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BIODIVERSITY RESEARCH

Geographic distribution of endemic dung beetles (Coleoptera, Scarabaeoidea) in the Western Palaearctic region

JEAN-PIERRE LUMARET and JORGE M. LOBO *Laboratoire de Zoogéographie, Université Paul Valéry, Route de Mende, F-34199 Montpellier Cedex 5 (France)*

Abstract. The distribution of endemic dung beetle species has been analysed in the West Palaearctic region (547 spp.). These species are concentrated in the Mediterranean Basin or in the neighbouring regions, with two main centres of endemism located on opposite sides of this Basin. The centres of endemism and the degree of endemicity were very different according to the three main dung beetle families. The possible explanation of these patterns has been examined.

Key words. Endemic species distributions, centres of endemism, Mediterranean region, dung beetles, Coleoptera Scarabaeoidea.

INTRODUCTION

A taxon can be considered as endemic when its geographical range is restricted to a limited and generally small area (Horton, 1973) for historical, ecological or physiological reasons (Major, 1988). However this definition is relative because it depends on the spatial scale considered (ultimately all species are endemic to the earth), as the size of the distribution area of a species depends on the size of the considered geographic area (Udvardy, 1969). Endemicity is not linked to the size of the area, but corresponds to the exclusive occurrence of a species in that area (Zunino & Zullini, 1995). However gradually, the term has been used also to define species restricted to small areas, as in the present work. In spite of this divergence in the definition, the study of endemic species is of great use, both for reconstructing the biogeographic history of life and areas (Humphries & Parenti, 1986; Blondel, 1995) and for making decision about conservation of species and areas (Myers, 1990; Rylands, 1990). At present conservation planning is recognized, but the distribution and location of reserves is haphazard, determined by economic, political and cultural factors. Many reserves are located on land which has no economic value (Eidsvik, 1980), whereas the definition of the areas to be securely protected has to take into account the number of species, but also the proportion of species with a small range of distribution (Platnick, 1992; Oosterbroek, 1994). The level of knowledge and the chorology established for the western Palaearctic dung beetles (Baraud, 1985, 1992) now allows a synthetic view of the biogeography of these Scarabaeoidea. The aims of the present work are (i) to define and illustrate the range of endemism in dung beetles at the species level in the W. Palaearctic region; (ii) to set apart areas with the highest rate of endemism; (iii) to verify if the areas of highest endemism are the same for the three main dung beetles families (Scarabaeidae, Aphodiidae, Geotrupidae).

MATERIALS AND METHODS

Levels of endemism

Gaston (1991) estimated that two distinctly different ways of measuring species geographical distributions could be recognized, their extent of occurrence and their area of occupancy. The relative crudity of distributional information makes their separation very difficult in practice. As recommended by Dennis & Shreeve (1991), one might determine the proportion of the area within the range boundaries that is occupied by a species. In the present work, the extent of occurrence of each dung beetle species was taken into account, as the occupancy

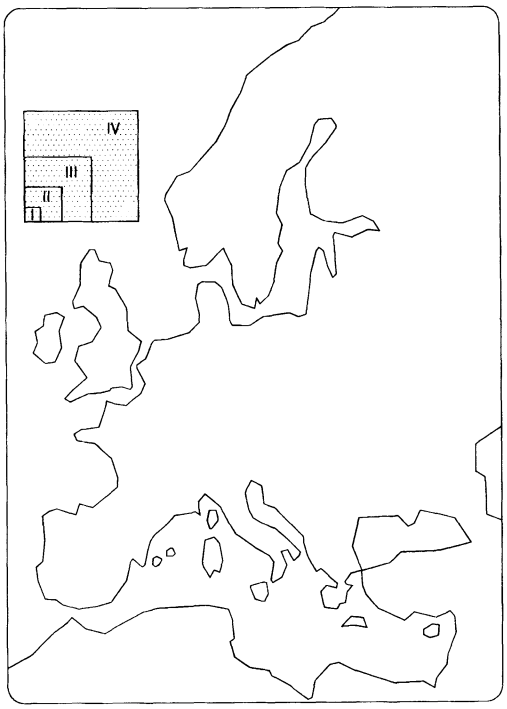

Fig. 1. Sizes of the four first classes of endemism defined for the Western Palaearctic region.

of all species was unknown. All the European and North African species belonging to the Aphodiidae, Scarabaeidae and Geotrupidae families have been considered. All the species reviewed recently by Baraud (1985, 1992) have been taken into account; additional data have also been considered (Carpaneto, 1976; Carpaneto & Kirgiz, 1988; Carpaneto & Piatella, 1989, 1990; Chromy & Kral, 1988; Clément, 1975; Pittino & Ballerio, 1994).

The Western Palaearctic region comprises North Africa from Morocco to Sinaï, and Europe from the Atlantic Ocean to the Oural mountains (60°E), including in its southern part the Caspian Sea and the western boundaries of Kazakhstan. The total surface of the W. Palaearctic region as defined was estimated at 12.10^6 km^2. Six classes of surface (I–VI) were established as subdivisions of the total surface area (Fig. 1). Transparent paper chips of surface corresponding to each six classes have been cut up at the scale 1:12,900,000 and compared with the surface of the distribution of each species drawn at the same scale. Species were allocated to one of the six geographic range-size classes:

(I) species with a distribution area less or equal to 0.1% of the total surface of the W. Palaearctic region (12.10^3 km^2);
(II) species with a distribution area between 0.1% and 0.5% of the total surface of the W. Palaearctic region (6.10^4 km^2);
(III) species with a distribution area between 0.5% and 1% of the total surface of the W. Palaearctic region (12.10^4 km^2);
(IV) species with a distribution area between 1% and 5% of the total surface of the W. Palaearctic region (6.10^5 km^2);
(V) species with a distribution area between 5% and 10% of the total surface of the W. Palaearctic region (12.10^5 km^2);
(VI) species with a distribution area over than 10% of the total surface of the W. Palaearctic region.

In the present work, species were considered as endemic when their distribution area was less or equal to 6.10^5 km^2 (classes, I, II, III and IV). This surface scale corresponds approximately to the surface of many sub-regions in the W. Palaearctic region (e.g. the Iberian Peninsula: $5.8.10^5$ km^2, the Maghreb: $6.3.10^5$ km^2; the Caucasus–Anatolian region: 7.10^5 km^2; or Italy–Balkan–Greece: $6.1.10^5$ km^2). Such a measure of endemicity, which can be defined as rarity in the form of restricted range-size (Williams & Humphries, 1994) is not fundamentally different from the definition given by several authors. For example, Thirgood & Heath (1994) considered as endemic bird species having breeding ranges below 5.10^5 km^2.

Statistical analysis

A contingency table procedure was used to analyse in each family the frequencies of all species occurring in the six classes of endemism. A χ^2 statistic test was used to assess the hypothesis of independence between geographic range-size classes and families. Similarly, a contingency table and a χ^2-test were performed to analyse the independence between families and the allotment of species among the ten biogeographic distribution types recognized in the W. Palaearctic region. Finally, the observed distributions of species among the six geographic range-size classes were compared (using a χ^2-test) with a theoretical evenness of species among the six classes.

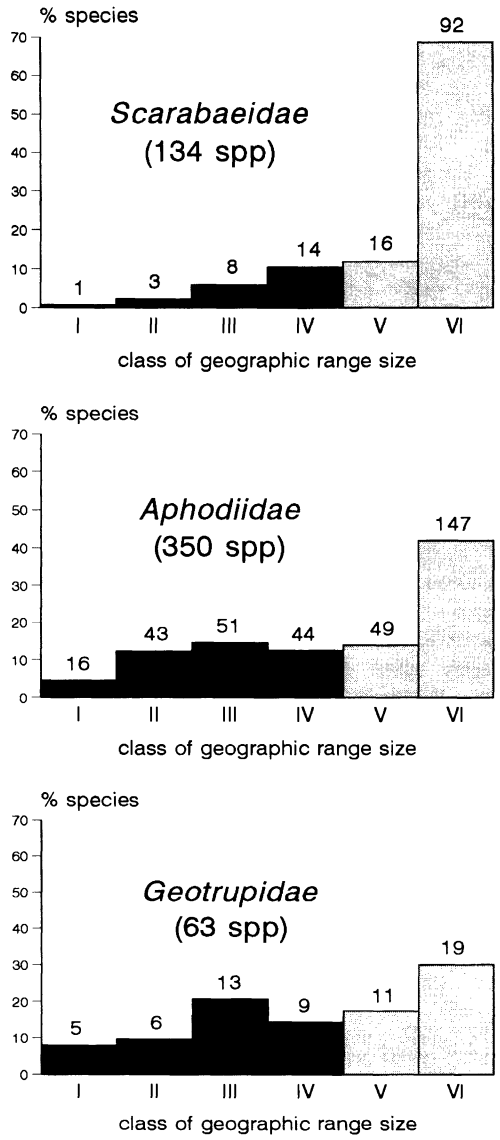

Fig. 2. Distribution of species belonging to the Scarabaeidae, Aphodiidae and Geotrupidae families, respectively, in the six geographical range-size classes. The number of species in classes is above each bar.

RESULTS

The distribution of species among the six geographic range-size classes significantly differed according to the families ($\chi^2 = 45.50$; df = 10; $P < 0.001$) (Fig. 2). In the Scarabaeidae, most species were widely distributed (80.6% of species gathered in classes V and VI). The observed distribution of species in the six geographic range-size classes significantly differed from species evenly distributed among classes ($\chi^2 = 262.54$; df. = 5; $P < 0.0001$) (Fig. 2). Conversely in Geotrupidae, classes V and VI only gathered 48% of species, and the observed distribution among classes weakly differed from an equidistribution of species in classes ($\chi^2 = 12.52$; df. = 5; $P = 0.03$). The Aphodiidae pattern was intermediate between Scarabaeidae and Geotrupidae. Classes V and VI contained 56% of species and the distribution of species among classes was significantly different from evenness ($\chi^2 = 175.47$; df. = 5; $P < 0.0001$).

Most of the species considered in the present work as endemic (classes I to IV) were distributed all around the Mediterranean Basin (Fig. 3). Three main areas gathered together 68% of endemic species: the Maghreb, the Iberian Peninsula and the Caucasian–Anatolian region (Fig. 4). The rate of endemic species in the Mediterranean Basin (34.2%) (Table 1) was close to the rate of endemic species observed in the whole W. Palaearctic region (3[illegible].9%) (Table 2). Such ratios were similar at the same time for Scarabaeidae (19.1% *v.* 19.4%), Aphodiidae (36.3% *v.* 44.0%) and Geotrupidae (51.9% *v.* 52.4%). The endemism rate in dung beetles in the Mediterranean Basin was higher than that observed in breeding birds and mammals in the same area (Blondel, 1995; Cheylan, 1991; Oosterbroek, 1994). Conversely, the endemism rate in all dung beetle families was less than that observed in amphibians, reptiles and plants in the Mediterranean Basin (Table 1). But when Geotrupidae were only considered, their endemism rate (51.9%) was close to that observed in plants (50%) and amphibians (56%).

The highest percentage of endemic species in the W. Palaearctic region was for Geotrupidae (52.4%) (Table 2), then for Aphodiidae (44.0%) and Scarabaeidae (19.4%). The geographic distribution of species significantly differed according to the families ($\chi^2 = 96.05$; df = 18; $P < 0.0001$) (Table 2). In Scarabaeidae, most endemic species had an Ibero-maghrebian (57.7%) and Balkanic (34.6%) distribution. In Aphodiidae, most endemic species originated from the Maghreb (31.2%), the Caucasian–Anatolian region (17.5%), the Iberian Peninsula (11%) and the Alps (9.7%) (Table 2). In Geotrupidae, endemic species were relatively more numerous in the Iberian Peninsula (39.4%), the Maghreb (30.3%) and the Corsican–Sardinian region (9.1%). Conversely endemic Geotrupidae were sparsely represented in the Caucasian–Anatolican region (6.1%) (Table 2 and Fig. 3).

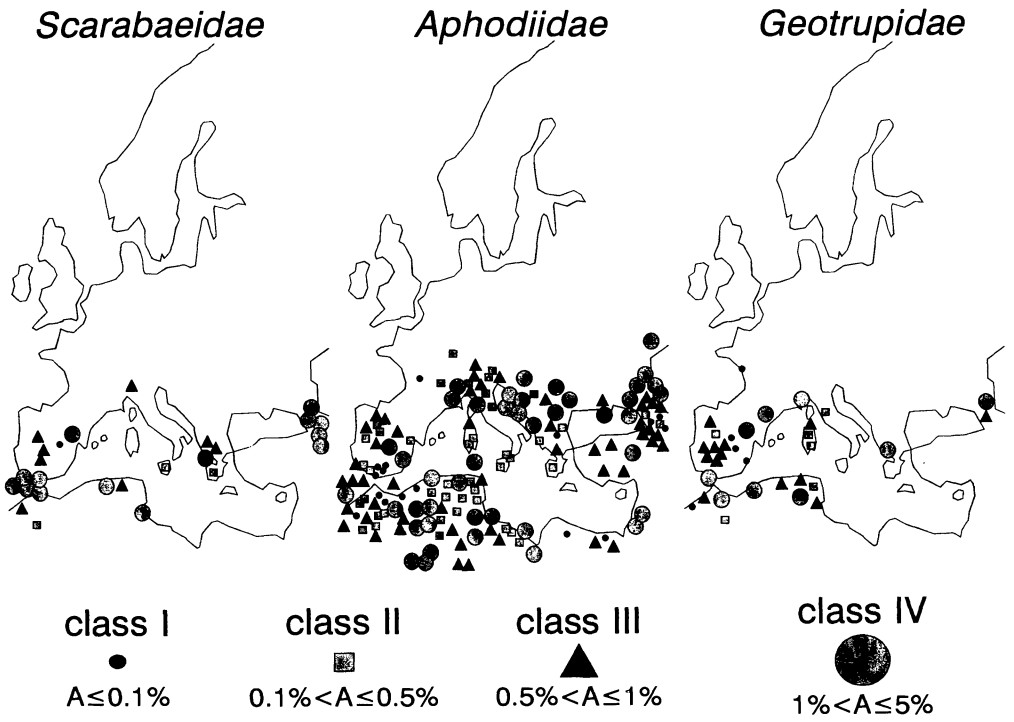

Fig. 3. Distribution of endemic species (Scarabaeidae, Aphodiidae and Geotrupidae, respectively) in the four first geographical range-size classes (classes I, II, III, and IV). Class I corresponds to a distribution area (A) of species ≤0.1% the total surface of the W. Palaearctic region. All symbols are located in the approximate centre of distribution of species.

DISCUSSION

In general many species have a restricted distribution and few species are widely distributed (Gaston, 1996). In the present case, many species of the three dung beetle families have a distribution area over more than 10% of the total surface of the W. Palaearctic region. Classes V and VI represent respectively 80.6% of Scarabaeidae species, 56% of Aphodiidae species and only 47.6% of Geotrupidae. The high tolerance to environmental variables and the high dispersal capacity of species can explain these results, as dung beetle are adapted to exploit ephemeral microhabitats (dung pats). 53.5% of endemic species (classes I to IV) and 61% of the dung beetle fauna occurring in the W. Palaearctic region were strictly concentrated in the Mediterranean Basin whereas the remaining endemic species were distributed in the neighbouring regions of the Mediterranean Basin. Most of these extramediterranean species belong to the Aphodiidae family. They occurred in the southern borders of the Palaearctic Africa (North-west Africa, as far south as the southern slopes of the High Atlas and the Saharian Atlas), in the European alpine areas, in the oriental plains of Europe and in the Ukrainian and Russian steppes.

Hanski, Kouki & Halkka (1993) established a positive correlation between the mean abundance of a species in a site and the size of its distribution area. In general, the adaptations which permit a species to have large populations are related to the adaptations of a good colonizer. Almost no endemic species occurred North of 47° in latitude (Table 2). During the last ice period (Würm–Weichsel, 115 000–130 000 yr BP), trees were very scarce North of 45° in latitude, and the polar vegetation roughly began near the 52° N (Pons, 1981; Huntley & Birks, 1983; Huntley, 1990). Due to such conditions, the dung beetle fauna occurring today North these latitudinal limits probably originated from more southern areas. So it is not surprising that most species occurring today in Northern Europe are generalist and widely distributed species.

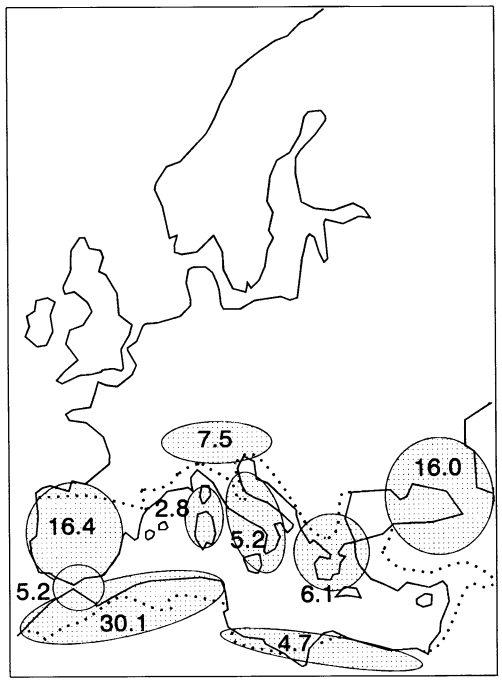

Fig. 4. Localization of the main centres of endemism. Numbers refer to the rate of endemism in each biogeographic sub-region (= the number of species in classes I–IV in the sub-region compared with the total number of species of classes I–IV in the whole W. Palaearctic region). Dotted line corresponds to the limits of the Mediterranean climatic influence (from Cheylan, 1991).

The distribution of endemic species in the W. Palaearctic shows an amphimediterranean pattern, with two centres at opposite sides of the Mediterranean Basin. Together they contain the majority of endemic species (67.7%). The Western part of the Mediterranean Basin (mostly Maghreb and Iberian Peninsula) constitutes the main centre where endemic species occur nowadays (51.7% of endemic species) (Table 2). The Caucasian–Anatolican region constitutes the second centre of endemism (16%).

Why do two main centres of dung beetles endemism occur? The amphimediterranean type of distribution was recognized many years ago by Jeannel (1942). Actually it is known that the oldest elements of the fauna are limited to the western part of the Mediterranean region, which was already part of Eurasia before the Miocene (Oosterbroek & Arntzen, 1992). Conversely, the eastern Mediterranean region constitutes a more recent part of Eurasia. The last vicariance involving faunal elements of West and East Mediterranean lineages dates from at least 10 MYBP, which coincides with the final structuring of the Alps and Neo-Pyrenees (Oosterbroek & Arntzen, 1992). Thus, the actual amphimediterranean distribution of endemic centres might be the result of evolution and cladogenesis in these two isolated areas over a long period of time. For these reasons, the oldest isolated parts of the Western Mediterranean region (mostly Iberian Peninsula and adhering fragments of north-western Africa) would have the higher rate of endemism.

The centres of endemism and the degrees of

Table 1. Total endemic species in dung beetle families compared with other taxonomic groups in the Mediterranean Basin.

Taxonomic groups	Number of species	% endemic species	Sources
Plants	25,000	50	Quezel (1995)
Mammals	184	25	Cheylan (1991)
Birds	343	11	Blondel (1995)
Reptiles	179	62	Cheylan & Poitevin (1994)
Amphibians	62	56	Cheylan & Poitevin (1994)
Insects	150,000	?	Balleto & Casale (1991)
Scarabaeidae	89	19.1	Present work
Aphodiidae	190	36.3	Present work
Geotrupidae	54	51.9	Present work
Total	333	34.2	Present work

Table 2. Comparison of endemicity in the dung beetles of the W. Palaearctic region according to the families and the origin of species.

Biogeographic distributions		Families						Total species
		Scarabaeidae		Aphodiidae		Geotrupidae		
		species	%	species	%	species	%	
I	Iberian peninsula	5	19.2	17	11.0	13	39.4	35
II	Iberian peninsula-Maghreb	4	15.4	6	3.9	1	3/0	11
III	Maghreb	6	23.1	48	31.2	10	30.3	64
IV	Cyrenaica	0	0.0	10	6.5	0	0.0	10
V	Italy	1	3.85	8	5.2	2	6.1	11
VI	Corsica–Sardinia	0	0.0	3	1.95	3	9.1	6
VII	Alps	1	3.85	15	9.7	0	0.0	16
VIII	Balkan	4	15.4	8	5.2	1	3.0	13
IX	Caucasus–Anatolia	5	19.2	27	17.5	2	6.1	34
X	Others	0	0.0	12	7.8	1	3.0	13
Total endemic species		26		154		33		213
Total species		134		350		63		547
% endemism		19.4		44.0		52.4		38.9

endemicity were very different according to families. Scarabaeidae and Aphodiidae are the largest families, with respectively 25% and 64% of the Scarabaeoidea species in the W. Palaearctic region. In Scarabaeidae the degree of endemicity is lesser than in Aphodiidae (20% *v.* 44% of species are endemics) and most species are widely distributed. This pattern is probably due to many Scarabaeidae species which have recently colonized western Europe (Martin–Piera, 1983). The Scarabaeidae, being probably less cool-resistant than Geotrupidae and Aphodiidae, may have arrived after these families (Cambefort, 1991). In Scarabaeidae and Aphodiidae, the two main centres of endemism were located in the western and eastern Mediterranean regions. But the Alps acting as a refuge and offering a large surface area may also be considered as a specific and important centre of endemism for Aphodiidae, which are cool adapted species (Jay–Robert, Lobo & Lumaret, 1997). Conversely, Geotrupidae constitute a small family (11% of the total Scarabaeoidea species in the W. Palaearctic region), with a high degree of endemicity (52% of species are endemic). This high rate of endemism is close to that observed in plants. The apterous *Thorectes* Mulsant genus contributes largely to this situation (74% from the thirty-one *Thorectes* species were considered as endemic). The western part of the Mediterranean Basin constitutes practically the only centre of endemism for Geotrupidae. Krikken (1981) and Zunino (1984), using phylogenetic and biogeographic reconstructions, also considered the western Tethys as the principal centre of origin for Geotrupidae. Such a pattern can be considered as the result of a very old isolation of basal lineages in the western part of the Mediterranean region, as Oosterbroek & Arntzen (1992) proposed for other faunal groups.

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