ASSEMBLAGE ORGANIZATION OF SURFACE-ACTIVE ARTHROPODS IN SONORAN DESERT DUNE ECOSYSTEMS

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ABSTRACT

I tested the hypothesis, in northwestern Sonora, that temporal patterns of organization among surface-active arthropods resemble each other in dune and interdune habitats from coastal (Puerto Peñasco) and inland (Gran Desierto) dune ecosystems. Seasonal (October and May) counts of arthropods at 12-h intervals were made from pitfall-trap grids at both sites. Although the coastal interdune had the greatest plant cover (32%), rarefaction analysis showed its expected species richness of arthropods, E(Sn), to be similar to richness in the inland interdune. In both interdune habitats, E(Sn) was significantly greater in spring than fall, and generally much greater than in dune habitats. Both E(Sn) and trap-capture frequencies averaged higher at night than during the day in all habitats.

Values of Hill's N2 diversity and Hill's modified E5 evenness in coastal and inland interdune assemblages were similar at night in spring. Otherwise, few correlations involving habitat, season, and diel time were evident, except that evenness was usually greatest at night. Neither plant cover nor recent precipitation at the coast were correlated with species richness. Species turnover (Sørensen's Index) was greater between inland habitats than between interdune habitats when sites were compared. Overall, evidence for consistent resemblance in assemblage organization between similar habitats -- especially dunes -- over seasonal and diel time was not strong.

RESUMEN

En el noroeste de Sonora probé la hipótesis de la similitud de los patrones de organización temporal de artrópodos en hábitats de dunas e interdunas de los ecosistemas de la costa (Puerto Peñasco) y continental (Gran Desierto). Conteos de artrópodos con intervalos de 12-h fueron efectuados temporalmente (Octubre y Mayo) usando transectos de trampas de agujero (pitfall trap) en ambos sitios. Aunque el área de interduna en la costa tenía la mayor cobertura vegetal (32%), el análisis de "rarefaction" mostró que la riqueza calculada de especies de artrópodos, E(Sn), es similar a la del área de interduna continental. En ambos hábitats de interduna, E(Sn) fue significativamente mayor en primavera que en otoño, y generalmente mayor que en los hábitats de dunas. Ambos valores, E(Sn) y la frecuencia de captura por trampa, promediaron valores más altos durante la noche que durante el día en todos los hábitats.

Los valores de diversidad de Hill N2 y el modificado E5 de similitud de Hill, en las congregaciones de interduna de la costa y continental fueron similares durante la noche en primavera. Por otro lado, hubo muy poca correlación entre hábitats, temporada y hora del día, excepto en que la similitud fue mayor durante la noche. Ni la cobertura vegetal ni la reciente precipitación pluvial en la costa tuvieron correlación con la riqueza de especies cuando fueron comparadas. El índice de incorporación de especies (índice de Sørensen) fue mayor entre hábitats continentales que el de interdunas. En general, la evidencia de similitudes en la organización de las congregaciones, entre hábitats semejantes, especialmente en dunas, durante temporadas y hora del día no fue evidente.

INTRODUCTION

Arthropod assemblages in desert dune ecosystems consist of unexpectedly large numbers of species (e.g. Pierre 1958, Holm and Scholtz 1979) that vary considerably in space and time wherever their populations have been studied (e.g. Ghabbour et al. 1977, Crawford and Seely 1987, Crawford 1988). Climatic and topographic instability clearly account for some of this variation (Seely and Louw 1980), as should the age and degree of isolation of a given dune field.

Little attention, however, has been paid to patterns of species richness and diversity that underly assemblage organization in different desert dune ecosystems. In this paper I examine such patterns, as they relate to diel and seasonal time, in coastal and inland dune ecosystems of northwestern Sonora. In doing so I test the null hypothesis that there are no important differences in the temporal organization of assemblages from similar coastal and inland dune ecosystem habitats.

STUDY AREA

Study sites with dune and interdune habitats (Fig. 1) were located approximately 1) 5 km east of the Centro de Estudio Desierto y Oceaneo (CEDO) on the coastal outskirts of Puerto Peñasco, Sonora, and 2) 10 km northeast of Gustavo Sotelo, a small railroad stop about 35 km northwest of Puerto Peñasco and 6 km inland from Adair Bay on the upper Gulf of California. The coastal site consisted of low dunes within 50-200 m of the intertidal zone, together with more level "interdune" plains beyond. Separated from the coastal site by 40 km, the inland site was situated roughly 2 km into the Gran Desierto dune field. A faint vehicular track connects Gustavo Sotelo with the dune field.

Rainfall at Puerto Peñasco is sparse and variable (Ezcurra and Rodriguez 1986); it averaged 122 mm between 1960 - 1977 (Durrenberger and Xicotencatl Murrieta 1978), with most arriving between September and December. Monthly temperatures averaged about 30°C in July and August and 11°C in December and January (Durrenberger and Xicotencatl Murrieta 1978). Climatic data do not exist

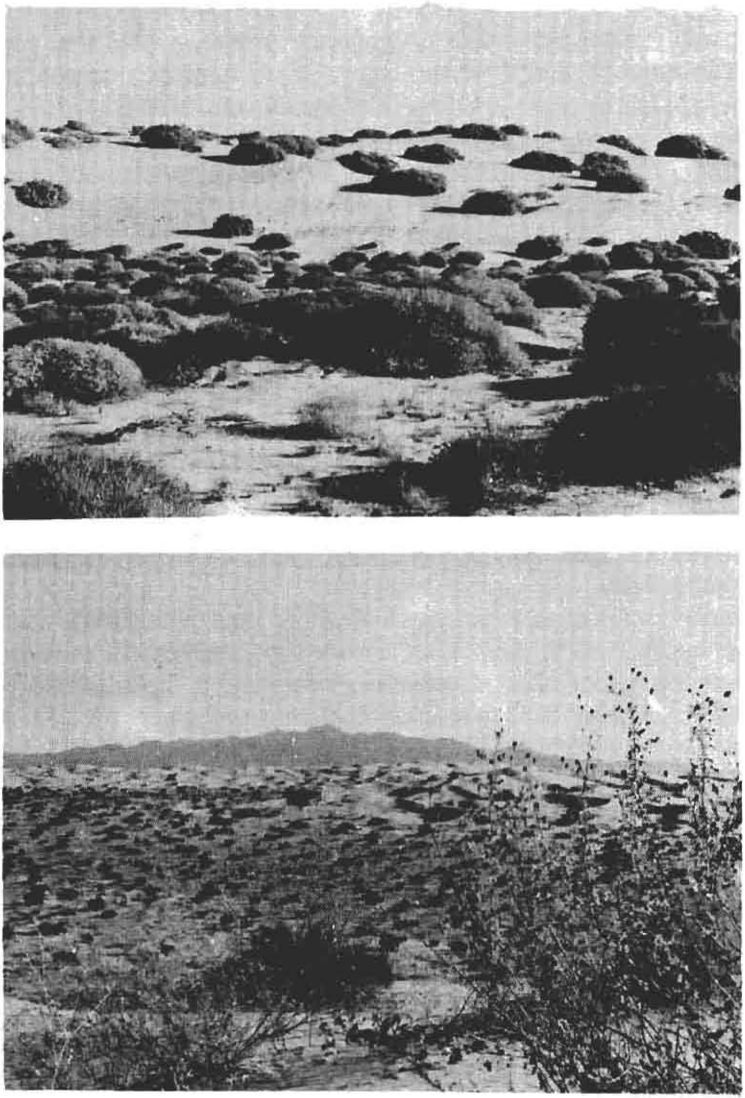

Fig. 1. Dune-interdune study sites. Top: coastal site with large *Atriplex canescens* on dune, and *Ambrosia dumosa* (light) as well as *Frankenia palmeri* (dark) shrubs in interdune. Bottom: Inland site showing dune with *Croton wigginsii* (foreground, right) and possibly *Asclepias subulata* (foreground, center) and *Ephedra trifurca* part way down slope, also mainly *E. trifurca* and *Helianthus niveus* in broad interdune; Sierra Pinacate in distance above the dunefield.

for the inland region, but should be generally similar, except that dewpoint is occasionally reached at night on the coast (CEDO weather records).

Colorado Valley type vegetation, i.e. pure stands of widely spaced shrubs, characterizes the region as a whole (Johnson 1982). Study site descriptions are given below. Habitats studied had sandy substrates that were more consolidated in interdunes than dunes. Sand grain texture was coarser at the coast than inland.

MATERIALS AND METHODS

Surface activity of arthropods was measured using pitfall traps, usually in single grids of 25, each trap being 5 m apart. Except for one inland interdune grid, each was used for at least two seasons. Traps were constructed of plastic cups, 9 cm in diameter at the opening and 11.5 cm deep. Two cups, one inside the other, were positioned with their openings at the ground surface. The inner trap was removed for specimen counts; arthropods not retained as vouchers were released, after counting, on the surface at least 1 m from a given trap. Diurnal and nocturnal specimen counting occurred as close as possible to sunset and sunrise, respectively.

Sampling at the coast took place in October 1983 (nine successive 12-h grid counts per habitat) and in May 1984, October 1984, and May 1985 (each of these periods with four successive grid counts per habitat). Sampling at the inland site took place only in May 1984 (two interdune grids and one dune grid, each with four successive counts) and October 1984 (four successive grid counts per habitat).

Specimens were identified to species when possible; alternatively they were described as morphospecies. Functional categories included 1) "carnivores," i.e. species with at least mainly predaceous immature stages; 2) "detritivores," i.e. mainly saprophagous species, at least as juveniles; 3) "herbivores," and 4) ants, which I considered to be mostly omnivores or granivores. Surface-active mites and collembolans were not counted, while tiny *Anthicus* sp. coleopterans (Anthicidae) were counted but not included in analyses because of their size.

Indices of richness (i.e. rarefaction), 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). Importance value of vegetation was calculated as relative density + relative dominance + relative frequency (Cox 1985).

RESULTS

Habitat-specific vegetation

Vegetation at the coastal and inland sites differed markedly; however, shrubs were visually dominant relative to forbs and grasses in both places. There was no overlap of obvious plant species between coastal and inland interdune habitats (Tables 1 and 2). In the latter, low-lying hummocks of the borage, *Tiquilia palmeri*, accounted for over half of the total plant cover. Total cover at the coastal interdune was 3 - 4 times that of the inland interdune, which was in turn about twice that of each dune habitat.

Vegetation characteristics within circles 1 metre in diameter around each pitfall trap are summarized in Table 3. In dune habitats, distances from traps to nearest plants averaged 4 - 5 times those of interdune habitats. Plant species richness and cover in interdune habitat circles at both sites greatly exceeded richness and cover in dune habitat circles.

Trap capture frequencies

The habitat-specific capture frequencies of surface-active arthropods averaged between 0% and 77% (Table 4). Average frequencies were nearly always greater in spring than in fall, especially at night. Average frequencies from interdune habitats were always greater than those recorded simultaneously from dune habitats. The average $\pm$ SE percentage of captures with ants was 50.7 $\pm$ 3.4% (n = 60), compared to 42.9 $\pm$ 3.3% (n = 59) without ants.

Arthropod species richness, diversity, and evenness

Arthropod species and morphospecies collected in pitfall traps during study periods are listed, in Table 5, as a function of presumed trophic level, and relative to habitat, season, and diel intervals when trapping occurred. The list is conservative because I lumped species (e.g., of lycosid spiders) when unsure of their identities. The list includes a total of 61 "species." Of these, I considered 23 to be carnivores, 23 to be detritivores, and seven to be herbivores, while eight are ants. A breakdown of these categories, by site and habitat, is given in Table 6, which shows that while detritivore species were more abundant than those of carnivores in dune habitats, both trophic groups were about equally represented in interdune habitats.

Rarefaction analysis of all species except anthicid beetles and ants was used to compare habitat-specific species richness at the smallest sample size in any

Table 1

Importance values (and percentage cover) at the coastal site of dune and interdune vegetation. Measured 3 November 1983.

Habitat	*Atriplex canescens*	*Atriplex* sp.	*Ambrosia dumosa*	*Frankenia palmeri*	*Aristida* sp.	Total cover (%)
Dune	113 (3.5)			187 (0.1)		(3.6)
Interdune	34 (0.7)	8 (2.2)	66 (11.0)	128 (17.4)	126 (0.7)	(32.0)

Table 2

Importance values (and percentage cover) at the inland site of dune and interdune vegetation. Measured 15 May 1984.

Habitat	*Tiquilia palmeri*	*Dalea* sp.	*Helianthus niveus*	*Larrea tridentata*	*Ephedra trifurca*	*Croton wigginsii*	Total cover (%)
Dune						3 (4.4)	(4.4)
Interdune	210 (4.8)	51 (1.8)	11 (0.5)	16 (1.1)	13 (0.6)		(8.8)

Table 3.

Pitfall trap distances to nearest plant, and vegetation characteristics within 1-m diameter circles surrounding pitfall traps in coastal and inland dune and interdune habitats.*

Site/habitat	Distance (m) to nearest plant $\bar{x} \pm SE$	No. of plant species in circles $\bar{x} \pm SE$	Estimated plant cover in circles $\bar{x} \pm SE$
Coastal dune	2.22 ± 0.90	0.24 ± 0.10	7.20 ± 3.20
Coastal interdune	0.45 ± 0.09	1.76 ± 0.91	19.40 ± 4.52
Inland dune	2.75 ± 0.52	0.08 ± 0.06	1.20 ± 0.90
Inland interdune	0.48 ± 0.12	1.20 ± 0.25	10.00 ± 2.27

* All measurements made between 12-15 May 1984.

Table 4

Mean seasonal and diel trap capture frequencies (%) relative to site and habitat and to presence and absence of ants. (n = number of 12-h sampling periods)

Habitat/traps with or without ants	Diurnal $\bar{x} \pm$ SE	(n)	Nocturnal $\bar{x} \pm$ SE	(n)	Diurnal $\bar{x} \pm$ SE	(n)	Nocturnal $\bar{x} \pm$ SE	(n)
Costal dune/with	3.0 ± 1.9	(4)	70.0 ± 13.5	(4)	31.4 ± 6.1	(7)	49.0 ± 4.7	(6)
Coastal dune/without	0	(4)	70.0 ± 13.5	(4)	29.7 ± 6.3	(7)	49.3 ± 4.7	(6)
Coastal interdune/with	77.0 ± 3.4	(4)	74.0 ± 3.8	(4)	64.0 ± 7.2	(7)	58.7 ± 10.4	(6)
Coastal interdune/without	35.0 ± 7.7	(4)	73.0 ± 4.7	(4)	52.6 ± 8.4	(7)	50.0 ± 8.9	(6)
Inland dune/with	0	(2)	24.0 ± 12.0	(2)	50.0 ± 10.0	(2)	34.0 ± 10. 0	(2)
Inland dune/without	0	(2)	24.0 ± 12.0	(2)	36.0 ± 2.0	(2)	34.0 ± 10.0	(2)
Inland dune/with	52.0 ± 2.3	(3)	73.0 ± 9.1	(4)	40.0	(1)	59.0 ± 27.0	(2)
Inland interdune/without	29.3 ± 4.8	(3)	69.0 ± 8.7	(4)	40.0	(1)	42.0 ± 14.0	(2)

Table 5

Species richness and relative abundance+ of surface-active arthropods from pitfall traps relative to habitat, season, and diurnal (D) or nocturnal (N) activity.

Trophic category	Coastal dune				Coastal interdune				Inland dune				Inland interdune			
Order: family	Spring		Fall		Spring		Fall		Spring		Fall		Spring		Fall	
Genus/species	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N
Carnivores																
Araneae: Agelinidae																
Gen. sp. #1						*										
Araneae: Caponiidae																
Gen. Sp. #1						*										
Araneae: Gnaphosidae																
Gen. sp. #1				*												
Araneae: Lycosidae																
Geolycosa sp.						*										
Gen. sp. #1						*		*						*		*
Araneae: Pholcidae																
Modismus sp.		*														*
Araneae: Sparassidae																
Heteropoda sp.		*	*			*									*	*
Olios sp.																

+ * = presence; ** =>an average of one individual/trap; *** =>an average of 10 individuals/trap.

Table 5 (continued)

Trophic category	Coastal dune				Coastal interdune				Inland dune				Inland interdune			
Order= family	Spring		Fall		Spring		Fall		Spring		Fall		Spring		Fall	
Genus/species	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N
Araneae: Theridiiae																
Gen. sp. #1				*		*										
Araneae: Thomisidae																
Gen. sp.								*						*		
Pseudoscorpiones																
Gen. sp. #1						*										
Scorpiones: Buthidae																
Centruroides sp.								*								
Scorpiones: Vaejovidae																
Gen. sp. #1						*										
Gen. sp. #2						*										
Hemiptera: Reduviidae																
Gen. sp. #1						*										
Neuroptera: Myrmeliontidae																
Gen. sp. #1		*											*	*		
Coleoptera: Carabidae																
Tetragonoderus sp.														**		

+ * = presence; ** => an average of one individual/trap; *** => an average of 10 individuals/trap.

Table 5 (continued)

Trophic category Order = family Genus/species	Coastal dune Spring D	 N	 Fall D	 N	Coastal interdune Spring D	 N	 Fall D	 N	Inland dune Spring D	 N	 Fall D	 N	Inland interdune Spring D	 N	 Fall D	 N
Hymenoptera: Multillidae																
Dasymutilla sp.													*	*		
Sphaeropthalama sp. #1						*				*				*		
Sphaeropthalama sp. #2														*		
Sphaeropthalama sp. #3														*		
Sphaeropthalama sp. #4						*								*		
Hymenoptera: Tiphiidae																
Gen. sp. #1		*				*								*		*
Detritivores																
Isopoda: Tylidae																
Tylos punctatus Holmes & Gay				*		**		*								
Thysanura: Lepismatidae																
Gen. sp. #1						*								*		
Gen. sp. #2																*
Orthoptera: Rhaphidophoridae																
Ceuthophilus imperialis Cohn		*				*								*		
Macrobaenetes sierrapintae Tinkham										*		*			*	
Blattodea: Polyphagidae																
Arenivaga sp.		*						*				*		*		*
Dermaptera:																
Gen. sp. #1																*

+ * = presence; ** =>an average of one individual/trap; *** =>an average of 10 individuals/trap.

Table 5 (continued)

Trophic category	Coastal dune				Coastal interdune				Inland dune				Inland interdune			
Order = family	Spring		Fall		Spring		Fall		Spring		Fall		Spring		Fall	
Genus/species	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N
Coleoptera: Anthicidae																
Anthicus sp.		***		*		*		*								
Coleoptera: Ptinidae																
Niptus ventriculus LeConte		*				*								*		
Coleoptera: Tenebrionidae																
Areoschizus sp.		*				*				*				**		
Agroporis sp. A								*								
Argoporis sp. B						*										
Asbolus laevis LeConte		*				*	*						*	*		
Asbolus verrucosus LeConte		*			*	*								*		
Cayptadius tarsalis Blaisdell		*														
Edrotes arens La Rivers				*						*		*				
Edrotes ventricosus LeConte		*		*				*								
Eleodes armatus LeConte			**	**			**	*	*		*	*		*	*	**
Eleodes blalselli Doyen						*	*	*								
Eusattus dilatatus LeConte								*								
Notibius puberulus Le Conte					**	*	*	*					*	*		
Gen. sp. #1		*														
Gen. sp. #3														*		
Herbivores																
Phasmida: Phasmatidae																
Gen. sp. #1								*								

† * = presence; ** => an average of one individual/trap; *** => an average of 10 individuals/trap.

Table 5 (continued)

Trophic category	Coastal dune				Coastal interdune				Inland dune				Inland interdune			
Order = family	Spring		Fall		Spring		Fall		Spring		Fall		Spring		Fall	
Genus/species	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N
Hemiptera: Miridae																
Gen. sp. #1											*					
Hemiptera: Cydnidae																
Gen. sp. #1		*		*		*	*	*						*		
Homoptera: Cicadellidae																
Gen. sp. #1											*					
Coleoptera: Crysomelidae																
Gen. sp. #1							*				*					
Coleoptera: Curculionidae																
Gen. sp. #1												*				
Gen. sp. #2												*				
Ants																
Hymenoptera: Formicidae																
Crematogaster sp.							*									
Myrmecocystus sp.							*									
Pogonomyrmex sp. A					**	*	**	*					**	*	*	*
Pogonomyrmex sp. B													*	*	*	*
Gen. sp. #1														*		
Gen. sp. #2														*		
Gen. sp. #3						**										
Gen. sp. #4						*										

+ * = presence; ** =>an average of one individual/trap; *** =>an average of 10 individuals/trap.

Table 6

Site and habitat species richness comparisons of trophic levels and ants.

Site/habitat	Carnivores	Detritivores	Herbivores	Ants
Coastal dune	5	12	1	0
Inland dune	1	5	5	0
Coastal interdune	12	14	1	4
Inland interdune	15	15	3	4

set of comparisons. Figures 2 and 3, for example, give expected levels of species richness, E(Sn), in the coastal interdune habitat (four season/diel interval combinations) and the inland interdune habitat (two such combinations). E(Sn) values for sample sizes of 80 individuals (coastal) and 30 individuals (inland) reveal close similarities between both interdune habitats during periods of greatest surface activity, e.g., spring nights (most) and fall nights (next most). This relationship, as well as the dominance of nocturnal over diurnal E(Sn) levels in both coastal habitats (Fig. 3), is quantified in Table 7 for 10 site/habitat/season/diel period combinations in which at least 30 nonsocial arthropods were trapped. Interestingly, both the highest (13.4) and lowest (1.3) E(Sn) values came from the same habitat (coastal dune) but at opposite seasons and diel periods (spring nights and fall days, respectively).

Indices of Hill's N2 diversity and Hill's modified E5 evenness, calculated relative to season, diel period, sampling effort, and individuals captured are given in Table 8 for all but two habitat combinations. Except for the remarkable similarity of all parameters relating to coastal and inland interdune spring nights, few other correlations are evident. However, when the remaining two habitat combinations (dune, spring, day) having either one and no captures (inland and coastal habitats, respectively) are added to the list, several distinctions can be made between combinations having evenness rankings higher or lower than eight.

First, in the top-ranked group, six combinations are nocturnal compared with two in the other group. Second, in the top-ranked group, the correlation between E5 and N2 values is very poor ($r = 0.17$), while in the group with low evenness (numbers 9 - 14) it is much better ($r = 0.50$), indicating a tendency for very abundant species to dominate in diurnal situations. Overall, the five most dominate species, ranked in order of abundance per sampling effort, were *Eleodes armatus* (tenebrionid detritivore: 10 combinations), *Tetragonoderus* sp. (carabid carnivore: one combination), *Tylos punctatus* (isopod detritivore: three combinations), *Areoschizus* sp. (tenebrionid detritivore: four combinations), and unidentified tenebrionid detritivore no. 2: six combinations.

The possible influence of habitat-specific plant cover on species richness was assessed by linear regression analysis. When estimated plant cover in 1-m diameter circles around each pitfall trap was compared with that trap's total individual spring or fall captures, the corresponding r-value was always low (<0.5).

Additionally, the possible influence of seasonal precipitation on species richness, and individual densities, was assessed at the coastal site (where weather

Table 7

Species richness rankings of site/habitat/season/diel period combinations at sample sizes of 30 pitfall-trapped arthropods (excluding ants, anthicid beetles and microarthropods). Expected number of species, E(Sn), for all combinations are based on rarefaction curves. Rankings are based on non-overlapping 95% confidence intervals.

Rank	Site/habitat/season/diel period	E(Sn)
1	Coastal dune spring night	13.4
2	Coastal/inland interdune spring night	10.5 - 11.0
3	Coastal/inland interdune fall night	7.0
4	Inland dune fall night	5.5
5	Coastal dune fall night	3.7
6	Coastal interdune spring day	3.4
7	Coastal interdune fall day	3.2
8	Coastal dune fall day	1.3

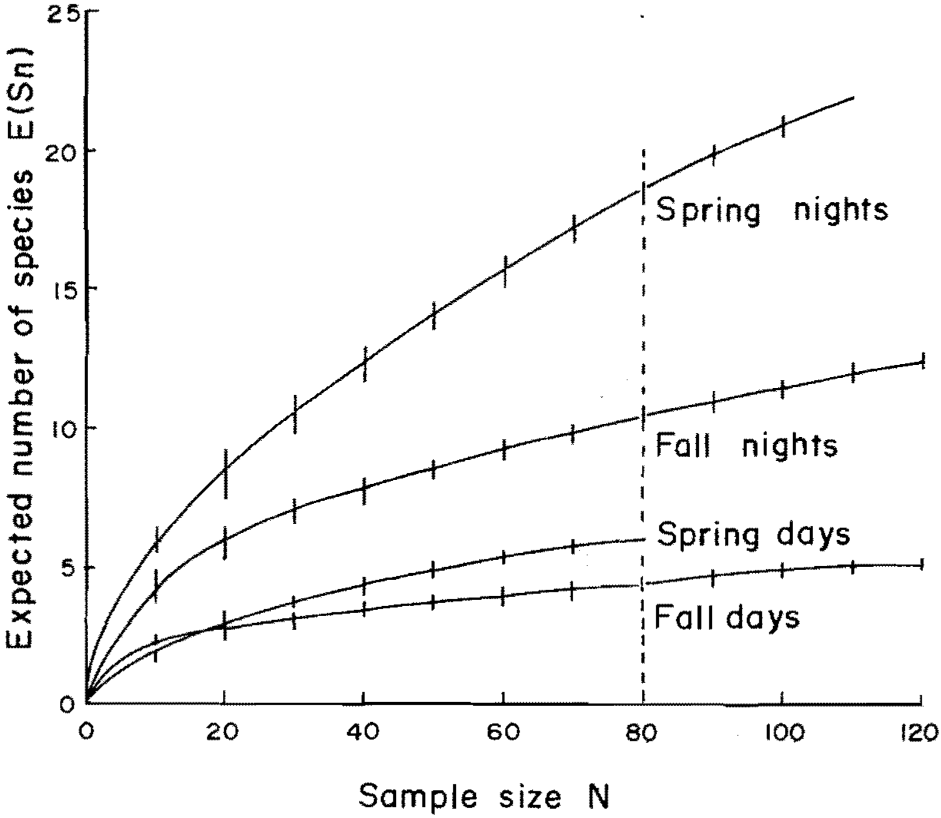

Fig. 2. Rarefaction curves for the expected number of surface-active arthropod species pitfall-trapped in the coastal interdune habitat. Vertical bars represented 95% confidence intervals. Dotted line shows E(Sn) for samples of 80 individuals.

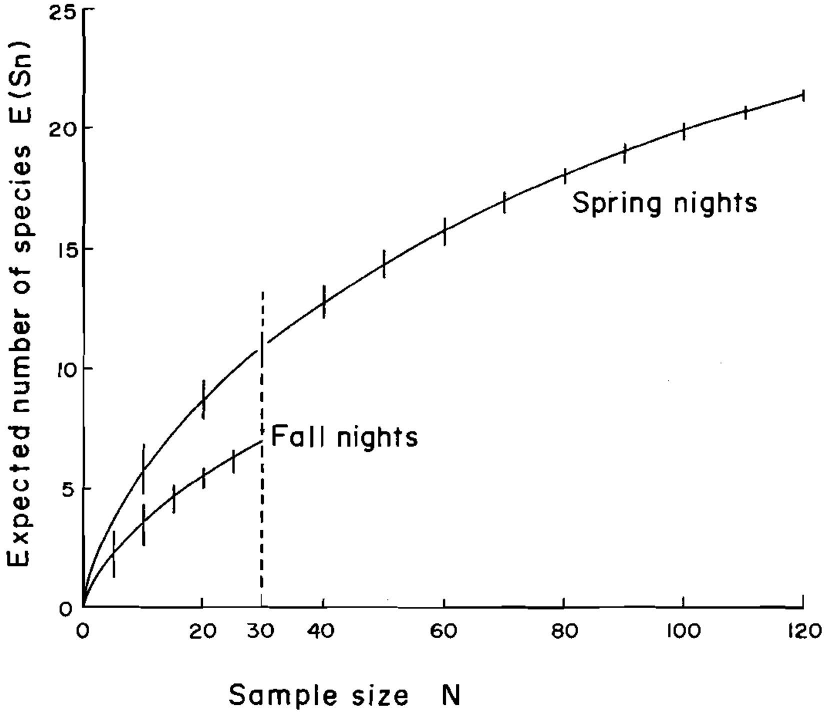

Fig 3. Rarefaction curves for the expected number of surface-active arthropod species pitfall-trapped in the inland interdune habitat. Vertical bars represent 95% confidence intervals. Dotted line shows E(Sn) for samples of 30 individuals.

Table 8

Habitat-specific species evenness (Hill's E5, ranked) and species diversity (Hill's N2) relative to season, diel period, and number of 12-h sampling periods, and total numbers of species and individuals. Habitats with one or fewer species not included.

E5 rank	Site/habitat/season/diel period	E5	N2	Sampling periods	Numbers of spp.	Numbers of indiv.
1	Inland dune spring night	1.62	5.00	2	4	6
2	Coastal dune s pring night	0.87	8.94	4	14	33
3	Inland dune fall night	0.75	2.84	2	6	36
4	Inland interdune spring day	0.72	2.59	2	5	18
5	Coastal interdune fall night	0.66	3.75	6	13	132
6	Inland dune fall day	0.63	1.83	2	4	12
7	Coastal interdune spring night	0.59	5.73	4	23	119
8	Inland interdune spring night	0.58	5.93	4	22	128
9	Coastal interdune fall day	0.56	1.56	7	7	165
10	Inland interdune fall day	0.54	1.14	2	2	16
11	Inland interdune fall night	0.50	1.98	2	7	31
12	Coastal interdune spring day	0.44	1.22	4	4	42
13	Coastal dune fall night	0.39	1.27	6	6	81
14	Coastal dune fall day	0.35	1.02	7	2	102

records applied) for interdune faunas (which were more consistently abundant than dune faunas). Regressions were made of total precipitation in the 30-day period preceding each fall and spring sampling versus seasonally corresponding E(Sn) values at n = 20 (smallest sample size). The relationship, r = -0.69, was not significant at P = 0.05. When average numbers of individuals trapped per sampling period were substituted for E(Sn) values the relationship was again non-significant (r = -0.54).

Patterns of beta-diversity

Species turnover between dune and interdune habitats at the inland site was twice that of the coastal site (Table 9). Turnover between interdune habitats at both sites was also twice that occurring between interdune habitats at both sites (Table 10).

When seasonal and diel patterns of beta-diversity are compared relative to location, season, and diel period, three patterns in particular become evident (Table 11). First, seasonal turnover in coastal dunes was distinctly greater than in inland dunes; seasonal turnover percentages in interdunes at both sites were similar and intermediate. Second, nocturnal-diurnal turnover percentages in dune habitats were twice those recorded from interdune habitats. Third, the usually species-rich habitats (interdunes) were more similar to each other in terms of diel time and seasonal time than were the usually species-poor dunes.

DISCUSSION

A diverse arthropod fauna populates soil surfaces of the warm coastal and inland dune ecosystems of northwestern Sonora. Especially well represented are spiders, mutillid wasps, tenebrionid beetles, and -- in the interdunes -- ants. Although these and other species comprise assemblages with often distinctive spatial and temporal patterns of species richness and diversity (Crawford et al. 1989), they collectively exhibit certain broad patterns as well. Therefore, before addressing the hypothesis of pattern similarity between similar habitats, I will compare some of this study's general findings with pitfall-trap results from 1) a much larger, cooler, and more arid coastal desert, the Namib (Crawford and Seeley 1987); and 2) a much smaller dunefield in the more mesic desert grasslands of central New Mexico (Crawford 1988).

Trap-capture efficiencies in the two larger deserts were similar, averaging about 51% (± 4 - 7%), while the average efficiency in New Mexico was 66 ± 8%.

Table 9

Habitat-specific species turnover between inland and coastal sites.

Site	Habitat-specific richness Dune	Habitat-specific richness Interdune	Number of shared species	Community coefficient (%)
Inland	11	30	5	24.5
Coastal	19	36	11	40.0

Table 10

Site -specific species turnover between inland and coastal sites.

Habitat	Site-specific richness Coastal	Site-specific richness Inland	Number of shared species	Community coefficient (%)
Dune	19	11	4	26.7
Interdune	36	30	17	51.5

Table 11

Seasonal and diel species turnover relative to sites and habitats.

Site/habitat	Comparative seasonal/diel richness		Number of shared species	Community coefficient (%)
	Fall vs	*Spring*		
Coastal dune	7	15	3	27.3
Inland dune	9	5	3	42.9
Coastal interdune	17	27	8	36.4
Inland interdune	10	26	6	33.3
	Day vs	*Night*		
Coastal dune	2	19	2	19.0
Inland dune	4	8	1	16.6
Coastal interdune	11	32	8	37.2
Inland interdune	9	29	8	42.1

Carnivore-detritivore species ratios in the Sonoran and Namib dune ecosystems were also similar, both approaching unity, while the ratio in New Mexico favored detritivores. It is possible that relative desert size may be associated with these findings, as may be desert location (within and between continents), regional climates, and biotic histories. Desert age, however, may be less relevant: the main Namib Sand Sea probably dates from the Pliocene (Ward et al. 1983), in contrast to the two North American ecosystems, which are probably no older than the late Pleistocene (Bowers 1982, S. Wells personal communication).

Similarly, geological time -- albeit less extensive in the present instance -- seems not to have been a major impediment to dispersal between the coastal and inland ecosystems considered in the present study, since about half of the coastal and inland interdune species were common to both of these sites. Fossils of the extant marine gastropod, *Muricanthus nigritis*, occur at the western edge of the inland dunes (personal observation) and were probably laid down there before the end of the Pleistocene (J.J. Schreiber, personal communication). Therefore that site has probably not been part of a coastal ecosystem since that time.

Regardless of whether they occurred at the coast or inland, or at both places, surface-active species displayed some similar habitat- and time-specific patterns of assemblage organization. For example, estimated species richness in both the coastal and inland interdunes was seasonally similar at night, greater in spring than in fall, and greater at night than in daytime. (By contrast, in the Namib, Seely and Crawford (1987) trapped diurnally and nocturnally active species from many sites in approximately equal numbers.) Another similar pattern was that of interdune species richness, which greatly exceeded richness in the dunes, except on the coast, in spring, at night.

Otherwise, most combinations of site, habitat, and seasonal as well as diel period were relatively unique as regards species richness and diversity. The greatest variation in richness occurred in the coastal dunes. There, in the daytime a small number of species dominated surface assemblages; however, at night the proportional distribution of species was more even. Thus, in that habitat in particular, carnivory, detritivory, and herbivory may well vary extensively in seasonal and diel time, assuming surface activity is indicative of these processes.

Factors influencing assemblage organization were not obvious, suggesting that species' activities may be relatively independent of each other -- and therefore relatively non-interactive -- within assemblages. This observation is supported by the lack of any clear correlation between plant cover with species richness, or between recent precipitation with richness and numbers of individuals trapped.

These findings agree with most other studies of this kind to date (Crawford in press). However it is still probable that unusually heavy rainfall events occasionally enhance both richness and individual numbers in the upper Gulf of California region, as they do in other deserts (Seely and Louw 1980, Ghabbour and Shakir 1982, Crawford and Seely 1987).

Finally, resemblance of assemblages in similar habitats was not particularly good, especially in dunes, at the beta-diversity level. However, estimates of low species richness in the inland dunes may have to be revised (thereby decreasing estimated turnover) following greater long-term sampling effort, which is needed if we are to understand the ecology of surface-active assemblages in the Gran Desierto. Overall, the hypothesis of organizational pattern resemblance between 1) dune habitats and 2) interdune habitats from the coastal and inland dune fields of Sonora appears simplistic. While seasonal and diel patterns do show some similarity, in the interdunes, assemblages in dune habitats exhibit little consistent organization over time.

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