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Assessing the origin of Neotropical mountain dung beetle assemblages (Scarabaeidae: Scarabaeinae): the comparative influence of vertical and horizontal colonization

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ABSTRACT

Aims The fauna of mountains and their surrounding regions are likely to be influenced principally by two biological processes: horizontal colonization along similar altitudinal levels by elements originating from lineages inhabiting higher latitudes; and vertical colonization by lineages from the same latitude, but at lower altitudes. We examine whether the expected patterns derived from the latter process can be observed in mountain dung beetle assemblages. Specifically, we study the variation in species composition and richness with altitude in five regions spanning elevation gradients, analysing whether the altitudinal rates of change in the number of species and genera differ, and whether beta-diversity scores for adjacent sites in each altitudinal gradient are different for species and genera.

Location Eastern Cordillera of the Colombian Andes.

Methods Field work was carried out in 1997–99 at 27 sites in five regions with elevation gradients, with 10–32 pitfall traps placed in each site. For each altitudinal level the numbers of species and genera were analysed with respect to altitude, and the slope of the linear regression between these variables was calculated. The slope of the curve of the altitude against the cumulative number of species and genera was also calculated for each altitudinal gradient to describe the compositional change between adjacent sites (beta diversity). Species and generic slopes were compared using analysis of covariance. The turnover of species along each altitudinal gradient was measured using presence/absence data and Cody's beta-diversity index between adjacent pairs of sites. A cluster analysis was used to detect faunistically homogeneous groups of localities.

Results Species richness always decreased with altitude, although the slopes did not differ significantly from zero. The number of genera also decreased with increasing altitude, but generally at a significantly slower rate than for species. Variation in the species beta-diversity scores between altitudinal levels did not follow a homogeneous pattern in the different regions. Two main altitudinal groups of sites with a boundary *c.* 1500–1750 m a.s.l. can be detected with respect to faunistic similarity. Low- and mid-altitude sites are inhabited by all of the genera (19) and 80% of all species collected. Eight genera and 61 species (*c.* 60% of the total) are unable to inhabit high-altitude sites, and only 20 species appear to be exclusive to these high-altitude environments (> 2000 m a.s.l.).

Main conclusions The dominant processes explaining dung beetle composition in the high north-eastern Andean mountains are probably those of vertical colonization. The limited role of horizontal colonization processes, or colonization from northern or southern lineages, could be a consequence of the isolation and recent geological origin of these mountains.

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INTRODUCTION

It has long been recognized that some of the biota that currently occur in temperate and tropical mountains are physiognomically similar to groups that inhabit higher latitudes, and that changes in the assemblages with altitude are equivalent to latitudinal changes (von Humboldt, 1805; Merriam, 1894; Flenley, 1979; Stevens, 1992). Biogeographers have now established that behind this general pattern of similarity lies an evolutionary process tied to the recent climatic cycles of the Pleistocene and the associated disruption of the assemblages that co-evolved and persisted for millions of years (Brown & Lomolino, 1998; Hewitt, 2000). Owing to this process, the mountainous biota of some low-latitude regions may be phylogenetically related to that inhabiting high-latitude biomes (Vuilleumier & Simberloff, 1980; Brown, 1995). However, when low-latitude mountain areas are disconnected or isolated from the temperate regions to the north and the south of them, the possibility of dispersal by lineages from these regions may be impeded, resulting in a tropical mountain biota with a low species richness that is phylogenetically related to the biota of surrounding lowlands (Janzen, 1967; Brown & Lomolino, 1998; Channell & Lomolino, 2000).

Taking these ideas into account, studies of the altitudinal variation in dung beetle species richness and community composition around the world have proposed two non-mutually exclusive processes to explain the origins of mountain fauna, the patterns of species richness and variation in composition across altitude: horizontal colonization by elements originating from lineages inhabiting higher latitudes; and vertical colonization by lineages inhabiting the same latitude but at lower altitudes (Lobo & Halffter, 2000 and references therein). These processes represent the two primary reactions that species can have to changes in environmental conditions: spatial adaptation, which involves shifts in their distribution (Hengeveld, 1997); or morpho-ecological adaptation, involving local adaptation to new conditions (Moritz et al., 2000). The effects of these processes are comparable with the biogeographical consequences of phylogenetic niche conservatism and niche evolution concepts (Wiens & Donoghue, 2004), and can help explain the two main types of endemism: allochthonous endemism (the reduction of a formerly larger range); and autochthonous endemism (local speciation).

These processes would be expected to differ not only in their consequences, but also in the spatial and temporal scales on which they operate. Horizontal colonization assumes the geographical displacement of taxa or of their ancestors in relatively recent geological times, and would generate both a clear pattern of altitudinal substitution between higher-level taxa with different evolutionary histories, and an attenuated gradient of reduction in species richness with altitude, because the decrease of species richness with altitude is attenuated by the incorporation of species from distant regions. In contrast, vertical colonization suggests a lower degree of regional dispersal of taxa but a higher relevance of long term speciation processes. In this case, the elevational substitution pattern detected would be lower, but the decrease in species richness would be greater.

As in some European mountain regions (Martín-Piera et al., 1992; Jay-Robert et al., 1997), the Mexican Transition Zone exemplifies horizontal colonization processes, as high-altitude communities are dominated by mountainous Palaeo-American and Nearctic species belonging to genera with diversification centres in the Holarctic region, whereas lowland assemblages are dominated by Neotropical elements (Halffter, 1976; Halffter et al., 1995; Lobo & Halffter, 2000). The horizontal colonization pattern would then be due to the southward shift of northern lineages that have taken place in response to climate changes (Halffter, 1976; Elias, 1994), facilitated by the north–south orientation of North American mountain ranges (Halffter, 1976; Lobo & Halffter, 2000; Escobar et al., 2005), whereas only a minor role is played by speciation and adaptive evolutionary changes resulting from the isolation and evolutionary divergence after these colonization events (Cruzan & Templeton, 2000; Hewitt, 2000). In contrast, vertical colonization dominates the expected pattern of species richness and variation in composition observed in some island dung beetle assemblages of south-eastern Asia (Hanski, 1983; Hanski & Niemelä, 1990; Hanski & Krikken, 1991).

There is no empirical evidence about the role of vertical colonization and its hypothesized effects on species richness and compositional patterns in continental areas. Evidently, the relative importance of both processes depends on the orientation and location of the mountains, and on their degree of isolation and biogeographical history, as these characteristics greatly influence the refuge and 'corridor' capacity of mountain areas (Rickart, 2001). In this study, we examine five Neotropical altitudinal gradients between 1000 and 2250 m a.s.l. in the Eastern Cordillera of the Colombian Andes, and determine whether patterns supposedly derived from vertical colonization can be observed, as they are relatively isolated both from northern and southern ranges. Assuming that when the mountain fauna is derived primarily from vertical colonization processes, the compositional and richness variation with altitude should be a consequence of the turnover of species belonging to the same phylogenetic lineages, we examine specifically whether the altitudinal rates of change in the numbers of species and genera are different,

and whether beta diversity for adjacent sites on each altitudinal gradient differs for species or genera.

METHODS

Study area and sampling design

A detailed description of the area and sampling procedures is presented by Escobar *et al.* (2005). Briefly, the study was carried out on the eastern slope of the Eastern Cordillera in the Colombian Andes (between 00°28′ N, 77°17′ W and 00°23′ N, 72°23′ W; Fig. 1), a south-to-north mountain range that separates the territory into large lowland regions (the Amazonian and Orinoquian regions to the east and the Chocó region to the west). Field work was carried out between February 1997 and November 1999 in five areas (Fig. 1). After dividing each area into six 250-m-interval transects, between 1000 and 2500 m a.s.l., 27 sites were sampled with 330 traps. At each site, 10–32 pitfall traps (12.2 ± 4.8; mean ± SD; traps 1000 mL capacity, 13 cm deep, 11 cm diameter) were placed in the forest 25 m apart and baited with 50 mL of human dung. Each trap was left in the field for 48 h. A total of 7894 specimens belonging to 101 species were captured. An evaluation of data completeness using accumulation curves showed that a detectable asymptote was reached in many sites (Escobar *et al.*, 2005), and that in 21 sites (78%) > 80% of species appeared to be collected, although in the remaining six sites the mean value of the estimates was 76%. The nonpar-

ametric richness estimates indicated that between 75% and 86% of the expected maximum number of species for the entire territory were collected (Escobar *et al.*, 2005).

Data analysis

For each sampling area, the elevational change in number of species and the number of genera were analysed. Curves for the cumulative numbers of observed species and genera against altitude were calculated for each area to describe the compositional change between adjacent sites (beta diversity). The slope of the linear regression of the altitude of sites against the cumulative number of species or genera was calculated for each area. These slopes were compared using analysis of covariance (ANCOVA) to test whether the effect of taxonomic category (species or genus) was statistically significant.

The turnover of species along the altitudinal gradient in each area was measured using presence/absence data and by calculating Cody's beta-diversity index (Cody, 1993) between adjacent pairs of sites (β_{co}) as:

$$\beta_{co} = 1 - \left[\frac{a(2a + b + c)}{2(a + b)(a + c)} \right]$$

where a is the total number of species or genera that occur in any pair of adjacent sites along a transect, and b and c are the number of exclusive species or genera (those that occur in each site but not in the adjacent one). This index was selected from the large number of beta-diversity measures available because
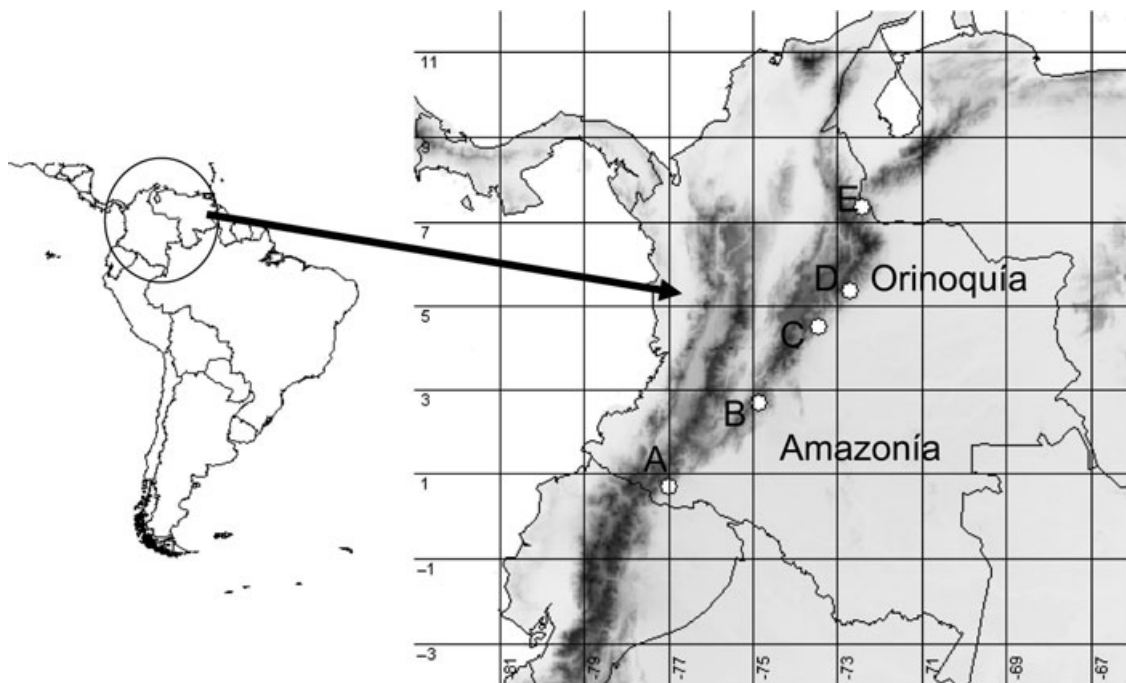

Figure 1 The Colombian Andes and geographical locations of the five altitudinal regions sampled (white circles) in the Eastern Cordillera of the Colombian Andes (dark grey). A = Putumayo (00°28′ N, 77°17′ W); B = Los Picachos (02°47′ N, 74°51′ W); C = Farallones de Medina (05°35′ N, 73°25′ W); D = Alto Río Cusiana (05°23′ N, 72°42′ W); E = Tamá National Park (07°07′ N, 72°14′ W). The two main tropical lowland regions are also indicated. Cells represent a 2° grid in latitude/longitude co-ordinates.

it is one of eight measures recently recommended (Koleff *et al.*, 2003) for its capacity to focus on compositional differences rather than on species richness, and for the higher scores it gives when the proportion of shared species is low and the percentages of species lost and gained are similar. As beta-diversity indices do not reveal whether the values are produced by a gain or loss in the number of species, we also calculated the number of species or genera gained and lost between neighbouring sites. A triangular *Q*-mode similarity matrix of sites was computed from the rectangular matrix of species abundance on each site using the percentage dissimilarity measure (PD; Ludwig & Reynolds, 1988). To define groups of sites with similar composition, cluster analysis was carried out using the Ward method as clustering strategy, as it allows detection of clusters that are relatively homogeneous with respect to all the variables (Legendre & Legendre, 1998). Significant clusters were estimated by randomly assigning the cases (500 random trials) to a given initial partition by a *k*-means procedure, to improve the Euclidean sum of squares (ESS), selecting the solution with the lowest ESS (Wishart, 2000; http://www.clustan.com).

RESULTS

Species richness of dung beetles decreased with altitude in all five areas, at a rate varying between 3.4 and 13.6 species per 1000 m altitude, but with a general increase in the number of species at intermediate elevations (Fig. 2). The estimated number of species using three different nonparametric richness estimators (the incidence-based coverage estimator, Chao1 and first-order jackknife; Colwell & Coddington, 1994), follow the same tendency as that of observed richness (Fig. 2; cf. Escobar *et al.*, 2005). The number of genera also decreased with increasing altitude (slopes from −2.57 to −6.0 genera per 1000 m). The rate of decrease in the number of genera was generally lower, without an increase at intermediate altitudes (Fig. 2), suggesting that the intermediate peak in species richness is probably the result of an increase in species of the same genera that inhabit adjacent altitudes.

The slopes of the cumulative number of species varied from 8.6 to 22.0 species per 1000 m, with the lowest slope occurring in the northernmost elevational gradient; slopes for the number of genera were significantly lower, varying from 1.6 to 3.6 genera per 1000 m (Table 1; Fig. 2). Thus the addition of new species with increasing altitude is much higher than the accumulation rate of genera, suggesting that species that appear with increasing altitude generally belong to the same genera that inhabited lower altitudinal levels.

Variations in species beta diversity (β_{co}) between altitudinal levels do not follow a homogeneous pattern in the different regions (Fig. 3), although there is a general increase in beta diversity between sites at the two highest altitudes. However, these higher β_{co} scores are mainly due to the loss of species, except in the case of the northern altitudinal gradient (site E), where the lack of data for the sites at 1500 and 1750 m a.s.l. produces an apparent increase in species turnover rates. The beta-diversity scores for generic replacement (mean ± SE: 0.23 ± 0.04) are significantly lower than for species (0.49 ± 0.05; Wilcoxon matched pairs, $Z = 3.26$, $P = 0.001$), but show the same general pattern as that observed for species (Fig. 4), so the higher beta scores are mainly due to the loss of genera between altitudinal levels.

As occurs when a presence/absence matrix is used (Escobar *et al.*, 2005), two main altitudinal groups of sites with a boundary around 1500–1750 m a.s.l. can be identified according to their faunistic similarity (Fig. 5). Mid-altitude sites harbour all the genera collected (19) and 80% of total species. Eight genera and 61 species (around 60% of total) did not inhabit high-altitude sites, and only 20 species appear to be exclusive to these high-altitude environments (Table 2). These belong to the genera *Bdelyrus* (one species), *Canthidium* (three species), *Canthon* (one), *Cryptocanthon* (two), *Deltochilum* (five), *Dichotomius* (one), *Ontherus* (one), *Scybalocanthon* (one) and *Uroxys* (five). Examining the distribution of the two genera with more exclusive species in the group of high-altitude sites, closely related species appear to be segregated both with respect to altitude and between the different mountain regions (Fig. 6).

DISCUSSION

The decline in species richness with altitude is common, but altitudinal patterns for different groups vary (Rahbek, 1995; Patterson *et al.*, 1998). Elevational patterns in diversity have been related to many contemporary environmental variables (Huston, 1994), but the underlying causal mechanisms behind these correlations remain elusive. It is likely that current patterns are greatly influenced by past environmental changes, and present-day environmental conditions only allow their maintenance (Brown, 2001; Davis & Shaw, 2001). That is why, rather than identifying the environmental variables correlated with the species richness and variations in faunistic composition, we have sought to explain how mountain species have been able to inhabit these environmentally favourable regions. In our study the results of the accumulation curves, the variation in beta-diversity scores, and the faunistic similarity between sites all suggest that the dominant processes able to explain the observed altitudinal patterns of dung beetle assemblages in the eastern Andean mountains are those of the vertical colonization model. However, it should be taken into account that the present study comprises only a portion of the altitudinal gradient (between 1000 and 2500 m), which suggests that caution is needed in proposing generalizations.

As for dung beetles of other tropical regions with high and isolated mountains (Davis *et al.*, 1999), the distinction between low- and high-elevation fauna is well established in the Andes, as is the distinction between lower- and upper-montane fauna (Patterson *et al.*, 1998; Kessler *et al.*, 2001). Although few species are added as altitude increases, and most of the turnover at high-altitude sites is due to the occurrence of a small number of species belonging to the same genera collected at lower altitudes, there are some examples indicative
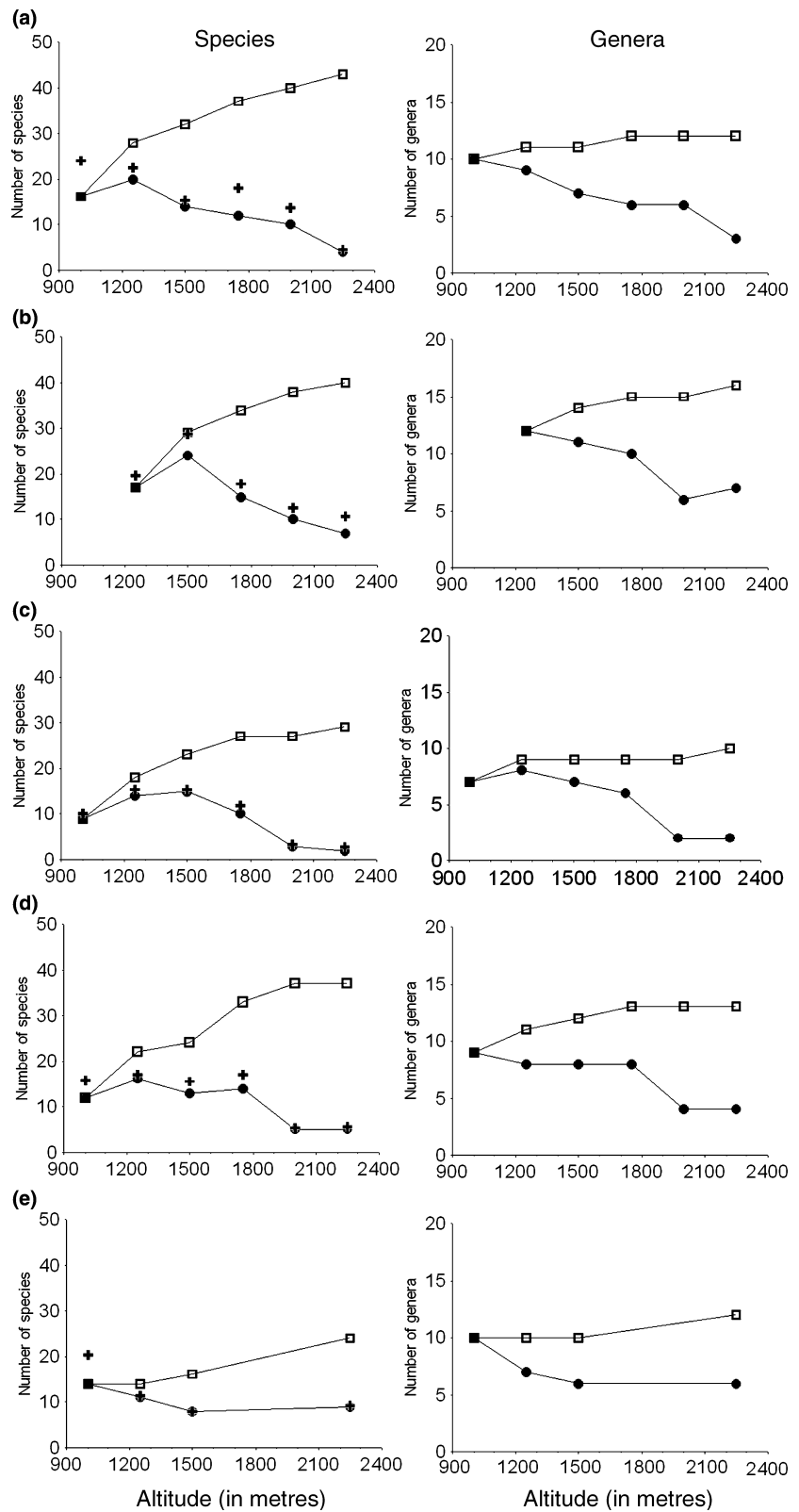
Figure 2 Elevational variation in number of species or genera (solid circles) and cumulative number of species and genera (squares) in each region. Sites as in Fig. 1. Crosses represent mean number of species estimated by three common nonparametric richness estimators that use species-by-sample data (Escobar *et al.*, 2005).

of possible *in situ* speciation, probably resulting from the local adaptation of populations coming from the lowlands. The current spatial segregation among presumed sister species, both between altitudes and between the different mountain

regions (genera: *Deltochilum*, *Uroxys* and *Cryptocanthon*), suggests that the complex geological and climatic history of the north Andean mountains could also have favoured the isolation and speciation of populations. Additional phylogeographical

Table 1 Slopes of variation in the cumulative number of dung beetle species and genera by altitude for the five mountain regions (see Fig. 1)

Region	Species	Genus	F	P
A	20.11**	1.60**	$F_{(1,9)} = 54.66$	< 0.001
B	22.00**	3.60*	$F_{(1,7)} = 36.56$	< 0.001
C	14.97**	1.71*	$F_{(1,9)} = 34.93$	< 0.001
D	20.46**	3.09*	$F_{(1,9)} = 32.61$	< 0.001
E	8.57*	1.71 ns	$F_{(1,5)} = 17.10$	0.009

F, ANCOVA results indicate whether the effect of taxonomic category (species or genus) is statistically significant for these slope scores: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

studies are needed to delimit the relevance of speciation processes across elevational gradients, and also across the different mountain chains. The strong environmental gradient that a mountain represents can result in adaptive divergence and speciation (gradient model of speciation; Moritz *et al.*, 2000), while the occurrence of related species in different mountain regions is better explained by a traditional vicariance model of speciation.

Recent evidence suggests that climatic oscillations during the Plio-Pleistocene played a minor role in generating vertebrate species in the lowland tropics, perhaps because species responded mainly by migration rather than by adaptive differentiation (Moritz *et al.*, 2000). However, these climatic changes are frequently mentioned as a main source of speciation when the aim is to explain the current distribution of Andean biota (frogs: Duellman, 1979; plants: Gentry, 1982; butterflies: Descimon, 1986; birds: Vuilleumier, 1986). Thus species found at high elevations in tropical America would be recent and geographically limited, possibly indicating the existence of an association between modern diversification processes and recent geological activity (Hewitt, 2001). At least for some vertebrate groups, molecular studies indicate that the tropical Andes contain a higher proportion of young species (Fjeldså, 1994; da Silva & Patton, 1998), probably owing to the environmental heterogeneity that emerged after the uplift of the Andes beginning in the Miocene (18 Ma), and the speciation processes that occurred during the Plio-Pleistocene glacial periods (García-Moreno *et al.*, 1999; García-Paris *et al.*, 2000). The rapid shifts in the climate and associated changes in the composition and distribution of vegetation during the last two glacial cycles would have generated sufficient opportunity for speciation (Moritz *et al.*, 2000 and references therein).

A clear example of the role of elevation and isolation in the Andean mountains is provided by *Cryptocanthon*, a genus for which one species occurs in each mountain region. According to Cook (2002), there are 35 species of *Cryptocanthon*, 23 of which have a narrow geographical distribution occurring at elevations above 1000 m a.s.l. (Cook, 2002). This high level of endemism is closely related to the loss of the ability to fly.
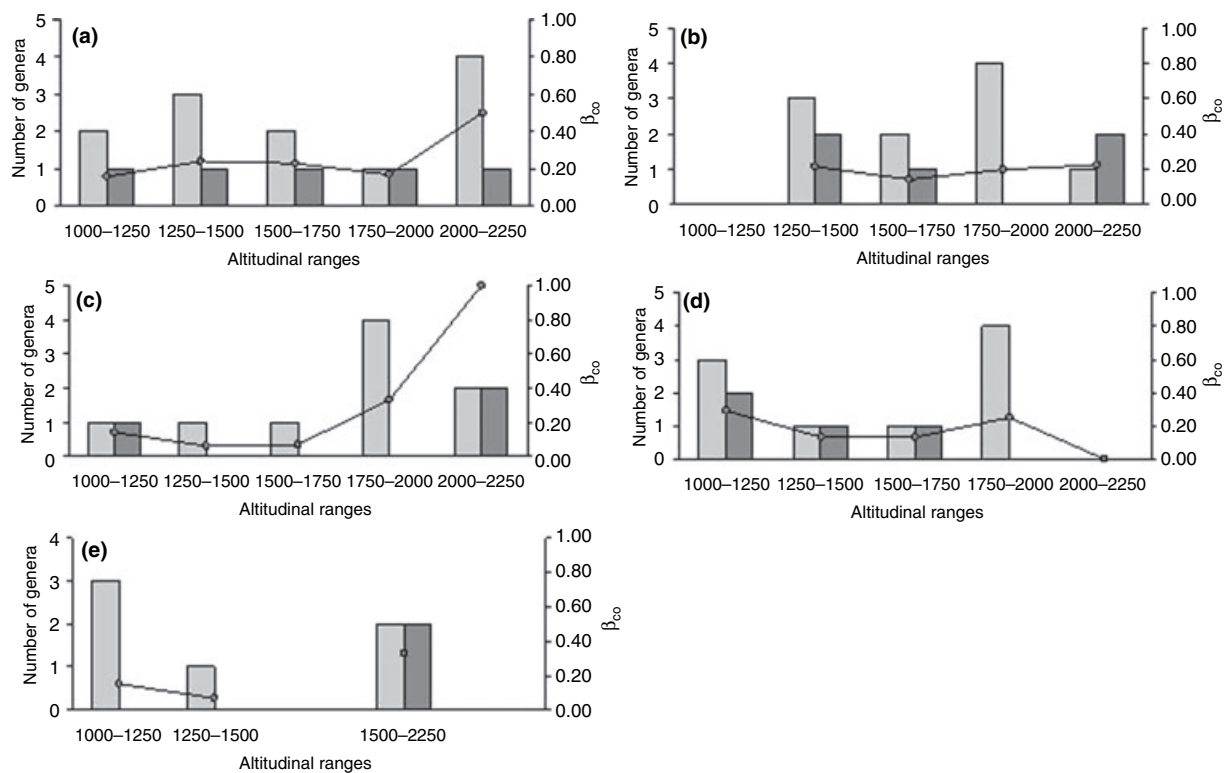

Figure 3 Changes in beta diversity (β_{co}) for species along each elevational gradient (line). Beta diversity was calculated between two adjacent altitudinal levels. Grey bars, number of species lost; dark bars, number of species gained.

Figure 4 Changes in beta diversity (β_{co}) for genera along each elevational gradient (line). Beta diversity was calculated between two adjacent altitudinal levels. Grey bars, number of species lost; dark bars, number of species gained.
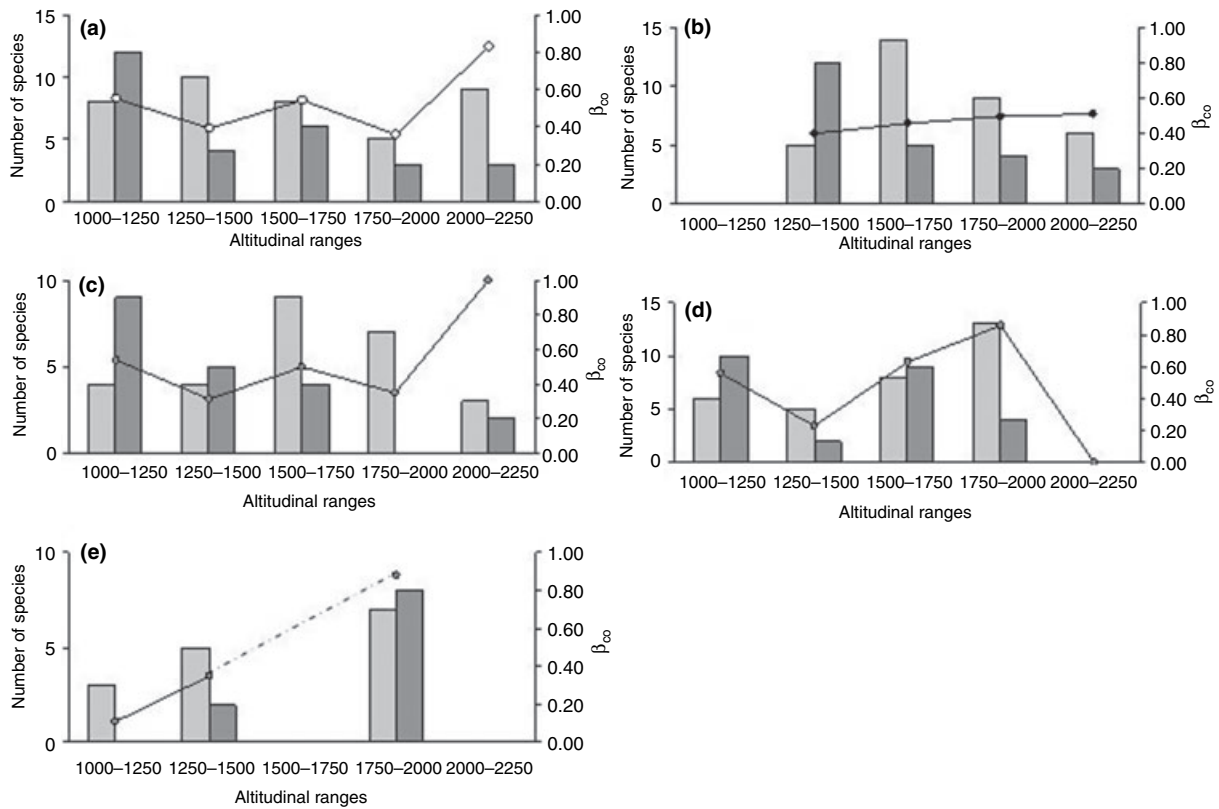
Flightlessness is unusual among dung beetles, because most species need fly to reach ephemeral food resources such as fresh dung (Halffter & Matthews, 1966). The tendency towards a reduction of metathoracic wings in mountain habitats is a pattern that occurs repeatedly in other Coleoptera (Carabidae; Darlington, 1943). These features are suggestive of old taxa that are phylogenetically isolated within their respective lineages, and could indicate a close adaptation to the environment and a relatively long residence time (Ball & Shpeley, 2000). So beetles with a tendency towards flightlessness, such as *Cryptocanthon*, have been profoundly affected by the repeated climatic disruptions of the Plio-Pleistocene (Cook, 2002).

Our results show that these Neotropical high-altitude dung beetle assemblages are poor in species, but are singular and distinctive. As found in other tropical studies (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, mainly due to the loss of species. 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 by lineages distributed at lower altitudes would have been very difficult (Lobo & Halffter, 2000). Other restrictions to colonizing mountain environments include the general shape of mountains, where area decreases and isolation increases

with increasing elevation, resulting in high extinction rates and low colonization rates. Both factors would contribute to a decrease in diversity with altitude (Brown, 2001). Although our collecting efforts did not include sampling above 2250 m a.s.l., studies carried out on different mountains in the Colombian Andes (Amat-García *et al.*, 1997; Medina *et al.*, 2002) confirm the predominant role of vertical colonization, dominated by species belonging to widely distributed genera with a long evolutionary history in lowlands: species such as *Dichotomius*, *Ontherus* and *Uroxys*.

In contrast to findings for the Mexican Transition Zone (Halffter, 1987; Lobo & Halffter, 2000), where the north–south orientation of the mountain ranges facilitates the arrival of northern elements, in the northern Andes a lack of horizontal colonization could be a result of the isolation and recent origin of these mountains relative to more northern and southern mountain chains. We suggest that these mountains are being colonized, without much success, by the surrounding Neotropical fauna. However, the presence of the genus *Onthophagus* in South America could have resulted from the horizontal colonization of elements that have recently penetrated the lowlands, such as species of the *clypeatus* group. American *Onthophagus* lineages probably derive from Oriental or Palaearctic taxa, although African lineages appear to be basal in the phylogeny of the genus (Emlen *et al.*, 2005). Currently the distribution of this genus is restricted mostly to
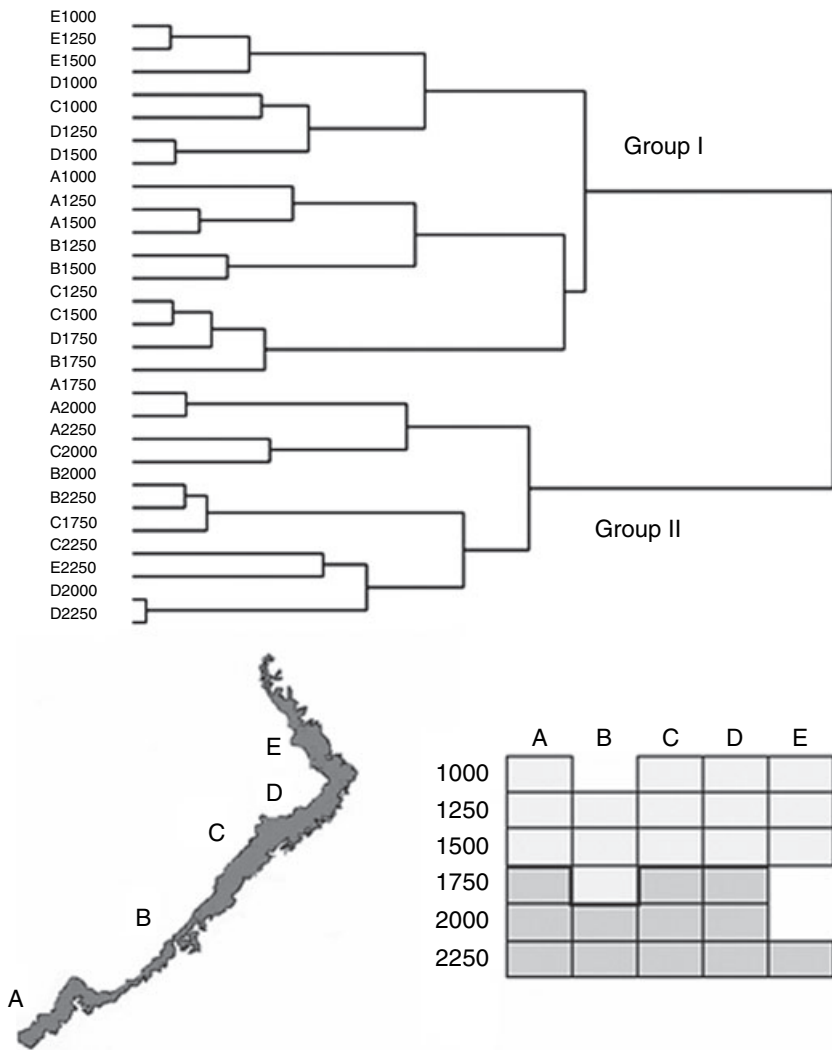
Figure 5 Cluster analysis of sites (27) using the Ward method as the linkage rule and Euclidean distance as the measure of similarity. A triangular Q-mode similarity matrix of sites was computed from the rectangular matrix of species abundance on each site using the percentage dissimilarity measure (PD; Ludwig & Reynolds, 1988). Below, locations of the two main clusters of sites derived. Sites in the dendrogram are represented by the combination of letters (Fig. 1) and altitudes (m).

Table 2 Number of genera, species (mean ± SD) and number of shared species of dung beetle according to cluster analysis (group I, sites < 1500–1750; group II, sites > 1750–2000 m a.s.l.)

Group	Genera Number	Genera Mean number per site	Species Number	Species Mean number per site	Shared Genera (number)	Shared Species (number)
I	19	8.5 ± 1.6	81	14.5 ± 3.8		
					8	20
II	11	4.7 ± 1.8	40	7 ± 3.4		

forest below 2000 m a.s.l. (Zunino & Halffter, 1997), with only a few species successfully colonizing the high Andean mountains.

The concepts of vertical and horizontal colonization allow us to explain the altitudinal turnover in fauna and, to a lesser extent, the changes in species richness along the elevational gradient, but principally aim to elucidate the role played by historical dispersal and speciation in the formation of mountain assemblages. Integrating large spatial and temporal processes to contemporary patterns, vertical and horizontal

colonization concepts provide a theoretical tool for understanding the processes behind the dissimilarity of the altitudinal variation in assemblages, as well as the differences in the rate of species richness decrease with altitude. As Pielou (1979) asks: 'Does the differential migration of species in response to change reinforce or obscure the zonation caused by the zoned climates on a rotating sphere warmed by a small, distant sun?' We believe that dispersal expanding the geographical ranges of species can reinforce the observed biotic zonation in some situations when physical connections are
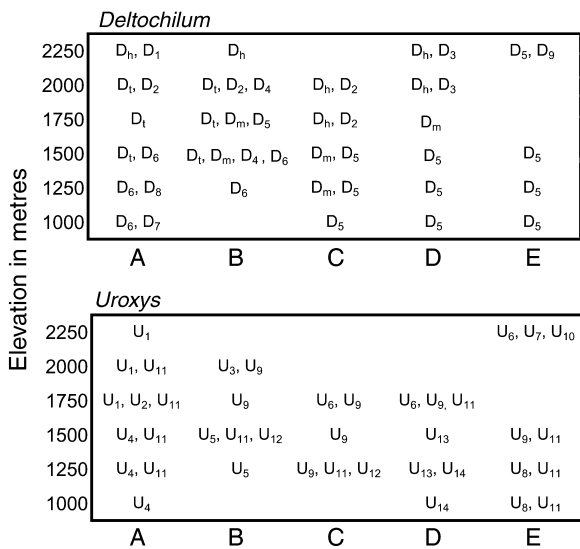
Deltochilum

Elevation (m)	A	B	C	D	E
2250	D_h, D_1	D_h		D_h, D_3	D_5, D_9
2000	D_t, D_2	D_t, D_2, D_4	D_h, D_2	D_h, D_3	
1750	D_t	D_t, D_m, D_5	D_h, D_2	D_m	
1500	D_t, D_6	D_t, D_m, D_4, D_6	D_m, D_5	D_5	D_5
1250	D_6, D_8	D_6	D_m, D_5	D_5	D_5
1000	D_6, D_7		D_5	D_5	D_5

Uroxys

Elevation (m)	A	B	C	D	E
2250	U_1				U_6, U_7, U_{10}
2000	U_1, U_{11}	U_3, U_9			
1750	U_1, U_2, U_{11}	U_9	U_6, U_9	U_6, U_9, U_{11}	
1500	U_4, U_{11}	U_5, U_{11}, U_{12}	U_9	U_{13}	U_9, U_{11}
1250	U_4, U_{11}	U_5	U_9, U_{11}, U_{12}	U_{13}, U_{14}	U_8, U_{11}
1000	U_4			U_{14}	U_8, U_{11}

Figure 6 Spatial distribution for the genera *Deltochilum* and *Uroxys* along each elevational gradient. Letters represent the sites as in Figure 1. Note the apparent elevational segregation with some species exclusive to mid and high altitude mountains. *Deltochilum* (D_m = *D. mexicanum*; D_t = *D. teselatum*; D_h = *D. hypponum*; D_1 = *D.* sp. 1; D_2 = *D.* sp. 2; D_3 = *D.* sp. 3; D_4 = *D.* sp. 4; D_5 = *D.* sp. 5; D_6 = *D.* sp. 6; D_7 = *D.* sp. 7; D_8 = *D.* sp. 8; D_9 = *D.* sp. 9). *Uroxys* (U_1 = *U.* sp. 1; U_2 = *U.* sp. 2; U_3 = *U.* sp. 3; U_4 = *U.* sp. 4; U_5 = *U.* sp. 5; U_6 = *U.* sp. 6; U_7 = *U.* sp. 7; U_8 = *U.* sp. 8; U_9 = *U.* sp. 9; U_{10} = *U.* sp. 10; U_{11} = *U.* sp. 11; U_{12} = *U.* sp. 12; U_{13} = *U.* sp. 13; U_{14} = *U.* sp. 14).

likely. In the case of high northern Andean mountain dung beetles, this does not appear to have been possible.

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BIOSKETCHES

Federico Escobar has worked for the past 10 years on biodiversity patterns of dung beetles and their use as indicators of effects of human disturbance on the environment. He is interested in the design of biodiversity surveys and in sampling theory, as well as 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 macro-ecological perspective, and in the management of biodiversity information as well as in conservation biology.

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

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