Biodiversidad y variación altitudinal de los escarabajos estercoleros (Scarabaeidae: Scarabaeinae) en la cuenca del Oglán Alto, Amazonia ecuatoriana

Biodiversity and Altitudinal Variation of Dung Beetles (Scarabaeidae: Scarabaeinae) in the Oglán Alto Watershed, Ecuadorian Amazon

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RESUMEN

Los escarabajos peloteros se consideran un taxón útil para describir patrones espaciales y temporales de biodiversidad. Este estudio se llevó a cabo durante 18 meses, en un gradiente altitudinal, de la cuenca del Oglán Alto, situada en la provincia de Pastaza, Ecuador. Se recolectaron un total de 10.227 individuos pertenecientes a 59 especies. Se analizó la preferencia alimentaria y se observó que las especies de escarabajos coprófagos son superiores a las especies necrófagas y generalistas. El grupo funcional de los cavadores fue más abundante que rodadores y moradores. Los efectos de la altitud y precipitación sobre la diversidad de escarabajos estercoleros se analizó mediante modelos lineales generalizados. Se utilizaron seis estimadores de riqueza para comparar los dos tipos de cebo utilizados (excremento y carroña). Se

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realizó un análisis de correspondencia, según los tipos de trampas y especies capturadas, con respecto a la variación del gradiente altitudinal. Se concluyó que la riqueza y abundancia de los escarabajos peloteros se ven influencias negativamente con la altitud y la precipitación. Pero, el grupo de cavadores evidenciaron una influencia positiva con la precipitación. Aunque la relación de gradiente altitudinal y promedio de riqueza por trampas es muy similar en el gradiente altitudinal muestreado, mostrando una mezcla de especies de escarabajos copronecrófagos asociados a tierras bajas amazónicas, con pocas especies de bosque siempreverde de piedemonte del oriente ecuatoriano. Se recomienda continuar los estudios en este tipo de vegetación, principalmente en un gradiente altitudinal mayor.

Palabras clave — Abundancia, grupo funcional, preferencia alimentaria, riqueza, transectos.

ABSTRACT

Dung beetles are considered a useful taxon to describe and to monitor spatial and temporal patterns of biodiversity. This study was carried out over 18 months, on an altitudinal gradient in the Oglán Alto watershed, located in Pastaza Province, Ecuador. A total of 10,227 individuals belonging to 59 species were collected. Food preference was analyzed and it was observed that species of coprophagous beetles are superior to necrophagous and generalists species. Tunnelers functional group was more abundant than rollers and dwellers groups. The effects of altitude and precipitation on dung beetle diversity were analyzed using generalized linear models. Six richness estimators were used for comparison between the two types of bait used (excrement and carrion). Correspondence analysis was performed, according to the types of traps and species captured, with respect to the variation of altitudinal gradient. We concluded that the richness and abundance of dung beetles are negatively influenced by altitude and precipitation. However, the group of tunnelers evidenced a positive influence on precipitation. Although the relation of altitudinal gradient and average of richness by traps is very similar in the altitudinal gradient sampled, showing a mixture of species of copronecrophagous beetles associated to Amazon lowlands, with few species of foothill evergreen forest of the Ecuadorian east. It is recommended to continue studies in this type of vegetation, mainly in a higher altitudinal gradient.

Keywords — Abundance, food preference, functional group, richness, transects.

INTRODUCTION

The dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are considered a useful taxon to describe and to monitor spatial and temporal patterns of biodiversity (Favila y Halffter, 1997; Nichols et al., 2007). Tropical communities of dung beetles are usually diverse, abundant, and habitat specific; these scarabs respond quickly to many types of environmental changes and their composition and abundance can be sampled with relative accuracy and low cost (Favila and Halffter, 1997; Larsen and Forsyth, 2005).

These insects have important ecological functions in the forests, such as recycling decomposing organic matter, fertilization, soil aeration, water penetration into the soil, control of pest flies and enteric parasites of vertebrates, and secondary seed dispersal of seeds defecated by frugivorous vertebrates (Halffter and Edmonds, 1982; Davis, et al., 2001; Andresen, 2005; Nichols et al., 2007). They are a highly diverse group, with generalist and specialist species very sensitive to environmental variability (Favila and Halffter, 1997).

Vegetation coverage determines the abundance and species richness of these beetles, but these variables also may be correlated to other environmental features, such as soils, rainfall and mammal communities (Forsyth and Spector, 1997). The association of the species with a given type of habitat seems to be related to its microclimate requirements (i.e. temperature, relative humidity, light intensity) and to its close dependence on mammalian feces for feeding and reproduction (Halffter and Matthews, 1966).

The composition and dynamics of dung beetle communities in tropical habitats have been studied in detail in tropical lowland forest, tropical flooded forests, semi-deciduous forests and tropical dry forests (Peck and Forsyth, 1982; Escobar, 2000a; Andresen, 2005; Carpio, Donoso, Ramón, Dangles, 2009; Domínguez, Marín-Armijos, Ruiz, 2015). However, mid-elevation habitats in the Ecuadorian Amazon occupied by the foothill evergreen forest have not been studied yet. Except for a complete list of species in the locality of the present study (Chamorro et al., 2019) and other study shows preliminary results in an altitudinal gradient between 400 - 2200 m (Espinoza and Noriega, 2018).

The dung beetle, Scarabaeinae, is a group largely adapted to warm or warm-temperate conditions, dominate in the lowlands and show a decrease in species richness as altitude increases (Escobar, 2000b; Lobo and Halffter, 2000). In the transitional zone between lowland forest and mountain forests of region the number of species decreases consistently, with a peak of richness in forests located in intermediate altitudes (554 - 944 m) and then decrease dramatically (Escobar, 2000b). The dung beetle fauna of the intermediate and high altitudes on the mountains is derivative of the one found in the neighboring lowlands. This is a product of the process of vertical colonization and can be explained by the restrictions imposed by altitude in terms of the environment (decreasing temperature) and the reduction in food availability; conditions that require physiological adjustments if the higher altitudes of the mountains are to be colonized (Escobar, Halffter, Arellano, 2007).

Through altitudinal gradients across the mountains, the species turnover is much more pronounced in relatively short distances, which often do not exceed 7 km (Escobar, 2000b). Overall, the changes in flora and fauna in mountainous areas are determined by elevation and precipitation levels; however, factors such as geological history, topography, orientation and inclination of the mountains could explain the diversity and distribution patterns in species (Escobar, 2000b). The objectives of this study are to determine the variation in richness, abundance and composition of dung beetle communities along an altitudinal gradient from 577 to 947 meters in foothill evergreen forest at the Ecuadorian Amazon and to examine seasonal changes in richness and abundance during 18 months of sampling.

MATERIALS AND METHODS

Study Area

The study was carried out in the Oglán Alto watershed, that belongs to the Pablo López Kichwa community and Shuar Washents community, located in the upper basin of the Oglán river (1º19'29" N, 77º41'20" W), Arajuno and Pastaza Province, Ecuador (Figure 1). The mean annual temperature varies between 16 and 30ºC and the mean annual rainfall exceeds 4000 mm (Palacios and Ontaneda, 2009). The study site is covered by two principal vegetation formations: evergreen lowland forest and foothill evergreen forest (Palacios, Cerón, Valencia, Sierra, 1999).

Fieldwork

Fieldwork was performed from March 2008 until August 2009 (18 months), during the last six days of each month. Dung beetles were sampled using pitfall traps, consisting of plastic containers 140 mm tall and 120 mm in diameter, with 30 grams of two types of bait: human feces and fish carrion. Traps were placed along four lineal transects of 200 m each along the following altitudinal gradient (altitudes estimated at the center of each transect): T1: 947 m, T2: 820 m, T3: 640 m and T4: 577 m. The first three transects were located in foothill evergreen forest and the last one in evergreen lowland forest (Figure 1). Along each transect 10 sampling points were placed, separated by 22 meters. In each sampling point a trap with human feces was placed on the left side at distance of four meters perpendicular to the transects and a trap with carrion bait was placed at the right side also at 4 meters. The traps were left 48 hours each month, and the beetles collected were killed and preserved in 70 % alcohol for subsequent determination in the laboratory using taxonomic keys, photographs and literature. We used the taxonomic specific articles (Cook, 1998; Génier, 1996, 2009; Arnaud, 2002; Vaz-De-Mello, Edmonds, Ocampo, Schoolmeesters, 2011) for the identification of all species.

Species with at least 10 registered individuals were classified into three defined trophic groups, following criteria: (1) Coprophagous, species which at least 70 % of individuals were captured in dung-baited traps; (2) Necrophagous, species which at

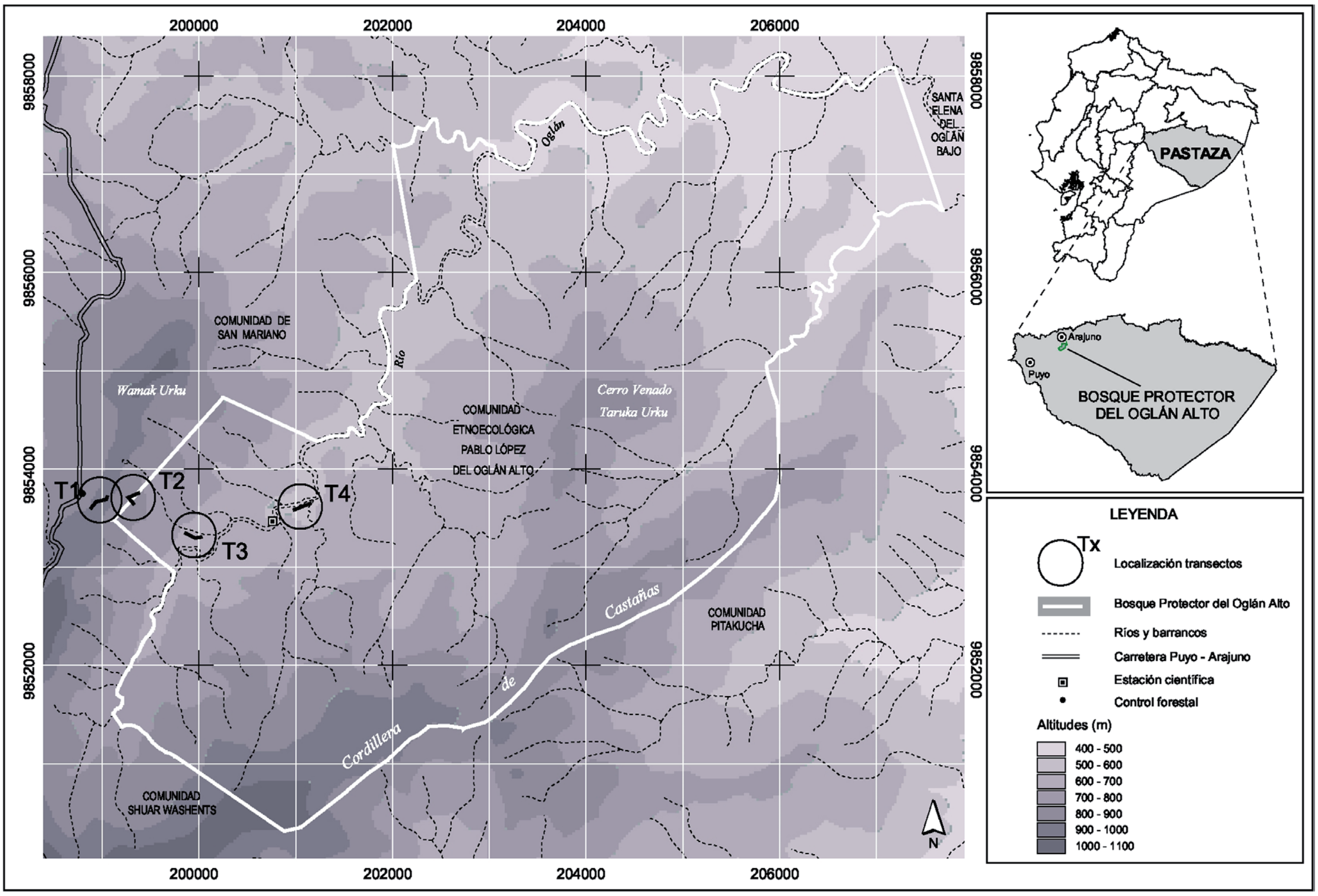

Figure 1. Map of the study area with the location of the four altitudinal transects where copronecrophagous scarabs were collected.

Figura 1. Mapa de la zona de estudio con la ubicación de los cuatro transectos altitudinales donde se recolectaron escarabajos copronecrófagos.

least 70 % of individuals were captured in carrion-baited traps; and (3) Generalists, the ones that do not follow the previous criteria (Halffter and Favila, 1993). These percentages [$\geq$ 70% (trophic groups)] were well defined, no statistical tests were applied and are understood as preferences or not for each resource. The species were also classified into three functional groups: (A) dwellers or endocoprids, referring to the ones that feed and reproduce directly in the dung pat, without digging galleries; (B) tunnelers or paracoprids, referring to the ones that dig galleries and build their nest directly under the dung pat; and (C) rollers or telecoprids, referring to the ones that make balls of dung and roll them away from the dung pat for burial in the soil (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991).

Data Analysis

The effects of altitude and seasonality on dung beetle richness and abundance were determined using advanced statistical methods, specifically generalized linear models (GLM). These models directly measure the influence of the independent variables (altitude and precipitation) on the response variables (Richness and Abundance). The analysis was further stratified by trophic groups to identify possible differences between these groups. Seasonality, defined as the monthly precipitation during sampling, was also analyzed with one [Precipitation (1)] or two [Precipitation (2)] months of delay; a delayed effect of the rains on the dung beetles is already probable (Table 1). Additionally, the altitudinal variation of the copronecrophagous scarab community composition was studied through correspondence analysis (CA) of traps per transect and per type of bait.

The variation of species richness accumulation in relation to the altitudinal gradient was calculated using six non-parametric estimators (ACE, ICE, Chao 1, Chao 2, Jackniffe 1 and Jackniffe 2) (Jiménez-Valverde and Hortal, 2001) and 200 aleatorizations. Species accumulation curves were performed for richness values (presence-absence) per trap, for the four altitudinal transects, in feces as well as in carrion. The degree of exhaustiveness and the altitudinal variation were determined, in each functional group, with the use of six non-parametric estimators.

Cumulative average species richness per transect and mean abundance per trap were determined for each type of bait in all four altitudinal transects to assess their variation throughout the 18 months of sampling. All statistical analysis was performed using the programs Estimate 9.1.0 (Colwell, 2013) and R software (R Development Core Team, 2017).

RESULTS

Effect of altitude and seasonality on the abundance and diversity of copronecrophagous scarab

The number of species and abundance of dung beetles were influenced by altitude and seasonality. The total abundance of beetles is negatively related to higher altitudes ($z = -10.817$, $p < 0.000$) and to months with more significant rainfall ($z = -4.6230$, $p < 0.000$). The abundances stratified by functional group mainly negatively influenced altitude and the rainiest months (Table 1). Only the group of tunnelers positively influenced more significant rainfall ($z = 4.4430$, $p < 0.000$). The number of species, similar to abundance, showed a negative relationship with altitude ($z = -10.9640$, $p <0.0000$) and with precipitation ($z = -7.779$, $p <0.0000$). The species stratified by functional groups also show a negative influence concerning higher altitudes and precipitation, except the tunnelers group were positively related to rainfall ($z = 3.3610$, $p =0.0008$) and rollers that showed no influence ($z = -1.4830$, $p =0.1380$) (Table 1).

Table 1. Effect of altitude and precipitation on the abundance and diversity of copronecrophagous scarabs.

Response variable	Model	*Std. error*	*z value*	*p*
Abundance	Altitude	0.0001	-10.8170	0.0000
	Precipitation (1)	0.0098	-4.6230	0.0000
Abundance Tunnelers	Altitude	0.0001	-6.6780	0.0000
	Precipitation	0.0165	4.4430	0.0000
Abundance Dwellers	Altitude	0.0002	-2.6100	0.0090
	Precipitation (1)	0.0234	-6.8220	0.0000
Abundance Rollers	Altitude	0.0001	-8.4630	0.0000
	Precipitation	0.0146	-2.4130	0.0158
Species	Altitude	0.0001	-10.9640	0.0000
	Precipitation (2)	0.01015	-7.779	0.0000
Species Tunnelers	Altitude	0.0002	-4.3140	0.0000
	Precipitation	0.0213	3.3610	0.0008
Species Dwellers	Altitude	0.0002	-2.4540	0.0141
	Precipitation (1)	0.0335	-2.7760	0.0055
Species Rollers	Altitude	0.0002	-2.3420	0.0192
	Precipitation	0.0219	-1.4830	0.1380

Legend: ( ) = The value represents that the precipitation was analyzed one (1) or two (2) months late.

Altitudinal variation of copronecrophagous scarab community composition

The first axis of correspondence analysis CA explains 36.3 % of variation in community composition and clearly separates carrion-baited traps from feces-baited traps. The second axis explains the 12.2 % of total inertia and represents a gradient that ordinates the traps in function of the transect they were placed (Figure 2A). Thus, the traps at 947 m (T1) were distributed in low values in this axis, followed by a little higher values for traps at 820 (T2), 577 (T4) and 640 m (T3). Even though this pattern was observed for both types of bait, carrion-baited traps are more similar to each other as they show higher proximity between them on axis 2 (Figure 2A). In contrast, the higher separation between feces-baited traps on axis 2 shows a higher variation in the composition of species attracted to this kind of bait along the altitudinal gradient.

The CA shows that those species that prefer feces where placed on the far right of the first axis, like *Canthon luteicollis* Erichson, 1847 (Canlu), *Onthophagus rubrescens* Blanchard 1843, (Ontru) and *Canthidium* sp. 3 (Cants3). The species that prefer carrion are located on the far left of the axis, such as *Coprophanaeus telamon* Erichson, 1847 (Coptel) and *Canthon sericatus* Schmidt, 1922 (Canser). The second axis shows the preferences of species at an altitudinal level, in other words, it shows in which transect species were collected in higher numbers. The species collected at 947 (T1) and 820 m (T2) were located at the lower end of the axis, such as *Oxysternon conspicillatum* Weber, 1801 (Oxcon), *Eurysternus lanuginosus* Génier, 2009 (Eulan) and *Oxysternon silenus smaragdinum* d'Olsouefieff, 1924 (Oxsil) for feces-baited traps; while for carrion-baited traps there are *Canthidium* sp 2 (Cants2), *Deltochilum crenulipes* Paulian, 1938 (Deltsc) and *Deltochilum* sp. (Deltsp). The species captured at 640 (T 3) and 577 m (T4) are found at the higher end of the axis, like *Uroxys* sp. 3 (Urosp3), *Eurysternus cayennensis* Castelnau 1840 (Eucay) and *Dichotomius ohausi* Luederwaldt, 1923 (Dicoh) for feces-baited traps; for carrion-baited traps there are

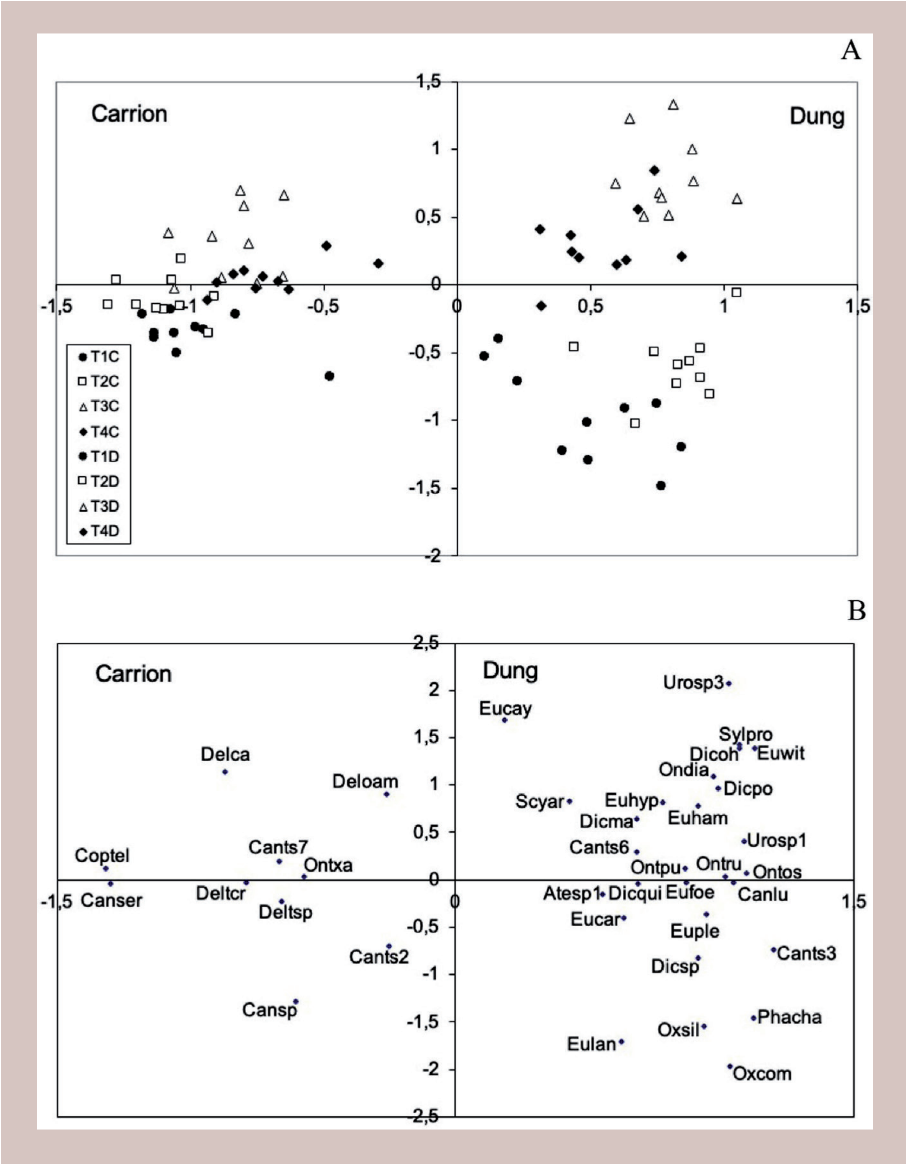

Figure 2. Results of correspondence analysis for the copronecrophagous scarab community by (A) traps ordination and (B) species ordination.

Figura 2. Resultados del análisis de correspondencias para la comunidad de escarabajos copronecrófagos mediante (A) disposición por trampas y (B) disposición por especies.

Deltochilum carinatum (Westwood 1837) (Delca) and *Deltochilum orbignyi amazonicum* (Bates 1887) (Delam) (Figure 2B).

Richness and abundance

A total of 10,227 individuals were classified into 37 known species, and 22 were classified as morphospecies. The 86.13% of the total of collected individuals from the subfamily Scarabaeinae were identified to species level, while the 13.86% were identified just as morphospecies. Five species (*Deltochilum crenulipes* Paulian, 1938; *Dichotomius quinquelobatus* (Felsche, 1901); *Eurysternus caribaeus* (Herbst, 1789);

Deltochilum sp., and *Coprophanaeus telamon* Erichson, 1847) were the most abundant, representing the 67 % of the total capture (Appendix 1).

The total species number observed in each transect was as followed: 43 at 947 m (T1), 48 at 820 m (T2), 45 at 640 m (T3) and 46 at 577 m (T4). The figures (Figure 3A and 3B), shows the estimated cumulative richness using the estimator Mao Tau in all four of the altitudinal levels for each type of bait. The traps in the transect located at the highest altitude (947 m T1) for both types of bait captured a lower

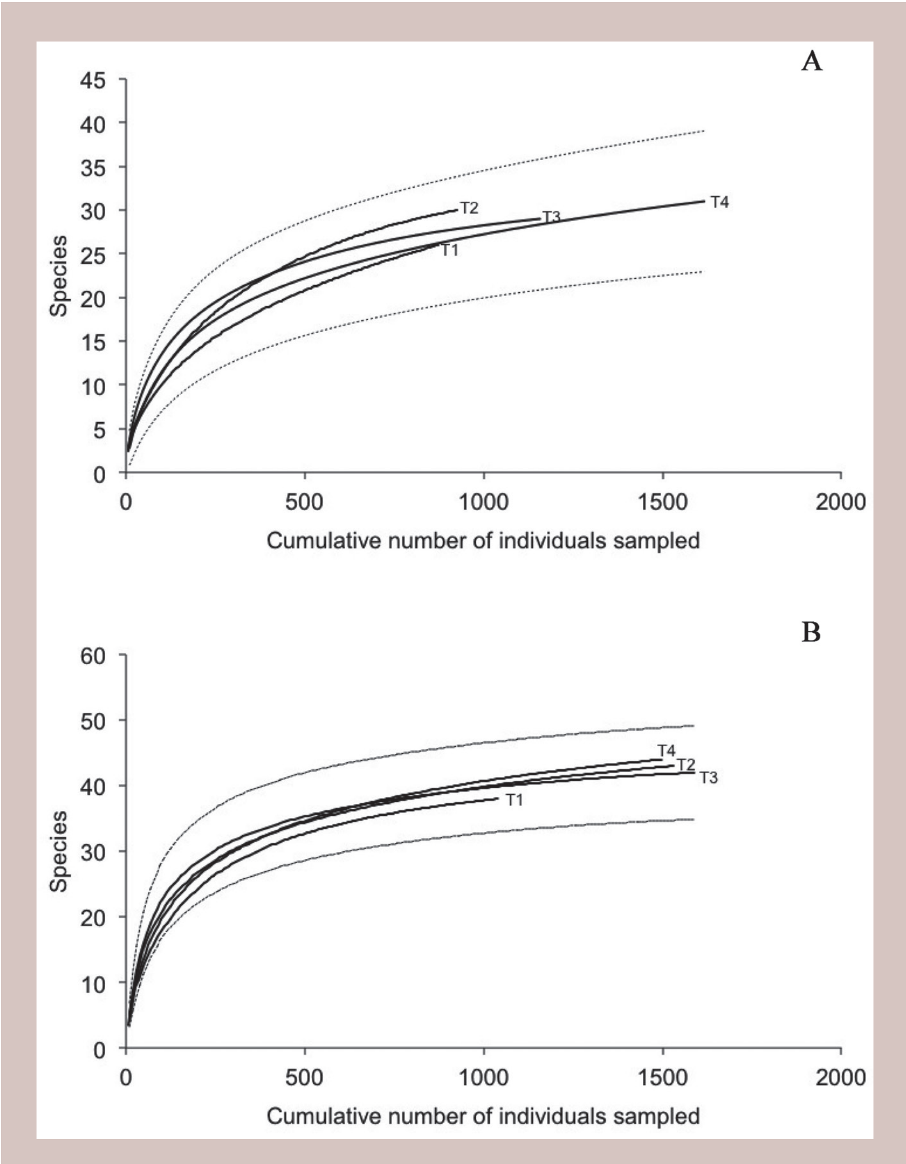

Figure 3. Species accumulation curves based on the number of individuals and on observed species (Mao Tau) for four transects with traps baited with (A) carrion and (B) feces. The confidence interval is shown for the transect with the higher number of individuals captured for each type of bait (T4 in carrion and T3 in feces).

Figura 3. Curvas de acumulación de especies basadas en el número de individuos y en las especies observadas (Mao Tau) para cuatro transectos con trampas cebadas con (A) carroña y (B) heces. Se muestra el intervalo de confianza para el transecto con mayor número de individuos capturados para cada tipo de cebo (T4 en carroña y T3 en heces).

number of individuals during the study. The curves for all the transects and their confidence intervals widely overlap, this indicates similar richness at all sites.

Transects at altitudes of 640 m (T3) and 577 m (T4) with carrion, showed the highest values of average species richness per transect, and they showed the highest values of mean abundance per trap throughout the 18-month survey. At 640 m (T3) showed the highest peak of richness on April 2008 and its highest peak of abundance on July of the same year, while 577 m (T4) had its highest peaks of richness on March 2008, June and July 2009, and its highest peaks of abundance on March 2008 (Figure 4A and 4C). Transects at 640 m (T3) and 820 m (T2) with feces bait, showed higher values of average species richness per transect and mean abundance per trap throughout the 18-month survey. Both transects had its highest peak of richness and abundance on March 2008 (Figure 4B and 4D).

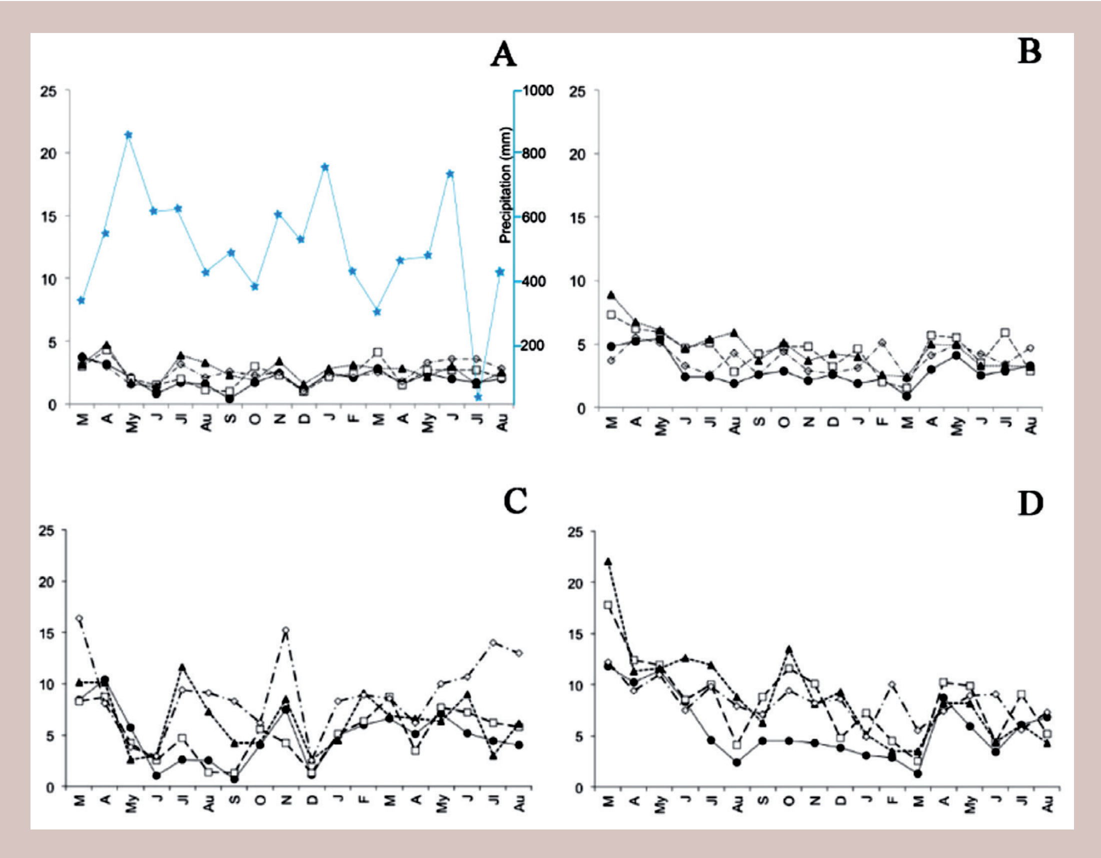

Figure 4. Mean values of richness (A and B), and abundance (C and D) per transect and per trap, and monthly rainfall (A, blue stars, precipitation mm) for Scarabaeinae in four altitudinal transects (● = T1; □ = T2; ▲ = T3; ◇ = T4) and in two types of bait (carrion and feces), in 18 months of sampling (March 2008 – August 2009).

Figura 4. Valores medios de riqueza (A y B) y abundancia (C y D) por transecto y por trampa, y precipitación mensual (A, estrellas azules, precipitación en mm) para Scarabaeinae en cuatro transectos altitudinales (● = T1; □ = T2; ▲ = T3; ◇ = T4) y en dos tipos de cebo (carroña y heces), en 18 meses de muestreo (marzo 2008 - agosto 2009).

Richness by feeding preference

In accordance with its feeding preference, 27 coprophagous species (71.05 %), five necrophagous species (13.15 %) and six generalist species (15.78 %) were registered. Coprophagous individuals were classified into 17 tunneler species, seven dwellers and three rollers. Necrophagous individuals were classified into three roller species, two tunneler species and one dweller (Appendix 1).

The total estimated species richness for each type of bait using several non-parametric estimators. For the traps baited with carrion, richness fluctuated between 49.4 and 59 species, which represents between the 72.9 and 8 % of species attracted to this kind of bait. For the traps baited with feces, richness was estimated between 64.7 and 74 species, which represents exhaustiveness between 75.7 and 86.4 %. All of the estimators showed values higher for feces than for carrion (Table 2).

Table 2. Copronecrophagous Scarabaeinae species richness estimation by type of bait.

Diet	Sobs	SD	Single-tons	Double-tons	Uni-ques	Dupli-cates	ACE*	ICE*	Chao 1*	SD	Chao 2	SD	Jack 1	SD	Jack 2*
Carrion	43	4.47	8	3	9	2	49.6	49.4	50	6.66	54.9	10.77	51.9	2.98	58.9
Dung	56	4.37	9	3	10	2	64.7	65.0	65	8.05	70.9	12.84	65.9	3.14	73.9

Legend: * = SD value was zero, for this reason it was not placed in the table.

Richness by functional groups

This study registered 35 tunneler species, 17 roller species and eight dweller species. By the six estimators used in this study, there should be between 42 and 53 tunneler species, 18 to 21 roller species and only eight dweller species in this study area (Table 2). Taking into account the estimated richness, the tunneler species represent the 61.8 - 64.6 % of the community, the rollers represent the 25.6 - 26.5 % and the dwellers the 9.8 - 11.8 %.

With the use of six estimators, it was determined that the level of sampling exhaustiveness varied depending on the functional group. It was found that a 100 % of dweller species for the area were detected. Between 65 - 81.6 % of tunneler species were registered for carrion traps and between 72.8 - 81 % of species were registered for feces traps. For roller species, between 76.5 - 91.2 % of species were registered for carrion traps and between 72.8 - 88.7 % for feces traps (Table 3).

DISCUSSION

Effect of altitude and seasonality on the abundance and diversity of copronecrophagous scarab

At higher altitudes and in rainier months, the richness and abundance of dung beetles were reduced. However, the group of tunnelers beetles shows a positive relationship with precipitation. Variables such as altitude and precipitation have shown significant variations in the richness, abundance, and composition of the dung beetle group (Lobo and Halffter 2000, Escobar, Lobo, Halffter, 2005, Herzog et al. 2013, Carrión-Paladines et al. 2021).

Table 3. Copronecrophagous Scarabaeinae species richness estimation by functional groups, in four altitudinal transects for two types of bait (feces and carrion).

Functional Group	Transects	Sobs	SD	Single-tons	Double-tons	Uni-ques	Dupli-cates	ACE*	ICE*	Chao 1	SD	Chao 2	SD	Jack 1	SD	Jack 2*
Dwellers	Global	8	0	0	0	0	0	8	8	8	0	8	0	8	0	0
	Carrion	8	0	0	0	0	0	8	8	8	0	8	0	8	0	8
	T1	4	1.49	1	1	2	0	5	7.82	4	0.25	4.96	2.08	5.91	1.91	7.74
	T2	5	1.37	0	1	0	1	5	5	5	0.01	5	0.07	5	0	4.1
	T3	5	1.37	0	0	0	0	5	5	5	0	5	0	5	0	5
	T4	6	1.33	0	2	1	1	6	6.57	6	0	6	0.24	6.98	0.98	7
	Dung	8	0	0	0	0	0	8	8	8	0	8	0	8	0	8
	T1	7	0.94	0	1	0	2	7	7	7	0	7	0	7	0	5.06
	T2	8	0	0	2	0	2	8	8	8	0	8	0	8	0	6.05
	T3	7	0.94	0	0	0	0	7	7	7	0	7	0	7	0	7
	T4	8	0	0	0	0	0	8	8	8	0	8	0	8	0	8
Tunnellers	Global	35	3.58	8	3	9	2	52.5	52.33	42	6.66	46.99	10.77	43.99	2.98	50.98
	Carrion	24	3.78	6	2	7	1	29.4	29.27	29	5.54	34.47	10.56	30.98	2.62	36.95
	T1	12	2.92	4	1	5	2	16.91	17.86	15	4.18	15.29	4.08	16.93	2.14	19.88
	T2	17	3.11	6	1	6	4	23.09	23.55	24.5	8.18	19.97	3.39	22.95	2.37	24.95
	T3	15	3	4	2	4	3	18.5	18.76	17	2.89	16.48	2.21	18.96	1.95	19.97
	T4	15	3.04	2	5	5	3	16.89	21.62	15.17	0.54	17.48	3.14	19.96	2.59	21.95
	Dung	32	3.21	6	3	7	2	39.53	40.74	35.75	4.21	38.99	7.11	38.99	2.63	43.97
	T1	19	3.05	2	1	3	2	20.15	20.46	19.5	1.3	19.99	1.8	21.97	1.7	22.97
	T2	24	2.87	2	3	3	3	25.43	25.43	24.25	0.74	24.74	1.42	26.98	1.71	27
	T3	25	2.75	3	4	3	5	27.1	27.12	25.6	1.19	25.5	1.02	27.98	1.71	26.04
	T4	25	2.93	5	3	5	4	29.02	28.9	27.5	3.16	26.99	2.57	29.96	2.19	30.98
Rollers	Global	17	0.97	2	0	2	0	17.98	17.97	18	2.3	18	2.3	19	1.41	20.99
	Carrion	13	1.9	2	0	2	0	14.26	14.17	14	2.28	14	2.28	15	1.41	16.99
	T1	10	2.19	3	2	3	2	12.38	12.1	11	1.82	10.99	1.81	12.98	1.71	13.98
	T2	8	2.07	1	2	1	3	8.45	8.81	8	0.17	8	0.12	8.99	0.99	7.04
	T3	9	2.06	1	0	1	0	9.7	9.64	9	0.47	9	0.47	9.99	0.99	10.98
	T4	10	2.11	1	1	2	0	10.86	11.48	10	0.25	10.99	2.25	11.99	1.4	13.96
	Dung	16	1.79	3	0	3	0	18.03	17.89	19	4.55	18.99	4.54	18.99	1.73	21.98
	T1	12	2.3	3	1	3	1	14.29	13.99	13.5	2.6	13.49	2.58	14.97	1.7	16.94
	T2	11	2.39	3	1	4	0	14.27	16.53	12.5	2.6	16.95	7.1	14.97	1.96	18.91
	T3	10	2.07	1	1	1	1	10.66	10.59	10	0.25	10	0.25	10.99	0.99	11
	T4	11	2.22	3	0	3	0	14.63	14.11	14	4.51	13.98	4.47	13.98	1.71	16.93

Legend: * = SD value was zero, for this reason it was not placed in the table.

Although the altitudinal range in Oglán Alto is small (577-947 m), the richness and abundance of dung beetles decreased with altitude, as reported in previous studies (Escobar et al., 2005; Herzog et al., 2013; Domínguez et al., 2015; Nunes, Braga, Figueira, Neves, Fernandes, 2016; Carrión-Paladines et al., 2021). The decrease in diversity at higher altitudes and higher rainfall is a result that could be attributed to the decrease in biomass at higher altitudes (Nunes et al., 2016). We consider that the dung beetle group is associated with the excrement of large mammals (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991). This resource is limited in that case since mammals also reduce their diversity at higher altitudes (McCain, 2007). Although high diversity of mammalian carnivores has been recorded in humid montane forests (1250 -1450 m) (Hodge and Arbogast, 2016). Our results are consistent with previous studies, and with generalities of this group, because the highly diverse areas of dung beetles are at lower altitudes (Escobar et al., 2005; Herzog et al., 2013) since they are a group of adapted species to heat (Lobo and Halffter, 2000).

The direct effect of precipitation not only occurs on the diversity of dung beetles but also on the food resource (Sun, Tang, Wu, He, Wu, 2023). The most significant number of species and individuals occurred when rainfall was lower. However, the group of tunnelers beetles showed a positive relationship with rainfall. This richness is more significant when the rains are light (Sun et al., 2023) or in the rainiest months (Correa, da Silva, Puker, Gil, Ferreira, 2021). However, abundance has diverse effects depending on rainfall (Domínguez et al., 2015; Correa et al., 2021; Sun et al., 2023). It has not even affected the temporal patterns of richness and abundance of dung beetles (Ferreira, Da Silva, Paladini, Di Mare, 2019). In our study, the characteristic of tunnelers has a positive effect on precipitation since they build galleries under or near the food resource, their larger size (Hanski and Cambefort, 1991), and their reproductive strategies (Halffter and Edmonds, 1982) make them less prone to inclement rainfall, compared to rollers and dwellers who would possibly be more affected, by the way to transfer the food resource and the washing of the resource. Thus, the low availability of food, given the ephemeral nature of carrion and feces upon contact with precipitation, could wash them away during heavy rainfall but not necessarily negatively affect the tunnelers. The response of richness and abundance stratified by functional groups tends to be more specific to climatic variables, including precipitation. Studies have demonstrated specific responses by taxonomic groups or species to climatic conditions (Herzog et al., 2013; Domínguez et al., 2015).

The precipitation variation registered for group for tunnelers could be due to this group predominance within the copronecrophagous scarab community from the Oglán River basin. In agreement with what was stated by Hanski (1989), the availability of feces is higher than carrion, mainly in lowland forests, due to the higher diversity of big mammals in that area. Another factor is the adaptation to lower temperatures, as mentioned by Forsyth y Spector (1997) who stated that dominant tunneler species from the genus *Dichotomius* are relatively corpulent and have the capacity to regulate their internal temperature and stay active in low environmental temperatures.

Altitudinal variation of the composition of copronecrophagous scarab communities

The results of the correspondence analysis concur with what Lobo and Halffter (2000) stated since the composition of the copronecrophagous scarab fauna is similar between transects at 947 m (T1) and 840 m (T2) and between transects at 640 m (T3) and 577 m (T4), which are not too far apart in altitude and are very close to each other. In this study, the majority of species share similar habitats, such as terra firme and foothill forest, with few species from different habitats like the montane cloud forests. Therefore, numerous species share morphological, sympatric, behavioral, and nutritional characteristics, these patterns correspond to the vertical colonization stated by the authors mentioned above, that stated that species that inhabit low altitudes are highly related phylogenetically. Another important argument is the one raised by Escobar et al. (2005), where they concluded that altitude in the sampling sites is the main factor that influences over the diversity of dung beetle communities. The peak of species richness was recorded at mean elevations and the higher number of species geographically restricted occur at low altitudinal levels.

The correspondence analysis showed that the main gradient variation for capture composition was due to the type of bait since there are species specialized to feed on carrion or on human feces. But the second composition gradient of this dung beetle community is due to the altitude since the traps are ordinated in the second axis in function to the transect that they were placed on, so that there are clearly two groups consisting of transects located at the upper river basin (between 800 and 950 m), and the ones located at the lower river basin (550 - 650 m). This differentiation is even much clearer in feces-baited traps.

Richness and Abundance

The number of species registered for Oglán is within the range of species found in other localities across the Amazon in Ecuador and other countries. In similar studies at “Terra Firme” forests, 46 to 97 species were found, like at Chiruisla Field Station, Ecuador [69 species (Carpio et al., 2009)]; Leticia, Colombia [52 species (Howden and Nealis, 1975)]; Tambopata, Perú [94 species (Spector and Forsyth, 1998)]; Noel Kempff National Park, Bolivia [97 species (Forsyth, Spector, Gill, Guerra, Ayzama, 1998)]; North of Manaos, Brazil [55 species (Klein, 1989); 59 species (Andresen, 2002)] and Nourages Field Station, French Guyana [87 species (Feer and Pincebourde, 2005)]. In studies conducted in different types of Amazon forests, between 48 and 61 species were registered; for instance at Natural Serranía del Chiribiquete National Park, Caquetá, Colombia [61 species (Pulido Herrera, Riveros, Harders, Hildebrand, 2003)] and at Nukak Natural Reserve, Guaviare, Colombia [48 species (Escobar, 2000a)]. The most similar study to our present research is the one conducted in foothill evergreen forest (Bosque Siempreverde Piemontano) at Untsuant, Kutukú mountain range, with an altitude between 500 to 900 m, which represents a similar altitudinal range as the present study (Celi, Terneus, Torres, Ortega, 2004), registered 78 species in 3 months in 5 localities with 3,084 individuals captured, which shows higher species richness in that mountain range due to the fact that in Oglán with 10,227 captured individuals, only 59 species were registered. This difference could be due to the methodology used, since in the study conducted five localities were studied and in each locality a transect 950 m long was sampled, with 20 pairs of traps, thus covering a larger sampling surface (Celi et al., 2004). Additionally, the foothill evergreen forest (Bosque Siempreverde Piemontano) at Untsuant is located next to the montane cloud forest (Bosque de Neblina Montano), while at the upper basin of the Oglán River there are no cloud forest areas nearby. It is possible that higher elevations, 1100 m or even 900 m at Kutukú range, could have an influence from cloud forest species that would increase its species richness.

The effort to taxonomically classify the individuals was high, which strengthens the study reliability, since the percentage of morphospecies was 40 %, which is lower than the ones registered in the majority of other studies conducted in Ecuador and South America, for instance: 52.44 % [Ecuador (Celi et al., 2004)], 52 % [Ecuador (Carpio et al., 2009)], 43 % [Peru (Larsen and Forsyth, 2005)], 45.4 % [Brazil (Durães, Martins, Vaz-de-Mellos, 2005)], 45.45 % (Brazil, (Klein, 1989), 45.6 % [Bolivia, (Vidaurre and Gonzales, 2008)], 61 % [Brazil, (Andresen, 2002)], 65.3 % (Colombia, (Escobar et al., 2005)] and 54 % (Colombia, (Pulido Herrera et al., 2003)]. Only the work from French Guyana shows a low morphospecies percentage at 29.6 % (Feer, 2000). Currently, there is more literature available about these groups of scarab beetles, which allowed our study to have a higher taxonomic precision than the studies listed previously.

With the six richness estimators we obtained a high percentage of exhaustiveness; however, we consider that the trapping method using pitfall traps probably was not sufficient to capture all of the copronecrophagous scarab fauna from Oglán simply because other species have been captured in other forest strata using other methodologies (intersection traps, canopy fogging, yellow plates, beating sheet, manual collecting and aerial carrion-baited traps), counting up to 65 species (Chamorro et al., 2019). Species collected using these other methods include: *Canthon quadriguttatus* (Olivier, 1789), *Deltochilum larseni* Silva, Louzada and Vaz-de-Mello, 2015 and *Eurysternus vastiorum* Martínez, 1988. In other forest strata there is less competition and different types of feeding resources such as monkey feces, millipede, and decomposing plant material, which allows the adaptation of other species to certain habitats (Jacobs, Nole, Palminteri, Ratcliffe, 2008; Silva, Vidaurre, Vaz-de-Mello, Louzada, 2012). Therefore, we suggest that to know all the copronecrophagous fauna that inhabit all of the forest strata from one locality, it is necessary to apply different collecting techniques besides carrion and human feces-baited traps.

Richness by feeding preference

The community composition of dung beetles from the Oglán river bassin was represented in its majority by coprophagous followed by generalists and necrophagous. Similarly, in other localities with different ecosystems it was observed that coprophagous dominated, for example in: in Fench Guyana (coprophagous 46.43 %, generalists 28.27 % and necrophagous 25 %) (Feer, 2000); at Nouragues Field Station, French Guyana (coprophagous 63.49 %, generalists 19.04 % and necrophagous 17.46 %) (Feer and Pincebourde, 2005); in a cloud forest in Mexico (coprophagous 44.44 %, generalists 33.33 % and necrophagous 22.22 %) (Halffter, Pineda, Arellano, Escobar, 2007) and in a dry tropical forest in Mexico (coprophagous 40 %, generalists 26.67 % and necrophagous 33.33 %) (Andresen, 2005). For the other trophic groups (generalists and necrophagous), even though the cited authors used an unequal criteria for category selection that varies from 70 to 90 % of captures in one type of bait, the necrophagous groups represented the minority in most of the compiled studies. This result suggests that there is higher availability of "feces" than of "carrion" in tropical forests due to high abundance of mammals which provide this feeding resource (Hanski, 1989). Our results showed that there is higher species richness of coprophagous than necrophagous (27 versus five species that meet the criteria of at least 10 individuals captured), which concurs with the studies mentioned above. The higher altitudinal segregation of coprophagous species could be related to the higher number of species in high interspecific and intraspecific competition over the feces resource, which could have produced higher differentiation in their niches and extreme specialization to the type of food (Hanski and Cambefort, 1991).

Richness by functional groups

The estimated proportions of tunneler, roller, and dweller species registered in this study are similar to the ones registered in other studies in the Neotropical region. Those studies show a higher number of tunneler species, which represent twice as many roller species, and these latter ones represent twice as many dwellers. Thus, in tropical humid forests, tunnelers are between 58.33 and 69.57 %, rollers are between 23.45 and 33.33 % and dwellers are between 6.52 and 12.96 % (Klein, 1989; Escobar, 2000a; Feer, 2000; Andresen, 2002; Pulido Herrera et al., 2003; Celi et al., 2004; Feer and Pincebourde, 2005; Carpio et al., 2009). Also, studies conducted in South American dry forests registered a very low percentage of dweller species. For instance at Sierra Nevada in Santa Marta (Colombia), where only 5.88 % of species were dwellers in contrast with 35.29 % roller species and 52.94 % tunneler species (Martínez et al., 2010).

In another South American ecosystem, with xerophytic vegetation known as "Caatinga" in Pernambuco (Brazil), the percentage of dweller species is similar to the one described above for Colombia: 3.57 % dweller species, 35.71 % roller species, and 60.71 % tunneler species (Barbosa Silva, Medina Hernández, Ide, De Moura, 2007). Finally, there are also studies conducted on dry forests that do not report dweller species, like at Chamela Biological Station in Jalisco (Mexico) (Andresen, 2005).

Tunneler and roller species have the capacity to rapidly remove their food from the dung pat; this trait makes them superior competitors above dwellers. In contrast, dwellers can only reproduce successfully in dung that stays fairly intact for several weeks. If the number of tunnelers and rollers is high, dwellers do not have any possibility for reproduction. This uneven competition between the three functional groups clearly explains an important tendency in the geographic distribution of copronecrophagous scarab beetles, that shows that dwellers typically represent an almost insignificant component of the tropical copronecrophagous scarab communities, where tunnelers and rollers show dominance and the competition is severe, mainly in habitats forests with a high degree of modification and fragmentation (Hanski and Cambefort, 1991; Nichols et al., 2007).

Taxonomically, in the Neotropical area the tunneler tribes such as Dichotomiini, Phanaeini, Onthophagini and Coprini have a higher number of species (821) than the roller tribes Canthonini, Eucraniini and Sisyphini (318), and this latter ones have a higher number of species than the tribe Eurysternini (22), which include the dweller or endocoprid species (Davis, Scholtz, Philips, 2002). It is important to take into account that dweller species from the tribe Eurysternini are endemic to the Neotropical realm (Génier, 2009). Therefore, according to Davis et al., (2002), dweller species represent only 2 % of the copronecrophagous species, while our study shows that dwellers represent approximately 10 %, which is a similar percentage showed by other studies conducted in the Amazon.

The richness values found for Oglán (our study) and Kutukú (Celi et al., 2004) are far superior to the ones that should correspond to this altitudinal area according to the bibliographic revision (Escobar, 2000b). The regression model proposed by this author predicts between 22 to 26 species for the altitudinal range covered in the cited localities, while in our study we found richness between 43 and 48 species. This results show that the current vision about richness variation specific for this group, in a gradient from the Amazon to the Andes, is very much influenced by the scarcity of studies at the specific altitudinal range addressed in this survey, and for that reason it should be reviewed. Furthermore, the majority of studies had been conducted in the lower Amazon at Guyana, Colombia, Peru, Bolivia and Brazil, therefore this work is one of the first at giving information about copronecrophagous scarab diversity at the Amazon foothills.

The areas in the foothill evergreen forest showed a significant diversity of dung beetles similar to that reported for the Amazonian lowland forest cited in this study. Two groups of dung beetles are present, some restricted to low altitudes and others to high altitudes. The richness and abundance of the dung beetle group decreased with increasing altitude and only the tunnelers increased with higher precipitation. This particular condition is because most of the tunnelers beetles were coprophagous, an excellent whose food resource may be higher at lower altitudes, and probably more resistant to low temperatures in the rains. But, other factors that we could not identify, such as temperature or intra and interspecific relationships, may be influencing this relationship. Nevertheless, the dynamics of the dung beetles recorded during the study provide concordant, essential, and new information that shows that species composition at higher altitudes, although less diverse, is still vital in conservation.

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AUTHOR CONTRIBUTIONS

Study design, data collection, analysis, and writing: William Romel Chamorro, Sandra Enríquez and Germán López-Iborra; Data collection and writing: Freddy Gallo-Viracocha, Soraya Delgado, Verónica Guasumba and Pablo Araujo.

DECLARATION OF CONFLICTING INTERESTS

The authors declared no potential conflicts of interest with respect to the research, authorship and/or publication of this article.

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Appendix 1. List of copronecrophagous scarab species (Coleoptera: Scarabaeidae: Scarabaeinae), diet, functional group, and abundance registered at Bosque Protector Oglán Alto, Pastaza, Ecuador, March 2008 to August 2009.

Tribes	Species	Code	Functional Group	Diet	Abundance
Ateuchini	*Ateuchus scatimoides* Balthasar, 1939	Atesca	Dwellers		4
	Ateuchus sp 1	Atesp1	Dwellers	Coprophagous	28
	Ateuchus sp 2	Atesp2	Dwellers		1
	Bdelyrus genieri Cook, 1998	Bdege	Dwellers		1
	Uroxys sp 1	Urosp1	Dwellers	Coprophagous	72
	Uroxys sp 2	Urosp2	Dwellers		7
	Uroxys sp 3	Urosp3	Dwellers	Coprophagous	18
Coprini	*Canthidium onitoides* Perty, 1830	Canton	Dwellers		2
	Canthidium sp 1	Cants1	Dwellers		10
	Canthidium sp 2	Cants2	Dwellers	Generalist	18
	Canthidium sp 3	Cants3	Dwellers	Coprophagous	18
	Canthidium sp 4	Cants4	Dwellers		2
	Canthidium sp 5	Cants5	Dwellers		1
	Canthidium sp 6	Cants6	Dwellers	Coprophagous	173
	Canthidium sp 7	Cants7	Dwellers	Necrophagous	23
	Ontherus diabolicus Génier, 1996	Ondia	Dwellers	Coprophagous	100
	Ontherus pubens Génier, 1996	Ontpub	Dwellers	Coprophagous	40
Dichotomiini	*Dichotomius compressicollis* Luederwaldt, 1929	Dicco	Dwellers		1
	Dichotomius mamillatus Felsche, 1901	Dicma	Dwellers	Coprophagous	181
	Dichotomius ohausi Luederwaldt, 1923	Dicoh	Dwellers	Coprophagous	58
	Dichotomius podalirius Felsche, 1901	Dicpo	Dwellers	Coprophagous	177
	Dichotomius quadrilobatus Chamorro, Lopera, & Rossini, 2021	Dicqua	Dwellers		1
	Dichotomius quinquelobatus (Felsche, 1901)	Dicqui	Dwellers	Coprophagous	1351
	Dichotomius sp.	Dicsp	Dwellers	Coprophagous	207
Deltochilini	*Canthon luteicollis* Erichson, 1847	Canlu	Rollers	Coprophagous	227
	Canthon sericatus Schmidt, 1922	Canser	Rollers	Necrophagous	31
	Canthon ohausi Balthasar, 1939	Canoh	Rollers		10
	Canthon sp.	Cansp	Rollers	Generalist	37
	Cryptocanthon aff. *curticrinis*	Crypcu	Rollers		8
	Deltochilum barbipes Bates, 1870	Deltbar	Rollers		4
	Deltochilum carinatum (Westwood 1837)	Delca	Rollers	Necrophagous	49
	Deltochilum crenulipes Paulian, 1938	Deltcr	Rollers	Necrophagous	3039
	Deltochilum orbiculare (Lansberge 1874)	Delor	Rollers		7
	Deltochilum orbignyi amazonicum Bates 1887	Deloam	Rollers	Generalist	77
	Deltochilum sp.	Deltsp	Rollers	Generalist	725
	Scybalocanthon kastneri Balthasar, 1939	Scybka	Rollers		3
	Scybalocanthon arnaudi Silva & Valois, 2019	Scyar	Rollers	Coprophagous	266
	Scybalocanthon sp.	Scysp	Rollers		1
	Sylvicanthon bridarollii Martínez, 1948	Sylsp	Rollers		7
	Sylvicanthon proseni (Martínez, 1949)	Sylpro	Rollers	Coprophagous	138
Epilissini	*Canthonella* sp.	Canthsp	Rollers		1
Oniticellini	*Eurysternus caribeus* (Herbst, 1789)	Eucar	Tunnellers	Coprophagous	1054
	Eurysternus cayennensis, Castelnau 1840	Eucay	Tunnellers	Generalist	223
	Eurysternus foedus Guérin-Méneville, 1830	Eufoe	Tunnellers	Coprophagous	81
	Eurysternus hamaticollis Balthasar, 1939	Euham	Tunnellers	Coprophagous	23
	Eurysternus hypocrita Balthasar, 1939	Euhyp	Tunnellers	Coprophagous	256
	Eurysternus lanuginosus Génier 2009	Eulan	Tunnellers	Coprophagous	252
	Eurysternus plebejus Harold, 1880	Euple	Tunnellers	Coprophagous	16
	Eurysternus wittmerorum Martínez, 1988	Euwit	Tunnellers	Coprophagous	13
Onthophagini	*Onthophagus rubrescens* Blanchard 1843	Ontru	Dwellers	Coprophagous	80
	Onthophagus xanthomerus Bates, 1887	Ontxa	Dwellers	Generalist	83
	Onthophagus aff. *osculatii*	Ontos	Dwellers	Coprophagous	68
Phanaeini	*Coprophanaeus telamon* Erichson, 1847	Coptel	Dwellers	Necrophagous	686
	Oxysternon conspicillatum Weber, 1801	Oxcom	Dwellers	Coprophagous	28
	Oxysternon silenus smaragdinum d'Olsouefieff, 1924	Oxsil	Dwellers	Coprophagous	186
	Oxysternon spiniferum Laporte, 1840	Oxspi	Dwellers		2
	Phanaeus camberforti Arnaud 1982	Phacam	Dwellers		1
	Phanaeus chalcomelas (Perty, 1830)	Phacha	Dwellers	Coprophagous	50
	Phanaeus haroldi Kirsch, 1871	Phahar	Dwellers		1