An intercontinental comparison of dung beetle diversity between two mediterranean-climatic regions: local versus regional and historical influences

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Abstract. The species richness of biological communities is influenced by both local ecological, regional ecological, and historical factors. The relative importance of these factors may be deduced by comparison between communities in climatically and ecologically equivalent, but geographically and historically separate regions of the world. This claim is based on the hypothesis that community processes driven by similar local ecological factors lead to convergence in species richness whereas those driven by differing regional or historical factors lead to divergence. An intercontinental comparison between the winter rainfall regions of South Africa and the Iberian Peninsula showed that overall species richness of dung beetles was dissimilar at local, subregional and regional scales in Scarabaeidae *s. str.* but similar at all scales in Aphodiinae. Removal of species widespread in the summer rainfall region of Africa or the temperate region of Europe (regional component) resulted in dissimilarity in species richness of mediterranean

endemics at all scales in both dung beetle taxa. However, the lines joining each set of species richness values were parallel which may indicate similarities in processes between different mediterranean climatic regions despite slight differences in latitudinal range. The dominant pattern of dissimilarity or non-convergence may be related primarily to intercontinental differences in regional biogeographical and evolutionary history (faunal dispersal, glaciation effects in relation to geographical barriers to dispersal, speciation history, long-term disturbance history). The limited pattern of similarity or convergence in overall species richness of Aphodiinae may be a chance result or primarily related to intercontinental similarities in local ecological factors.

Key words. Convergent species richness, dung beetles, historical factors, Iberian Peninsula, mediterranean-type regions, Scarabaeoidea, South Africa.

INTRODUCTION

The present-day composition and diversity of biological communities derives from a complex of local and regional processes (Ricklefs, 1987). On the one hand, present-day diversity stems partly from historical processes (Ricklefs, 1987; Schluter & Ricklefs, 1993a; Westoby, 1993) which include biogeographical events, adaptive radiation, speciation, disturbance history and extinction. On the other hand, it stems partly from current functional ecological processes (discussed by Cornell & Karlson, 1996) which may limit maximum diversity according to available

resources. This limitation operates through the functional processes of resource partitioning and species packing which can hypothetically continue up to the point where niche overlap reaches the maximum possible ecological similarity between species for coexistence to continue (limiting similarity). Beyond this species saturation point, there will be no increase in diversity owing to competitive exclusion either of existing community members or of further regional immigrants. Thus, present-day diversity results from the balance between these current local ecological processes, the regional process of dispersal and the enduring effects of preceding history (Ricklefs, 1987).

This scenario leads to a prediction. If local processes are predominant in determining species richness, the diversity of distant communities in ecologically similar

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environments will be convergent regardless of the origins of their components. In opposition to this process, composition and diversity of distant communities will be divergent if they are predominantly influenced by the unique geographical characteristics of each region and its particular historical circumstances (Orians & Paine, 1983; Ricklefs, 1987; Schluter & Ricklefs, 1993a; Ricklefs & Schluter, 1993). Thus, by comparing the degree of convergence in species richness between ecologically similar but geographically separate communities, it is possible to examine the relative contribution of local, regional and historical factors to diversity (Westoby, 1993; Schluter & Ricklefs, 1993b).

Methods for such comparison have to deal with the difficulty in separating the effects of ecological from those of historical factors (Schluter, 1986; Schluter & Ricklefs, 1993b; Westoby, 1993). For a strongly supported indication of convergence, it is necessary to quantify the relative contribution of habitat and history to the overall variation in diversity (ANOVA procedure; Cody & Mooney, 1978; Schluter, 1986). However, as this method requires a large number of replicated samples for many areas, it cannot be applied to assess convergence where data are limited (Wiens, 1991), as in the present case. Since no additional data will be available in the near future, we have compared regional diversity patterns using methods reviewed by Westoby (1993).

Of four hypothetical patterns obtainable by comparing local and regional diversity of climatically and ecologically similar areas on different continents, three have been demonstrated in nature (Westoby, 1993). Convergent local diversity, but divergent regional diversity ('V'-shaped pattern), has been demonstrated for plants in mediterranean-climatic regions of Australia and South Africa. Proportionately divergent local and regional diversity (parallel lines) has been demonstrated for several animal groups (Australian and Caribbean reef fishes, Australian and North American lizards; Westoby, 1993). Convergence at both local and regional scales (congruent lines) has also been demonstrated for Australian and North American birds but this is interpreted as a chance result (Westoby, 1993). There are also conflicting results for the same taxonomic group (see, for example, Tonn *et al.*, 1990 and Oberdorff, Hugueny & Guégan, 1997 for European and North American fishes). In view of these findings, we would suggest that greater frequency of a particular pattern defines the dominant intercontinental trend.

The present study compares species richness of dung beetle assemblages at different spatial scales between two mediterranean climatic regions located in distant continents. These are the winter rainfall region of the Western Cape in South Africa and the west mediterranean region of Europe and north Africa, principally the Iberian Peninsula. This comparison considers separately the data for two principal taxonomic groups of dung beetles (Scarabaeidae *s. str.*, Aphodiinae) which have different ecological adaptations and evolutionary histories (Hanski & Cambefort, 1991). Firstly, we made an intercontinental comparison between local species richness and the slopes and intercepts of their species-area relationships. Then, we analysed the increase in species richness at three spatial scales (local, subregional and regional). This analysis used both observed species richness and values estimated from the species-area relationships. We end by discussing the probable processes selecting for convergence or non-convergence in the intercontinental comparisons. Separation of ecological from historical influences on the data collected for these groups is assisted by the relatively extensive knowledge of dung beetle ecology and biogeography (Hanski & Cambefort, 1991). Such knowledge is used to test intercontinental similarity in both overall species richness and that in mediterranean climatic endemics (specialized local component) after removal of widespread elements (regional component).

As South Africa and the Iberian peninsula show higher differences in their biogeography and history (Jaeger *et al.*, 1987; Loftus *et al.*, 1994; Deacon, 1992), we hope that the effects of divergent biogeographical histories are greater than those of local ecological processes, and so a stronger trend at intercontinental divergence in diversity than at convergence.

METHODS

We used both unpublished and published data from mediterranean climates for the intercontinental comparison of species richness at different spatial scales. Published data have been drawn mainly from local journals whereas unpublished data have been drawn mainly from theses. Origins of data are cited in Tables 1 and 2.

To ensure that the South African species lists were exhaustive, we plotted species accumulation or 'collector's' curves (Colwell & Coddington, 1995) for the ten traps placed in each of the eleven localities

Table 1. Species richness of Scarabaeidae (Sscar) and Aphodiinae (Sapho) recorded in study areas of shrubland and pasture in the winter rainfall regions of South Africa and the western Mediterranean region of Europe. The number of winter rainfall endemic species remaining after the removal of species also widespread in the adjacent temperate (Iberian Peninsula) or summer rainfall (South Africa) climate types is placed in brackets.

Locality	Surface area	Latitude	Sscar	Sapho	References
West Mediterranean					
1 Colmenar Viejo	0.2 km²	40° 40′	16 (12)	21 (7)	Veiga (1982)
2 Sierra de Alfacar	1 km²	37° 10′	14 (9)	21 (9)	Fernández-Sigler (1986)
3 Cabo de Gata	1 km²	36° 40′	10 (7)	12 (7)	Rozas & Avila (1990)
4 La Hiruela	1 km²	41° 00′	8 (4)	20 (7)	Baz (1988)
5 El Ventorrillo	1 km²	40° 25′	10 (6)	27 (8)	Martín-Piera, Veiga & Lobo (1986)
6 Chiclana de la Frontera	4 km²	36° 25′	25 (18)	26 (12)	Avila, Sánchez-Piñero & Pascal (1989); Avila & Sánchez-Piñero (1988, 1990)
7 Aldehuela de la Bóveda	4 km²	40° 50′	15 (9)	—	Galante *et al.* (1991)
8 Pego-Oliva	9 km²	38° 53′	8 (6)	6 (3)	Micó, Verdú & Galante (1998)
9 Valle del Alberche	25 km²	40° 30′	19 (14)	25 (6)	Lobo (1982)
10 Font Roja	25 km²	38° 40′	5 (3)	10 (5)	Verdú (1994)
11 Villafáfila	28 km²	41° 50′	13 (9)	21 (7)	Salgado-Costas (1983)
12 Sierras Subbéticas	50 km²	37° 25′	17 (13)	20 (9)	Hidalgo & Cárdenas (1994)
13 Macizo Central Gredos	100 km²	40° 15′	22 (14)	31 (11)	Lobo (1992)
14 Ceuta	150 km²	35° 50′	24 (18)	32 (21)	Ruiz (1995)
15 Depresión Guadix-Baza	400 km²	37° 30′	18 (13)	29 (17)	Sánchez-Piñero (1994)
16 Sierra Nevada	1250 km²	37° 50′	22 (15)	28 (15)	Avila & Pascual (1988)
17 Salamanca	12 300 km²	40° 45′	31 (22)	38 (12)	Galante (1979, 1981, 1983)
18 Albacete	14 800 km²	38° 45′	28 (21)	35 (16)	Ruano-Marco, Martín-Piera & Andújar Tomás (1988); Sánchez-Ruiz, Sánchez-Ruiz & López-Colón (1994)
19 Caceres	19 900 km²	39° 50′	31 (21)	37 (10)	Rodríguez-Romo, Galante & García-Román (1988); Galante & Rodríguez-Romo (1988); Galante, Rodríguez-Romo & García-Román (1989); Galante & Stebnicka (1993)
20 Mediterranean Iberian Peninsula	476 000 km²		52 (35)	94 (54)	Veiga & Martín-Piera (1988); Baraud (1992)
South Africa					
1 Cape Peninsula	145 km²	34° 20′	18 (13)	20 (16)	Davis (1993a)
2 West coast, Western Cape	330 km²	33° 20′	40 (28)	30 (24)	Davis (1993a)
3 South-western tip, Western Cape	475 km²	33° 50′	45 (32)	34 (28)	Davis (1993a)
4 South-west of Western Cape	1614 km²	33° 20′	49 (37)	—	Davis & Lobo (unpublished ms)
5 South African winter rainfall region	115 800 km²		88 (67)		Ferreira (1972); Scholtz & Howden (1987a,b); Howden & Scholtz (1987)

(Table 2). We remove the effect of sample order by computing the number of species in a single trap at random, after we select a second trap added in random order (100 randomizations) and re-computed the species richness using the pooled data from both samples, and so on until all traps are included (Colwell, 1997). All eleven curves reached an asymptote indicating that most species present had been recorded (Fig. 1A). In the studies conducted in the Iberian Peninsula, we could not test the exhaustiveness of the scarabaeid and aphodine data by this method because there is no measure of the recording effort in most studies. However, we have estimated the true richness at each locality by applying the Abundance-base Coverage Estimator (ACE) using the EstimateS package (Colwell, 1997). ACE was first proposed by

Table 2. Species richness of Scarabaeidae (Sscar) and Aphodiinae (Sapho) recorded over one year at 1 km² study sites in the western Mediterranean region of Europe and in mediterranean-type localities in South Africa. The number of winter rainfall endemic species remaining after the removal of species also widespread in the adjacent temperate (Iberian Peninsula) or summer rainfall (South Africa) climate types is placed in brackets.

Locality	Sscar	Sapho	References
West Mediterranean			
Aldehuela de la Bóveda	15 (9)	—	Galante *et al.* (1991)
Colmenar Viejo	16 (12)	21 (7)	Veiga (1982)
La Hiruela	8 (4)	20 (7)	Baz (1988)
El Ventorrillo	10 (6)	27 (8)	Martín-Piera *et al.* (1986)
Valle del Alberche (El Barraco)	19 (14)	19 (4)	Lobo (1982)
Macizo de Gredos (Hiruela Cimera)	16 (9)	18 (6)	Lobo (1992)
Macizo de Gredos (Hiruela Mediana)	18 (10)	22 (9)	Lobo (1992)
Depresión Guadix-Baza (Barranco del Espartal)	11 (8)	18 (12)	Sánchez-Piñero (1994)
Depresión Guadix-Baza (Rambla del Grao)	11 (8)	17 (9)	Sánchez-Piñero (1994)
Depresión Guadix-Baza (Ladihonda)	13 (8)	19 (10)	Sánchez-Piñero (1994)
Sierras Subbéticas (La Nava)	14 (10)	17 (6)	Hidalgo & Cárdenas (1994)
Sierra de Alfacar	14 (9)	21 (9)	Fernández-Sigler (1986)
Sierra Nevada (800 m)	12 (8)	11 (6)	Avila & Pascual (1988)
Sierra Nevada (1000 m)	14 (9)	15 (6)	Avila & Pascual (1988)
Sierra Nevada (1100 m)	17 (11)	21 (7)	Avila & Pascual (1988)
Sierra Nevada (1300 m)	14 (9)	13 (5)	Avila & Pascual (1988)
Cabo de Gata	10 (7)	12 (7)	Rozas & Avila (1990)
Chiclana de la Frontera (El Chaparral)	22 (18)	22 (10)	Avila *et al.* (1989); Avila & Sánchez-Piñero (1988, 1990)
Ceuta (Ceuta)	18 (13)	22 (14)	Ruiz (1995)
Mean ± SD	14.3 ± 3.6	18.6 ± 4.0	
Mean ± SD after removal	(9.6 ± 3.1)	(7.9 ± 2.5)	
Western Cape, South Africa			
Cape Peninsula (Bonne Attente)	14 (9)	15 (13)	Davis (1993a)
West Coast (Groote Post)	23 (14)	21 (16)	Davis (1993a)
West Coast (Waylands)	17 (10)	20 (15)	Davis (1993a)
West Coast National Park (pasture)	22 (14)	16 (13)	Davis (1993a)
West Coast (Oranjefontein)	20 (12)	22 (17)	Davis (1993a)
Cape Peninsula (Cape of Good Hope Nature Reserve, 9–10 yr old fynbos)	12 (10)	14 (11)	Davis (1993a)
Cape Peninsula (Cape of Good Hope Nature Reserve, 2–3 yr old fynbos)	13 (11)	12 (11)	Davis (1993a)
West Coast (Modderrivier)	33 (23)	17 (13)	Davis (1993a)
West Coast National Park (shrubland)	24 (17)	16 (15)	Davis (1993a)
West Coast (Pampoenvlei, sand)	30 (22)	18 (13)	Davis (1993a)
West Coast (Pampoenvlei, sandy loam)	25 (17)	17 (13)	Davis (1993a)
Mean ± SD	21.2 ± 6.8	17.1 ± 3.0	
Mean ± SD after removal	(14.5 ± 4.8)	(13.6 ± 1.9)	

Chazdon *et al.* (1988) and is a modification of Chao & Lee's (1992) estimator which eliminates the consistent overestimate of species richness yielded by Chao & Lee's method (Colwell & Coddington, 1995). We have considered all those studies with abundance values for the two considered taxonomical groups of dung beetles (seventeen studies). As shown in Fig. 1B, there are no important differences between the number of species estimated by ACE and that listed in a particular inventory. On average, 93.8% of the maximum species richness estimate was inventoried in the Iberian Peninsula.

The first analysis of species-area patterns generates species area curves for Scarabaeidae *s. str.* and Aphodiinae using observed species richness data for both shrubland and pasture habitats. European data
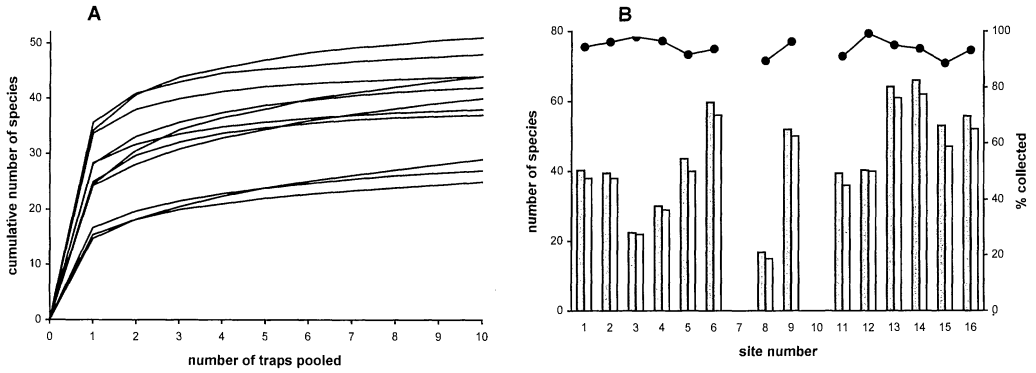
Fig. 1. (A) Species accumulation curves for dung beetle species across different number of traps pooled (100 randomizations) at each of eleven South African localities listed in Table 2. These calculations have been made using the EstimateS package (Colwell, 1997). (B) Number of species recorded at the Iberian localities listed in Table 1 (white bars), the maximum possible species richness (black bars) calculated by the Abundance-base Coverage Estimator (ACE) (Chazdon *et al.*, 1988), and the percentage of this maximum that were recorded (broken line).
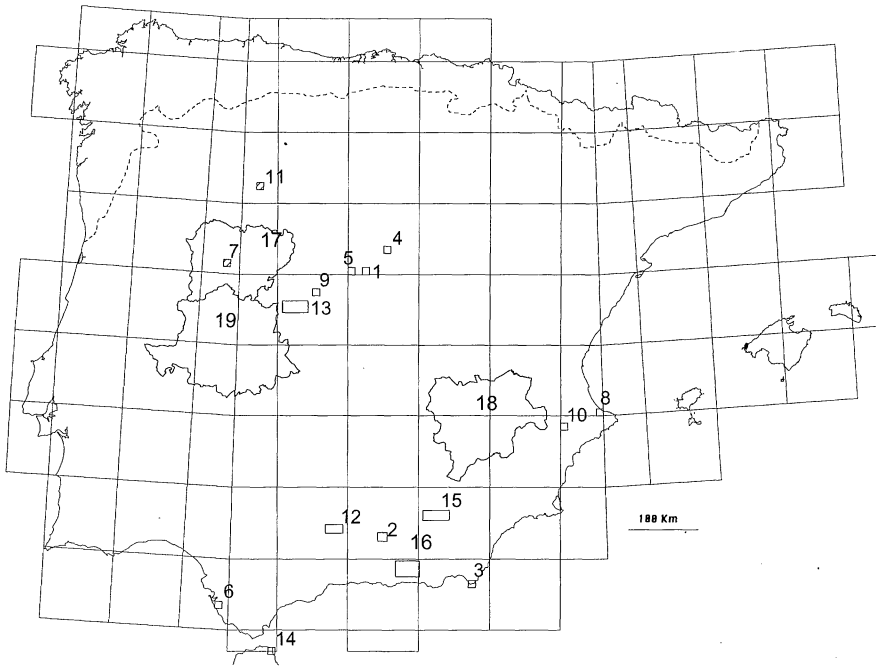

Fig. 2. Approximate location of the nineteen west mediterranean studies cited in Table 1. The broken line is the approximate limit of the Eurosiberian region.

are drawn from eighteen Iberian and one north African study conducted in areas of various size from 1 km² to 19,900 km² (Table 1 and Fig. 2). The total species observed in the mediterranean Iberian Peninsula (476, 000 km²) were determined using the general information of Veiga & Martín-Piera (1988) and Baraud (1992), together with the data of Avila (1986), Veiga (1988) and Galante & Verdú-Faraco (1994). Southern African data are drawn from eleven localities of 1 km² (Table 2) and four larger areas of different

size from $145 \, km^2$ to $1,614 \, km^2$ (Table 1). These data are derived from two extensive studies conducted in the Western Cape (Davis, 1993a; Davis & Lobo, unpublished). The total number of species in the Western Cape, winter rainfall region of South Africa were derived from the data of Ferreira (1972), Scholtz & Howden (1987a,b), Howden & Scholtz (1987), and from the reference collection of the former CSIRO Dung Beetle Research Unit which is now part of the National Collection of Insects in Pretoria, South Africa. Although there may be differences in taxonomic knowledge between the dung beetle fauna of Europe and that of South Africa, we consider that these inventories are fairly complete.

The second analysis also generates species area patterns for Scarabaeidae *s. str.* and Aphodiinae from both shrubland and pasture habitats. However, this analysis uses mean observed and predicted values for species richness to which linear regression lines are fitted. At the three spatial scales selected for the study, missing values were predicted using the species-area equation, $S = CA^z$, in which S is the predicted species richness, C is the species richness over $1 \, km^2$, A is the area, and z is a constant. In reference to the selected spatial scales, we use the term 'local diversity' to refer to species richness at sites of approximately $1 \, km^2$. In all cases, the data are derived from one year studies using similar capture methods, i.e. baited pitfall traps or natural dung pats. We use the term 'subregional diversity' in reference to species richness in an area of $475 \, km^2$. This is the area calculated for the study region in the Western Cape using the species area equation. We use the term 'regional diversity' when referring to the species richness in a region of $115,800 \, km^2$. This is the area measured for the entire winter rainfall region of South Africa. For this second analysis, the mean number of species at local scale ($1 \, km^2$) in Europe was calculated from data for nineteen shrubland and pasture sites (Table 2) whereas the predicted number of species at subregional ($475 \, km^2$) and regional scales ($115,800 \, km^2$) were calculated using the species area equation. The mean number of species at local scale in South Africa were calculated using the data from eleven localities cited in Table 2. The species-area equation was used to predict the number of aphodine species at regional scale in the Western Cape. All other South African data for subregional and regional scales were derived from observations.

In the first two analyses of species-area patterns, species richness is influenced by both local ecological, regional and historical influences. Therefore, in further

analyses, the regional component was partly removed by deleting all species widespread beyond the borders of mediterranean-type climate so that only the endemic species component remained. In the Iberian Peninsula, the principal groups of widespread species occurred also in the cooler, temperate regions of central and northern Europe. The endemic species were considered to be those showing either a Mediterranean or an Euroturanian distribution (La Greca, 1964). In South Africa, the principal groups of widespread species occurred also in the warmer, summer rainfall region of Africa (Davis, 1993b, 1997). The endemic species were considered to be those restricted (most species) or centred on (three species) the winter and bimodal rainfall regions. Biogeographical data were incomplete for southern African Aphodiinae. However, as most widespread Scarabaeidae were primarily active in summer (Davis, 1993b), species of Aphodiinae were deleted either if they were widespread or if they were active during summer in the Western Cape.

Slopes and intercepts of the regression equations generated by the analyses were compared using analysis of covariance (Sokal & Rohlf, 1969). As the slopes and intercepts of the power function are interdependent parameters, only intercepts from regressions of equal slope may be compared (Gould, 1979).

Whittaker's β-diversity index was used as a measure of species turnover between assemblages. In this index, $\beta = (S/a) - 1$, a is the mean species richness in a standard area of $1 \, km^2$ (local scale) and S is the overall species richness predicted for $115,800 \, km^2$ (regional scale). These indices indicate the amount of within region variability between species assemblages. Within taxon, intercontinental comparison of indices indicate to what degree the African and European communities are ecologically similar or dissimilar in terms of partitioning of space.

RESULTS

The observed species-area patterns for Scarabaeidae *s. str.* are shown in Fig. 3. For the South African Scarabaeidae, the species-area relationship is described by the equation, $\log S = 1.29347 + 0.11507 \log A$, $(F_{(1,14)} = 23.65; \ P = 0.0003; \ R^2 = 0.6281)$, whereas, for the Iberian Peninsula, it is described by the equation, $\log S = 1.04494 + 0.10192 \log A$, $(F_{(1,18)} = 20.71; \ P = 0.0003; \ R^2 = 0.5350)$. The slopes of the two regression lines (Fig. 3) are similar $(F_{(1,32)} = 0.02; \ NS)$ but the intercepts are significantly different $(F_{(1,33)} =$
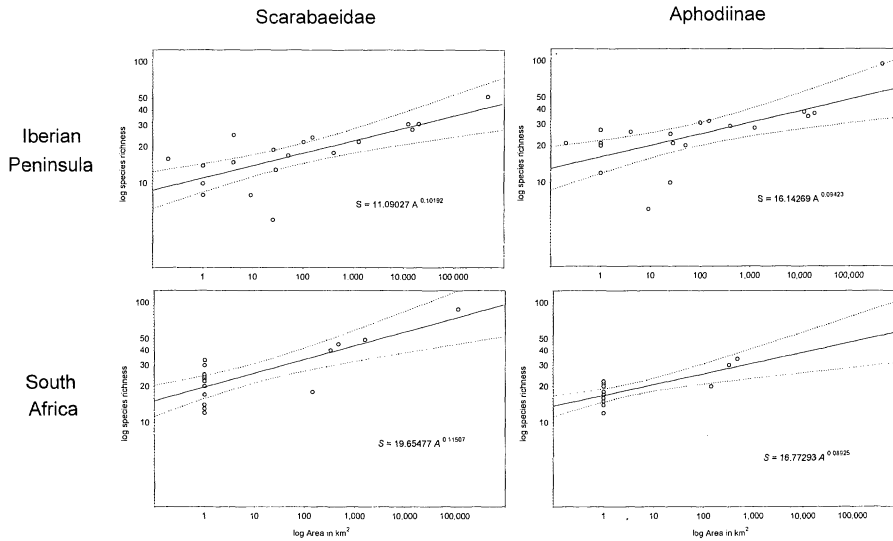
Scarabaeidae   Aphodiinae

Fig. 3. Species-area relationships for Scarabaeidae and Aphodiinae in mediterranean climatic regions of South Africa and the Iberian Peninsula. The dotted line is the 95% confidence interval.

23.51; $P = 0.0001$). In other words, both species-area curves are similar in shape but the species richness in South Africa is greater than that in the Iberian Peninsula (species richness comparison at local scale, t test $= 3.64$, df $= 28$, $P = 0.001$). On a similar spatial scale, real and estimated richness values for both continents (Fig. 4A) confirm that local, subregional and regional diversity are greater in the mediterranean areas of South Africa than in the Iberian Peninsula. The diversity lines are parallel or slightly convergent at local scale and the value of β-diversity for the Iberian Scarabaeidae is much lower than that for the South African Scarabaeidae (Table 3).

The observed species-area patterns for Aphodiinae are shown by Fig. 3. For the South African Aphodiinae, the species-area relationship is described by the equation, log $S = 1.22461 + 0.08925$ log A, $(F_{(1,12)} = 17.16$; $P = 0.001$; $R^2 = 0.5885)$ whereas, for the Iberian Peninsula, it is described by the equation, log $S = 1.20798 + 0.09423$ log, $(F_{(1,17)} = 13.84$; $P = 0.002$; $R^2 = 0.4487)$. In this case, neither the slopes of the two regression lines $(F_{(1,29)} = 0.43$; NS) nor the intercepts are significantly different $(F_{(1,30)} = 0.05$; NS) (Fig. 3). The two species-area curves are similar in shape and the local species richness is similar on both continents (species richness comparison at local scale, t test $= 1.08$, df $= 27$, $P = 0.29$). On a similar spatial scale, the lines that connect the three species richness values are clearly

congruent (Fig. 4B) (convergence at local and regional scales). The β-diversity for the Iberian Aphodiinae is slightly lower than that for the South African Aphodiinae (Table 3).

As there is a similar decrease at each spatial scale, deletion of non-endemic species (regional component) maintains the greater species richness of Scarabaeidae *s. str.* in the mediterranean region of South Africa compared to that in the Iberian Peninsula (Fig. 4A, Table 3). The inventory for the entire winter rainfall region of South Africa decreases by 24% (twenty-one spp.) from eighty-eight to sixty-seven species (Table 3) whereas that for the Iberian Peninsula decreases by 33% (seventeen spp.) from fifty-two to thirty-five species (Table 1). The predicted regional species richness for the Iberian Peninsula decreases by 28% (ten spp.) (Table 3). In South Africa, mean species richness at local scale decreases significantly by 32% from 21.2 ± 6.8 to 14.5 ± 4.8 species $(t = 2.67$, df $= 20$, $P = 0.02)$ whereas, in the Iberian Peninsula, it decreases significantly by 33% from 14.3 ± 3.6 to 9.6 ± 3.1 species $(t = 4.38$, df $= 36$, $P = 0.0001)$. Local species richness remains significantly different between the two continents $(14.5 \pm 4.8 / 9.6 \pm 3.1$; $t = 3.39$, df $= 28$, $P = 0.002)$. As in the analysis of the entire scarabaeid fauna, the slopes of the species-area regressions continue to be similar $(F_{(1,32)} = 0.26$; NS) and the intercepts continue to be significantly different $(F_{(1,33)} = 23.40$; $P < 0.0001)$. The
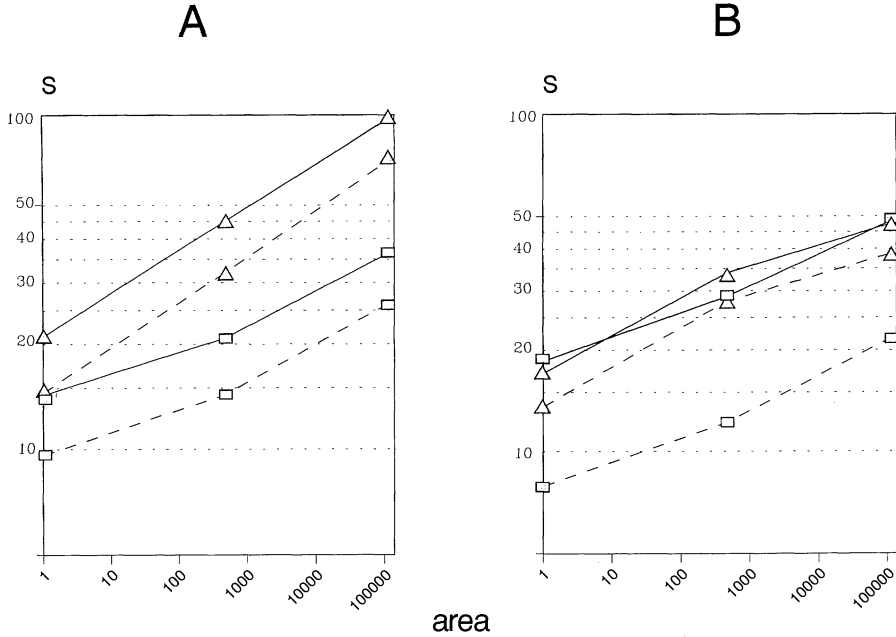
A
B

Fig. 4. Schematic representation of the increase in species richness with area for Scarabaeidae (A) and Aphodiinae (B) comparing the overall species richness (solid line) in the winter rainfall region of South Africa (triangle) and the mediterranean region of the Iberian Peninsula (square). The dotted line represents species richness of taxa endemic to the mediterranean climate in South Africa or the Iberian Peninsula with the more widespread species component removed. Species richness values are presented on a similar spatial scale for both continents (1 km², 475 km², 115,800 km²—see Methods for explanation).

Table 3. Values of z, beta diversity (β), and the numbers of species recorded or predicted ($S = CA^z$) at local, subregional and regional scales in the winter rainfall region of South Africa and the mediterranean region of the Iberian Peninsula. The values calculated for winter rainfall endemic species after the removal of species also widespread in the adjacent temperate (Iberian Peninsula) or summer rainfall (South Africa) climate types are placed in brackets (*Predicted S).

Surface area	Local 1 km²	Subregional 475 km²	Regional 115 800 km²	Slope of species-area regression (z)	β-diversity
South Africa	Mean $\pm$ SD	Total S	Total S		
Scarabaeidae	21.2 $\pm$ 6.8 (14.5 $\pm$ 4.8)	45 (32)	88 (67)	0.11507 (0.12435)	3.15 (3.62)
Aphodiinae	17.1 $\pm$ 3.0 (13.6 $\pm$ 1.9)	34 (28)	47.5 (38.7)*	0.08925 (0.09064)	1.78 (1.85)
Iberian Peninsula	Mean $\pm$ SD	Predicted S	Predicted S		
Scarabaeidae	14.3 $\pm$ 3.6 (9.6 $\pm$ 3.1)	20.8 (14.3)	36.4 (26.1)	0.10192 (0.10896)	1.55 (1.72)
Aphodiinae	18.6 $\pm$ 4.0 (7.9 $\pm$ 2.5)	28.9 (12.2)	48.4 (21.7)	0.09423 (0.10391)	1.60 (1.75)

lines connecting the three richness values (Fig. 4A) also continue to be parallel or, slightly convergent, at local scale and the value of β-diversity for the Iberian Scarabaeidae continues to be much lower than that for the South African Scarabaeidae *s. str.* (Table 3).

Deletion of non-endemic species of Aphodiinae increases the differences between mediterranean regions

(Fig. 4B) so that aphodine species richness now becomes much greater at all spatial scales in South Africa (Table 3). In South Africa, the predicted inventory of Aphodiinae for the entire winter rainfall region decreases by 19% (nine spp.) from 47.5 to 38.7 species whereas that observed for the Iberian Peninsula (Table 1) decreases by 43% (forty spp.) from ninety-

four to fifty-four species. The predicted regional species richness in the Iberian Peninsula decreases by 55% (twenty-seven spp.) (Table 3). In South Africa, the mean species richness at local scale decreases significantly by 20% from 17.1 ± 3.0 to 13.6 ± 1.9 species ($t = 3.21$, df $= 20$, $P = 0.04$) whereas that in the Iberian Peninsula decreases significantly by 58% from 18.6 ± 4.0 to 7.9 ± 2.5 species ($t = 9.57$, df $= 34$, $P < 0.0001$). Thus, the loss of richness due to deletion of non-endemic species is practically double in the Iberian Peninsula compared to South Africa. This results in local species richness of mediterranean endemics becoming significantly different between the two continents ($13.6 \pm 1.9/ 7.9 \pm 2.5$; $t = 6.50$, df $= 27$, $P < 0.0001$). As in the analysis of the entire aphodine fauna, the slopes of the species-area regressions are similar ($F_{(1,29)} = 1.08$; NS) but now the intercepts are significantly different ($F_{(1,30)} = 25.58$; $P < 0.0001$). The lines connecting the three richness values (Fig. 4B) are parallel, rather than congruent, and the value of β-diversity for the Iberian Aphodiinae continues to be lower than that for the South African Aphodiinae (Table 3).

DISCUSSION

Differences in species richness patterns

Species richness of dung beetles has been compared between mediterranean South Africa and the Iberian Peninsula. The dominant pattern comprises dissimilar but parallel increase in species richness with increasing spatial scale (three out of four cases). Such parallelism suggests similarities between the processes operating on each continent and conforms with the pattern shown by intercontinental comparisons between several other animal groups (Westoby, 1993; Oberdorff *et al.*, 1997). Despite this possible ecological similarity between continents, the absence of convergence suggests that differing historical or geographical factors have also strongly influenced both regional and local diversity (Schluter & Ricklefs, 1993a,b). In the remaining case, there is close intercontinental similarity in overall species richness of Aphodiinae at all spatial scales (Fig. 4B). This may represent convergence assuming that it is not a chance result. In this case, local ecological factors may be more important determinants of diversity (Schluter & Ricklefs, 1993a,b) than historical factors.

Species richness patterns differ between the Scarabaeidae and the Aphodiinae (Fig. 4). At all spatial scales, the overall scarabaeid fauna of the mediterranean region of South Africa is more species rich than that of the Iberian Peninsula. This pattern is maintained even when the species with extra-mediterranean distribution are deleted since this species component is similarly rich in each region (seventeen spp. in the Iberian Peninsula/twenty-one spp. in the Western Cape, South Africa). Therefore, the greater species richness in South African Scarabaeidae is not due to recent immigration from the summer rainfall region of Africa. Species richness patterns were more variable in Aphodiinae than in Scarabaeidae. Overall species richness was similar between the Iberian Peninsula and South Africa. However, this pattern was radically modified by the deletion of species showing extra-mediterranean distribution. Species richness then became much greater at all spatial scales in South Africa. Thus, the extra-mediterranean species component (forty spp. in the Iberian Peninsula/twelve spp. in the Western Cape, South Africa) is a much more important contributor to species richness in the Iberian Peninsula than in South Africa.

Regional and historical processes influencing species richness

The history of regional processes differs between continents. The different histories may be responsible for the increase in dissimilarity between the patterns shown by overall species richness to those shown by endemic mediterranean species alone. Intercontinental differences in geographical position would be the principal influence on regional and historical factors which would include dispersal, biogeographical history, climatic history, and disturbance history. It appears that these factors have influenced the Scarabaeidae and Aphodiinae in different ways. This is only to be expected considering the differing ecology and evolutionary histories of the taxa.

Differences in geographical position have strongly influenced the composition of modern dung beetle communities in South Africa and the Iberian Peninsula. Aphodiinae are the numerically dominant coprophagous group in the dung beetle communities of northern higher latitudes (Hanski, 1986; Biström, Silfverberg & Rutanen, 1991). Proximity of the Iberian Peninsula to northern Europe and the absence of geographical barriers probably explains why the extra-mediterranean contribution to species richness in Aphodiinae was much greater than in South Africa. Greater diversity of Aphodiinae in temperate biomes

may be related to higher cool-resistance (Cambefort, 1991) and lower dung removal. In contrast, most phylogenetic lines of the Scarabaeidae *s. str.* show a Gondwanaland origin (Halffter & Matthews, 1966; Halffter, 1974; Cambefort, 1991). Species of Scarabaeidae are the numerically dominant coprophagous group in torrid Afrotropical biomes. The extra-mediterranean component of Scarabaeidae in South Africa was somewhat greater than that of the Aphodiinae. Consequently, proximity to the centre of distribution of each taxon may be a strong contributor to regional differences in species richness patterns between Scarabaeidae and Aphodiinae.

The differing positions of geographical barriers has strongly influenced dispersal into South Africa and the Iberian Peninsula. At present, geographical isolation from temperate regions bars dispersal from these regions into South Africa. However, barriers are lacking between the winter rainfall and warmer, summer rainfall regions of Africa. A number of pasture Scarabaeidae are common to both regions (Davis, 1993b, 1997). These species show primarily summer activity periods and are uncommon in shrubland in the winter rainfall region. They have probably dispersed from the tropics into the winter rainfall region in response to the clearance of the dominant natural shrubland vegetation and its replacement by pasture (Davis, 1993b). Such a summer rainfall dispersal component is practically absent from the scarabaeid fauna of the Iberian Peninsula due to its relative isolation from tropical regions. Only one Iberian scarabaeid species, i.e. *Euoniticellus pallens* (Olivier, 1789), and three aphodine species, i.e. *Aphodius lividus* (Olivier, 1789), *A. unicolor* (Olivier, 1789) and *A. vitellinus* Klug, 1845, can be considered as Afrotropical immigrants (unpublished data). However, in the Iberian Peninsula, geographical barriers are lacking between mediterranean climate and cooler, temperate climates of northern Europe (i.e. climate types VI and VII after Walter & Lieth, 1964). A number of Scarabaeidae and many Aphodiinae are common to both climatic regions. This differing permeability of each region to temperate and afrotropical elements is, probably, a principal determinant of local and regional species richness.

Owing to the different positions of geographical barriers to dispersal, cooler climates during the Pleistocene glaciations may have influenced species richness in different ways on each continent. In South Africa, retreat towards the equator has been possible throughout the Pleistocene. However, the Iberian Peninsula has been separated from Africa for 5 MY

since the Pliocene (Jaeger *et al.*, 1987) so barring retreat southwards towards the equator. During glacial maxima, the barrier to southwards retreat could conceivably have contributed to extinctions of warm-adapted species in the Iberian Peninsula whereas equatorwards retreat may have permitted their survival in South Africa. As in other groups (Blondel & Vigne, 1993), there is fossil support for both northwards and southwards dispersal of European dung beetle species during the glacial/interglacial phases which is related to their temperature associations (Coope & Angus, 1975; Coope, 1979, 1990; Foddari, 1994). In the Iberian Peninsula, there is a greater proportional extra-mediterranean contribution to overall species richness of dung beetles (33% in Scarabaeidae, 43% in Aphodiinae, primarily of higher latitudinal origin) than in South Africa (24% in Scarabaeidae and, approximately, 19% in Aphodiinae, all of lower latitudinal origin). The greater addition of extra-mediterranean species in Europe may reflect greater species losses in the Pleistocene.

The history of habitat disturbance may be more influential on species richness in the Iberian Peninsula than in South Africa since fragmentation of woodland habitats commenced as early as 10–8000 BP in Europe (Loftus *et al.*, 1994; Mönkkönen & Welsh, 1994). In South Africa, widespread clearance of natural shrubland dates only from the arrival of Europeans *c.* 350 BP although burning of natural vegetation to promote the growth of pasture or geophytes dates, respectively, from 2000 BP and 100,000 BP (Deacon, 1992). These differences may be responsible for the scarcity of specialist woodland species and the extreme dominance of pasture or habitat generalist species of Scarabaeidae in the Iberian Peninsula (Martín-Piera & Lobo, 1996). By contrast, in the winter rainfall region of South Africa, shrubland specialists are equally as well represented as pasture specialists and habitat generalists (Davis, 1993a).

Local ecological processes influencing species richness

The results suggest that regional processes have more influence on species diversity than local ecological processes except, possibly, in one instance. In this instance, the broad intercontinental divergence in species richness which was shown by endemic mediterranean Aphodiinae changed to similarity or convergence in species richness by the addition of different numbers of species with extra-mediterranean

distribution. Does this represent a chance result or the achievement of community saturation on each continent due to the dictates of similar local ecological factors? At present, it is not possible to answer this question. However, it is noteworthy that various recent studies have been unable to demonstrate saturated communities in nature (Hugueny & Paugy, 1995; Cornell & Karlson, 1996; Griffiths, 1997; Caley & Schluter, 1997).

Slopes of species richness at different spatial scales showed clear intercontinental parallels despite the slight latitudinal differences between study sites in South Africa and those in the Iberian Peninsula which lie from 1 to 8° further away from the equator. Although this parallelism implies similarity between ecological processes in each continent (Westoby, 1993), β-diversity was greater in South Africa than in the Iberian Peninsula in all comparisons. This higher rate of species turnover suggests that many South African species occupy smaller ranges than those in the Iberian Peninsula. This may be related to the greater habitat specialization shown by the extent dung beetle fauna of South Africa which, in turn, may result both from the differences between continental disturbance histories and the influence of slight latitudinal differences on climate.

CONCLUSION

The diversity and composition of modern communities result from the historical juxtaposition of species with different biogeographical and phylogenetic origins which presently coexist in a state of dynamic interaction with their immediate environment and with each other. It has been predicted that species richness of communities will be wholly convergent when they are subject to similar environmental conditions even if they occur on distant continents and show differing taxonomic composition. This hypothesis is poorly supported by the present study. However, similarities in processes are suggested between mediterranean climatic regions due to intercontinental parallels in species richness at a range of spatial scales. Closer convergence may be excluded since intercontinental differences outweigh similarities.

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