SPECIES DIVERSITY AND COMPOSITION OF DUNG BEETLE (COLEOPTERA: SCARABAEOIDEA) ASSEMBLAGES IN NORTH AMERICA

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Abstract
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Data from 18 studies carried out on dung beetles from temperate North America (north of 25° latitude) are compared to verify the existence of some geographical pattern in the variation of three parameters: (1) species number, (2) taxonomic composition, and (3) number of introduced species. Southern localities are characterized by a larger number of species and a significantly higher number of scarabaeine species than northern localities (only southern communities located inside the Chihuahuan desert do not conform to this pattern). To explain the latitudinal pattern in faunistic composition and number of species, historical factors are postulated. Foreign species of the tribe Aphodiini seem to be more frequent in the northern localities where more aphodiine native species occur. In contrast, foreign species of the subfamily Scarabaeinae are not more frequent in the southern localities with a greater number of native scarabaeine species. These results are consistent with the hypothesis that the more diverse assemblages of native dung beetle are more resistant to invasion by foreign species.

Résumé

Ce travail met en relation la richesse en espèce, la composition taxonomique, ainsi que le nombre des espèces introduites dans les communautés de Scarabaeidae coprophages d'Amérique du Nord. L'objetif était de verifier l'existence d'une règle de la variation géographique de ces differents paramètres en traitant les informations de dix-huit études réalisées dans les régions au dessus des 25° de latitude. L'analyse des donnés montre que les régions méridionales se caractérisent par une plus grande richesse et un nombre d'espèces de la sous-famille Scarabaeinae plus élevé que les regions septentrionales. Seules les régions méridionales situées à l'intérieur du désert de Chihuahua ne suivent pas cette règle. On suggère que les facteurs historiques peuvent expliquer cette variation latitudinale en composition faunistique et nombre d'espèces. La présence d'espèces introduites d'Aphodiini paraît être plus fréquente dans les localités plus septentrionales, lesquelles contiennent le plus grand nombre d'espèces indigènes. Au contraire, la présence des espèces de Scarabaeinae introduites n'est pas plus fréquente dans les localités méridionales, là où les espèces indigènes sont plus nombreuses. Ces résultats appuient l'hypothèse selon laquelle les communautés indigènes de Scarabaeidae coprophages d'Amérique du Nord les plus riches sont plus résistantes à l'invasion par des espèces introduites.

Introduction

Studies about the variation in species number and faunistic composition along a geographical gradient are necessary (Lubchenco *et al.* 1991) because they allow us to describe and propose explanatory hypotheses for geographical distribution patterns (Gaston and Williams 1996). Hanski (1986, 1991) pointed out for European dung beetle communities a latitudinal European gradient in the number of species which is

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associated with a faunistic turnover between two principal dung beetle groups. The cool-adapted species of Aphodiini (*sensu* Scholtz 1990) dominate the species-poor northern communities, whereas the warm-adapted species of Scarabaeinae dominate the species-rich southern communities. In Euro-Mediterranean conditions, this latitudinal replacement between higher taxonomic groups also appears on a seasonal or altitudinal gradient (Martin-Piera *et al.* 1992; Jay-Robert *et al.* 1997). It is not known if these gradients also exist for North American dung beetle communities.

One of the most striking characteristics of the North American dung beetle communities is the relative importance of accidentally or intentionally introduced species. Most of these species were introduced during the past few hundred years (Blume and Aga 1978; Gordon 1983; Legner 1986; Fincher 1986). Most accidentally introduced species are trophic generalists coming from central and northern Europe (Hanski 1991; Hanski and Cambefort 1991). Also, some African species were introduced intentionally to improve the yield of pasturelands through efficient removal of dung and to limit the proliferation of some plagues of flies or nematodes that inhabit the dung (Fincher 1986).

Unlike introduced species, a striking characteristic of most native North American dung beetles is their limited aᵇ⁺ʲlity to colonize cattle dung (Gordon 1983). This characteristic constitutes another fundamental difference from the European dung beetle communities. To explain this difference, Mönkkönen and Welsh (1994) and Martín-Piera and Lobo (1996) postulated that the western Palaearctic dung beetles have been subjected for hundreds of years to a selection process caused by human activity which has favoured species adapted to domestic ungulate dung.

This paper uses the data from published dung beetle studies carried out in temperate North American localities. The objectives were (1) to determine if a geographical pattern in the number of species and faunistic composition of North American dung beetle communities exists, (2) to estimate the relative importance of introduced species in these communities, and (3) to determine if the geographical variation of the species number and the relative importance of the introduced species are related to spatial or climatic variables.

Methods

Samples and Species Names. Data from 18 North American studies including 39 species of Scarabaeinae and 28 species of Aphodiini carried out in localities situated north of the 25° parallel have been used for this study (Fig. 1). The localities form two spatial groups, one located north of the 35° parallel and the other located south of this parallel. These studies differ in their sampling efforts and aims (Table 1). Three studies do not offer a complete set of data because either they did not consider aphodiine species (Nealis 1977; Howden and Scholtz 1986), or they did not report the identification of these species (Dajoz 1994). As well, the type of dung used as bait varies among studies: human dung (Nealis 1977; Howden and Scholtz 1986), bovine and equine dung (Schoenly 1983), bovine and sheep dung (Kessler *et al.* 1974), and bovine dung in the remaining 13 studies. Although these methodological differences make the comparison among localities less precise than one would prefer, I expected that the main geographical variation patterns would be detected.

The name of each species listed in these studies (Table 2) conforms with recent taxonomic reviews and monographs (Matthews 1962; Howden and Cartwright 1963; Halffter and Martínez 1977; Gordon 1983; Kohlmann 1984; Dellacasa 1987, 1988, 1991, 1995; Edmonds 1994; Dellacasa and Gordon 1994, 1997). For example, *Canthon laevis* (Drury) and *Copris tullius* Olivier are conspecific with *Canthon pilularius* (L.)
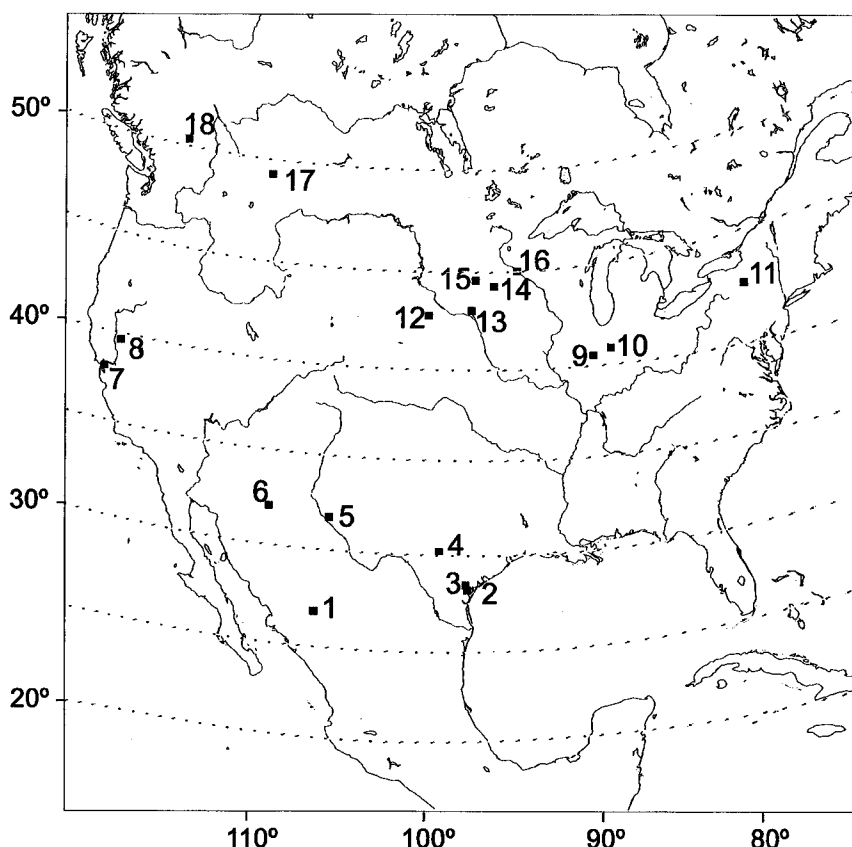
FIGURE 1. Approximate location in North America of the study sites on dung beetles (Coleoptera: Scarabaeoidea) considered in this study. Site numbers correspond to those listed in Table 1.

and *Copris fricator* (Fabricius), respectively. *Aphodius vestiarius* Horn and *Aphodius cuniculus* Chevrolat are conspecific with *Aphodius nigrita* Fabricius (Dellacasa 1987; Bordat *et al.* 1990). *Aphodius ruricola* Melsheimer = *Aphodius rusicola* Melsheimer, *Aphodius stercorosa* Melsheimer = *Aphodius stercorosus* Melsheimer (Dellacasa 1987), and *Aphodius rubeolus* Beauvois = *Aphodius rubeolus* Palisot (Dellacasa 1991).

Source Regions. The source region of each species is estimated as the biogeographical region of maximum diversity of the genus or subgenus to which the species belongs (Table 2). For each aphodiine species, this region was estimated by considering the type locality of all species contained in the subgenus to which the species in question belongs. For each aphodiine subgenus the biogeographic region where most type localities occur is estimated, according to the catalogue of Dellacasa (1987), assigning that biogeographic region to the species of this subgenus. For the Scarabaeinae, this region was established using the data of Cambefort (1991) and Halffter and Martínez (1977). All American species of *Onthophagus* belong to the Oriental subgenus *Onthophagus* sens.str. (Zunino and Halffter 1997).

Data Analysis. As sample sizes are not equal, the rarefaction method (Hurlbert 1971) was used to compare the number of species among localities. This method allows the number of species expected in each sample to be calculated as if all samples were of a

TABLE 1. Sampling characteristics and biological, geographical, and climatic data for each of the 18

Site*	No. of Scarabaeinae species		No. of Aphodiini species		Total no. of species		Abundance of species	
	Native	Introduced	Native	Introduced	Native	Introduced	Native	Introduced
1	3	2	3	3	6	5	3 002	2 967
2	16	0	Unknown	Unknown	·Unknown	Unknown	14 742	0
3	15	1	Unknown	Unknown	Unknown	Unknown	844	200
4	14	0	6	4	20	4	Unknown	Unknown
5	3	0	0	0	3	0	Unknown	Unknown
6	18	0	10	Unknown	28	Unknown	2 533	Unknown
7	0	0	4	3	4	3	Unknown	Unknown
8	0	0	6	4	6	4	Unknown	Unknown
9	5	0	10	4	15	4	Unknown	Unknown
10	2	0	4	3	6	3	658	261
11	3	1	8	6	11	7	Unknown	Unknown
12	2	0	6	4	8	4	547	199
13	3	0	10	6	13	6	3 686	2 707
14	2	0	7	7	9	7	2 664	2 444
15	3	0	10	6	13	6	2 308	1 716
16	3	1	11	7	14	8	2 941	2 906
17	2	1	14	7	16	8	156 465	148 889
18	2	1	9	5	11	6	Unknown	Unknown
Mean	5.3	0.4	7.4	4.6	11.4	5.0		

* 1, Reserva de Mapimí, Durango, Mexico (Lobo 1996); 2, San Patricio, Texas (Nealis 1977); 3, San Patricio, Texas (Schoenly 1983); 6, Cochise County, Arizona (Dajoz 1994); 7, Marin County, California (Poorbaugh *et al.* 1968); 8, 10, Lafayette, Indiana (Sanders and Dobson 1966); 11, Ithaca, New York (Valiela 1969); 12, Mead County, Nebraska 14, Brown County, Minnesota (Cervenka and Moon 1991); 15, Brookings County, South Dakota (Kessler *et al.* 1974); (Floate and Gill 1998); 18, Kamloops, British Columbia (Macqueen and Beirne 1974).

† Sampling effort is the number of baited pitfall traps or dung pats.

standard size ($n = 300$; Magurran 1988). Faunistic comparison of sites sampled differently is possible for dung beetles because samples taken from a few baited traps accurately represent the main assemblage composition (Lobo *et al.* 1998).

A triangular Q-mode matrix of similarity was computed from the rectangular presence–absence matrix (Table 2) using the Jaccard similarity coefficient (Ludwig and Reynolds 1988). To define groups from localities of similar composition, a nonmetric multidimensional scaling (NMDS) was carried out. NMDS (Statsoft Inc. 1999) is a non-linear ordination technique which, like other ordination techniques, derives an axis system that shows the relationships between sampling units (sites). In computing these axes, information loss is minimized. NMDS was chosen because any kind of similarity matrix may be used and normality and linearity of data are not required (Kruskal and Wish 1978). To evaluate how many dimensions are needed to reproduce the similarity between localities a *stress* value was computed (the smaller the stress value, the better is the fit of the reproduced similarity matrix to the observed similarity matrix). The scores of each locality for the first three NMDS dimensions were subjected to a cluster analysis to describe how these groups of localities are related. The squared euclidean distance was used as the measure of resemblance and the UPGMA method as the clustering method (Ludwig and Reynolds 1988).

To estimate the variables related to the faunistic similarity of the localities, the nonparametric Spearman rank correlation coefficient (Siegel and Castellan 1988) was calculated using the scores of the first three NMDS dimensions as dependent variables

North American dung beetle (Coleoptera: Scarabaeidae) studies considered.

Sampling		Location		Mean annual temp. (°C)	Mean annual precip. (mm)
Years	Effort[†]	Lat. N	Long. W		
1993	150	26°40′	103°40′	21	284
1977	85	28°12′	97°33′	22	879
1985	25	28°12′	97°33′	22	879
1968	204	30°03′	99°09′	18	737
1981	48	31°44′	106°04′	17	211
1991	470	32°06′	109°56′	20	250
1964–1965	120	37°55′	122°15′	14	500
1972–1973	798	39°27′	121°34′	16	610
1930–1933	Unknown	40°07′	88°12′	10	850
1962–1963	98	40°25′	86°54′	10	890
1965–1967	Unknown	42°26′	76°30′	11	940
1985	330	42°46′	99°50′	11	460
1969–1970	208	43°00′	96°42′	10	820
1984	239	44°15′	94°58′	7	645
1969	Unknown	44°19′	96°47′	6	551
1984	479	45°00′	93°10′	7	670
1993–1995	1600	49°38′	112°48′	6	398
1970–1972	Unknown	50°39′	120°24′	9	270

(Howden and Scholtz 1986); 4, Kerr and Bexar County, Texas (Blume 1970, 1972); 5, El Paso, Browns Valley, California (Merritt and Anderson 1977); 9, Urbana, Illinois (Mohr 1943); (Peitzmeier *et al.* 1992); 13, Big Sioux River, South Dakota (Kessler and Balsbaugh 1972); 16, Washington County, Minnesota (Cervenka and Moon 1991); 17, Lethbridge, Alberta

and values of the following variables as explanatory variables: latitude, longitude, annual mean temperature, annual precipitation, total number of species, total introduced species, total native species, number of scarabaeine species, number of introduced scarabaeine species, number of native scarabaeine species, number of aphodiine species, number of introduced aphodiine species, and number of native aphodiine species. All possible pairwise correlations among these 13 variables were also computed in a triangular correlation matrix using the Spearman rank correlation coefficient. As several tests of significance are carried out simultaneously, the Bonferroni-corrected significance level was applied, where the significance level $\alpha = 0.05$ is replaced by an adjusted level $\alpha' = \alpha/$(number of simultaneous tests). The pattern of covariation between variables has been displayed performing a new NMDS using this triangular correlation matrix.

Results

Comparison of the Number of Species. Most scarabaeine species belong to a genus or subgenus with most of its species in the Neotropical and Oriental regions (61.5%) and, to a lesser extent, in the Nearctic region (Table 3). Most of the aphodiine species belong to a subgenus with most of its species in the Palaearctic, Holarctic, and Nearctic regions (82.2%). Only three species of Scarabaeinae (7.7% of the total) have been

TABLE 2. Abundance or presence (+) – absence (0) of the dung beetle species (Coleoptera: Scarabaeidae) for each study.

	Study site																		Region
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
Scarabaeinae																			
Ateuchus histeroides Weber	0	9	11	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Canthon (Boreocanthon) ebenus (Say)	0	13	1	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	Nearctic
Canthon (Boreocanthon) lecontei Harold	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Nearctic
Canthon (Boreocanthon) melanus Robinson	0	0	0	0	+	105	0	0	0	0	0	0	0	0	0	0	0	0	Nearctic
Canthon (Boreocanthon) simplex LeConte	0	0	0	0	0	140	0	0	0	0	0	0	0	0	0	0	0	+	Nearctic
Canthon (Boreocanthon) praticola LeConte	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	7	0	Nearctic
Canthon (Boreocanthon) probus (Germar)	0	0	0	+	0	8	0	0	0	0	0	0	0	0	0	0	0	0	Nearctic
Canthon (Boreocanthon) puncticollis LeConte	35	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Nearctic
Canthon (Canthon) cyanellus LeConte	0	12	0	+	0	6	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Canthon (Canthon) imitator Brown	0	800	97	+	0	139	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Canthon (Canthon) indigaceus Harold	0	0	0	0	0	367	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Canthon (Canthon) pilularius (Linneo)	0	146	1	+	0	0	0	0	+	0	0	0	0	0	0	0	0	0	Neotropical
Canthon (Canthon) vigilans LeConte	0	51	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Canthon (Glaphyrocanthon) viridis (P. de Beauvois)	0	115	2	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Melanocanthon bispinatus (Robinson)	0	13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Nearctic
Melanocanthon nigricornis (Say)	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Nearctic
Pseudocanthon perplexus LeConte	0	115	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Dichotomius carolinus (L.)	0	0	0	+	0	0	0	0	+	0	0	0	0	0	0	0	0	0	Neotropical
Dichotomius colonicus Say	0	0	0	0	0	58	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Copris fricator (Fabricius)	0	38	0	0	0	0	0	0	+	0	0	0	17	8	0	0	0	0	Neotropical
Copris lecontei Matthews	0	0	0	0	0	371	0	0	0	0	0	0	0	0	7	0	0	0	Afrotropical
Copris moechus LeConte	0	0	0	0	0	180	0	0	0	0	0	0	0	0	0	0	0	0	Afrotropical
Phanaeus difformis LeConte	0	215	137	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Phanaeus quadridens Say	0	0	0	0	0	343	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Phanaeus triangularis (Say)	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical
Phanaeus vindex Macleay	0	0	0	0	0	132	0	0	0	0	0	0	0	0	0	0	0	0	Neotropical

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Region
Digitonthophagus gazella (Fabricus)*	1913	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Afrotropical
Onthophagus (Onthophagus) alluvius Howden & Cartwright	0	200	211	+	0	0	0	0	0	0	0	0	0	0	0	0	0	Oriental
Onthophagus (Onthophagus) coproides Horn	0	0	0	0	54	0	0	0	0	0	0	0	0	0	0	0	0	Oriental
Onthophagus (Onthophagus) hecate (Panzer)	2901	23	+	0	206	0	0	0	86	+	138	629	212	360	21	0	0	Oriental
Onthophagus (Onthophagus) hoepfneri Harold	0	0	0	0	51	0	0	0	0	0	0	0	0	0	0	0	0	Oriental
Onthophagus (Onthophagus) knulli Howden & Cartwright	0	0	0	0	91	0	0	0	0	0	0	0	0	0	0	0	0	Oriental
Onthophagus (Onthophagus) medorensis Brown	660	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Oriental
Onthophagus (Palaeonthophagus) nuchicornis (L.)*	0	0	0	0	0	0	0	0	0	+	0	0	0	0	74	60 403	+	Palaearctic
Onthophagus (Onthophagus) oklahomensis Brown	1341	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Oriental
Onthophagus (Onthophagus) pennsylvanicus Harold	8133	105	+	0	0	0	0	0	306	+	52	99	0	86	5	0	0	Oriental
Onthophagus (Onthophagus) schaefferi Howden & Cartwright	180	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Oriental
Onthophagus (Onthophagus) subopacus Robinson	0	0	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	Oriental
Euoniticellus intermedius (Reiche)*	965	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Afrotropical
Aphodiini																		
Aphodius (Agoliinus) congregatus Mannerheim	0	nd	0	0	nd	0	0	0	0	0	0	0	0	0	0	0	+	Holarctic
Aphodius (Agrilinus) pectoralis Leconte	0	nd	0	0	nd	0	0	0	0	0	0	0	0	0	0	0	+	Palaearctic
Aphodius (Agrilinus) rusicola Melsheimer	0	nd	0	0	nd	0	0	+	0	0	141	49	0	84	5	291	0	Palaearctic
Aphodius (Amidorus) lentus (Horn)	0	nd	0	0	nd	0	0	0	0	0	0	0	0	0	1	0	0	Holarctic
Aphodius (Amidorus) lutulentus Haldeman	0	nd	0	+	nd	0	0	0	0	0	0	0	0	0	0	0	0	Holarctic
Aphodius (Aphodius) fimetarius (L.)*	0	nd	+	+	nd	+	+	+	24	0	108	282	172	145	621	9 649	+	Palaearctic
Aphodius (Calamosternus) granarius (L.)*	0	nd	+	+	nd	+	+	+	0	0	0	625	424	653	259	990	+	Palaearctic
Aphodius (Chilothorax) distinctus (Müller)*	0	nd	0	0	nd	+	+	0	0	0	0	68	232	36	335	21 955	+	Palaearctic
Aphodius (Chilithorax) leopardus Horn	0	nd	0	0	nd	+	0	0	0	0	0	0	0	0	0	3	0	Palaearctic
Aphodius (Chilothorax) pardalis (Leconte)	0	nd	0	0	nd	0	0	+	0	0	0	0	0	0	0	0	0	Palaearctic

TABLE 2 (concluded).

	Study site																		Region
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
Aphodius (Cinacanthus) bicolor Say	0	nd	nd	0	0	nd	0	0	+	5	0	0	0	0	0	0	0	0	Nearctic
Aphodius (Colobopterus) erraticus (L.)*	0	nd	nd	0	0	nd	0	0	0	97	+	13	0	648	0	453	1	0	Palaearctic
Aphodius (Diapterna) pinguellus Brown	0	nd	nd	0	0	nd	0	0	0	0	0	0	0	0	0	0	67	0	Nearctic
Aphodius (Diapterna) pinguis Haldeman	0	nd	nd	0	0	nd	0	0	0	0	0	0	0	0	0	0	29	0	Nearctic
Aphodius (Drepanocanthoides) walshi Horn	0	nd	nd	0	0	nd	0	0	0	0	0	0	0	0	0	2	0	0	Australian
Aphodius (Koshantschikovius) rubeolus Palisot	0	nd	nd	0	0	nd	0	0	0	0	0	17	0	0	0	0	0	0	Afrotropical
Aphodius (Koshantschikovius) stercorosus Melsheimer	0	nd	nd	0	0	nd	0	0	+	0	+	0	34	0	11	1	0	0	Afrotropical
Aphodius (Labarrus) lividus (Olivier)*	27	nd	nd	+	0	nd	+	+	0	0	0	10	0	0	0	0	0	0	Afrotropical
Aphodius (Melinopterus) femoralis Say	0	nd	nd	0	0	nd	0	0	+	0	0	0	0	0	0	0	0	0	Palaearctic
Aphodius (Melinopterus) prodromus (Brahm)*	0	nd	nd	0	0	nd	0	0	0	0	+	0	2	40	1	265	54 601	0	Palaearctic
Aphodius (Nialaphodius) nigrita Fabricius*	60	nd	nd	+	0	nd	0	0	0	0	0	0	0	0	0	0	0	0	Afrotropical
Aphodius (Otophorus) haemorrhoidalis (L.)*	2	nd	nd	+	0	nd	0	+	+	140	+	68	1702	902	871	858	736	+	Palaearctic
Aphodius (Planolinus) tenellus Say	0	nd	nd	0	0	nd	0	0	0	0	0	0	0	0	0	0	0	+	Holarctic
Aphodius (Planolinus) vittatus Say	0	nd	nd	+	0	nd	+	+	+	0	0	0	109	0	58	0	6 943	+	Holarctic
Aphodius (Platyderides) iowensis Wickham	0	nd	nd	0	0	nd	0	0	0	0	0	0	0	0	0	0	1	0	Nearctic
Aphodius (Pseudoagolius) terminalis Say	0	nd	nd	0	0	nd	0	0	+	0	0	0	0	0	0	0	0	0	Nearctic
Aphodius (Pseudagolius) coloradensis Horn	0	nd	nd	0	0	nd	0	0	0	0	0	0	42	0	19	0	235	0	Nearctic
Aphodius (Teuchestes) fossor (L.)*	0	nd	nd	0	0	nd	0	0	0	+	+	0	28	26	10	41	554	+	Palaearctic

Note: Site codes as in Table 1. The biogeographical region with most species for the genus or subgenus to which each species belongs is also represented. nd, data not available.

* Introduced species.

TABLE 3. Total number (percentage in parentheses) of dung beetle species (Coleoptera: Scarabaeidae) in all studies considered depending on their biogeographical source region, which was estimated as that for most species of the genus or subgenus to which each species belongs (see Methods).

	Australian	Neotropical	Afrotropical	Oriental	Nearctic	Holarctic	Palaearctic	Total	Introduced species
Scarabaeinae	0	14 (35.9)	5 (12.8)	10 (25.6)	9 (23.1)	0	1 (2.6)	39	3 (7.7)
Aphodiini	1 (3.6)	0	4 (14.3)	0	6 (21.4)	5 (17.9)	12 (42.9)	28	9 (32.1)
Total	1 (1.5)	14 (20.9)	9 (13.4)	10 (14.9)	15 (22.4)	5 (7.5)	13 (19.4)	67	12 (17.9)

TABLE 4. Total number of Scarabaeinae (Coleoptera) species (S_{tot}), Scarabaeinae richness (S_{sca}), and species richness (S) estimation by the rarefaction method (Magurran 1988) for 300 individuals (n).

Site No.	Location	S_{tot}	S ($n = 300$)	S_{sca}	S ($n = 300$)	References
1	Mapimi, Durango, Mexico	6	5.1	3	3.0	Lobo 1996
3	San Patricio, Texas	—	—	15	12.0	Howden and Scholtz 1986
6	Cochise County, Arizona	28	25.5	18	17.1	Dajoz 1994
10	Lafayette, Indiana	6	5.9	2	2.0	Sanders and Dobson 1966
12	Mead, Nebraska	8	8.0	2	2.0	Peitzmeier et al. 1992
13	Big Sioux River, South Dakota	13	11.7	3	3.0	Kessler and Balsbaugh 1972
14	Brown County, Minnesota	9	8.6	2	2.0	Cervenka and Moon 1991
15	Brookings County, South Dakota	13	11.2	3	3.0	Kessler et al. 1974
16	Washington County, Minnesota	14	10.1	3	3.0	Cervenka and Moon 1991
17	Lethbridge, Alberta	16	8.0	2	1.0	Floate and Gill 1998
—	Northern European assemblages	23	13.5	0	0.0	Hanski 1991
—	Southern European assemblages	40	22.1	18	14.8	Lumaret et al. 1992

NOTE: Only those North American studies with abundance data for both Scarabaeinae and Aphodiini are included (sites 2, 3, 4, 5, 7, 8, 9, 11, and 18 are excluded; see Table 2).

introduced into North America from the Afrotropical and Palaearctic regions, whereas nine aphodiine species (32.1% of the total) were introduced within the past few hundred years from the Palaearctic region (seven species) and from the Afrotropical region (two species). The percentage of individuals of the introduced species in this survey of 18 studies ranges between 36.4 and 98.8% of the total (mean = 76.1%; Table 1).

Taking into account the total number of species estimated by rarefaction, the number of species for sites north of the 40° parallel is similar to or lower than values estimated for northern European assemblages (Table 4). The number of species for the Chihuahuan desert (site 1) is the lowest, whereas that on the desert's edge (site 6) is similar to or greater than that for southern European assemblages. This pattern was repeated when only scarabaeine species were considered (Table 4): low values for number of species were found in sites north of the 40° parallel, much higher values near the 30° parallel (sites 3 and 6), and low values in the Chihuahuan desert.

Comparison of Composition. A three-dimensional configuration reproduces the site similarity matrix (stress value = 0.09) almost as well as a four-dimensional configuration (stress value = 0.05) but much better than a two-dimensional configuration (stress value = 0.14). The cluster analysis of the three NMDS dimensions clearly delimited two groups: the first group comprises the 12 localities north of the 35° parallel (see Fig. 1) and the most southern locality (site 1), and the second group includes sites south of the 35° parallel (Fig. 2). The clustering of sites 1, 7, and 8 with those from the north
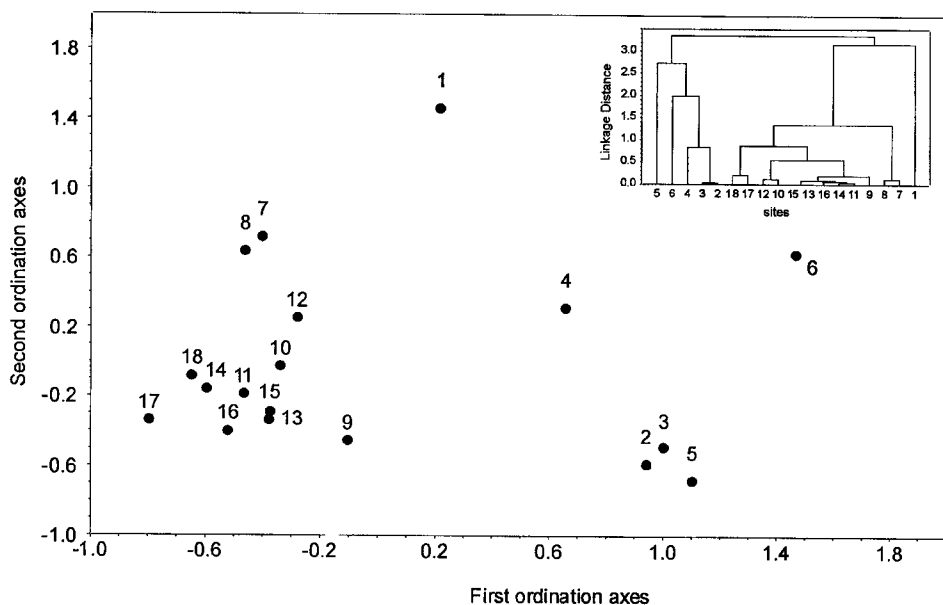
FIGURE 2. Two-dimensional representation of the grouping of sites according to the degree of similarity between each pair of sites measured by means of the Jaccard index (presence–absence data). Sites are arranged in the first two ordination axes which provides the maximum information about their faunistic similarities. The nonlinear nonmetric multidimensional scaling procedure has been used as an ordination method. Site scores for the three first axes have been grouped by means of a cluster analysis (dendrogram), with the squared euclidean distance as a measure of resemblance and the UPGMA method as the clustering technique (Ludwig and Reynolds 1988).

appears marginal, thus pointing out the faunistic singularity of these sites. The first NMDS dimension is positively correlated with the number of scarabaeine species ($r_S = 0.72$, $n = 18$, $P = 0.0007$), the number of native scarabaeine species ($r_S = 0.73$, $n = 18$, $P = 0.0005$), and the mean temperature ($r_S = 0.77$, $n = 18$, $P = 0.0002$), but negatively correlated with the number of introduced aphodiine species ($r_S = -0.73$, $n = 15$, $P = 0.002$), the number of total introduced species ($r_S = -0.70$, $n = 15$, $P = 0.004$), and latitude ($r_S = -0.81$, $n = 18$, $P = 0.0001$). Therefore, the first dimension discriminates the southern localities with greater environmental temperature and more scarabaeine species but fewer introduced (mostly aphodiine) species. The second NMDS dimension is negatively correlated with the total number of native species ($r_S = -0.54$, $n = 15$, $P = 0.04$), discriminating the localities with a higher number of native species. The third NMDS dimension is positively correlated with longitude ($r_S = 0.58$, $n = 18$, $P = 0.01$) but negatively correlated with precipitation ($r_S = -0.51$, $n = 18$, $P = 0.03$).

Variables Correlated with the Number of Introduced Species. The correlation matrix contains 13 variables, thus 78 tests of significance were carried out simultaneously. The Bonferroni-corrected significance level (α') was $0.05/78 = 0.0006$. The relationships among the 13 variables, taking into account all pairwise correlations, revealed a strong positive correlation between the total number of introduced species and the number of aphodiine species ($r_S = 0.78$, $n = 15$, $P = 0.0006$; Fig. 3). These two variables are also positively correlated with the number of introduced aphodiine species ($r_S = 0.93$, $n = 15$, $P < 0.0001$; and $r_S = 0.86$, $n = 15$, $P < 0.0001$, respectively). The total number of species is positively correlated with the number of native aphodiine species ($r_S = 0.78$, $n = 15$, $P = 0.0006$) and the total number of aphodiine species ($r_S = 0.81$, $n = 15$, $P = 0.0002$). The number of introduced aphodiine species is positively correlated with
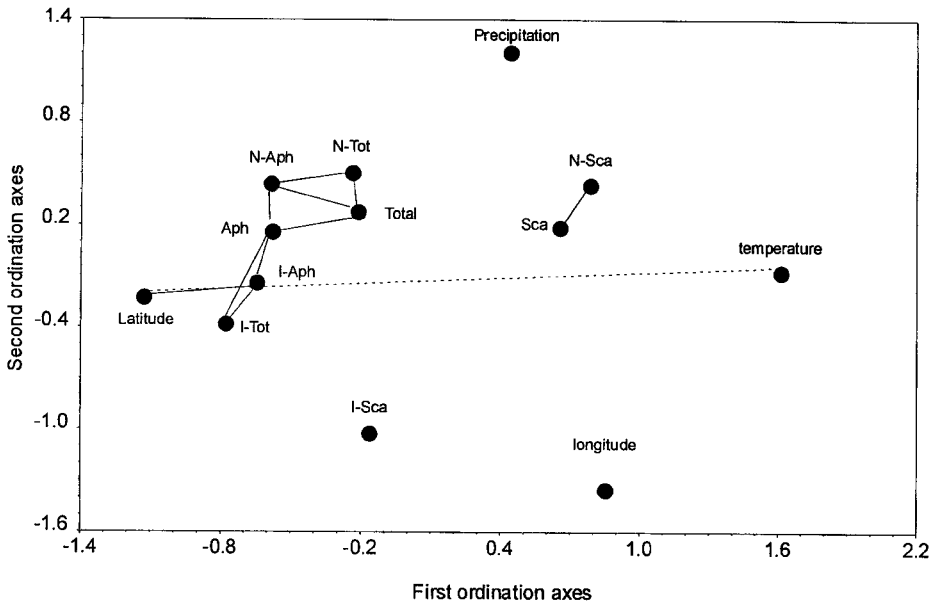
FIGURE 3. Two-dimensional representation of all the pairwise possible correlations between 13 variables using the Spearman rank correlation coefficient. The variables are latitude, longitude, mean annual temperature, mean annual precipitation, total number of species (Total), total number of introduced species (I-Tot), total number of native species (N-Tot), number of Scarabaeinae species (Sca), number of introduced Scarabaeinae species (I-Sca), number of native Scarabaeinae species (N-Sca), number of Aphodiini species (Aph), number of introduced Aphodiini species (I-Aph), and number of native Aphodiini species (N-Aph). To represent the pattern of covariation between variables a nonmetric multidimensional scaling procedure has been computed using the triangular correlation matrix between variables selecting the two first ordination axes. Continuous lines represent positive and significant correlations between variables, and broken lines represent negative and significant correlations. As several tests of significance are carried out simultaneously, the Bonferroni-corrected significance level was applied, where the significance level $\alpha = 0.05$ is replaced by an adjusted level $\alpha' = \alpha/$(number of simultaneous tests).

latitude ($r_S = 0.80$, $n = 15$, $P = 0.0004$), but negatively correlated with mean annual temperature ($r_S = 0.77$, $n = 15$, $P = 0.0007$). The total number of scarabaeine species is positively correlated with the number of native scarabaeine species ($r_S = 0.90$, $n = 18$, $P < 0.0001$). The correlation between the total number of scarabaeine species and mean annual temperature is not significant at the Bonferroni-corrected level ($r_S = 0.49$, $n = 18$, $P = 0.04$), although a weak relationship likely exists between both variables. The number of scarabaeine species and the number of aphodiines are not correlated, considering both the native species ($r_S = 0.17$, $n = 15$, $P = 0.55$), the introduced species ($r_S = 0.28$, $n = 15$, $P = 0.31$), and the total number of species ($r_S = 0.27$, $n = 16$, $P = 0.31$). The numbers of introduced and native Scarabaeinae in North America are not correlated ($r = -0.33$, $n = 18$, $P = 0.18$), whereas the weak positive correlation between the numbers of introduced and native Aphodiini ($r_S = 0.56$, $n = 15$, $P = 0.03$) indicates that a relationship possibly exists between the two variables.

A stepwise multiple regression analysis of the percentage of total introduced species as a function of number of native species and climatic and spatial variables (latitude, longitude, mean annual temperature, annual precipitation, total native species, number of native scarabaeine species, number of native aphodiine species) shows that the only variable significantly negatively correlated with the proportion of introduced species is the total number of native species [$b = -0.598$; $t(13) = 2.69$; $P = 0.02$; $R^2 = 35.77\%$].

Discussion

Excluding the sites within the Chihuahuan desert, the number of species in sites north of the 35° parallel is less than that in sites south of the 35° parallel. Moreover, the number of species in northern communities of North America seems less than that in northern European dung beetle communities (Hanski 1991), whereas the number of species in the southern communities is equal to or greater than those in the southern European communities (Lumaret et al. 1992). The number of species in desert sites (1 and 5) in the southern portion of the territory under study is less than that of northern localities, but the relative weight of the scarabaeine species is greater. Schoenly (1983) reported only three species of Scarabaeinae in the Chihuahuan desert. Lobo (1996) found six dung beetle species in Mapimí, but three species of Scarabaeinae accounted for more than 98% of the total abundance. The remaining southern sites are characterized as geographical transition sites between the desert region and the steppes of the American Great Plains (sites 4 and 6) and between the steppes and the eastern wet subtropical climate region (sites 2 and 3). The higher number of species for communities from southern North America could be the result of the overlap of "cool-adapted" and "warm-adapted" biogeographical groups. This region in general, and Mexico in particular, has been recognized for a long time as a transition zone between the Nearctic and Neotropical regions (Halffter 1964, 1976).

The latitudinal variation in the number of species correlates with a modification in the qualitative composition of the communities. The cluster analysis shows that the northern sites constitute a clearly defined group. The southern sites, except Mapimí (site 1), form another group that is less homogeneous. Two other results support the recognition of a latitudinal gradient in the composition and in the number of species: (1) the first dimension of NMDS, which clearly distinguishes between the northern and southern localities, is correlated with both the number of scarabaeine species and the number of native species of this subfamily; and (2) these last two variables are negatively correlated with latitude but positively correlated with mean annual temperature. Northern localities with relatively higher annual rainfall and lower temperatures have lower values for the total number of species and fewer species of Scarabaeinae. Conversely, southern localities are characterized by higher values for total number of dung beetle species and dominance of scarabaeine species.

A similar geographical contrast is evident among dung beetle faunas of the mediterranean and temperate European regions (Hanski 1986, 1991; Hanski and Cambefort 1991): less diverse communities dominated by aphodiine species in the northern localities, and more diverse communities dominated by scarabaeine species in the southern localities. Explanatory hypotheses postulated that this latitudinal pattern may be either the result of ecological turnover between two groups with different competitive capacity, or a consequence of the latitudinal increase southward in the variety of resources (Hanski 1986; Hanski and Cambefort 1991). Alternatively, an historical hypothesis could explain this pattern. The co-occurrence of species in an area can be simply a consequence of the degree of similarity in their ecological responses. As species are adapted to the same environmental conditions that existed when they originated, the current adaptations of many species are the result of ancient evolutionary selections (Hengeveld 1990, 1997). The native scarabaeine species of North America have Oriental and Neotropical lineages principally, whereas the native aphodiine species come from lineages arising mostly in the Palaearctic and Nearctic regions. As these lineages differ in their climatic tolerance, the latitudinal gradient may be the result of rigid adaptations to the specific environmental conditions of the diversification centre for each taxon. For example, Farrell et al. (1992), Latham and Ricklefs (1993), and Beerling and Woodward (1996) attribute current diversity and distribution of species to a response to

differences in the climatic tolerance among higher phylogenetic lineages. Field experiments and more rigorous and consistent sampling must be carried out to assess the relative importance of historical and ecological factors in this latitudinal pattern.

The main difference between dung beetle communities of North America and those of Europe is the relative importance of introduced species. Almost a third of the aphodiine species considered here are foreign species. The number of introduced species of Scarabaeinae is not related to the number of introduced aphodiine species (the number of native species and the total number of species of both taxa are also not correlated). Therefore, foreign aphodiine species are more frequent in the northern localities where more native aphodiine species occur; however, introduced scarabaeine species are not more frequent in the southern localities where a large number of native species of this subfamily occur.

Two complementary and nonexclusive hypotheses may explain the importance of the introduced species: (i) the probability of a successful introduction will be lower in the more diverse assemblages of dung beetles; and (ii) the less diverse and aphodiine-dominated assemblages have a greater number of introduced species due to the extended human-caused connection between North America and the northwest Palaearctic region where Aphodiini also dominate. Although the first hypothesis should be viewed with caution (Lodge 1993), these preliminary results are consistent with the hypothesis that the more diverse assemblages of native dung beetle species are more resistant to invasion by foreign species.

Acknowledgements

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