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DIVERSITY AND SPATIAL TURNOVER OF DUNG BEETLE (COLEOPTERA: SCARABAEOIDEA) COMMUNITIES IN A PROTECTED AREA OF SOUTH EUROPE (DOÑANA NATIONAL PARK, HUELVA, SPAIN)

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ABSTRACT

Diversity and Spatial Turnover of dung beetle (Coleoptera: Scarabaeoidea) communities in a protected area of South Europe (Doñana National Park, Huelva, Spain).

Diversity and spatial turnover of the spring dung beetle community of Doñana National Park (Huelva, Spain), one of the most important wildlife reserves in the Mediterranean area, were examined. The entire dung beetle community is estimated to comprise around 68 species. Coastal dunes and marsh proved to be the most singular habitats within Doñana Reserve. Response of Scarabaeidae and Aphodiidae to habitat heterogeneity was different. Scarabaeidae fauna was highly homogeneous throughout the habitats whereas Aphodiidae showed higher rates of species turnover and some singular local communities, thus contributing to a greater extent to the regional diversity. Scarabaeidae family presents more ubiquitous species and lower values of beta diversity, so that its local and regional diversity converge. It is suggested that different adaptive strategies regarding resource partitioning (Scarabaeidae: tunnellers and ball-rollers; Aphodiidae: dwellers) can account for these differences. Although Doñana National Park is home to a richer wild mammal fauna and non-human altered habitats, its dung beetle diversity is similar to that of other Spanish regions.

Key words: Coleoptera, Scarabaeoidea, Dung beetle diversity, habitat heterogeneity, species turnover, spatial distribution, Doñana, Southern Spain.

INTRODUCTION

Studies on local dung beetle communities in Western Europe have been greatly developed (HANSKI, 1980; LUMARET, 1978-79a, b; HOLTER, 1982; LUMARET & KIRK, 1987; HANSKI, 1991; LUMARET & KIRK, 1991; HIRSCHBERGER & BAUER, 1994; WASSMER, 1995; GITTINGS & GILLER, 1997). Although knowledge available for Southern Europe communities has increased notably in the last few years (AVILA & PASCUAL, 1986; KIRK & RIDSDILL-SMITH, 1986; BAZ, 1988; GALANTE *et al.*, 1991; LOBO, 1992; MARTIN-PIERA *et al.*, 1992; LOBO & MARTIN-PIERA, 1993; MENENDEZ & GUTIERREZ, 1996), there are not still standardized sampling protocols which allow effective diversity comparisons between localities or regions.

In this paper we examine the spring dung beetle community of the best preserved wildlife reserve in Southwestern Europe, Doñana National Park. No quantitative study of this community has been made, the only available information being a catalogue based on sporadically collected data (COMPTE, 1986). Dung beetle communities colonizing wild and domestic faeces in Doñana Park include two main families (Scarabaeidae and Aphodiidae), representatives of at least five different (or even six: kleptoparasites; MARTIN-PIERA & LOBO, 1993) functional groups as defined by DOUBE (1990). Previous studies have showed that habitat heterogeneity is an important dimension of the dung beetle niche (FINCHER *et al.*, 1970; MERRIT & ANDERSON, 1977; NEALIS, 1977; DOUBE, 1983; GALANTE *et al.*, 1991), which can be related to climatic changes (MENENDEZ & GUTIERREZ, 1996). However, no one has tried to ascertain the diverse influence of this factor on these two families.

Turnover in species composition across habitats (beta diversity) is as important as local richness in determining diversity. Beta diversity is a measure of the rate of change in species composition across a range of samples or habitats. The fewer species the different communities have in common, the higher the beta diversity will be (WHITTAKER, 1960, 1972; WILSON & SCHMIDA, 1984; MAGURRAN, 1988). Species turnover patterns in space may be expected to vary among taxa (HARRISON *et al.*, 1992).

The purpose of this study was therefore threefold: *i*) to obtain an inventory of the spring coprophagous Scarabaeoidea community of Doñana; *ii*) to compare dung beetle diversity of Doñana with those Iberian Central System regions that had been sampled using an equivalent methodology; *iii*) to compare community composition and diversity among different habitats, measuring species turnover at a regional scale in Scarabaeidae and Aphodiidae.

MATERIAL AND METHODS

Doñana National Park is situated in El Rocio, Huelva, Spain, UTM: 29SQB812, one of the most important wildlife reserves in the Mediterranean area. Doñana is unique due to the presence of singular habitats: coastal dunes and marshes, at present largely absent from the Iberian shore.

Eight types of habitats were sampled across 300 km^2: coastal sand dunes devoid of vegetation («corrales») (habitat 1); stationary dunes reforested with pines (habitat 2); scrub fringes of semi-permanent lagoons (habitat 3); a grassland in the marsh-holm oak ecotone (habitat 4); marsh (habitat 5); a cleared area in the primary holm and cork oak wood (habitat 6); a cleared area in a reforested pinewood (habitat 7) and a nearby stream bank primary wood (habitat 8). See figure 1 for geographic location, labels and description of these habitats.

Two sampling programmes were carried out during spring of 1992 and 1993, the season of maximum diversity of dung beetles in Iberobalearic communities (MARTÍN-PIERA *et al.*, 1992; LOBO & MARTÍN-PIERA, 1993). In order to cover the entire season, the first sampling was carried out at the beginning of spring (22-25 April of 1992) and the second at the end of it (7-10 June of 1993). A pitfall trap design recommended by LOBO *et al.*, (1988) and VEIGA *et al.*, (1989) was used. Three traps, baited with 1,000 g. of fresh cow dung, were set in each of the eight habitats, one during the 1992 sampling and two others in 1993. In all, 24 traps were used. Traps were placed 10 meters apart, with a trapping period of 48 hours.

There is evidence that a density of three traps per habitat will adequately represent the dung beetle community structure in the Mediterranean regions. A field experiment of LOBO *et al.* (1998), carried out in Southern France, with twenty five traps per locality (0.01 km^2) proved that a number of 3 traps is enough to catch 60 % of the spring species of a given locality. These species are the most representatives of the local community, they representing 89 % of the total abundance and biomass.

In 1992, 14 additional traps were set in habitat 6. They were of identical construction but baited with dung of different mammals occurring at the reserve: horse, deer, fallow deer, wild boar, badger, lynx, fox, human and cow. Two traps were used for each kind of dung, except for lynx, fox, human and cow with one trap each. In that same year, a supplementary manual sampling of the commonest faeces (cow, rabbit, lynx, fallow deer, wild boar, badger, horse and sheep) was carried out in 14 other localities of the Park.

Taxonomic criteria of VEIGA & MARTÍN-PIERA (1988), BARAUD (1992) and DELLACASA (1983) have been followed in the determination of specimens.

The HORN simplified Morisita index (1966), as recommended by WOLDA (1981), was used as a measure of faunistic similarity between habitats. The resultant similarity matrix was analyzed under three different clustering strategies, Single, Complete and UPGMA, using the program NTSYS-pc version 1.70 (ROHLF, 1992). Although only dendrograms computed by UPGMA have been illustrated, groups mentioned in the text are those common to all strategies at the highest level.

Species replacement patterns in Scarabaeidae and Aphodiidae were examined by measuring alpha, beta and gamma diversity (WHITTAKER, 1960, 1972; CODY, 1986). We have determined alpha diversity, that is, the number of species coexisting within a uniform habitat (intrahabitat diversity), as the average species number per trap in each of these habitats. Beta diversity, which is the faunistic change along an environmental gradient (between habitat diversity), has been calculated for adjacent habitats using the WHITTAKER Index (1960), as recommended by WILSON & SCHMIDA (1984). Gamma diversity, defined as the richness in species for the range of habitats (regional diversity), depends on both alpha diversity for each community and beta diversity between communities; in this paper, the cumulative curve of species richness is shown to properly describe how gamma diversity arises.

RESULTS AND DISCUSSION

Faunistic Inventory

As a result of this sampling 10,648 specimens representing 46 species were collected (Table 1). An increase in sampling intensity, by covering different variables (space, time and trophic sources), did not lead to a great increase in species number (Fig. 2).

The species abundance distributions fit a truncated lognormal model well ($\chi^2 = 11.67$, df= 9, $0.1 < p < 0.5$) yielding an estimate of the theoretical total number of species in the community (MAGURRAN, 1988): S* = 48, a figure quite similar to the total species collected (46) in Table 1. Other Iberian studies (MARTIN-PIERA *et al.* 1992; LOBO & MARTIN-PIERA, 1993) enable us to estimate the number of species caught in cow dung in spring as around 75 % of the total annual inventory. In Doñana, that would mean an entire cow dung beetle community of around 64 species, that is 15-20 more species than those found in spring in this study. Table 2 shows the possible missing species according to previous inventories of the same (COMPTE, 1986) and a near locality: Chiclana de la Frontera (AVILA *et al.*, 1989; AVILA & SANCHEZ PIÑERO, 1988 and 1990). Taking into account all these species, the Doñana dung beetle community comprise about 68 species, a figure quite similar to our previous estimation.

Comparison with other Iberian regions

Comparison of biodiversity between areas requires methodologically equivalent samplings, that is, similar collecting method and sorting of data, per sampling unit and per range value of the variables considered (seasonality, altitude, habitat, etc.). Only two studies, carried out in the Iberian Central System, fulfil these requirements: MARTÍN-PIERA *et al.* (1992) in Sierra Guadarrama and LOBO (1992) in Gredos Massif, so only the spring dung beetle community diversity of these two areas have been compared with Doñana. Comparison was further restricted to grassland biomes with limited or no forest cover, which present the greatest diversity values.

As shown in Table 3, Doñana does not have the largest values of diversity and richness. According to all estimators, the richest communities are found in Sierra Guadarrama, although this is probably a consequence of the larger size of the sampling area. The most interesting difference is probably that related to the taxonomic composition of the two main families: Scarabaeidae and Aphodiidae.

Because of the proportional increase in Aphodiidae richness (Table 3), the species- number ratio Scarabaeidae/Aphodiidae appears unbalanced in Doñana, a case contrary to that of Guadarrama and Gredos. Nevertheless, the number of Scarabaeidae species does not significantly differ from the value expected assuming equal species numbers in the two families ($\chi^2 = 2.78$; $p = 0.5$).

Despite its lower richness of Scarabaeidae, Doñana shares an important number of species with areas as far away as Sierra Guadarrama or Gredos Massif in Central Spain.

Among the non-shared species, only one, *S. cicatricosus* Lucas, 1846, is restricted to the Southwestern Iberian sandy regions. *S. sacer* Linnaeus, 1758, and *C. hispanus* Linnaeus, 1764, colonize the Central System too but they occur in altitudes below those sampled by MARTÍN-PIERA *et al.* (1992); *O. marginalis andalusicus* Waltl, 1835, is mainly restricted to the South Iberian Peninsula although it has been recently found in North of Cáceres (Central Spain) (GALANTE *et al.*, 1989).

As for Aphodiidae, there is a larger number of characteristic species in Doñana. Those with a northernmost distribution, such as *A. bonvouloiri* Harold, 1860, *A. coenosus* (Panzer, 1798), *A. fossor* (L., 1758) *A. frigidus* Brisout, 1886, *A.*

Table 1: Inventory of four samplings carried out at the National Park of Doñana: TH-1992: Trapping carried out over 22-25/IV/1992 at eight habitats (see Table 4). TR-1992: Trapping carried out over 22-25/IV/1992 at habitat 6, with nine types of faeces. H-1992: Complementary sampling by hand over 22-25/IV/1992. TH-1993. Trapping carried out over 7-10/VI/1993 at eight habitats.

Samplings	TH-1992	TR-1992	H-1992	TH-1993	TOTAL
SPECIES					
Scarabaeus cicatricosus	434	14	9	2692	3149
Scarabaeus sacer	33	1	1	76	111
Copris hispanus	0	3	1	3	7
Euoniticellus fulvus	20	18	1	10	49
E. pallipes	22	41	3	9	75
Onitis belial	4	1	4	2	11
Bubas bison	0	5	1	0	6
B. bubalus	0	1	2	0	3
Onthophagus furcatus	7	24	3	3	37
O. maki	262	206	24	887	1379
O. punctatus	12	5	6	190	213
O. similis	449	1116	8	580	2153
O. opacicollis	67	383	0	81	531
O. taurus	278	88	15	685	1066
O. vacca	18	3	2	3	26
O. marginalis andalusicus	0	0	2	2	4
Caccobius schreberi	16	91	6	27	140
Aphodius baraudi	41	35	2	0	78
A. erraticus	111	22	17	0	150
A. fimetarius	5	4	6	6	21
A. foetidus	8	29	1	0	38
A. granarius	9	3	1	0	13
A. haemorrhoidalis	3	0	0	0	3
A. ictericus	23	17	0	1	41
A. immundus	46	16	9	6	77
A. lineolatus	42	78	1	0	21
A. castaneus	0	0	0	1	1
A. lividus	1	2	1	1	5
A. longispina	2	2	0	0	4
A. ghardimaouensis	0	0	0	16	16
A. luridus	1	4	0	0	5
A. merdarius	1	11	0	1	13
A. satellitius	1	1	2	0	4
A. striatulus	275	117	2	8	402
A. klugi	0	0	0	26	26
A. vitellinus	0	0	0	332	332
A. sturmi	5	2	0	3	10
A. tersus	73	104	7	2	186
A. unicolor	47	1	2	0	50
Heptaulacus algarbiensis	1	0	0	0	1
Sericotrupes niger	0	0	0	7	7
Thorectes hispanus	0	1	14	0	15
Typhaeus momus	11	28	11	2	52
Trox cotodognanensis	1	0	4	0	5
T. scaber	0	0	1	0	1
T. perlatus	0	0	11	0	11
TOTAL N	2329	2477	180	5662	10648
TOTAL S	34	35	33	29	46

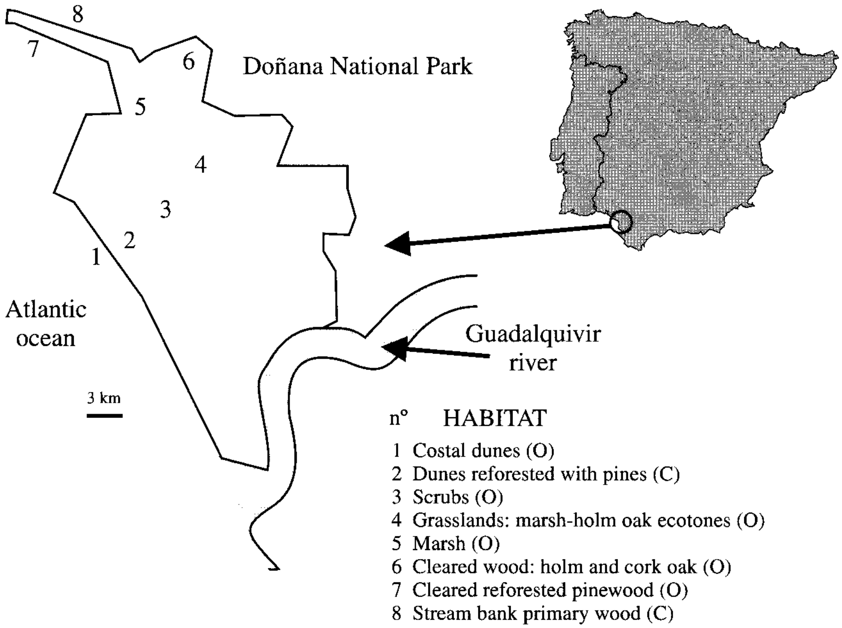


Fig. 1: Localization and characteristics of the sampling habitats. O= open, C= closed biomes.

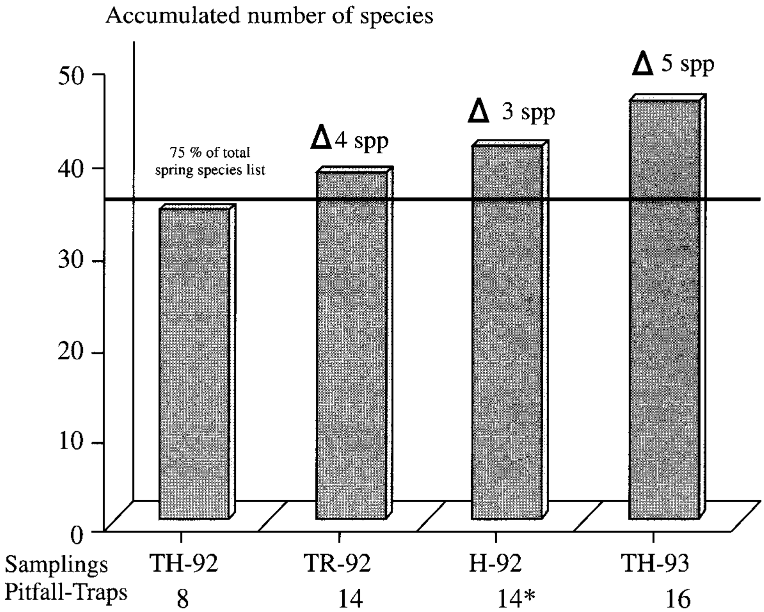


Fig. 2: Cumulative number of species in four samplings carried out in Doñana National Park (Abbreviations as in Table 1). (*) = Number of sites sampled by hand

Table 2: Possible added species to Doñana catalogue of dung beetles according to current literature. A: COMPTE (1986), B: AVILA *et al* (1989); AVILA & SANCHEZ-PIÑERO (1988, 1990).

A	B
Ceratophyus hoffmanseggi Fairmaire	*Gymnopleurus flagellatus* Fabricius
Aphodius lusitanicus Erichson	*G. sturmi* MacLeay
A. hydrochaeris Fabricius	*G. mopsus* Pallas
	Onitis ion Olivier
	Chironitis hungaricus Herbst
	Euoniticellus pallens Olivier
	Onthophagus melitaeus Fabricius
	O. latigena d'Orbigny
	O. ruficapillus Brülle
	O. hirtus Illiger
	Aphodius elevatus Olivier
	A. sphacelatus Panzer
	A. villareali Baraud
	A. tingens Reitter
	A. quadriguttatus Herbst
	A. mayeri Pilleri
	Heptaulacus brancoi Baraud
	Geotrupes ibericus Baraud
	Thorectes laevigatus Fabricius

scrofa (F., 1787) *A. scrutator* (Herbst, 1789) and *A. sphacelatus* (Panzer, 1798), are replaced in Doñana by *A. baraudi* Villareal, 1975, *A. longispina* Kuster, 1854, *A. ghardimaouensis* Balthasar, 1929, *A. lividus* (Olivier, 1789), *A. castaneus* Illiger, 1803, *A. luridus* (F., 1775), *A. klugi*, Schmidt, 1910, *A. vitellinus* Klug, 1845, and *Heptaulacus algarbiensis* Branco & Baraud, 1984. Thus, the richness of Aphodiidae does not decrease in Doñana. Besides, 37 Doñana species have been collected in Chiclana de la Frontera (Cádiz) (AVILA & SANCHEZ PIÑERO, 1990), suggesting that the Doñana dung beetle community is not particularly different.

Why Doñana does not have more diverse communities?

The Doñana National Park, despite its rich wild mammal fauna, does not yield a greater dung beetle diversity when compared with other Spanish regions. Historical and ecological causes can explain this fact. Domestication of livestock goes back to 10,000-8,000 years BP (LOFTUS *et al.*, 1994). Also, the major change in European forests (from full forest to predominantly open cultivated land), started 10,000-8,000 years ago in the Mediterranean area, and about 5,000 ago in Western and Central Europe (MÖNKÖNEN & WELSH, 1994 and references therein). Hence, mammal populations may have been modified troughout the Neolithic by human activity, in particular by livestock herding, possibly leading

Table 3: Comparison of dung beetle communities of three Iberian Regions. SUs: Sample Units (Traps: Doñana and Guadarrama, dung pads: Gredos). S: Richness. N: Abundance. ST: Number of species estimated by fitting to truncated lognormal curve (Krebs 1989). Raf. 1,000: Species estimated by means of rarefaction curve (1,000 individuals) (Hulbert 1971). H': Shannon Diversity Index. Scar/Apho: Scarabaeidae/Aphodiidae Richness ratio. (*) = Estimation.

	Sampling Dates	Size Area	Nº SUs	S (Annual)	S (Spring)	S mean/trap Range	N mean/trap Range	ST	Raf. 1,000 Ind.	H'	car/Apho
Sª Gredos	1-3/V and 11-13/VI/1985	100 Km^2	30	61	43	12 2 - 20	436 8 - 1733	50	27	1.58	19/20
Sª Guadarrama	24-27/VI/1986; 18/21/VI/1987	2600 Km^2	20	74	50	14 6 - 23	211 26 - 886	54	40	2.61	24/23
Doñana National Park	23-25/IV/1992; 1-7/VI-1993	300 Km^2	24	64-69(*)	41	13 7 - 24	380 45 - 1017	45	30	2.17	15/23

Table 4: Spring inventory of Scarabaeoidea dung beetles in the National Park of Doñana from two samplings carried out over 22-25/IV/1992 (TH-1992: Table 1) and 7-10/VI/1993 (TH-1993: Table 1). Habitat numbers as in figure 1.

Sampling stations	1	2	3	4	5	6	7	8	Total
SPECIES									
Scarabaeus cicatricosus	605	798	907	672	0	16	77	51	3126
Scarabaeus sacer	18	8	38	30	1	0	9	5	109
Copris hispanus	0	0	0	0	0	3	0	0	3
Euoniticellus fulvus	2	1	3	13	4	2	3	2	30
E. pallipes	4	0	8	11	7	1	0	0	31
Onitis belial	0	0	1	4	0	1	0	0	6
Onthophagus furcatus	1	0	5	1	1	1	1	0	10
O. maki	2	20	563	395	0	70	54	45	1149
O. punctatus	1	6	1	76	1	89	8	20	202
O. similis	6	8	225	385	0	293	57	55	1029
O. opacicollis	0	1	15	9	13	78	18	14	148
O. taurus	12	48	461	382	8	22	16	14	963
O. vacca	0	0	0	11	4	2	1	3	21
O. marginalis andalusicus	0	0	0	0	0	0	1	1	2
Caccobius schreberi	0	0	0	5	3	14	15	6	43
Aphodius baraudi	5	18	12	3	0	2	1	0	41
A. erraticus	0	0	0	82	0	6	22	1	111
A. foetidus	0	0	0	3	0	5	0	0	8
A. fimetarius	0	1	0	5	0	1	2	2	11
A. granarius	0	0	0	0	0	0	7	2	9
A. haemorrhoidalis	0	0	0	2	1	0	0	0	3
A. ictericus	0	3	7	1	0	12	1	0	24
A. immundus	0	0	0	15	3	6	28	0	52
A. lineolatus	0	1	3	1	0	35	2	0	42
A. castaneus	0	0	0	0	1	0	0	0	1
A. lividus	0	0	0	0	1	0	1	0	2
A. longispina	0	0	0	0	1	0	1	0	2
A. ghardimaouensis	6	1	4	0	0	5	0	0	16
A. luridus	0	0	0	1	0	0	0	0	1
A. merdarius	0	0	0	0	0	1	1	0	2
A. satellitius	0	0	0	1	0	0	0	0	1
A. striatulus	12	9	183	23	17	32	7	0	283
A. klugi	1	0	1	0	24	0	0	0	26
A. vitellinus	0	0	4	0	319	7	2	0	332
A. sturmi	1	3	0	0	0	3	1	0	8
A. tersus	1	0	2	20	0	29	23	0	75
A. unicolor	0	0	0	0	0	0	47	0	47
Heptaulacus algarbiensis	0	0	1	0	0	0	0	0	1
Sericotrupes niger	0	0	5	1	0	0	1	0	7
Typhaeus momus	3	3	5	0	0	2	0	0	13
Trox cotodognanensis	0	1	0	0	0	0	0	0	1
Total N	680	930	2454	2152	409	738	407	221	7991
Total S	16	17	22	26	17	27	28	14	41

Table 5: Mean species per trap and habitat in Scarabaeidae and Aphodiidae, and regional richness (S) in Doñana National Park.

	Traps		Habitats		Regional
	Mean	SE	Mean	SE	S
Scarabaeidae	7.58	0.90	10.75	1.32	15
Aphodiidae	4.21	1.33	9.13	2.76	23

to drastic reduction and even extinction of trophic-specialized dung beetles, as well as to major dietary restrictions in truly trophic-generalist species (MARTÍN-PIERA & LOBO, 1996). More herbivore-euryphagous species may have prospered and extended their geographic range. Dung beetles, having evolved for a long time and coped mainly with ungulate dung, are able to react quickly to sudden changes in dung type. The guild diversity and the complexity of reactions among native dung beetle species have made their communities highly adaptable to change (LUMARET *et al.*, 1992). As a consequence, present dung beetle communities are hardly sensitive to human activity, having been ecologically structured over a period covering the last several thousands of years.

Habitat comparison

Table 4 displays the list of captured species and their abundances in the eight habitats. In all, 15 Scarabaeidae, 23 Aphodiidae, 2 Geotrupidae, and only 1 Trogidae species, were collected.

Cluster analysis of habitats yielded a different clustering pattern depending on the family considered: Aphodiidae or Scarabaeidae (Fig. 3). In the case of Scarabaeidae, there are four clusters: *i*) inland bushy and grassland areas, and bank river areas in the northwestern border of the Park, are clustered together (habitats 3,4 and 7,8); *ii*) a second cluster is made up of coastal dunes (habitats 1,2); *iii*) only one habitat, the cleared Mediterranean wood (6) and the marsh (5) make up the third and fourth clusters, respectively.

Fauna of habitats 7 and 8 is nearly the same (Table 4). Grassland biomes placed in the centre of Doñana (habitat 4) have a very similar fauna: dominant species do become more dominant but there are just three non-common species: *E. pallipes* (F., 1781), *O. marginalis andalusicus* Waltl, 1835, and *Onitis belial* F., 1798, all of them with low abundances. On the contrary, fauna inhabiting habitat 3 may be considered as a poor faunistic subset of that in nearby habitat 4, where a few species show still increasing dominance (Table 4).

Coastal dune fauna is a poor version of that found on inland habitats, and is dominated by the presence of ball roller *Scarabaeus cicatricosus* (Lucas, 1846). No new species occur with respect to inner habitat 3. Thus, species loss and the increasing dominance of *S. cicatricosus* lead to a decrease in equitability and diversity as we approach coastal dunes (Fig. 3). Marsh (habitat 5) has an still poorer fauna, as just a few species of the close grassland biomes occur, showing very low abundances. Only the fauna of the cleared holm oak wood (habitat 6) differs to some extent from that found in the faunistic core habitats of Doñana territory, (habitats 3,4 and 7,8): a new species, *Copris hispanus* (L., 1764) is present; *S. cicatricosus* abundance decreases; another ball roller, *S. sacer* L., 1758 disappears; and the dung beetle community becomes dominated by Onthophagini tribe, which includes the most typical species of Mediterranean grassland biomes (Table 4).

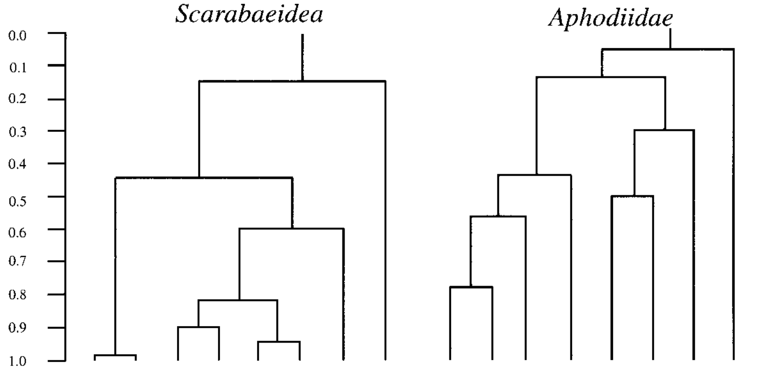
Aphodiidae's grouping pattern of habitats is rather different (Fig. 3). The dendrogram shows three clusters: habitats 4, 7 and 8 are grouped together, the second cluster consists of habitats 1, 3, 2 and 6, and marsh (habitat 5) makes up the third cluster. The two cleared wood areas placed in the northern part of Doñana territory (habitats 6, 7) have communities with the greatest equitability and diversity; their faunas, however, exhibit different dominant species and six non-common species. Fauna occurring in habitat 8, a wooded area, is only an impoverished subset of that of close habitat 7, whereas fauna of the grassland biome (habitat 4) is quite different: there are eleven non-common species from a total of nineteen (58%). Regarding the other cluster, there is a great similarity between dune communities (habitats 1, 2) and the richer fauna of close bushy areas (habitat 3). They share dominant species *A. baraudi* Villareal, 1975 and *A. striatulus* Waltl, 1835; only species rare in dunes, such as *A. sturmi* Harold or *A. fimetarius* (L., 1758) are absent from the habitat 3 community. Thus, a loss of dominance and richness can be observed as we move from inland to coast (Fig. 3). There are important differences, however, between the fauna of habitat 6 and that of other habitats forming the second cluster, habitats 1, 2 and 3; habitat 6 shows four new non-abundant species and a big turnover in dominant species (Table 4). Finally, the marsh community clearly differs from all others because of the dominance of such relatively rare species as *A. klugi* Schmidt, 1910 and *A. vitellinus* Klug, 1845, and because ubiquitous species (e.g. *A. baraudi* Villareal, 1975) or those very dominant in other habitats (e. g. *A. erraticus* (L., 1758) and *A. tersus* Erichson, 1848) are missing.

The spring Scarabaeidae community of Doñana is rather homogeneous, different habitats not presenting singular faunas. Only the cleared holm and cork oak wood in the northern part of Doñana has a somewhat different community, characterized by the absence of ball rollers and the dominance of species belonging to Onthophagini. This habitat, widely spread over the Mediterranean area, defines the northern border of the Park.

In the case of Aphodiidae, however, almost all habitats have their particular fauna. There are just similarities between the faunas of habitats 7 and 8, and likewise, between 1, 2 and 3. Marsh, dunes, holm oak and stream bank woods seem each to have a different Aphodiidae community.

Three species stand out for their great population size and niche breadth: *S. cicatricosus*, *O. similis* (Scriba, 1790) and *O. maki* (Illiger, 1803) (Fig. 4). *S. cicatricosus* is a large ball roller dominating mostly in the coastal dune communities. Only in the marsh the dominant species is an Aphodiidae, *A. vitelllinus*, a small species with a very restricted niche (Fig. 4).

Dunes are characterized by their faunistic scarcity and the dominance of large ball rollers, such as *S. cicatricosus* and *S. semipunctatus* (F., 1792) (LUMARET & KIRK, 1987; LOBO & MARTÍN-PIERA, 1993). Because of their loose texture, dunes make difficult the building of vertical and deep tunnels by tunnelling species,



Habitats	1	2	3	4	7	8	6	5	1	3	2	6	4	7	8	5
S	9	8	11	13	12	11	13	9	6	9	7	13	12	15	3	8
N	651	890	2227	1994	260	216	592	42	26	217	36	144	157	146	5	367
1/D	1.16	1.24	3.53	4.37	5.18	5.48	3.32	5.41	3.25	1.40	3.04	6.06	3.11	5.17	2.78	1.31
E	0.15	0.22	0.79	0.84	0.88	0.90	0.76	0.92	0.83	0.32	0.78	0.91	0.74	0.86	1.00	0.27

Fig. 3: Similarity clustering among Doñana sampling habitats. S: Richness. N: Abundance. 1/D: Simpson's reciprocal index diversity (D). E: Eveness (E = D/Dmax) (Krebs 1989). Ch: Similarity Index (Simplified Morisita Similarity Index) (Horn 1966). Clustering method: UPGMA.

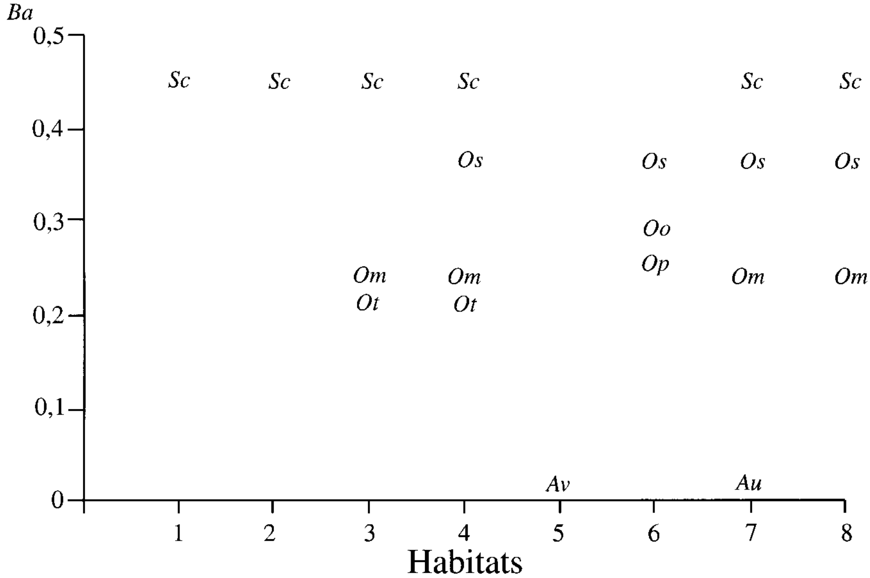
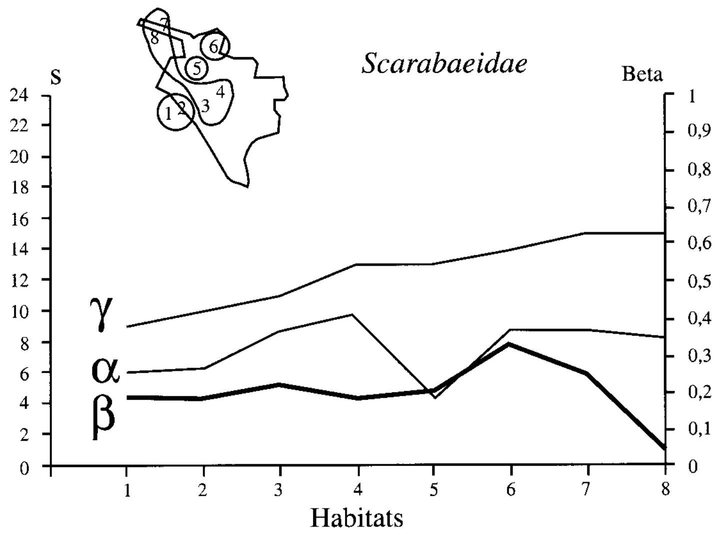


Fig. 4: Habitat niche breadth for those species with more than 10% of the total abundance in each sampling habitat. Av: *Aphodius vitellinus*; Au: *Aphodius unicolor*; *Om: Onthophagus maki*; Oo: *Onthophagus opacicollis*; Op: *Onthophagus punctatus*; Os: *Onthophagus similis*; Ot: *Onthophagus taurus*; Sc: *Scarabaeus cicatricosus*. BA is the Levins index of standardized niche breadth (Krebs, 1989).



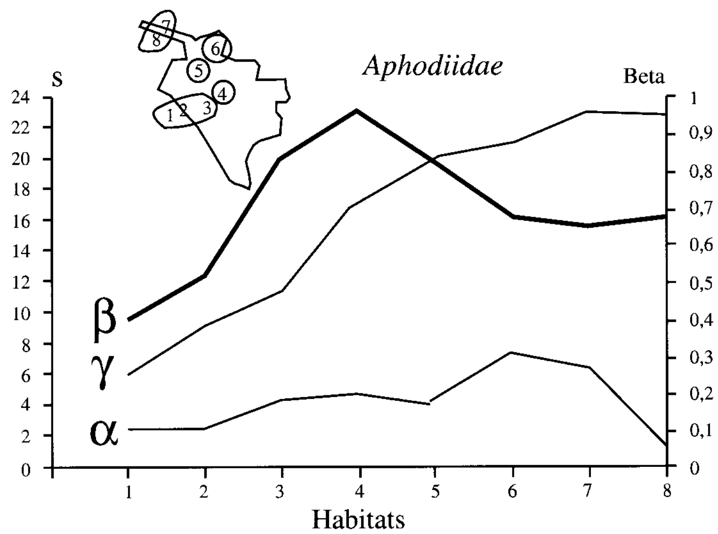


Fig. 5: Alfa, Beta and Gamma diversity variation in dung beetle Scarabaeoidea communities of Doñana National Park. Upper left figures: Habitats clustering as shown in figure 3. Left ordinate Y axis (S): Number of species; right ordinate Y axis (Beta): Beta diversity Index of Whittaker (1960). Gamma diversity variation is represented as the cummulative richness curve.

as in *Onthophagus* or *Caccobius* genera. On the contrary, soil texture does not appear to be a relevant factor for ball rolling species, which build shallower and more horizontal tunnels (HALFFTER & EDMONDS, 1982). There is no straightforward biological explanation to the habitat specialization of *A. vitellinus*, the reproductive and nesting behaviour of this dwelling species being still unknown.

Turnover in Species Composition

Spatial diversity patterns show that Doñana Scarabaeidae fauna is quite homogeneous in all habitats, there being no detectable increase in collected species as the number of localities increases (Fig. 5). Only the holm oak wood community (habitat 6) differs to some extent from all others. That explains the increase in beta diversity observed in this habitat (Fig. 5). When Aphodiidae are considered, this pattern changes sharply. As previously seen, almost all habitats are characterized by their own Aphodiidae fauna. Consequently, beta diversity values for each habitat and the slope in the cumulative richness curve are greater than in Scarabaeidae (Fig. 5).

Since Scarabaeidae communities are very similar in all habitats, the regional richness depends on Aphodiidae: 50 % of the collected species are Aphodiidae and 37 %, Scarabaeidae; Geotrupidae and Trogidae merely represent 13 % of richness. In contrast, local communities are clearly dominated by Scarabaeidae, which comprise 84 % of the total specimens. In terms of biomass, this dominance becomes clearer because the mean dry weight of Scarabaeidae ranges between 760 and 30 mg whereas Aphodiidae never weigh over 11 mg. (LOBO, 1992). Thus, although the mean species number per trap is significantly greater in Scarabaeidae ($t = 4.11$, $df = 46$, $p < 0.001$), the average richness per habitat is similar in both families ($t = 1.04$, $df = 14$, ns), and the regional richness is clearly greater in Aphodiidae (Table 5). This pattern is also found in other sampled areas of the Iberian Central System (Fig. 6). Although not yet demonstrated, this pattern is likely to be a general rule which would explain the Aphodiidae/Scarabaeidae ratio in the Iberian Peninsula: 129/54 (VEIGA & MARTÍN PIERA, 1988).

Literature dealing with biodiversity topics underlines some biological characteristics which would explain the diversity pattern of Aphodiidae and Scarabaeidae in Doñana.

Turnover in species composition has been related to species vagility (CODY, 1986). HARRISON *et al.* (1992), however, found that turnover is clearly not higher in poorly dispersing taxa than in good dispersers, and consequently turnover with distance may be a relatively minor component of regional diversity. High beta diversity results from a high habitat specificity, habitat specialists being particularly rare if their preferred habitats are scarce (CODY, 1986; HARRISON *et al.*, 1992).

Although there are important exceptions, mainly among autumn-winter species (LOBO, 1992), Aphodiidae species may be considered rare. They have narrow environmental tolerances and high reproductive rates so as to balance a high larvae mortality. Since Aphodiidae larvae are free-living, growing up without parental care, they are more sensitive to the environment. Also, Aphodiidae adults do not relocate excrement but feed inside it (dwellers), becoming sensitive to environmental conditions too. In contrast, Scarabaeidae species have low fecundity (ovarial reduction) and maximize their reproductive efficiency by increasing parental

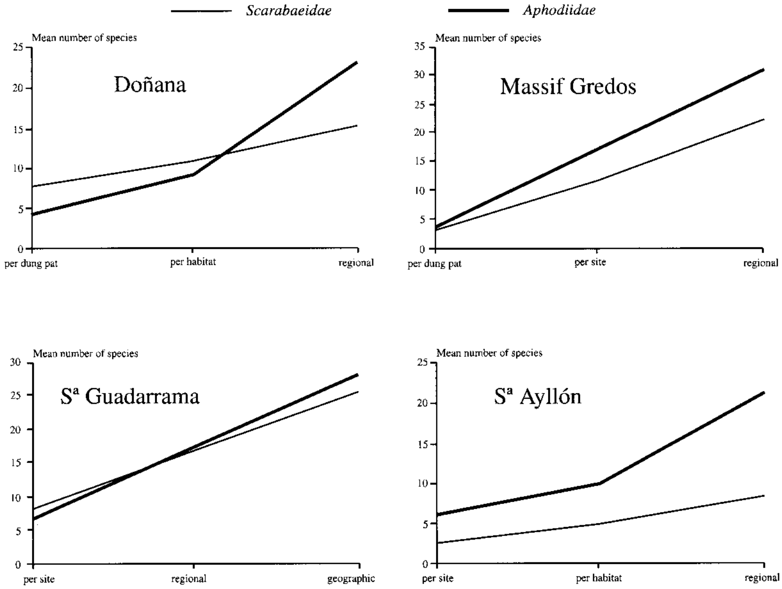


Fig. 6: Mean species number at different spatial scales. Data from Lobo (1992): Gredos Massif; Martín-Piera et al. (1992): Sierra Guadarrama, and Baz (1988): Sierra Ayllón.

investment in each progeny. Larvae are brought up inside subterranean nests made by adults and with enough food for their development (HALFFTER & EDMONDS, 1982). Food availability and nest protection make them more independent of environmental conditions than Aphodiidae.

These biological characteristics could account for the differences in population size and spatial distribution observed in both families. While Doñana Aphodiidae have small or moderate populations and small niche breadths, Scarabaeidae species present much greater abundance and larger niches (Fig. 7). CORNELL & LAWTON's theoretical framework (1992) would, then, suggest that deterministic ecological processes, such as niche packing and competitive dominance, play the major role in structuring the Scarabaeidae community, whereas in the case of Aphodiidae, stochastic and historical factors would be the fundamental structuring forces, thus explaining the higher values of gamma diversity in this family (CODY, 1986).

CONCLUSIONS

1. The entire spring dung beetle community of Doñana National Park is estimated to comprise around 68 species. Coastal dunes and marsh proved to be the most singular habitats within Doñana Reserve. Both are characterized by little diversity of fauna and dominance of *Scarabaeus cicatricosus* in dunes and *Aphodius vitellinus* in marsh.

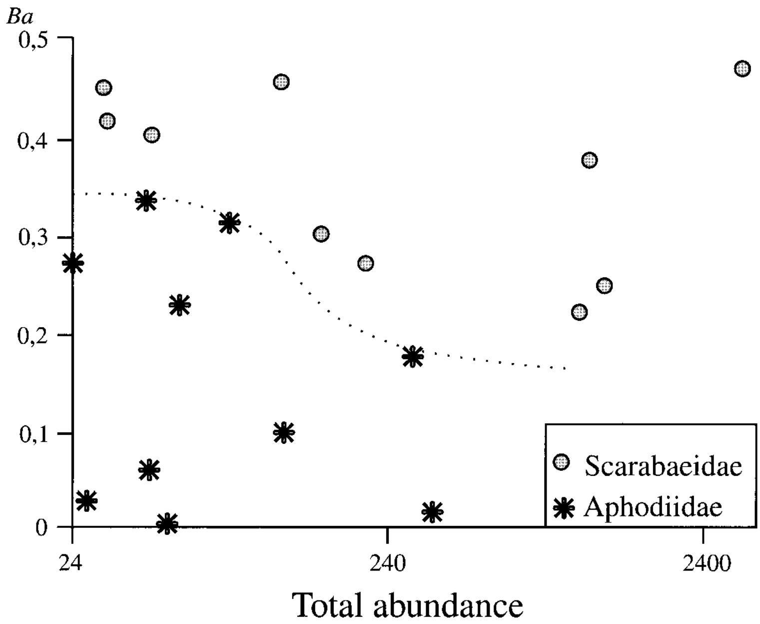


Fig. 7: Abundance and habitat niche breadth relationship for those species with abundance larger than 24 individuals (3 individuals per habitat). Niche breadth measure (BA) is the Levins index of standardized niche breadth (Krebs, 1989).

2. The two main families of dung beetles respond differently to habitat heterogeneity. Scarabaeidae fauna was highly homogeneous throughout the habitats whereas Aphodiidae showed high rates of species turnover and some singular local communities, thus contributing to a greater extent to the regional diversity. The Scarabaeidae family presents more ubiquitous species and lower values of beta diversity, so that its local and regional diversity converge. It is suggested that different adaptive strategies regarding resource partitioning (Scarabaeidae: tunnellers and ball-rollers; Aphodiidae: dwellers) can account for these differences.

3. Although Doñana National Park is richer in wild mammal fauna and non-human altered habitats, its dung beetle diversity is similar to that of other Spanish regions. There is a slight decrease in Scarabaeidae richness with respect to other areas of the Iberian Central System, mainly due to the lack of some species with Central European distribution (especially Onthophagini). On the contrary, the absence of Aphodiidae species with Northern distribution is compensated for by the presence of Southern species.

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