Biogeographical and Ecological Factors Affecting the Altitudinal Variation of Mountainous Communities of Coprophagous Beetles (Coleoptera: Scarabaeoidea): a Comparative Study

JORGE M. LOBO[1] AND GONZALO HALFFTER

Instituto de Ecología, A.C., Departamento de Ecología y Comportamiento Animal, Apartado Postal 63, Xalapa 91000, Veracruz, Mexico

ABSTRACT The altitudinal variation in the richness and composition of communities of coprophagous beetles in a mountainous landscape in Mexico is analyzed and the results obtained are compared with those of similar studies carried out in other parts of the world. Two nonexclusive processes are proposed as responsible for the assemblage of mountain fauna: horizontal colonization by elements originating from lineages distributed at higher latitudes and vertical colonization by lineages distributed at the same latitude but at different altitudes. The current analysis supports the hypothesis that when the horizontal colonization dominates, mountain faunas show a clear altitudinal substitution between large taxa with different evolutionary histories (e.g., Scarabaeinae and Aphodiinae) and the gradient of reduction in species richness is attenuated. This occurs in mountains of different continents and depends primarily on the degree of isolation and general orientation of the mountain ranges. Conversely, when vertical colonization dominates, mountain faunas show only slight altitudinal substitution, and the reduction in richness is greater.

KEY WORDS Scarabaeinae, Aphodiinae, dung beetles, mountain biogeography

ALTITUDINAL VARIATION IN communities of copropha-gous beetles has been studied in Europe (Avila and Pascual 1988; Lumaret and Stiernet 1989, 1991; Martín-Piera et al. 1992; Jay-Robert et al. 1997), in Mexico (Martín-Piera and Lobo 1993, Halffter et al. 1995), and in Southeast Asia (Hanski 1983, Hanski and Niemelä 1990, Hanski and Krikken 1991). From these studies a first conclusion is that the number of species dimin-ishes with increasing altitude, as in other groups of insects (Wolda 1987, McCoy 1990). However, this conclusion does not have as much general value as global figures would suggest. Within the Scarabae-oidea there are 3 taxa with essentially coprophagous habits: Scarabaeinae, Geotrupinae, and Aphodiinae. In the Scarabaeinae, a group mostly adapted to warm or warm-temperate conditions, the decrease in richness with increasing altitude is notable. Geotrupinae and Aphodiinae are predominantly adapted to cold tem-perate conditions, and where the biogeographic his-tory has made the presence of these groups possible, the number of species does not decrease and may even increase with increasing altitude. Under these circum-stances there is altitudinal replacement: Aphodiinae and Geotrupinae dominate at higher altitudes and Scarabaeinae dominate in the lowland. Because these taxa have distinct biogeographical distributions and different evolutionary histories, it has been proposed

that the altitudinal variation must be a consequence of unique and unrepeatable historical and geographical factors (Martín-Piera et al. 1992, Martín-Piera and Lobo 1993, Jay-Robert et al. 1997).

To explain the altitudinal variation in the richness of coprophagous beetles we considered the following 3 hypotheses: (1) that mountain fauna is a rarefied equivalent of lowland fauna; (2) that mountain fauna is composed of a lesser number of phylogenetically related species relative to that which inhabits lower altitudes (vertical colonization model); and (3) that mountain fauna may or may not have a lower number of species, but is composed of elements with a differ-ent evolutionary history and origin than those occu-pying the lowlands (horizontal colonization model). From the 1st hypothesis, one would expect to find mountains that, owing to their geographic isolation, limited surface area, high altitude, or relatively recent formation, have not accumulated their own assem-blage of fauna. This appears to be the case for the most southern mountains of the Iberian Peninsula (Sierra Nevada) where mountain species also occur at lower levels, although with different seasonal occurrence (Avila and Pascual 1988, Jay-Robert et al. 1997). In the vertical colonization model, mountain species would originate through allopatric speciation of elements distributed at lower altitudes. The mountains of South-east Asia appear to be a good example of this process (Hanski 1983, Hanski and Krikken 1991). Conversely, in the horizontal colonization model, geographic and historical factors acquire special relevance, as is the

[1] Departamento de Biodiversidad y Biología Evolutiva, Museo Na-cional de Ciencias Naturales, C/José Gutiérrez Abascal, 2., 28006, Madrid, Spain. E-mail: mcnj117@mncn.csic.es

case with the central mountains of the Iberian Peninsula (Martín-Piera et al. 1992) and the mountains of Mexico (Halffter 1987).

Naturally, the mountain fauna for a given territory results from the combined effects of ecological (vertical colonization) and historical factors (horizontal colonization). The relative importance of each effect depends on the orientation, location, and degree of isolation of the mountains under study and, even more importantly, on their biogeographic history. The more isolated a mountain is, the lower its capacity to act as a refuge for and maintain allochthonous elements during climatic change. Consequently, under these conditions, the horizontal model of colonization will be less relevant and the species assemblage will therefore be an outcome of possible vertical colonization.

The possibilities of both horizontal and vertical colonization must be considered in analyzing how mountain faunas have achieved their current composition. Horizontal colonization assumes that the evolutionary histories of mountain faunas and adjacent lowlands to be different and (2) that a reduction on the tendency of species diversity to decrease with increasing elevation. When horizontal colonization has dominated the integration of mountain fauna, one expects a much greater degree of phylogenetic diversity between its elements and those of the lowlands than that resulting primarily from vertical colonization. In addition, the phylogenetic inertia represented by the maintenance of affinities toward certain ecological conditions is greater. For example, richness decreases less in the higher levels of the central European mountains than in tropical mountains because many Aphodiinae species with geographic distributions restricted to cold climates can survive there (Jay-Robert et al. 1997). These mountains act as a refuge, and even as areas of speciation, for elements with a more northerly current distribution that were trapped after the retraction of the glaciers. Horizontal colonization and its consequences are also notable in the Mexican Transition Zone (MTZ) where the composition and biogeographical origin of the fauna differ from those of lowland fauna (Halffter 1964, 1976, 1987; Martín-Piera and Lobo 1993; Halffter et al. 1995).

We present a study of the distribution of coprophagous mountain Scarabaeoidea in eastern Mexico (State of Veracruz) using transects at altitudes above 1,800 m. Through a comparision with former studies, we analyze the relative importance of horizontal versus vertical colonization to explain mountain faunas.

Materials and Methods

Characterization of Biogeographical Parameters. The distribution patterns defined by Halffter (1976, 1987), Halffter et al. (1995), and Zunino and Halffter (1988) have been used as a biogeographic tool. These studies propose the existence of different distribution patterns to explain the populations of insects in the MTZ, based on a synthesis of the available distributional, systematic, and biogeographical information. The distribution patterns are categories associating

species that probably have a common history and have colonized a given region during the same geological period. Following previous studies, it is not difficult to assign a pattern type to the various species of Scarabaeinae and Geotrupinae. For the Aphodiinae, we estimated its distribution pattern taking into account the available information about the geographical distribution of the genus and subgenus to which they belong (Dellacasa 1987).

Description of the Area and Sampling Sites. Field work was done in an area covering ≈1,200 km², located in central Veracruz, Mexico, ≈100 km from the Gulf of Mexico (19° 30′ N). The highest point of this area is the Cofre de Perote volcano (4,282 m). This area belongs to the Transverse Volcanic System; a group of mountains with a generally east–west orientation that stretches across Mexico from coast to coast, and covers 950 km between 19 and 21° N latitude. The current configuration of this mountain system is primarily a result of volcanic activity during the Plio-Pleistocene, although this region has been subject to prolonged volcanic activity since the Miocene. The Cofre de Perote region is located in the eastern sector of the Transverse Volcanic System and is characterized by rock from the 2 main periods of volcanic activity: the Oligo-Miocenic and the Plio-Pleistocenic periods.

The edaphic composition of the Cofre de Perote region is almost completely lava, scoria, and volcanic ash, together with Plio-Pleistocenic alluvial deposits located above rock packs, also of volcanic origin. Above 2,500 m, climate is temperate with a mean annual temperature between 10 and 12°C and total annual precipitation is between 1,000 and 1,500 mm. Above 3,500 m, mean annual temperature varies between 5 and 12°C and total precipitation is 1,200–1,500 mm/yr. At 2,000 m, vegetation varies between oak-pine forest, predominantly *Pinus* forest and *Abies* forest. From 4,000 m upward there is alpine grasslands. It is estimated that ≈60% of the surface area was covered with forest before the Spanish arrived (Gerez-Fernández 1983). Coniferous forests are still abundant from 2,500 to 4,000 m, covering ≈39% of this zone. There is an unquantified but notable presence of sheep and goats, as well as cattle and horses.

In this region, 10 sites between 1,900 and 4,000 m were sampled along an east–west transect (Fig. 1). Sampling sites were in grasslands or pasture without arboreal cover. Only at Malpaís (cite number 2) and Cruz Blanca (number 3) were the grasslands selected surrounded by extensive coniferous forest.

Sampling Design and Data Analysis. Three independent samples of coprophagous beetle species were obtained in each of the 10 sites (16–19 March, 18–21 May, and 28–31 July 1993). At each site and for each sample, 3 pitfall traps, of widely demonstrated efficacy, were used (Lobo et al. 1988, Veiga et al. 1989). The traps were separated by 10 m and baited with ≈1 kg of cow dung. A total of 90 baited pitfall traps (3 traps × 3 sampling visits × 10 sites) was used. Two additional pitfall traps (15 cm deep, 20 cm high) baited with pieces of meat or fish were placed beside these
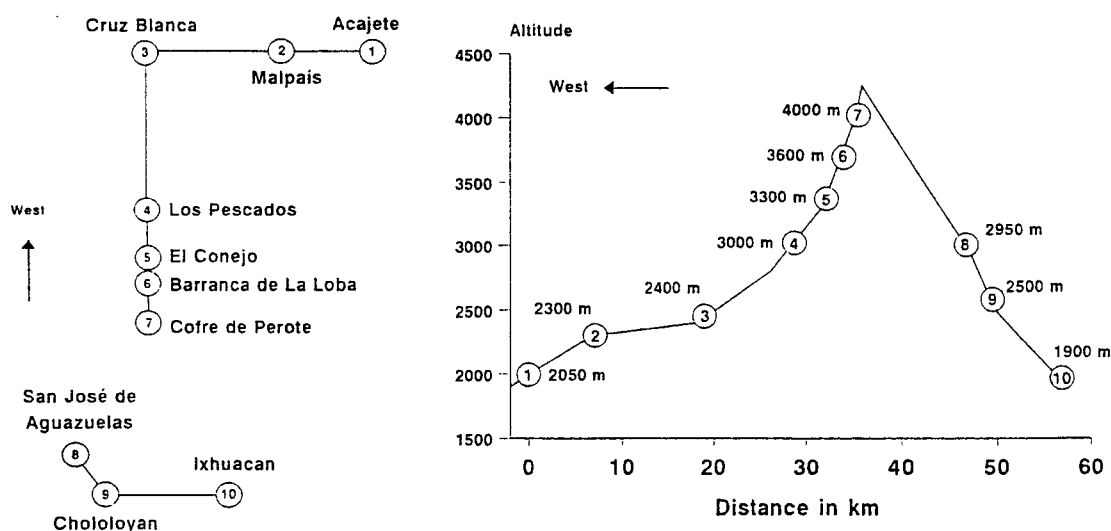
Fig. 1. Location and altitude of the 10 sampling sites in the Cofre de Perote region of Mexico.

traps. The bait was covered with large rocks to permit access to insects, but to prevent other animals from stealing the bait. A total of 60 traps baited with meat or fish was used (2 traps × 3 sampling visits × 10 sites; Table 1). Trap contents were collected 72 h after the traps had been set. A complementary study of the faunal content of all types of feces found in situ was carried out for each site, with the exception of 2 sites (number 2, Malpaís and number 7, Cofre de Perote) where no feces were found. For the other sites, 10 fecal samples were examined per site, with the exception of the 18–21 May field period in Ixhuacan (number 10) where only 5 fecal samples were examined owing to the large number of individuals captured. A total of 235 fecal samples (10 samples × 3 sampling visits × 8 sites - 5 fecal samples) were examined. The majority of these samples were cow, sheep, and horse dung (93.6%), the rest were human and canine (Table 1).

Using a rectangular matrix with the abundance data for each species in each site, a triangular similarity matrix was generated using the "chord distance" recommended by Ludwig and Reynolds (1988). The value of this index ranges from zero (maximum similarity) to $\sqrt{2}$ or ≈1.41 (minimum similarity). Cluster analysis was performed on the resulting similarity matrix to determine which groups of sites were most similar to each other. The unweighted pair-group method with arithmetic average (Ludwig and Reynolds 1988) was used as the linkage rule. The mean number of species per pitfall trap baited with excrement was calculated for each site, allowing for a more precise comparison of species richness because the sampling effort is equivalent in all sites. The number of species expected per trap if all traps had caught the same number of individuals ($n = 150$) was also used as a measure of diversity.

Groups of species were established using the principal components analysis. By considering the appearance of species in different traps and fecal samples, we used this technique to represent the species in a two-dimensional scheme where their relative positions reflect ecological similarities between them (Ludwig and Reynolds 1988). To see whether the values assigned to different species by the principal components analysis vary according to the factors studied

Table 1. Number of pitfall traps baited with cow dung, meat or fish, number and type of excrement samples examined in situ, total number of species and individuals and mean number of species and individuals captured per capture method

	No.	% of total	No. of samples	Total species (S)	Total abundance (N)	S mean	N mean
Pitfall traps baited with cow dung			90	15	697	1.42	7.74
Pitfall traps baited with meat or fish			60	3	6	0.08	0.1
In situ excrement							
Cow dung	34	14.5%					
Horse dung	56	23.8%					
Sheep dung	130	55.3%					
Human dung	10	4.3%					
Dog dung	5	2.1%					
	235		235	18	4,459	0.26	18.97
		Total	385	21	5,162		

Table 2. Distribution of the number of individuals of each species captured in the 10 sampling sites

Species	Sampling site										Total	Mean capture altitude masl	Taxonomic group	Distribution Pattern	Biogeographic region
	1	2	3	4	5	6	7	8	9	10					
Canthon humectus Robinson, 1948	0	0	1	0	0	0	0	0	0	0	1	2,400	*Scarabaeinae*	Mexican Plateau	Neotropical
Onthervus mexicanus Harold, 1869	252	0	0	0	0	0	0	0	69	47	368	2,115	*Scarabaeinae*	Meso-American	Neotropical
Phanaeus amethystinus Harold, 1863	0	0	0	0	0	0	0	0	0	1	1	1,900	*Scarabaeinae*	Meso-American	Neotropical
Copris incentus (Say), 1835	0	0	0	0	0	0	0	0	0	2	2	1,900	*Scarabaeinae*	Tropical Paleo-Am.	Afrotropical
Copris lugubris Boheman, 1858	0	0	0	0	0	0	0	0	0	1	1	1,900	*Scarabaeinae*	Tropical Paleo-Am.	Afrotropical
Copris armatus Harold, 1869	0	0	3	0	0	0	0	0	0	0	3	2,400	*Scarabaeinae*	Montane Paleo-Am.	Afrotropical
Onthophagus (s. str.) *incensus* (Say), 1835	35	0	0	0	0	0	0	0	0	41	76	1,969	*Scarabaeinae*	Tropical Paleo-Am.	Oriental
Onthophagus (s. str.) *mextexus* Howden, 1970	1	0	0	0	0	0	0	0	0	1	2	2,050	*Scarabaeinae*	Meso-American	Oriental
Onthophagus (s. str.) *cyanellus* Bates, 1887	0	0	0	0	0	0	0	0	30	24	54	2,233	*Scarabaeinae*	Meso-American	Oriental
Onthophagus (s. str.) *chevrolati* Harold, 1869	41	2	44	83	50	0	0	138	71	2	431	2,776	*Scarabaeinae*	Montane Paleo-Am.	Oriental
Aphodius (*Amidorus*) *glyptus* Bates, 1887	0	0	0	19	0	0	0	0	0	0	19	3,000	*Aphodiini*	Montane Paleo-Am.	Palearctic
Aphodius (*Agrilinus*) prope *duplex* Leconte, 1878	0	0	0	15	2	0	0	0	0	0	17	3,035	*Aphodiini*	Montane Paleo-Am.	Palearctic
Aphodius (*Agrilinus*) *azteca* Harold, 1863	0	0	0	0	0	0	0	0	1	0	1	2,500	*Aphodiini*	Montane Paleo-Am.	Palearctic
Aphodius (*Chilothorax*) *pumilio* Schmidt, 1907	16	18	57	0	0	0	0	0	1	6	98	2,295	*Aphodiini*	Montane Paleo-Am.	Palearctic
Aphodius (*Chilothorax*) *multimaculosus* Hinton, 1934	0	0	4	0	0	0	0	0	0	0	4	2,400	*Aphodiini*	Montane Paleo-Am.	Palearctic
Aphodius (*Planolinus*) *vittatus* Say, 1825	0	0	10	0	0	0	0	0	1	17	28	2,100	*Aphodiini*	Nearctic	Palearctic
Aphodius (*Planolinus*) prope *tenellus* Say, 1823	0	0	0	0	0	0	0	2	0	0	2	2,950	*Aphodiini*	Nearctic	Palearctic
Aphodius (*Platyderides*) *hogei* Bates, 1887	0	0	0	0	0	0	0	23	0	0	23	2,950	*Aphodiini*	Nearctic	Nearctic
Aphodius (*Trichaphodius*) *opisthius* Bates, 1887	506	0	17	0	0	0	0	1	570	2,915	4,009	2,006	*Aphodiini*	Neotropical	Afrotropical
Atanus prope *scutellaris* Harold, 1867	0	0	0	0	0	0	0	0	0	14	14	1,900	*Eupariini*	Neotropical	Neotropical
Onthotrupes herbeus (Jeckel), 1865	0	0	0	0	0	0	0	8	0	0	8	2,950	*Geotrupinae*	Montane Paleo-Am.	Nearctic
Abundance	851	20	136	117	52	0	0	172	743	3,071	5,162				
Richness	6	2	7	3	2	0	0	5	7	12	21				

Site number corresponds to that presented in Fig. 1. For each species, mean capture altitude, taxonomic group, distribution pattern according to those proposed by Halffter (1964, 1976, 1987) and Halffter et al. (1995); and the biogeographic region with the greatest number of species belonging to the captured species' genus or subgenus, are indicated.
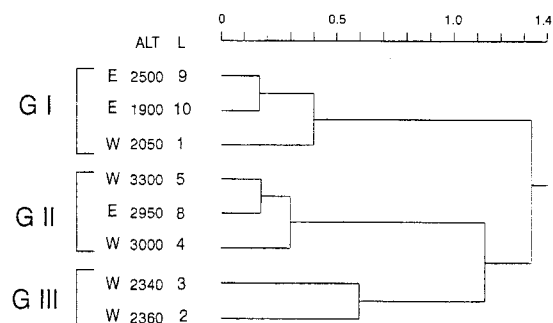
Fig. 2. Dendrogram of the cluster analysis done on the sampling sites. The similarity matrix was generated using the chord distance and the unweighted pair-group method with arithmetic average linkage rule was used. L, sampling site (see Fig. 1); ALT, sampling site altitude (m); E, east slope; W, west slope.

(i.e., systematic position, distribution pattern, or biogeographic region with the most species belonging to the genus or subgenus of the captured species), we used the Kruskall–Wallis nonparametric analysis of variance (ANOVA). Contingency analysis of two-way frequency tables were used to test association between factors.

Results

Analysis of the mountain fauna of the Cofre de Perote. A total of 21 species and 5,162 individuals were captured. Their distribution in the ten sampling sites is shown in Table 2. The pitfall traps baited with meat or fish only caught 6 individuals belonging to 3 species. The pitfall traps baited with cow dung and the strategy of collecting and examining dung were far more effective (Table 1). Table 2 presents species information: mean captures altitude, taxonomic position to subfamily or tribe, distribution pattern according to those proposed by Halffter (1964, 1976, 1987) and Halffter et al. (1995), and the biogeographic region where most species belonging to the genus or subgenus of the captured species occur.

Cluster analysis indicates that there are 3 groups of sites with respect to the composition of the fauna (Fig. 2). The 3 highest sites (4, 5 and 8) form a well defined group (group II) regardless of slope. The same is true of the 2 eastern sites and the western site, located at the lowest altitude (1, 9 and 10; group I). Group III includes the 2 western sites located at an intermediate altitude in forested zones (2 and 3). These 2 sites differ notably in total richness and mean number of species per trap (Table 2). Site 2 (Malpaís), where only 2 species (*O. chevrolati* and *A. pumilo*) were found, has a very species poor community compared with that of site 3 (Cruz Blanca) where these and other species occur (Table 2). Therefore, we feel that the characteristics of group III are well defined by the data from site 3.

Compared with the sites of group I, group II (high altitude sites) has a lower species richness per trap

value (0.7–1.1 species per trap). However, according to the estimate obtained with the rarefaction method (Table 3), richness is similar for the 3 groups of sites. The groups differ significantly in the percentage of species according to the different taxonomic categories ($\chi^2 = 69.6$, df $= 4$, $P < 0.001$), distribution pattern ($\chi^2 = 166.5$, df $= 10$, $P < 0.001$) and biogeographic region with the greatest number of species of the genus considered ($\chi^2 = 102.3$, df $= 8$, $P < 0.001$; Table 3). Most species of group I are Scarabaeinae, with Meso-American, Tropical Paleo-American, Mountain Paleo-American, and, to a lesser degree, Neotropical distribution patterns. The species of group III are Scarabaeinae and Aphodiinae, with a Mountain Paleo-American distribution pattern. The species of group II are mainly Aphodiinae, with a Mountain Paleo-American or Nearctic distribution pattern and belong to genera for which the majority of species occur in Palearctic and Nearctic regions.

The results of the principal components analysis for the 21 species collected throughout the study region indicate that (Fig. 3) together, the two 1st axes or components account for 78.6% of the variance of the system (component I: 42.4%, component II: 36.2%) and explain the regional distribution of species. The value for each species on component I explains the altitudinal variation of these communities because there is a high degree of correlation between these values and the mean altitude where individuals of each species were captured (Spearman rank correlation: $r_s = -0.926$, $n = 21$, $P < 0.0001$). There are 3 groups of species that correspond to the 3 site groups. The 1st is composed of 10 species restricted to or abundant at the low altitude sites (group I). The next is composed of 7 species characteristic of sites with the altitudinal range of group II. The 3rd is comprised of 4 species that characterize the sites of group III. As such, component II is related to vegetation cover.

The values of component II are not significantly different with respect to the taxonomic group, distribution pattern, or the biogeographical region with most species belonging to the same genus (Table 4). The values of each species on component I are not significantly different with respect to taxonomic group, but are with respect to distribution pattern and the biogeographical region where most of congeneric species occur.

Comparison with Other Regions. Table 5 summarizes presence–absence data, with intervals of 300 m, for all species captured above 1,800 m. There is a total of 32 species (γ diversity) in this mountain landscape at the extreme east of the transverse volcanic system, 11 more than those captured in the transect. Using this data set we have compared the altitudinal variation between different biogeographic regions.

In Europe, the Alps have been studied in detail (Lumaret and Stiernet 1989, 1991, 1992). The greatest diversity for an altitudinal range occurs at intermediate altitudes (between 1,500 and 2,100 m), whereas above 2,400 m the number of species diminishes, although not abruptly (Fig. 4A). In contrast, in southern Europe (Sierra Nevada), the decrease in the number

Table 3. Mean number of species per trap (S_{mean} per trap) and total number of species (S) for each sampling site

Group Sampling site	I			II			III	
	1	9	10	4	5	8	3	2
				Diversity measures				
S_{mean} per trap	2.4	2.7	3.1	0.9	0.7	1.1	2.4	0.9
S	6	7	12	3	4	5	7	2
S_{total}		13			7			7
S_{raref} 150		6.29 ± 1.08			6.12 ± 0.68			6.96 ± 0.19
				Taxonomic position				
Scarabaeinae		62%			14%			43%
Aphodiini		31%			72%			57%
Others		7%			14%			0%
				Distribution pattern				
Neotropical		15%			14%			14%
Tropical Paleo-American		23%			0%			0%
Meso-American		31%			0%			0%
Montane Paleo-American		23%			57%			57%
Nearctic		8%			29%			14%
Mexican Plateau		0%			0%			14%
				Biogeographic region with the greatest number of species				
Neotropical		23%			0%			14%
Afrotropical		23%			14%			29%
Oriental		31%			14%			14%
Palearctic		23%			43%			43%
Nearctic		0%			29%			0%

Site number corresponds to that presented in Fig. 1. Total number of species collected (S_{total}) in each of the 3 groups of sites according to the cluster analysis (Fig. 2) and the number of species expected in a sample of 150 individuals (S_{raref} 150) according to the rarefaction method (Ludwing and Reynolds 1988). Percentage of species in each of the site groups according to taxonomic position, distribution pattern and the biogeographic region with the greatest number of species belonging to the genus or subgenus of the captured species. The sampling sites 6 and 7 do not appear because no species were captured in them.

of species with increasing altitude is notable from 1,200 m (Avila and Pascual 1988). Below 1,500 m the communities of the Sierra Nevada appear to be much richer that those of the Alps. At higher elevations there are more species in the Alps than in the Sierra Nevada (Fig. 4B). There is a marked altitudinal substitution in the Alps: Scarabaeinae species dominate communities at lower altitudes while Aphodiini predominate at greater altitudes (Fig. 5A). Under these conditions there is a negative correlation between the numbers of species of both taxa that occur at each altitudinal interval (Spearman rank correlation: r_s = -0.14, n = 8, not significant). In the Sierra Nevada there is a similar percentage of species from both families at all altitudes (Fig. 5B) and the richness of both taxa is positively and significantly correlated (Spearman rank correlation: r_s = 0.85, n = 7, P < 0.04).

In the Cofre de Perote region (Fig. 4C) the number of species decreases starting at 2,600 m and richness appears to be less than in European communities. For the interval with the greatest number of species (2,300–2,600 m) species richness is similar to that of the altitude intervals with the lowest species richness in Europe (Fig. 5C). In the mid-mountain zones (1,500–2,600 m) the number of Scarabaeinae is higher than in the Alps and similar to that of the Iberian Peninsula. The opposite is true for the number of Aphodiinae species, which is low up to 2,600 m, although it comprises most coprophagous beetle community above this altitude. Between 2,700 and 3,000 m species richness is similar to that of the high altitude grasslands in Europe (Figs. 4C and 5C). As a result,

there is no significant correlation between Scarabaeinae and Aphodiinae richness by altitudinal range (Spearman rank correlation: r_s = -0.12, n = 6, not significant), where there is a clear altitudinal substitution between these 2 groups. This altitudinal substitution between the 2 main taxonomic groups of coprophagous beetles can also be observed in the distribution patterns (Table 4) where the Neotropical, Tropical Paleo-American, and Meso-American Patterns become less important from 2,600 m upward (only 2 species, 15%) and where the Nearctic (3 species, 23%) and, above all, the Mountain Paleo-American (8 species, 62%) patterns become more dominant.

In the mountain region of Mulu, Borneo (Hanski 1983), the number of species declines rapidly above 1,300 m and there is no altitudinal substitution between the large taxonomic groups (Figs. 4D and 5D). There are no studies on the altitudinal variation of the communities in the tropical regions of South America or Africa. However, at least in the case of Africa, we can obtain an estimate based on the extensive data from the taxonomic and distributional study done by Endrödi (1964) on the Aphodiinae of equatorial Africa and the results of a biogeographical study carried out by Davis and Dewhurst (1993) on the Scarabaeinae of eastern equatorial Africa. The study of these data indicate that the number of species of Aphodiini found in different regions of eastern Africa clearly increases with altitude, although the same does not occur in other tribes of Aphodiinae, and that the number of
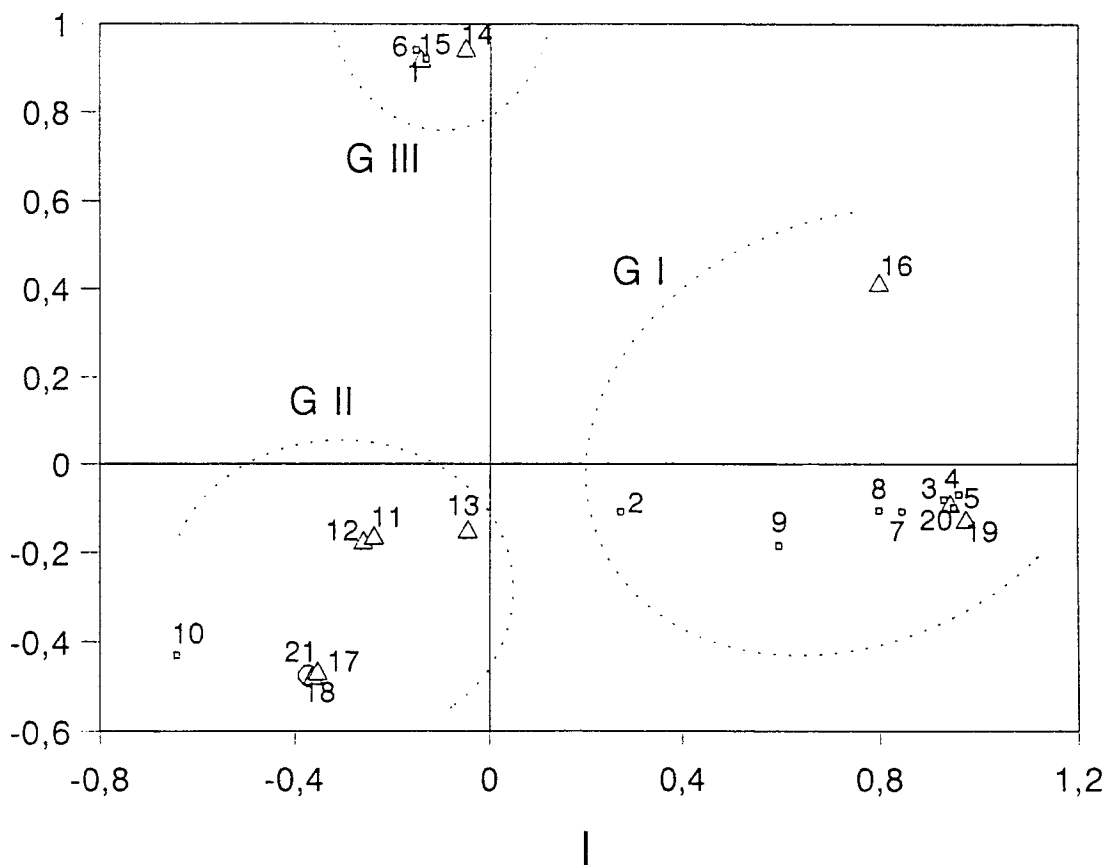
Fig. 3. Position on the first 2 axes of the principal components analysis for the 21 species captured. Small squares, subfamily Scarabaeinae; triangles: Tribe Aphodiini; octagons: subfamily Geotrupinae. GI, GII, and GIII are the site groups mentioned in Fig. 2. The number of individuals captured for each species is shown in Table 1.

Scarabaeinae species decreases markedly with increasing altitude.

Discussion

Three groups of sites in the Cofre de Perote region above 1,800 m appear to be distinguishable by 3 well defined groups of coprophagous beetles. First, there is a group of sites that extend up to ≈2,500 m. Scarabaeinae species characterized by Mountain Paleo-American, Tropical Paleo-American, Meso-American, and Neotropical distribution patterns dominate this group. Other studies demonstrate that with decreasing altitude, the importance of Scarabaeinae with a typically Neotropical distribution pattern progressively increases (Martín-Piera and Lobo 1993, Halffter et al.

Table 4. Nonparametric analysis of variance (Kruskall–Wallis) value and associated probability (p), to test whether the values of the first axes of the principal components analysis for each of the species captured (Fig. 3) differ with respect to taxonomic position, distribution pattern or the biogeographic region with the greatest number of species belonging to the captured species' genus or subgenus

	Taxonomic position			Distribution pattern					Biogeographic region with the most species				
	Scarabaeinae	Aphodiini	Others	NT	TPA	MA	MPA	NA	NT	AF	OR	PAL	NA
Component I													
Avg value	0.44	0.03	0.29	0.96	0.91	0.65	−0.24	0.02	0.77	0.66	0.13	−0.01	−0.36
Kruskall–Wallis test		1.75 ($P = 0.42$)			14.09 ($P = 0.007$)					10.67 ($P = 0.03$)			
Component II													
Avg value	0.06	0.08	−0.28	−0.11	−0.10	−0.12	0.18	−0.18	−0.09	0.15	−0.22	0.25	−0.48
Kruskall–Wallis test		0.38 ($P = 0.54$)			1.85 ($P = 0.76$)					7.77 ($P = 0.10$)			

NT, Neotropical; TPA, tropical Paleo-American; MA, Meso-American; MPA, Montane Paleo-American; NA, Nearctic.
NT, Neotropical; AF, Afrotropical; OR, oriental, PAL, Palearctic; NA, Nearctic. The mean for each component is presented above this value for the species of each category.

Table 5. Species present in the Cofre de Perote region above 1,800 masl

Species	Altitude interval					Distribution Patterns
	1,800 to 2,100	2,200 to 2,500	2,600 to 2,900	3,000 to 3,300	over 3,400	
Canthon humectus Robinson, 1948	1	1				Mexican Plateau
Deltochilum mexicanum Burmeister, 1848	1					Neotropical
Ontherus mexicanus Harold, 1869	1	1	1	1		Meso-American
Phanaeus amethystinus Harold, 1863	1	1				Meso-American
Copris incertus (Say), 1835	1					Tropical Paleo-American
Copris lugubris Boheman, 1858	1					Tropical Paleo-American
Copris armatus Harold, 1869		1				Montane Paleo-American
Onthophagus hoepfneri Harold, 1869	1					Tropical Paleo-American
Onthophagus fuscus Boucomont, 1932	1	1				Montane Paleo-American
Onthophagus lecontei Harold, 1871		1				Tropical Paleo-American
Onthophagus incensus (Say), 1835	1					Tropical Paleo-American
Onthophagus aureofuscus Bates, 1887	1	1	1	1		Montane Paleo-American
Onthophagus mextexus Howden, 1970	1	1				Meso-American
Onthophagus corrosus Bates, 1887	1					Tropical Paleo-American
Onthophagus cyanellus Bates, 1887	1	1				Meso-American
Onthophagus chevrolati Harold, 1869	1	1	1	1		Montane Paleo-American
Onthophagus hippopotamus Harold, 1869			1	1		Montane Paleo-American
Aphodius (Amidorus) glyptus Bates, 1887			1	1	1	Montane Paleo-American
Aphodius (Agrilinus) prope duplex Leconte, 1878				1	1	Montane Paleo-American
Aphodius (Agrilinus) azteca Harold, 1863		1	1		1	Montane Paleo-American
Aphodius (Chilothorax) pumilio Schmidt, 1907	1	1				Montane Paleo-American
Aphodius (Chilothorax) multimaculosus Hinton, 1934		1				Montane Paleo-American
Aphodius (Planolinus) vittatus Say, 1825	1	1				Nearctic
Aphodius (Planolinus) prope tenellus Say, 1823				1		Nearctic
Aphodius (Platyderides) hogei Bates, 1887			1	1		Nearctic
Aphodius (Platyderides) pierai Lobo & Deloya, 1996			1	1		Nearctic
Aphodius (Trichaphodius) opistius Bates, 1887	1	1	1	1		Neotropical
Aphodius (Trichonotulus) perotensis Deloya & Lobo, 1996			1	1		Montane Paleo-American
Ataenius prope scutellaris Harold, 1867	1					Neotropical
Ceratotrupes bolivari Halffter & Martinez, 1962	1	1				Montane Paleo-American
Onthotrupes nebularum (Howden), 1964	1	1				Montane Paleo-American
Onthotrupes herbeus (Jeckel), 1865	1	1	1	1		Montane Paleo-American
Total species	20	18	11	12	3	

Data from this study and from Martín-Piera and Lobo (1993), Lobo and Halffter (1994), Halffter et al. (1995), Deloya and Lobo (1995) and Arellano (unpubl. data). Distribution Pattern is indicated for each species.

1995). The 2nd group of sites occurs between 3,000 and 3,300 m. Communities appear to possess a lower mean richness per trap. Dominant species are Aphodiinae with Mountain Paleo-American and Nearctic distribution patterns for which the genera and subgenera have most of their species in Palearctic and Nearctic Regions. These are poorer communities with species from lineages that possibly originated in the Holarctic and penetrated the MTZ before or during the Plio-Pleistocene. Finally, there is a small group of sites located at intermediate altitudes, and characterized by the presence of oak-pine forests. Halffter et al. (1995) pointed out that forests in this region that occur between 1,800 and 2,600 m are dominated by elements of northern distribution. Our data corroborate this. This group of sites is characterized by Aphodiini species with a Mountain Paleo-American distribution pattern and genera and subgenera whose primarily occur in the Palearctic.

For the sites and the species that occur above 1,800 m, we found the same pattern as that reported in other studies carried out in this region (Martín-Piera and Lobo 1993, Halffter et al. 1995) and in western Europe (Lobo 1992, Martín-Piera et al. 1992, Jay-Robert et al. 1997). The main segregation of fauna resulting from altitudinal variation occurs in high range taxa (Scarabaeinae, Aphodiini) with different biogeographic distributions and evolutionary histories. The distribution of these 2 taxa could be the consequence of physiological limitations that do not permit them to cross certain climatic boundaries. Most Scarabaeinae lineages would have difficulty colonizing and inhabiting cold temperate climates, whereas some Aphodiini would have difficulties in warm or tropical climates.

A peculiarity of the coprophagous beetle fauna in the European mountains is the conspicuous altitudinal substitution between the 2 principal groups of beetles (Scarabaeinae and Aphodiini). In the most northern regions of Europe only a few Aphodiini species comprise the coprophagous communities (Hanski 1986, Biström et al. 1991). In both the northern and southern Alps, as well as in the central and northern mountains of the Iberian Peninsula, there is altitudinal substitution for these 2 taxa. However, in the most southern reaches of the Iberian Peninsula mountain range this substitution is less evident (Jay-Robert et al. 1997). This could be a result of 3 factors that have made access by northern elements difficult: the lower latitude of these mountains, their east–west orientation, and the small surface area of the zones located at
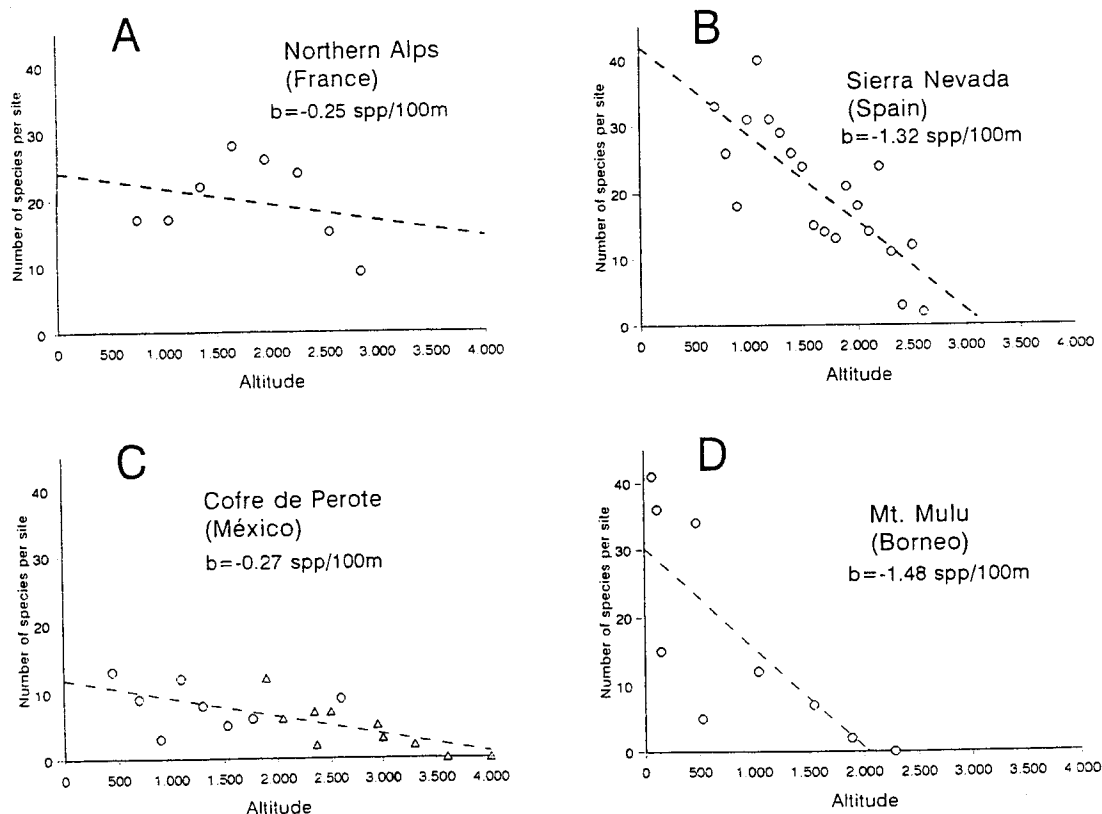
Fig. 4.   Variation in the number of species with altitude in (A) the northern French Alps (Lumaret and Stiernet 1989), (B) the Sierra Nevada in southern Spain (Avila and Pascual 1988), (C) the Cofre de Perote in eastern Mexico (circles, Halffter et al. 1995; triangles, current study), (D) Mount Mulu in Borneo (Hanski 1983), where b is the slope of the linear regression between altitude and the number of species (dashed line).

higher altitudes. This chain of mountains has not served as a refuge for northern fauna.

What is the situation in the mountainous regions of Mexico? Midmountain communities of this region appear to have lower richness than their European counterparts. This is partly a result of the species poor Aphodiinae fauna that inhabits them. Nevertheless, at higher elevations most of the species are Aphodiinae and the altitudinal substitution is similar to that of Europe. The grasslands of the Cofre de Perote located at ≈3,300 m are almost exclusively inhabited by Aphodiini and have a richness similar to that of the high alpine grasslands of Europe.

High altitude communities in the MTZ would be dominated by Mountain Paleo-American or Nearctic elements belonging to genera with diversification centers in the Holarctic, whereas lowland communities would be dominated by Neotropical elements (Halffter, 1964, 1976, 1987). The occurrence of elements with such different biogeographic origins within the MTZ is precisely what characterizes this transition zone. The altitudinal version of this transition is also found in the mountains, especially in the Sierra Madre Occidental and in the eastern and western extremes of the transverse volcanic system of Mexico (Halffter et

al. 1995). The fauna with northern affinity that characterizes the higher altitudes of the MTZ mountains is a notable example of horizontal colonization with strong speciation resulting from vicariance (for an example of a Scarabaeinae see Onthophagus of the chevrolati group in Zunino and Halffter 1988). In general terms there is clear evidence of the importance of dispersal phenomena during the Pleistocene (Coope 1979; Noonan 1988; Elias 1994) and is also evidence that some northern taxa emigrated south war during the Pleistocene and currently find refuge in the mountains of Mexico (McDonald 1993). However, many of the current species, or their ancestors, inhabited higher zones of the Mexican High Plain and the Transverse Volcanic System long before the Pleistocene (Liebherr 1994, Lobo and Halffter 1994; and literature cited therein). For these species, precisely those to which we assign the Mountain Paleo-American distribution pattern, speciation processes have been favored by 2 factors: (1) alternating volcanic activity and inactivity since 30 million years BP, which has resulted in population isolation and fragmentation, and (2) limited contact between southern and northern alpine zones of Mexico during the last glaciation period (McDonald 1993).
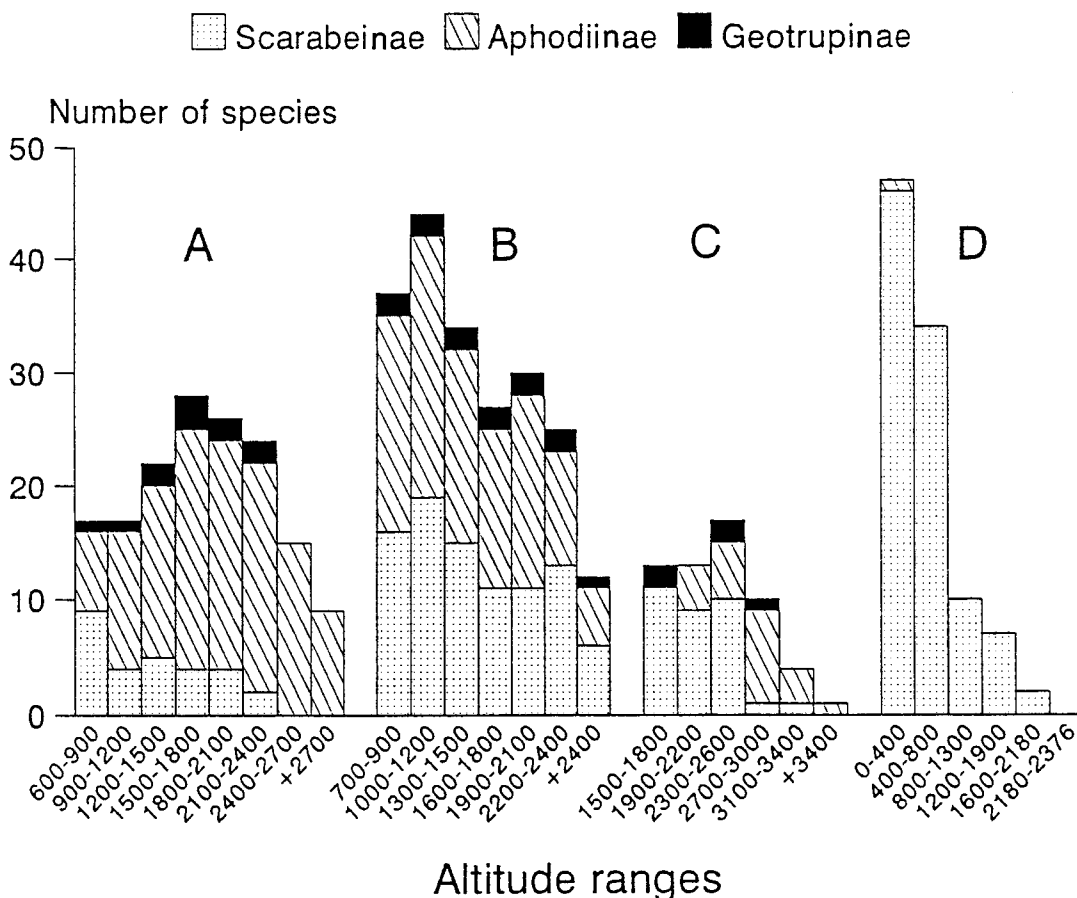
Fig. 5. Altitudinal variation in the number of species belonging to the 3 main dung beetle taxa (Scarabaeoidea) by altitudinal interval. (A) Northern French Alps (Lumaret and Stiernet 1989). (B) Sierra Nevada in southern Spain (Avila and Pascual 1988). (C) Cofre de Perote in eastern Mexico (Halffter et al. 1995, current study). (D) Mount Mulu in Borneo (Hanski 1983).

Despite the marked dominance of horizontal colonization in the integration of the coprophagous beetle fauna in the Cofre de Perote (see Table 4, Mountain Paleo-American and Nearctic patterns), there are several species whose presence results from vertical colonization. These species have Tropical Paleo-American, Mountain Meso-American and Neotropical distribution patterns and penetrate locations of lower altitude in the transect. Among these species, *Ontherus mexicanus* demonstrates high colonization capacity (see Halffter et al. 1995), climbing the mountain from lower, tropical levels by following pastures and other heliophilic formations.

Another curious aspect of the Cofre de Perote data are the poverty of species at intermediate altitudes compared with the richness of communities in western Europe. This is primarily because of the few Aphodiinae species in these communities. In the coprophagous communities of temperate biomes all species of Aphodiinae belong to Aphodiini, a tribe of ≈2,000 species and 134 subgenera (Dellacasa 1987). In the western Palearctic, there are lines of Aphodiini that

are primarily distributed at intermediate and high latitudes and altitudes, as well as lines distributed in regions with Mediterranean climate and low altitudes. On the American continent the Aphodiinae fauna includes many species of Eupariini a tribe with a principally tropical distribution and ≈600 species (Dellacasa 1987). We believe that there is latitudinal and altitudinal separation between the Eupariini and the Aphodiini in the Neotropical region. The scarcity of Aphodiinae species halfway in the Cofre de Perote Transect could be a consequence of the inadequate environmental conditions of this altitudinal band, for both the Neotropical Eupariini and the Holarctic Aphodiini.

There are some data available on the altitudinal variation of coprophagous communities under tropical conditions in southeastern Asia (Hanski 1983, Hanski and Niemelä 1990, Hanski and Krikken 1991). As we have seen, the number of species falls rapidly with increasing altitude in Borneo and there is no altitudinal substitution between large taxa because the only species of Aphodiinae appears between 50 and 100 m

(Hanski 1983). Data from a nearby altitudinal transect on a much lower mountain in Sulawesi (1,150 m) show that the decrease in richness is less abrupt if the mountain under study is not isolated, but rather forms part of a mountain chain (Hanski and Niemelä 1990, Hanski and Krikken 1991). However, the altitudinal substitution between the Scarabaeinae and the Aphodiinae is not observed in Sulawesi either, because only 4 species of *Aphodius* were captured and all of these at 200 m (Hanski and Krikken 1991). In southeastern Asia, mountain beetle fauna has its origin in tropical lowland fauna as a result of vertical colonization

If, as is mostly the case in the northern hemisphere, the altitudinal substitution between large taxonomic groups is primarily a result of their altitudinal stratification according to their biogeographical origin, it would be expected that as distance from the mountain range to temperate regions increases, the presence of Aphodiini with Holarctic affinity would decrease and high altitude communities should be poorer in species. As we have seen, the data from the southern Iberian Peninsula indicate a tendency of this kind (Jay-Robert et al. 1997). In the Mexican transverse volcanic system, our results indicate the importance of Holarctic Aphodiini in high altitude communities, its richness at 3,000 m being similar to that of other regions. The latitude has less effect in Mexico on rarefaction with altitude because of the demonstrated "corridor effect" of the longitudinal American mountain ranges as contrasted with the transverse European ranges (McDonald 1993).

It is commonly supposed that, for a given change in altitude, mountains in the tropics present a barrier that is less penetrable to species than that of mountains located in temperate zones (Janzen 1967, Smith 1975, Huey 1978). This would explain why altitudinal decrease in richness is greater in tropical zones than in temperate zones. This hypothesis might be somewhat simplistic because it assumes that the source of colonization at higher altitudinal horizons is principally fauna from the lowlands. Altitudinal variation may result from horizontal colonization. In this case, the degree of connectedness of each territory with temperate regions would be a key factor in explaining both the altitudinal substitution of species and the decrease in the number of species with increasing altitude.

Acknowledgments

References Cited

Avila, J. M., and F. Pascual. 1988. Contribución al conocimiento de los escarabeidos coprófagos (Coleoptera, Scarabaeoidea) de Sierra Nevada: III. Distribución altitudinal y temporal. Boll. Mus. Reg. Sci. Nat. Torino 6(1): 217–240.

Biström, O., H. Silverberg, and I. Rutanen. 1991. Abundance and distribution of coprophilus Histerini (Histeridae) and *Onthophagus* and *Aphodius* (Scarabaeidae) in Finland (Coleoptera). Entomol. Fenn. 27: VIII.

Coope, G. R. 1979. Late Cenozoic Coleoptera: evolution, biogeography and ecology. Annu. Rev. Ecol. Syst. 10: 247–267.

Davis, A.L.V., and C. F. Dewhurst. 1993. Climatic and biogeographical associations of Kenyan and northern Tanzanian dung beetles (Coleoptera: Scarabaeidae). Afr. J. Ecol. 31: 290–305.

Deloya, C., and J. M. Lobo. 1995. Descripción de dos nuevas especies mexicanas de *Aphodius* de los subgéneros *Platyderides* y *Trichonotulus* (Coleoptera: Scarabaeidae: Aphodiinae) asociadas con *Pappogeomys merriami* (Rodentia: Geomyidae). Folia Entomol. Mex. 94: 41–55.

Dellacasa, M. 1987. Contribution to a world-wide catalogue of Aegialiidae, Aphodiidae, Aulonocnemidae, Termitotrogidae. Mem. Soc. Entomol. Ital. 66: 1–455.

Elias, S. A. 1994. Quaternary insects and their environments. Smithsonian Institution Press, Washington, DC.

Endrödi, S. 1964. Die Aphodiinae des Congo-Gebietes in rahmen der fauna von Zentral-Afrika (Coleoptera, Scarabaeidae). Ann. Mus. Res. Afr. Centr. Tervuren 123: 1–415.

Gerez-Fernández, P. 1983. Crónica del uso de los recursos naturales en la cuenca de Perote-Libres, pp. 11–16. *In* A. D. Golberg [ed.], El Cofre de Perote. Investigaciones ecológicas en un área conflictiva. Instituto Nacional de Investigación sobre Recursos Bióticos, Xalapa, Mexico.

Halffter, G. 1964. La entomofauna americana. Ideas acerca de su origen y distribución. Folia Entomol. Mex. 6: 1–108.

Halffter, G. 1976. Distribución de los insectos en la Zona de Transición Americana. Relaciones con la entomofauna de Norteamérica. Folia Entomol. Mex. 35: 1–64.

Halffter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. Annu. Rev. Entomol. 32: 95–114.

Halffter, G., M. E. Favila, and L. Arellano. 1995. Spatial distribution of three groups of Coleoptera along an altitudinal transect in the Mexican transition zone and its biogeographical implications. Elytron 9: 151–185.

Hanski, I. 1983. Distributional ecology and abundance of dung and carrion-feeding beetles (Scarabaeidae) in tropical rain forest in Sarawak, Borneo. Acta Zool. Fenn. 167: 1–45.

Hanski, I. 1986. Individual behaviour, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe. Acta Oecol. Gen. 7: 171–187.

Hanski, I. and J. Krikken. 1991. Dung beetles in tropical forest in Southeast Asia, pp. 179–197. *In* I. Hanski and Y. Cambefort [eds.], Dung beetle ecology. Princeton University Press, Princeton, NJ.

Hanski, I., and J. Niemelä. 1990. Elevational distribution of dung and carrion beetles in northern Sulawesi, pp. 145–152. *In* W. J. Knight and J. D. Holloway [eds.], Insects and the rain forest of Southeast Asia (Wallacea). The Royal Entomological Society, London.

Huey, R. B. 1978. Latitudinal patterns of between-altitude faunal similarity: Mountain passes might be higher in the tropics. Am. Nat. 112: 225–229.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Am. Nat. 101: 233–249.

Jay-Robert, P., J. M. Lobo, and J. P. Lumaret. 1997. Elevational turnover and species richness variation in European mountain dung beetle assemblages. Arctic Alpine Res. 29(2): 196–205.

Liebherr, J. K. 1994. Biogeographic patterns of montane Mexican and central American Carabidae (Coleoptera). Can. Entomol. 126: 841–860.

Lobo, J. M. 1992. Modificación de las comunidades de Scarabaeoidea coprófagos (Coleoptera) en pastizales de altura del sistema Central Ibérico (España) a lo largo de un gradiente altitudinal. Acta Zool. Mex. 53: 15–31.

Lobo, J. M., and G. Halffter. 1994. Relaciones entre escarabajos (Coleoptera: Scarabaeoidea) y nidos de tuza (Rodentia: Geomyidae): Implicaciones biológicas y biogeográficas. Acta Zool. Mex. 62: 1–9.

Lobo, J. M., F. Martín-Piera, and C. M. Veiga. 1988. Las trampas *pitfall* con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeoidea (Col.). I. Características determinantes de su capacidad de captura. Rev. Ecol. Biol. Sol. 25: 77–100.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical ecology: a primer on methods and computing. Wiley, New York.

Lumaret, J. P. and N. Stiernet. 1989. Inventaire et distribution des coléoptéres scarabéides coprophages dans le massif de la Vanoise. Trav. Sci. Parc Natl. Vanoise 17: 193–228.

Lumaret, J. P., and N. Stiernet. 1991. Montane dung beetles, pp. 242–254. *In* I. Hanski and Y. Cambefort [eds.], Dung beetle ecology. Princeton University Press, Princeton, NJ.

Lumaret, J. P., and N. Stiernet. 1992. Biogeography of dung beetle communities in the western and central Alps (Coleoptera, Scarabaeoidea), pp. 425–436. *In* B. Baccetti [ed.], II popolamento delle Alpi occidentali. Biogeographia XVI.

Martín Piera, F., and J. M. Lobo. 1993. Altitudinal distribution patterns of copro-necrophage Scarabaeoidea (Coleoptera) in Veracruz, Mexico. Coleopt. Bull. 47: 321–334.

Martín Piera, F., C. M. Veiga, and J. M. Lobo. 1992. Ecology and biogeography of dung-beetle communities (Coleoptera, Scarabaeoidea) in an iberian mountain range. J. Biogeogr. 19: 677–691.

McCoy, E. D. 1990. The distribution of insects along elevational gradients. Oikos 58: 313–322.

McDonald, J. A. 1993. Phytogeography and history of the alpine-subalpine flora of Northeastern Mexico, pp. 681–705. *In* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa [eds.], Biological diversity of Mexico: origins and distribution. Oxford University Press, Oxford.

Noonan, G. R. 1988. Biogeography of North American and Mexican insects, and a critique of vicariance biogeography. Syst. Zool. 37: 366–384.

Smith, A. P. 1975. Altitudinal seed ecotypes in the Venezuelan Andes. Am. Midl. Nat. 94: 247–250.

Veiga, C. M., J. M. Lobo, and F. Martín-Piera. 1989. Las trampas *pitfall* con cebo, sus posibilidades en el estudio de las comunidades coprófagas de Scarabaeidea (Col.). II: Análisis de efectividad. Rev. Ecol. Biol. Sol. 26(1): 91–109.

Wolda, H. 1987. Altitude, habitat and tropical insect diversity. Biol. J. Linn. Soc. 30: 313–323.

Zunino, M., and G. Halffter. 1988. Análisis taxonómico, ecológico y biogeográfico de un grupo americano de *Onthophagus* (Coleoptera: Scarabaeidae). Monografie IX, 211 pp. Museo Regionale di Scienze Naturali, Torino, Italy.