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RESEARCH LETTER

Diversity, biogeographical considerations and spatial structure of a recently invaded dung bettle (Coleoptera: Scarabaeoidea) community in the Chihuahuan desert

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Abstract. Analysis of the faunal composition and diversity of Mapimí dung beetle communities indicates that, while much poorer than those near the edges of the Chihuahuan desert, they may possibly have been even more so in the recent past, since at least four of the six captured species were introduced recently into North America. While their overall diversity and composition appear explicable in terms of historic and topographic factors, the regional variation in these communities between sample sites is argued to be a function of the interplay of the environmental requirements of the species and the quantity and quality of trophic resources available.

Key words. Dung-beetles, *Scarabaeidae*, introduced species, regional distribution, Chihuahuan desert.

INTRODUCTION

Although some effort has been made to evaluate the effect on autochthonous communities of exotic dung beetle species introduced into North America (Howden & Scholtz, 1986), intentionally (Fincher, 1986) and otherwise (Gordon, 1983; Blume, 1985) in recent times, no spatial distribution or community composition data are available from localities in which the participation of these new species is fundamental. Two species of dung beetle intentionally introduced previously in the U.S.A. have been found together in the 'Bolsón de Mapimí'; Chihuahua desert, Mexico: *Digitonthophagus gazella* (Fabricius) and *Euoniticellus intermedius* (Reiche). *D. gazella*, an Indo-African species, has been introduced into various parts of the globe (Barbero & López-Guerrero, 1992; Huchet, 1992). First recorded in Mapimi Reserve in August, 1984 (Zunino & Halffter, 1988), 12 years after it was released in south Texas (Blume & Aga, 1978), it must now have been in the area for about 10 years. *E. intermedius*, an African species, has spread to the area after its release in Central Texas in 1979 and 1980 (Blume, 1984). First found in Mexico in Mapimí Reserve in August, 1992 (Montes de Oca, Anduaga & Rivera, 1994), it has been there for 2 or 3 years at most, also 12 years after its release.

Although the community structure prior to the arrival of these introduced species is unfortunately unknown, it is to be hoped that their short stay has not yet had an irreversible impact on the native community. This paper intends to provide: (i) an introduction to the composition, origin, structure and regional distribution of this community to facilitate future comparisons; (ii) an estimation of its diversity, compared with that of other nearby territories; (iii) an evaluation of the possible impact of introduced species on local fauna.

METHODS

The area under study is located in the Mapimí Biosphere Reserve (1600 km^2), Durango, on the northern Mexican plateau, approximately midway between the Sierra Madre Occidental, to the west, and the Sierra Madre Oriental northern ranges, to the east. This area lies within the southern part, the Bolsón de Mapimí, of the 357,000 km^2 Chihuahua desert, between the parallels 26° 29′ and 26° 52′ and the meridians 103° 58′ and 103° 32′, and includes portions of Coahuila, Chihuahua and Durango States. Its arid climate (283.8 mm annual precipitation, 1978–88) is characterized by: average monthly temperature varying from 12°C (January) to 28°C (June); a dry season from

October to May; torrential rainfall, highly irregular both annually and seasonally (Cornet, 1988), limited regionally and to the hot, rainy June–September season. Regional environment and flora are described in Montaña (1988) and Montaña & Breimer (1988).

The data presented here were collected between 20 September and 3 October, 1993, at the end of the rainy season, favourable to the growth of vegetation (Cornet, 1988), when the average temperature begins to fall (24.7°C) and the average monthly rainfall reaches a maximum (60.8 mm). The main sampling was done at the 'Laboratorio del Desierto', from September 21 to 25, with three transects of twenty pitfall traps of proven efficiency (Lobo, Martín-Piera & Veiga, 1988; Veiga, Lobo & Martín-Piera, 1989). Each pitfall trap was baited with 250 g of cow dung and placed at 6-m intervals through an environmentally uniform 200 m^2 area. Beside each of these pitfall traps, from 21 to 28 September, sixty 1 kg dung pats were set out. The traps and the dung pats were examined for faunal content after 24 h.

In addition, from 28 September to 2 October, five identical pitfall traps were set in each of six other localities (Fig. 1). The total surface area covered by these stations is 210 km^2 and the localities are separated by an average distance of 6.2 km (between 3.5 and 10 km), all at nearly the same altitude (1100–1200 m). The most important difference between sites had to do with the number of cattle present.

This limited seasonal sampling effort can give an adequate picture of dung beetle diversity due to: (i) the low seasonal variation in the structure of desert-soil arthropod communities (Cepeda-Pizarro & Whitford, 1989); and (ii) the rapidity of collection of the majority of species of the dung beetle community. With five pitfall traps it was possible to collect 71.4% of the species at one locality (95% confidence interval = ± 2.8). These species represent 94% of total abundance (J. M. Lobo & J. P. Lumaret, unpublished data). The statistical tests used are nonparametric: the Wilcoxon signed ranks test for comparison of means and Spearman's rank correlation coefficient (*rs*). Values for mean species biomass are calculated on the basis of a linear length-to-body weight relationship (Lobo, 1993).

RESULTS AND DISCUSSION

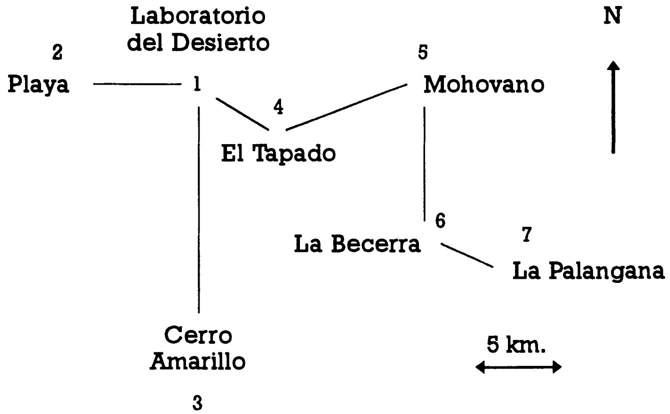
Comparative Diversity

Table 1 gives a break-down of captures according to sample site. Only six species were found in the 150 traps and dung pats examined. In other sites in the Chihuahuan desert, Schoenly (1983) captured only three species, using a similar sampling programme. However, in a sampling programme carried out in tropical Chiapas, Mexico, during a similar period of time, using only fifty traps, around forty species were found (unpublished data). Severely restricted as to the number of species able to survive in the harsh environment of this arid zone, the dung beetle community in Mapimí is undoubtedly very poor in species, even in comparison with the northern temperate biomes. The expected number of species, estimated by rarefaction (Krebs, 1989) is 2.6 times greater in northern European pastures than in Mapimí ($n = 300$; Hanski & Cambefort, 1991). Dung beetle communities established on the northern edge of the Chihuahuan desert seem also to be rather richer. Results available from three similar sampling programmes there provide a basis for the comparison of community diversity; in south Texas (Nealis, 1977), twelve species were found in sandy open grassland, and eight species in clay-soil open grassland; in the south of Arizona (Dajoz, 1994), twenty-eight species of dung beetles were captured.

There could be three more dung beetle species, *Canthon (Boreocanthon) praticola* Leconte, *Canthon (Canthon) imitator* Brown, and perhaps one species of *Onthophagus* (Halffter & Halffter, 1989; Halffter, G. & Moron, M.A., pers. comm.) in the Mapimí area. In other nearby Mexican sites outside of this desert area, dung beetles have been found in association with rodent dens (Anduaga & Halffter, 1991). During the Pleistocene, rodent dens in Mapimí were associated with a rich dung beetle fauna (Elias, 1992; Elias, Van Devender & De Baca, 1995), but today this seems not to be the case. During this study four *Neotoma* burrows were examined, yielding nothing, as did previous inspections (Halffter, G. & Reyes-Castillo, P., pers. comm.). Furthermore, only specimens of *Digitonthophagus gazella* (Fabricius) were found in the seven horse, ten human and seven tortoise (*Gopherus flavomarginatus*) faeces examined. Thus the Mapimí inventary may be composed of very few additional species.

Biogeographical and Taxonomic considerations

While the dung beetle communities in Mapimí are poor today, they may possibly have been even more so in the recent past. Certainly four of the six species studied



Site	Landscape	Cattle numbers
1	grasslands and low woodland	moderately abundant
2	grassland with low scrub cover	scarce
3	sparse scrub and grasslands	unobservable
4	floodplain with tall woodland, low woodland and grasslands	abundant
5	grasslands and low woodland	scarce
6	floodplain with tall woodland, low woodland and grasslands	unobservable
7	grasslands and low woodland	unobservable

Fig. 1. Approximate numbered sample site layout with selected characteristics.

Table 1. Number of individuals captured in each of seven sample sites, with both manipulated dung pats (DP) and pitfall traps (PT)

Species	Sites Type of sampling	1 DP	1 PT	2 PT	3 PT	4 PT	5 PT	6 PT	7 PT	Total
Digitonthophagus gazella (Fabricus)		715	954	42	42	83	69	3	5	1913
Euoniticellus intermedius (Reiche)		238	553	11	81	54	10	5	13	965
Canthon (Boreocanthon) puncticollis LeConte		12	21	—	—	1	1	—	—	35
Aphodius (Labarrus) lividus Olivier		4	8	—	1	4	—	9	1	27
Aphodius (Otophorus) haemorrhoidalis (L.)		—	—	—	—	2	—	—	—	2
Aphodius (Nialaphodius) nigrita Fabricius		—	1	3	—	53	3	—	—	60
Total individuals		969	1537	56	124	197	83	17	19	3002
Total species		4	5	3	3	6	4	3	3	6
Total sampling units		60	60	5	5	5	5	5	5	150

here, *D. gazella*, *E. intermedius*, *A. haemorrhoidalis* (L.) and *A. lividus* Olivier are not indigenous to North America. These species account for 96.8% of the specimens captured in this study, and 99.6% of the biomass (mg dw). Moreover, there is a high probability that the other species of *Aphodius* (*A. nigrita* Fabricius) was also introduced.

As mentioned above, the African species *D. gazella* and *E. intermedius* have spread to the area after release in Texas in 1972 and 1979–1980 respectively (Blume & Aga, 1978; Blume, 1984). *A. haemorrhoidalis*, a Paleartic bovine-dung specialist, frequently found in northern and southern European grasslands (Dellacasa, 1983), was accidentally introduced in to North America. In 1915 Schaeffer reported it for the first time in New Jersey (Woodruff, 1973). This is the first record south of Rio Grande and thus represents the new southern boundary of the species range (Lobo, 1994).

The case of *A. lividus* is more complicated. According to Balthasar (1941), this is a name given to a complex of species; within it, first he, and later Petrovitz (1961a, b; 1965) and Dellacasa (1987), recognized a total of twelve species. Accordingly, the captured individuals of this study should be classified as *A. pseudolividus*. Nevertheless, other authors, in disagreement, maintain that the African taxa of the '*lividus* complex' belong to an infra-species category (Endrodi, 1964; Endrodi & Rakovic, 1981). *A. lividus*, considered to be cosmopolitan, is the only representative of this species complex recognized as present in North America by American authors (see, for example, Gordon, 1983; Woodruff, 1973; Morón, Villalobos & Deloya, 1985; Morón, Deloya & Delgado-Castillo, 1988; Deloya, 1992). One of many species accidentally introduced into North America (Blume, 1985), recorded there since the end of the last century (Horn, 1887), it is today found throughout the continent (Woodruff, 1973). It may be viewed either as a case of a polymorphic species, or as a complex of very closely related species, most probably introduced into America.

The case of *A. (Nialaphodius) nigrita* is also difficult, but, unlike the previous one, because it is the name given in common to twelve different taxa, eight described in Africa, and four, *A. vestiarius* Horn, *A. cuniculus* Chevrolat, *A. guadaloupensis* Fleutiaux and Salle and *A. haroldi* Deyrolle, in America (Dellacasa, 1987; Bordat, Paulian & Pittino, 1990; Bordat, 1993). The American distribution of *A. nigrita* would take in practically all of the southeastern U.S.A., the Caribbean, Central America and Mexico. In Africa, apparently a widely distributed species, it frequently appears together with *A. lividus* (Endrodi, 1955, 1964, 1973; Petrovitz, 1972), as it does in America. As it is found on both sides of the Atlantic with hardly any morphological modification, its recent introduction also cannot be ruled out.

Although ranching in Mapimí was impeded by native peoples' opposition until almost the end of the nineteenth century (Barral & Hernández, 1992), bison could have been present before the arrival of the Spanish (Barral, H. & Hernández, L., pers. comm.). Mapimí dung beetle communities, probably very much poorer in the absence of exotic species, very probably lacked species colonizing cattle faeces as recently as 20 years ago. Exotic species would hardly have been able to replace autochthonous fauna in such a short time. In southern Texas, the introduction of *D. gazella* does not seem to have greatly affected pre-existing communities (Howden & Scholtz, 1986). Only between 2% and 40% of biological invasions produce a perceptible impact on native communities (Lodge, 1993) and, in general, species invasions are rarely accompanied by the complete exclusion of native competitors (Valentine & Jablonski, 1993). It would seem that Mapimí dung beetle communities were not saturated, lacking both species and individuals. In the northern Chihuahuan desert, where the average dung beetle density was 3.6 individuals per trap, not a single exotic, among only three species was found (Schoenly, 1983); whereas, in Mapimí, a total of six species were found and twenty individuals per trap, due to the presence of the exotics.

If these desert communities are not saturated, as suggested above, the limit to the number of co-existing species would not have been established solely by adverse environmental conditions. Historical causes may have played a part. Generally speaking endemic American dung beetles are unable to exploit cow dung effectively (Gordon, 1983; Hanski, 1991a), hence the need to introduce foreign species (Fincher, 1986). There is not a convincing explanation for this impoverished fauna of native pasture species in North America. Perhaps the climatic conditions which occur in the Great Plains (low precipitation and humidity) are generally unfavourable for dung beetles that use bovine droppings (Hanski, 1991a). Or perhaps the lengthy duration of the effects of the human presence in the Palaeartic region and the geographical configuration of the continental land masses have selected the most generalist species (Mönkkönen & Welsh, 1994).

It would seem that in Mapimí we find dung beetle communities whose structure may at present be developing, based on some species well-adapted to arid Afro-Tropical and Palaeartic biomes. The much richer African Sahel dung beetle community includes *D. gazella*, *E. intermedius* and *A. lividus* among its dominant species (Rougon & Rougon, 1991). *A. nigrita* and *A. lividus*, both part of communities scattered about the African continent (Endrodi, 1964, 1973; Petrovitz, 1972), are also the only two species of *Aphodiini* found in cleared southern Mexican jungle (Morón *et al.*, 1985). *A. haemorrhoidalis* is one of the few European summer *Aphodius* (Lumaret, 1990).

As the Sierra Madre Occidental has probably impeded species penetration from the arid west, the source of the species of these communities would seem to lie to the north or northeast (the south and southeastern U.S.A.), from where all the introduced species, except for perhaps *A. nigrita*, would have entered Mapimí. *Canthon (Boreocanthon) puncticollis* LeConte, the only species that may be considered autochthonous, also probably colonized the territory from the north. Its autochthonous presence may be due to the fact that it is the only Scarabaeidae in the Chihuahuan desert attracted by the intestinal contents of mammalian carcasses (Schoenly & Reid, 1983). *C. puncticollis* belongs to a phylogenetically recent subgenus, a typically neotropical northern vicariant of the *Canthon* subgenus (Halffter, 1958). The 'Depresión del Balsas' may be considered the southern distribution limit of the subgenus *Boreocanthon* (Halffter & Martinez, 1977), and Mapimí may be considered the southern distribution limit of this species, found in Baja California, Arizona and Chihuahua (Robinson, 1948).

The biogeographic characteristics of these communities are: (i) their poverty, (ii) the lack of authoctonous elements, (iii) northern penetration, and (iv) the important role of recently introduced species. These characteristics contrast markedly with: the richness; importance of endemic species; Neotropical affinity; and phylogenetic antiquity of this arid region's flora (Rzedowski, 1973, 1988, 1993). A high proportion of the plants (and vertebrates) present in the Chihuahua desert in the Late Wisconsin survive (Elias, 1992). This is not the case for the insects, whose distributional ranges vary greatly in response to environmental changes (Coope, 1970; Elias, 1992; Elias *et al.*, 1995), most probably thanks to their mobility and short generation lifespan. The Mapimí region was a refugium for desert biota during the late Pleistocene, but neither these dung beetles (13,590–12,280 yr BP), nor the species present only 1000–3000 yr BP, are now found there (Elias, 1992; Elias *et al.*, 1995), probably due to climate changes (Nordt *et al.*, 1994). This process of endemic species impoverishment very probably continued until the arrival from the north of species introduced by man.

Similarity between sites and regional distribution

While there is no major regional variation in the Mapimí dung beetle community composition, the abundance of its two dominant, truly characteristic species, *D. gazella* (64% of captured individuals, 71% of total biomass) and *E. intermedius* (32% of captured individuals, 29% of total biomass), appearing in all seven localities, is greatest in the localities of the sampled region where richness, density and average biomass are greatest (Figs 2 and 3). But attention should be drawn to the species segregation reflected in the greater abundance of *D. gazella* where livestock was present, while *E. intermedius* predominated where livestock was absent (Fig. 2). The abundance of both species in the ninety pitfall traps is not significantly correlated ($rs = 0.118$) and neither is the mean abundance of each per locality ($rs = 0.560$, df $= 5$). But in the localities with livestock, *D. gazella* have a significant higher mean abundance per trap (Wilcoxon test, $Z = 3.79$, $n = 75$, $P = 0.0002$). In localities with no livestock *E. intermedius* has a significant higher median abundance per trap ($Z = 2.73$, $n = 15$, $P = 0.007$). *C. puncticollis*, the only *Canthonini* found, was similarly abundant in northern sample sites near El Tapado (Fig. 2). *A. haemorrhoidalis* was captured only in El Tapado, also the site of the largest populations of *A. nigrita* (Fig. 3). *A. lividus* populations appear to be linked with floodplains.

Within the sampling area, livestock density was greatest near the abundant water and pasture available around El Tapado, site of traps yielding the greatest densities and biomass (Fig. 3), and the only site in which all six species were captured (Table 1). The Bray-Curtis percent dissimilarity index (Ludwig & Reynolds, 1988), using El Tapado data as a base, was employed to compare regional variation in communities. In particular (Fig. 4): site 1 (near El Laboratorio) is very similar; site 5 (Mohovano) is next in similitude, primarily due to the dominance of *D. gazella*; in site 2 (La Playa), much poorer in species (only 3), *D. gazella* is also dominant; the similitude of site 3 (Cerro Amarillo), to the southwest, is comparable to that of

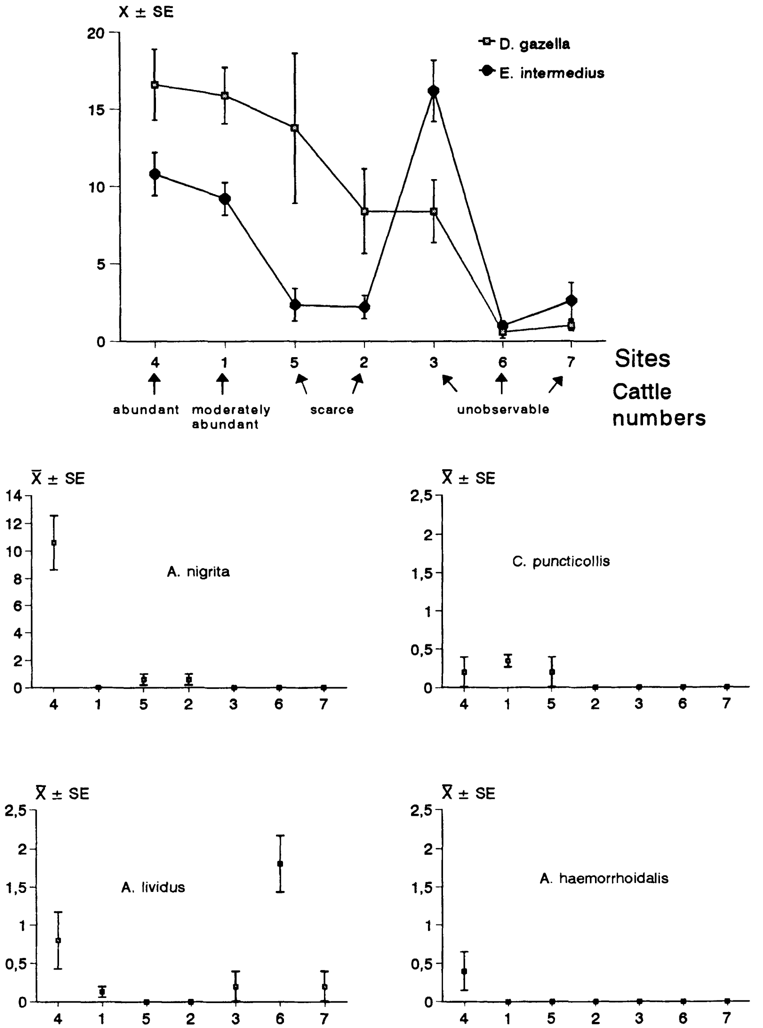


Fig. 2. Variation with site of mean number of individuals per pitfall trap of each one of the six species.

Mohovano, but *E. intermedius* is dominant (Table 1); *D. gazella* was of minor importance in the two southeastern sites, characterized by poor diversity.

These results support the idea that regional variation in population density and diversity is a consequence of resource abundance. Yet there must be another ecological mechanism responsible for the spatial segregation of the two dominant species in these communities: *D. gazella* dominant in the rich communities with livestock and pastures, and *E. intermedius* relatively dominant in the poorest communities with fewer resources.

In an experiment designed to establish the times of immigration and emigration from droppings of both species, sixteen dung pats were set out at intervals of 5 m on 30 September, at 10 a.m. Four of them, chosen at random, were examined at 24-h intervals thereafter. Average populations of both species increased in the dung pats during the first 48 h, thereafter, emigration exceeded immigration, so that after 96 h *E. intermedius* was the only species found (Fig. 5). In the process of faeces consumption, dung beetle immigration rates are roughly similar, to a certain extent a function of population abundance. Emigration rates, on the other

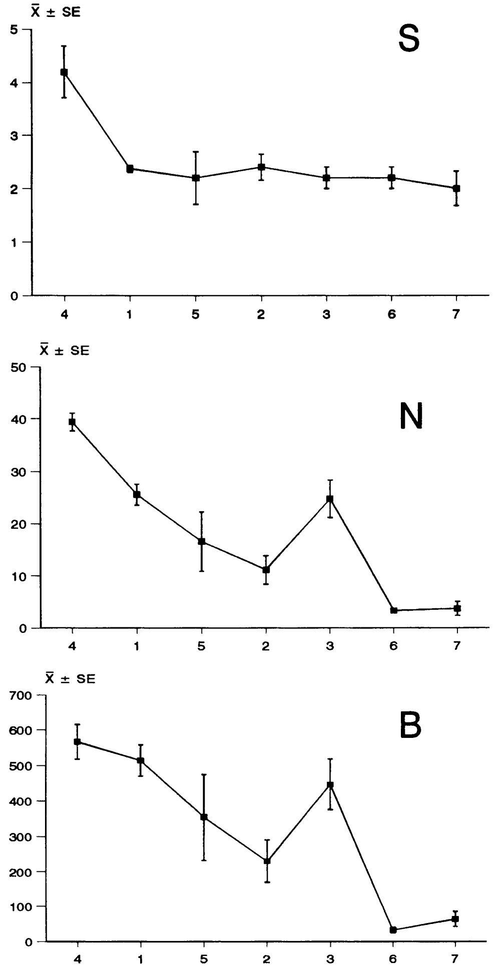


Fig. 3. Variation of average richness (S), abundance (N) and biomass (B, in mg dw) per pitfall trap at each sample site.

hand, may differ (Lobo, 1992), due to differences in environmental tolerance or trophic requirements.

While both species are prolific, their environmental requirements differ: *E. intermedius* laying fewer eggs (ninety per female) and developing more quickly (28 days) than *D. gazella* (120 eggs, 41 days) (Rougon & Rougon, 1991; Hanski, 1991b), whose adults require adequate soil moisture to emerge (Doube *et al.*, 1991). *E. intermedius* pupation can occur, and adults emerge, in the absence of rainfall. Clearly seasonally segregated in the African Sahel, *D. gazella* appears above all during the rainy season (Rougon & Rougon, 1991), building its nest at depths of 20–35 cm. Nests types of *E. intermedius*, at depths of 3–8 cm, depend on soil humidity; in dry soil, onitidian-type, in wet, onthophagian-type (Rougon & Rougon, 1982).

Evidently, *E. intermedius* is able to nest even during drought, emerge in dryer conditions, use dryer faeces, and is better adapted toward aridity and scarcity of resources than *D. gazella*. The fact that the observed emigration rates differ for the two species means that *E. intermedius* probably spends more time in dung pats, and thus is more likely to be found in sites where there is little livestock. The movement of cattle in the Mapimí area is related to their use of permanent sources of water (Barral, 1988). In some places, cattle are present permanently, in others, intermittently. In the former, *D. gazella* would always find fresh resources available, and so become dominant thanks to its greater fertility. In the latter, where the spreading between dung pats of both species is not favoured, the *E. intermedius* population would be greater, due to the above-mentioned factors (ability to exploit dry faeces, hatch in the absence of rainfall, and develop more quickly). In such places with intermittently-available trophic resources, *E. intermedius* should be able to colonize rapidly the first dung pats of newly-returned livestock, maintaining its population size above that of *D. gazella*, until the latter's greater fertility rate allowed its numbers to surpass the former's. This model could be used to explain regional differences in both populations, and would imply that: (i) both species, but above all *D. gazella*, would colonize areas after the arrival of livestock; (ii) the dung beetle community make-up in an area would be a reflection of the time elapsed without livestock; (iii) the regional diversity variation, or spatial segregation, of both species would be positively correlated with regional livestock aggregation. In the dry season, when cattle are less spatially aggregated (Barral, 1988), both species would be less regionally segregated. In the wet season, when herds are more aggregated, species segregation would increase. Without a doubt, a study of the regional dynamics of cattle and dung beetles, today a complete unknown, should shed new light on the colonization process of new territories by these species.

CONCLUSIONS

Dung beetle communities in Mapimí are much poorer today than those of other temperate and tropical biomes and also much poorer than those near the edges of the Chihuahua desert. These communities probably

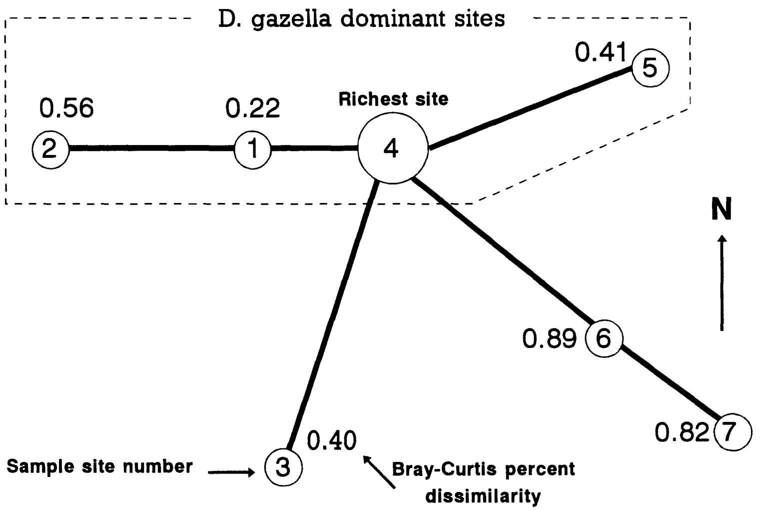


Fig. 4. Faunal similitude of sample sites compared with the richest site (site 4, El Tapado) according to the Bray-Curtis percent dissimilarity index (Ludwig & Reynolds, 1988).

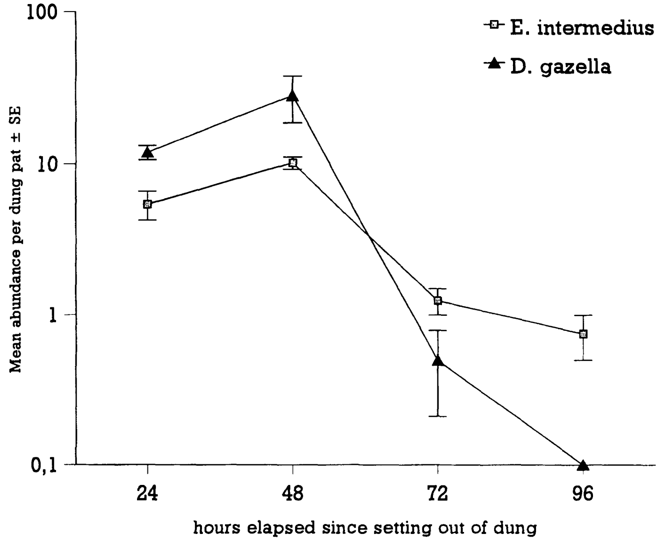


Fig. 5. Variation with time of *D. gazella* and *E. intermedius* average abundance per dung pat.

were even poorer as recently as perhaps 20 years ago. At least three of the six species found there colonized Mapimí less than 10 years ago, and two others probably were introduced relatively recently.

Due to their poverty, lack of autochthonous elements, northern penetration and the important role of recently introduced species, actual Mapimí dung beetle communities are today probably in the process of becoming saturated in both individuals and species. For these reasons competitive displacement of autochthonous species by exotics is considered very improbable.

On a geographic scale, the diversity and composition of the dung beetle communities of Mapimí seem to be primarily functions of historic and topographic factors. Adverse environmental conditions, while limiting the number of coexisting species, would not seem to be the principal cause of species poverty. The latter is probably a function of the scarcity and geographical isolation of American species capable of colonizing this type of biome.

Cattle having been in this area for nearly a century at least (Barral & Hernández, 1992), dung bettle community composition and diversity would seem to be only secondarily a function of resource availability, a factor which does, however, become important on a regional scale (between sampling sites). For even though there is no major regional variation between communities, diversity and density is greater in sites where cattle graze. The response to the presence of cattle of the two species characterizing these communities is remarkable, insofar as *D. gazella* dominates in sites grazed by cattle, while *E. intermedius* does so in the others. Such segregation could be the result of their different ontogenetic, behavioural and eco-physiologic adaptation to the arid environment.

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