Composition and Structure of Dung Beetle (Coleoptera: Aphodiidae, Geotrupidae, Scarabaeidae) Assemblages in Mountain Grasslands of the Southern Alps

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ABSTRACT This study attempts to estimate the influence of local environmental conditions on dung beetle assemblages in a bioclimatic transition area. Dung beetle assemblages were monitored by monthly dung-baited pitfall trapping from July to October at five sites in the Southern Alps (Verdon Valley). The sites were characterized by both elevation ($\approx$1,000, 1,500, and 2,000 m a.s.l., respectively) and exposure (north/south). Exposure had a noteworthy influence. In summer, Coprinae showed by far the highest numbers and biomass in the sites facing south regardless of elevation. In the north-facing sites, Aphodiinae dominated the assemblages. In autumn, the abundance of Coprinae decreased and, in turn, Aphodiinae became dominant in most assemblages. Species composition changed with assemblage structure and dynamics. When Coprinae were numerous, few species were predominant in the assemblages and diversity was negatively related with elevation. In the Southern Alps, the alternate predominance observed between Coprinae and Aphodiinae species, which develop at distinct elevation ranges, is analogous to the supramediterranean vegetation range, which characterizes Mediterranean mountains.

KEY WORDS Scarabaeoidea, Aphodiinae, Coprinae, European mountain, bioclimatic transition

DUNG BEETLES (SCARABAEOIDEA) belong to three distinct taxonomic groups: Scarabaeidae (Scarabaeinae and Coprinae), Geotrupinae, and Aphodiinae (Baraud 1992). The first group is well adapted to warm conditions, whereas the other two groups are predominantly adapted to cold, temperate conditions (Hanski and Cambefort 1991). This main difference, which is caused by distinct evolutionary histories, brings about a segregation of the fauna in Europe. Scarabaeidae are largely restricted to the southern Mediterranean part of Europe, whereas Geotrupinae and Aphodiinae are well distributed all over the continent (Hanski 1986, 1991, Lumaret and Kirk 1991, Lobo et al. 2002). A conspicuous altitudinal substitution between Scarabaeidae and Aphodiinae occurs in the mountain ranges of Central Europe (Jay-Robert et al. 1997). This altitudinal pattern is observed in the Northern and Southern French Alps as well, although the exposure and climates of the northern and southern slopes are very different (Ozenda 1985). The Northwestern Alps are included in a broadly temperate region, whereas the Southwestern Alps constitute a part of the northern boundary of the Mediterranean region. In the Southern Alps, the transition between the Mediterranean lowland and high altitude ($\approx$3,000 m a.s.l.) generates a range of habitats, which form a complex landscape. Jay-Robert et al. (1997) showed that the dung beetle fauna was roughly similar throughout the Alps, but that local distribution of dung beetles in such a mosaic has never been analyzed. Several studies carried out in European mountain areas showed that dung beetle distribution was controlled by elevation (Lumaret and Stiernet 1991, Martín-Piera et al. 1992, Menéndez and Gutiérrez 1996). In the Southern Alps, thermal contrasts between slopes are equivalent to a 400-m change in elevation (0.5°C decrease every 100 m in elevation). However, exposure was never considered as a significant factor when it did not correspond to a change in vegetation structure (forest versus pasture). The aim of our work is to study the distribution of the dung beetle fauna and the dynamics of assemblages in open pastures along an altitudinal gradient in the Southwestern Alps to determine whether exposure may change the composition, the structure, and the functioning of the species assemblages on a regional scale (a few kilometers).

Materials and Methods

Sampling sites

Dung beetle pitfall trapping was conducted from July to October 1995 in the Verdon Valley, Southern

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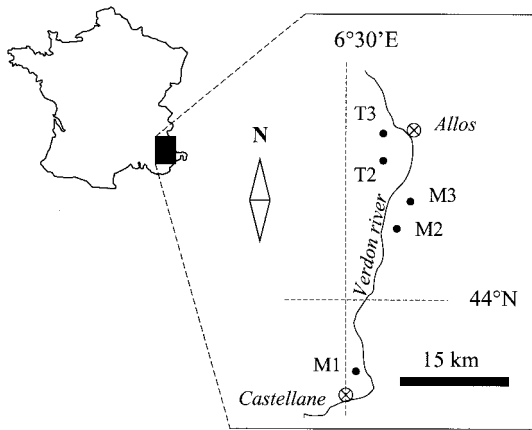
Fig. 1. Location of sampled sites.

Alps. This valley is open to the opposing influences of Mediterranean and meso-European climates. From the analysis of the vegetation composition, it has been shown that the Mediterranean climate has a significant effect on south-facing slopes, regardless of elevation, whereas the biotopes facing north are influenced by meso-European climatic conditions (Barbero et al. 1977, Archiloque et al. 1980, Barbero et al. 1990). Above 1,000 m a.s.l., human activity is restricted to pastoralism and has little impact on the composition of grasslands.

Five sites were sampled in distinct environmental conditions, which combined climatic influence and elevation. The three sites open to Mediterranean influences (facing south) were designated by [M], whereas the two meso-European sites (facing north) were designated by [T] (=temperate) (Fig. 1). Locally, the climatic influence (Mediterranean versus meso-European) was deduced from vegetation composition (Barbero et al. 1977, Archiloque et al. 1980, Barbero et al. 1990). Three elevation levels were distinguished, namely lower [1], medium [2], and high [3] montane sites corresponding approximately to 1,000, 1,500, and 2,000 m a.s.l., respectively. Site M[1] (1,060 m) was a *Bromus erectus* grassland in the supra-Mediterranean collinear level. Site M[2] (1,520 m) consisted of an *Astragalus sempervirens* and *Eryngium spina-alba* grassland in the upper montane level, and site M[3] (2,020 m) was a *Anthoxanthum odoratum* and *Deschampsia flexuosa* grassland in the subalpine level.

In the valley, at low elevation, the influence of the meso-European climate is very weak (Barbero et al. 1977, Archiloque et al. 1980, Barbero et al. 1990), so that no grazed area constituting putatively site T[1] could be sampled. Site T[2] (1,670 m) was a *Trisetum flavescens* grassland in the lower alpine level, and site T[3] (1,920 m) corresponded to a *Festuca paniculata* grassland in the upper alpine level.

The most distant sites, M[1] and T[3], were 45 km apart. All the five sites were situated on deep brown soils on limestone. The pastures had been regularly grazed rotationally by sheep for more than 10 yr before the beginning of our study. M[1] was grazed by a 600-head permanent flock, principally in December–January and in May–June. M[2] was grazed from June to September by a 400-head permanent flock, and all the others by migratory flocks. M[3] was grazed mainly in September and October by a 1,700-head flock. T[2] was grazed from June to August and in October by a 3,850-head flock. T[3] was grazed from July to October by a 1,200-head flock. All of these five sites were close to the Mercantour National Park, and consequently, throughout the year, the pastures were also grazed by wild fauna, including deer, chamois, and wild sheep.

At each site, pitfall traps were put in open pastures, and they remained in a fixed position throughout the sampling period. Because of climatic conditions (snow in upper sites from November to June), sampling was restricted to the July–October period, which corresponds to 20 dung beetle assemblages in total (5 sites × 4 mo).

Trapping methods

The pitfall design corresponded to the Cebo-Suspendido-Rejilla (CSR) model described in Lobo et al. (1988) and Veiga et al. (1989). Each trap consisted of a plastic basin 210 mm in diameter, buried to its rim in the soil, containing a water-formalin-liquid soap mixture. Fresh cow dung (1 liter) was supported on a wire grid at the top of a bucket. At all sites, a set of traps was used, consisting of four replicate traps per site, each replicate being at each corner of a 10-m square. At both regional and local scales, Lobo et al. (1998) demonstrated that the use of only four pitfall traps sampled most species present at a site (between 60 and 70% species, which corresponded to a 89 and 93% abundance range, respectively). The trap contents were collected 1 wk later, and fresh dung baits were deposited 3 wk later for a further sampling event.

Data analysis

All trapped beetles were identified to species level and counted. To compare assemblages and constituent species, the variation among sites and months was described by parameters that include species richness, monthly changes in assemblage numbers and biomass, composition and diversity, and analyses of assemblage variability.

Biomass estimations are based on species dry weights (Lumaret and Kirk 1987; Lumaret and Stiernet 1994; Lumaret, unpublished data; Lobo 1992). Weather and availability of additional dung can affect the number of species and individuals (Lobo et al. 1998). Regional species richness is a product of the stand-level species richness (α-diversity), and the variation in species composition (β-diversity) among individual stands. We studied α-diversity by calculating the D_M Margalef index (Magurran 1988), as this balances the richness by the beetle numbers. $D_M = (S - 1)/\ln N$, where S is the number of species, N the

number of trapped individuals. The β-diversity index of Whittaker (βw) expresses the faunistical change either between site assemblages (regional space scale) or, over time, between monthly assemblages at the same site (temporal scale) (Whittaker 1960). $\beta w = (S/\alpha) - 1$, where S is the total number of species in assemblages and α the average number of species observed in each assemblage. βw varies between 0 (identical specific composition) and 1.

The numbers of all individuals were $\ln(x + 1)$ transformed and used in correspondence analysis (CA) to explore the compositional variation in the assemblages to find possible differences among sites and months. Rank-abundance diagrams were drawn, plotting the log-transformed abundance of beetles (expressed in biomass) against rank. Monthly species assemblages were fitted to the log-linear Motomura's model (Motomura 1932): $\log(N) = a * R + b$, where N is the biomass of beetles collected for a species and R is the rank of the species. The adjustment of abundance distribution to the model is made by plotting beetle biomass (log-transformed data) against species rank. The antilogarithm m of the regression slope ranges between 0 and 1. The higher the slope (absolute value), the more the assemblage is organized with few predominant species, which appropriate most of the trophic resource (Daget 1976, Lumaret and Stiernet 1992, Stiernet and Lumaret 1993, Lumaret and Iborra 1996, Galante and Cartagena 1999). The m value corresponds to Motomura's environmental constant (Iganaki 1967). The adjustment to the model was tested using the Kolmogorov-Smirnov test (Tokeshi 1993). When the variance of the residues was the same in the five site assemblages for every month (Bartlett test; see Scherrer 1984), the homogeneity of the slope values was tested by using a covariance analysis (Scherrer 1984).

The analyses were performed with Statgraphics Plus 2 (Manugistic, Rockville, MD) and Stat-Itcf 2.0 (Institut Technique des Céréales et des Fourrages, Paris, France) statistical package software.

Results

Efficiency of the pitfall trapping method is shown by the species accumulation curves plotted in Fig. 2. On average, one trap collected 74.5% of the total number of species observed in a site, whereas two and three traps resulted in 86.7 and 94.1% species, respectively.

Species composition

The pooled sample included 20,910 beetle individuals belonging to 48 species. Species belonged to Geotrupinae (6 species), Aphodiinae (29 species), Scarabaeinae (1 species), and Coprinae (12 species) (Table 1). The total species richness in each dung beetle subfamily was not significantly different between the five sites ($\chi^2 = 8.6$, df = 12, $P = 0.74$) (Table
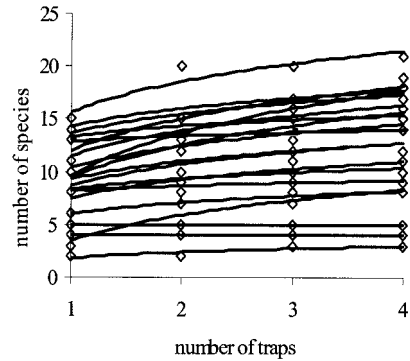

Fig. 2. Cumulative number of species trapped according to the number of pitfall traps used in the 20 samples (i.e., monthly dung beetle assemblages). For each sample, the four traps are randomly located. Logarithmic adjustment of data.

2), and the sites did not differ with regard to species chorology ($\chi^2 = 17.29$, df = 20, $P = 0.63$) (Table 2).

Conversely, highly significant differences were observed among subfamilies when monthly abundance in assemblages was compared (July, $\chi^2 = 3284.57$, df = 12; August, $\chi^2 = 3230.73$, df = 12; September, $\chi^2 = 910.49$, df = 12; October, $\chi^2 = 810.95$, df = 8; all $P < 0.001$). During the July and August periods, Coprinae (mostly *Onthophagus* spp.) were predominant in most Mediterranean sites (in five assemblages of six; 71.5–95.2% of total individuals), while Aphodiinae (*Aphodius* spp.) predominated both in temperate sites (65.3–98.2% of total individuals) and in the M[2]-August assemblage (59.3%). During the September–October period, Coprinae decreased and, in turn, Aphodiinae became predominant in most assemblages: Coprinae only predominated in September in sites M[1] and M[2], with 91.1 and 50.9% of total individuals, respectively, and in October in site M[2] (65.4%). Elsewhere, Aphodiinae predominated in the assemblages (67.7–97.7% of total individuals).

The CA showed the combined influence of space and time and identified exposure as a greater influence than elevation in the studied area. In the CA, the main gradient in the ordination, running approximately from right to left, clearly discriminated Mediterranean sites (successively M[1], M[2], M[3]) from temperate sites (T[2], T[3]) (Fig. 3A). Site differences diminished from the positive (M[1]) to the negative (T[3]) pole of axis 1, which explained 41.6% of the total variation. The second gradient, running approximately from top to bottom, opposed summer and autumnal assemblages in each site, and axis 2 could be considered as a temporal axis. This single variable explained 17.3% of the total variation in the species data. The seasonal differences regularly decreased according to increasing elevation. This gradient in the ordination, running from top to bottom (axis 2), highlighted species active in summer against species active in autumn (positive and negative coordinates, respectively) (Fig. 3B). Summer species were distributed exclusively along axis 1. Except *Onthophagus baraudi*

Table 1. Monthly variation of dung beetle assemblages

Species	Abbr.	Site M[1]				Site M[2]				Site M[3]				Site T[2]				Site T[3]			
		VII	VIII	IX	X	VII	VIII	IX	X	VII	VIII	IX	X	VII	VIII	IX	X	VII	VIII	IX	X
Geotrupinae																					
Anoplotrupes stercorosus (Scriba)	Ans														1			50		6	
Geotrupes spiniger (Marsh.)	Gsp			3	2			1													
Geotrupes stercorarius (L.)	Gst										2				4	2	3	7		1	1
Sericotrupes niger (Marsham)	Sen	5	2		1																
Trypocopris alpinus (Sturm & Hagenbach)	Tra																	4		4	
Trypocopris vernalis (L.)	Trv	2	1	4		28	9	3	2	7					21	2		6			
Aphodiinae																					
Aphodius alpinus (Scopoli)	Aal														14		1	130	2	61	4
Aphodius biguttatus Germar	Abi	1																			
Aphodius borealis Gyllenhal	Abo													1							
Aphodius consputus Creutzer	Acs				22				1												
Aphodius contaminatus (Herbst)	Acn			1	747			4	362			1	3			1					1
Aphodius corvinus Erichson	Acr											5			24		3			17	
Aphodius elevatus (Olivier)	Ael		4	5																	
Aphodius erraticus (L.)	Aer	162	21	4		79	260	3	8	17	49			86	436	5		1	25	18	
Aphodius fimetarius (L.)	Afi	3	1	8	124	1	5	37	331	18	20			9	234	365	33	80		31	13
Aphodius foetidus (Herbst)	Afe				2																
Aphodius fossor (L.)	Afo					2				1											
Aphodius granarius (L.)	Agr		1								1										
Aphodius haemorrhoidalis (L.)	Aha	3	67	2		1	12			2	1				1			1			
Aphodius immaturus Mulsant	Aim														1	2					
Aphodius obscurus (Fabricius)	Aob	4		1		44	154	2	1	105	53			15	331	17	2	105	111	37	2
Aphodius paracoenosus Balthasar & Hrubant	Apa	9																			
Aphodius porcus (Fabricius)	Apo								1												
Aphodius prodromus (Brahm)	Apr			1																	
Aphodius pusillus (Herbst)	Apu	11				19	6			4					16					1	
Aphodius quadrimaculatus (L.)	Aqu					1															
Aphodius rufipes (L.)	Aru															23	2	55	6	5	
Aphodius satyrus Reitter	Asa									3	27				1			262	2	64	2
Aphodius scrutator (Herbst)	Asr			1			3				2								1		
Aphodius scybalarius (Fabricius)	Asc			2			3	3			3				124	11	3	1	13	83	23
Aphodius suarius Faldeman	Asu				1																
Aphodius thermicola Sturm	Ath				98				43												
Aphodius uliginosus (Hardy)	Aul								9	2	14	692	120			47	83			139	8
Aphodius zenkeri Germar	Aze		1	2																	
Euheptaulacus carinatus (Germar)	Eca					1	1				8										
Scarabaeinae																					
Sisyphus schaefferi (L.)	Ssc	11	1	17		1															
Coprinae																					
Euoniticellus fulvus (Goeze)	Efu	10	9			1	3								1						
Euonthophagus gibbosus (Scriba)	Egi	2	1				3	1			1										
Onthophagus baraudi Nicolas	Oba					255	7	1		738	273	1		2	77			61			
Onthophagus emarginatus Mulsant	Oem	38	148	54	11																
Onthophagus fracticornis (Preyssler)	Ofr	3	9	37	263	41	227	49	1,429	1,884	1,294	311	15	6	207	111		210	3	217	3
Onthophagus grossepunctatus Reitter	Ogr	41	13	6																	
Onthophagus illyricus (Scopoli)	Oil	2	2			2	2														
Onthophagus joannae Goljan	Ojo	2,509	1,650	368	52	93	53	4	2	1	1										
Onthophagus lemur (Fabricius)	Ole	91		2		2				16	4				1						
Onthophagus ovatus (L.)	Oov	299	118	37	4																
Onthophagus vacca (L.)	Ova.	1	4	6	1		1														
Onthophagus verticicornis (Laicharting)	Ove	173	2			51				11	1										
Total species		21	19	19	14	17	16	11	12	14	18	4	3	5	18	10	8	15	8	14	9
Total beetles		3,380	2,055	560	1,329	622	749	108	2,190	2,809	1,759	1,005	138	118	1,494	586	129	974	164	684	57
Total Geotrupinae		7	3	7	3	28	9	4	2	7	2	0	0	0	26	4	3	67	0	11	1
Total Aphodiinae		193	95	26	995	148	444	49	756	152	183	693	123	110	1,182	471	126	636	161	456	53
Total Scarabaeinae		11	1	17	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total Coprinae		3,169	1,956	510	331	445	296	55	1,432	2,650	1,574	312	15	8	286	111	0	271	3	217	3

M and T: Mediterranean and meso-European (temperate) climatic influence in sites, respectively.
[1], [2], [3]: lower, medium, and higher montane sites, respectively.

Nicolas (Oba) and *O. fracticornis* (Preyssler) (Ofr), all the species belonging to Scarabaeinae and Coprinae showed positive coordinates along axis 1, whereas Aphodiinae and Geotrupinae species were evenly distributed along axis 1.

Diversity

α-Diversity (Margalef index, D_M) varied significantly between sites exclusively in July and in September (Table 3). Pairwise comparisons showed sig-

Table 2. Species diversity in subfamilies according to sites and chorotype distributions of species in sites

Sites elevation (m)	M[1] 1,060	M[2] 1,520	M[3] 2,020	T[2] 1,670	T[3] 1,920
Geotrupinae	3	2	2	3	4
Aphodiinae	18	15	14	14	14
Scarabaeinae	1	1	0	0	0
Coprinae	11	9	6	4	2
Palearctic	7	9	7	7	6
Eurosiberian	6	5	4	3	3
Euroturanian	7	4	2	1	1
European	9	7	6	6	6
Mediterranean	4	1	1	1	0
Alpine	0	1	2	3	4

M and T: Mediterranean and meso-European (temperate) climatic influence in sites, respectively.

[1], [2], [3]; lower, medium, and higher montane sites, respectively.

nificant differences between M[2]-M[3], T[2]-T[3], M[2]-T[2], M[3]-T[3] in July, and between M[2]-M[3], T[2]-T[3], M[3]-T[3] in September (Mann-Whitney tests: $U = 16$, $P = 0.015$). In the Mediterranean sites, diversity decreased with increasing elevation. Conversely, α-diversity increased in the temperate sites with elevation. In both July and Sep-

Axis 2 (17.3 %)

Axis 1 (41.6%)

Axis 2 (17.3 %)

Axis 1 (41.6 %)

Fig. 3. (A) CA ordination of dung beetle assemblages. (B) CA ordination of dung beetle species (see Table 1 for abbreviations).

tember, α-diversity was significantly higher in T[3] than in M[3] (Mann-Whitney test: $U = 16$, $P = 0.015$).

α-Diversity varied significantly between months in sites M[3], T[2], and T[3] (Table 3). For M[3], pairwise comparisons showed that diversity decreased between August and September. For T[2], diversity increased between July and August and, for T[3], it decreased between July and August, but increased in September (Mann-Whitney test: $U = 16$, $P = 0.015$).

Species turnover

The variation in species composition (β-diversity) was higher between sites (median = 0.43) than between consecutive months (median = 0.33). Geographical comparisons showed that the highest βw values were observed between M[2] and T[2] ($\beta w = 0.55$) and between T[2] and T[3] ($\beta w = 0.50$) in July; between M[3] and T[3] ($\beta w = 0.62$) in August; between M[2] and M[3] ($\beta w = 0.60$) and between M[3] and T[3] ($\beta w = 0.77$) in September; between M[2] and M[3] ($\beta w = 0.60$), M[2] and T[2] ($\beta w = 0.60$), and M[3] and T[3] ($\beta w = 0.50$) in October. Most of the faunistical changes occurred between Mediterranean and temperate sites.

Temporal comparisons showed that the highest βw values were found between September and October ($\beta w = 0.52$) in M[1]; between August and September ($\beta w = 0.73$) in M[3]; between July and August ($\beta w = 0.57$), between August and September ($\beta w = 0.43$), and between September and October ($\beta w = 0.6$) in T[2].

Assemblage structure

The adjustment to Motomura's geometric series model was statistically correct in all the assemblages (Kolmogorov-Smirnov test: $F < 1.23$; $P \geq 0.1$), but only 14 slope comparisons were possible (Bartlett's test; Table 4).

In July, the environmental constant m value decreased significantly along the succession M[1]-M[2]-M[3] (Fig. 4), but increased from T[2] to T[3]. In August, significant difference was observed exclusively between M[1] and M[2] ($m = 0.71$ and 0.67, respectively; $F \leq 30.86$). In September, the m value decreased from M[2] to M[3], but it increased from T[2] to T[3] (Fig. 4). In October, the m values decreased with elevation in Mediterranean sites, but the slope comparison was not possible (Pb (probability of Bartlett's test) < 0.05; see Table 4). An m value decrease was also observed between T[2] and T[3] in October.

Discussion

Finn et al. (1999) underlined the problems involved in the interpretation of data when using baited pitfall traps. To prevent a possible methodological bias, we used standardized traps (Lobo et al. 1988, Veiga et al. 1989, Lobo et al. 1998), which collected ≈1,000 beetle individuals per assemblage, i.e., about 3 times more
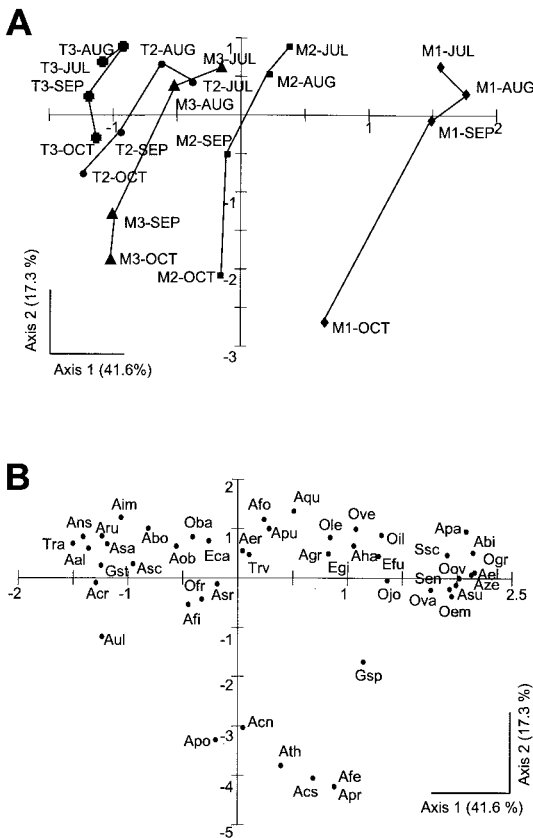
Table 3. Diversity of dung beetle assemblages in sites

		M[1]	M[2]	M[3]	T[2]	T[3]	Kruskal-Wallis test according to sites	P
July	D_M	2.13	1.98	1.38	1.06	1.92	14.43	0.006
Aug.	D_M	1.64	2.01	1.81	1.82	1.25	8.74	0.067
Sept.	D_M	2.19	1.35	0.27	1.48	1.91	13.04	0.011
Oct.	D_M	1.40	1.03	1.03	1.04	1.82	9.21	0.055
Kruskal-Wallis test according to time		6.84	6.70	12.18	9.42	7.83		
P		0.077	0.081	0.007	0.024	0.049		

Values of D_M Margalef index according to months and comparison of D_M values according to months at the same site and to site distribution in the same month, respectively, by using a Kruskal-Wallis test.

M and T: Mediterranean and meso-European (temperate) climatic influence in sites, respectively.

[1], [2], [3]: lower, medium, and higher montane sites, respectively.

beetles than obtained by Martín-Piera et al. (1992) and Finn et al. (1999) in similar studies.

In the current study, in only five sites distributed over an area covering 400 km^2 (40 km in latitude $\times$ 10 km in longitude), 48 species were sampled, i.e., 31% of the whole dung beetle richness in continental France $(550,000 \text{ km}^2)$ (Lumaret 1990, Lumaret et al. 1996, Bordat 1999). As a comparison, Lumaret and Stiernet (1989) collected only 40 species in Vanoise (Northern Alps) from $\approx$200 sites prospected over $2,500 \text{ km}^2$.

Lobo and Martín-Piera (1999) modeled the relationship between dung beetle species richness and surface. By comparison, in both Geotrupinae and Aphodiinae, our results show that the numbers of species collected over 4 mo (6 and 29 species, respectively) were $\approx$6% higher than the richness predicted by models, whereas the number of Scarabaeidae (13 species) was 30% lower than predicted. The species richness did not differ between the five sites, both for subfamilies and chorotypes. From a biogeographical point of view, the fauna observed at this regional scale was apparently the same everywhere. Aphodiinae species, which belonged to Palaearctic, Eurosiberian, and European chorotypes, were predominant. These results agree with Jay-Robert et al. (1997), who showed that, in the Western Alps, >50% of species were widely distributed or belonged to the Eurosiberian chorotype. Conversely, the fauna of the Western Alps differs from faunas of the massifs located in the Mediterranean region (e.g., Iberian Central System, Sierra

Nevada), which gather >20% Mediterranean species in the assemblages.

In the Southern Alps, at elevations ranging from 1,000 to 2,000 m, change in exposure induced a higher species turnover (βw median = 0.53) than that caused by either elevation or monthly variation (βw median = 0.38 and 0.33, respectively), and strong differences were observed in the relative species abundance between sites. Sites located at a similar elevation level, but with opposite exposures (M[2]/T[2], M[3]/T[3]) represented very different assemblages. In July and August, Coprinae largely dominated (abundance and biomass) in the Mediterranean sites regardless of elevation, whereas Aphodiinae dominated in the temperate sites. In September and October, Coprinae abundance strongly decreased because most of these insects have a typical spring-summer adult activity period (Lumaret 1990), but the assemblages of the Mediterranean and temperate grasslands remained different.

In the Southern Alps, a change in the exposure (north versus south) induces a 2°C difference in the mean temperature (Douguedroit 1976). This contrast in the temperature conditions can explain the differences observed in the assemblages. Coprinae species, which are well adapted to warm conditions and which predominate in the south-facing sites, are mostly restricted to the Mediterranean region (Lumaret and Kirk 1991, Lobo et al. 2002). Conversely, most of the Aphodiinae species, which are predominant in the

Table 4. Slope comparison of the adjustment to Motomura's model

	July	Aug.	Sept.	Oct.
M[1]-M[2]	$Pb = 0.078$	$Pb = 0.700$	$Pb = 0.025$	$Pb = 0.012$
	$F = 28.15***$	$F = 30.86***$	‖	‖
M[2]-M[3]	$Pb = 0.166$	$Pb = 0.969$	$Pb = 0.282$	$Pb = 0.048$
	$F = 25.11***$	$F = 0.01^{NS}$	$F = 10.14**$	‖
M[3]-T[3]	$Pb = 0.550$	$Pb = 0.512$	$Pb = 0.466$	$Pb = 0.979$
	$F = 9.02**$	$F = 3.63^{NS}$	$F = 0.53^{NS}$	$F = 0.14^{NS}$
M[2]-T[2]	$Pb = 0.265$	$Pb = 0.013$	$Pb = 0.919$	$Pb = 0.037$
	$F = 4.02^{NS}$	‖	$F = 13.43***$	‖
T[2]-T[3]	$Pb = 0.327$	$Pb = 0.039$	$Pb = 0.053$	$Pb = 0.774$
	$F = 8.08*$	‖	$F = 18.03***$	$F = 5.91*$

Pb, probability value of Bartlett's test; F, value of covariance test.

* , $P_F < 0.05$; ** , $P_F < 0.01$; *** , $P_F < 0.005$; NS, not significant; ‖, statistical comparison impossible ($Pb < 0.05$).

M and T: Mediterrancan and meso-European (temperate) climatic influence in sites, respectively.

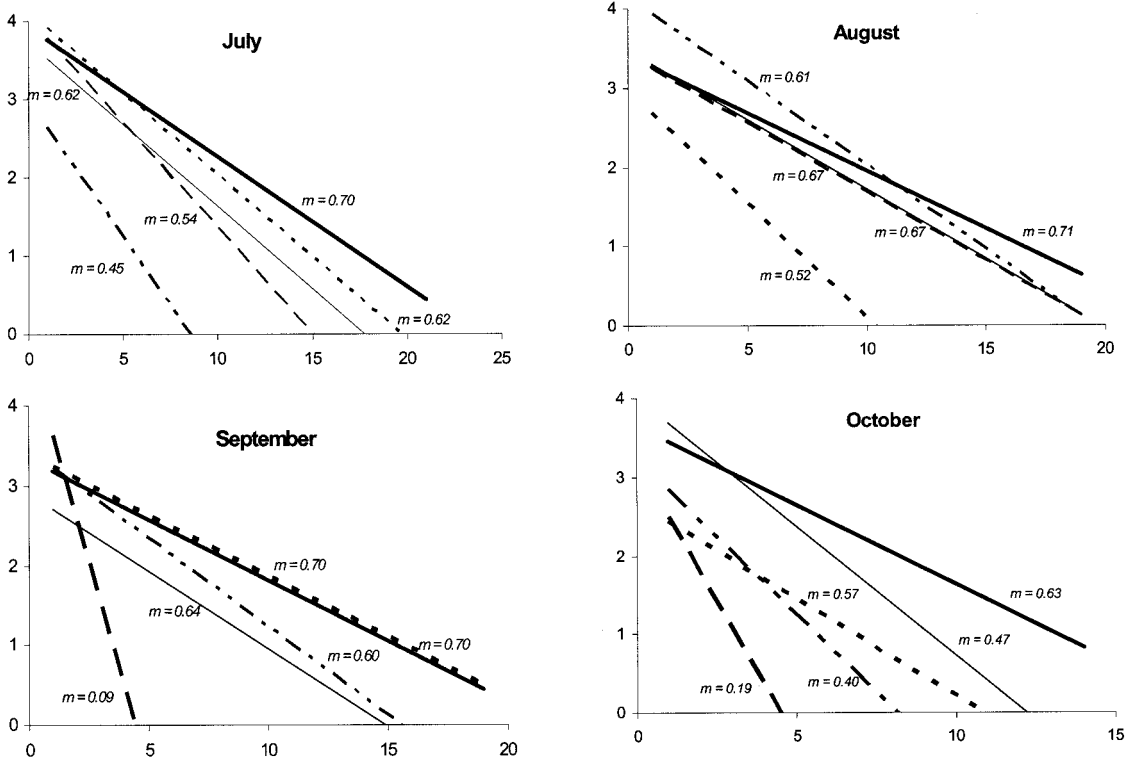[1], [2], [3]: lower, medium, and higher montane sites, respectively.

Fig. 4. Adjustment of species assemblages to Motomura's (1932) geometric series model (biomass of species, log value) according to the rank of species: ——, M[1]; ——, M[2]; – – –, M[3]; –·–·–, T[2]; ·····, T[3].

north-facing sites and which are well adapted to cold, temperate conditions, predominate in the dung beetle assemblages of central and northern Europe (Hanski 1991, Wassmer 1994, Finn et al. 1998, Finn et al. 1999). Such segregation reflects distinct biogeographical origins of the species and probably corresponds to distinct ecophysiological constraints (Jay-Robert et al. 1997).

The altitudinal substitution between Coprinae and Aphodiinae is peculiar to the dung beetle fauna of the European mountains (Martín-Piera et al. 1992, Jay-Robert et al. 1997, Lobo and Halffter 2000). In the Southern Alps, the altitudinal substitution is very clear when the species richness of assemblages is considered (Jay-Robert et al. 1997).

Variations in exposure led to an evident difference in both the structure of assemblages and species abundance, mainly in the 1,000- to 2,000-m range of elevation. In the Mediterranean sites, both species diversity and Motomura's environmental constant (m) diminished when elevation increased, because the fauna at altitude was roughly a rarefied sample from the valley fauna, as was shown in most southern mountains in the Iberian Peninsula (Jay-Robert et al. 1997). On the contrary, in temperate sites, α-diversity and m generally increased with increasing elevation and many Aphodiinae species exploited a large range of niches. Consequently, at 2,000-m elevation, the dung beetle assemblages in the Mediterranean sites were

poorer, but more structured (predominance of few species represented by many individuals) than temperate sites.

Both in the northern Alps (Lumaret and Stiernet 1991) and southward in the Iberian Peninsula (Martín-Piera et al. 1992, Menéndez and Gutiérrez 1996), little difference in species distribution was observed between slopes, and the assemblage composition was determined by elevation. Martín-Piera et al. (1992) argued that the absence of differences between slopes in the Iberian Central System could be caused by the high flying power of dung beetles or by the reduced geographic extension of the mountain range. Our results showed that the flying power of beetles, which was the same in both massifs, did not prevent differences emerging between slopes, and, consequently, the hypothesis of Martín-Piera et al. (1992) is not totally relevant. The massif location and its size could play a crucial role by controlling environmental factors. The substitution of species according to slope exposure was possible because both Coprinae and Aphodiinae species were in contact, but elevation and exposure did not play the same role for all dung beetles. For example, Aphodiinae were abundant in site T[2], but not in site M[3], which was only 350 m higher in elevation. In the Southern Alps, the dung beetle assemblages present in south-facing slopes were very similar to the assemblages observed in lowland Mediterranean assemblages. So, in the Southern

Alps, one can consider that the south-facing exposure allows the existence of an original fauna, which is analogous to the supramediterranean vegetation level well represented in this region.

Acknowledgments

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