# Altitudinal Turnover and Species Richness Variation in European Montane Dung Beetle Assemblages

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## Abstract

The dung beetles (Coleoptera, Scarabaeoidea) are divided into several guilds, particularly dwellers and small tunnelers. We analyzed and compared the faunistic composition and the organization of these guilds from several mountain systems in Western Europe. Variation in species richness with altitude, altitudinal turnover, and the taxonomical and biogeographical characteristics of beetles were analyzed. A global analysis enabled an estimation of the importance of the local speciation mechanisms and historical processes, respectively, in the formation of the assemblages in each mountain system. The roles played by each mountain system in the historical perspective of the early Quaternary and in the biogeographical context of the Western Palaearctic are discussed.

## Introduction

There is a well-documented relationship between number of species and altitude, both in insects (Wolda, 1987; McCoy, 1990) and other animals (Terborgh, 1977, 1985). When the complete altitudinal gradient is analyzed from sea level to mountain tops, entomological richness varies according to the altitude, with the highest diversity at intermediate altitudes (Janzen et al., 1976; McCoy, 1990). This is probably due to the limiting effect of environmental conditions at low and high altitudes and to the contact at intermediate levels between faunas of low and high altitudes. Many factors that have been put forward to explain the latitudinal gradients of species richness (e.g. productivity gradient, differences in history, spatial heterogeneity, environmental variability, etc.) (Pianka, 1966; Rohde, 1992) can also be applied to the altitudinal gradients. However, these altitudinal gradients present a peculiarity, because they are accompanied by a progressive decrease in surface area. This effect may in part account for the decrease in community richness observed when altitude increases (MacArthur, 1972).

Altitude, as well as latitude, also strongly influences the distribution of species and produce a zonation. It has been known since the 1920s that the altitudinal turnover of species largely corresponds to that found by latitude (Dansereau, 1957). However, in each case, the scales and the phenomena coming into play are vastly different as mountains give little opportunity for survival when species require extensive areas for finding food or for maintaining minimal population size with minimal genetic variation. Latitudinal environmental variation encompasses much larger regions (Hengeveld, 1990). In Europe, both latitudinal and altitudinal gradients produce a similar zonation. Several authors have argued that this convergence was due to the effects of the last glaciation which brought about a southward movement of the Nordic species and the mixing of fauna around the Mediterranean basin (Blondel, 1995). Studies of mutually exclusive altitudinal ranges in birds and in insects suggest that ecologically and phylogenetically closely related species have mutually exclusive altitudinal ranges more frequently than expected by chance (Mayr and Diamond, 1976; Diamond, 1978; Schluter and Grant, 1982; Hanski, 1983; Hanski and Krikken, 1991). If altitudinal turnover concerns closely related species, it

may be due to a local speciation which is the result of the competition existing in the present or in the past between the two species or their ancestors (Brooks and McLennan, 1993). In that case, local ecological processes are probably important in forming altitudinal zonation. On the other hand, if the altitudinal turnover occurs between species which are not closely related (i.e. genera or subgenera are different), one may suppose that it is a matter of multi-origin species brought into contact by their biogeographical history (Connell, 1980; Brooks and McLennan, 1993). This zonation is probably due to nonlocal factors related to historical processes (Schluter and Ricklefs, 1993). A recent study proposed that the altitudinal segregation of the dung feeding families of Scarabaeoidea in the central mountains of the Iberian peninsula was probably due to historical processes (Martín-Piera et al., 1992).

The goals of this paper are (1) to analyze the altitudinal gradient of species richness in several European montane dung beetle faunas; (2) to examine the altitudinal zonation in the same dung beetle faunas in order to evaluate the relative importance of both ecological and historical processes in the altitudinal patterns; and (3) to compare the general characteristics of European montane dung beetle faunas.

## Methodology

### DEFINITION OF FUNCTIONAL GROUPS

Our data concern dung beetles (Coleoptera, Scarabaeoidea), a taxonomically well-studied group of around 490 species in Europe (Baraud, 1992) belonging to Geotrupidae (51 sp.), Aphodiidae (260 sp.), and Scarabaeidae (180 sp.). They exploit mammal feces, a simple, well-defined food resource. Dung beetles are classified into several functional groups according to the way they exploit dung (Doube, 1990; Hanski and Cambefort, 1991).

In spite of a few exceptions (Rojewski, 1983; Yoshida and Katatura, 1992), most Aphodiidae species are dwellers in the dung or just below the pats and do not construct nests. The small tunneler species belong to the Onthophagini and Oniticellini tribes in the Scarabaeidae family. They dig more or less vertical tunnels below the dung pats and bury dung for adult feeding or for breeding. Due to their importance in numbers and species in the Palaearctic assemblages, the dwellers (DW) and the small

tunnelers (ST) constitute the main functional groups. Two other groups occur in the West Palaearctic area: the large tunnelers and the rollers. Despite their large body size (range from 13 to 40 mm in length), they normally represent a small proportion of the total number of beetles in regional faunas.

## SAMPLING DATA

Our analyses focus on European montane dung beetle assemblages. The main data are extracted from a study in progress managed in the Verdon and the Var valleys of the Southern French Alps. This corresponds to a contact area between Mediterranean and Alpine ecological influences. Beetles were trapped using two dung-baited pitfall traps of standard design (CSR model, Lobo et al., 1988; Veiga et al., 1989) set up in open pastures. Traps consisted of a plastic basin 210 mm in diameter, buried to its rim in the soil, containing a water-for-malin-liquid soap mixture. Fresh cattle dung was supported on a wire grid on top of a bucket. Trapped beetles were collected 1 wk later. Trapping was made during three consecutive years (1992, 1993, 1994) in June and July, a season when most dung beetle montane species are active.

The other consistent data come from (1) the French Vanoise National Park (Northern Alps) (Lumaret and Stiernet, 1989, 1991); (2) the Iberian Central System (Lobo, 1992; Martín-Piera et al., 1992), a massif which constitutes a contact between the Eurosiberian and the Mediterranean subregions; and (3) the Sierra Nevada, which is situated in the Mediterranean subregion of southern Spain (Avila and Pascual, 1988). Finally, to complete the study at the European scale, spring data from two other regions have been added: (1) data from the Cantabrian Mountains, which are located in the Eurosiberian subregion of northern Spain (Galante and Rodríguez-Menéndez, 1989; Galante and Stebnicka, 1994), and (2) data from Viiala, in southern Finland (Hanski and Koskela, 1977).

## SPECIES BIOGEOGRAPHIC CHARACTERIZATION

The species were divided into five geographic categories according to the criteria defined by La Greca (1964): (1) Widely distributed elements, corresponding to an Euroasiatic, Palaearctic, Holarctic or Cosmopolitan distribution. Their geographic range includes the Mediterranean Basin as a minor part; (2) Eurosiberian elements, which are clearly Eurosiberian, European, and Boreoalpine. Their geographic range seldom includes the Mediterranean Basin; (3) Euroturanian elements, which extend almost all over Europe to the Aralocaspian plain and frequently colonize the northern, or even the entire, Mediterranean basin; (4) Mediterranean elements, which have a geographic range primarily limited to the Mediterranean basin, but which do not extend beyond the Sahara desert; (5) Endemic elements, which are limited to localized regions.

## DATA ANALYSIS

The diversity analysis in each montane assemblage was made by means of a study of alpha ($\alpha$), beta ($\beta$), and gamma ($\gamma$) diversity patterns (Whittaker, 1960, 1972). $\alpha$-diversity is the number of species coexisting within an uniform habitat (intra-habitat diversity). $\alpha$-diversity was measured as the species number per altitudinal site or per range of close altitudinal sites. To estimate the relation between $\alpha$-diversity and altitude in each mountain system, the slope value (b) of the linear regression between both variables was calculated. The $\beta$-diversity, which

is the faunistic change along an environmental gradient (between habitat diversity), measured the species turnover along the altitudinal gradient. The $\beta$-diversity between adjacent sites was calculated with Cody's index ($\beta_c$) (1975), expressed as a percentage of $\alpha$-diversity and calculated as:

$$\beta_C = (Sg + Sl)/2\alpha \times 100$$

where $Sg$ is the increase in number of species between two consecutive altitudinal sites; $Sl$ is the number of species lost; and $\alpha$ is the average of the $\alpha$-diversity for the two sites.

The $\beta$-diversity along the complete altitudinal gradient for each mountain system was calculated using Whittaker's index ($\beta_w$) (1960):

$$\beta_W = (S/\alpha) - 1$$

where $S$ is the total number of species recorded and $\alpha$ is the average of the $\alpha$-diversity for all sites of the mountain system.

Both $\beta_c$ and $\beta_w$ were recommended by Wilson and Shmida (1984) as reliable indicators of $\beta$-diversity and their values are strongly correlated. The species turnover measured with $\beta$-diversity indices does not reveal whether the values are produced by an increase or by a loss in species number. In order to know the relative importance of both processes, we calculated the percentage of the species gained and lost between consecutive sites over the total number of species present in the two sites.

$\gamma$-diversity is defined as the richness in species for the whole of the altitudinal gradient of each mountain system (regional diversity). Its value depends on both the $\alpha$-diversity of each site and of the $\beta$-diversity among them. The cumulative curve of species richness against rise in altitude helps to explain the process of development of the $\gamma$-diversity. To estimate this process of development, we calculated the slope of the linear regression curve of the altitude of sites (independent variable) against the cumulated number of species (dependent variable).

Due to the differences in sampling effort and in the size of sampled areas, it was not possible to make effective $\gamma$-diversity comparisons. However, we were able to compare the qualitative resemblance among montane assemblages. The Jaccard (1908) association coefficient was used to make a cluster analysis of the European regions, using the UPGMA clustering strategy (Sokal and Rohlf, 1981). This coefficient is expressed as:

$$Qj_{(x1,x2)} = a/(a + b + c)$$

where $a$ is the number of species which were present in both samples ($x1$, $x2$); $b$ the number of species which were only present in $x1$; and $c$ the number of species which were only present in $x2$. One of the advantages of the Jaccard coefficient is that it allowed us to estimate the probability of finding an observed value by chance (Baroni Urbani, 1980). Only species present above 1500 m in altitude were considered in the analysis.

The Spearman rank correlation coefficient (rs) was used to measure the covariation between altitude and richness.

# Results

## ALTITUDINAL GRADIENT OF $\alpha$-DIVERSITY

In the Southern Alps, the variation in species number per site was negatively correlated with altitude for the samples of year 1992 (rs = $-0.563$; df = 11; $P$ = 0.05) and 1994 (rs = $-0.443$; df = 27; $P$ = 0.02). In contrast to this, the variation in species number was not correlated with altitude in 1993 samples (rs = 0.049; df = 14; $P$ = 0.85) because of an unusually high number of species in the three samples from the highest altitudes

## Southern Alps
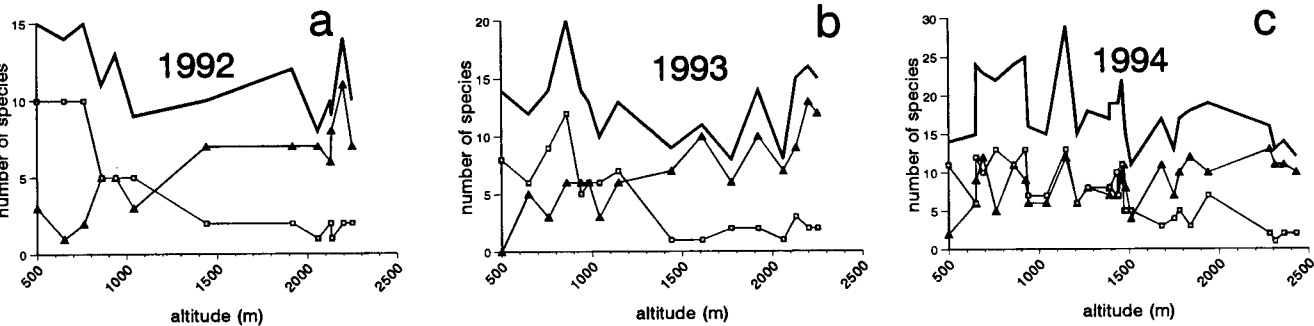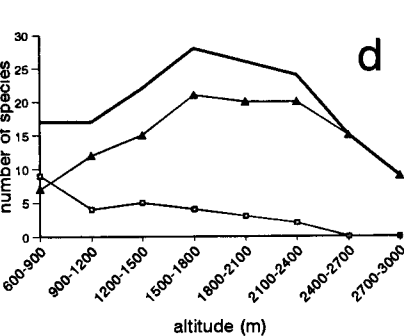


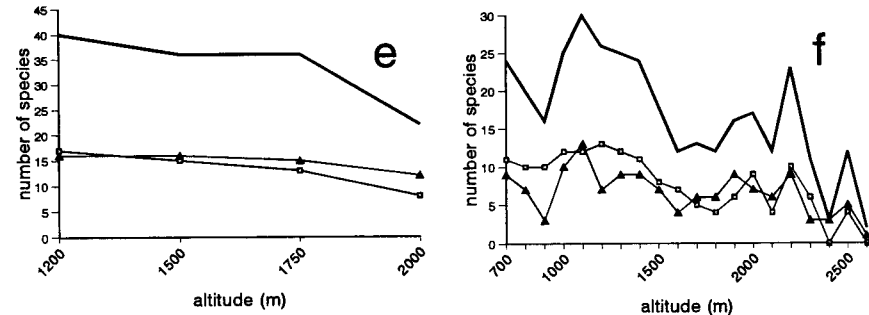## Northern Alps    Iberian Central System    Sierra Nevada



FIGURE 1. Altitudinal variation in the number of species (S) of the four mountain systems. The continuous line is the total species variation; ▲——▲ = dwellers variation. □——□ = small tunnelers variation.

(Fig. 1a, b, c). According to the year, the decrease in richness with altitude ranged between 0.20 and 0.67 species lost per 100 m in altitude (Table 1). The patterns of variation in the altitudinal species number differ according to the functional groups of beetles which were considered (Fig. 1 a, b, c). The α-diversity in dwellers (DW) was clearly higher in the high altitude versus low altitude assemblages (from 0.24 to 0.41 species gained with every 100 m). Conversely, the number of small tunnelers (ST) decreased as altitude increased (from 0.44 to 0.53 species lost with every 100 m) (Table 1). A significant negative correlation was found between the DW and ST dung beetle α-diversity, in 1992 (rs = −0.896; df = 11; P = 0.002) and in 1993 (rs = −0.727; df = 14; P = 0.005). In 1994, the negative correlation between the DW and ST α-diversity was not significant (rs = −0.278; df = 27; P = 0.14).

Throughout the Alps, the pattern of variation of the whole species number with altitude was the same. The ST α-diversity decreased with altitude rise (rs = −0.952; df = 6; P = 0.01), with a loss of 0.37 species per 100 m (Table 1). Conversely, the DW α-diversity increased slightly of 0.17 species per 100 m (rs = 0.229; df = 6; P = 0.55). Above 2400 m in altitude, the DW α-diversity decreased in turn (Fig. 1d).

In the Iberian Central System (ICS) and in the Sierra Nevada (SN), a negative correlation was observed between species number and altitude (rs = −0.947; df = 2; P = 0.1 and rs = −0.734; df = 18; P = 0.01, respectively). In both mountain systems, the altitudinal α-diversity decreased at once for ST (1.08 and 0.53 species lost with every 100 m in the ICS and the SN, respectively) and for DW (0.48 and. 0.26 species lost with every 100 m in the ICS and the SN, respectively) (Fig. 1e, f).

TABLE 1

Slope values of the linear regression between altitude and richness by site and between altitude and accumulated richness for dwellers and small tunnelers in the four mountain systems

| | Northern Alps | | | Southern Alps | | Iberian Central System | Sierra Nevada |
|---|---|---|---|---|---|---|---|
| Altitudinal range (m) | 600–3000 | | | 500–2430 | | 1200–2000 | 700–2600 |
| | | 92 | 93 | 94 | | | |
| General slope (spp/100 m) | −0.25 | −0.20 | −0.67 | −0.37 | | −2.01 | −0.94 |
| Dwellers slope | 0.17 | 0.34 | 0.41 | 0.24 | | −0.48 | −0.26 |
| Small tunnelers slope | −0.37 | −0.46 | −0.44 | −0.53 | | −1.08 | −0.53 |
| Accumulated richness slope | | | | | | | |
| Dwellers | 0.98 | 0.87 | 0.95 | 1.10 | | 1.37 | 0.47 |
| Small tunnelers | 0.05 | 0.19 | 0.26 | 0.26 | | 0.23 | 0.10 |

# Southern Alps



accumulated richness

a

b

c

βc DW

βc ST

altitude (m)

# Northern Alps

d

accumulated richness
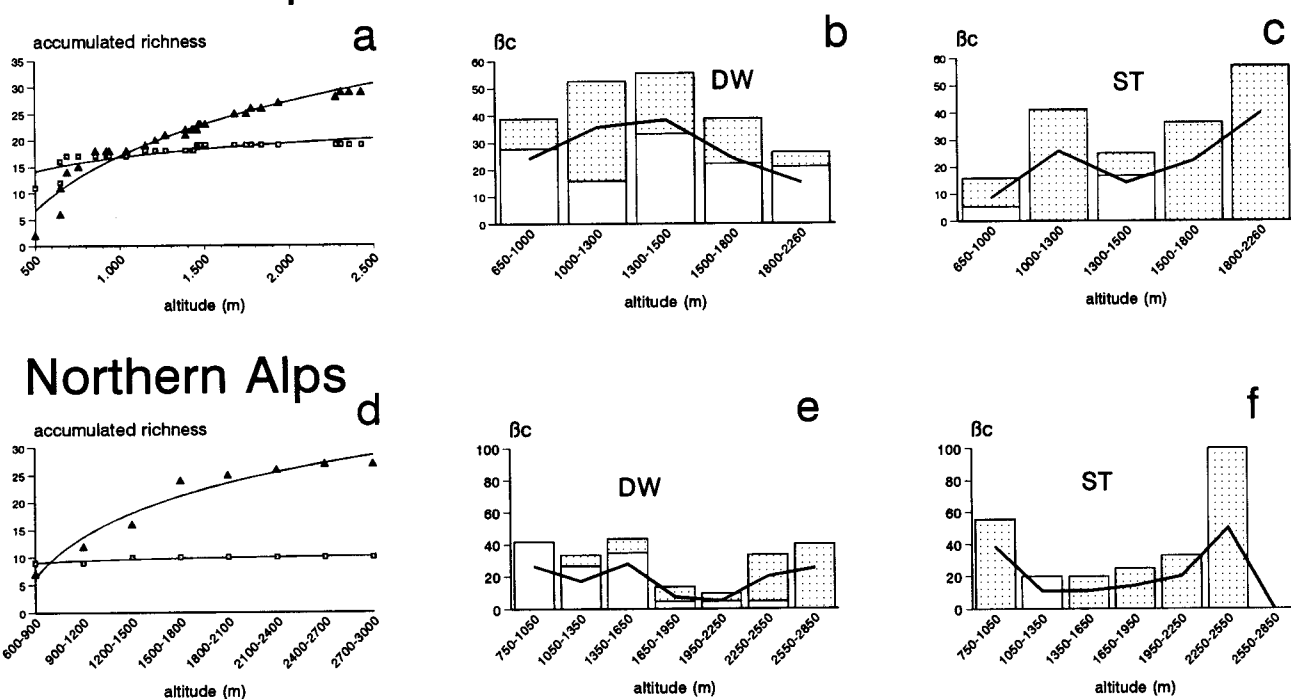
e

f

βc DW

βc ST

altitude (m)

FIGURE 2. *Accumulated richness of dwellers (▲) and small tunnelers (□) according to altitude in Southern Alps (a) and Northern Alps (d). Beta-diversity variation (βc) for dwellers (DW) and small tunnelers (ST) in Southern (b, c) and Northern (e, f) Alps. The beta-diversity was calculated between two adjacent altitudinal levels with the Cody's measure (1975) expressed as a percentage of alpha-diversity (gross-line). The dotted-bars correspond to the percentage of species lost between two consecutive altitudinal levels and the empty bars to the percentage of species gained. For the Southern Alps the calculation was made using the 1994 data.*

In the ICS, the decrease in α-diversity was more important than for other mountain systems, probably due to samples collected along a restricted altitude range (from 1200 to 2000 m) (Table 1, Fig. 1f).

## SPECIES TURNOVER AND ALTITUDINAL ZONATION

In the Southern Alps, the slope of the curve of cumulative richness versus altitude increased slightly for the small tunnelers (from 0.19 to 0.26 species more in every 100 m), but much more distinctly for the dwellers (from 0.87 to 1.1 species more with every 100 m) (Table 1). For the ST dung beetles, the highest value for cumulative richness was observed at 1500 m altitude (plateau), with no further increase in species number at higher altitudes. Conversely, the cumulative richness for DW continued to increase until 2300 m altitude (Fig. 2a). The β-diversity (Fig. 2b, c) was mainly due to a loss of species in the ST and an equilibrium between losses and gains of DW throughout the altitudinal gradient.

In the Northern Alps, the slope of the curve of cumulative richness versus altitude was more pronounced in DW than in ST (Table 1, Fig. 2d). The high values of the ST β-diversity were due to species losses (Fig. 2f), while a species turnover occurred in the DW until 2400 m altitude (Fig. 2e).

The Iberian Central System (ICS) presented the same cumulative richness curve pattern seen in the other mountain systems, both for the DW species (1.37 species more with every 100 m rise) and the ST species (0.23 species more with every 100 m rise) (Fig. 3a, Table 1). Unlike that which was observed previously, the β-diversity was nearly constant in the DW (Fig.

3b), due to a negative balance between losses and gains in species above 1700 m altitude. In the ST, the β-diversity increased regularly (Fig. 3c), even when the gain of new species was stopped at the 1500-m level (Fig. 3a). The gain in species at the 2000-m level was an artefact and corresponded to species present at the 1200- and/or 1500-m levels, absent at the 1750-m level, and again present at 2000 m (Fig. 3c).

Lastly, in the Sierra Nevada, the cumulative richness curves and the β-diversity patterns were not very different for DW and ST (Fig. 3d, e, f, Table 1). For both functional groups, we observed an irregular but persistent turnover of species with altitudinal rise. In ST, this did not correspond with a gain of new species, but with successive disappearances of species followed by their reappearance.

The analysis of the global variation in beta diversity (βw) for species and for subgenera along the latitudinal gradient from the Northern Alps to the Sierra Nevada showed that species turnover was higher than subgenera turnover (Wilcoxon signed ranks test: $Z = 2.1$, $P = 0.04$; and $Z = 1.89$, $P = 0.06$ for DW and ST, respectively) (Fig. 4). However, when the Iberian Central System and the Sierra Nevada were considered separately from the other massifs, the values of the β-diversity in species and subgenera were quite similar both for DW and ST.

## EUROPEAN SCALE ANALYSIS

A cluster analysis using the Jaccard index (Fig. 5) divided the six studied areas into three groups: (1) Northern Europe assemblage; (2) Alpine and North Iberian assemblages; and (3) Central and South Iberian assemblages ($P = 0.01$). Along the
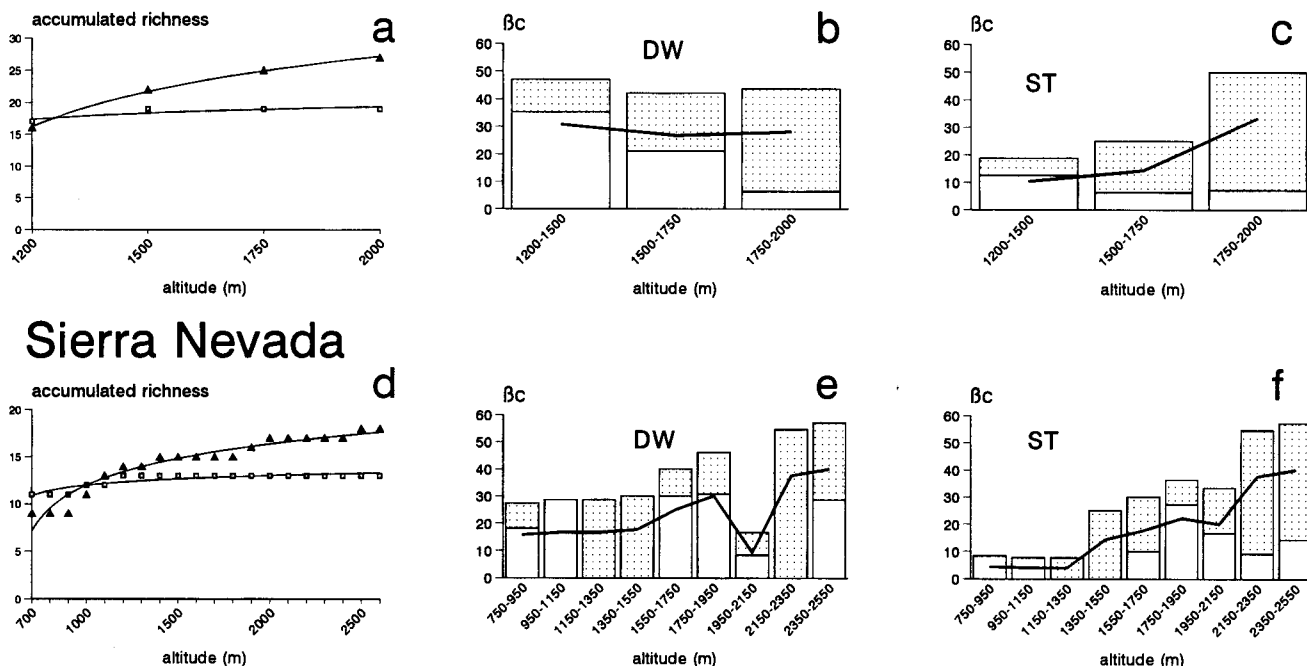
# Iberian Central System



# Sierra Nevada



FIGURE 3. Accumulated richness of dwellers (▲) and small tunnelers (□) according to altitude in Iberian Central System (a) and Sierra Nevada (d). Beta-diversity variation (βc) for dwellers (DW) and small tunnelers (ST) in Iberian Central System (b, c) and Sierra Nevada (e, f). The beta-diversity was calculated between two adjacent altitudinal levels with Cody's measure (1975) expressed as a percentage of alpha-diversity (gross-line). The dotted-bars correspond to the percentage of species lost between two consecutive altitudinal levels and the empty bars to the percentage of species gained.

southward latitudinal gradient, the DW : ST ratio mainly decreased because of the rise in ST number (Table 2). There were no ST species in the Scandinavian site and few ST in the Alpine and Cantabric systems. In the ICS and Sierra Nevada, the number of ST was two to three times greater when compared with the other mountain systems. In the Sierra Nevada, the decrease in number of DW gave an equal importance to ST and DW (13 and 15 species, respectively).

The Finnish assemblage was essentially composed of Eurosiberian species (64%) (Table 2). Eurosiberian, widely distributed, and Euroturanian elements were dominant in the Alpine and Cantabrian assemblages but Mediterranean elements were poorly representated (from 0 to 3.2%). Conversely, in the ICS, Mediterranean elements constituted a large part of the dung



FIGURE 4. Species beta-diversity and subgenera beta-diversity variation among mountain systems for both dwellers and small tunnelers. βw is the Beta Whittaker index (1960): βw = (S/α) − 1 where S is the total number of species (or subgenera) recorded and α is the average of the alpha-diversity. NA = Northern Alps; SA = Southern Alps (1992, 1993, 1994 data); ICS = Iberian Central System; SN = Sierra Nevada.

beetle fauna (22.2%). Finally, in the Sierra Nevada, the Eurosiberian elements almost disappeared (3%) and the Euroturanian and Mediterranean species increased considerably (48.5 and 24.2%, respectively). The ICS was the only massif where all five biogeographic elements were equally represented ($\chi^2 = 10.9$; $P = 0.03$).

No endemic species were found in the Finnish site (Table 2). Throughout the Alps, in the Cantabric Mountains and in the ICS, endemic species were numerous (from 13.3 to 22.6% of total). But in the Alps, all the species were true montane endemics. Conversely, in the Spanish mountain systems, the rate of endemism decreased southward from the Cantabric mountains to the ICS and the Sierra Nevada (83, 50, and 0%, respectively). In the Sierra Nevada, endemism was very low (3%), due to a preponderance of *Geotrupes ibericus* (Baraud), an Iberian endemic species widely distributed in the Iberian peninsula.
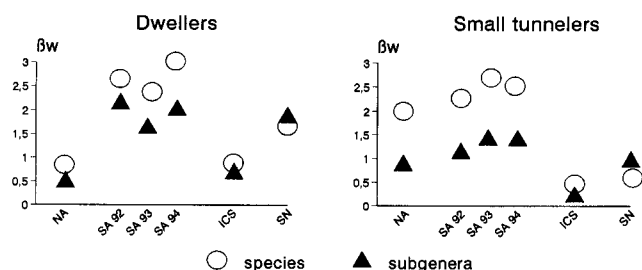
## Discussion

The study of montane dung beetle faunas in Europe showed a general negative gradient of α-diversity with altitude: the higher the altitude, the lower the α-diversity. However, the altitudinal drop was more obvious in the southern montane systems compared with the Alps. These differences with altitude were mainly due to dissimilar responses of DW and ST with the latitudinal location of the massifs. The α-diversity of ST always decreased as altitude increased and it was the same for DW in the southern Iberian peninsula. But in the Alps, the α-diversity of DW increased with altitude up to a threshold of about 2400 m. These altitudinal patterns of DW and ST produced a differential zonation which led to different
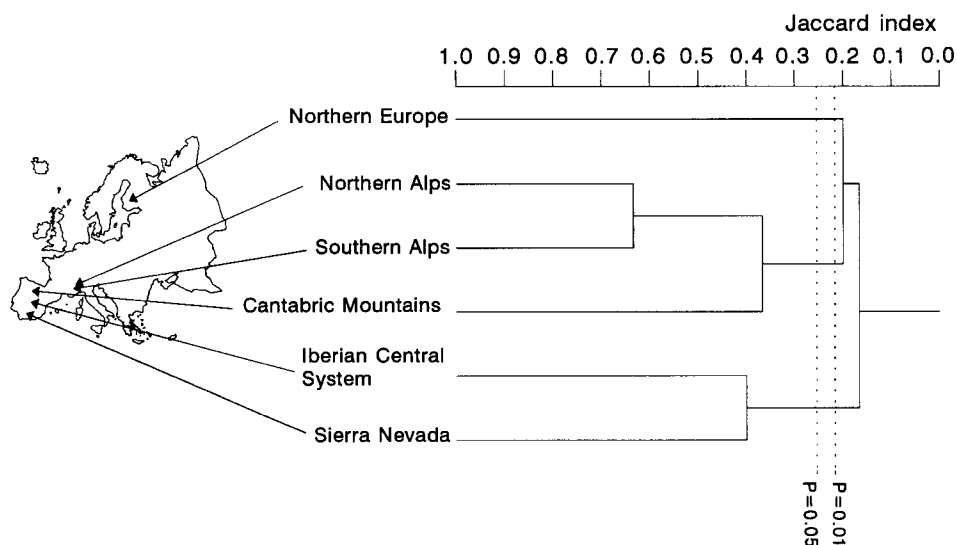
FIGURE 5. Cluster analysis of the six European areas. The resemblance was calculated using the Jaccard's (1908) association coefficient; the clustering strategy was UPGMA (Sokal and Rohlf, 1981). Vertical dashed lines indicate the critical values of the Jaccard coefficient at the probablity levels 0.05 and 0.01, according to Baroni Urbani (1980). In the montane areas, only species present above 1500 m were considered.

faunal assemblages. Such zonation was more marked in the Alps, but also exists in Spain (Martín-Piera et al., 1992). In any case, ST species (Scarabaeidae) represented the bulk lowland faunas while DW species (Aphodiidae) were dominant at higher altitudes. This altitudinal differentiation between DW and ST currently corresponds well at the geographic scale of Europe. The distribution of both groups shows a well known latitudinal gradient (Hanski, 1986). Dwellers are dominant in the dung beetle assemblages of northern Europe. They are the only group that reach Scandinavia (Biström et al., 1991) and they have numerous montane endemic species in the rest of Europe (32 species, i.e. 9.1% of all the European Aphodiidae). Small tunnelers constitute the dominant group in southern European dung beetle assemblages (Lumaret and Kirk, 1987). Most ST have a Mediterranean or Euroturanian distribution, with few montane endemic species (6 species,

4.5% of total Scarabaeidae in Europe). There is paleontological evidence of successive dominances of DW and ST at the same site: the Aphodiidae were the dominant group in the temperate interlude which occurred in the middle of the last glaciation, but the Scarabaeidae were dominant in the interglacial period (Coope, 1974, 1979, 1990; Coope and Angus, 1975). The correspondence of this segregation in time may be due to ecophysiological restrictions related to a temperature control (Landin, 1961; Martín-Piera et al., 1992). The differences between cold and temperate species reflect a physiological barrier to colonization of cold zones that can be crossed only by the evolution of freezing tolerance mechanisms. Latham and Ricklefs (1993) proposed this explanation for temperate and tropical trees and Farrell et al. (1992) suggested it for insects. The segregation observed between ST and DW is probably due to a biogeographical difference in

TABLE 2

Main characteristics of the six areas clustered in the figure 4, total number of recorded species, dweller:small tunneler ratio (DW: ST), and percentage of the occurrence of all species among geographical categories defined according to La Greca (1964).

| | Northern Europe[a] | Northern Alps[b] | Southern Alps[c] | Cantabric Mountains[d] | Iberian Central System[e] | Sierra Nevada[f] |
|---|---|---|---|---|---|---|
| Sampling effort | 270 | — | 46 | — | 36 | — |
| Period | Jun/Aug | Jun/Aug | Jun/Jul | Jun/Jul | Jun/Jul | Jun/Jul |
| Area (km²) | — | 530 | 200 | 15,000 | 100 | 400 |
| Altitudinal range (m) | — | 600–3000 | 500–2430 | — | 1200–2000 | 700–2600 |
| Total number of species | 14 | 31 | 29 | 31 | 45 | 33 |
| DW/ST ratio | 13/0 | 24/4 | 20/5 | 21/8 | 21/16 | 15/13 |
| Geographical distribution | | | | | | |
| Wide distribution | 28.57 | 19.35 | 20.69 | 19.35 | 13.33 | 18.18 |
| Eurosiberian | 64.29 | 32.26 | 34.48 | 29.03 | 20.00 | 3.03 |
| Euroturanian | 7.14 | 22.58 | 31.03 | 29.03 | 31.11 | 48.48 |
| Mediterranean | 0 | 3.22 | 0 | 3.22 | 22.22 | 24.24 |
| Endemic | 0 | 22.58 | 13.79 | 19.35 | 13.33 | 3.03 |
| mountain endemics | 0 | 100 | 100 | 83 | 50 | 0 |
| other endemics | 0 | 0 | 0 | 17 | 50 | 100 |
| $\chi^2$ | 150.02 | 22.28 | 38.52 | 22.28 | 10.87 | 70.42 |
| $P$ | <0.0001 | <0.001 | <0.0001 | <0.001 | 0.03 | <0.0001 |

The sampling effort is the number of pitfall-traps or dung pats considered. The percentage of mountain endemics and other endemics refer to the total of endemic species. The equal distribution of species among the five geographical categories was tested using a $\chi^2$ test.

Data from: [a] Hanski and Koskela (1977); [b] Lumaret and Stiernet (1989, 1991); [c] authors data; [d] Galante and Rodríguez-Menéndez (1989), Galante and Stebnicka (1994); [e] Lobo (1992), Martín-Piera et al. (1992); [f] Avila and Pascual (1988).
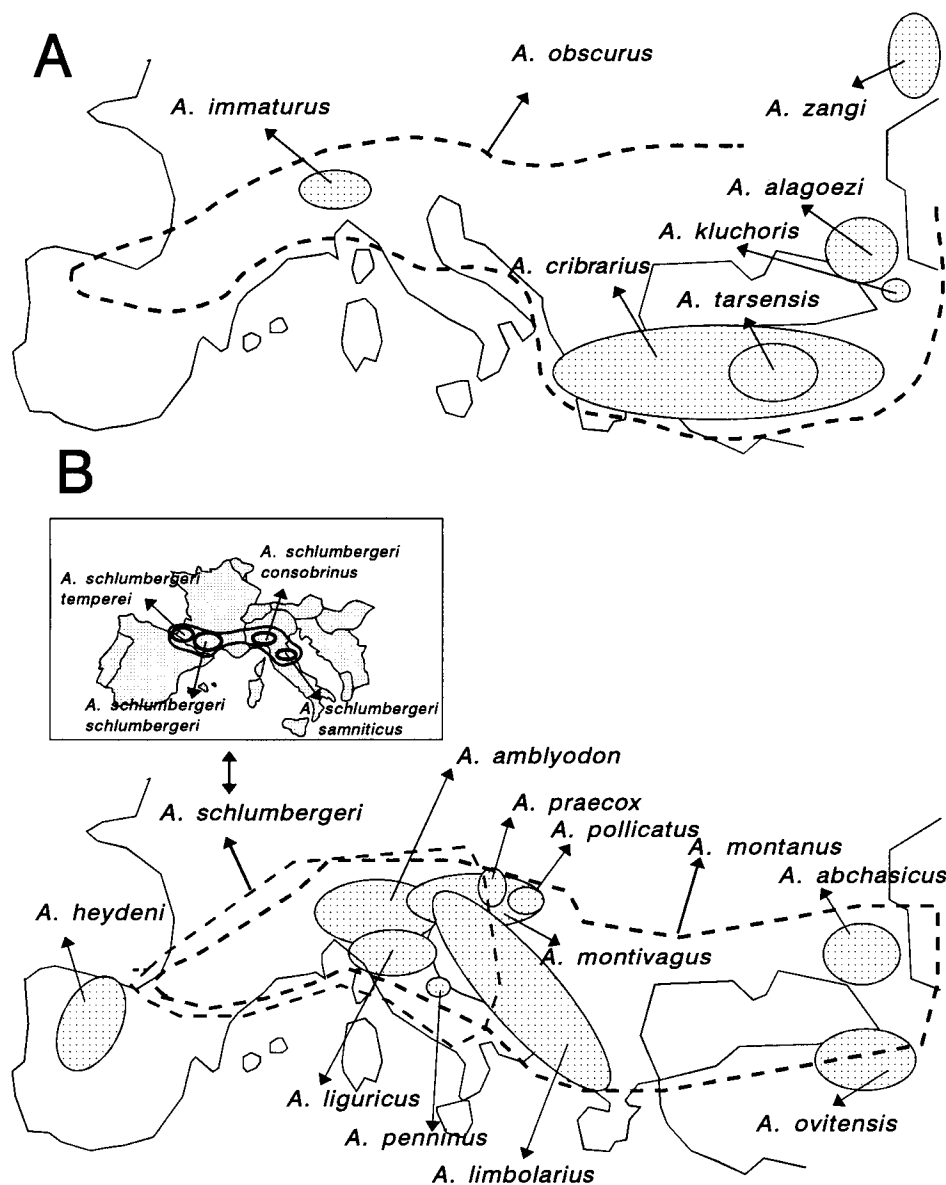
FIGURE 6. A—Distribution of the Aphodius obscurus group; B—Distribution of the Aphodius montanus group (according to Baraud, 1992; Dellacasa, 1987; Lumaret and Stiernet, 1992).

origin and their actual distribution in altitude probably reflects more the ecophysiological constraints than a strong competition between ST and DW.

Is the altitudinal segregation observed between small tunnellers and dwellers also partly observed within each group, at the specific and/or supra-specific level? The altitudinal distribution of ST showed neither a marked and structured zonation nor an altitudinal enrichment. Moreover, in the Iberian massifs where the importance of ST in the high-altitude ecosystems was obvious, subgenera turnover was quite similar to species turnover. That suggests little importance of species interactions at the community level in the explanation of the altitudinal zonation. Conversely, DW showed a marked and structured zonation with an altitudinal enrichment. Both zonation and enrichment were especially evident in the Alps, with a turnover higher for species than for subgenera. This establishes that altitudinal zonation of DW in the Alps is partly the result of ecological interactions at the community level.

When the faunistic composition of dung beetle assemblages, the biogeographic origin of faunas and the level of endemism are all considered, two groups of mountain systems are defined: (1) the West Mediterranean massifs, with the Iberian

Central System and the Sierra Nevada; (2) the Western Eurosiberian massifs, including the Alps and the Cantabric mountains. The Iberian Central System (ICS) and the Sierra Nevada (SN) present a noteworthy entomological composition and organization of assemblages. In both massifs, the altitudinal zonation of assemblages was indefinite and subgenera turnover along the altitudinal gradient was high. In the ICS, the species percentage of each of the five established geographical categories was similar. These results mean that these massifs have a mixture of species from different biogeographical origins. Such an hypothesis was already suggested for the ICS by Martín-Piera et al. (1992) and by Lobo (1992). Moreover, the fauna from SN does not contain any true montane species or any montane endemic species. All the montane endemic species found in the ICS were not restricted to this massif, but were also found in the Cantabrian massif. In the ICS the mountain tops have probably acted as refuges for the Pleistocene fauna that migrated to higher altitudes as the ice retreated during deglaciation. This hypothesis is partly validated by the fact that two of the five present endemic species found in the ICS were found in earlier times in the British Isles: Aphodius (Agolius) bonvouloiri during the last glaciation and Aphodius (Acrossus) carpetanus during the last

interglacial (Coope, 1979, 1990). In the ICS and SN, it is remarkable that the occupation of successive altitudinal niches was due to the turnover of species having different geographical distributions and belonging to many phylogenetical groups (many genera and subgenera). History takes the main place in the origin and composition of assemblages.

The situation of the Alpine fauna is outstandingly different: the Alps are the only mountain region to present diversified communities for almost all the studied altitudinal gradients, with the exception of a slight decrease in species number above 2400 m in the Northern Alps. The Alps constitute the European mountain system with the highest percentage of endemic species (13.8% in Southern Alps; 22.6% in Northern Alps). Furthermore, the distribution of all species was well structured and a distinct altitudinal zonation was observed. Unlike the pattern which occurs in the Spanish massifs, the zonation in the Alps concerns often closely related species. So, it is most likely that some altitudinal species turnovers are the result of ecological interactions at the community level. An example of altitudinal turnover probably due to local community processes is shown by the alpine species *Onthophagus baraudi* Nicolas. This endemic species belongs to the *ovatus*-group, a phyletic line with recent speciation processes (Martín-Piera and Zunino, 1986). Along an alpine altitudinal gradient, the regular turnover of the species *O. ovatus* vs. *O. joannae* vs. *O. baraudi* is noticed from sea level to 2300 m in the Alps. The altitudinal turnover of the species *Aphodius (Acrossus) luridus* vs. *A. (A.) rufipes* vs. *A. (A.) depressus* vs. *A. (A.) laticollis* is another example of such processes among closely related species.

Two other processes could be responsible for species turnover and for the presence of endemic species in the Alps: (1) the isolation of populations in the inner Alps; and (2) the character of refuge habitats in the Alps. Many subfossil species (insect exoskeletons) were found in organic deposits of Quaternary age. The Pleistocene records suggest the modern species have existed for many hundred of thousands of years, and longer in some cases (Coope, 1979, 1990; Elias, 1994; Ponel et al., 1995). This means a morphological stability of species along generations. However, when species were restricted in small refuge habitats in few numbers then local populations could have become extinct or have diverge into new taxa according to their genetic potentiality (Blondel, 1995). The possibility of speciation by an isolation mechanism is illustrated by the *Aphodius* species of the subgenera *Amidorus* and *Neagolius*. In the *Amidorus* subgenus, inside the large distribution area of the *A. (Amidorus) obscurus* (Fabr.) species which extends from Spain to the Caucasus mountains, each closely related phylogenetically species differentiated in a mountain system (Fig. 6a). In the same way, the subgenus *Neagolius* shows a radiative differentiation from *A. (Neagolius) montanus* Erichson or its ancestors, into 12 species which occur in the mountain systems of the western Palaearctic. Inside this group, *A. (Neagolius) schlumbergeri* Seidlitz has differentiated into 4 or 5 new subspecies, each occupying the whole or a part of one mountain system (Fig. 6b). Contrary to what was observed in the Iberian massifs, the role of a Pleistocene refuge played by the Alps was less evident, probably limited to the southern slopes where trees could survive (Reille et al., 1996). The boreo-alpine migration, associated with the retreat of ice, is represented by two currents: one towards the north (Arctic region), and one towards the Alps and other southern European mountains (Marcuzzi, 1990). Few dung beetle species have a true boreo-alpine distribution, as observed for *Aphodius (Agoliinus) piceus* Gyllenhal and *A. (Parammoecius) gibbus* Germar.

In conclusion, the montane assemblages of the central and southern European mountains are very different. In the southern massifs, the temperate species can extend their altitudinal ranges to high altitudes and only few cold species are actually restricted to mountain tops. For that reason, the montane assemblages are a mixture of species that have different biogeographic, taxonomic, and ecological characteristics. On the contrary, the montane assemblages in the Alps are not primarily composed by temperate species, but by cold-adapted species that principally speciated *in situ* by isolation or by community processes. Why are the richness of true montane assemblages and the rate of true montane endemism higher in the Alps than in the southern massifs? Several explanations can be argued: e.g., the geographic situation of the Alps placed them on the boundary of the glacial area during the Pleistocene and, today, on the boundary of the Mediterranean region; the east-west orientation of the mountain range and its role as a faunistic corridor between Europe and Asia; or the high surface of the massif and its associated environmental heterogeneity.

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