Ecology and biogeography of dung-beetle communities (Coleoptera, Scarabaeoidea) in an Iberian mountain range

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Abstract. The role of the Eastern Mountains of the Iberian Central System (EMICS) as both a barrier to the dispersion of, and ecologic refuge for, Scarabaeoidea dung beetles is studied. An Ecogeographic Patterns comparison method (EP = set of ecologic features common to, and present geographic range shared by, a group of species) to weight the historical and ecological causes of geographic distribution is proposed. This method is based on the assumption that species now sharing geographic ranges, with common structural and non-structural features, also have a (to some extent) common evolutionary history.

The data studied indicate that (i) fauna of the N and S slopes are identical. Euroturanian and Mediterranean species, and those which belong to the Scarabaeidae family, predominated in all samples. Except for very few species, the EMICS have not impeded dispersal of Scarabaeoidea dung beetles; minor regional differences should be explained in terms of ecological causes. (ii) The variation in abundance,

richness, characteristic species, systematic composition and EP was found to relate mainly with altitude. Principally endemic, European or wider-range species of the Aphodiidae and Geotrupidae families, prevented from dispersing toward lower altitudes by a climatic discontinuity, colonize the higher altitudes, having taken refuge in the EMICS after Pleistocene glaciations. (iii) The explanation of the causes of the present vertical distribution of Scarabaeoidea dung beetles in the EMICS must take into account the historical events there, and major modifications of the geographic distribution of the species inhabiting it.

The agreement of inferences drawn from EP analysis with those drawn from paleontologic and phylogenetic evidence (for some species) supports the use of EP, and validates the assumption made in their application.

Key words. Eco-geographical patterns, dung-beetles, Scarabaeoidea, distribution, historical biogeography, Iberia.

INTRODUCTION

This paper deals with the biogeographical topics of (i) barriers, (ii) refuges, and (iii) the role played by historical and ecological causes in species distribution.

There have been many attempts to arrive at acceptable definitions for the terms dispersal and migration. Dispersal means a scattering of a population leading to an increase in the mean distance between individuals (Danthanarayana, 1986) as a result of (i) short-distance non-migratory movements (behavioural range); (ii) long-distance migratory movements (ecological range), and (iii) truly migratory movements and/or repeated short- and/or long-distance movements during more than one generation (geographical range); see Southwood (1962) and Hanski (1980a). Over a large space–time scale the geographic range of a species may be extended by combinations of these three kinds of movements, affected by variations in the balance between intrinsic, migration-favouring attributes (dispersal-favouring: structure, physiology, ecology, behaviour, etc.) and extrinsic, environmental factors (both biotic, species interaction; and non-biotic, climate, topography, history, etc.).

Non-biotic environmental factors (mountains, rivers, deserts, seas) may act either as a barrier to dispersal, or as a refuge for different taxonomic groups. Now, as Udvardy (1969) rightly argued, the distinction between geographical and ecological barriers is a semantic one. In fact, a mountain chain accommodates an environmental mosaic which may be an ecologic barrier for some species or a refuge for others.

The Pleistocene climates of ice-free regions (and hence their biotic histories) were greatly affected by the great climatic oscillations of the glacial/interglacial cycles. Several colder and warmer intervals within glacial stages (stadial and interstadial) have been recognized and named (Turner & Hannon, 1988). In response to these climatic changes of the Quaternary, large-scale alterations have taken place in the geographical ranges of species of Coleoptera (Coope, 1979). During warm periods (interglacial/interstadial) the mountain ranges and other areas within ice-free regions became ecological refuges for northern biotas which were widespread in colder periods (Halffter, 1987; Turner & Hannon, 1988). This effect has probably been heightened by the transversal orientation of the Eastern Mountains of the Iberian Central System (EMICS). Aubert (1963), Gangwere & Morales

Agacino (1970) and Pascual (1978), among others, investigated the possible effect of Iberian mountain range orientation on the relative abundance of endemisms.

When attempting to explain the distribution of a species, one must consider both historical and ecological factors (Blondel, 1979). The former are taken here to be those that greatly modify the geographical range of a species over many generations through dispersal. The latter are factors that scarcely modify the geographical range. Thus historical factors are measured on a geological scale and take effect over an evolution time period, while ecological factors are measured on a habitat scale, over ecological time.

Historical and ecological information can be 'decoded' from its species carriers, but rarely can the historical contribution to variations of geographical range be distinguished from the ecological.

As is widely accepted by biologists, the closer the phylogenetic relationships among species, the greater the likelihood of a common evolutionary history. Usually, phylogenetic inferences are based on structural features since knowledge of ecology, behaviour and other non-structural features is less complete than that of morphology. Nevertheless, common non-structural features, and shared geographic range among species, may also be indicative of a (to some extent) common evolutionary history. If this is so, we would then be enabled to draw historical inferences based on these common ecologic and geographic features.

We define the Ecogeographic Pattern (EP) of the species as the set of ecologic features common to, and present geographic ranges shared by, a group of species (see Methodology for particular definitions). Therefore, common EP among species is taken to mean a common (at least partially) evolutionary history. Then species EP become a means of facilitating comparisons of the fauna of different areas, and may also provide a means for breaking down the contribution to distribution variations into their historic and ecologic components. Thus EP would provide an alternative line of historical biogeography research in cases where phylogenetic data are lacking.

A biogeographic sampling of areas might produce the following data sets.

(1) The EP and species are common. Obviously no biogeographic inferences are possible.

(2) Species are not identical, but are characterized by similar EP. Although the species involved have adapted differently to ecological conditions, they probably have a common evolutionary history, in so far as their geographic ranges spread simultaneously (especially if they are closely related). In this case ecological factors have led to differences in fauna.

(3) Neither the species nor their EP are common. Probably the species' evolutionary histories are very different, and presumably their geographical ranges have not spread simultaneously. In this case historical factors have led to differences in fauna.

Starting from these theoretical premises, this paper aims to answer the following questions.

(1) Have EMICS (Eastern Mountains of the Iberian Central System) been an insurmountable barrier to the dispersal of Scarabaeoidea dung beetles ?

(2) Are EMICS an ecological refuge for some species of this group of Coleoptera ?

(3) Have historic factors played an important role in the spatial distribution variations of coprophagous Scarabaeoidea throughout EMICS ?

METHODOLOGY

Sampling design

EMICS were divided into three sampling sectors: East, Central and West (Fig. 1). In each sector three sampling stations were established on a north–south transect; two stations at similar altitudes on both slopes (at 1200 m. in the lower limit of the Supramediterranean phytoclimate approximately) and the third higher, on the upper limit of the Supramediterranean phytoclimate (for botanical terminology see Rivas-Martinez, 1987 and Rivas-Martinez *et al.*, 1987), which might or might not correspond with the mountain crests.

The easternmost transect was situated in the Macizo de Ayllón; Riaza (1240 m: R) and Colmenar de la Sierra (1210 m: CS) were, respectively, the north and south stations. The highest point was in Puerto de la Quesera (1600 m), where three samples of different biomes were collected: mat-grasses, *Nardus stricta* (PQMl), Pyrenean oak woodland, *Quercus pyrenaica* (PQQp), and beech woodland, *Fagus sylvatica* (PQFs).

In the central transect, set up in the Macizo Central de Guadarrama, the north and south stations were El Robledo (RO) and Navacerrada (N) respectively, both at 1170 m. The highest altitude station was in the Puerto de Cotos where two samples were collected: the first in a closed pine woodland, *Pinus sylvestris* (CT1:1630 m), and the other in mixed zones of mat-grasses, pines, and broom, *Cytisus purgans* (CT2: 1760 m).

Finally, the western transect was established in the Sierra de Malagón by fixing the stations in Aldeavieja (A) and Navalperal de Pinares (NP), both at 1200 m. The highest station, in Puerto de la Cruz de Hierro (CH), was on the line of the mountain crest (1560 m).

Besides the above-mentioned three transects, two samples (T1: 1220 m, grasslands, pastures; T2: 1240 m, closed Pyrenean oak woodland) were collected in the westernmost station, El Tiemblo, on the southern slope. This station is in the Valley of the Alberche river, the transition zone between the Sierra de Guadarrama and the Sierra de Gredos (Fig. 1). It has a unique mesoclimate (with high rainfall) and a healthy forest, the only zone sampled in which the Supramediterranean series of *Q. pyrenaica* (see below) predominates.

Every sample in the low-altitude stations, as well as in the highest one of the western transect (Sierra de Malagón), was collected in open biomes, i.e. pastures, grasses or very open meadows.

Sampling was done in forestal habitats to investigate (i) the unique phytoclimate of the chestnut grove, *Castanea sativa*, of El Tiemblo and the relict beech woodland of the Puerto de la Quesera and (ii) the possible effects of open and closed biomes on the abundance and distribution of Scarabaeoidea dung beetles (Lumaret & Kirk, 1987; Baz, 1988;
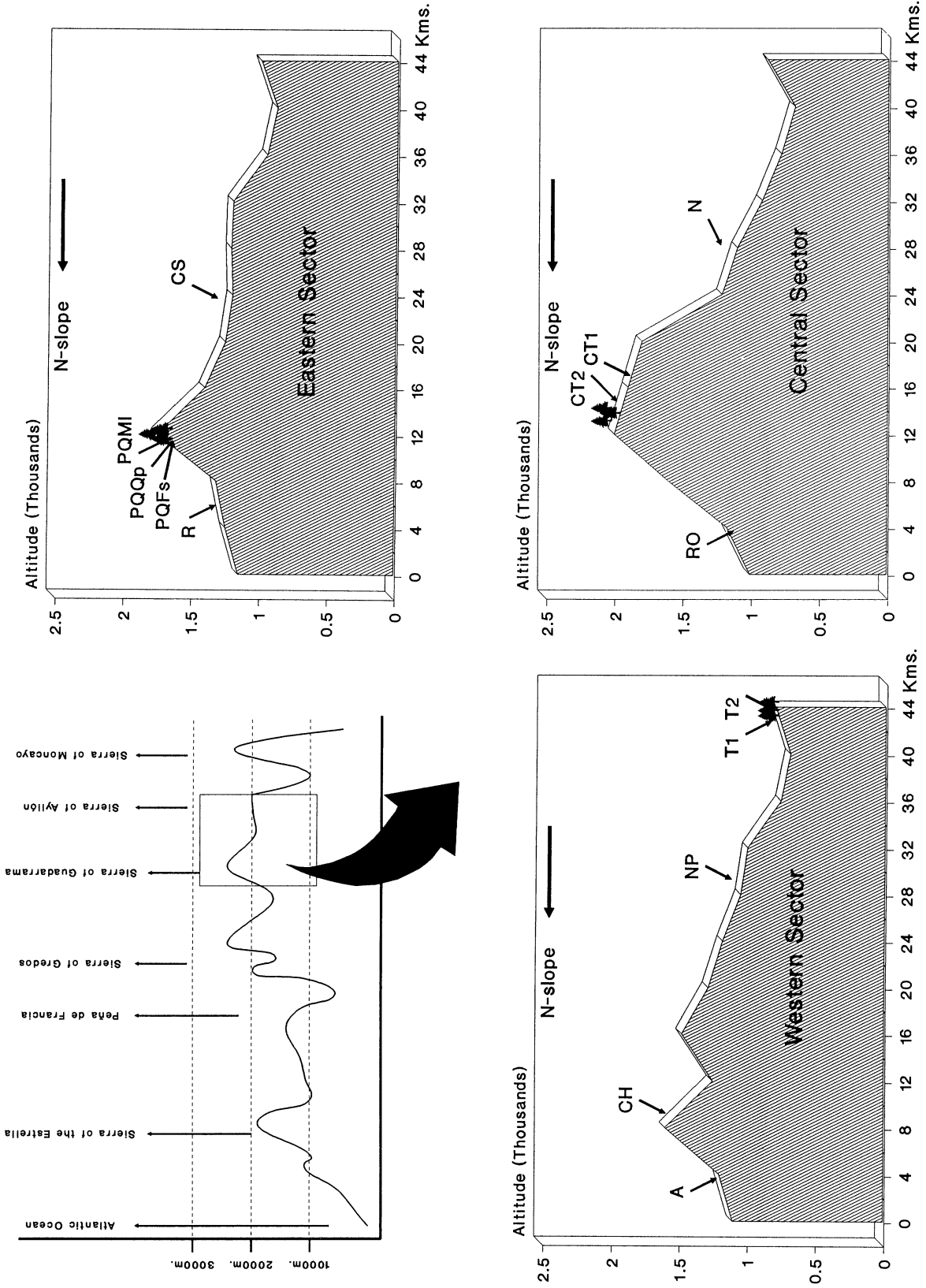
FIG. 1. Block diagram with the topographical vertical section of the N–S sampling transects. Abbreviations as in Table 1.

TABLE 1. Sampling design and variables. Meaning of abbreviations: A: Aldeavieja; CH: Puerto de la Cruz de Hierro; CS: Colmenar de la Sierra; N86/N87: Navacerrada, years 1986 & 1987; CT1: Puerto de Cotos (*Pinus sylvestris* woodland); CT2: Puerto de Cotos (mixed zone of mat-grass, *Nardus stricta*, pines, and broom, *Cytisus purgans*); NP: Navalperal de Pinares; PQFs: Puerto de la Quesera (*Fagus sylvatica* woodland); PQM1: Puerto de la Quesera (mat-grass); PQQp: Puerto de la Quesera (Pyrenean oak woodland, *Quercus pyrenaica*); R: Riaza; RO: El Robledo (San Ildefonso); T1: El Tiemblo (grasslands, pastures); T2: El Tiemblo (Pyrenean oak woodland and Chestnut grove, *Castanea sativa*).

Stations	Samples	U.T.M. coordinate	Altitude	Slope	Biome	Date/hour of setting pitfall-trap	Date/hour of collecting pitfall-trap	Number of species	Number of individuals	
Riaza	R	30TVL6067	1240	North	Open	24.6.86/9.00	27.6.86/9.13	15	374	
Puerto	PQMI	30TVL6564	1600	Top	Open	24.6.86/9.50	27.6.86/10.00	12	102	Eastern
de la	PQQp	30TVL6564	1600	Top	Close	24.6.86/9.55	27.6.86/10.27	7	54	Sector
Quesera	PQFs	30TVL6563	1600	Top	Close	24.6.86/11.00	27.6.86/11.25	6	17	
Colmenar de la Sierra	CS	30TVL6448	1210	South	Open	24.6.86/11.40	27.6.86/12.58	16	280	
Navacerrada	N86*	30TVL1509	1170	South	Open	24.6.86/7.15	27.6.86/7.15	20*	581*	Central
	N87*	30TVL1509	1170	South	Open	18.6.87/6.40	21.6.87/6.50			Sector
Puerto de	CT1	30TVL2120	1630	Top	Close	18.6.87/7.25	21.6.87/7.09	9	52	
Cotos	CT2	30TVL1919	1760	Top	Open	18.6.87/7.47	21.6.87/7.35	10	61	
Robledo	RO	30TVL1228	1170	North	Open	18.6.87/9.00	21.6.87/8.39	18	478	
Aldeavieja	A	30TUL7611	1200	North	Open	18.6.87/10.16	21.6.87/9.45	18	184	Western
Cruz de Hierro	CH	30TUL7707	1560	Top	Open	18.6.87/10.55	21.6.87/11.28	14	52	Sector
Navalperal de Pinarea	NP	30TUK8092	1200	South	Open	18.6.87/11.57	21.6.87/11.28	24	342	
El Tiemblo	T1	30TUK7067	1220	South	Open	18.6.87/13.28	21.6.87/13.10	25	1773	El
	T2	30TUK7067	1240	South	Close	18.6.87/13.45	21.6.87/13.20	14	481	Tiemblo

*The samples of this station were combined and taken randomly as sample units of each year, see Table 3. Further explanation in the text.

Doube, 1983). Sample variables and physiographic and phytoclimatic characteristics of the different samples are summarized in Table 1.

The sampling was done with a dung-baited pitfall trap model selected in an earlier study (Lobo, Martín-Piera & Veiga, 1988; Veiga, Lobo & Martín-Piera, 1989). Each sample station consisted of two identical traps (sample units: SUs) about 10 m apart, baited with 1000 g of fresh cattle dung. The traps were left in the field for an uninterrupted 72-h period. The choice of bait as well as timing of the sampling (15–30 June) were found to be optimum in a previous study (Martín-Piera, Veiga & Lobo, 1986), where abundance, diversity and richness in cattle dung was maximum during the spring.

Because of the size of the area (nearly 2600 km²), the sampling programme took 2 years: the Eastern Sector was sampled in 1986; El Tiemblo, and Western and Central Sectors were sampled in 1987. As Scarabaeoidea dung beetle populations are seasonally variable, to ensure that the phenological conditions of both sampling periods were identical, the populations of the Navacerrada station samples for both years (1986/87) were compared at weekly intervals to select a comparable sampling period. These two samples (N86 and N87) were combined into one, to be used in comparisons with the remaining samples.

Fifteen samples were collected at ten stations: five samples in the eastern transect; three in the central one, plus two in Navacerrada (one each year); three in the western transect, and finally two samples in the station of El Tiemblo. Eleven samples were collected in open biomes (pastures, grasses, and very open meadows) and four samples in closed biomes:

Puerto de la Quesera (Pyrenean oak and beech woodlands), Puerto de Cotos (pine woodland) and El Tiemblo (mixed Pyrenean oak woodland and chestnut grove). Thirty pitfall traps were used. There were more samples than stations, because in some of them more than one sample was taken (see Table 1).

Ecogeographical patterns (EP); see Table 2

We have defined the Ecogeographic Pattern of the species as the set of ecologic features common to, and present geographic ranges shared by, a group of species (see Introduction). We consider that this concept was given precedent by Halffter (1962, 1974, 1976, 1987) when he coined Dispersal Pattern. This in its turn in based on the Reig's earlier concept (1962) of Coenochrom: 'an animal or plant group or community, whatever its origin, which enters into a given area between definite limits of geological time'. Both concepts implicitly embody the basic assumption which enable us to weight the role of historic and ecologic factors in determining distribution variations, by means of species EP: species which share ecological and geographic features share, to some extent, evolutionary history. Neither Coenochrom nor Dispersal Pattern incorporate a strict recognition of monophyly as Erwin's Theory (1985, pp. 440–441) of Taxon Pulses does; EP does not either. If we recognized monophyly in species sharing EP, we would then be dealing with a true Taxon Pulse. Therefore, we emphasize once again the potential usefulness of EP when phylogenetic data are lacking.

TABLE 2. List of species and EP. E, Eurosiberian distribution; En, endemisms; Et, Euroturanian distribution; M, Mediterranean distribution; W, wide Palaerctic or Holarctic type of distribution. L, Lower level of the Supramediterranean phytoclimate (transition to Mesomediterranean); U, upper level of the Supramediterranean phytoclimate (transition to Oromediterranean).S/A, species of Spring and/or Autumn; S/S, species of Spring and/or Summer. C, species of closed biomes (thick forests). O, Species of open biomes (pastures, grasses or open meadows).

Eco-Geographical Patterns (EP)	W	W	W	W	E	E	E	E	E	Et	Et	Et	Et	M	M	M	M	M	En	En	En	En	T
	U	U	L	L	U	U	U	L	L	U	L	L	L	U	U	L	L	L	U	U	U	L	O
	S/A	S/S	S/A	S/S	S/A	S/A	S/S	S/A	S/S	S/A	S/A	S/A	S/S	S/A	S/S	S/A	S/A	S/S	S/A	S/S	S/S	S/S	T
	O	O	O	O	C	O	C	O	C	O	C	O	O	C	O	C	O	O	O	C	O	O	A
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	L
Fam. SCARABAEIDAE																							
1. Bubas bubalus																	15						
2. Caccobius schreberi													153										
3. Chironitis hungaricus																	1						
4. Copris lunaris												114											
5. Euoniticellus fulvus													734										
6. Euonthophagus amyntas													14										
7. E. gibbosus													1										
8. Gymnopleurus flagellatus													42										
9. Onitis belial																	2						
10. Onthophagus coenobita											37												
11. O. fracticornis										21													
12. O. furcatus													271										
13. O. grossepunctatus																		414					
14. O. illyricus													23										
15. O. joannae									4														
16. O. lemur												45											
17. O. maki																		6					
18. O. punctatus																9							
19. O. similis								1052															
20. O. stylocerus																			90				
21. O. taurus													46										
22. O. vacca													177										
23. O. verticicornis											147												
24. Scarabaeus laticollis																		1					
25. Sisyphus schaefferi				609																			
No species	-	-	-	1	-	-	-	1	1	1	2	2	9	-	-	1	3	3	1	-	-	-	25
No individuals	-	-	-	609	-	-	-	1052	4	21	184	159	1461	-	-	9	18	421	90	-	-	-	4028
Fam. APHODIIDAE																							
26. Aphodius annamariae																						1	
27. A. bonvouloiri																					7		
28. A. carpetanus																				2			
29. A. coenosus				4																			
30. A. depressus			3																				
31. A. erraticus													311										
32. A. fimetarius			38																				
33. A. foetidus																	27						
34. A. fossor		8																					
35. A. frigidus														18									
36. A. granarius			7																				
37. A. haemorrhoidalis		19																					
38. A. ictericus																		4					
39. A. inmundus						4																	
40. A. lugens													110										
41. A. merdarius			13																				
42. A. pusillus	64																						
43. A. quadriguttatus																	14						
44. A. satellitius																	2						
45. A. scrofa												22											
46. A. scrutator															5								
47. A. scybalarius							3																
48. A. sphacelatus						1																	
49. A. sticticus					1																		
50. A. striatulus														1									
51. A. sturmi													5										
52. A. unicolor																	23						
53. Pleurophorus caesus			3																				
No species	1	2	4	1	2	2	1	-	-	-	-	1	3	2	1	-	4	1	-	1	1	1	28
No individuals	64	27	61	4	4	5	3	-	-	-	-	22	426	19	5	-	66	4	-	2	7	1	720
Fam. GEOTRUPIDAE																							
54. Anoplotrupes stercorosus							41																
55. Bolbelasmus gallicus																1							
56. Geotrupes stercorarius						1																	
57. Trypocopris pyrenaeus																					40		
No species	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	4
No individuals	-	-	-	-	-	1	41	-	-	-	-	-	-	-	-	1	-	-	-	-	40	-	83
TOTAL species	1	2	4	2	2	3	2	1	1	1	2	3	12	2	1	2	7	4	1	2	1	1	57
TOTAL individuals	64	27	61	613	4	6	44	1052	4	21	184	181	1887	19	5	10	84	425	90	42	7	1	4831

The set of geographic and ecological features which we use here is the set of geographic and altitude ranges, phenology (seasonal variation) and vegetative cover which reflect a species' niche dimensions, i.e. temperature, humidity, insolation degree, etc. Their different variable ranges have been established in accordance with the extensive literature on the group (see Martín-Piera *et al.* 1986) and references quoted therein.

Optimum (not arbitrarily selected) ranges have been assigned to each species. Since they can vary over the entire geographical range (e.g. altitude range, phenology) obviously they must be defined for each study area. For instance, for phenology, a seasonal range can be set to describe the species as spring/summer or spring/autumn. However, beyond the EMICS, this formal definition is not applicable for widely ranging species such as Euroturanian, Eurasiatic, etc. Once again, these optimum variable ranges have to be defined for each particular study area.

Geographic distribution

The geographic range of each species has been defined according to the criteria of La Greca (1964). Here they are summed up as five.

(1) Widely distributed elements (W). These are species with a Euroasiatic, Palearctic, Holarctic or Cosmopolitan distribution, whose geographic range includes the Mediterranean basin as a minor part.

(2) Eurosiberian elements (E). Clearly Eurosiberian, European, and Boreoalpine elements; their geographic ranges seldom include the Mediterranean area.

(3) Euroturanian elements (Et). Species that extend almost all over Europe to the Aralocaspian plain and frequently colonize the northern or even the entire Mediterranean area.

(4) Mediterranean elements (M). Species whose geographic range is primarily the Mediterranean basin, and which does not extend beyond the Sahara desert not even in some cases the north African Mountain ranges.

(5) Endemic elements (En). Geographic range limited to the Iberian Peninsula.

Altitude distribution

Altitude ranges were assigned in accordance with the altitude preferences of species in the Iberian Peninsula. To facilitate consideration of this variable, the Supramediterranean horizon was divided into a lower level (L) in contact with the Mesomediterranean phytoclimate and an upper level (U) in the transition zone with the Oromediterránean phytoclimate.

Phenology

Previous works (Veiga, 1985; Lobo *et al.*, 1988) on the effects of rainfall on the emergence of populations in the EMICS indicated two ranges for this variable.

(1) Spring/Autumn species (S/A). Humidity-dependent; population maximum occurs during seasons of maximum rainfall (spring, autumn). Includes species of spring or autumn only, spring/autumn, or longer phenology.

(2) Spring/Summer species (S/S). Species of a strictly summer phenology, and those whose phenology coincides with the end of spring and the beginning of summer (Spring/summer species). In both cases the phenologies are marked

by moderate to high temperatures and absence of rainfall, in the time of the Mediterranean summer drought.

Plant cover

As commonly refered to in the literature (Lumaret, 1980; Cambefort, 1982; Doube, 1983; Martín-Piera, 1984; Baz, 1988) the vegetative cover is classified as either of open biome (pastures, grasses or open meadows - O -) or of closed (thick forests - C -).

Data processing

The resemblance of the fauna of the thirty SUs and the fifteen samples was checked by means of Pearson's correlation coefficient (quantitative mode) of species abundance and the value of the chi-square test (qualitative mode) for the number of the common and non-common species.

Three linkage rules (criteria for combining two clusters), were used: (i) single linkage (minimum distance between, or maximum similarity of, the two clusters over all pairings of the variables); (ii) complete linkage (maximum distance or minimum similarity), and (iii) average linkage (average distance or similarity: the arithmetic average of similarity using all possible pairings of the variables between the two clusters); see Dixon *et al.* (1985). In the interpretations and analysis of results, reliable groups were taken to be those for which the three linkage rules and two resemblance measures produced identical well-defined clusters. These have been illustrated in the dendrograms of Figs 2–5.

Data was processed by BMDP software (Dixon *et al.*, 1985), run on a CYBER computer of the CSIC Computing Center.

With respect to the EP, the Bray–Curtis dissimilarity Index (Clifford & Stephenson, 1975) was applied as a measure of ressemblance:

$$I = \frac{\sum_{1}^{n} |X_{1i} - X_{1j}|}{\sum_{1}^{n} (X_{1i} + X_{1j})}$$

where X_{1i} = number of species belonging to the EP '1' in the sample 'i', X_{1j} = number of species belonging to the EP '1' in the sample 'j' and n = total of the EP.

The dendrograms were computed using the unweighted pair-grouping clustering strategy (UPGMA method, Sneath & Sokal, 1973) by a program run on a PC microcomputer.

RESULTS

Analysis of the community

The entire sample consisted of 4831 individuals belonging to fifty-seven species, from the samples indicated in Table 3.

The inventories obtained from earlier studies made of closed sites (Lobo, 1982; Veiga, 1982; Martín-Piera *et al.*, 1986; Baz, 1988) as well as the data assembled for this work, consisted of seventy-four species for the EMICS, more than 42% of the Iberian coprophagous fauna belonging to the Scarabaeidae, Aphodiidae and Geotrupidae families (Veiga & Martín-Piera, 1988). So, during the six days of sampling, 77% of the known fauna in the zone was captured (the other species being of mainly autumn/winter phe-
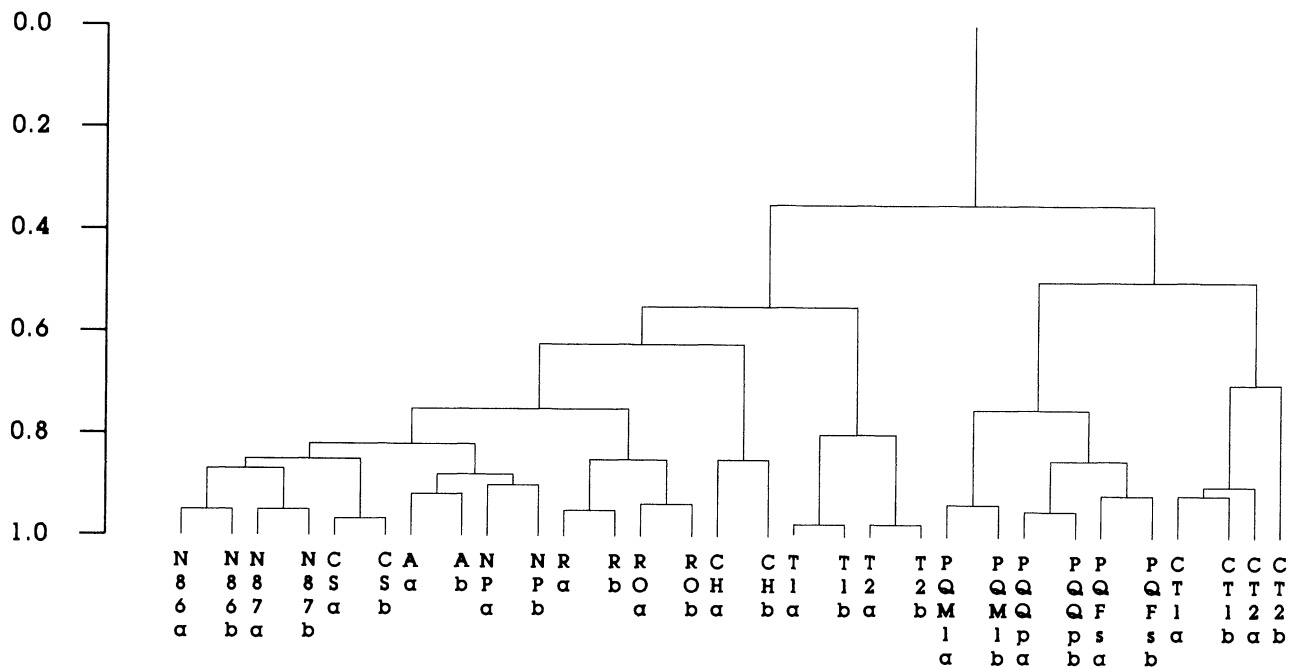
FIG. 2. Dendrogram drawn by means of a cluster analysis of the total SUs obtained with BMDP Software. Similarity measure: Pearson's Correlation Coefficient. Linkage rule in the clustering procedure is average similarity. Abbreviations as in Table 1; a/b are the SUs of a same sample.
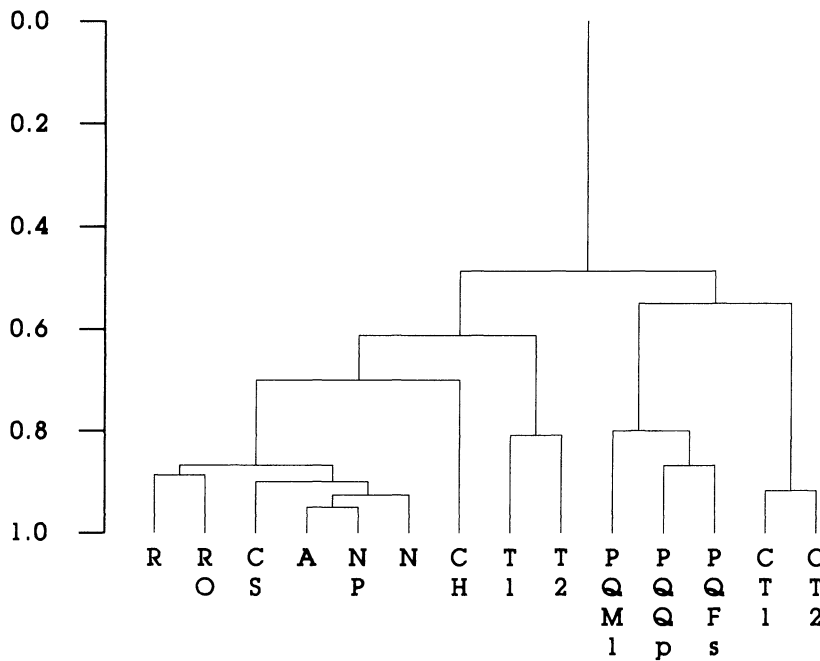

FIG. 3. Dendrogram drawn by means of a cluster analysis of samples obtained with BMDP Software. The similarity measure is the Pearson's Correlation Coefficient between the number of individuals of each species in all pairs of samples. Linkage rule in the clustering procedure, is average similarity. Abbreviations as in Table 1.

nology), a representative sample size for comparisons of fauna from different sample sites.

As shown in Table 4, the Scarabaeoidea dung beetle community is comprised of a similar proportion of Scarabaeidae and Aphodiidae species, while individuals of the Scarabaeidae family are almost six times more abundant in the data. Scarabaeidae is represented by dominant species in all the samples except those in the upper limit of the Supremediterranean phytoclimate, while the Aphodiidae is comprised of numerous but not abundant species (see also Table 3).

With regard to their distribution, 59.6% of the captured species can be considered Euroturanian or Mediterranean; 31.5% of Wide distribution or Eurosiberian and 8.8% endemisms of the Central System. Also worthy of note is the Eurotu-
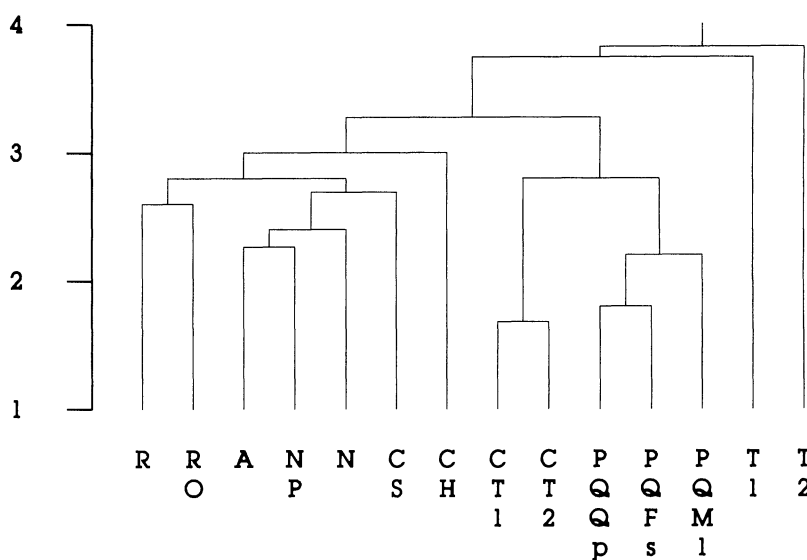
FIG. 4. Dendrogram drawn by means of a cluster analysis of samples obtained with BMDP Software. The similarity measure is the value of the Chi-square test applied to presence/absence data of species. Linkage rule is single linkage. Abbreviations as in Table 1.
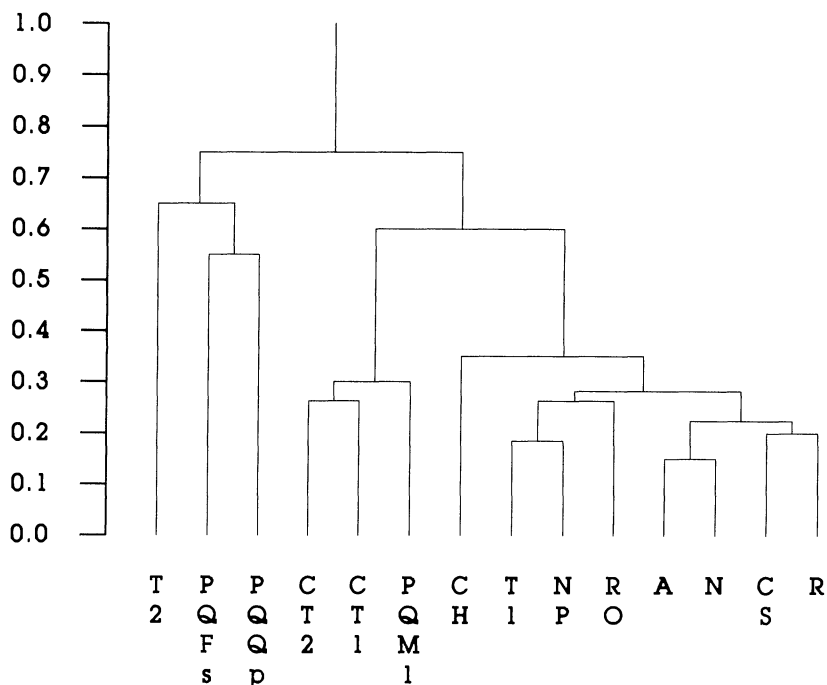

FIG. 5. Dendrogram drawn by means of a cluster analysis of samples. The ressemblance measure is the Bray-Curtis Dissimilarity Index applied to the number of species belonging to each EP in every sample (presence/absence data). The clustering strategy is UPGMA method. Abbreviations as in Table 1.

ranian and Mediterranean distribution of 84% of Scarabaeidae (Table 4), whereas the species of Aphodiidae are more dispersed among the different biogeographical categories.

Regarding vertical distribution, 31.5% of the species were caught within the upper limit of the Supramediterranean phytoclimate, 89% belonging to Aphodiidae and Geotrupidae families.

With respect to phenology, the three families are almost equally distributed between the two variable ranges considered.

Finally, Aphodiidae as well as Scarabaeidae clearly predominate in open or exposed habitats; not so the Geotrupidae species, two of which show preference for thick forestal habitats (see Table 3).

TABLE 3. List of species and samples. Abbreviations as in Table 1.

Species	PQMR	PQQl	PQFp	Cs	S	N	CT1	CT2	RO	A	CH	NP	T1	T2	TOTAL
Fam. SCARABAEIDAE															
1. Bubas bubalus	3					2		1	3	2	4				15
2. Caccobius schreberi	2				18	14		21	36		1	45	16		153
3. Chironitis hungaricus											1				1
4. Copris lunaris	1					4			3	32	5	36	30	3	114
5. Euoniticellus fulvus	203				75	172	1	3	13	42	1	94	130		734
6. Euonthophagus amyntas		1			7					1	2	1	2		14
7. E. gibbosus												1			1
8. Gymnopleurus flagellatus											8	32	2		42
9. Onitis belial											1	1			2
10. Onthophagus coenobita													2	35	37
11. O. fracticornis						1					1		15	4	21
12. O. furcatus					34	156			1	17		55	8		271
13. O. grossepunctatus										1			358	55	414
14. O. illyricus													23		23
15. O. joannae			4												4
16. O. lemur		1	2	2	4								30	6	45
17. O. maki												1	5		6
18. O. punctatus						5				1		3			9
19. O. similis	13	8			93	50	3		214	2	2	19	583	65	1052
20. O. stylocerus		61	2					4	18				5		90
21. O. taurus	3				1	14			4	1			23		46
22. O. vacca	39	2			16	3			58	19	21	6	13		177
23. O. verticicornis													48	99	147
24. Scarabaeus laticollis													1		1
25. Sisyphus schaefferi													423	186	609
No species	7	5	3	1	8	10	3	2	9	10	11	13	19	8	25
No individuals	264	73	8	2	248	421	8	21	316	154	45	298	1717	453	4028
Fam. APHODIIDAE															
26. Aphodius annamariae														1	1
27. A. bonvouloiri		2		1			3	1							7
28. A. carpetanus									1	1					2
29. A. coenosus		1			2			1							4
30. A. depressus				3											3
31. A. erraticus	77	2			5	38		1	137	19		7	25		311
32. A. fimetarius	ʻ5				4				1	2			24	2	38
33. A. foetidus	6				12	2			2	1	1	2	1		27
34. A. fossor	5	2	1												8
35. A. frigidus			1											17	18
36. A. granarius									7						7
37. A. haemorrhoidalis	8				1	4		2	1	1		1	1		19
38. A. ictericus						3						1			4
39. A. immundus						4									4
40. A. lugens	1				1	83			1			24			110
41. A. merdarius							2	2	9						13
42. A. pusillus		1					33	30							64
43. A. quadriguttatus					4	2				2		2	4		14
44. A. satellitius	2														2
45. A. scrofa	6				3	2	4	2	3		1	1			22
46. A. scrutator											5				5
47. A. scybalarius							1					1	1		3
48. A. sphacelatus							1								1
49. A. sticticus														1	1
50. A. striatulus												1			1
51. A. sturmi						5									5
52. A. unicolor						17				3		3			23
53. Pleurophorus caesus				1						1		1			3
No species	8	5	2	3	8	10	6	7	9	8	3	11	6	4	28
No individuals	110	8	2	5	32	160	44	39	162	30	7	44	56	21	720
Fam. GEOTRUPIDAE															
54. Anoplotrupes stercorosus		13	20	8											41
55. Bolbelasmus gallicus														1	1
56. Geotrupes stercorarius								1							1
57. Typocopris pyrenaeus		8	24	2										6	40
No species	-	2	2	2	-	-	-	1	-	-	-	-	-	2	4
No individuals	-	21	44	10	-	-	-	1	-	-	-	-	-	7	83
TOTAL species	15	12	7	6	16	20	9	10	18	18	14	24	25	14	57
TOTAL individuals	374	102	54	17	280	581	52	61	478	184	52	342	1773	481	4831

TABLE 4. Number of species (s) and individuals (n) of the three families considered, and distribution of the former according to the variables which define EP. Abbreviations as in Table 2.

	Number of species	Number of individuals	Geographical distribution					Altitude		Phenology		Habitat	
			W	E	Et	M	En	L	U	S/A	S/S	O	C
Scarabaeidae	25	4028	1	2	14	7	1	23	2	11	14	21	4
Aphodiidae	28	720	8	5	4	8	3	15	13	16	12	22	6
Geotrupidae	4	83	0	2	0	1	1	1	3	2	2	1	3
Total	57	4831	9	9	18	16	5	39	18	29	28	44	13

TABLE 5. Values obtained from the comparison of each pair of sample units (SUs: pitfall traps) in all of samples Specific affinity $= (2\,C/A+B)$ 100; being C. the common species; A and B species number of each SU respectively. Abundance Affinity $= (2\,W/N1+N2)$ 100; W being the sum of the highest abundance values in all the common species, and $N1$ and $N2$ total abundance values of each pair of SU respectively. Pearson's Correlation Coefficient calculated on species's abundance in both SUs and associated probability. Abbreviations as in Table 1.

Samples	R	PQM1	PQQp	PQFs	CS	CT1	CT2	RO	A	CH	NP	T1	T2
Specific affinity	88.9	66.9	83.3	40.0	85.7	50.0	46.1	61.5	61.5	52.6	54.6	81.0	81.8
Abundance affinity	98.1	88.9	96.3	54.5	95.2	75.0	83.6	96.0	92.4	78.8	92.7	99.3	98.3
Pearson's correlation	0.97	0.90	0.93	0.54	0.93	0.41	0.79	0.89	0.86	0.71	0.79	0.95	0.95
Probability	**	**	**	NS	**	NS	*	**	**	*	**	**	**

NS $P>0.05$; * $P<0.01$, ** $P<0.001$.

TABLE 6. Values obtained on the comparison of the SUs taken at Navacerrada reference station, over two consecutive years (1986/87). Statistics as in Table 5 and abbreviations as in Table 1; a/b are the SUs of a same sample.

	Specific affinity	Abundance affinity	Pearson's correlation	
N86a-N86b	70.97	98.18	0.95	(P<0.001)
N86a-N87a	78.79	93.33	0.80	(P<0.001)
N86a-N87b	58.06	92.49	0.70	(P<0.001)
N86b-N87a	82.35	97.07	0.83	(P<0.001)
N86b-N87b	81.25	96.86	0.77	(P<0.001)
N87a-N87b	88.24	98.89	0.96	(P<0.001)

Analysis of sample units (SUs)

The similarity of the pair of pitfall traps (SUs) of each sample was analysed, as well as that of the two pairs of the Navacerrada reference stations of 1986 and 1987, to verify affinities, and in the case of Navacerrada to check the sampling period phenology similarity, and consequently comparability, between both years.

As seen in Table 5, the different SUs of each sample are very similar to one another. The Pearson's correlation coefficients between species abundance are high, positive, and significant except for two samples (PQFs and CT1). SUs share a notable number of species (Specific Affinity) and these common species constitute a high percentage of the total abundance (Abundance Affinity). Only SUs belonging to the samples with a low richness (see Table 3), were remarkably dissimilar. On the other hand, the results of two consecutive years of sampling in Navacerrada are similar

(Table 6), and sample population means were not significantly different either.

To double-check the similarity of each pair of traps, and of the traps of both years in Navacerrada reference station (4 SUs), we performed a cluster analysis of all 30 SUs and found that trap pairs, including those of Navacerrada, had the highest similarity values (Fig. 2).

Thus there is no good reason not to treat each trap pair as one, including those of two randomly selected from Navacerrada.

Analysis of samples

Figures 3 and 4 display the results of a cluster analysis of sample populations.

The high altitude samples from the Eastern and Central Sector (PQMl, PQQp, PQFs and CT2) are notably different from the lower altitude ones.

(i) The individual abundance is almost nine times greater in the lower altitude samples than in the higher ones.

(ii) The species richness of the lower altitude samples is twice that of the higher ones.

(iii) The percentage of endemisms (13%), Eurosiberian elements (35%) and Wide-type distributions (22%) in the above cited high altitude samples is greater than in samples from any other sites. Almost 70% of species and 92% of individuals occurred in the high altitude samples from the Eastern and Central Sector, belong to these distributional ranges (Table 7).

Lower altitude, N and S slope samples are clustered, along with high altitude Western Sector (CH) sample to a certain extent. Percentages of Euroturanian and Mediterra-

TABLE 7. Captures made in the upper levels of the Supramediterranean phytoclimate from the Eastern and Central Sectors: Number of individuals (N), and species (S) of the three families of Scarabaeoidea dung beetles (Scarabaeidae, Aphodiidae and Geotrupidae) in each geographic range.

Family		Wide distribution	Eurosiberian	Euroturanian	Mediterranean	Endemic	Total (%)	
Scarabaeidae	N	0	15	12	0	85	112	(39.2)
	S	0	2	4	0	1	7	(30.4)
Aphodiidae	N	74	7	9	1	7	98	(34.3)
	S	5	4	2	1	1	13	(56.5)
Geotrupidae	N	0	42	0	0	34	76	(26.5)
	S	0	2	0	0	1	3	(13.1)
Total N (%)		74 (25.9)	64 (22.4)	21 (7.3)	1 (0.4)	126 (44.0)	286	
Total S (%)		5 (21.7)	8 (34.8)	6 (26.1)	1 (4.4)	3 (13.0)	23	

TABLE 8. Captures made in the lower levels of the Supramediterranean phytoclimate including the high altitude sample of Western Sector (Cruz del Hierro). Number of individuals (N), and species (S) of the three families of Scarabaeoidea dung beetles (Scarabaeidae, Aphodiidae and Geotrupidae) in each geographic range.

Family		Wide distribution	Eurosiberian	Euroturanian	Mediterranean	Endemic	Total (%)	
Scarabaeidae	N	609	1041	1813	448	5	3916	(86.2)
	S	1	1	14	7	1	24	(48.0)
Aphodiidae	N	82	5	439	93	3	622	(13.6)
	S	7	3	4	8	2	24	(48.0)
Geotrupidae	N	0	0	0	1	6	7	(0.2)
	S	0	0	0	1	1	2	(4.0)
Total N (%)		691 (15.2)	1046 (23.0)	2252 (49.6)	542 (11.9)	14 (0.3)	4545	
Total S (%)		8 (16.0)	4 (8.0)	18 (36.0)	16 (32.0)	4 (8.0)	50	

nean range species (36% and 32% respectively) are higher in the lower altitude samples than in those from high altitude samples (26.1% and 4.4%; see Tables 7 and 8).

Samples taken at the westernmost station (T1 and T2) are marginally clustered to other samples (Fig. 4), mainly due to the exclusive presence of five species in T1 (20% of total) and six in T2 (43%), and the remarkable abundance of the others (see Table 3).

Cluster-EP analysis of samples yields the results shown in Fig. 5, where the following are found.

(i) Highest altitude Central and Eastern sector samples are clustered, with the exception of Eastern sector (PQQp and PQFs) forest habitat stations,

(ii) All low altitude (except the El Tiemblo forest habitat sample: T2) and the highest altitude Western sector (CH) sample are clustered,

(iii) High degree of association of open biome samples. Cluster analysis of sample populations grouped both closed and open biome samples by geographic proximity and altitude (see Figs 3 and 4); furthermore, species from closed habitats differed markedly one from the other. However, EP analysis distinguished three of the four closed biome samples

(PQQp, PQFs, and T2) from those of open biomes, because of the higher degree of association of all open habitat samples.

DISCUSSION

Northern and southern EMICS slope fauna are very similar, so sample population differences are attributable to ecological factors as well as to the presence of accessory species and to minor fluctuations in the abundance of common species.

Fauna are very similar on both N and S slopes perhaps because of the following.

(1) Flying power of these beetles (Hanski, 1980 a, b).

(2) Dispersion effects of 'corridors', such as the upper valley of the Alberche River.

(3) Reduced geographic extension of mountain range (major axis: 130 km.) relative to distributional range of most of its colonizing species;

(4) Age of mountains. Beginning in the Tertiary, alpine orogenic processes formed the EMICS, part of the 'Escudo Hespérico', after the disappearance of the mesozoic seas.

Taxonomic composition of sample population as well as EP are slope independent. The community model for the

lower Supramediterranean pastures is very similar on both slopes, (which lack ligneous plants) consisting of an average of 300–500 individuals of fifteen to twenty species per sample. The most abundant species belong to the Scarabaeidae family which include about 86% of individuals. Aphodiidae is represented by the same number of species, but of lowest abundance (Table 8). The Euroturanian and Mediterranean ranges together account for 61.5% of individuals and 68% of species. Of these, 81% of individuals and 62% of species belong to the family Scarabaeidae.

There is a moderate increase of Mediterranean range species from NE to SW, higher in the southern slope (Eastern Sector/Central Sector/Western Sector: 2/6/9) than in the northern (2/5/5), probably influenced by the NE–SW orientation of these mountains. The sample population of the highest station of the Western Sector (CH) (vegetative cover entirely lacking) clustered to the lower altitude stations in all the dendrogrammes, probably due to the similarity of their environments. The El Tiemblo station sample population has the greatest species richness; EP are similar to those which predominate on both slopes. We think that this richness in fauna is due to its unusual climate (higher rainfall). El Tiemblo samples are also clustered to the other lower altitude samples of both slopes.

With respect to vegetative cover, there is little correlation of sample fauna with biome type (Figs 3 and 4).

In the Eastern sector (PQQp, PQFs) and the upper valley of the Alberche (T2), both with forest vegetative cover, the richness is approximately half and abundance almost four time less than in those of the open biome samples (Table 3). The richness and abundance of the Central sector stations CT1 and CT2 are as low as those of PQQp, PQFs and T2, probably due to the greater sample population homogeneity, in spite of differing plant cover.

These small differences suggest that the nature of vegetation (forest or herbaceous) seems to act as an ecological selective species filter. For example, it seems clear that *E. fulvus* (Goeze, 1777); *O. grossepunctatus*; *A. erraticus* (L. 1758) and *O. stylocerus* Gräells, 1851 have a marked preference for herbaceous biomes whereas *O. verticicornis, O. coenobita, A. frigidus, A. stercorosus* (Scriba, 1796) and *T. pyrenaeus* (m. *coruscans* Chevrolat, 1840) are not very frequent or abundant outside the forest. These findings agree with the view of Lumaret & Kirk (1987), Lumaret (1980) and Baz (1988), that vegetation directly influences the distribution and richness of coprophagous scarabeid communities. However, the findings contradict Doube's (1983) conclusions that fauna differences are most influenced by forestal and open habitat light-intensity differences.

With respect to vertical distribution, a change in altitude of 400–500 m. within the same phytoclimatic zone is accompanied by a greater difference in; abundance, richness, characteristic species, systematic composition and EP than that which accompanies a N–S slope change. Richer and more abundant Aphodiidae and Geotrupidae families, and a larger proportion of elements belonging to Eurosiberian endemic and widespread ranges are found. However, as Tables 7 and 8 show, species and individual numbers decrease drastically in the highest altitudes, above all in Mediterranean and, to a lesser extent, in Euroturanian species, while almost 70% of

species and more than 92% of individuals are of endemic, eurosiberian or wider ranges. As for taxonomic groups, more than 60% of individuals and almost 70% of species at higher altitudes belong to Aphodiidae and Geotrupidae. 44% of sample individuals belong to the three species endemic to these altitudes: *A. bonvouloiri, O. stylocerus,* and *T. pyrenaeus.*

The percentage of endemic species (8.8% of the total sampling) is similar to that of Staphylinidae of Guadarrama (Outerelo, 1979). It falls between the estimated 29% for the relatively poor flyers, Acridoidea (Presa, 1977) and the 2.7% for the strong flyers of Apoidea (Pérez-Iñigo, 1980).

The differences in diversity, richness and abundance among communities of different altitude levels can be attributed to environmental factors. Such a difference correlates with different taxonomic composition and EP, i.e. Aphodiidae and Geotrupidae in the highest zones, Scarabaeidae in the lower levels; Eurosiberian, Endemic and Widespread elements in the upper levels, Mediterranean and Euroturanian elements in the lower altitude areas.

This altitudinal segregation also occurs in the Caucasus (Dzhambazishvilli, 1973) and the Mexican Transition Zone (Halffter & Matthews, 1966; Halffter 1976). A corresponding latitudinal segregation can also be seen in southern latitudes, where Aphodiidae and Geotrupidae are replaced by Scarabaeidae; see, for example, the studies on communities of Northern Europe (Hanski, 1980c, 1986), Central Europe (Desiere, 1983) and Southern Europe (Lumaret, 1979, 1980; Carpaneto, 1985; Lobo, 1982) and those on Asia (Hanski, 1983) and tropical Africa (Cambefort, 1982; Walter, 1978).

There is also paleontologic evidence indicating a predominance of Aphodiidae (Aphodiinae) during the temperate interlude in the middle of the last glaciation and interglacial Scarabaeidae predominance (Coope & Angus, 1975; Coope, 1974, 1979). On a seasonal scale, Aphodiidae and Geotrupidae predominate in autumn and winter and Scarabaeidae in summer in Central Spain (Lobo, 1982).

These facts seem to indicate both an ecological and a historic dimension to the climatic requirements of the three groups. Therefore, we argue that eco-physiologic adaptations of high-rank taxa reflect long-period macroclimatic conditions occurring in their primitive (hypothetic or not) geographical areas of origin and/or dispersion. This idea agrees with the assumption of Atkinson, Briffa & Coope (1978) that the present climate tolerance range of species, enable us to deduce the paleoclimate.

For example, a late Cretaceous origin in herbaceous biomes has been proposed for Scarabaeidae (Halffter & Matthews, 1966), as well as an Afro-tropical origin for a several genera: *Onthophagus, Copris, Oniticellus, Liatongus, Drepanocerus* and *Sisyphus* (Halffter, 1976). The maximum taxonomic diversity of others, such as *Scarabaeus, Gynmopleurus* and *Onitis* occurs in Africa. As Halffter & Matthews (1966) indicate, all these genera are associated with widely differing ecologies, although they are found mainly in hot and hot-temperate climates. Except for very special cases of colonization in the highest altitudes of tropical mountains, they cannot be considered to be typical elements of cold climates (Halffter, 1976).

On the other hand, paleontologic evidences and phylogenetic inferences suggest an Asiatic-oriental dispersion centre for the Geotrupinae (Geotrupidae) subfamily, present in the early Cretaceous of the Gobi Desert, the Tian-Shan, Tibet and Central China (Zunino, 1984). There is no similar evidence for Aphodiidae, but the subfamily Aphodiinae (the only one involved in this study) is at least an essentially holarctic group (most taxonomically diverse in the Palearctic and Nearctic regions at present). There seems to be a correlation of macroclimatic adaptations with biogeographic history, as Lobo (1985) noted in a study of the present structure of the coprophagous communities in the Iberian Peninsula. This sort of relation for a specific group would support the definition of Dispersal Patterns (Halffter, 1976) for Iberian fauna of Scarabaeoidea.

Although the EMICS have not been a topographic barrier to the dispersal of the coprophagous Scarabaeoidea, it is the southern distribution limit for a few rare, non-abundant species. All are either endemic (*C. martinezi* not represented in our sample populations, *A. bonvouloiri*, *O. stylocerus*) or european (*O. joannae*, *A. stercorosus*, *T. pyrenaeus*), or of wider ranges (*O. semicornis*, not in our sample populations either but recently found by Baz (1986) and by us).

The species in our sample population are mainly orophilous. Has the barrier effect of the highest biomes of the EMICS been great enough to favour speciation? There is no evidence of morphologic evolution over the last half a million years but there is a great variation in the geographic range of species (Coope, 1979). This is particularly true for one of the two endemic species of the Sierra (*A. bonvouloiri*) which colonized Great Britain 43,000 years ago (Coope, 1975), and today is an orophilous endemic confined to the Iberian mountains, its area of refuge, not its centre of origin.

As for *O. stylocerus*, there is no fossil record, but it belongs to one of the most recent Onthophagini Iberian lines of turanian origin (subgenus *Palaeonthophagus* of the *vacca* group; see Martin-Piera, 1983, 1985). An early allopatric evolution from some orophilous Iberian *Palaeonthophagus* population is suggested by phylogenetic inferences based on the apomorphic characters of the male genitalia. However, present geographic restriction of a taxon is not evidence *per se* of an origin centre (Coope, 1970, 1979) as is demonstrated by Quaternary fossils of *A. bonvouloiri*. See also Halffter (1987) regarding flora and fauna of Mexican Transition Zone.

There is no paleontological evidence for *O. joannae*; however biogeographic and phylogenetic data suggest that (i) it belongs to the earlier (Middle-Upper Oligocene/Upper Miocene) cladogenetic event of the subgenus *Palaeonthophagus* and (ii) the internal cladogenesis undergone by the *O. joannae* phyletic line, should be related to the Quaternary climatic fluctuations (Martín-Piera & Zunino, 1986).

The case of the two orophilous Geotrupidae species is different. The phylogenetic and biogeographical data suggest that *Anoplotrupes* is a relict from the Tertiary (Zunino, 1984), which fits in an Euroamerican distribution pattern (Noonan, 1988). The presence of *A. stercorosus* in the Iberian mountains is restricted to ombrophilous environments similar to those of an essentially Eurosiberian geographical range. There is no palaeogeographic evidence of possible variations in its distribution area.

According to Zunino (1984), the origin of the *Trypocopris* is more recent; its differentiation dates from no later than the Pleistocene. The Iberian species *T. pyrenaeus* is linked with the same forestal habitats as *A. stercorosus*. However, unlike the latter, evidence of morphologic evolution exists. As stated in the literature, and seen in all specimens of our sample population, *T. pyrenaeus* in the whole Iberian Central System display a phenotype characterized by integument colouring (*coruscans* aberration Chevrolat), which would justify considering it a subspecies, according to Baraud (1977).

Minor morphological evolution in some populations of *A. bonvouloiri* has resulted in Pittino (1981) according them subspecific rank as *A. bonvouloiri cantabricus*. This subspecies colonizes the Cantabric Cordillera, lending support to the hypothesized morphologic evolution of endemic populations (whatever their formal taxonomic rank) having occurred in the highest biomes of the EMICS.

However, Coope (1979) suggests that local morphological variations are not necessarily a result of reproductive isolation, but an attribute of polymorphic species (as *T. pyrenaeus* is), which enable them to enlarge their geographic range and better adapt themselves to changing environments, such as those of the recent Quaternary.

In summary, scant paleontologic and phylogenetic evidence indicate that unique fauna have colonized the highest biomes of the EMICS. Published data can be used to investigate the geographic distribution of some orophilous species. But in the case of the other species mentioned in this paper there is no published data. For this reason, we have proposed the Ecogeographical Pattern (EP) method, to weight the historical and ecological causes of distributions based on the assumption that species at present sharing a geographic range, with common adaptations, have to some extent a common evolutionary history. This assumption takes precedent from the idea of Williams (1964 in Hutchinson, 1979) which is: 'organisms which share a common ancestor have a high probability of inheriting a common way of life'. Also it is implicit in the Mutual Climatic Range method (Atkinson *et al.*, 1987), in Erwin's Theory (1985) of Taxon Pulses, and in Dispersal Pattern and Coenochron concepts (Reig, 1962; Halffter, 1962, 1987).

The verification of the results of EP analysis by paleonotologic and phylogenetic evidence (for the orophilous species discussed above) supports the use of EP, and validates the assumption made in their application. We suggest that further verification might be possible through the definition of EP for taxonomic groups (e.g. mammals and birds) whose structural and non-structural (ecological, behavioural, etc.) adaptations, phylogenies and fossil records are best known.

Since our assumption seems valid from an evolutionary viewpoint, the use of EP may be considered useful for biogeographic analysis, in the evaluation of the role of historic and/ or ecologic factors in determining distribution variations, in cases where fossil records and phylogenetic data are lacking.

CONCLUSIONS

Analysis of present data enable us to draw the following conclusions.

(1) Northern and southern EMICS (Eastern Mountains of the Iberian Central Sistem) slope fauna are very similar. Therefore, with very few exceptions (*O. joannae, O. stylocerus, T. pyrenaeus, A. stercorosus,* and *A. bonvouloiri*) the EMICS has not been an insurmountable ecological barrier to dispersal. Minor regional differences should be explained in terms of ecological factors, i.e. in a reduced and short space-time scale. In all samples the Euroturanian and Mediterranean-ranges species and those which belong to the Scarabaeidae family predominated.

(2) Abundance, richness, characteristic species, systematic composition and Eco-geographical Patterns varied most with altitude. Endemic, Eurosiberian or wider distributional-range species, and those which belong to the Aphodiidae and Geotrupidae families, colonize the higher biomes, a consequence of a climatic discontinuity which presents dispersal toward lower altitudes.

(3) The explanation of the causes of the present vertical distribution of Scarabaeoidea dung beetles in the EMICS is not possible without taking into account the historical events there, therefore, large space-time scale modifications of the geographic distribution of species inhabiting it.

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