

## Between-group differences in the Iberian dung beetle species-area relationship (Coleoptera: Scarabaeidae)

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**Abstract** — Between-group  $\alpha$ - and  $\beta$ -diversity differences were derived from species-area relationships fitted to field data. The accuracy of spatial richness variation predictions based on area size was also checked. The log-log model ( $\log S = c + z \log A$ ) was found to be the best-fit linear model, with slopes ( $z$ ) ranging from 0.089 to 0.142. Between-group comparisons of  $z$  (slope) and  $q$  (intercept) parameters, using the  $S = q + cA^z$  curvilinear regression model, corroborated early results, indicating a lower  $\beta$ -diversity (slope) for Scarabaeinae than for Geotrupinae and Aphodiinae. The latter group, probably more sensitive to environmental heterogeneity, should contribute more to species richness in large areas.  $\alpha$ -Diversity is greater for Aphodiinae, more relevant to local diversity (1 km<sup>2</sup>), than for Scarabaeinae and considerably greater for these two groups than for Geotrupinae. As earlier results show that the richness of a single dung pat is rather more a function of the Scarabaeinae species pool, richness on dung pat scales is probably due more to the between-dropping mobile Scarabaeinae, while Aphodiinae contribute mainly to local and regional pool richness. Nearly 88 % of the total richness variance is explained by area size. This percentage decreases to 37 % when the spatial structure of area size and species number are extracted. The corresponding figures for Scarabaeinae, Aphodiinae and Geotrupinae are 44, 22 and 31 %, respectively. © 1999 Éditions scientifiques et médicales Elsevier SAS

Species-area / dung beetles / Scarabaeidae / beta-diversity / Iberian Peninsula / richness comparison

### 1. INTRODUCTION

Variation in species number with variation in area, which has been much studied [13, 72], is usually expressed as a power function:

$$S = cA^z$$

or, to linearise the relationship, as:

$$\log S = c + z \log A \quad (1)$$

where  $S$  is the number of species,  $A$  the area,  $z$  the slope (species richness rate of accumulation with increment in area) and  $c$  a species-dependent constant. Connor and McCoy [26] compared (1) with  $S$  vs.  $A$ ,  $S$  vs.  $\log A$  and  $\log S$  vs.  $A$  and found, as have others [26, 53, 84, 91], that for practical values of  $S$  and  $A$ , (1) best expresses the species-area relationship. However, non-linear regression techniques can yield improved parameter estimates compared to those derived from linear equations [72], whose popularity is due, in any

case, to the ease of both computation and comparison with previously published results.

While theoretically  $z$  can vary from negative values (fewer species in large areas than in small ones) to greater than one (larger areas contain a relatively greater number of species than smaller ones), a range of only  $0.20 > z > 0.40$  has been found for the many different areas and groups [26, 72, 91]. The biological meaning of the slope has been widely disputed ([1, 26, 72, 84] and references therein): why do species numbers accumulate with increments of area? [8, 23, 49, 60, 61, 90, 91, 92]; and why does  $z$  typically vary between a rather limited range? [1, 26, 29, 53, 65, 70, 84]. While ecologists have addressed these questions for a long time, proposing many biological and non-biological hypotheses, for the purpose of this paper, the slope is considered to be the rate at which species numbers vary with area, the turnover in species composition or  $\beta$ -diversity [19], a useful measure of species replacement on a spatial scale. For example, a zero value of  $z$  means that the same number of species

is found in all samples (i.e. regional and local diversity are equal), while a slope of one means that doubling the area doubles the number of species.

The taxon- and biogeographic-region-dependent parameter  $c$ , taken as the number of species within an unit-area sample [26], can measure local richness. Additionally, thanks to Rosenzweig [72],  $c$  can be considered the slope of a function whose x-axis is  $A^z$  and whose y-axis is  $S$ . Thus, for the modified species-area equation:

$$S = q + cA^z \quad (2)$$

$q$ , the  $S$ -intercept when area has vanished [72], becomes a measure of local richness ( $\alpha$ -diversity). Comparisons of  $z$  and  $q$  parameters highlight diversity variation differences between groups.

Turnover in species composition, related primarily to both the vagility [22] and habitat specificity of species [46], has been reported to differ significantly in southern Spain on a local scale for Aphodiinae and Scarabaeinae [59], the two major monophyletic Iberian dung beetle lineages. Scarabaeinae intra-habitat ( $\alpha$ ) diversity, measured as dung pat richness, is higher than that of Aphodiinae, whose between-habitat ( $\beta$ ) diversity is higher than that of Scarabaeinae. Such higher Aphodiinae  $\beta$ -diversity is thought to be mainly the result of the free life style of Aphodiinae larvae [59] and their concomitant heightened sensitivity to environmental heterogeneity. The greater heterogeneity of larger areas, expected to contain proportionally more Aphodiinae than Scarabaeinae species, should lead to differentiation of the slope and intercept values for their respective species-area relationships.

The first aim of this paper is to check differences in Iberian Scarabaeinae, Aphodiinae (sensu Browne and Scholtz [15]) and Geotrupinae (sensu Zunino [93])  $\beta$ - and  $\alpha$ -diversity by estimating slope and intercept values of (2). Second, the area effect on species richness is ascertained. By means of a trend surface analysis [52], spatial structure was subtracted from  $S$  and  $A$  and the residuals used to formulate another species-area relationship, theoretically more acceptable as a predictive tool.

## 2. MATERIALS AND METHODS

To examine the species-area relationship of Iberian dung beetles, data from 26 Iberian studies (figure 1, table I), plus the complete Iberian inventory, were used. The majority of the available information has been obtained either from unpublished theses or from

studies published in regional journals. The data from 'Ceuta' (North Africa, locality 14, table I) and Balearic islands (locality 19, table I) were not included in species-area calculations, but were graphed to check if their values fall within the regression confidence limits. The total number of species observed in the Iberian Peninsula was determined using the general information of Veiga and Martín-Piera [87] and Baraud [10] as well as the data of Avila [2], Veiga [86] and Galante and Verdú-Faraco [38].

To record all the species occurring in the area, only intensive studies of at least an entire year sampling programme were used (table I). In all cases, the data come from time-extensive catalogues, compilations of all the available regional information [7, 18, 27, 28, 31–33, 35, 36, 39, 47, 62, 71, 74, 77–79, 81] or from 1-year local studies using similar capture methods, i.e. dung-baited pitfall traps or natural dung pats [3–6, 12, 30, 34, 37, 40, 48, 54, 55, 64, 66, 67, 73, 75, 76, 80, 85, 88].

Data from exhaustive inventories is not accompanied by estimates of sampling effort. Hence, total richness cannot be extrapolated by means of the species accumulation, or 'collector's curve' [25]. But an estimate can be gained from relative species abundance. A corrected version of Chao and Lee's estimator [20, 25], the abundance-based coverage estimator (ACE) [21], was calculated with the EstimateS package [24], on data from all those studies with abundance values for the three main Iberian dung beetle subfamilies ( $n = 21$ ). There is no significant difference between the ACE-estimated species numbers and those listed in any inventory. On average, 97.3 % of the estimated species richness was inventoried (figure 2). In any case, the tendency for a given inventory's number of species to give an underestimate of an area's species richness should be mitigated by Mediterranean conditions, where only two baited pitfall traps collected 53 % of site species representing around 85 % of total beetle abundance and total biomass [58] (fifteen traps collected 95 % of site species).

The standard error of the estimate ( $S_{yx}$ ), and not the correlation coefficient scores [82, 84], has been used to check the appropriateness of the different linear models ( $\log S$  vs.  $\log A$ ,  $S$  vs.  $A$ ,  $\log S$  vs.  $A$  and  $S$  vs.  $\log A$ ). Subfamily values of  $S_{yx}$  clearly indicated that (1) fits the data best, which was also chosen because of the ease of comparison of results and its common usage. Regression curves were least-squares fitted to log-transformed data. Area measurements are in  $\text{km}^2$ . The two unique zero data of Geotrupinae (see table I)

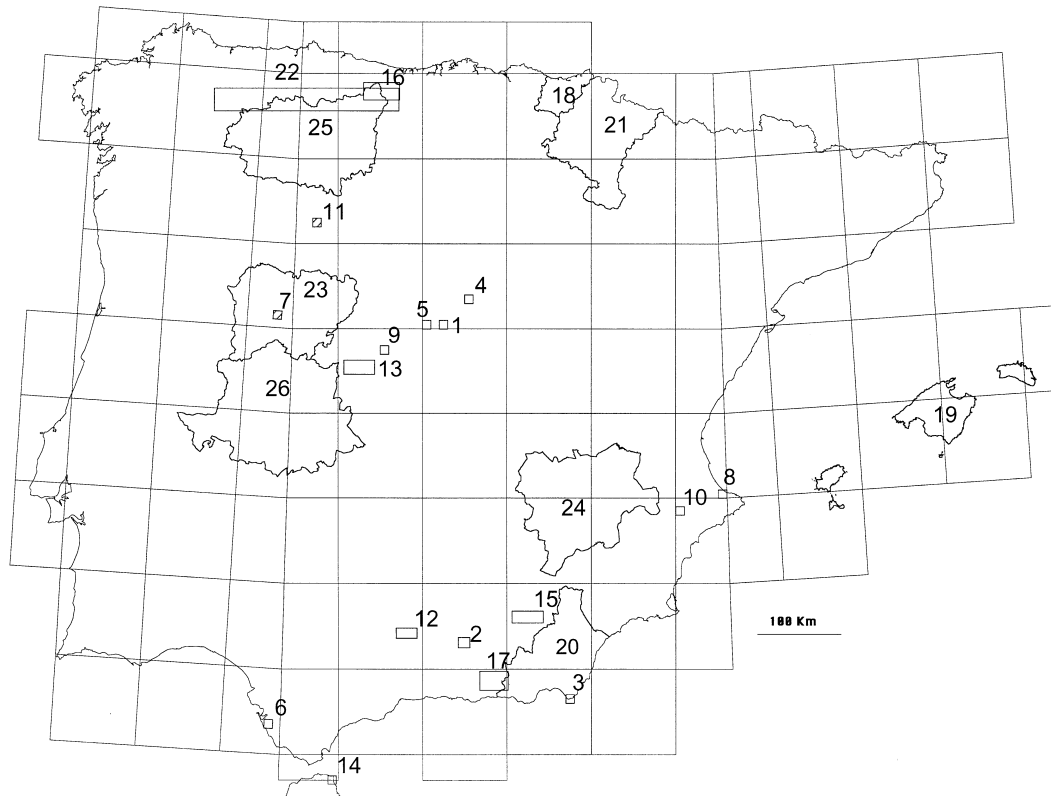


Figure 1. Iberian location of dung beetle faunistic inventories used for calculations of the species-area relationship.

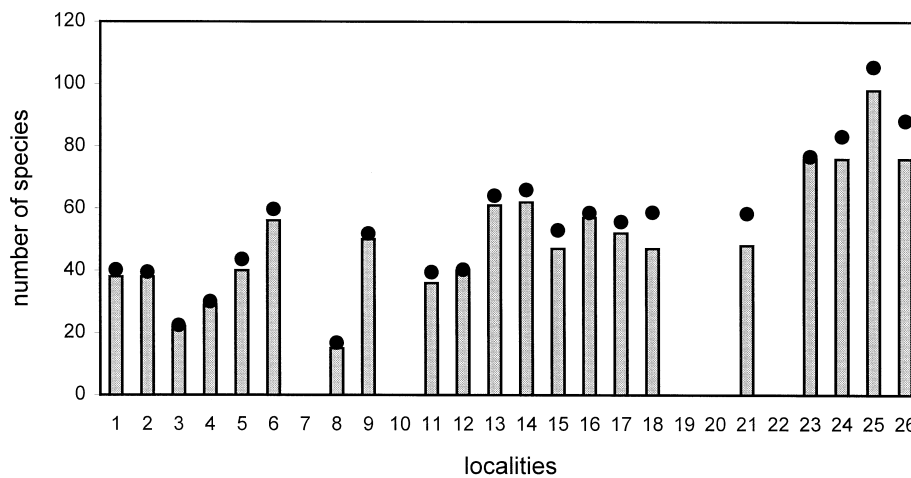


Figure 2. Number of collected species in the localities listed in table 1 (bars) and maximum richness (black dots) estimated by means of the abundance-based coverage estimator (ACE) [21].

**Table I.** Scores for calculations of species-area relationship. Numbers of localities correspond to those in *figure 1*. STOT, Total richness; SScA, Scarabaeinae richness; SAph, Aphodiinae richness; SGeo, Geotrupinae richness.

Code number	Localities	Reference	Area (km <sup>2</sup> )	Latitude (N)	Longitude (W)	STOT	SScA	SAph	SGeo
1	Colmenar Viejo	[85]	0.2	40.67	3.75	38	16	21	1
2	Sierra de Alfacar	[30]	1	37.17	3.50	38	14	21	3
3	Cabo de Gata	[73]	1	36.67	2.17	22	10	12	0
4	La Hiruela	[12]	1	41.00	3.50	29	8	20	1
5	El Ventorrillo	[64]	1	40.75	4.00	40	10	27	3
6	Chiclana de la Frontera	[4, 5, 6]	4	36.42	6.17	56	25	26	5
7	Aldehuela de la Bóveda	[40]	4	40.83	6.00	–	15	–	3
8	Pego-Oliva	[67]	9	38.87	0.08	15	8	6	1
9	Valle del Alberche	[54]	25	40.50	4.67	50	19	25	6
10	Parque Natural de la Font Roja	[88]	25	38.67	0.53	18	5	10	3
11	Villafáfila	[76]	28	41.83	5.67	36	13	21	2
12	Sierras Subbéticas	[48]	50	37.42	4.33	40	17	20	3
13	Macizo Central de Gredos	[55]	100	40.25	5.33	61	22	31	8
14	Ceuta	[75]	150	35.83	5.25	62	24	32	6
15	Depresión Guadix-Baza	[80]	400	37.50	3.17	47	18	29	0
16	Picos de Europa	[34, 37, 66]	866	43.08	5.08	57	16	34	7
17	Sierra Nevada	[3]	1 250	37.08	3.50	52	22	28	2
18	Vizcaya	[7]	2 217	43.17	2.83	47	13	27	7
19	Baleares	[62]	5 014	39.63	–2.76	39	13	23	3
20	Almería	[18]	8 774	37.29	2.40	54	28	21	5
21	Navarra	[47]	10 421	42.67	1.67	48	17	21	10
22	Cordillera Cantábrica	[34, 37]	10 569	43.00	5.58	–	23	45	–
23	Salamanca	[31, 32, 33]	12 336	40.75	6.00	76	31	38	7
24	Albacete	[74, 81]	14 858	38.75	1.83	76	28	35	13
25	León	[27, 28, 77, 78, 79]	15 468	42.67	5.92	98	35	55	8
26	Cáceres	[35, 36, 39, 71]	19 945	39.83	6.33	76	31	37	8
27	Iberian Peninsula	[2, 10, 38, 86, 87]	596 750	39.89	3.05	198	55	110	33

were handled (log 0 is undefined) using log  $x+1$  transformations, leading to much smaller errors than those stemming from omitting zeroes [89].

Since (2), used to make comparisons for the three subfamilies, is non-linear, a non-linear regression (Quasi-Newton method, STATISTICA software [83]) was used to obtain parameter estimates [72]. While linear model slopes and intercepts must be compared using analysis of covariance [82], in the absence of any analogue procedure for non-linear models, a jackknife technique was applied to a data-set of 24 localities (25 for the Scarabaeinae; see *table 1*) calculating 24  $q$  and  $z$  scores leaving out one locality each time. Between-group comparisons of slopes ( $z$ ) and  $\alpha$ -diversity scores ( $q$ ) were made by the non-parametric Kruskal-Wallis ANOVA and Mann-

Whitney U-test. The null hypothesis of similar  $z$  and  $q$  between-group parameters was rejected at  $P \leq 0.01$ . Non-linear regression techniques can manage  $S = 0$  data [89].

When investigating the variation in species number at sites of different sizes, correction must be made for possible non-random geographic distribution, i.e. spatially autocorrelated species number and site size [51, 52, 69]. Iberian peninsula site size is not homogeneous geographically (*figure 1*) and neighbouring sites' species number is probably similar because of decisive spatially structured environmental variables. To eliminate the effects of spatial autocorrelation, forward stepwise analysis was performed for both  $S$  and  $A$  (dependent variable), using the nine terms of a third-degree polynomial equation of latitude and longitude

as independent variables (trend surface analysis – TSA; [52]). Residuals for each locality from each regression, good measures of *S* and *A* independent of spatially structured environmental variables [52], were retained. The species-area linear regression was calculated again with these ‘new’ non-spatially structured scores of *S* and *A* variables.

Species richness variance accounted for by space ( $R^2_S$ ) has been estimated by means of a TSA with the number of species as dependent variable. That not accounted for by space ( $R^2_{NS} = 1 - R^2_S$ ) includes the variance explained by the area ( $R^2_A$ ) and the remaining unexplained variance ( $R^2_{UE}$ ):  $R^2_{NS} = R^2_A + R^2_{UE}$ . To get an estimate of the percentage of richness variance accounted for by the area ‘in itself’, the species richness variance explained using the ‘new’ non-spatially structured variables in the species-area relationship ( $R^2_{TSA}$ ) was calculated. As  $R^2_{TSA}$  is a fraction of the variance not explained by space ( $R^2_{NS}$ ),  $R^2_A$  may be estimated because  $R^2_A = (R^2_{TSA} \times R^2_{NS})$ . Lastly, the unexplained ( $R^2_{UE}$ ) variance can be estimated as  $R^2_{UE} = 1 - (R^2_S + R^2_A)$ .

Latitude and longitude were taken at the central point of each area, except for the entire Iberian Peninsula which was not taken into consideration because on the spatial scale analysed, the ‘central point’ of the whole Iberian Peninsula makes no sense.

### 3. RESULTS

#### 3.1. Dung beetle slopes in log-log species-area curve

The linear species-area relationship for the Iberian Scarabaeinae is

$$\log S = 1.036 + 0.092 \log A$$

$$(R^2 = 0.5074; F_{(1,23)} = 23.69, P < 0.0001);$$

for the Aphodiinae,

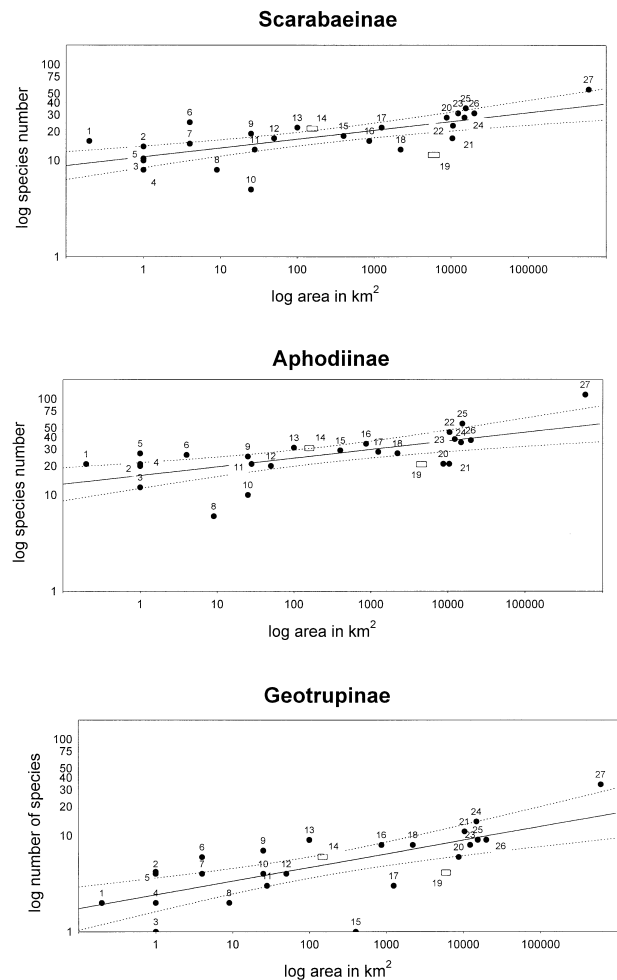
$$\log S = 1.202 + 0.090 \log A$$

$$(R^2 = 0.4303; F_{(1,22)} = 16.61, P = 0.0005);$$

and for the Geotrupinae,

$$\log S = 0.382 + 0.142 \log A$$

$$(R^2 = 0.5095; F_{(1,22)} = 22.86, P = 0.0001).$$



**Figure 3.** Log-log species-area relationship for Scarabaeinae, Aphodiinae, and Geotrupinae Iberian dung beetle groups. Numbered black dots are localities indicated in *table I*. Numbered white squares are Balearic Islands and Ceuta (N-Africa) (14 and 19, respectively). Dotted lines correspond to 95 % confidence limits.

The species-area curve based on all species is:

$$\log S = 1.457 + 0.098 \log A$$

$$(R^2 = 0.5470; F_{(1,21)} = 25.36, P < 0.0001).$$

In all cases, the scores corresponding to North Africa (‘Ceuta’, locality 14) and those of Balearic islands (locality 19) are respectively above and below the corresponding regression lines. There is a great dispersion of the points along the species-area curve and some other Iberian areas are outside the 95 % confidence interval (*figure 3*).



**Table II.** Between-group comparisons of the slope ( $z$ ) and intercept ( $q$ ) of the curvilinear species-area model ( $S = q + cA^z$ ). Twenty-four  $q$  and  $z$  scores were calculated leaving out one locality each time (table I). Comparisons of  $q$  and  $z$  parameters were performed using a non-parametric ANOVA Kruskal-Wallis test (\*\*\*)  $P \leq 0.001$ . Pairwise significant differences between subfamilies ( $P \leq 0.01$ ) for  $q$  and  $z$  parameters are shown in Mann-Whitney U-test columns.

	$c$	Mann-Whitney U-test		$z$	Mann-Whitney U-test	
		$q$				
Total	1.019	34.367		0.382		
Scarabaeinae	1.100	11.710	Aphodiinae, Geotrupinae	0.277	Aphodiinae, Geotrupinae	
Aphodiinae	0.305	19.713	Scarabaeinae, Geotrupinae	0.428	Scarabaeinae	
Geotrupinae	0.115	2.453	Scarabaeinae, Aphodiinae	0.420	Scarabaeinae	
Kruskal-Wallis test ( $n = 73$ )		64.00***		40.82***		

### 3.2. $\alpha$ - and $\beta$ -diversity comparison between groups

Both the slopes ( $\beta$ -diversity) and intercepts ( $\alpha$ -diversity) of the curvilinear regressions for the three subfamilies are significantly different (table II). The slope of Scarabaeinae is significantly less than Aphodiinae (Mann-Whitney U-test = 5.50;  $n_1 = 25$ ,  $n_2 = 24$ ,  $P < 0.0001$ ) and Geotrupinae (Mann-Whitney U-test = 5.16;  $n_1 = 25$ ,  $n_2 = 24$ ,  $P < 0.0001$ ). However, those of Aphodiinae and Geotrupinae do not differ at a statistically significant level such as  $P < 0.01$  (Mann-Whitney U-test = 2.19;  $n_1 = 24$ ,  $n_2 = 24$ ,  $P = 0.03$ ). The scores of  $\alpha$ -diversity, as indicated by the  $q$  parameter, significantly differ for all pairwise comparisons: Scarabaeinae vs. Geotrupinae (Mann-Whitney U-test = 6.0;  $n_1 = 25$ ,  $n_2 = 24$ ,  $P < 0.0001$ ), Scarabaeinae vs. Aphodiinae (Mann-Whitney U-test = 6.0;  $n_1 = 25$ ,  $n_2 = 24$ ,  $P < 0.0001$ ), and Aphodiinae vs. Geotrupinae (Mann-Whitney U-test = 5.94;  $n_1 = 24$ ,  $n_2 = 24$ ,  $P < 0.0001$ ). The  $\alpha$ -diversity score of Aphodiinae is nearly twice that of the Scarabaeinae and is eight times greater than that of Geotrupinae (table II).

### 3.3. How predictive is the area?

Nearly 89 % of total richness variance is explained by area size with the curvilinear model of species-area relationships. The corresponding  $R^2 \times 100$  scores are similar both in Aphodiinae and Geotrupinae (around 84 %), but higher than that of Scarabaeinae (77 %) (table III). Space explains around 39 % of total species number variability, scoring the highest percentage for Aphodiinae (55 %), the lowest for Geotrupinae (15 %), and in-between for Scarabaeinae (29 %). It is remarkable that the percentage of total species number variability explained by area is similar to that explained by space. However, the species number variance of Aphodiinae is accounted for by the environmental spatially structured variables rather than area size. Conversely, species number variation of both

Scarabaeinae and Geotrupinae is better explained by area size. Lastly, except for Geotrupinae (54 %), the percentage of unexplained variance, 27 and 23 % (table III), is similar and low in Scarabaeinae and Aphodiinae, respectively.

## 4. DISCUSSION AND CONCLUSIONS

Regarding the linear models of the species-area relationships, Scarabaeinae (0.092), Aphodiinae (0.089), and Geotrupinae (0.142) slopes are very low. Small  $z$  values indicate low species-accumulation rates with increasing area. Out of one hundred studies mentioned by Connor and McCoy [26], only eight have scores lower than 0.10, and sixteen lower than 0.15. Such low slopes are also known for protozoans, spiders, other insects, birds and mammals [26]. This rare pattern can be in agreement with the general ecological features of dung beetles, an insect group well adapted to the colonisation of dung pats, ephemeral habitats. It has been widely argued that dung beetles are taxa with good dispersal ability and, probably, habitat generalists operating in dung resources everywhere [44, 45]. As expected, North Africa ('Ceuta', locality 14) and Balearic islands (locality 19), are, respectively, above and below the corresponding regression lines. North African territories host a rich regional pool of dung beetle species [9, 75] while dung beetle communities inhabiting Balearic Island represent a rather qualitatively and quantitatively impoverished Iberian fauna [57]. Many other sites also show important deviations from the predicted line (figure 2).

Species number increment rate with increasing area differs significantly between Scarabaeinae and the other two subfamilies, and to a lesser extent, between Aphodiinae and Geotrupinae (table II). That means that on a geographic scale, remarkable differences in

**Table III.** Percentages of the species richness variance ( $R^2$ : coefficient of multiple determination  $\times 100$ ) for total Iberian dung beetle fauna, Scarabaeinae, Aphodiinae, and Geotrupinae subfamilies.  $S = q + cA^z$  is the curvilinear model of the species-area relationship [72].  $R^2_S$  is the species richness variance accounted for by space. The nine terms of a third-degree polynomial equation of latitude and longitude were taken as independent variables in the species-space regression (trend surface analysis – TSA; [52]). SST, Significant spatial terms in the species-space regression with in brackets, the sign of the relationship;  $R^2_{NS}$ , species richness variance not explained by space ( $R^2_{NS} = 1 - R^2_S$ );  $R^2_{TSA}$ , percentage of species richness variance accounted for by the species-area regression, removing spatial structure of both variables by means of a TSA;  $R^2_A$ , species richness variance explained by area [ $R^2_A = (R^2_{TSA} \times R^2_{NS})$ ];  $R^2_{UE}$ , unexplained variance [ $R^2_{UE} = 1 - (R^2_A + R^2_S)$ ].

	Total	Scarabaeinae	Aphodiinae	Geotrupinae
$S = q + cA^z$	88.57 %	77.23 %	84.35 %	84.49 %
$R^2_S$	39.44 %	29.34 %	55.40 %	15.29 %
SST	Latitude <sup>2</sup> $\times$ longitude [-]	longitude <sup>3</sup> [-]	latitude <sup>2</sup> $\times$ longitude [-]	latitude <sup>3</sup> [+]
$R^2_{NS}$	60.56 %	70.66 %	44.60 %	84.71 %
$R^2_{TSA}$	61.33 %	61.87 %	48.77 %	36.42 %
$R^2_A$	37.14 %	43.72 %	21.75 %	30.85 %
$R^2_{UE}$	23.42 %	26.94 %	22.85 %	53.86 %

species turnover should be observed, especially between Scarabaeinae on the one hand, and Aphodiinae and Geotrupinae on the other. As the larger areas tend to be environmentally more heterogeneous, and the rate of species increase with area differs significantly between groups, on a geographical scale, the effect of habitat variety on Aphodiinae and Geotrupinae richness must be more pronounced than on that of Scarabaeinae. These results are in agreement with those of Lobo et al. [59], who found that on a regional scale, Aphodiinae species are more sensitive than Scarabaeinae to environmental heterogeneity. No comparative data are available for Geotrupinae.

The values of  $\alpha$ -diversity also are significantly different for the three subfamilies. The Aphodiinae  $q$  score is 1.7 times greater than that of Scarabaeinae and nearly eight times greater than that of Geotrupinae (table II). So, Aphodiinae species are more relevant to local diversity (1 km<sup>2</sup>) than are Scarabaeinae. Early results show, however, that the richness of a single dung pat is rather more a function of the Scarabaeinae species pool [59]. This contradiction is more apparent than real, taking into account vagility, the other major biological characteristic of species with high spatial turnover rates [22]. If, on average, Aphodiinae species are less able to disperse between neighbouring droppings than Scarabaeinae species, on a scale of 10 m (between-dropping movements), group differences in dispersal capacity may lead to: i) a greater contribution to dung pat richness from the group (Scarabaeinae) with greater between-dropping mobility; and ii) greater species homogeneity of this group between neighbouring sites (lower  $\beta$ -diversity). Verification of Scarabaeinae species' greater dispersal ability would be enough to explain both groups' relative contribu-

tion to  $\beta$  and  $\alpha$ -diversity on a scale of 10 m (between dropping movements) and on a local scale (1 km<sup>2</sup>). The conclusion is that Scarabaeinae dominates  $\alpha$ -diversity on a between-dropping scale, while Aphodiinae does so on local to larger scales. In other words, the richness of communities established in each dung pat depends on the Scarabaeinae species, but the local and regional pool richness depends on Aphodiinae.

The potential mechanisms that influence local species number are many and not mutually exclusive [50]. In the case of Iberian dung beetles, unique geographical and historical circumstances seem to have been decisive in the formation of present local richness [56]. Some species attributes which are the result of their specific evolutionary history, such as habitat specialisation and dispersal capacity, seem also to play a fundamental role in the determination of local and regional richness. Both factors have been invoked as responsible for  $\beta$ -diversity [22, 46]. In dung beetle, habitat specialisation would act on between-habitat to larger scales, while the low dispersal capacity would mainly determine the spatial turnover of species on a within-habitat scale. However, the degree of dependence of the whole geographic range on ecological dispersal capacity and the latter's interdependence on habitat specialisation still remains unknown. At present, some progress has been made on searching for habitat selection [45], and data on good dispersal ability of a variety of successful medium-sized, high-fecundity species with a high population growth rate are well known ([11, 44, 68] and references therein). However, data on dispersal rate are badly needed [44], and most concretely, dispersal capacity differences between Aphodiinae and Scarabaeinae species have not yet been empirically demonstrated. Therefore, it

remains to be proven whether presence in a greater number of dung pats (low local  $\beta$ -diversity) is a consequence of differences in between-dropping movements.

The percentage of total richness variance explained by area is rather high. Area also accounts for high percentages of species richness variance for Aphodiinae, Geotrupinae, and to lesser extent for Scarabaeinae. But if the spatial structure of both the area ( $A$ ) and species counts ( $S$ ) is extracted, its explanatory power greatly decreases, to roughly 37 % for the total dung beetle species. A considerable fraction of the richness variation, around 39 %, must be related with some other ignored spatially structured environmental variables. This area effect is also low (22 %) in Aphodiinae and slightly greater in Geotrupinae (31 %). Area size has more predictive power (43 %) on Scarabaeinae richness. Hence, area size per se is not as good a predictor variable as has been commonly argued. The removal of the spatial structure of variables  $S$  and  $A$  significantly reduces the explanatory power of the area, but this decrease probably would be still greater if the effect of other simple environmental variables such as temperature, rainfall, soil type, insolation, etc., were considered. Actually, area is a multi-factor variable that summarises other causal and truly explicative environmental variables, but it is currently used when no detailed environmental information is available.

As expected, the fraction of richness variation related with ignored spatially structured variables is greater in Aphodiinae, considered to be more of a habitat specialist than Scarabaeinae [59]. The former shows greater species turnover, from local to higher scales, than the latter. Also remarkable is the high percentage of unexplained variance in Geotrupinae (nearly 54 %), suggesting a complex multiplicity of historical and/or ecological factors which potentially account for its species richness variance.

However, a major question which still remains is: why Iberian Scarabaeinae species seem to be more habitat generalists than Iberian Aphodiinae species? We advance two non-exclusive explanations, one behavioural and another historical. First, most of Aphodiinae species are relatively small, the adults living and eating within fresh droppings (dwellers). Unlike Scarabaeinae and Geotrupinae species, the majority of Aphodiinae species deposit their eggs in dung pats without constructing any kind of nest or chamber [17]. Due to the free life style of the Aphodiinae larvae, these species should be more exposed to environmental heterogeneity; and therefore be more

habitat specialists than Scarabaeinae species. The historical explanation is related with the between-group differences in the geographical barriers and proximity to the centre of distribution of each taxon. Aphodiinae are the numerically dominant coprophagous group in the dung beetle communities of northern high latitudes [14, 43]. Greater diversity of Aphodiinae in temperate biomes may be related to greater tolerance of low temperatures [16]. In contrast, most phylogenetic lines of the Scarabaeinae are of a Gondwanaland origin [16, 41, 42], and are the numerically dominant coprophagous group in torrid Afrotropical biomes. Thereby, the arrival of generalist invader species may have made a greater contribution to species richness in Iberian Scarabaeinae species than in Aphodiinae species. The lengthy duration of the effects of human presence in the Iberian region would enhance this process [63].

New insights and more investigation on the environmental and historical factors causing the geographical distribution patterns of the Iberian dung beetles not correlated with area size are needed.

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