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Sección Básica / Basic
Artículo de investigación / Research paper

Spatial diversity of dung beetle assemblages (Coleoptera: Scarabaeidae: Scarabaeinae) in five ecoregions from Sucre, Colombian Caribbean coast

Diversidad espacial del ensamblaje de escarabajos coprófagos (Coleoptera: Scarabaeidae: Scarabaeinae) en cinco ecorregiones de Sucre, costa Caribe colombiana

YINA AMELL-CAEZ[1]; INDRADATTA DECASTRO-ARRAZOLA[2]; HÉCTOR GARCÍA[3]; JOSÉ D. MONROY-G.[4]; JORGE ARI NORIEGA[5]

[1] B. Sc. Biología, Universidad del Magdalena, Santa Marta, Colombia, *yinamellbio@gmail.com*. [2] Ph. D. Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, Madrid, España, *indra@mncn.csic.es*, https://orcid.org/0000-0001-6558-5730. [3] B. Sc. Universidad del Magdalena, Santa Marta, Colombia, *coleopterocoprofago@yahoo.es,* https://orcid.org/ 0000-0003-2832-3699. [4] M. Sc. Laboratorio de Zoología y Ecología Animal – LAZOEA, Universidad de Los Andes, Bogotá, Colombia, *dannielmonroy@gmail.com*, https://orcid.org/0000-0002-0893-4727. [5] Ph. D. Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, Madrid, España. Laboratorio de Zoología y Ecología Animal – LAZOEA, Universidad de Los Andes, Bogotá, Colombia, *jnorieg@hotmail.com,* https://orcid.org/0000-0003-1760-7020.

Corresponding author: Jorge Ari Noriega, Ph. D. Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, Madrid, España. Laboratorio de Zoología y Ecología Animal – LAZOEA, Universidad de Los Andes, Bogotá, Colombia, *jnorieg@hotmail.com,* https://orcid.org/0000-0003-1760-7020.

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Abstract: Biodiversity changes in space and time generate complex gradients. These gradients affect community structures, generating beta diversity replacement patterns. The two main patterns of spatial replacement are turnover and nestedness. However, there are very few studies that analyze diversity changes along environmental gradients in the Colombian Caribbean region. In an attempt to understand these spatial changes, a complete sampling was conducted in five Colombian Caribbean ecoregions (Golfo de Morrosquillo, Montes de María, Sabanas, San Jorge, and La Mojana) using dung beetles as an indicator. In each region, a linear transect with 20 pitfall traps baited with dung was established. Differences in abundance, richness, Shannon-index, evenness, and beta diversity between ecoregions were evaluated. A total of 923 individuals belonging to 27 species were collected. The tribe Deltochilini and the genus *Canthon* were the most diverse. The most abundant species was *Silvicanthon aequinoctialis*. Significant differences were found in the parameters measured between the ecoregions. A Beta diversity index established a clear spatial pattern demonstrating high turnover with low nestedness values. The Montes de María ecoregion has the highest diversity, which was linked with the maintenance of conserved forest fragments. It is advisable to generate conservation strategies and the designation of a new National Natural Park for Montes de María in order to stop the negative impact caused by agricultural and cattle farming expansion in the region. This study represents the first effort to understand dung beetle spatial patterns within the ecoregions of the Colombian Caribbean region through connecting environmental gradients and spatial diversity dynamics.

Keywords: Bioindicators, beta diversity, ecoregions, Scarabaeidae, spatial heterogenity, Colombia, Neotropical region.

Resumen: La biodiversidad cambia en el espacio-tiempo generando gradientes complejos. Estos gradientes afectan la estructura de las comunidades creando dos posibles patrones de recambio espacial, reemplazo o anidamiento. Existen pocos estudios que busquen analizar los cambios de la diversidad a lo largo de gradientes ambientales en la región Caribe de Colombia. Buscando entender estos cambios, se realizó un muestreo en cinco ecorregiones del Caribe colombiano (Golfo de Morrosquillo, Montes de María, Sabanas, San Jorge y La Mojana) usando a los escarabajos coprófagos como un grupo bioindicador. En cada región se estableció un transecto lineal con 20 trampas de caída cebadas con excremento. Se evaluaron las diferencias en la abundancia, riqueza, Shannon-índice, equidad y grupos funcionales entre ecorregiones y condiciones ambientales. Un total de 923 individuos pertenecientes a 27 especies fue recolectado. La tribu Deltochilini y el género *Canthon* fueron los más diversos. La especie más abundante fue *Silvicanthon aequinoctialis*. Se encontraron diferencias significativas en los parámetros medidos entre las ecorregiones. La diversidad Beta presenta un claro patrón espacial demostrando un alto recambio y un bajo anidamiento. Los Montes de María presentaron la mayor diversidad, asociada con la conservación de fragmentos de bosque. Es fundamental generar estrategias de conservación y crear un nuevo Parque Nacional Natural para los Montes de María, previniendo el impacto negativo causado por la expansión de la frontera agrícola y ganadera. Finalmente, este estudio representa un primer esfuerzo para entender los patrones espaciales de los escarabajos coprófagos en el Caribe colombiano, relacionando los gradientes ambientales con la dinámica espacial de la diversidad.

Palabras clave: Bioindicadores, diversidad beta, ecorregiones, Scarabaeidae, heterogeneidad espacial, Colombia, región Neotropical.

Introduction

Biodiversity changes in space and time, following complex interactions between gradients, such as altitude, precipitation or temperature (Sanders and Rahbek 2012). Some of the best-known gradients in different regions of the world are those associated to changes in space, such as altitude and latitude (Willig *et al.* 2003). Along these spatial gradient's biodiversity can present replacement patterns in beta diversity that affect community structure and dynamics (Myers and LaManna 2016). Beta diversity can change in space evidencing two easily recognizable patterns that are antagonistic in nature, namely turnover (*i.e.*, replacement of established species by new ones) and nestedness (*i.e.,* a non–random process of species loss without replacement generating a subset of the biota of richer sites) (Baselga 2010). Despite their importance, there are few studies that analyze spatial patterns of species turnover diversity along environmental gradients in the Neotropical region (Escobar 1997; Barraza *et al*. 2010; Louzada *et al*. 2010; Silva and Hernández 2016; Villada-Bedoya *et al*. 2017).

One of the most interesting biogeographical regions in the Neotropics for analyzing spatial turnover is the Caribbean region of Colombia. This area consists of seven Departments (*i.e.,* Atlántico, Bolívar, Cesar, Córdoba, La Guajira, Magdalena, and Sucre) encompassing a broad variety of ecosystems (*i.e.,* dry and rainy forests, mountain forests, valleys, savannas, swamps, and mangroves) with a strong environmental gradient reaching from the dry coastal areas to the extremely humid areas in the interior (Rangel-Ch. and Carvajal-Cogollo 2012; IDEAM 2013). Within the Caribbean region, the Sucre department is one of the Colombian areas with the greatest spatial heterogeneity, presenting a marked environmental gradient that ranges from its coastal dry forests to the extreme humidity of its flooded marshes and the San Jorge and Cauca river basin systems (Aguilera 2005). This diversity in landscape, climate, topography, and vegetation is reflected in the five subregions of the department. Despite the great diversity that defines this area, the ecosystems of the Colombian Caribbean have been severely affected in the last decades by human intervention due to livestock breeding, agriculture, and mining (Rudas *et al.* 2007); a situation that has brought up the necessity to search for strategies that can evaluate the degree of disturbance caused by these activities within them.

A recurrent strategy applied to evaluate anthropological perturbation on biodiversity is the use of bioindicators that allow the estimation and quantification of the degree of environmental disturbance. For this purpose, the dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae) are frequently employed, having been used in different regions of the world as an effective bioindicator group to evaluate and monitor the status of ecosystem health and its conservation (Halffter and Favila 1993; McGeoch *et al*. 2002; Spector 2006; Nichols *et al*. 2007; Otavo *et al*. 2013). The intimate association between this group and vertebrate excrement has important consequences in ecosystem function, contributing to nutrient cycling, soil aeration, parasite control, and seed dispersal (Nichols *et al*. 2008).

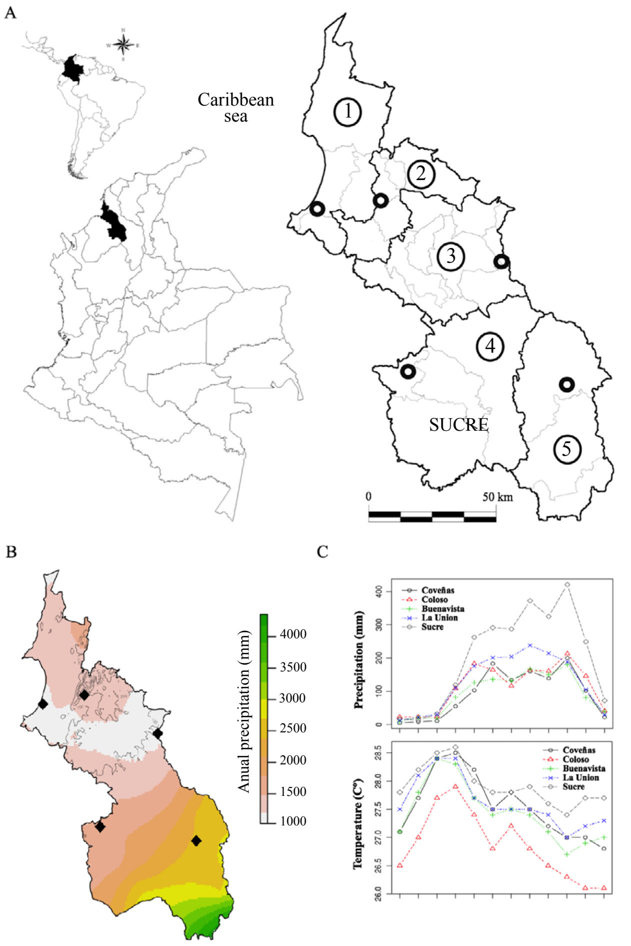
The Sucre Caribbean region in Colombia presents one of the largest knowledge gaps in dung beetles biodiversity patterns in the country due to the lack of appropriate studies (Noriega *et al*. 2013; 2015). Therefore, the main objective of the current study is to analyze the spatial turnover and its effects on the biodiversity of dung beetle's assemblages within the five ecoregions of the Sucre department in the Colombian Caribbean region. The main questions were: How biodiversity changes between the different ecoregions of the Sucre department?, and whether or not these changes present a relationship with spatial environmental variations in temperature, precipitation, and/or humidity? It was hypothesized that the change in dung beetle composition along the assemblages in Sucre will be due to spatial turnover rather than species loss (nestedness), and that the biodiversity maximum will coincide with the optimal environmental conditions for this bioindicator group.

Materials and methods

Study area. The Sucre Department, in the Caribbean region at the north of Colombia (between 10º08'03" - 08º16'46"N and 74º32'35" - 75º42'25"W) has an extension of 10,364 km^2 (Peroza and De la Ossa 1997). The climate is warm with an aridity gradient stretching from dry coastal areas to the more humid areas around the San Jorge river basin. Average annual temperatures oscillate between 25.5 and 28.7 °C, average humidity is 85 % and seasonality is bimodal with two rainy seasons that alternate with dry ones. Rainfall values vary greatly from 1,000 mm along the coastal strip to 3,000 mm in the lower San Jorge region (Aguilera 2005). These environmental gradients originate five physiographic ecoregions within the Sucre department: 1) Golfo de Morrosquillo, 2) Montes de María, 3) Sabanas, 4) San Jorge, and 5) La Mojana (Fig. 1).

Dung beetle sampling. Sample collections were carried out during the rainy season between September and October 2011. One observation station was chosen in each of the five ecoregions (Fig. 1, Table 1), taking into consideration the access routes, conservation status, and the biogeographical and ecological characteristics of each ecoregion. Pitfall traps consisting in 500 ml plastic cups with a diameter of 10 cm and containing 300 ml of 70 % ethanol were buried at ground level (Noriega and Fagua 2009). The bait (50 g mixed 1:1 human-pig excrement) was wrapped in gauze and suspended with a wire above the trap. A white plastic plate was suspended above the trap with another wire, preventing the bait from desiccation and from rainfall. Traps were placed along two 500 m linear transects separated 100 m from each other. Each transect consisted of 10 traps separated 50 m from each other (Larsen and Forsyth 2005), consisting of a total of 20 traps per station and 100 traps for the five ecoregions. Traps were baited at 17 h and maintained for 72 h.

Sample processing. Samples were preserved in 70 % ethanol and their number, transect, and ecoregion recorded. Specimens were then deposited at the Entomological Laboratory of the Universidad del Magdalena (INTROPIC) where morph types were generated. Species identification was carried out at the Zoology and Aquatic Ecology Laboratory of the Universidad de Los Andes (LAZOEA) based on taxonomical keys (Edmonds 1994; Kohlmann and Solis 2001; Solis and Kohlmann 2002; Camero 2010; Vaz-de-Mello *et al*. 2011). Each species was allocated to a trophic relocation guild (*i.e.*, paracoprids, telecoprids, and endocoprids) following the traditional classification (Halffter and Edmonds 1982;



D

No	Subregion	Sampling coordinates	Altitude (masl)	Life zone	T (°C)	P (mm/year)	H (%)
1	Morrosquillo	9º28'11.30"N - 75º35'16.65"W	15	BsT	27.4	1,000	70
2	Montes de María	9º30'56.21"N - 75º21'31.30"W	120	BsT	26.8	1,100	75
3	Sabanas	9º19'14.89"N - 74º57'15"W	85	BsT/S	27.2	1,350	80
4	San Jorge	8º50'50.10"N - 75º16'17.67"W	50	BhT/S	28.1	2,200	82
5	Mojana	8º46'41.25"N - 74º44'24.12"W	30	BhT/H	28.5	2,550	85

Figure 1. Location and climatic characteristics of the studied areas: **A.** Map of the ecoregions in the Sucre Department and sampling sites: (1) Morrosquillo (Mpio. Coveñas), (2) Montes de María (Mpio. Coloso), (3) Sabanas (Mpio. Buenavista), (4) San Jorge (Mpio. La Union), and (5) Mojana (Mpio. Sucre). **B.** Ecoregional annual precipitation map. **C.** Ecoregional variation in annual precipitation and temperature. **D.** Geographical coordinates of sampled locations and environmental values (T: average annual temperature, P: average annual precipitation, and H: average annual relative humidity).

Doube 1990) and the dung-relocation behavior of each genus. Individuals were mounted, labelled, and deposited at the Universidad del Magdalena Entomological Collection (CEUM) and the last author reference collection (CJAN).

Environmental values. Three bioclimatic variables: annual average temperature (°C), annual average precipitation (mm), and annual average humidity (%) of WorldClim were used (see www.worldclim.org; Hijmans *et al*. 2005), at a resolution of 2.5 minutes (approximately 25 km^2), as environmental predictors (Fig. 1).

Data analysis. Relative species abundances were evaluated by means of species accumulation curves in EstimateS v. 8.2 (Colwell 2011). Alfa diversity was described using the total number of species (S), Margalef's richness parameter (d), the Shannon-Wiener index (*H'*), and Pielou's evenness index (*J'*) with PRIMER 6.0 (Clarke and Gorley 2006). Normality in the data was checked with the Shapiro-Wilk test and homogeneity of variances with Bartlett's test. To determine whether there were differences between abundance and richness between ecoregions a Kruskall-Wallis test was performed in Statistix v. 8.1 with a significance threshold of $\alpha = 0.05$. The similarity between ecoregions was estimated with the Jaccard (I_J) and Sorensen indexes (I_S) (Moreno 2001). Beta diversity was assessed with the index proposed by Baselga (2010), which decomposes total beta diversity into turnover and nestedness components (β_{SIM}: Simpson dissimilarity - spatial turnover, β_{NES}: nestedness dissimilarity, and β_{SOR}: Sørensen dissimilarity – total Beta diversity; measuring additive fractions: $\beta_{SOR} = \beta_{SIM} + \beta_{NES}$) performed in R v. 3.1.1 program (R Development Core Team 2016), using the *betapart* package (Baselga and Orme 2012). Likewise, the Colwell and Coddington (1994) complementarity index was calculated to understand the composition overlap of assemblages. An NMDS (non-metric multidimensional scaling) analysis of the Bray-Curtis similarity index, transforming the abundances to log $(x + 1)$ (Clarke and Gorley 2006), was performed in PRIMER v. 6 (Clarke and Gorley 2006) to determine spatial turnover between ecoregions considering abundance of species.

Results

Interpretation of the sampling effort curves for each ecoregion evidence that the number of observed species was above 90 % of the total species expected (1 = 95 - 100 %, 2 = 90 - 100 %, 3 = 99-100 %, 4 = 97 - 100 %, 5 = 99 - 100 %) when applying the values for singletons, doubletons, and the ACE, Chao 1, Chao 2, and Jack 1 indexes (Fig. 2). These values demonstrate that the number of traps used was adequate to sample a representative percentage of species of the dung beetle assemblage within the five ecoregions.

Composition, abundance, richness, and functional guilds. A total of 923 individuals were collected belonging to 27 species, 12 genera, and eight tribes (Table 1). The tribe with the largest number of species was Deltochilini (n = 9), followed by Onthophagini (n = 6). *Canthon* was the most diverse genera with six species (Table 1). The species *Pseudocanthon perplexus* (LeConte, 1847) was registered for the first time within the Sucre department. The most abundant species was *Sylvicanthon aequinoctialis* (Harold, 1868) (n = 370, 40.08 %), followed by *O. marginicollis* Harold, 1880 (n = 166, 17 %), and *P. perplexus* (n = 99, 10 %) (Table 1). Significant differences in abundance ($H = 49.61$, $P \leq 0.001$, n = 20; Fig. 3A) and richness ($H = 50.75$, $P \leq 0.001$, n = 20; Fig. 3B) were observed between ecoregion stations. Twenty-three species (n = 647) were collected at station 2, seven (n = 52) at station 1, five (n = 105) at station 4, four (n = 28) at station 3, and three (n = 91) at station 5 (Table 1, Fig. 3). Ecoregion 2 registered the highest Margalef's richness index (d = 3.55) and the highest Shannon-Wiener value (*H'* = 1.72), while ecoregion 5 the smallest value (Table 1). Evenness values (*J'*) displayed large differences between ecoregions, from 0.85 (ecoregion 1) to 0.43 (ecoregion 5) (Table 1). In relation to the functional guilds, 17 species were paracoprids (tunnelers, 63.0 %), nine telecoprids (rollers, 67.8 %), and one endocoprid (dweller,

Tabla 1. Diversity of dung beetles present within the five ecoregions: (1) Morrosquillo, (2) Montes de María, (3) Sabanas, (4) San Jorge, and (5) Mojana of the Sucre Department, Colombian Caribbean. Relocation guilds (G): paracoprids (P), telecoprids (T), and endocoprids (E).

Tribe	Species	G	Ecoregions					Total (%)
			1	2	3	4	5	
Ateuchini	*Ateuchus* sp. 1	P	0	3	0	0	0	3 (0.3)
	Ateuchus sp. 2	P	0	4	0	0	0	4 (0.4)
Coprini	*Canthidium euchalceum* Balthasar, 1939	P	0	4	0	0	0	4 (0.4)
	Canthidium aurifex Bates, 1887	P	0	5	0	0	0	5 (0.5)
	Dichotomius cf. *agenor* (Harold, 1869)	P	4	30	0	0	0	34 (3.7)
Coptodactylini	*Uroxys* sp. 1	P	0	3	0	0	0	3 (0.3)
	Uroxys sp. 2	P	0	1	0	0	0	1 (0.1)
	Uroxys sp. 3	P	0	5	0	0	0	5 (0.5)
	Uroxys sp. 4	P	0	9	0	0	0	9 (1.0)
Deltochilini	*Sylvicanthon aequinoctialis* (Harold, 1868)	T	0	370	0	0	0	370 (40.1)
	Canthon cyanellus Harold, 1863	T	0	2	0	0	0	2 (0.2)
	Canthon juvencus (Harold, 1868)	T	0	0	0	4	3	7 (0.8)
	Canthon mutabilis Lucas, 1857	T	0	0	14	0	0	14 (1.5)
	Canthon lituratus (Germar, 1813)	T	3	5	2	0	0	10 (1.1)
	Canthon septemmaculatus (Latreille, 1811)	T	3	7	0	0	0	10 (1.1)
	Canthon subhyalinus Harold, 1867	T	0	18	0	0	0	18 (2.0)
	Deltochilum guildingii (Westwood, 1835)	T	0	10	0	0	0	10 (1.1)
	Pseudocanthon perplexus (LeConte, 1847)	T	13	0	0	4	82	99 (10.7)
Demarziellini	*Trichillidium pilosum* (Robinson, 1948)	P	0	5	0	0	0	5 (0.5)
Oniticellini	*Eurysternus caribaeus* (Herbst, 1789)	E	2	7	0	0	0	9 (1.0)
Onthophagini	*Digitonthophagus gazella* (Fabricius, 1787)	P	12	0	0	0	0	12 (1.3)
	Onthophagus acuminatus Harold, 1880	P	0	9	0	0	0	9 (1.0)
	Onthophagus marginicollis Harold, 1880	P	15	63	12	70	6	166 (18.0)
	Onthophagus landolti	P	0	61	0	24	0	85 (9.2)
	Onthophagus cf. *clypeatus* Blanchard, 1843	P	0	16	0	0	0	16 (1.7)
	Onthophagus sp. 1	P	0	1	0	3	0	4 (0.4)
Phanaeini	*Phanaeus hermes* Harold, 1868	P	0	9	0	0	0	9 (1.0)
	Abundance		52	647	28	105	91	923
	Richness		7	23	3	5	3	27
	Margalef index (d)		1.87	3.55	0.98	1.14	0.57	-
	Shannon index (H')		1.66	1.72	0.85	0.94	0.47	-
	Pielou index (J')		0.85	0.56	0.62	0.58	0.43	-

3.7 %) (Table 1, Fig. 4). Species from ecoregions 2 and 4 tended to be paracoprids (67.8 %, n = 19), while those from ecoregions 3 and 5 were predominantly telecoprids (66.6 %, n = 4) (Fig. 4). The most abundant guild in ecoregions 2, 3, and 5 was the telecoprids (66.9 %, n = 513), while in 1 and 4 paracoprids were most abundant (81.5 %, n = 128) (Fig. 4).

Table 2. Complementarity analysis between the five ecoregions of the Sucre Department, Colombian Caribbean. In parenthesis: the number of species shared between ecoregions.

	Ecoregions				
	1	2	3	4	5
	Morrosquillo	Montes de María	Sabanas	San Jorge	Mojana
1) Morrosquillo	-	(5)	(2)	(2)	(2)
2) Montes de María	0.81	-	(2)	(2)	(1)
3) Sabanas	0.72	0.92	-	(1)	(1)
4) San Jorge	0.81	0.92	0.87	-	(3)
5) Mojana	0.75	0.96	0.83	0.41	-

Complementarity, beta diversity, and spatial pattern between regions. The complementarity index (C) revealed that ecoregion 2 was the most dissimilar in relation to species composition, sharing only one species with ecoregion 5 (C = 0.96), but showing similar values with ecoregions 2 and 3 and 2 and 4 (C = 0.92; Table 2); ecoregions 4 and 5 were the most similar with a complementarity index of C = 0.4. The partition of beta diversity index presented an overall high total Beta diversity (βsor > 0.6 in all 5 ecoregions) with a marked pattern of high turnover (βsim around 60-70 % of total Beta) with low

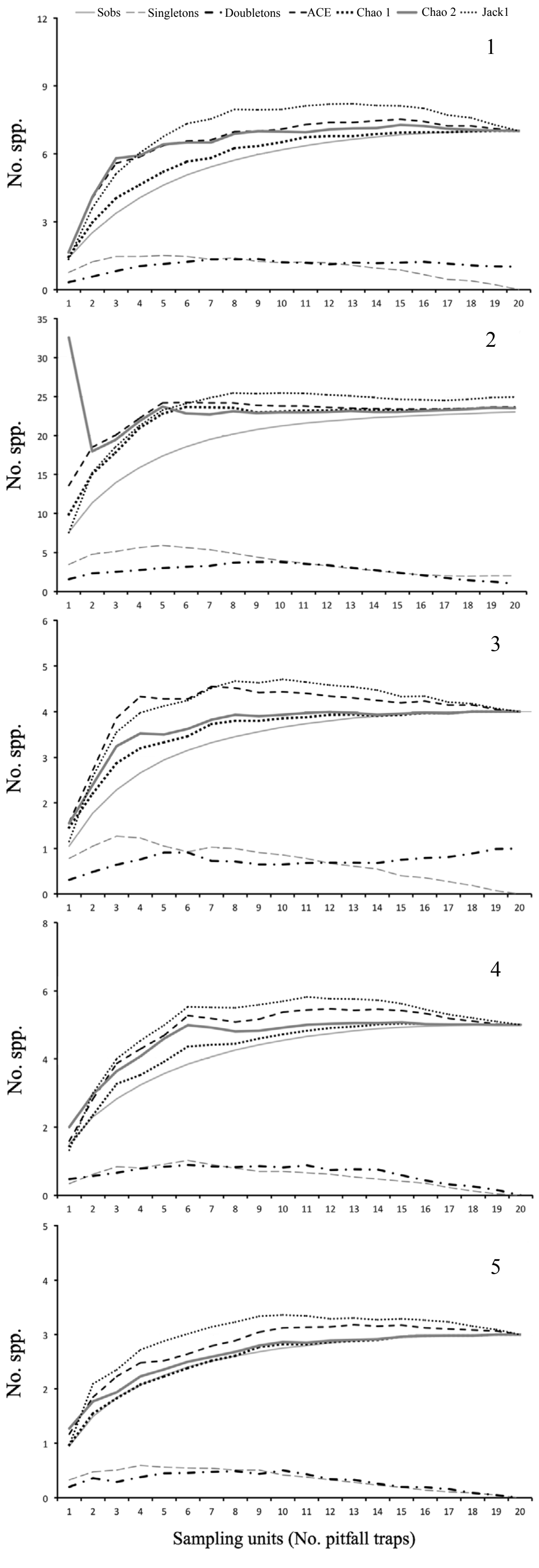


Figure 2. Sampling effort curves for the dung beetle's species (Coleoptera: Scarabaeinae) in the five ecoregions: (1) Morrosquillo, (2) Montes de María, (3) Sabanas, (4) San Jorge, and (5) Mojana, Sucre Department, Colombian Caribbean. N = 20 traps per region.

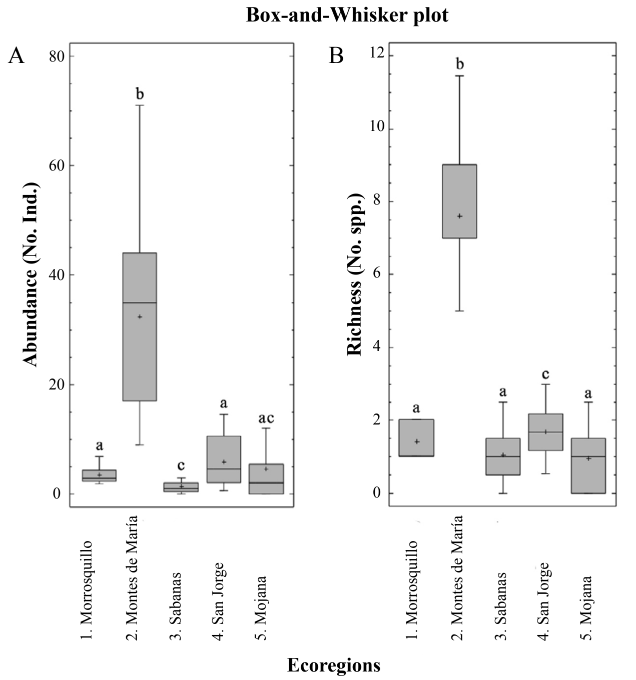


Figure 3. Boxplots illustrating differences in: **A.** Abundance and **B.** Richness between the five ecoregions of the Sucre Department, Colombia. N = 20 traps per region.

nestedness values in the five ecoregions (βnes around 25 % of total Beta) (Fig. 5). The Sabanas region presented the highest species turnover, and Montes de María the most nested composition (βnes). This pattern is even clearer if abundance is considered, using Bray-Curtis. In addition, the NMDS analysis displayed a spatial separation of the five ecoregions, indicating a strong spatial pattern (Fig. 6).

Environmental values and diversity. The Spearman correlation coefficients for species richness and abundance of dung beetles in the five ecoregions demonstrated that temperature have the highest relationship with richness (r = 0.679) and abundance (r = 0.564), followed by precipitation and humidity (Table 3).

Discussion

Biodiversity changes in space results in complex interaction gradients that affects the structure of communities (Sanders and Rahbek 2012). One of the most interesting biogeographical regions in the Neotropics for analyzing spatial diversity changes is the Caribbean region of Colombia, due to the high spatial turnover between different ecosystems in a reduce space. Because of this, we asked the following question: How biodiversity changes between different ecoregions of the Sucre department? Using dung beetles as a bioindicator tool we hypothesize that the change in dung beetle diversity between regions will be due to a spatial turnover pattern. In general terms, important differences were observed in abundance, richness, Shannon index, evenness, and functional groups between the different ecoregions. The beta diversity index established a marked spatial pattern demonstrating high turnover and validating our hypothesis. In addition, the results we obtained on this study constitute one of the first efforts to

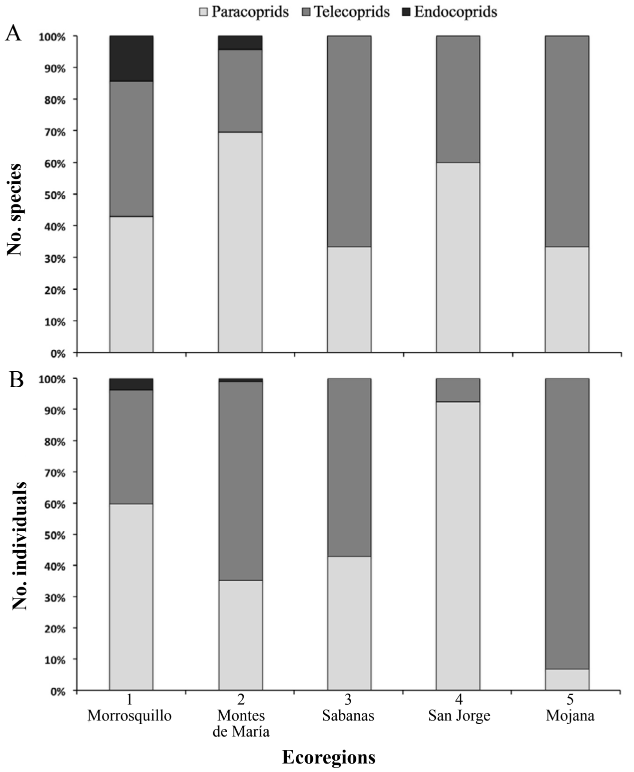


Figure 4. Cumulative percentage of: **A.** Number of species and **B.** Number of individuals classified by relocation guild (paracoprids, telecoprids, and endocoprids) in the five ecoregions: (1) Morrosquillo, (2) Montes de María, (3) Sabanas, (4) San Jorge, and (5) Mojana, of the Sucre Department, Colombian Caribbean. N = 20 traps per region.

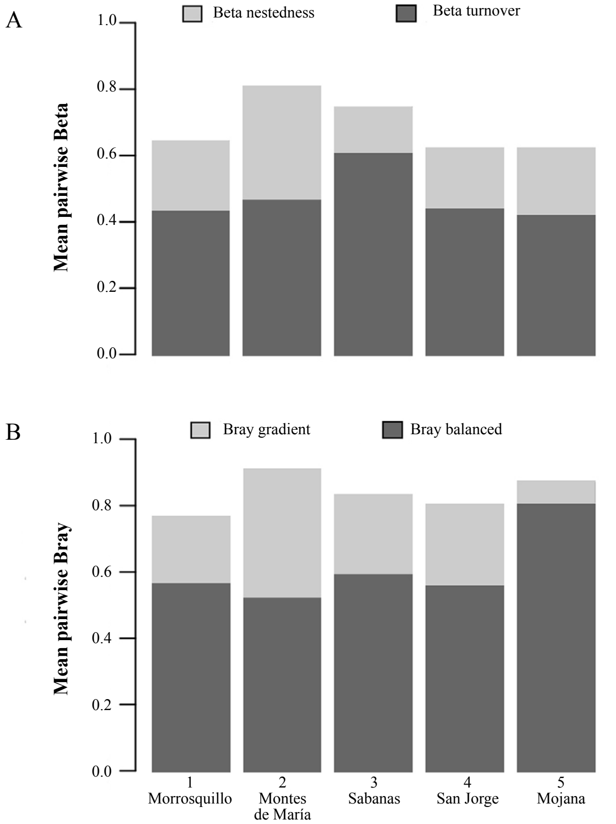


Figure 5. Turnover values for: **A.** Beta (nestedness and turnover) and **B.** Bray-Curtis (gradient and balanced) indices for the five ecoregions of the Sucre Department, Colombia. N = 20 traps per region.

systematically understand dung beetle spatial patterns within the ecoregions of the Colombian Caribbean, including the effects of environmental gradients on the spatial dynamics of diversity.

Composition, abundance, and richness. Species composition, abundance, and richness appear to be in accordance to what has been observed in other studies related to climate seasonality (Janzen 1983; Davis 1996; Andresen 2005; Labidi *et al*. 2012; Noriega *et al*. 2016). However, species richness varies substantially between ecoregions, presenting its highest value in the Montes de María region due to an inferior level of perturbation and higher degree of conservation. In addition, this region accommodates the most adequate climatic conditions in temperature, precipitation, and humidity (*i.e*., 26.8 °C, 1,100 mm, and 75 % humidity; variables strongly related with the conservation level of the vegetation cover) to maintain dung beetles' populations, as registered in other studies for other regions (Nunes *et al*. 2016; Silva *et al*. 2016; Gómez-Cifuentes *et al*. 2017). Likewise, the low richness observed in other ecoregions may be due to a higher level of perturbation and habitat degradation as a result of extensive livestock breeding (Aguilera 2005). Other possible factors that could contribute to this pattern are the reduction of wild mammal populations, the fragmentation of forests, and especially the growth of agricultural frontier (Gill 1991; Halffter 1991; Escobar 1997). In accordance with the indexes of diversity, a marked difference between ecoregions is observed, that may be related to the typology of the soil that is less compact and humid in forests in contrast to those found in the savannas, which obstruct the establishment of dung beetles since they are lacking a plant cover (Howden and Nealis 1975; Halffter *et al*. 1992; Estrada and Coates-Estrada 2002).

Of the 12 genera and 27 species registered in this study, *P. perplexus* is a new record for the Sucre department; this observation evidences the necessity for more in-depth surveys in this area. The species richness encountered in the five ecoregions coincides with those registered in punctual studies within the department (Navarro *et al*. 2011a, 2011b; Tovar *et al*. 2016) and with others carried out in the Colombian Caribbean (Noriega *et al*. 2007; Martínez *et al*. 2009; Solis *et al*. 2011; Cárdenas-Bautista *et al*. 2012; Delgado-Gómez *et al*. 2012). In this manner, the genus *Canthon* was the most abundant in all ecoregions as reported by other authors (Jiménez-Ferbans *et al*. 2008; Martínez *et al*. 2009, 2010; Solis *et al*. 2011), suggesting that this taxon is one of the widely distributed in the Colombian Caribbean region. The dominance of tunnelers species in certain ecoregions may be related to the differential availability of trophic resources and with the type of soil; the latter represents a fundamental

Table 3. Spearman correlation coefficients for species richness and abundance of dung beetles in the five ecoregions versus temperature, precipitation, and humidity in the Sucre Department, Colombian Caribbean.

	Temperature	Precipitation	Humidity
Richness	0.679	0.522	0.471
Abundance	0.564	0.345	0.261

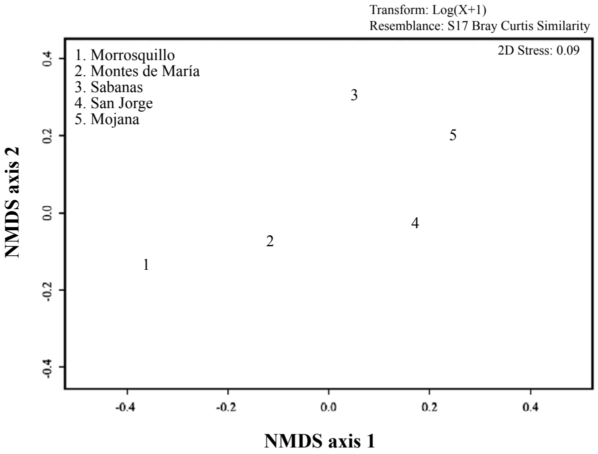


Figure 6. NMDS analysis employing the Bray-Curtis similarity index for the dung beetle's assemblage in the five ecoregions of the Sucre Department, Colombia.

factor that determines the abundance of this group (Halffter 1991; Hanski and Cambefort 1991; Osberg *et al*. 1994). The marked abundance of *S. aequinoctialis* may be attributed to its unambiguous association with primate excrement, which is especially abundant in the Montes de María ecoregion (Galván 2010). Lastly, the presence in the ecoregion of Morrosquillo of an introduced species from Africa (*D. gazella* (Fabricius, 1787)) that is strongly associated to disturbed areas with livestock (Navarro *et al*. 2009; Noriega *et al*. 2011) suggest the high level of perturbation that exists in this area due to an increase in the cattle industry.

Functional guilds and spatial diversity patterns. It was evident that the structure of the assemblage, in terms of the abundance and richness of each ecoregion, affects the presence of the three main functional guilds. The paracoprids were dominant in terms of richness (N = 17 spp.), meanwhile the telecoprids were dominant in abundance (due to the high numbers of *S. aequinoctialis*, N = 370 ind.). The non–appearance of any endocoprid species in region 3, 4, and 5 corroborate the impoverishment of the assemblage structure in these areas. There is a slight tendency to equilibrium in the proportion between paracoprids and telecoprids in all regions, except on region 2 where the high diversity numbers increase the number of paracoprids species. This high richness (especially of telecoprids) might be also connected to the food resource offer in the area, and especially the presence of primates that could support a high diversity of rollers (Estrada *et al*. 1993, 1999; Noriega 2012). Furthermore, there is a high proportion of telecoprids species in the Caribbean region in comparison with other areas in Colombia, where the proportion of rollers is lower (Neita and Escobar 2012; Otavo *et al*. 2013; Villada-Bedoya *et al*. 2017).

Species turnover was exceptionally different between ecoregions, displaying near zero values for the Jaccard and Sorensen indexes, and demonstrating a marked spatial pattern and strong turnover due to varying environmental conditions. In addition, the complementarity index displayed high values, which indicates that the number of species shared between ecoregions is low. In general terms, there is a strong spatial turnover in species richness (*i.e.,* turnover, Bsim) between the five ecoregions, which increases towards the central area of the environmental gradient (Sabanas ecoregion). Although some species loss (*i.e.,* nestedness, Bnes) is observed in all ecoregions, these values are very low in comparison to the real turnover between them. This pattern is consistent with that observed in studies carried out in other parts of the world presenting accentuated environmental variance (Labidi *et al.* 2012).

Conservation interest. It is manifest that the Montes de María ecoregion is an area of great biotic importance (Rudas *et al.* 2007; Rangel-Ch. and Carvajal-Cogollo 2012) regarding it hosts a high richness of dung beetle species associated to the remaining forest fragments in this region. Our results suggest that the five ecoregions are strikingly different in their species assemblage structure since they presented few similarities in their composition, abundance, and richness. The diversity of the dung beetle's assemblage exhibits a spatial pattern associated to the heterogeneity of the landscape, conservation status of the forest cover, climate, and soil use in this region (Aguilera 2005). A decline in the diversity associated with environmental variation, conservation status, change of ecosystem function, and degree of soil compaction was observed.

It is essential to propose and generate conservation strategies for the Montes de María ecoregion in the interest of potentially creating a novel conservation zone and the designation of a new National Natural Park. At present, the Sucre department only counts with two protected area systems, which shares with the Bolivar Department: (1) PNN Islas del Rosario and San Bernardo in ocean territory, and (2) Santuario de Fauna y Flora El Corchal El Mono Hernández in the continental territory. This sanctuary was created in 2002 for protection of the mangroves and has a surface area of 38.5 km^2, of which little more than 50 % is located within the Sucre Department. This makes Sucre at the national level one of the departments with the lowest percentage of protected areas in Colombia (less than 0.02 % of 142,682 km^2 in total) (SINAP 2018). Furthermore, the existing reserves in the region should be enlarged to increase the spatial connection between small and medium forest fragments with existing corridors. Finally, it is important to generate governmental strategies at the municipal and departmental levels to try to stop the negative impact caused by the expansion of the agricultural and cattle farming into the Caribbean region.

The degree of fragmentation and the loss of vegetation cover to which the few remaining forest relicts are subjected in this region generate a marked effect in the registered biodiversity. The extension of the agricultural and cattle farming frontier has caused a sharp decline in the diversity of this group of insects; bioindicators that have been evidenced to play an irreplaceable role in the stability and functionality of the ecosystems where they inhabit. It is crucial to continue performing similar studies in this area on a landscape scale with the purpose of contributing to the understanding of how the different agricultural and livestock practices influence ecosystem degradation in the ecoregions, and consequently develop management and conservation strategies.

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Author contributions

Jorge Ari Noriega and Yina Amell-Caez conceived the idea and designed the research and designed and structured the manuscript. Yina Amell-Caez gathered the data. Jorge Ari Noriega, Yina Amell-Caez, José D. Monroy-G, and Indradatta Decastro-Arrazola analyzed the data; Jorge Ari Noriega and Yina Amell-Caez wrote a first version of the paper with the help of Héctor García and Indradatta Decastro-Arrazola. All authors discussed results and approved the last version of the paper.