



**ASSEMBLAGE ORGANIZATION OF SURFACE-ACTIVE  
ARTHROPODS ALONG HORIZONTAL  
MOISTURE GRADIENTS IN A COASTAL  
SONORAN DESERT ECOSYSTEM.**

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## RESUMEN

Examinamos las diferencias a corto plazo en la organización de las comunidades de artrópodos activos en la superficie del suelo en una porción restringida del ecosistema de dunas cerca de Puerto Peñasco, Sonora, México. Para probar la hipótesis de que el gradiente de humedad del suelo influye en tal organización, se establecieron tres transectos de 32 m en dirección oeste hacia la costa 1) área de estero, 2) estanque de agua salada, y 3) área intermedia de desierto seco (control). El gradiente de humedad varió en el estero y estanque de 15% y 11% a <1% respectivamente, mientras que la humedad del suelo en la área control fue de <1% (valores promedio a 15 cm de profundidad). Cuatro lotes, proporcionalmente espaciados de 3 x 7 m a lo largo del transecto con trampas "pitfall" capturaron artrópodos continuamente por períodos de 12 horas, el número de trampas fue ocho en el estero, ocho en el estanque y seis en el control.

Se capturaron 558 artrópodos pertenecientes a 50 especies, se excluyeron las numerosas hormigas del género *Solenopsis*. El análisis de "rarefaction" con 80 como tamaño de muestra, mostró valores de 27 en el estero, 21.5 en el estanque y 18 para el sitio de control, cuando se eliminó el efecto de pantano de *Uca latimanus* (cangrejo que fue dominante en el estero y ausente en los otros dos sitios).

Los artrópodos, excluyendo cangrejos, fueron doblemente abundantes en el estero durante el día y cuatro veces más abundantes en la noche que en los otros dos sitios durante el día.

La proporción carnívoros-detritívoros en los tres sitios fue aproximadamente 2:1 (estero), 1:1 (estanque) y 1:2 (control). El valor de similitud (modificado de Hill E5) sin *Uca* fue similar en todos los sitios; sin embargo, grandes valores en diversidad (Hill N2) confirman la presencia de numerosas especies en el estero (escarabajos Carabidae y arañas Lycosidae). No se encontró relación significativa entre el porcentaje de cobertura vegetal y la densidad de artrópodos capturados. La medida del valor beta-diversidad (coeficiente de comunidad de Sørensen) reafirma la particularidad de la organización en el estero. Nuestra hipótesis inicial fue parcialmente apoyada porque la diferencia de especies, abundancia de individuos y proporción carnívoros-detritívoros tendió a incrementarse con el gradiente de humedad.

## ABSTRACT

We examined short-term differences in assemblage organization of surface-active arthropods from a restricted portion of a coastal dune ecosystem near Puerto Peñasco, Sonora, Mexico. To test the hypothesis that soil moisture gradients influence organization, we established three, 32-m transects running westward from real or simulated shorelines: of 1) an estuary terminus ("estero"),

2) a salt-water pond ("seep"), and 3) an intermediate dry desert site ("control"). Transect moisture gradients ranged, at the estero and seep sites respectively, from 15% and 11% to <1%, while soil moisture at the control site was <1% (mean values to 15cm depths). Four evenly spaced plots, each 3 x 7m, along each transect contained pitfall traps that captured arthropods continuously for eight (estero, seep), or six (control), 12-h periods.

We trapped 558 arthropods comprising 50 species, excluding abundant ants of the genus *Solenopsis*. Rarefaction analysis for sample sizes of 80 gave expected species numbers,  $E(S_n)$ , of 27 (estero), 21.5 (seep), and 18 (control) when the swamping effect of *Uca latimanus* (crabs which were dominant at the estero, absent elsewhere) was removed. Arthropods other than crabs were twice as abundant at the estero and four times as abundant at night, respectively, as they were at the other two sites and during the day.

Carnivore:detritivore species ratios at the three sites were approximately 2:1 (estero), 1:1 (seep), and 1:2 (control). Evenness (modified Hill's  $E_5$ ) values without *Uca* were similar at all sites; however, high diversity (Hill's  $N_2$ ) values for the estero assemblage confirmed the presence of a small number of abundant species (carabid beetles, lycosid spiders) there. We found no significant correlation between percent plant cover and total densities or species richness of trapped arthropods. Measurements of beta-diversity (Sørensen's community coefficient) reinforced the uniqueness of the estero assemblage. Our initial hypothesis received support in that species differences, individual abundances, and carnivore:detritivore ratios all tended to increase along moisture gradients.

## INTRODUCTION

The distribution and abundance of desert arthropods, including many species that are regularly active on the soil surface, is strongly influenced by the physical environment (Cloudsley-Thompson and Chadwick 1964, Crawford 1981, Wallwork 1982). Temperature and moisture extremes, in particular, can regulate the activities of individual species and species assemblages of these organisms (Cloudsley-Thompson and Idris 1964, Ghabbour et al. 1977, Holm and Scholtz 1980, Mispagel 1983). Use of suitable trapping methods, especially pitfall-trapping, enables one to assess the organizational patterns of such assemblages as patterns change between habitats and over time (Ghabbour and Shakir 1980, Pietruszka 1980, Crawford and Seely 1987, El-Shishiny and Ghabbour 1988, Pantis et al. 1988).

Differing patterns of assemblage organization can be attributed to soil conditions (Crawford 1988, in press) and local moisture regimes. Crawford and

Seely (1987) found that in relatively moist and recently wetted (by rain) soils, the species richness and population densities of carnivorous arthropods exceeded those of detritivorous arthropods. In deserts generally, species richness ratios of these two most common trophic groups are on average about even (Crawford in press).

In the present study we examined aspects of assemblage organization in two moist and one dry (control) desert habitats, all within < 1 km of each other. Since the latter typified local desert shrubland, we termed it the "control" habitat. Specifically, we use short-term pitfall-trap results to test the hypothesis that horizontal soil moisture gradients influence organizational patterns of surface-active arthropod assemblages in a restricted coastal desert ecosystem.

### Study Sites

The study area (Fig. 1, 2) was located directly inland of the Centro de Estudios de Desiertos y Oceanos (CEDO), Puerto Peñasco, Mexico, in the Lower Colorado Valley subdivision of the Sonoran desert.

Initially we chose a water-filled swale, the "seep" site, located approximately 0.5 km northeast of CEDO, and an estuarine site (the "estero"), located approximately 1 km northeast of the seep site, for assemblage comparisons. A day later we established a "control" site in the desert between the seep and the estero. Vegetation in all three sites was dominated by the shrubs *Ambrosia dumosa* (Gray) Payne, *Atriplex canescens* (Pursh) Nutt., *Frankenia palmeri* S. Wats., *Lycium pallidum* Miers, and the grass *Hilaria rigida* (Thurb.) Benth. The grass, *Monanthocloe littoralis* Engelm., was prominent along the shoreline at both the seep and (especially) the estero.

The seep site was a small, irregularly shaped pond of saline water. A few clusters of the halophyte, *Salicornia* sp., were present at the water's edge. Parts of the western and southern shores were encompassed by steep banks of the coastal dunes, but most of the shore graded gradually into the surrounding desert. The estero site was a slightly larger lagoon connected by a narrow channel to the western end of Estero Morua, into which the normally dry Rio Sonyita flows only on rare occasions, about 10 km to the east (CEDO News, Vol. 2, 1989). Water at the estero site fluxes slightly with tidal flows entering Estero Morua from the Gulf of California, and has a salinity equivalent to that of the local sea water. Low banks were present on the north and south shores of the estero site; the western bank had a relatively gradual incline. Both the seep and estero sites were visited by an assortment of waterfowl.

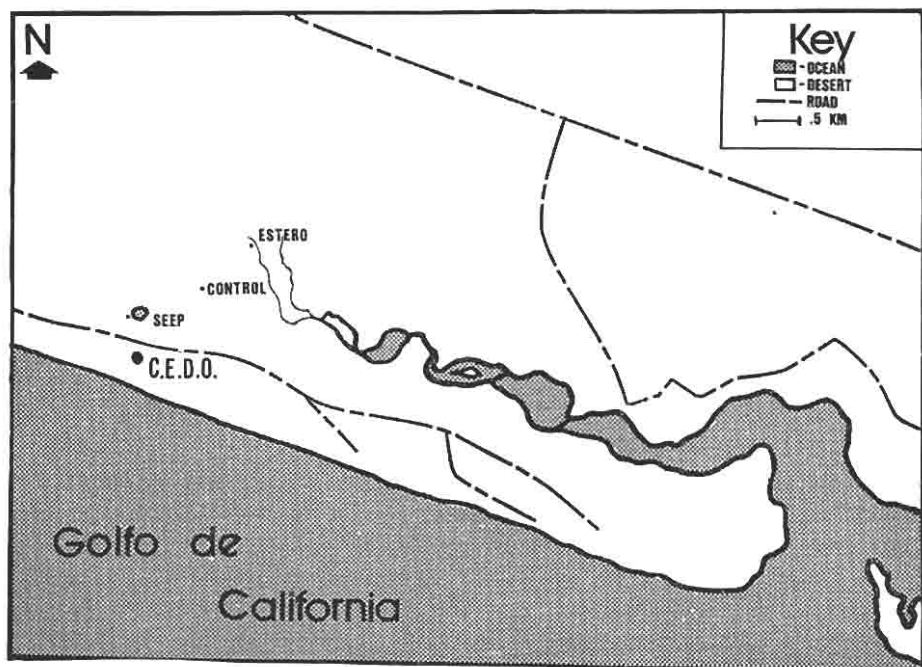


Fig. 1. Map of study sites and region near the study area.

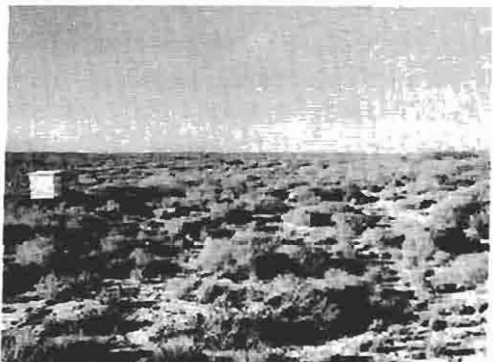


Fig. 2. Photographs, taken at time of sampling, of estero site (top), seep site (middle), and control site (bottom).

The control site was established on a relatively flat area of desert floor midway between the seep and the estero. We designated its eastern edge as simulated shoreline. Some *Opuntia bigelovii* was present on the western "bank".

## MATERIALS AND METHODS

Three transects, oriented westward and perpendicular to the shoreline, were established on the west shore at each site. Transects were separated by 30-50 m, and reflected local differences in elevation and vegetation. Beginning at 2m from the actual or simulated shoreline, the transects were intersected at 10m intervals by rows of four pitfall traps, 2m apart and centrally located in a 3 x 7m plot. Pitfall traps were composed of doubled plastic 12-oz Solo<sup>R</sup> cups, 9 cm wide at the opening and 12 cm deep.

Two maximum-minimum thermometers were buried 10 cm deep at the center of the two most central plots in the middle transect at the seep and estero sites. A weather station containing a recording hydrothermograph was placed adjacent to the control site.

Traps were checked and trap contents recorded each morning and evening. The study period ran from the morning of October 6 to the evening of October 9 at the seep and the estero; at the control site sampling did not begin until 24 hours later. Unknown specimens were preserved in alcohol for later identification. These and other voucher specimens were deposited in the University of New Mexico Insect Collection.

Indices of species richness (i.e., rare-faction), diversity (Hill's N2) and evenness (modified Hill's E5 ratio) were calculated using licensed software programs available in Ludwig and Reynolds (1988). Sørensen's similarity index (Magurran 1988) was used to calculate species turnover (beta-diversity).

Nonsocial arthropods other than crabs were classified according to trophic group following identification to species or morphospecies. Carnivores were defined as species having at least mainly predaceous immature stages, while detritivores were defined as mainly saprophagous species. The terms "omnivore," "algavore," and "ant" as used below are self-explanatory.

A vegetation survey was carried out in each plot. Height, width and length of each plant in the plot was recorded, and area of plant cover was determined by summing length x width measurements over the entire plot. Per cent cover was calculated as area of vegetation divided by the total area of the plot x 100.

Single samples from the upper 15 cm of soil were taken from each plot of the center transect at each site and placed in sealed plastic bags for soil moisture analyses. Soil moisture was determined from these samples by measuring mass loss after drying a small amount at 110° C for 24 h.

## RESULTS

### *Climate*

Twenty-four hour changes in air and soil temperatures and atmospheric relative humidity were recorded throughout the study. Diurnal high temperatures ranged between 30° C and 34° C (air), and between 33° C and 35° C (soil). Nocturnal lows ranged between 15° C and 22° C (air), and between 24° C and 27° C (soil). Atmospheric relative humidity ranged between 95% and 100% (nocturnal) and between 33% and 50% (diurnal).

### *Species Richness, Diversity and Evenness*

The most prevalent arthropods collected during the study period at all three sites were ants of the genus *Solenopsis*, which due to their overwhelming numbers were excluded from calculations. With the exception of *Solenopsis*, a total of 558 arthropods comprising 50 species were collected at the estero, seep and control sites. Table 1 lists numbers of individuals in each species trapped at each site. The greatest species richness and individual abundance occurred at the estero, where, except for *Solenopsis* and 233 *Uca latimanus* (fiddler crabs), 145 individuals of 34 other species were trapped. This contrasts with only 77 individuals of 21 species (no crabs) at the seep site, and 76 individuals of 18 species at the control site (which received three-fourths of the sampling effort given the two "moist" sites).

Numbers of species other than *Uca latimanus* and *Solenopsis* trapped per site at all sites averaged ( $\pm$  SE) 3.6  $\pm$  0.7 (diurnal) and 10.2  $\pm$  0.9 (nocturnal), while numbers of individuals averaged 6.1  $\pm$  1.4 (diurnal) and 24.0  $\pm$  2.5 (nocturnal). The only apparent correlation between surface activity and climate was a nearly significant positive correlation between nocturnal (low) air temperatures (3 nights) and total numbers of individuals trapped ( $r = 0.91$ ,  $p < 0.1$ ).

Recognizing from species-area curves shown in Fig. 3 that this study did not sample the full number of species present, we used rarefaction analysis (Fig. 4) for all species except ants to obtain expected levels of species richness,  $E(S_n)$ , at a sample size of 80 individuals, which approximates sample sizes at the seep



and control sites. Results are consistent with actual trap data (above) when the swamping effect of *Uca* crabs is excluded. Thus, rarefaction curves at  $n=80$  indicate significant  $E(S_n)$  differences (shown by 95% confidence intervals in Fig. 4) between the estero (27 species), the seep (21.5 species), and the control (18 species).

Diversity and evenness values at the estero were also affected by its high *Uca* density (Table 2). Without *Uca*, the low estero  $N_2$  indicates that proportionally few very abundant species dominated that site, compared to the other sites. The greatest dominance of such species occurred at the control site, where *Tylos punctatus* (isopods) were relatively abundant. Similar  $E_5$  values (when the contribution of *Uca* at the estero is excluded) at all sites indicate an overall similarity in their species' proportional distributions.

Numbers of individuals and species of arthropods in designated trophic levels varied at each site relative to distance from the shore or its artificial equivalent (Table 3). At the control site, detritivores outnumbered carnivores by two to one (species) and three to one (individuals). One crab, an omnivore, was identified. At the seep site, no crabs were present, and carnivores and detritivores were approximately equal in both numbers of species and individuals. At the estero, on the other hand, crabs were the dominant trophic group in terms of numbers of individuals. However, in terms of species richness, carnivores were dominant at the estero and outnumbered detritivores by two to one. At all three sites, the detritivore component consisted mainly of tenebrionid beetles and isopods (*Tylos*), whereas carnivores were largely spiders, scorpions and, at the estero, carabid beetles, which were found only within 14m of the shoreline.

Assuming that soil moisture measurements taken along the center transects at each site (Fig. 5) accurately reflected moisture in soil at similarly spaced points on the lateral transects, we obtained the following relationships between soil moisture and data shown in Table 3: (1) a highly significant direct correlation at the estero between soil moisture and density of *Uca latimanus* ( $r = 0.99$ ,  $p < 0.005$ , Spearman rank correlation, 1-tailed test), (2) strong inverse trends between soil moisture and detritivore density at the estero ( $r = -0.87$ ) and the seep ( $r = -0.82$ ), and (3) a strong positive trend between soil moisture and total arthropod density at the control ( $r = 0.85$ ). No other soil moisture relationships approached statistical significance.

Vegetative cover within plots ranged from <5% to 65%. No correlations approaching statistical significance were found between per cent cover and total

TABLE 1

Species richness and relative abundance of surface-active arthropods trapped at estero, seep, and control sites.

Trophic category:	Total numbers trapped		
	Estero	Seep	Control
Order: Family	(6 samples)	(6 samples)	(4 samples)
Carnivores			
Araneae: Sparassidae			
<i>Heteropoda sp.</i>	7	9	9
Araneae: Lycosidae			
<i>Pardosa sp.</i>	10		
<i>Lycosa sp.</i>		3	
Araneae: Pisauridae			
<i>Gen. sp. #1</i>	2		
Araneae: Clubionidae			
<i>Gen. sp. #1</i>	1	1	
Araneae: Linyphiidae			
<i>Gen. sp. #1</i>	1		
Araneae: Caponiidae			
<i>Gen. sp. #1</i>		2	
Araneae: Theridiidae			
<i>Gen. sp. #1</i>		1	
Araneae: Filistatidae			
<i>Gen. sp. #1</i>	1		
Araneae: Loxoscelidae			
<i>Loxosceles deserta</i>	1		

TABLE 1 (continued) p. 2

Araneae: Homalonychidae			
<i>Gen. sp. #1</i>			1
Araneae: unknown family			
<i>Gen. sp. #1</i>	1		
Scorpiones: Buthidae			
<i>Centruroides sp.</i>	1	1	
<i>Paruroctonus sp.</i>	1	6	6
Dictyoptera: Mantidae			
<i>Gen. sp. #1</i>	1	2	
Coleoptera: Histeridae			
<i>Gen. sp. #1</i>	5		
Coleoptera: Cicindellidae			
<i>Gen. sp. #1</i>	4		
Coleoptera: Carabidae			
<i>Dyschirius aratus</i> LeConte	30		
<i>Tachys sp. (?) #1</i>	17		
<i>Tachys sp. (?) #2</i>	7		
Coleoptera: Staphylinidae			
<i>Aleochara sp.</i>	1		
Hymenoptera: Bradynobaenidae			
<i>Gen. sp. #1</i>	1		
Hymenoptera: Mutillidae			
<i>Sphaerophthalama sp.</i>		1	1
<i>Dasymutilla sp.</i>	3	2	
<b>Detritivores</b>			
Isopoda: (Tyliidae)			
<i>Tylos punctatus</i> (Holmes and Gay)	16	24	33
Thysanura: Lepismatidae			
<i>Gen. sp. #1</i>	4	7	6
<i>Gen. sp. #2</i>			1
Thysanura: Nicoletiidae			
<i>Gen. sp. #1</i>	1		2

TABLE 1 (continued) p. 3

Dictyoptera: Polyphagidae			
<i>Arenivaga</i> sp.	2	1	
Dermaptera: Labiduridae			
Gen. sp. #1	1	1	
Coleoptera: Tenebrionidae			
<i>Areoschizus</i> sp.	1	1	
<i>Argoporis bicolor</i> LeConte	1	1	
<i>Asbolus verrucosus</i> LeConte		1	2
<i>Cayptaduis tarsalis</i> Blaisdell	3	8	8
<i>Edrotes ventricosus</i> LeConte	3		3
<i>Eleodes armatus</i> LeConte	5		
<i>Eleodes caudatus</i> (Horn)	3	2	
Gen. sp. <sub>s</sub> #1		1	
Gen. sp. <sub>s</sub> #2			1
Gen. sp. <sub>s</sub> #3			1
Coleoptera: Staphylinidae			
<i>Carpelimus</i> sp	9		
Coleoptera: Ptinidae			
<i>Niptus ventriculus</i> LeConte	1	2	1
<b>Algavores</b>			
Coleoptera: Staphylinidae			
<i>Bledius</i> sp. #1	1		
<i>Bledius</i> sp. #2	1		
<b>Omnivores</b>			
Crustacea:			
<i>Uca latimanus</i>	223		
<i>Uca crenulata</i>			1

**TABLA 1 (continued) p. 4**

**Ants**

Hymenoptera: Formicidae

Dolichoderine sp. #1			3
Dolichoderine sp. #2			1
<i>Gen. sp.</i> #1	3		
<b>TOTAL NUMBER OF SPECIES</b>	<b>34</b>	<b>21</b>	<b>18</b>
<b>TOTAL INDIVIDUALS*</b>	<b>145</b>	<b>77</b>	<b>76</b>

(\*excluding ants and *Uca*)

**TABLE 2**

Species diversity (Hill's N2) and evenness (modified Hill's E5) values for the three study habitats.

Habitat	N2 diversity	E5 evenness
Control	5.95	0.58
Seep	9.04	0.67
Estero (with <i>Uca</i> )	2.81	0.31
Estero (without <i>Uca</i> )	14.03	0.68

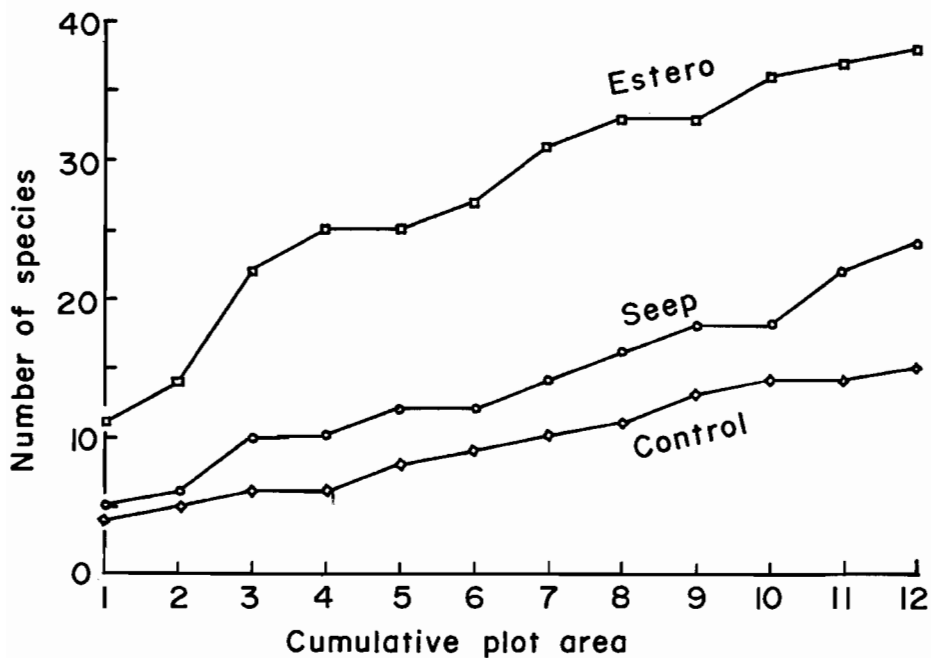


Fig. 3. Species-area curves for surface-active arthropod assemblages at the estero, seep, and control sites.

TABLE 3

Trophic group composition (carnivores, detritivores, *Uca* crabs) at control, seep, and estero sites.

Site position *	Number of species			Number of individuals		
	Car.	Det.	<i>Uca</i>	Car.	Det.	<i>Uca</i>
Control						
2 m	2	7	0	2	12	0
12 m	2	3	1	4	3	1
22 m	4	6	0	7	24	0
32 m	3	5	0	5	22	0
Total	5	11	1	18	61	1
Seep						
2 m	6	4	0	14	7	0
12 m	2	2	0	4	5	0
22 m	6	7	0	10	19	0
32 m	6	6	0	9	20	0
Total	12	11	0	37	52	0
Estero						
2 m	9	2	1	48	2	143
12 m	12	4	1	40	2	73
22 m	5	7	1	10	14	4
32 m	5	6	1	5	25	3
Total	22	12	1	103	48	223

\* Values refer to distance westward along transect from actual or simulated shoreline.

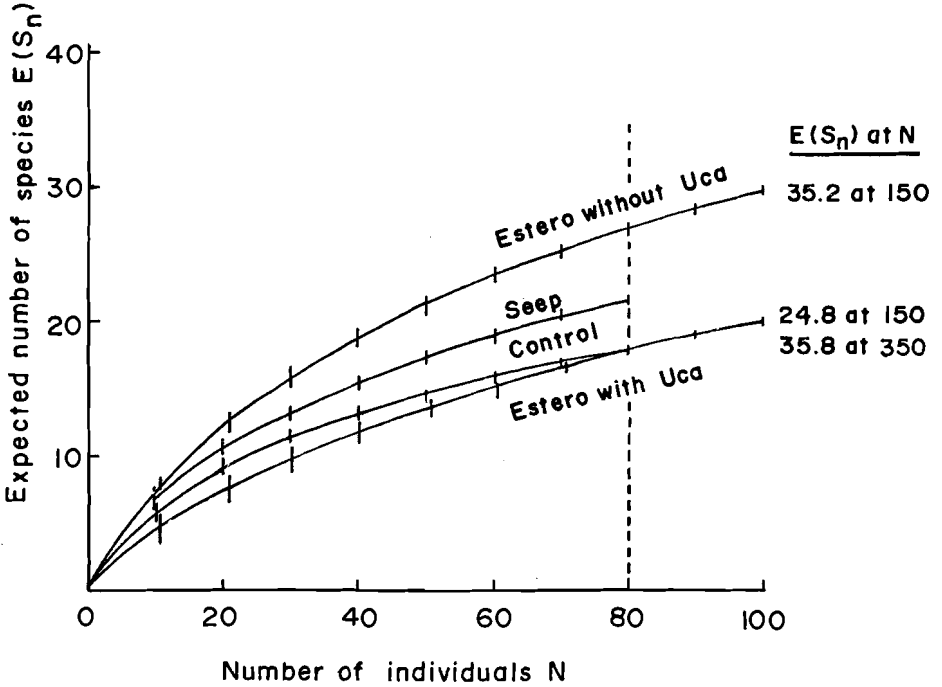


Fig. 4. Rarefaction curves for species trapped at estero, seep, and control sites. Vertical bars are 95% confidence intervals.



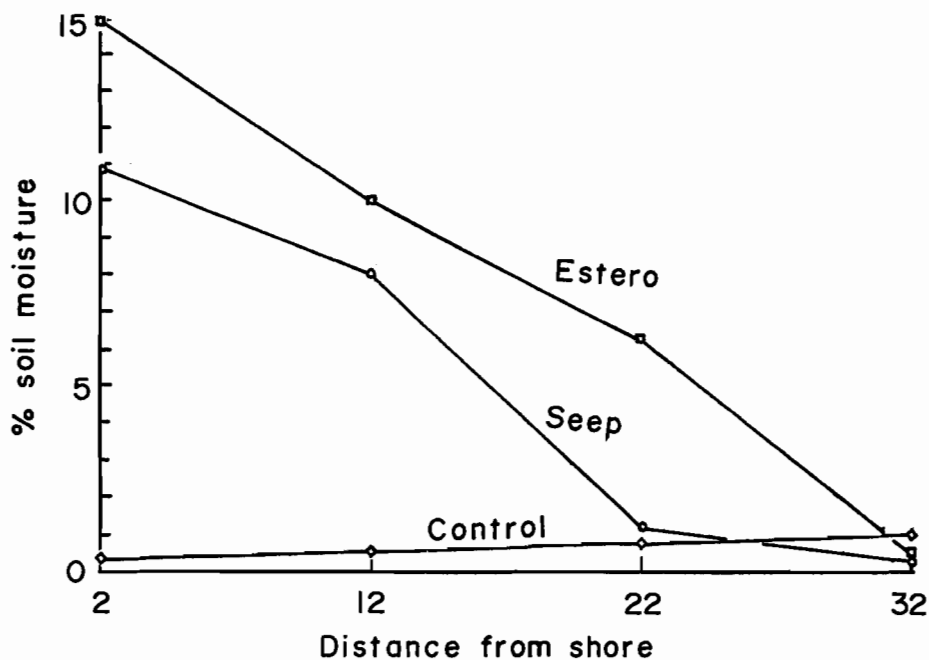


Fig. 5. Soil moisture gradients, representing single samples, for the estero, seep, and control sites.

densities or species richness of trapped arthropods when these were compared by regression analysis on a plot basis ( $n = 12$ ) at all sites.

At each site, we also examined capture trends for carnivores and detritivores. Using data in Table 3, we found a significant inverse relationship between individuals of these trophic groups at the estero ( $r = -0.52$ ,  $p < 0.05$ , Spearman rank correlation, 1-tailed test). No other correlations were significant.

### *Beta diversity*

Species turnover between the estero and control sites was greater than between the estero and the seep and control sites (Table 4). A major contributing factor was the relative uniqueness of the carnivore assemblage at the estero. The lowest turnover observed was between detritivores at the estero and seep sites.

## DISCUSSION

We found clear organizational differences among the surface-active arthropod assemblages at the three study sites. Moreover, all sites were surprisingly rich in species. Several years earlier, a more extensive study by Crawford (1989) at a dune-interdune site about 5 km to the east resulted in expected species numbers (also at  $n = 80$ ) that ranged from  $< 5$  to 18, compared to the 18-27 range in the present report. Thus, the presence of permanent water bodies (seep, estero) in a relatively confined, dune-associated landscape may promote relatively high numbers of surface-active species.

A specific, although untested, explanation for the estero's species richness may be that *Uca latimanus* is in some way acting as a "keystone species" (Paine 1969), since expected richness was significantly lower at the seep where *U. latimanus* did not occur. The possibility that the presence of this omnivore enhances species richness at the estero could be tested by constructing crab enclosures.

Assemblage organization was also most unique at the estero site, mainly due to the large population of crabs, and the many carnivores, particularly spiders and very small carabid beetles. The presence of crabs reflected the marine environment of the estuary. However, one *U. crenulata* was found dead in a control site trap some 300m distance from the estero, and bleached carapaces and claws of other *Uca* crabs were scattered between the control and estero sites. Perhaps intermediate swales become wet enough after winter rains to support a marginal inland crab population.

TABLA 4

Numbers of carnivores, detritivores, and total species\* shared between study sites, and corresponding community coefficients.

Habitat pairs/	Number of species	Community
	shared	coefficient (%)
<b>Estero/Seep</b>		
Carnivores	5	35.7
Detritivores	8	69.6
Total	14	49.1
<b>Estero/Control</b>		
Carnivores	2	17.4
Detritivores	4	36.4
Total	7	25.9
<b>Seep/Control</b>		
Carnivores	5	53.3
Detritivores	5	47.6
Total	9	43.9

\* Data from Table 1, plus *Solenopsis* ants which occurred at all sites.

The dominance of carnivores at the estero, and the excess of carnivores at the seep relative to the control site, tend to support the observation of Crawford and Seely (1987) that carnivore:detrivore ratios are high in moist desert habitats. However, the presence of very small carnivorous carabid and staphylinid beetles close to the estero shoreline was unexpected. Possibly they rely on a high microfaunal density made possible by elevated soil moistures. Numerous small dipterans were present during sampling; their eggs and larvae are a potential food source. Also, although we did not trap many ants (other than *Solenopsis*), tiny individuals that also may be prey were often fairly abundant on the surface. Paarman et al. (1986) reported that larvae of certain carabids in the Sahara Desert prey on ants and their broods.

Since soil in the vicinity of the seep was also moist, the unique aspects of the estero assemblage must have resulted from factors other than moisture alone. We speculate that the occasional connection in El Niño years of the estero and Río Sonyita has over time resulted in a mixed, partly relic assemblage of hydrophilic riparian arthropods and *Uca* crabs.

In other respects, assemblage organizations at the three sites were relatively similar. Thus proportional distributions of species were roughly the same, although a comparatively small number of very abundant species was present at the estero. Also, isopods (*Tylos*) occurred at all three sites, although they were trapped most frequently at the control site and least often at the estero (and there only in traps farthest from the shoreline). According to Hamner et al. (1969), this species orients away from soil moisture and up an elevational gradient. Finally, no trophic or taxonomic group showed a correlation with plant cover at any site. This is consistent with results obtained from studies of ground-dwelling desert beetles (Thomas 1983, Parmenter and MacMahon 1984), *Tylos punctatus* (Wood, unpublished data), and several assemblages of surface-active desert arthropods (Crawford, 1989).

In general, and despite the similarities just discussed, results of this study support the hypothesis that horizontal moisture gradients influence organizational patterns of arthropod assemblages in a restricted desert ecosystem. Species richness, individual abundances, and carnivore:detrivore ratios all appear to increase along moisture gradients involving scales that change by an order of magnitude from 32m (transect length) to 0.5 - 1 km (distances between sites). Long-term studies would help to verify these apparent trends.

## ACKNOWLEDGMENTS

We greatly appreciate the support of Peggy Turk and Rick Boyers of the Centro de Estudios de Desiertos y Oceanos (CEDO), and of the Biology Department at the University of New Mexico. We thank the following individuals for identifying arthropod specimens: R. L. Aalbu (Tenebrionidae), J. S. Ashe and A. F. Newton, Jr. (Staphylinidae), G. E. Ball (Carabidae), and S. L. Brantley (Araneae). William Martin gave author names of plants and Kenneth Schoenly provided a valuable review of the manuscript. The field assistance of Joe Frank is acknowledged, as is the figure drawing by Kenneth Schoenly.

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