation in species distribution (Baselga 2012, 2013, Leibold and Geddes 2005, Calderón et al. 2012).

On the other hand, the high beta diversity among the three fragments is due to turnover and nestedness, as few species were shared between the sites, reflecting a loss of species at the local level. The high turnover values between RCM and FLC could be attributed to biogeographic history as a result of spatial arrangement or historical constraints (Baselga 2010, 2012, 2013), with a low number of shared species despite these fragments have high similarity in their plant composition. For FLC, the wasp community is likely more influenced by the Sierra Nevada de Santa Marta (SNSM) due to its orogenic development, which affects the establishment of species not shared with other fragments. The fact that some species recorded in RCM are also found in RLF suggests that RCM is a subset of the more diverse RLF, with a loss of species possibly due to the reduction and fragmentation of TDF patches.

When comparing wasp composition between the two seasons in the three fragments, less than half of the total species were shared, suggesting that the high turnover of Polistinae species in the TDF of the Colombian Caribbean is related to temporal changes. Additionally, it is possible that many insects living in environments with marked seasonality, such as the TDF, have an emergence and activity period that synchronizes their life cycle with the season that offers a higher number of specific resources for each species. During the rainy season, species seek certain environmental conditions such as optimal temperatures, high vegetation cover, relative humidity, nutrients, and specific sites for building nests. Wasps recorded during the dry season correspond to species active throughout the year, indicating that they have more than one annual generation (multivoltine) or have adaptations necessary to survive during this period when water stress occurs. Although foliage decreases during this time, there is still the availability of food resources such as carrion, exudates, and mammal feces in the forest fragments, which are utilized by generalist species (e.g., *A. centralis*).

On the other hand, changes in the abundance and diversity of Polistinae between seasons can be attributed to phenological changes in vegetation and environmental variables (such as increased relative humidity) due to rainfall. This leads to increased canopy cover, reactivation of leaf and fruit production processes, nutrient dynamics in TDF plants, and the emergence of new ecological niches (Jaramillo et al. 2011). Additionally, the floristic composition has a direct influence on the fundamental and effective niches of social wasp species, providing them with nesting substrates and carbohydrate resources (Clemente et al. 2012), which are utilized by Polistinae for reproduction and colony mainte-

nance. In these fragments, we can infer that precipitation has a direct effect on the distribution of abundances and diversity of these wasps, as a higher proportion of individuals from different species were found during the rainy season.

Finally, ambient humidity and the respective changes between seasons and fragments were among the variables that best explained changes in the abundance and diversity of frequent and very frequent social wasp species. This aligns with the findings of Coutinho et al. (2014), who conducted a study in the Atlantic Forest of the Ubatuba region, Brazil, where relative humidity was one of the best predictors for changes in Polistinae diversity. This can be explained by the ecological tolerance observed in some species of certain genera. For example, nests of *Po. occidentalis* exhibit high foraging activity at low relative humidity (Hernández et al. 2009). Similar behavior was observed in *A. centralis* and *Parachartergus colobopterus* under comparable conditions described by these authors. It is suggested that *A. centralis* is one of the species that responds most effectively to seasonal changes in this region, contributing to the understanding of the biology of these wasps in the TDF of the Colombian Caribbean. It is important to note that species' preferences for habitats or certain environmental conditions are not only due to the resources provided by these factors for their survival but also likely represent an evolutionary response developed to coexist and reduce competition.

The results obtained in this study demonstrate that social wasp species exhibit seasonality in the TDF fragments, with many species showing a positive response in abundance and diversity with the arrival of the rains. This is attributed to the ecological requirements and behavior of different social wasp species, which exploit various resources and are more selective in their nesting habitats, resource foraging, adaptability to habitat changes, and environmental variables in the TDF fragments of the Colombian Caribbean.

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