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Altitudinal variation of dung beetle (Scarabaeidae: Scarabaeinae) assemblages in the Colombian Andes

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ABSTRACT

Aim We describe the changes in species richness, rarity and composition with altitude, and explore whether the differences in Scarabaeinae dung beetle composition along five altitudinal transects of the same mountain range are related to altitude or if there are interregional differences in these altitudinal gradients.

Location Field work was carried out on the eastern slope of the eastern Cordillera, Colombian Andes, between Tamá Peak to the north, in the Tamá National Park (07°23' N, 72°23' W) and the San Miguel River (00°28' N, 77°17' W) to the south.

Methods Sampling was carried out between February 1997 and November 1999 in five regions spanning elevation gradients. In each gradient, six sites were chosen at 250 m intervals between 1000 and 2250 m a.s.l.

Results We found a curvilinear relationship between altitude and mean species richness, with a peak in richness at middle elevations. However, the diversity of dung beetle assemblages does not seem to be related to the interregional differences in environmental conditions. The number of geographically restricted species is negatively and significantly related to altitude, with geographically restricted species more frequent at low altitude sites. Ordination delimited the two main groups according to altitude: one with all the highest sites (1750–2250 m a.s.l.) and a second group with the remaining sites (< 1750 m a.s.l.). Analysis of species co-occurrence shows that these dung beetle assemblages seem to be spatially structured when all sites have the same probability of being chosen. In contrast, the spatial structure of species assemblages seems to be random when the probability of choosing any site is proportional to its altitude.

Main conclusions The altitude of sites is the main factor that influences the diversity of these dung beetle assemblages. The peak in species richness at middle elevations, the higher number of geographically restricted species at lower altitudinal levels, and the compositional differences along these mountain gradients seem to result from the mixing at these altitudes of dung beetle assemblages that have different environmental adaptations and, probably, different origins. The relevance of altitude in these assemblages is related to the limited role of these Neotropical high altitude environments as centres of refuge and vicariance for a monophyletic group of warm-adapted species, for which the vertical colonization of these high mountain environments by lineages distributed at lower altitudes would have been very difficult.

Keywords

Altitudinal distribution, Colombian Andes, composition, diversity, dung beetles, Scarabaeinae, species co-occurrence.

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INTRODUCTION

Altitude is a variable that is frequently related to changes in the species richness and composition of assemblages (Huston, 1994).

The altitudinal variation in dung beetles has been studied at several locations in Europe, Mexico, and Southeast Asia (see Lobo & Halffter, 2000 and references therein), South Africa (Davis *et al.*, 1999) and Australia (Monteith, 1985). As for other insect groups

(Wolda, 1987; McCoy, 1990), the number of species generally diminishes with increasing altitude and there is an altitudinal replacement between the two main groups of dung beetles (Lobo & Halffter, 2000), similar to that which takes place along latitude both for European and North American dung beetle assemblages (Hanski, 1986, 1991; Lobo, 2000). The cool-adapted species of Aphodiini (*sensu* Scholtz, 1990) dominate the high altitude and species-poor northern communities, whereas the warm-adapted species of Scarabaeinae dominate the low altitude and species-rich southern communities. Because Aphodiini and Scarabaeinae have distinct biogeographical distributions and different evolutionary histories, it has been proposed that both altitudinal and latitudinal variation in dung beetle assemblages is conditioned by unique and contingent historical and geographical factors (Martin-Piera *et al.*, 1992; Jay-Robert *et al.*, 1997; Lobo & Halffter, 2000). The species of Aphodiini are only very occasionally present in South America, as the dung beetle assemblages are dominated almost exclusively by Scarabaeinae species. When only Scarabaeinae species are considered, all the mountains systems analysed show a negative and linear relationship between altitude and species richness (Monteith, 1985; Jay-Robert *et al.*, 1997; Davis *et al.*, 1999; Lobo & Halffter, 2000). However, as for many other groups, reliable altitudinal data for the Neotropical region is lacking (Lomolino, 2001).

To maintain stable populations in high altitude environments, warm-adapted Scarabaeinae species need to tolerate adverse conditions. These conditions, for instance, low temperatures and frost, demand special physiological adjustments by the species (Chown *et al.*, 2002). If the dispersion among mountains is not seriously physically hindered, the restrictive environmental conditions of high altitudes could generate similar diversity and

faunistic composition in the mountain assemblages. In contrast, if each mountain evolved independently of the others, historical and geographical factors should explain the dissimilarities in assemblages of mountain fauna. By analysing the data from five Neotropical altitudinal transects of Colombia located along a latitudinal gradient, we describe the altitudinal changes in species richness, rarity and faunistic composition of the Scarabaeinae dung beetle assemblages. We examine the interregional differences in these altitudinal variations in order to examine the relevance of the specific geographical and historical circumstances of each mountain region or, contrariwise, if the altitudinal effect on each mountain assemblage can be considered similar, independently of the geographical location of the mountain chain.

MATERIALS AND METHODS

Study area

The study was conducted on the eastern slope of the eastern Cordillera in the Colombian Andes, between the Tamá Peak to the north, in the Tamá National Park (07°23' N, 72°23' W; Department of Santander), and the San Miguel River (00°28' N, 77°17' W; Department of Putumayo) to the south (Fig. 1). The Colombian Andes are comprised of three mountain ranges that cover 30% of the country's area and cross from north to south, effectively separating the territory into two large lowland regions: the Amazonian and Orinoquian regions to the east, and the Chocó region to the west (Hernández *et al.*, 1992).

Of the three ranges, the eastern Cordillera, c. 1200 km long and 200 km wide, is the main mountain chain in the northern

Site number	Precipitation (mm)	Temperature (°C)
1	2398 ± 537	15.5 ± 3.6
2	1548 ± 456	12.5 ± 3.5
3	2320 ± 782	13.5 ± 3.0
4	1704 ± 165	19.1 ± 3.3
5	2495 ± 599	16.3 ± 4.6

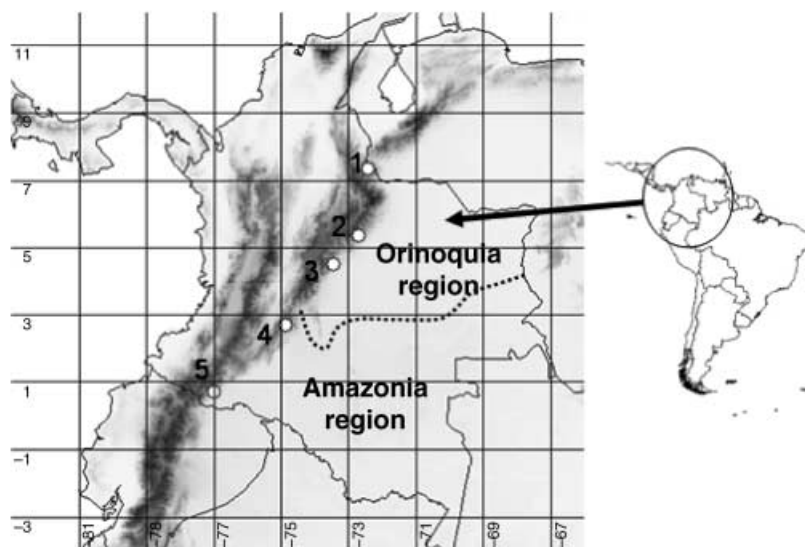


Figure 1 The geographical location of each of the five sampled altitudinal regions (circles) in the eastern Cordillera of the Colombian Andes. 1 = Tamá National Park (07°23' N; 72°23' W), 2 = Alto Río Cusiana (05°26' N; 72°41' W), 3 = Farallones de Medina (04°35' N; 73°26' W), 4 = Los Picachos (02°45' N; 74°51' W) and 5 = Putumayo (00°47' N; 77°00' W). The annual precipitation and annual temperature (± SD) was calculated for the 0.5 degree square, whose centre is the geographical position of each region, taking into account the scores of all 0.05 degree squares. Environmental data extracted using WORLDCLIM version 1.2 (see <http://biogeو.berkeley.edu/worldclim/worldclim.htm>). The two main tropical lowland regions are also indicated.

tropical Andes. Its geological origin goes back to the Miocene (18 Myr ago) and its final formation took place in the Pliocene, 3 to 5 Myr ago. It is considered the most recent mountain chain in the Colombian Andean system (van der Hammen, 1974). The eastern slope of this cordillera borders on two large biomes: the Amazonian lowlands in the south, and the savannas of Orinoquía (*Llanos Orientales*) in the north (Fig. 1). According to Hernández *et al.* (1992), these areas have different geological and biogeographical histories. The natural savannas in the Orinoquía region are predominantly characterized by flat relief, and are covered with grass and gallery forest. Annual precipitation varies between approximately 1000 and 2500 mm, with a long dry season that can last up to six months. The Amazonian region differs from the Orinoquían in its vegetation cover, which is essentially extensive forest on undulating relief, mixed with rocky outcrops. The latter emerged from the Guyana Shield, and is covered by savanna vegetation and low to medium height forests. Annual precipitation varies between 3000 and 4000 mm, with a short dry period.

The variation in the orientation of this mountain range relative to the easterly winds influences the amount of annual rainfall, which ranges from 2000 to 5000 mm. The greatest precipitation occurs at intermediate altitudes, where cloud forest dominates the vegetation, and rainfall decreases notably with elevation (Sarmiento, 1986). The vertical distribution of the forest in the Andes mainly depends on climatic conditions, but topographic and edaphic conditions can also modify the distributional range of the four main vegetation types: tropical lowland Amazonian forest is found up to 1000 or 1250 m a.s.l.; sub-Andean forest to 2000 m a.s.l.; Andean forest to 3500 m a.s.l.; and páramo occurs above 3500 m a.s.l. (van der Hammen, 1995).

Field work was carried out between February 1997 and November 1999 in five regions or elevation gradients located in the Colombian eastern mountain range which differ, not only in their latitudinal position, but also in the annual precipitation and mean annual temperature of the region they are located (Fig. 1). In this territory, the areas with greater anthropic impact are concentrated below 1000 m between 4° and 8°30' N (Armenteras *et al.*, 2003). The cartographic study (scale 1 : 50,000) on the distribution of forests and other types of vegetation in each one of the studied regions shows that in Putumayo, the vegetal cover corresponds to continuous primary forests (90%) at 500–600 m. In Los Pichachos, 70% of the region corresponds to forests with a lower degree of perturbation, concentrating the human intervention around the routes and some places destined to cattle farming and other agricultural activities. In the Farallones de Medina, 72% of the area is primary forest and the human land use is dominated by cattle farming. In Río Cusiana, the degree of transformation of the forest is comparatively greater, and around 50% of the area is covered by forests. Lastly, in the PNN Tamá, 60% of the area corresponds to primary forests, mainly above 1500 m, the remaining area being a mosaic of forests moderately transformed, pastures and crops (IAvH, 1999).

Sampling design

Each of the five regions was divided into six 250-m interval transects, approximately between 1000 and 2500 m a.s.l. Twenty-

seven of the 30 sites were sampled with 330 traps. It was not possible to sample three sites (region 1 at 1750 and 2000 m a.s.l., and region 4 at 1000 m a.s.l.). At each site, 10 to 32 pitfall traps (12.2 ± 4.8 ; mean \pm SD) were placed in the forest 25 m apart, and baited with 50 mL of human dung. The traps had a 1000 mL capacity, were 13 cm deep and 11 cm in diameter. In this study, strictly necrophagous species were not collected. Each trap was left in the field for 48 h, after which, beetles were collected, counted, preserved and transported to the laboratory for further identification. For the identification of morphospecies to genus, such as *Canthidium*, *Uroxys*, *Canthon* and *Deltochilum*, and where there are no recent taxonomic revisions, species identification was based on the characteristics of male genitalia (aedeagus). Voucher specimens were deposited in the arthropod collection of the Instituto Alexander von Humboldt (IAvH) in Colombia.

Data analysis

To examine if each of the 27 local inventories and if each of the elevation gradients could be considered an adequate description of their diversity, smoothed accumulation curves (500 randomizations) were produced, taking into account the number of individuals captured as a surrogate for the sampling effort, as recommended by Gotelli and Colwell (2001) when sampling effort varies. True species richness for each site and each elevation gradient was also estimated using incidence-based coverage estimator (ICE), Chao1 and first-order jackknife, three common non-parametric richness estimators that use species-by-sample data.

The EstimateS software package (Colwell, 1997) was used to generate the smoothed species accumulation curves and the estimators for true species richness. Detailed descriptions of these estimators can be found in Colwell and Coddington (1994).

Species rarity was calculated as $1 - (n_i/n)$, where n_i is the number of sites where species i was present, and n is the total number of sites ($n = 27$). For each site, mean species rarity was calculated by taking into account the rarity scores of the species present at a given site (see Kier & Barthlott, 2001). We define rare or geographically restricted species as those present only in one or two sites ($n = 60$). As the sampling intensity differs between sites, the mean number of species per trap was used as the dependent variable. However, the use of mean richness per trap does not preclude bias in the probability of recording rare species, so the inventories of arthropods in tropical biomes are frequently incomplete (Gotelli & Colwell, 2001; Longino *et al.*, 2002). Thus, although the number of traps used in each site is not significantly related to the number of geographically restricted species (Spearman rank correlation coefficient; $r_s = 0.34$, $n = 27$; $P = 0.08$), or to the mean species rarity at sites ($r_s = -0.02$, ns), we also use the following measures of species diversity that do not depend a priori on the sample size: the asymptotic value of the species accumulation curves estimated by the Clench equation (Soberón & Llorente, 1993) for each of the sites taking into account the number of individuals as surrogate of the sampling effort, as well as Hurlbert's (1971) PIE index. This diversity index gives the probability that two randomly sampled individuals from the assemblage represent two different species

and its estimates are based on rarefaction at 10 individuals with 1000 iterations, calculated using *ECOSIM* version 7.67 (Gotelli & Entsminger, 2004).

General regression models (StatSoft, 1999) were used to examine the relationships between dependent and independent variables, with the five regions treated as categorical factors and the remaining explanatory variables as continuous. Using mean species richness for each site as the dependent variable and the altitude and latitude of these sites as independent variables, a backward stepwise regression analysis was performed to evaluate the influence of these variables. Quadratic ($x + x^2$) and cubic ($x + x^2 + x^3$) functions of each independent variable were subjected to regression analysis to estimate curvilinear relationships between variables. Species richness was square root transformed to normalize its scores.

A triangular Q-mode matrix of similarity was derived from the rectangular presence/absence matrix using the Jaccard similarity coefficient (Ludwig & Reynolds, 1988). To define groups of sites with similar species composition, nonmetric multidimensional scaling (NMDS) was applied. NMDS (Statsoft, 1999) is a nonlinear ordination technique that, like other ordination techniques, derives an axis system that shows the relationships between sites. When these axes are computed, information loss is minimized. NMDS was chosen because any kind of similarity matrix may be used, and neither normality nor linearity of data is required (Kruskal & Wish, 1978), and because it is possible to establish a priori the number of dimensions being particularly appropriated when many rare species occur (Brehm & Fiedler, 2004). To evaluate how many dimensions are needed to reproduce the similarity between sites, a stress value was calculated (the smaller the stress value, the better the fit of the reproduced similarity matrix to the observed similarity matrix). The scores of each site for the first two NMDS dimensions were subjected to a cluster analysis to represent groups of similar sites (see Legendre & Legendre, 1998). The Euclidean distance was used as the measure of resemblance, and the single linkage method as the clustering strategy (Legendre & Legendre, 1998). Spearman rank correlation coefficients (Siegel & Castellan, 1988) were used to estimate the relationship between the pairwise variables.

Using the presence-absence matrix, the existence of a non-random pattern of species co-occurrence was tested using the co-occurrence module of the *ECOSIM* package (Gotelli & Entsminger, 2004). One thousand Monte-Carlo randomized matrices were generated so that each site had exactly the same number of species as in the real data, and each species in the null communities had the same number of occurrences as in the original data (Gotelli, 2000). The C-score co-occurrence index (Stone & Roberts, 1990) was calculated to compare statistically the patterns in the randomized communities with those in the real data matrix. The C-score is the average of all possible 'checkerboard units' across all possible species pairs in the matrix, where a 'checkerboard unit' is a pair of species that never co-occur at any site. The larger the C-score, the lower the average co-occurrence among species pairs. We ran *ECOSIM* three times: once under the assumption that all sites have an equal probability of being chosen, second under the assumption that the probability of choosing a site is proportional to its altitude and third under the assumption that

the probability of choosing a site is proportional to its latitude (i.e. that the occurrence of species is not randomly distributed among sites and depends on altitude or on latitude).

RESULTS

Species richness reliability

In total, 7894 specimens belonging to 101 species were collected from the 330 pitfall traps (see Appendix S1 in Supplementary Material). The number of species collected by region varied between 24 species for the Tamá National Park in the north and 43 species for Putumayo in the south (Table 1). Although in a large number of sites, the accumulation curves have a readily detectable asymptote (Fig. 2), in others – particularly in those sites located in the lowest part of regions 1, 2 and 5, as well as those in the high part of regions 3, 4 and 5 – the asymptotic phase of the species accumulation curve is less evident. Estimates of expected species richness at the local level show that at 21 sites (78%), on average more than 80% of the species were collected (minimum = 79.4% – maximum = 100%), whereas for the remaining six sites, the mean value of the estimates was less than 76% (minimum = 65%, maximum = 75.9%; Table 2). The species accumulation curves show an asymptotic tendency for region 1 (Tamá National Park) and region 3 (Farallones of Medina), where the number of species actually collected ranges from 84 to 96% of that predicted by the different estimators (Fig. 2, Table 1). In the remaining regions, the asymptotic tendency of the accumulation curves was less evident (Fig. 2). In region 2 (Alto Río Cusiana), the observed richness figures range from 84 to 90% of the predicted scores, in region 4 (Los Picachos) from 76 to 86%, and in region 5 (Putumayo) from 67 to 77%. The nonparametric richness estimates indicated that between 75% (Chao1 = 134 species) and 86% (ICE = 117 species) of the expected maximum number of species for the entire territory were collected (Table 1).

Variation in species richness

The mean species richness was significantly related to altitude ($F_{5,304} = 76.61$; $P < 0.0001$) and although to a lesser degree, the mean species richness also differed between the five regions ($F_{4,305} = 4.03$; $P < 0.004$). A posteriori comparison with the Tukey HSD test demonstrated that the mean richness of species differed significantly between all altitudes ($P < 0.01$), except between those located at 1000 and 1750 m a.s.l. In contrast, the mean richness of regions was very similar and only region 4 showed a significantly higher mean species richness than regions 1 and 3 ($P < 0.01$) (see Table 2).

The stepwise regression analysis with the terms of a third degree polynomial for altitude (altitude + altitude² + altitude³) showed that the three terms were statistically significant ($P < 0.001$) and that therefore, the relationship between altitude and mean species richness was curvilinear (Fig. 3). The highest mean species richness appears at 1250 m a.s.l., and decreases with altitude until it levels off around 2000 m a.s.l. The third degree

Table 1 Species richness estimators for each site (each of the five mountain regions and for the whole territory studied). N_p = number of pitfall traps, N_s = number of species and N_i = number of individuals. ICE = incidence-based coverage estimator, Jack1 = 1st order jack knife. Percentage indicates the average proportion of the number of species expected

Region/site	N_p	N_s	N_i	ICE	Chao1	Jack1	Mean \pm SD	%
Tamá National Park	69	24	1383	26.4	28.5	27.0	27.3 \pm 1.0	87.9
1000	12	14	227	19.1	26.5	18.6	20.3 \pm 4.4	68.8
1250	13	11	668	11.5	11.1	11.9	11.4 \pm 0.4	96.2
1500	12	8	186	8.0	8.0	8.0	8.0 \pm 0.0	100
2250	32	9	302	9.3	9.3	9.9	9.4 \pm 0.3	95.4
Alto Río Cusiana	60	37	1232	41.1	41.9	43.9	42.3 \pm 1.4	87.5
1000	10	12	280	17.2	15.5	16.6	15.8 \pm 0.8	76.0
1250	10	16	338	17.1	16.4	17.8	17.0 \pm 0.7	94.4
1500	10	13	187	16.6	14.6	16.7	15.5 \pm 1.1	83.6
1750	10	14	309	17.7	16.2	18.9	17.1 \pm 1.3	82.0
2000	10	5	52	5.8	5.1	5.9	5.5 \pm 0.4	90.6
2250	10	5	66	5.6	5.5	5.9	5.6 \pm 0.2	89.7
Farallones de Medina	60	29	1539	30.1	31.3	32.0	31.2 \pm 0.9	93.1
1000	10	9	82	10.4	9.4	10.8	10.0 \pm 0.7	89.7
1250	10	14	471	15.8	14.3	16.7	15.3 \pm 1.2	91.0
1500	10	15	618	15.5	15	15.9	15.4 \pm 0.4	97.4
1750	10	10	347	12.8	10.8	12.7	11.8 \pm 1.1	84.7
2000	10	3	9	3.7	3.5	3.0	3.3 \pm 0.3	89.7
2250	10	2	12	3.1	2.5	2.9	2.8 \pm 0.3	73.4
Los Picachos	72	40	2327	46.7	52.3	46.9	48.6 \pm 3.1	82.2
1250	12	17	578	18.5	21.5	19.8	19.5 \pm 1.5	87.1
1500	24	24	783	27.3	32	28.9	28.6 \pm 2.3	83.8
1750	12	15	463	19.9	15.8	19.5	17.9 \pm 2.2	83.7
2000	12	10	437	11.9	14.5	12.7	12.6 \pm 1.3	79.3
2250	12	7	66	13	10.5	10.6	10.7 \pm 1.4	65.1
Putumayo	69	43	1413	56.7	64.1	55.8	58.8 \pm 4.5	73.0
1000	13	16	101	25.3	27.4	23.4	24.0 \pm 2.0	66.5
1250	10	20	758	22.4	23.2	23.3	22.5 \pm 0.5	88.7
1500	14	14	378	15.0	16.0	15.8	15.3 \pm 0.5	91.1
1750	10	12	69	16.4	24.5	16.5	18.1 \pm 4.6	66.2
2000	12	10	93	17.1	11.8	14.5	13.8 \pm 2.6	72.3
2250	10	4	14	4.4	4.5	4.9	4.5 \pm 0.2	88.6
The whole territory	330	101	7894	117.7	134.3	120.9	124.3 \pm 8.8	81.2

polynomial function of altitude explained 77.6% of the variation in the mean species richness of sites ($F_{3,23} = 24.49$; $P < 0.001$). However, neither the mean annual temperature ($F_{1,25} = 1.16$; ns), the mean precipitation ($F_{1,25} = 0.23$; ns; see Fig. 1) nor the region ($F_{4,22} = 0.41$; ns) had a significant effect on the mean species richness of sites. Although Hurlbert's PIE index scores are not significantly correlated with the mean species richness, neither with the total richness of sites nor the estimated species richness from the Clench accumulation curves, altitude is again the only significant variable that is linear and negatively related to Hurlbert's PIE index scores ($F_{1,25} = 5.18$; $P < 0.03$). The asymptotic number of species estimated individually for each site is also negatively related to altitude ($F_{1,25} = 12.95$; $P < 0.001$), showing that all the considered species richness estimators suggest a decrease in the diversity of these dung beetle assemblages with altitude.

Rarity and species composition

The mean species rarity at the sites was not related to altitude ($F_{1,25} = 0.05$; ns) or region ($F_{4,22} = 1.78$; ns), nor the interaction between these variables ($F_{4,22} = 0.99$; ns). Evidently, the scores of

this variable are profoundly influenced by the rarity figures of the most widespread species, and also by the high number of species present at very few sites. The distribution of species by site shows that 38.6% of species occur at only one site, whereas 79.2% of the total number of species recorded occurs at four or fewer sites (Fig. 4a). We define geographically restricted species as those present only in one or two sites ($n = 60$), so most geographically restricted species inhabit the lower altitudinal levels of the mountain ranges, principally the southern ones, but are also found in the northernmost region at the highest altitudinal level (Fig. 4b). Moreover, the geographically restricted species shared between two sites occur mainly at adjacent altitudinal levels of the same mountain range. The number of geographically restricted species at each site is significantly and positively correlated both with the mean richness per trap ($r_s = 0.53$, $P = 0.005$), with the total richness per site ($r_s = 0.66$, $P = 0.0002$), the estimated richness by the Clench accumulation curve ($r_s = 0.59$, $P = 0.001$) and Hurlbert's PIE index scores ($r_s = 0.49$, $P = 0.01$). The number of geographically restricted species is also negatively and significantly related to altitude ($F_{1,25} = 14.4$, $P = 0.001$), but does not vary between regions ($F_{4,22} = 1.14$; ns) and is not related

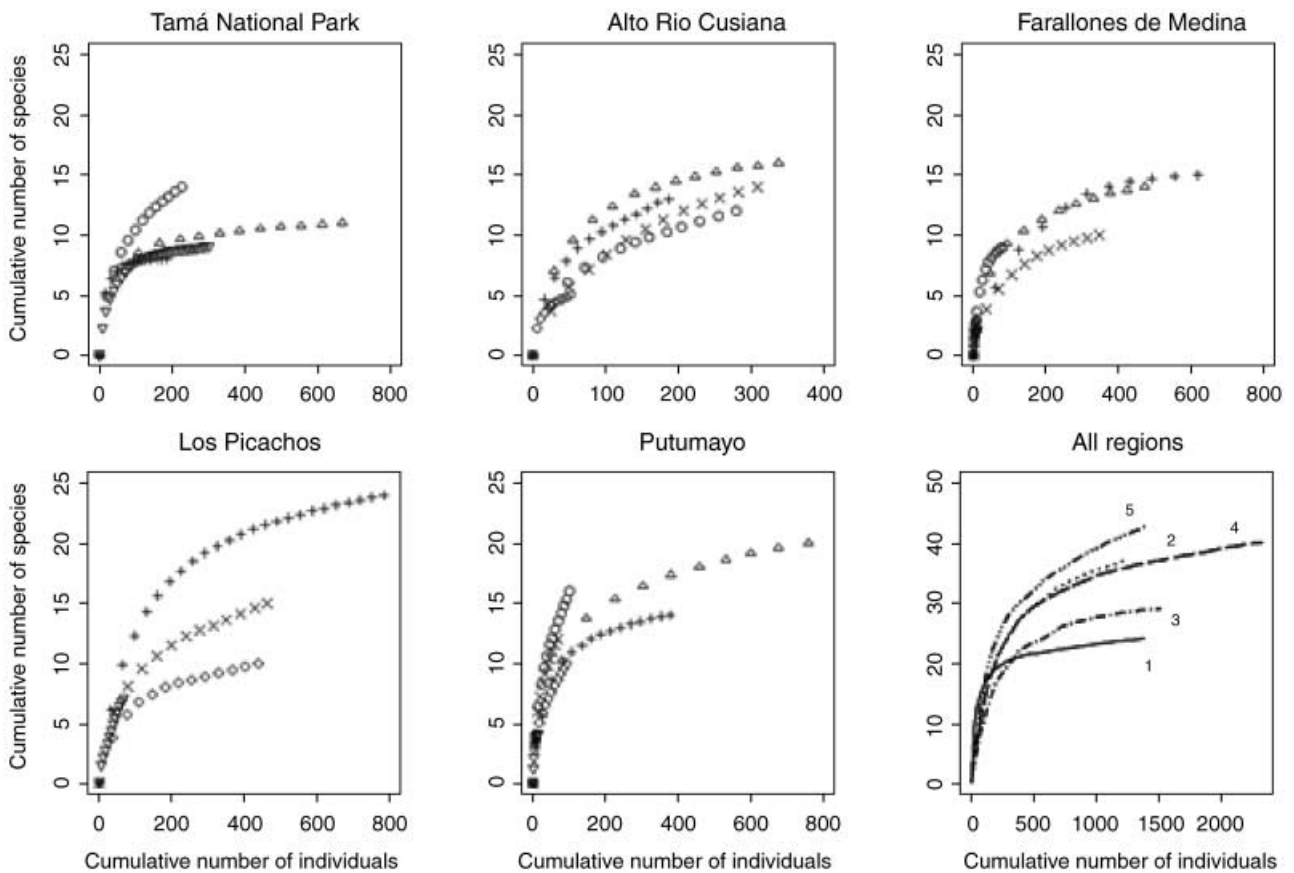


Figure 2 Smoothed species accumulation curves, taking into account the number of individuals as a surrogate for the sampling effort accomplished in each site for each of the five regions studied. The curves were generated by randomizing the order of the samples 500 times using EstimateS software (Colwell, 1997). ○ = 1000 m, △ = 1250, + = 1500, x = 1750, ◇ = 2000 and ▽ = 2250.

Table 2 The number of species at each altitudinal level for each of the five regions and the mean number of species per trap (in brackets). The estimated number of species (given in italics) was obtained from the Clench accumulation curves (Soberón & Llorente, 1993), using the number of individuals as a surrogate for sampling effort, whereas the rarefied Hubbert's PIE (1971) diversity index scores is given in bold letters

Altitudinal level (in m a.s.l.)	Tamá National Park	Alto Rio Cusiana	Farallones de Medina	Los Picachos	Putumayo	The whole territory
1000	14 (4.8), 17, 0.70	12 (5.9), 15, 0.59	9 (3.5), 11, 0.71	—	16 (4.2), 21, 0.86	42 (4.5)
1250	11 (7.0), 12, 0.75	16 (7.4), 18, 0.81	14 (6.9), 16, 0.59	17 (9.8), 18, 0.89	20 (10.2), 22, 0.68	53 (8.3)
1500	8 (5.2), 9, 0.81	13 (5.2), 16, 0.57	15 (5.6), 19, 0.29	24 (6.6), 27, 0.73	14 (5.5), 16, 0.53	48 (5.8)
1750	—	14 (4.2), 20, 0.56	10 (3.8), 12, 0.27	15 (5.9), 17, 0.52	12 (3.7), 16, 0.83	35 (4.5)
2000	—	5 (2.4), 6, 0.64	3 (1.2), 4, 0.67	10 (3.9), 11, 0.28	10 (3.5), 12, 0.76	19 (3.0)
2250	9 (2.2), 10, 0.69	5 (2.1), 6, 0.59	2 (1.0), 3, 0.17	7 (1.8), 15, 0.27	4 (1.3), 5, 0.74	21 (1.9)
Total	34 (4.0)	37 (4.5)	29 (4.1)	40 (6.0)	43 (4.9)	101 (4.7)

to the mean annual temperature ($F_{1,25} = 3.29$; ns), or the mean annual precipitation ($F_{1,25} = 0.56$; ns).

Cluster analysis of the two first NMDS dimensions (stress value = 0.19) clearly delimited two main groups by altitude: one comprised of all the highest sites (above approximately 2000 m a.s.l.) with the site at 1750 m a.s.l. from region 3, and the second included the remaining sites at lower altitudes (Table 1, Fig. 5). Interestingly, the site at 2000 m a.s.l. of the southernmost region is associated with the lowland sites. The group containing the

highest sites has a significantly lower mean species richness than the group containing sites at lower altitudes (mean ± SE: 2.2 ± 0.6 and 5.8 ± 0.4 , respectively; Mann–Whitney U -test; $Z = 3.86$, $P = 0.0001$), a significantly lower number of geographically restricted species (1.5 ± 0.8 and 3.7 ± 0.5 ; $Z = 2.3$, $P = 0.02$) and significantly lower estimated richness scores according to the Clench accumulation curve (8.1 ± 1.5 and 16.7 ± 1.0 ; $Z = 3.5$, $P = 0.0004$). The NMDS ordination reveals an arch-like structure (see Fig. 5) that probably indicates the control of the data set by

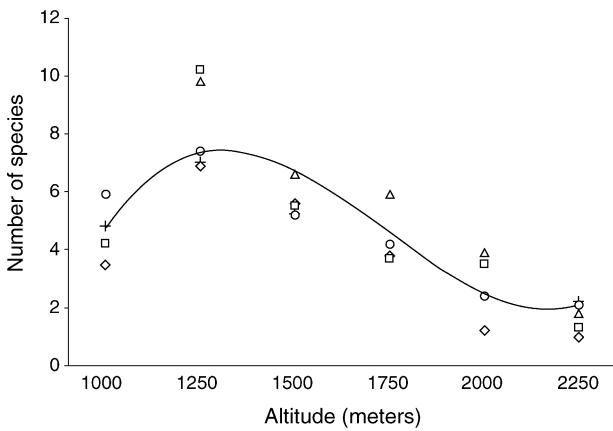


Figure 3 Variation in the mean number of species per trap with elevation for the five regions studied. The line is the third degree polynomial of altitude taking into account the data for all sites. + = region 1, O = region 2, ◇ = region 3, △ = region 4, □ = region 5.

the dominant altitudinal gradient (Brehm *et al.*, 2003a; Brehm & Fiedler, 2004). Therefore, the first NMDS dimension is negatively and significantly correlated with altitude ($r_s = -0.79$, $n = 27$, $P < 0.001$), but not with the mean annual temperature ($r_s = -0.16$, ns), or mean annual precipitation ($r_s = -0.02$, ns).

Co-occurrence

The average C-score of all the matrix pairwise values among species is 5.82 and none of the simulated matrices had a C-score as large as the observed (the mean of simulated indices is 5.76). Thus, there is much less co-occurrence of dung beetles in the observed matrix than expected by chance ($P < 0.0001$), suggesting that these dung beetle assemblages are spatially structured. When each site was proportionally weighted according to its latitude so that sites at lower latitudes would have a greater chance of receiving species, simulated matrices also had a significantly lower C-score than observed (4.39; $P < 0.00012$). However, when each

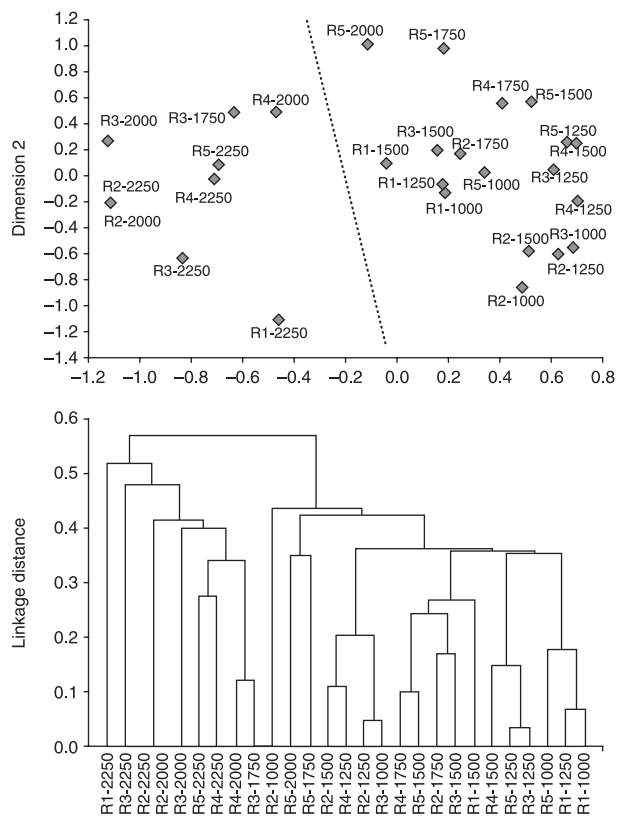


Figure 5 Cluster analysis of the 27 sites using the single linkage method as the linkage rule and Euclidean distance as the measure of similarity. A triangular matrix of similarity was generated using the rectangular matrix of presence-absence of species in each site and the Jaccard coefficient of similarity. A non-metric multidimensional scaling ordination technique was applied to the former triangular matrix of similarity, selecting the two main dimensions. These dimensions were used to build the cluster analysis. The upper graph represents the distribution of each site (for example, R1-1000 is the locality at 1000 m a.s.l. of region 1) in the two NMDS dimensions, and the broken line discriminates the two group of sites represented by the cluster analysis.

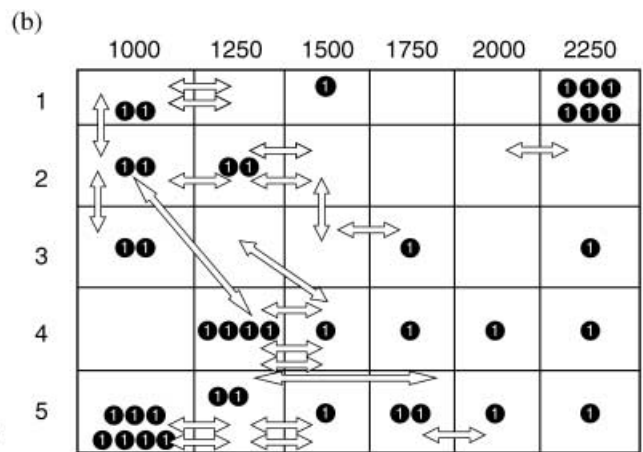
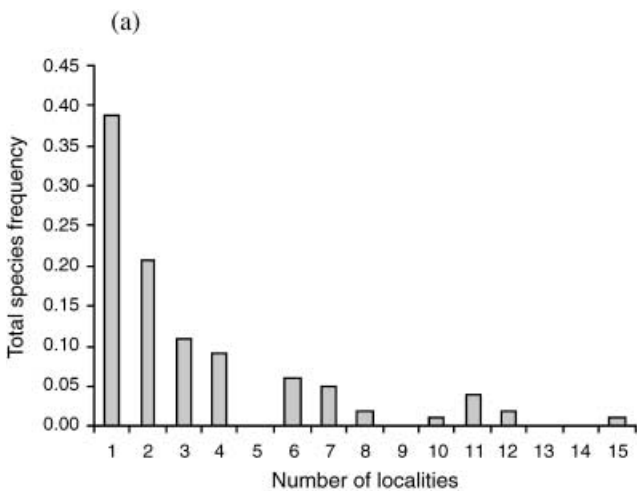


Figure 4 (a) Percentage of total species that occur in a given number of sites, and (b) location of the species exclusive to one site (●), or that occur in two sites (⇒). The arrows indicate the pairs of sites for those species that appear in two sites.

site was proportionally weighted according to its altitude (i.e. lower sites would have a higher chance of receiving species), there was a 0.70 probability that the observed C-score would be higher than the simulated value (average C-score = 5.96), showing that under these circumstances the assemblage seems to be randomly structured.

DISCUSSION

Site altitude significantly influences dung beetle species diversity. Both the observed mean number of species and the estimated richness by asymptotic curves or Hurlbert's PIE diversity index fluctuate markedly with altitude. The altitude of the sites accounts for a high proportion of the variation in species richness, as in all regions we observed a similar curvilinear relationship between altitude and species richness, with greater richness at intermediate altitudes. The number of geographically restricted species is also related to site altitude, with more geographically restricted species occurring at lower altitudinal levels. Thus, the number of geographically restricted species decreases linearly with altitude and the species richness of sites is positively correlated with the number of geographically restricted species.

In contrast to what happens with species richness, variation in rarity or endemism with elevation frequently differs between taxonomic groups (Kessler, 2002) because taxon-specific traits and independent evolutionary histories prevent the occurrence of a general pattern of variation. In none of the five altitudinal regions studied are geographically restricted species abundant at high altitudes and only the northernmost high altitude sites (i.e. Tamá National Park) have a relatively high number of geographically restricted species. The genus *Cryptocanthon* is a good example of this because at least one species occurs in each transect. The elevation gradients located within the Orinoquían lowland influence have three abundant species of *Cryptocanthon* (see Appendix S1). Of the 15 species of *Cryptocanthon* comprising the northern Andean species group, 10 are flightless local endemics occurring at higher elevations (Cook, 2002). Regarding compositional changes, the ordination of sites clearly delimits two main altitudinal groups of sites with their boundary around 2000 m a.s.l. These groups differ in their species richness and number of geographically restricted species (see Appendix S1), so low altitudinal levels have a higher number of species and also have more geographically restricted species. The relevance of altitude is also manifested in that, when low altitude sites have a higher probability of receiving species (weighting each site in inverse proportion to its altitude), a random pattern in the species co-occurrence of these dung beetle assemblages emerges across this mountain territory.

As for many other taxonomic groups, this altitudinal species richness pattern has also been documented for small mammals (Heaney, 2001; McCain, 2004), birds (Rahbek, 1995, 1997), plants (Kessler, 2001) and insects (Janzen, 1973; Holloway *et al.*, 1990; McCoy, 1990; Olson, 1994; Brehm *et al.*, 2003a), including dung beetles (Jay-Robert *et al.*, 1997; Lobo & Halffter, 2000), although this pattern may not be the rule (Brehm *et al.*, 2003b). Of the many causal mechanisms that have been put forth to explain this mid-domain species richness pattern (see Colwell & Lees, 2000; Zapata *et al.*, 2003), we propose that the contact and mixing of

faunas with different climatic tolerances (and probably different lineages and history) from the Amazonian and Orinoquían lowlands are the main factors responsible for the observed increase in the diversity at intermediate altitudes in the eastern Cordillera of the Colombian Andes (see also Brown, 2001; Lomolino, 2001), the magnitude of which depends on the total species richness of the juxtaposed assemblages (Lomolino, 2001). As the geographically restricted species that inhabit the lower altitudinal levels sampled (1000–1250 m a.s.l.) are widely distributed in the tropical lowlands, some with larger populations, the failure of the lowland tropical fauna to colonize these low altitudinal level could generate the remarkable observed pattern in the distribution of geographically restricted species. For example, *Eurysternus hirtellus*, *Dichotomius nisus*, *Dichotomius mamillatus*, *Oxysternon smaragdinum*, *Oxysternon conspicillatum* and *Phanaeus haroldii* are geographically restricted species found at the lower altitudinal levels of our study area, but are frequently collected in tropical Amazonian and Orinoquían lowlands (Escobar, 2000; Pulido *et al.*, 2003; Spector & Ayzama, 2003). Thus, we suggest that the increase in species richness detected at intermediate altitudes, the higher number of geographically restricted species at lower altitudinal levels, and the compositional differences along these mountain gradients are the result of the encounter of dung beetle assemblages characterized by different environmental adaptations and, probably, different origins.

The relevance of altitude in these assemblages may be related to the limited role of these Neotropical high altitude environments as centres of refuge and vicariance for dung beetles. Our results show that these Neotropical high altitude dung beetle assemblages are poor in species (around 7 species per site and 2.4 species per trap), but that they are singular and distinctive. As found in other studies (see Lobo & Halffter, 2000), the environmental changes associated with increasing altitude generate a notable decrease in species richness, and also a slight turnover in the composition of assemblages. This probably occurs because Scarabaeinae dung beetles are a monophyletic group (Scholtz, 1990), mostly comprised of warm-adapted species for which the vertical colonization of these high mountain environments would have been very difficult for lineages distributed at lower altitudes (Lobo & Halffter, 2000).

The importance of altitude in the variation of these Neotropical dung beetle assemblages contrasts the limited role of the interregional differences in topography or general climatic conditions. Species richness and rarity do not vary significantly between the elevation gradients studied. In these mountains, species composition changes rapidly with altitude over distances of only a few kilometres (21.2 ± 13.4 , mean \pm SD; average distance in kilometre between the lowest and highest sites in each transect), whereas the separation among regions ranges over distances greater than 900 km. Thus, we argue that the environmental similarity and connectivity of the montane biomes in the eastern Cordillera of Colombia has allowed many species to spread, especially in the south and particularly along the foothills (Hernández *et al.*, 1992), thus reducing the importance of the geographical separation of these assemblages, and consequently facilitating diversity and faunistic homogeneity. Hence, on the

scale of this study, the influence of environmental variation associated with these altitudinal gradients can be considered similar, independently of the geographical location of the mountain chain.

However, the high relevance of altitudinal gradients on diversity and composition of dung beetle assemblages does not hinder the existence of a biogeographical pattern in the studied territory. The northernmost and southernmost high altitude assemblages differ in the number of geographically restricted species they have, showing that at the limits of the sampled latitudinal gradient the isolated conditions of the high mountains may allow for the development of different communities. In the same way, most species occurring in more than one transect were centred on adjacent blocks of transects, suggesting also a biogeographical pattern. As the Orinoquian and Amazonian areas are two distinct tropical lowland territories in contact with the eastern slope of the Eastern Cordillera (Hernández *et al.*, 1992), interregional differences in species assemblages could be the result of differences in the tropical lowland species assemblages from which they are derived. According to van der Hammen (2001), the eastern Cordillera of the Colombian Andes emerged from the south to the northeast and when its final formation took place around 2–3 Myr ago, cyclic glaciation during the Plio-Pleistocene was reflected in the expansion and contraction of mountain forest. This allowed for the repeated connection and isolation of geographically separated locations and latitudinal interchange of biota (van der Hammen & Cleef, 1986; Brown & Lomolino, 1998). The difference in species richness and composition between the southern and northeastern Andean mountains could be also related to the presence of wet southern palaeoecological refugia [or ecologically extremely stable areas (EESAs), *sensu* Fjeldsø, 1995] in the adjacent lowlands during glacial periods. The Florencia, the Putumayo and the Kofan refugia are examples of this (Hernández *et al.*, 1992). At present, these refugia are connected by mountain forest where particular flora and fauna occur (Hernández *et al.*, 1992). With the final rising of the Andes in the Plio-Pleistocene, new environments with a cooler, temperate climate appeared and these offered 'empty' habitats ready to be occupied by lowland biota (van der Hammen, 2001). Exchange with the faunas of neighbouring tropical montane biomes at lower altitudes was relatively important, especially during the Plio-Pleistocene glaciation cycles, and probably continues to be important (Vuilleumier, 1986). So, many biotic elements of the Andean mountains have their origin in lowland rainforest, as reported for plants (Hernández *et al.*, 1992; report that more than 50 genera of Andean plants are from lowland vegetation) and birds (Vuilleumier, 1986). Much of the species level endemism of the plants, birds and mice of the high Andes occurred *in situ* (Moritz *et al.*, 2000), producing the present zonation of flora and fauna throughout tropical mountains (Vuilleumier, 1986; Kessler, 2001; Patterson *et al.*, 1998).

Finally, our results must be viewed with caution because of the difficulty in obtaining complete, reliable inventories. Considering the universe that has been defined by the chosen sampling method, accumulation curves suggest that we collected a high proportion of the species that inhabit this territory. For tropical insects, accumulation curves do not often reach an asymptote

(Novotny & Basset, 2000) probably owing to the failure to collect some geographically restricted species. In our case, the regions richest in species have more singletons or number species with one individual (Colwell & Coddington, 1994; see Appendix S1 in Supplementary Material), greater differences between estimated and observed species richness scores, and they probably contain a comparatively higher number of species. This underestimation of the true number of species in the richest regions implies that the differences in species richness and the turnover in species composition between southern and northern regions (see Fig. 5) may be even greater than estimated.

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SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com

Appendix S1 Scarabaeinae dung beetle species collected from five regions in the Colombian Andes

BIOSKETCHES

Federico Escobar has worked on the biodiversity patterns of dung beetles and their use as indicators of the effects of human disturbance on the environment for the last 10 years. He is interested in the design of biodiversity surveys and in sampling theory, as well as in the effects of habitat fragmentation caused by human disturbance on dung beetle populations.

Jorge M. Lobo is a specialist in the biogeography and ecology of dung beetles (Scarabaeoidea) working at the Department of Biodiversity and Evolutionary Biology of the Museo Nacional de Ciencias Naturales de Madrid. He is interested in the patterns and processes of species distribution from a macroecological perspective, and in the management of biodiversity information as well as in conservation biology.

Gonzalo Halffter is one of the world's leading specialists in the ecology, biology, and ethology of dung beetles, and has published two major works (one with Eric Matthews and the other with David Edmunds), in addition to a host of chapters and scientific papers on this subject. The biogeography and biodiversity of Mexico are also his strong areas of research. Most recently, he has been writing about biosphere reserves and their importance to the conservation of native biota.