STRUCTURE OF A SCARABAEINAE COMMUNITY: A NUMERICAL-BEHAVIOURAL STUDY (COLEOPTERA: SCARABAEINAE)

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ABSTRACT

The structure of a Scarabaeinae community in the tropical mountains of Mexico is studied using trophic and reproductive characters, which were analyzed by multivariate methods (cluster and ordination analysis). The results suggest that spatial-temporal characters play an important role in structuring the community. These characters along with resource utilization behaviour suggest that competition has a community ordering process. Species richness in this area is high due to a biogeographic overlap. The obtained results show the great potential of using multivariate analysis techniques for this type of study.

RESUMEN

En el presente trabajo se estudia la estructura de una comunidad de Scarabaeinae de las montañas tropicales de México, en el estado de Guerrero en un área de pastizales y de bosque tropical caducifolio. Se analizan tanto caracteres tróficos como reproductivos utilizando un análisis de agrupamientos y un análisis en coordenadas principales, el cual es un método reconstructivo que permite calcular com-

ponentes principales a partir de cualquier matriz de distancias geométricas (Euclidiana). La similitud entre especies fue calculada usando el coeficiente de similitud general de Gower. Estas técnicas fueron utilizadas en tres conjuntos de datos: para caracteres tróficos, reproductivos y ambos. El análisis de los caracteres tróficos muestra que las características de espacio y tiempo, dimensión corporal y abundancia relativa son factores importantes que determinan la estructura de la comunidad. Aparentemente, para las especies de bosque los caracteres de espacio y tiempo son más importantes, mientras que para las especies de pastizal lo son peso y dimensiones corporales. Se puede pensar que el grupo de especies de bosque se encuentra saturado, estando todas sus clases de peso y tamaño ocupadas, de tal forma que el siguiente cambio de estrategia es hacia una dimensión diurna dentro del bosque.

El análisis de los caracteres tróficos y reproductores muestra que la estrategia reproductora, tamaño del cuerpo, cooperación bisexual, estructura de la cámara del huevo, horario de actividad así como habitat son de importancia para la estructuración de la comunidad. El análisis de caracteres puramente reproductores no demostró una estructuración muy detallada de la comunidad. Los dos primeros tipos de análisis dan estructuras de la comunidad muy similares, lo cual sugiere que usar sólo caracteres tróficos da una buena caracterización de la misma. Se sabe que las comunidades coprófagas de bosque, en la América tropical son más ricas en número de especies que el mismo tipo de comunidades de pastizales. Sin embargo, en este caso la comunidad de pastizal en esta área es relativamente rica debido a una "mezcla" faunística. Se encuentran tanto especies de la Depresión del Balsas, como especies de regiones templadas de las montañas, así como de amplia distribución estableciéndose también un traslapamiento biogeográfico.

INTRODUCTION

The structure and fuction of biological communities are affected, and in several instances determined, by the characteristics of species that constitute them and by interactions between them. There are several historical, evolutionary and ecological factors that regulate coexisting species number in a particular place at a certain given moment.

Fundamental to the ideas of resource partitioning and competition is the concept of ecological niche as stated by Hutchinson (Cody, 1974; Dueser and Shugart, 1979; Fujii, 1969; Pianka, 1976, 1978). Although the multidimensional niche concept has a high heuristic value, the practical problems stemming from its application are well known.

The use of multifactorial or multivariate statistical analysis in ecology has been growing in these last years. It is in this context that ordination and cluster analysis techniques have been employed.

In the specific case of insects, multivariate analysis techniques have been used for taxonomic studies, but only in a few cases for ecological studies. The subfamily Scarabaeinae (Coleoptera: Scarabaeidae) is a relatively well known group from the taxonomic and natural history points of view (Halffter and Edmonds, 1982). Nevertheless few people have studied them using a mathematical ecological approach (Hanski and Koskela, 1977, Koskela and Hanski, 1977, Nealis, 1977; Hanski and Koskela, 1978; Lumaret, 1978; Hanski and Koskela, 1979; Hanski, 1980; Holter, 1982; Peck and Forsyth, 1982 and Stevenson, 1982).

In this paper we use multivariate analysis techniques for studying some aspects of resource utilization and community structure in Scarabaeinae of tropical deciduous forest in Mexican mountains using ecological, behavioural and morphological characters. These beetle communities are especially interesting because they make use of very particular resources (excrements, carrion or decomposing fruit), that have a patchy distribution and short life, and because they often comprise a large number of species.

The purpose of this study is to identify the most important factors that characterize and define the communities studied.

STUDY AREA

The studies were conducted during the month of August, 1980, 5 Km E of Teloloapan, State of Guerrero, on the Pacific slope of the Neovolcanic System, 1610 m (18^0 22' N and 99^0 52' W). The vegetation is tropical deciduous forest, according to Rzedowsky's (1978) classification. In this area several species of *Bursera* (Burseraceae) are a very common vegetation element. The climate is the $A(C)w_2(w)ig$ type of Köppen's classification, modified by García (1973), i.e. a warm, subhumid climate with summer rains. The average annual temperature is 21.9^0 C and average annual precipitation is 1264 mm.

Additional data were obtained from another, ecologically similar locality, Zacatlancillo, about 20 Km W of Teloloapan.

3

METHODS

Bettles were collected in 1 l plastic pitfall traps, baited with one of three type of baits: human excrement, rotting fish and

	Identification Number
Tribe ONTHOPHAGINI.	
Onthophagus mexicanus.	11
Onthophagus igualensis.	14
Onthophagus rostratus.	12
Onthophagus nitidor.	9
Tribe COPRINI.	
Subtribe DICHOTOMINA.	
Dichotomius carolinus.	3
Dichotomius centralis.	4
Ateuchus carolinae.	10
Ateuchus halffteri.	17
Scatimus ovatus.	8
Subtribe PHANAEINA.	
Phanaeus (P.) daphnis.	16
Phanaeus (P.) mexicanus.	5
Phanaeus. (C.) telamon corythus	1
Subtribe COPRINA.	
Copris klugi klugi.	6
Tribe SCARABAEINI.	
Subtribe SCARABAEINA.	
Canthon (C.) cyanellus cyanellus.	2.
Canthon (C.) humectus incisus.	15
Canthon (G.) viridis coorporali.	7
Deltochilum gibbosum.	13

Table 1
Species included in this study: Taxonomic position and identification co-de.

rotting fruit (papaya). Sets of three traps, one with each of the bait types, were placed in woodland and open-fields, always under shade cover to avoid dessication. The traps were checked and emptied daily and the collected material was killed and preserved in ethyl acetate for later identification and measurement at the laboratory.

STUDY ORGANISMS

The subfamily Scarabaeinae is cosmopolitan and comprises usually coprophagous, nocturnal and darkly coloured species; all of these traits are generally considered primitive in most cases in American groups, whereas necrophagic, diurnal, species having metallic colours are considered as derived. The systematic position of the treated species is shown in table 1.

The subfamily Aphodiinae, which was also present in the area and which has similar habits, is not included in this study because its taxonomy is poorly known and because very few specimens were collected.

CHARACTER SELECTION

The choice of characters for such a community study is always subjective, although one tries to select characters that are comparable among all treated species. Table 2 lists all characters used for this study.

One can distinguish two sets of characters that Young (1979) as well as we consider as relevant to the trophic structure of the community. The other set contains the last five characters, all of them related to reproductive strategies, especially nesting, they are based on Halffter and Edmonds, (1982).

It should be said that the forementioned authors consider r– and K-strategies as extremes of a continuum of life history traits, and not as mutually exclusive concepts.

We do not know *Dichotomius centralis* nests. We assume it nests as do ecologically similar South American woodland species.

Characters five, six and seven are related to dominance. Length is an explicit character, being an estimation of the

5

Character 1: FOOD TYPE
    0.—Saprophagous
    1.—Coprophagous
    2.—Necrophagous
Character 2: FORAGING TIME
    0.—Nocturnal
    1.—Diurnal
Character 3: USUAL HABITAT
    0.—Forest interior
    1.—Open tracts
Character 4: RESOURCE CONSUMPTION PATTERN
    0.—Burial under food source
    1.—Burial and/or pushing with head
    2.—Rolling with hind legs
Character 5: BODY LENGTH in mm (Average for collected specimens)
Character 6: WEIGHT in g (Average for collected specimens)
Character 7: ABUNDANCE (ind./trap)
Character 8: REPRODUCTIVE STRATEGY TREND
    0.—r trend
    1.—K trend
Character 9: NESTING PATTERN
    0.—Type I   2.—Type III
    1.—Type II   3.—Type IV
        4.—Type V
Character 10: BROOD CARE
    0.—No
    1.—Yes
Character 11: BISEXUAL COOPERATION
    0.—Absent or scarce
    1.—Present
Character 12: EGG CHAMBER
    0.—Non-isolated
    1.—Isolated

Table 2
Character key and code used for species description.

average individual size. Abundance has always been difficult to determine and in this case we have considered it to be the average number of individuals per species, per trap, per bait type, per habitat. In this way a comparison is at least possible. Average individual weight probably would furnish similar information as length, so we have elected to pool it with abundance for this analysis in order to obtain a rough estimate of biomass.

Character nine describes different nidification patterns proposed by Halffter and Edmonds, (1982). Type I: Nests single or compound, subterranean, paracoprid, brood balls with a linear or racemose distribution, ocasionally linear-racemose. Type II: Nests compound, subterranean, paracoprid, brood balls with a linear or racemose distribution when nest is compound. Type III: Nests compound, subterranean, paracoprid, brood balls grouped in a single chamber. Type IV: Nests simple, subterranean or superficial, telocoprid, brood balls rolled away and buried at a distance. Type V: Nests compound, superficial, telocoprid, brood balls rolled away and grouped in a shallow cavity. Nesting patterns were really described as a diagnosis of several characters (Halffter and Edmonds, 1982). Some of these characters (brood care and bisexual cooperation) were taken out from the diagnosis and separately analyzed in order to evaluate their importance, only the more architectural characters were left to describe the nesting patterns in this study.

Table 1 lists the identification code of the species. Table 3 constitutes the matrix of raw data and does not include the pooled weight and abundance characters.

DATA ANALYSIS

The biological characteristics determined for seventeen species allow us to define portions of their ecological niches (using the methods of Levins (1968) and Fujii (1969)). Three series of analysis were undertaken. The first, which considers only trophic characters (characters 1 to 7) permit us to visualize utilization of food resources. The second includes all characters (trophic and reproductive) and results in an overall view of each species' niche. The third considers only reproductive characters. The results of the third analysis are not presented here, because only two great groups were recognized: 1) K-strategy, bisexual cooperation and, in general, with an isolated egg

	Species.								
	1	2	3	4	5	6	7	8	9
1*	2	2	1	1	1	1	1	1	1
2*	0	1	0	0	1	0	1	0	0
3*	0	0	1	0	1	0	0	0	1
4*	0	2	1	1	1	0	2	0	0
5*	23	14	26	21	22	18	5	5	7
6*	.88	.04	2.08	.92	.68	.41	.01	.01	.02
7*	6.3	1.3	.6	9.3	1.3	4.0	1.6	7.3	15
8	1	1	0	1	1	1	1	0	0
9	1	4	0	1	1	2	3	0	0
10	0	1	0	0	0	1	0	0	0
11	1	1	0	1	1	1	1	0	0
12	1	1	0	1	1	0	0	0	0

Characters.

	Species.								
	10	11	12	13	14	15	16	17
1*	1	1	0	1	1	1	1	1
2*	0	1	1	0	1	1	1	0
3*	0	1	0	0	1	1	1	0
4*	0	0	0	2	0	2	1	0
5*	6.5	6.5	6.5	23	3.5	13	15	6.5
6*	.04	.01	.01	.68	.005	.21	.42	.04
7*	24 .3	1.3	14	1.3	0.3	8	3.3	0.3
8	0	0	0	1	0	1	1	0
9	0	0	0	3	0	3	1	0
10	0	0	0	0	0	0	0	0
11	0	0	0	1	0	1	1	0
12	0	0	0	0	0	0	1	0

Characters.

Table 3
Data matrix. See tables I and II for key to character and species codes.
Trophic characters are marked with an asterisk (*).

chamber; and 2) r-strategy, no or small bisexual cooperation and in general a non-isolated egg chamber.

The same methodology was used for all three analyses: First, a cluster analysis was performed to identify the number of species subgroups correlated with particular ecological characteristics. The species in each subgroup form an ecologically homogeneous guild *sensu* Root (1967).

The similarity between each species pair was calculated using Gower's General Similarity Coefficient, because this metric allows the use of mixed characters (i.e. binary, multistate and meristic characters).

Nevertheless geometric (Euclidean) distance or dissimilarity was used instead, since it gives a better representation of niche space. It was calculated taking the square root of the complement of Gower's Similarity Coefficient. Previously the interval covered by each character was adjusted to a unitarian interval, using the transformation proposed by Gower (1966).

The clustering strategy used is known as UPGMA (Unweighted pair-group method using arithmetic averages), which is polythetic, agglomerative and hierarchic causing a relatively small space distortion. The details of all these procedures are given in Cody (1974) and Sneath and Sokal (1973).

Figure 1 shows the resulting dendrogram using only trophic characters and figure 5 depicts the corresponding analysis using the totality of characters. Additionally the average dissimilarities of each species for the different analyses were computed and are reproduced in table 4. The discussion and interpretation of these results are given later.

The second step in the overall analysis was the use of an ordination technique. One of the main aims of these techniques is to reduce the dimensionality of data structure, having at the same time a minimal distortion.

Gower's (1966) "Principal Coordinates Analysis" was used, since it is a reconstructive method that allows us to compute principal components starting from any geometric (Euclidean) distance matrix. These matrixes are not reproduced here. The computational aspects of this method are given in Chatfield and Collins (1980), Orlóci (1978), Pielou (1977) and Sneath and Sokal, (1973).

In each analysis (trophic characters, totality of

9

Species number	Mean dissimilarity.	Species number	Mean dissimilarity.
1	0.7381	9*	0.5962
2	0.7874	10*	0.5745
3	0.6627	11*	0.6015
4	0.7239	12	0.6607
5	0.6878	13	0.6591
6	0.7002	14*	0.6098
7	0.6566	15	0.6650
8*	0.5765	16	0.6815
		17*	0.5721
		MEAN	0.6561

Table 4
Mean dissimilarity for each species: Trophic and reproductive character analysis. Species with mean dissimilarity less than average of mean dissimilarities are regarded as "core species" and marked with an asterisk (*). See explanation in the text.

characters) we tested the significance of the three first principal components using Frontier's (1974; in Daget, 1976) residual variance method. In both cases the three principal components were significant. Figures 2 and 6 are the corresponding ordination diagrams of the trophic and of the totality of characters, respectively.

The interpretation of the principal components was done using Daget's (1976) graphic method, where one compares the behaviour of the coordinates or saturation factors of the seventeen species in each principal components with the behaviour of the different characters of all species. Any character whose behaviour resembles the one of a component, can be suggested as the interpretation of that component. Figures 3 and 4 show graphic comparisons of those characters that seem to be best correlated with the first principal component of trophic character analysis. Figures 7 and 8 show the same for the totality of character analysis. The discussion and interpretation of these results are given in the next section.
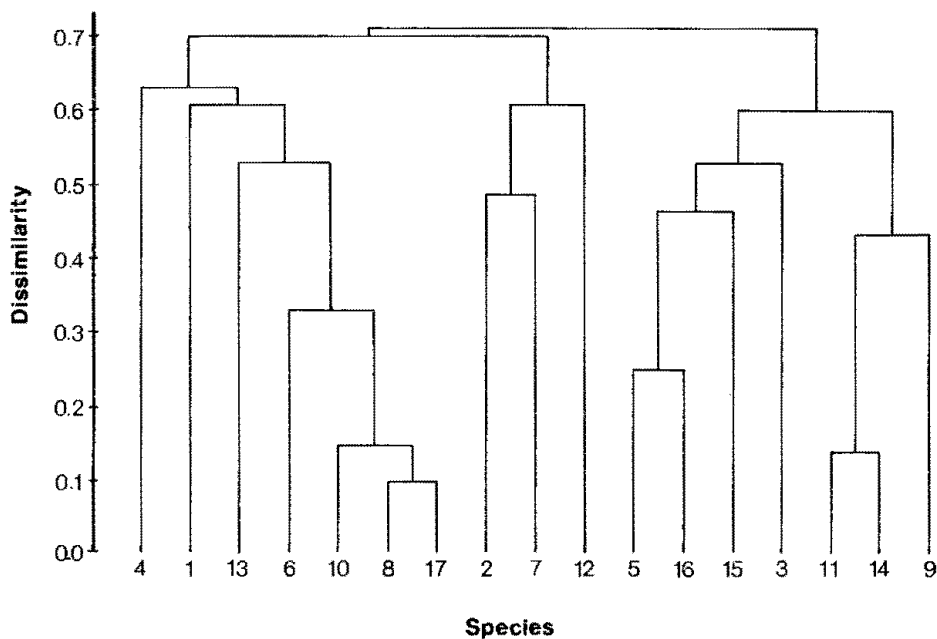
Figure 1
UPGMA dendrogram of simmilarity relationships between species
(trophic characater analysis). Dissimilarity is given as the square root of
the complement of Gower's General Simmilarity Coefficient. See Table 1
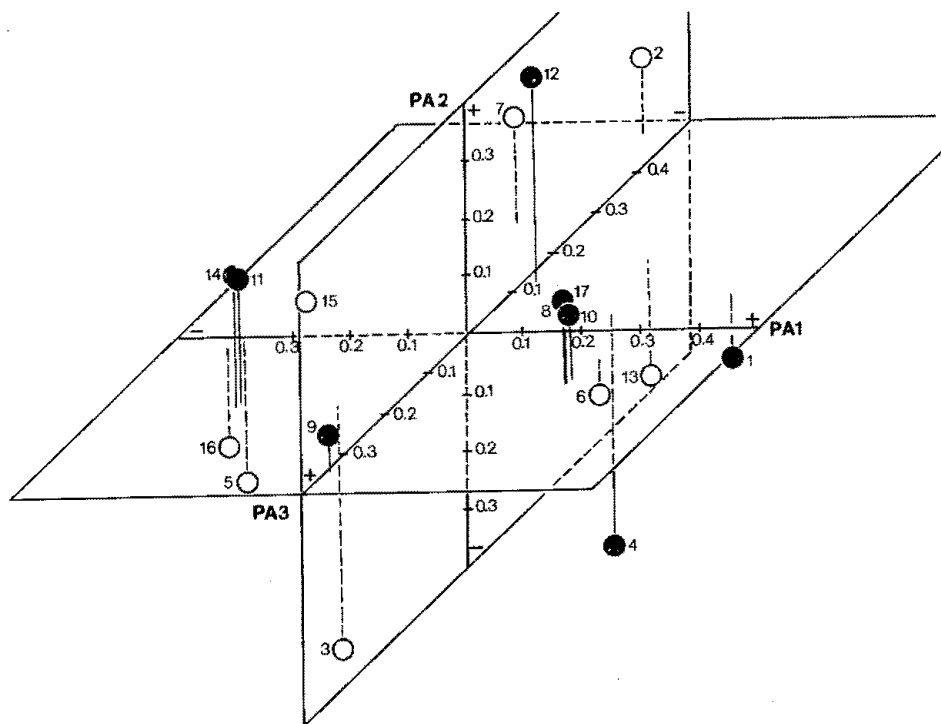for species code. Interpretation in the text.

Figure 2
Distribution of 17 species relative to the first three principal axes (trophic character analysis). These axes account for 73.5% of total variation. Interpretation in the text.
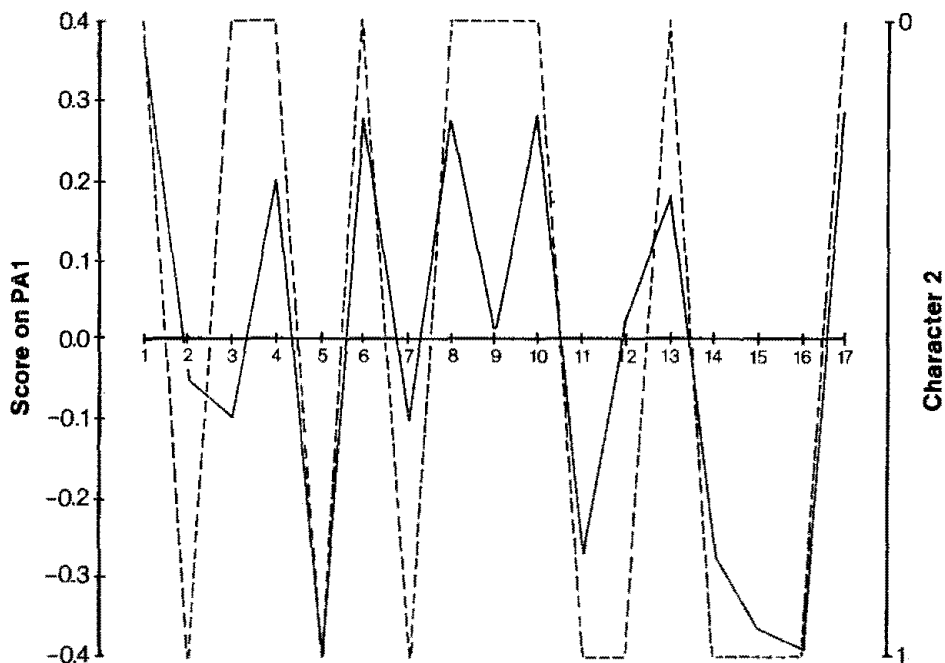
Figure 3
Relationship between score on P. A. 1 (continuous line) and character 2
(foraging time, broken line) in 17 species.
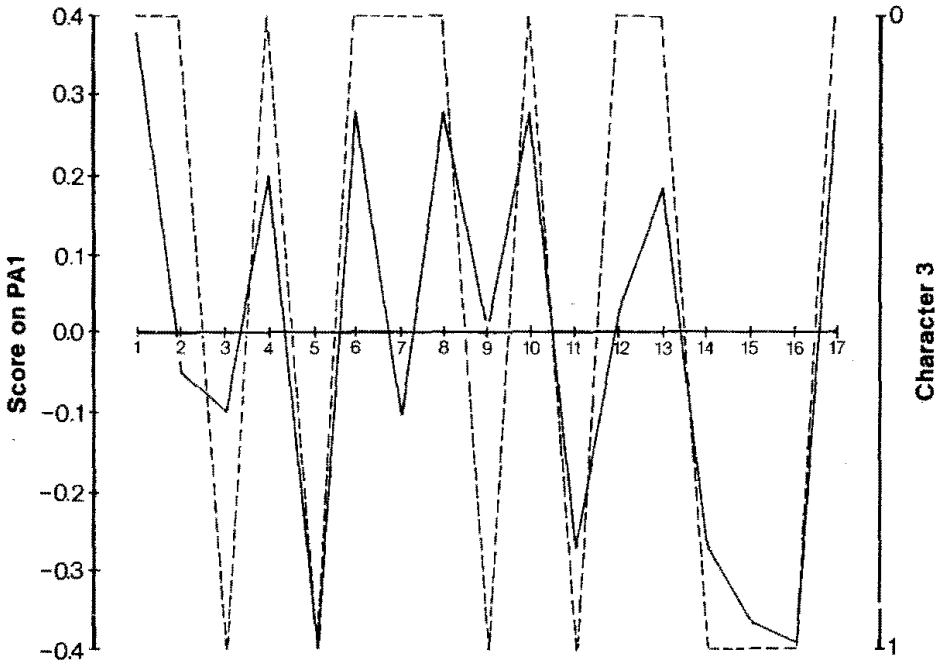
Figure 4
Relationship between score on P. A. 1 (continuous line) and character 3
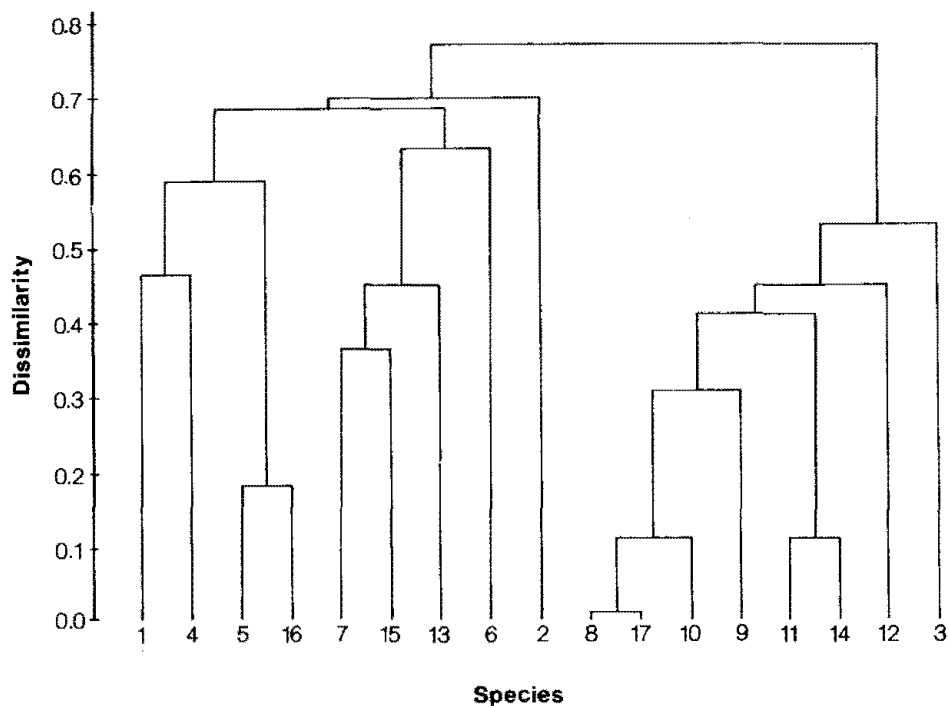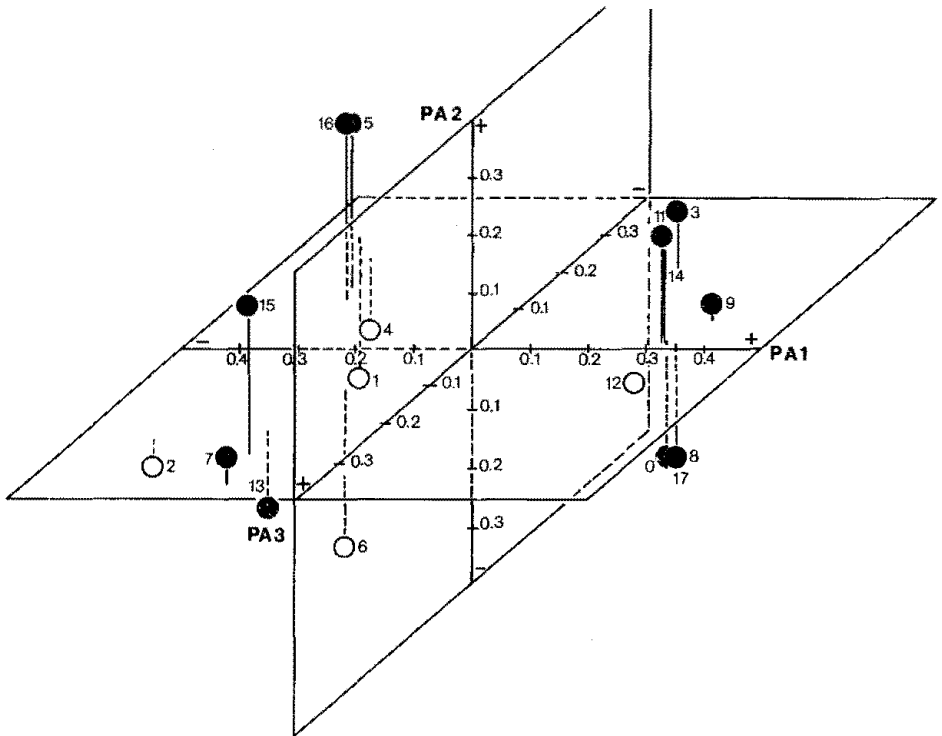(usual habitat, broken line) in 17 species.

Figure 5
UPGMA dendrogram of simmilarity relationships between species
(trophic and reproductive character analysis). Dissimilarity is given as the
square root of the complement of Gower's General Simmilarity
Coefficient. See Table 1 for species code. Interpretation in the code.

Figure 6
Distribution of 17 species relative to the first three principal axes (trophic
and reproductive character analysis). These axes account for 74.3% of
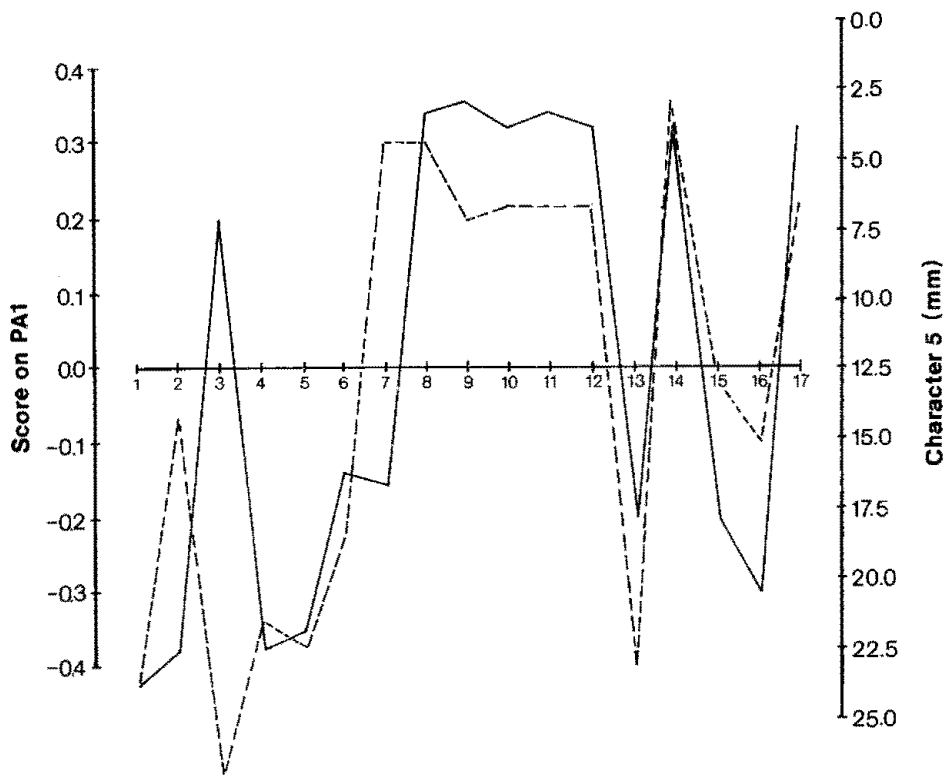variation. Interpretation in the text.

Figure 7
Relationship between score on P. A. 1 (continuos line) and character 5
(body length, broken line) in 17 species. r = −0.6791 (P<0.01).
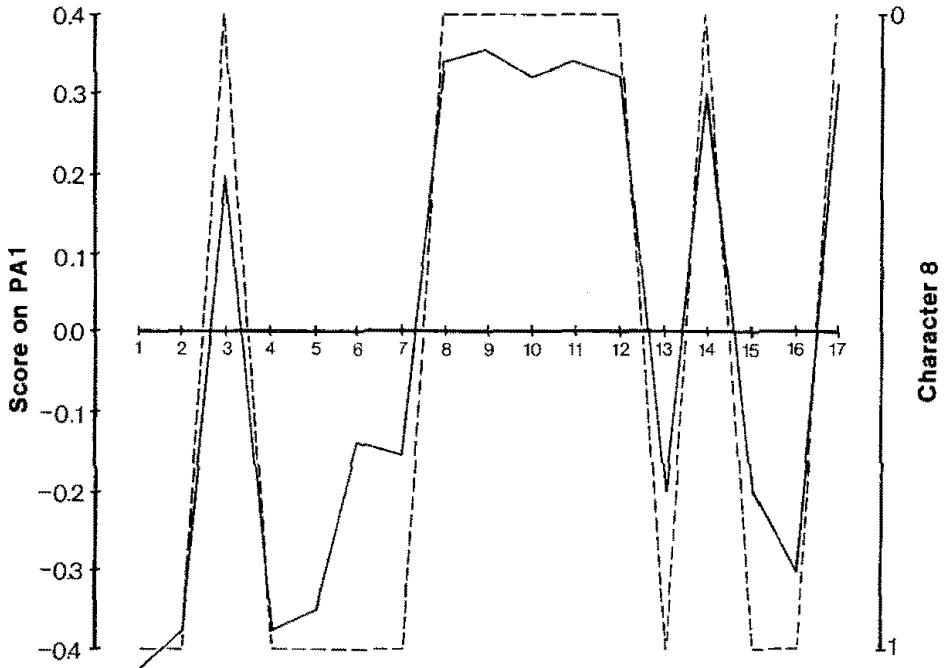
Figure 8
Relationship between score on P. A. 1 (continuous line) and character 8
(reproductive strategy, broken line) in 17 species).

DISCUSSION AND RESULTS

Analysis of Trophic Characters

The dendrogram obtained from this analysis (Fig. 1) reveals some general aspects of resource partitioning among the species of this community. First, two great species groups emerge: Woodland species (species 1, 2, 4, 6, 7, 8, 10, 12, 13, and 17), and open-field species (species 3, 5, 9, 11, 14, 15 and 16).

The woodland species-group clearly separates into two subgroups. One includes nocturnal species (species 1, 4, 6, 8, 10, 13 and 17), the other diurnal species (species 2, 7 and 12). These spatial and temporal segregation patterns are probably related to the differentiation and segregation of niches promoted by competition (Pianka, 1976, 1978).

The open-field species group divides again into two subgroups that differ in size and estimated biomass. One of them is formed by large, heavy species (species 3, 5, 15 and 16), the other by small and light species belonging to the genus *Onthophagus* (species 9, 11 and 14). This pattern is frequently observed in Mexico and it is possible that these size and biomass differences are of importance to resource partitioning since all open-field species here treated are coprophagous. Hanski (1980) has arrived at a similar conclusion for dung-inhabiting Hydrophilidae (Insecta: Coleoptera) in northern Europe.

The resulting groups consist of core species such as 6, 7, 8, 9, 10, 11, 14 and 17 which initiate the cluster or join it early; and fringe species such as 1, 2, 3, 4, 12, 13 and 15, which are relatively different from the others and could be treated in a certain way as specialists (Cody, 1974).

Core species generally show a low dissimilarity, table IV), whereas fringe species show a high dissimilarity value (Cody, 1974).

We have considered as core species those whose average dissimilarity is less than the total average dissimilarity of all species.

Each of the four derived subgroups includes species with similar ecological characteristics, where competition is potentially more intense than between species of different subgroups

(Cody, 1974). One can expect that among species of each subgroup some characteristics will operate to reduce competition intensity. However, the analysis does not furnish a finer differentiation, with the exception of open-field *Onthophagus,* which are separated into diurnal (species 11 and 14) and nocturnal (species 9) species.

Concerning ordination analysis, the first principal axis accounts for 31.32% of total variance. Figures 3 and 4 show that this axis can be interpreted as a combination of characters 2 (activity timetable) and 3 (type of habitat). In this way the most important differences for these species are given by spatial and temporal dimensions. We find towards the positive end of the first principal axis, nocturnal, woodland species and to the negative end, diurnal, open-field species (Fig. 2). Diurnal, woodland species and nocturnal open-field species are found on the central part of the first principal axis.

The second principal axis accounts for 23.27% of total variance and is correlated with average length and estimated biomass. One finds towards the positive end of the second principal axis small, light species and towards the negative end large, heavy species.

The third principal axis accounts for 18.91% of total variance and is correlated with resource utilization behaviour. Towards the positive end of the third principal axis we find species that stay at the food source and bury food beneath it, and towards the negative end those species that roll food fragments with their hind legs. Species that push away food fragments are situated on the centre of the third axis.

The tridimensional diagram (Fig. 2) shows the relative position of the species in relation to the three principal axes. One notes a remarkable dispersal that reveals existing differences between species.

Differentiation of these characters could be a factor contributing to the coexistence of great number of species. As a reference the "Los Tuxtlas" biological research station near Sontecomapan, Veracruz, is tropical evergreen forest and supports 27 species of Scarabaeinae (Morón, 1979). The high species richness of Teloloapan is caused by a "biogeographic overlap", the confluence of tropical woodland species with Balsas River Valley species and some temperate mountain elements.

Analysis of Trophic and Reproductive Characters

This analysis gives us a more complete picture of the existing affinities and differences between species and, therefore, of the community structure.

We notice in the dendrogram (Fig. 5) a first division into two groups. One includes K-strategists, medium or large sized species (with the exception of species 7) that have bisexual cooperation and several nesting patterns, excluding pattern I (species 1, 2, 4, 5, 6, 7, 13, 15 and 16). The other group comprises r-strategists, small sized species (with the exception of species 3) that do not show bisexual cooperation and present only nesting pattern I (species 3, 8, 9, 10, 11, 12, 14 and 17). This correlation between body size, bisexual cooperation and reproductive strategy agrees with theoretical arguments expressed by Pianka (1976, 1978).

Among the group of K-strategists, species 2 (*Canthon cyanellus*) shows an isolated position (average dissimilarity = 0.787), which is apparently determined by its nesting pattern (type V), brood care type and food source (necrophagy) besides being diurnal. The first subgroup (species 7, 13 and 15) comprises all species with nesting pattern IV and also species 6 (*Copris klugi*) with nesting pattern III. We observe here that species 8, 9, 10, 11, 14 and 17 are core species, species 5 and 16 are in an intermediate position and all the rest are fringe species.

In all analyses done so far a group of three very closely related species appears: *Scatimus ovatus, Ateuchs halffteri* and *Ateuchus carolinae*. Within this group *S. ovatus* and *A. halffteri* appear as the two most similar species. One would expect that both *Ateuchus* species should appear as more proximate since they are ecologically very similar. This apparent incongruity is due to the fact that *S. ovatus* as well as *A. halffteri* are not very abundant in this area (whereas *A. carolinae* is) and therefore appear as more similar in the analysis. Moreover there are some records of *S. ovatus* being found in broodballs of other dung beetles (G. Halffter, *pers. comm.*, and original observations) which suggests that cleptoparasitism exists in this species.

The dendrogram shows, reproductive characters play an important role in the general structuring of the community. This view is also supported by the ordination analysis, as discussed below.

The first principal axis accounts for 42.31% of total variance and is correlated with average length, reproductive strategy, bisexual cooperation and egg chamber isolation (Figs. 7 and 8). Towards the positive end of the first axis we find r-strategists and small species with no bisexual cooperation and non-isolated egg chambers; towards the negative end we find species with contrary characters. This division is essentially the same as the one found in the dendrogram.

The second principal axis accounts for 16.88% of total variance and is correlated with activity timetable and type of habitat. Towards the positive end of the second axis we find diurnal and open-field species and towards the negative end, nocturnal and woodland species. On the central part of the second axis one finds diurnal, woodland species and nocturnal, open-field species.

The third principal axis accounts for 15.15% of total variance and is correlated with different nesting patterns. Towards the negative end of the third axis we find nesting pattern I and the other patterns towards the positive end.

The tridimensional diagram (Fig. 6) shows the relative position of the species to the three principal axes. The observed dispersion shows existing differences between species. The diagram gives a synthetic description of the approximate community structure in relation to trophic and reproductive characters.

CONCLUSIONS

The analysis of trophic characters shows that spatial-temporal, body dimensions and relative abundance characters are important determinants of community structure. Apparently for wood-land species the spatial-temporal characters are more important, whereas for open-field species body weight and dimensions are of greater importance. One could think of the nocturnal, woodland group, which has the largest species number, as being saturated and having all its size and weight classes occupied so that the next available strategy shift is towards a diurnal, woodland dimension. On the other hand, the second largest group consists of the diurnal, openfield species, for which body size and weight are apparently more important. One could think of this community as showing a relative ecological vacuum (Pianka, 1978), which could still be filled along the body size and weight axis before shifting to a spatial-

temporal separation. In any case, in order to gain a deeper insight into this hypothesis; several different localities and conditions should be examined and compared in order to determine the limiting factors that would determine species number and community structure in this group.

The analyses of trophic and reproductive characters shows that reproductive strategy, body size, bisexual cooperation, egg chamber structure, activity timetable and typical habitat are of importance to community structure. The fact that reproductive characters explain a great fraction of total variance is due partly to the great concordance among them.

We conclude that the resulting community structures are very similar for both analyses. This could suggest that trophic characters alone give an adequate approximation of community structure.

Hanski (1980) and Peck and Forsyth (1982) think that the general structure of dung-beetle communities has been molded by past competition. We agree, particularly if we consider activity timetable and typical habitat segregation and, most importantly, resource utilization behaviour.

However other authors (Landin, 1961; Valiela, 1974 in Holter, 1982), think that abiotic factors or the tendency to facilitate the encounter between sexes (Holter, 1982) has been the driving force shaping the community. We think all these arguments are not mutually exclusive and their importance has varied throughout time and according to different situations. In any case it would be interesting to study Holter's aggregation findings, if there is no pheromone or sexual attractant playing a role in the process.

To this respect Bellés and Favila (1983) describe the production of an allomone in *Canthon cyanellus* (a necrophagous species) that has a repellent effect against *Calliphora* flies and it is thought that it also has a nest- and trail-marking effect.

It is known that in tropical America, coprophagous, woodland communities are richer in species number than coprophagous, open-field communities. Nevertheless the Teloloapan community is relatively rich because of faunal mixing. Balsas River Valley species (*Ph. mexicanus, Ph. daphnis, O. igualensis* and in a lax sense *C. h. incisus)* are found as well as some temperate mountain species (*O. mexicanus, O. nitidor* and *C. klugi*), and a widely distributed one (*D. carolinus*) creating here a biogeographical overlap.

If we compare this information with the results obtained by Halffter and Matthews (1966) who sudied a tropical evergreen forest in the state of Veracruz (along the Gulf Coast of Mexico) the following picture emerges. They concluded that (pp.: 71-72) the species found inside the tropical evergreen forest were strictly of Neotropical origin. It is the same for the area we study. Nevertheles the composition of the open areas although of Neotropical origin in its great part contains several elements which originated at higher elevations on mountains. This should be expected since the area lies at the altitudinal limit of the tropical deciduous forest.

They also found that the species were strictly stenotopic, there is a complete exlusion inside the forest of species which inhabit open areas and viceversa. The same conclusion can be applied here.

Lastly they concluded that two distinct faunas were present inside the forest, a diurnal and a nocturnal one. We arrive at the same conclusion when we say that spatial-temporal characters are important for structuring the forest community. Nevertheless in tropical evergreen forests necrophagous species are a very important component whereas they decrease in importance in tropical deciduous forests. Coprophagous species are more important in this type of habitat.

The comparison shows that a certain general behaviour underlies the structure of tropical forests concerning dung beetle communities.

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