Abundance and Diversity of Surface-active Collembola along a Watershed in the Northern Chihuahuan Desert

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ABSTRACT: Jackknife diversity estimates (N_2 = inverse Simpson diversity index) for surface-active Collembola were examined along a watershed in the Chihuahuan desert of southern New Mexico. Chord distance measures indicated low similarity in collembolan species composition among the six sites. However, assemblages at the top (black grama grassland) and bottom (mesquite fringe of playa) of the gradient were similar to each other, possibly reflecting available soil nitrogen. There was no significant correlation between Collembola and either weekly or long-term precipitation patterns. Populations of truly epigeic Collembola appeared unaffected by rainfall but were significantly, though weakly, correlated with long-term temperatures.

INTRODUCTION

Temporal and spatial distributions of soil microarthropods in desert ecosystems have been studied by several workers (Wood, 1971; Wallwork, 1972; Santos *et al.*, 1978; Franco *et al.*, 1979; Greenslade, 1981; Santos and Whitford, 1983; Steinberger and Whitford, 1984; Kamill *et al.*, 1985). Considerably less work has been done examining the distribution and activity patterns of epigeic microarthropods in arid environments. Greenslade and Greenslade (1973) reported that some epigeic Collembola (*e.g.*, *Entomobrya* spp.) in semiarid Australia were active on sand dunes throughout the hottest part of the year. Comparing the taxonomic similarities of, and adaptations by, collembolan faunas in arid areas of Australia and Africa, Greenslade (1981) found several genera which were resistant to desiccation and concluded that populations of many species are underestimated in arid or semiarid areas.

Pefaur (1981) showed that the abundance of epigeic microarthropods varied along an altitudinal gradient (300-1000 m) in a Peruvian desert, though there was little correlation between elevation and abundance of each species. Pefaur (1981) hypothesized that the abundance of epigeic species populations should increase in response to the increase of surface litter, which would provide greater shade and humidity. Except for Hypogastruridae (= Poduridae), he collected most Collembola from moist areas.

In the Chihuahuan Desert of southern New Mexico, differences in soil type and drainage patterns produce distinct plant communities. Some of these produce more organic litter than others. Our objectives in this study were to examine the composition of epigeic collembolan communities associated with different plant communities along a watershed and to determine the seasonal activity of epigeic Collembola in this system.

MATERIALS AND METHODS

The study was conducted at the Jornada Long Term Ecological Research Site (LTER) located 40 km NNE of Las Cruces, New Mexico. The LTER area encompasses a watershed extending from the base of Mt. Summerford down a drainage slope (bajada) to a temporary lake basin (playa) 2850 m distant. Soils vary from coarse gravels on the bajada to sandy loam on the playa edge and clay silt on the playa basin.

Pitfall traps were placed in six plant communities distributed along the watershed. From the bottom to the top of the drainage slope, these were: 1) playa, dominated by

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the perennial grass *Panicum obtusum* H.B.K.; (2) mesquite fringe (*Prosopis qlandulosa* [Torr.]); (3) herbaceous, basin slope area of sparse, low herbaceous cover, dominated by *Baileya multiradiata* Harv. & Gray, *Escholtzia mexicana* Greene, *Xanthocephalum* spp. and *Yucca* spp.; (4) creosote bush (*Larrea tridentata* [D.C.] Cov.) shrub region; (5) fluff grass, sparse grassland area composed of *Erioneuron pulchellum* (H.B.K.) Takeoka and *Bouteloua eriopoda* (Torr.) Torr. (black grama); and (6) black grama grassland dominated by *B. eriopoda*.

Pitfall traps were made of 300-ml paper cups placed in 375-ml paper cups left permanently in the ground. Leaving the outer cups in place allowed repeated sampling with little soil disturbance and its attendant "digging-in effect" (Joose, 1965; Joose and Kapteijn, 1968). A shallow layer of ethylene glycol was used as a preservative in all pitfall traps. Ethylene glycol does not evaporate like alcohol nor quickly mold as does glycerol. Voucher specimens will be deposited at the United States National Museum and the New Mexico State University Entomology Museum.

A grid of nine pitfall traps 1 m from each other was placed in each of the above plant communities. Sample dates are shown in Table 2. Pitfall traps were collected after 1 day for all samples, except 26 November 1984 (4 days), 6 March 1985 (6 days), 3 April 1985 (3 days) and 1 May 1985 (5 days). Because of heavy rain and flooding, samples could not be taken from the playa basin after 17 October 1984. Collection data were standardized by multiplying to make all equal to 1 day of exposure; inverse Simpson diversity (N_2) was calculated from these standardized data. Variances of collembolan numbers were normalized using the $N' = \log_e(N+1)$ transformation.

On 17 July 1984, we checked diurnal activity of surface Collembola. One half of all pitfall traps were collected and replaced after 12 hr intervals.

The inverse Simpson index (N_2) (Hill, 1973; Peet, 1974) was used to calculate collembolan species diversity at each site based on long-term "season" (see below). Variances and confidence intervals for N_2 were estimated using a jackknife procedure using species turnover along the entire gradient (Routledge, 1980, 1984).

Community similarities were analyzed using chord distance (Pielou, 1984). This was calculated using the formula:

$$C(j,k) = (2(1\text{-}\cos\Theta))^{1/2}$$

where j and k are the sampling units being compared, $\cos\Theta = \Sigma X_{ij}X_{ik}/(\Sigma X_{ij}^2\ \Sigma X_{ik}^2)^{1/2}$, and "$X_{ij}$" and "$X_{ik}$" represent the abundance of the "ith" species in the "jth" or "kth" sampling unit. Chord distance was chosen to determine the similarity between two communities because this procedure uses the relative proportions of each species within the assemblages. Relative measures of species, instead of absolute measures, were useful to us because they allowed us to look across community types, rather than restricting us to looking within a community type. Values range from 0-1.41, with 0 being most similar and 1.41 least similar.

A Pearson product-moment correlation analysis was performed between short-term precipitation and collembolan species diversity and abundance. The precipitation was averaged from total weekly rainfall collected for 2 weeks before each sample date. Precipitation averages included the collection site and one LTER station on each side of the site.

Based on monthly precipitation data from 1914-1983, the Jornada LTER has 3 seasons: warm-dry (minimum temperature >0 C), lasting from April-June with 28.4 mm average precipitation; warm-wet (minimum temperature >0 C), from July-October with 150.8 mm average precipitation; and cold-dry (minimum temperature <0 C), from November-March with 54.2 mm average precipitation. Collection dates were classified according to long-term "season" and correlation analysis was performed between long-term average precipitation and collembolan diversity and abundance.

RESULTS

The most abundant collembolan species were *Sminthurides pumilis* Krausbauer in the

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playa and mesquite fringe, *Brachystomella arida* Cristiansen and Bellinger in the mesquite fringe and black grama grassland, *Seira bipunctata* (Packard) in the mesquite fringe and creosote bush area, and *Entomobrya* (*Calx*) n. sp. in the mesquite fringe and herbaceous area. No species dominated the fluff grass area (Table 1).

According to PROC CORR (SAS Institute, 1982), there was no significant correlation ($P<0.05$) between either weekly precipitation or long-term average precipitation and collembolan species diversity or abundance. No collembolan species abundance was correlated with the abundance of other collembolan species. Species abundance was significantly correlated ($P<0.05$) with the long-term "seasons." However, the correlation coefficients were low (the highest was 0.32).

Percent composition varied seasonally. During the warm-wet and warm-dry seasons, *Seira bipunctata* and *Entomobrya* (*Calx*) n. sp. (Entomobryidae) were most abundant in the collections. During the cold-dry season, *Brachystomella arida* (Hypogastruridae) and *Cryptopygus ambus* (Isotomidae) were most abundant and entomobryids were virtually absent. In addition to seasonal effects, strong nocturnal effects were observed. Of the 262 Col-

TABLE 1.—Occurrence and relative abundance of surface-active Collembola on a desert watershed in southern New Mexico

Species	Site					
	P	M	H	C	F	G
Sminthuridae						
Bourletiella n. sp. 1	a	a	a	a	a	a
B. n. sp. 2		a	a	a	a	a
B. n. sp. 3		a	a		a	a
B. (Deuterosminthurus) wexfordensis (Snider)	a	a			a	a
B. unkn. spp.		a	a	a		a
Sminthurides (Sphaerida) pumilis Krausbauer	c	c	a	a	a	a
S. (Denisiella) sexpinnatus Denis		a				
Entomobryidae						
Seira bipunctata (Packard)		b	a	c	a	a
Entomobrya (Calx) n. sp.		b	b	b	a	a
Pseudosinella spp.		a	a			
Isotomidae						
Cryptopygus ambus Christiansen and Bellinger		a	a	a	a	a
Isotoma (Desoria) notabilis Schaeffer					a	
Folsomides americanus Denis		a				
Proisotoma minuta (Tullberg)			a			
P. minima (Absolon)				a	a	
Anurophorus (Anurophorus) utahensis (Wray)			a	a		
Hypogastruridae						
Brachystomella arida Christiansen and Bellinger		c	a	a	a	b
Pseudachorutes texensis Christiansen and Bellinger			a		a	
P. aureofasciatus (Harvey)					a	

Key: P = playa, M = mesquite, H = herbaceous, C = creosotebush, F = fluff grass, G = grama grass, a < 20/trap, b = 20-45/trap, c > 45/trap

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lembola collected from 27 pitfall traps on 17 July 1984, only two (*Bourletiella* n. sp. 1) were collected during daylight.

Total abundance varied according to the 3 seasons at the Jornada. Collembolan diversity and abundance were highest in the warm-wet season, and lowest during the cold-dry season (Table 2). Collembolan collections were highest in the mesquite area and lowest in the fluff grass and black grama zones.

Collembolan assemblages from all sites differed in species composition (Figs. 1-4). Based on the chord distances and cluster analysis of community similarity, the playa assemblage separated completely from all other sites. The herbaceous fluff grass and creosote bush communities had some degree of similarity, though not strong. The black grama and mesquite habitats were most similar, with a chord distance value of 0.68.

DISCUSSION

Typically, Collembola are soil or litter-dwelling and are limited to relatively mesic areas (Christiansen, 1964). Although some pine litter-dwelling species are adapted to xeric habitats (Knight and Read, 1969), generally epigeic Collembola are more tolerant of xeric conditions. The most prevalent epigeic Collembola at the Jornada LTER site

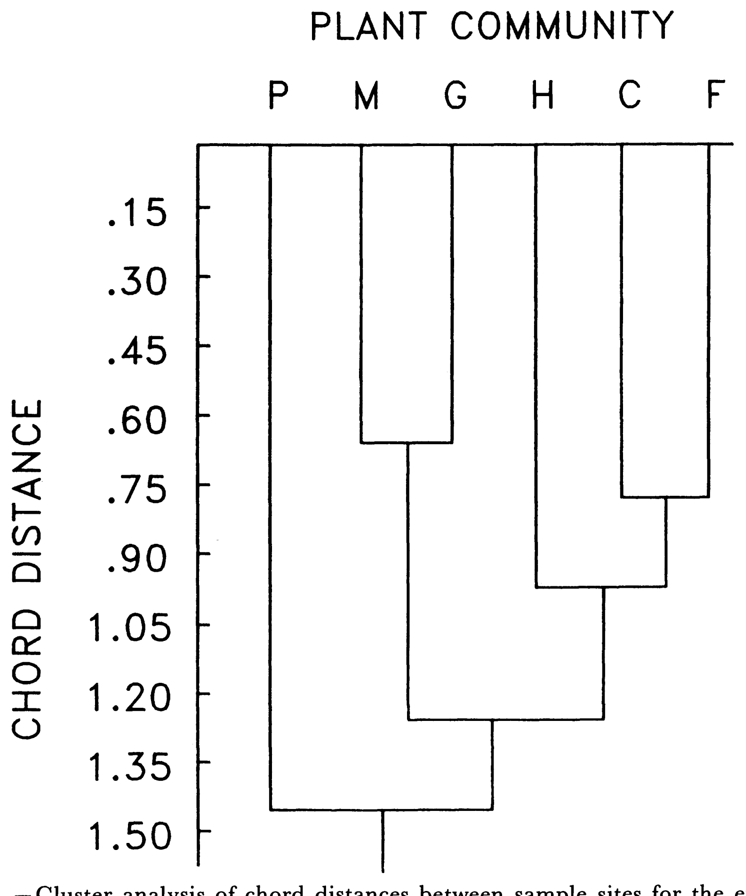

Fig. 1.—Cluster analysis of chord distances between sample sites for the entire year. P = playa, M = mesquite fringe, H = herbaceous, C = creosote bush, F = fluff grass, G = black grama

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TABLE 2.—Mean numbers of Collembola collected per date and site on the Jornada LTER

	Long-term season													
	Warm-wet						Cold-dry			Warm-dry				
	Date													
Habitat	7/17	7/30	8/13	9/10	9/24	10/17	11/12	11/26	1/21	3/6	4/3	5/1	Total	Mean
Playa	2.1	5.7	132.2	11.0	0.8	•	•	•	•	•	•	•	151.8	30.4
Mesquite	1.2	38.5	205.5	53.1	71.6	213.8	41.2	59.3	7.3	0.4	0.9	0.6	693.4	57.8
Herbaceous	30.0	19.5	28.4	29.3	50.9	12.3	1.3	4.3	0.2	5.0	3.1	15.4	199.8	16.6
Creosote bush	16.6	19.2	21.7	42.2	106.3	13.5	2.5	0.8	0.2	8.4	12.8	15.1	259.2	21.6
Fluff grass	7.6	13.2	14.2	8.5	6.2	0.8	0.3	7.7	1.9	3.0	7.5	5.0	75.8	6.3
Black grama	5.0	4.9	42.7	11.5	2.7	1.2	2.2	14.2	2.9	0	0.2	1.2	55.3	7.4
Total	62.4	100.9	444.8	155.6	241.5	47.5	86.3	86.3	12.5	9.3	24.6	37.3		
Mean	10.4	16.8	74.1	25.9	39.7	48.3	9.5	17.3	2.5	1.8	4.9	7.5		

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were entomobryids having scales and long setae that help maintain higher humidity near their bodies (Christiansen and Bellinger, 1980). Various *Bourletiella* spp. (Sminthuridae) were also routinely present; *Bourletiella* species are often xeromorphic (Betsch, 1980).

Greatest collembolan abundance occurred during the warm-wet season. Greatest collembolan species diversities at each plant community occurred during the warm-wet and warm-dry seasons. The jackknife estimates of diversity were weakly but significantly correlated with long-term temperature, although there is no significant correlation with precipitation. This agrees with the pattern observed by Whitford *et al.* (1983) where moisture was not the controlling factor affecting plant and animal responses at the Jornada LTER site, contrary to the predictions of Noy-Meir's (1973) pulse-reserve model.

The abundance of *Sminthurides* (*Sphaeridia*) *pumilis* Krausbauer, 1898 and *Sminthurides* (*Denisiella*) *sexpinnatus* Denis (Sminthuridae) showed the strongest correlation with precipitation (r = 0.32). Greenslade and Greenslade (1973) reported that *S. pumilis* quickly appeared following heavy rain in the Sudan. They also speculated that *S. pumilis* may

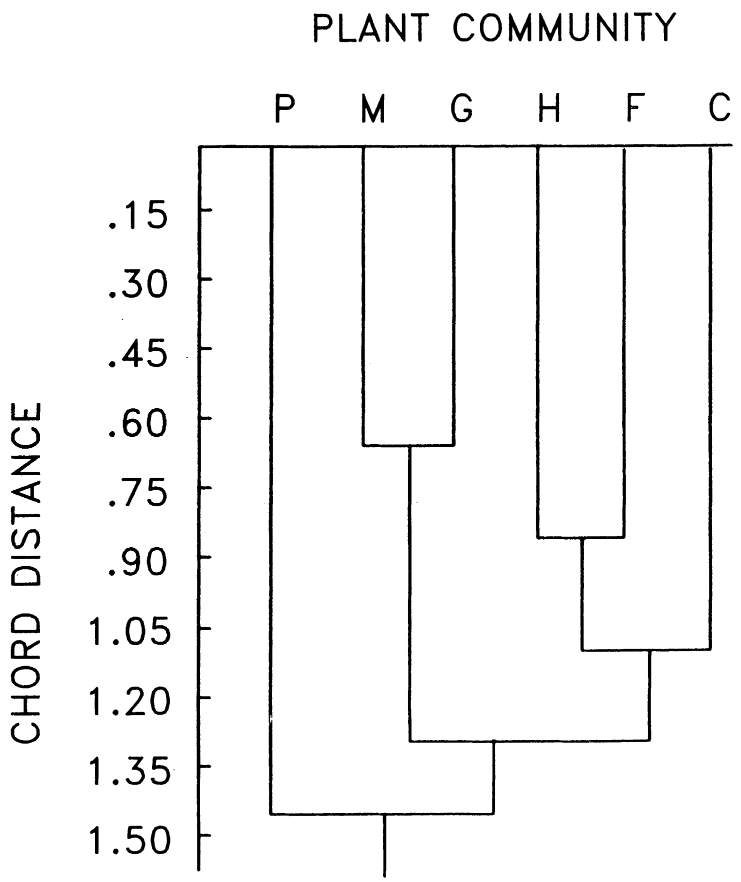

Fig. 2.—Cluster analysis of chord distances between sample sites for the warm-wet season. P = playa, M = mesquite fringe, H = herbaceous, C = creosote bush, F = fluff grass, G = black grama

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enter a diapause state resembling anhydrobiosis between rains. Other collembolan species can enter such a dehydrated state (Poinsot, 1974; Poinsot-Balaguer, 1976). However, populations of truly xeromorphic Collembola, such as *Bourletiella*, *Entomobrya* and *Seira*, appeared unaffected by rainfall. *Brachystomella arida*, a hemiedaphic species, was the dominant species in the mesquite area during the cold-dry season, although it was found in the other areas only immediately after rain. Apparently, increased soil moisture allowed more frequent surface activity by this species. Whitford *et al.* (1981) and Kamill *et al.* (1985) showed that Collembola increased their activity after rainfall or wetting of the soil. However, we found no meaningful correlation between collembolan surface-abundance (indicating activity) and precipitation in this study.

Surface activity of epigeic Collembola showed very strong nocturnal tendencies. Daytime soil surface temperatures may be in excess of 50 C during the summer. Restricting surface activity to night may be a response to these high temperatures.

Between the ends of the drainage gradient, diversity measures indicated little overall difference. However, the chord distance measure indicated great differences in community composition. The most interesting result was the degree of similarity between the

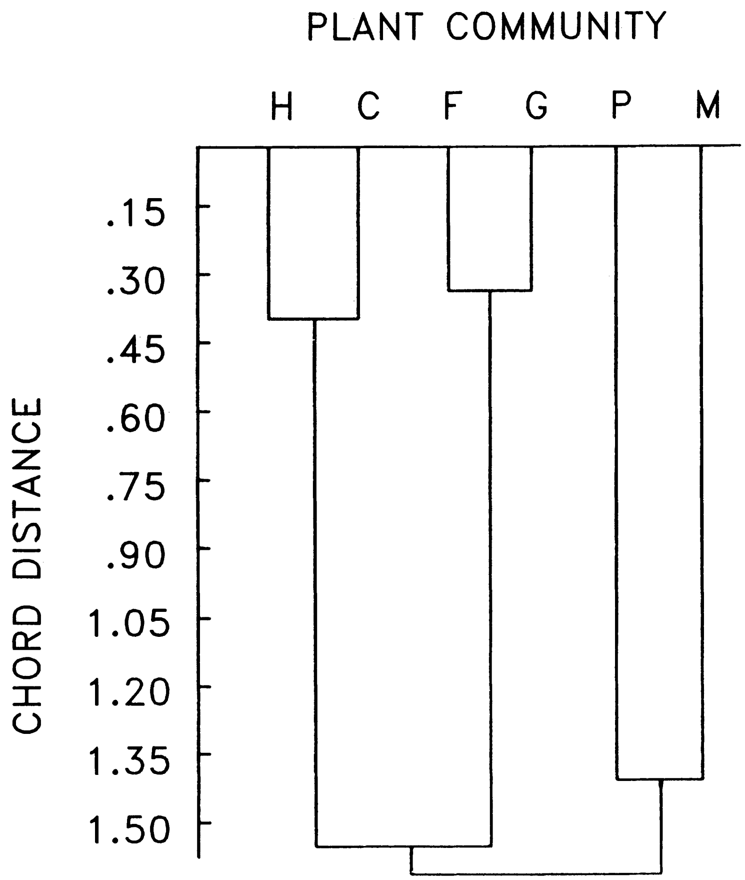

Fig. 3.—Cluster analysis of chord distances between sample sites for the cold-dry season. P = playa, M = mesquite fringe, H = herbaceous, C = creosote bush, F = fluff grass, G = black grama

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black grama and mesquite communities, which differed in vegetation, soil texture and location along the drainage gradient. This corresponds with high levels of available soil nitrogen along the gradient. Mesquite is a nodulated legume and the mesquite community has the highest amount of available nitrogen. Preliminary data indicate that black grama grass has high associative nitrogen fixation, with a sharp discontinuity of available nitrogen compared with the adjacent fluff grass community (F. Fisher, pers. comm.). Lightfoot and Whitford (1987) found that the amount of available nitrogen in creosote bush stems and leaves affected density and diversity of associated foliar arthropods. Similarly, the amount of plant protein, as influenced by available nitrogen, may have affected the diversity of epigeic Collembola.

The overall pattern changes when examined by season. During the warm-wet season (biologically most active period), community similarity is nearly identical to the generalized annual pattern (Fig. 2). During the cold-dry season, the community similarity pattern conforms to upper, middle and lower watersheds (Fig. 3). During the warm-dry season, community similarities have a pattern intermediate between the other two (Fig. 4).

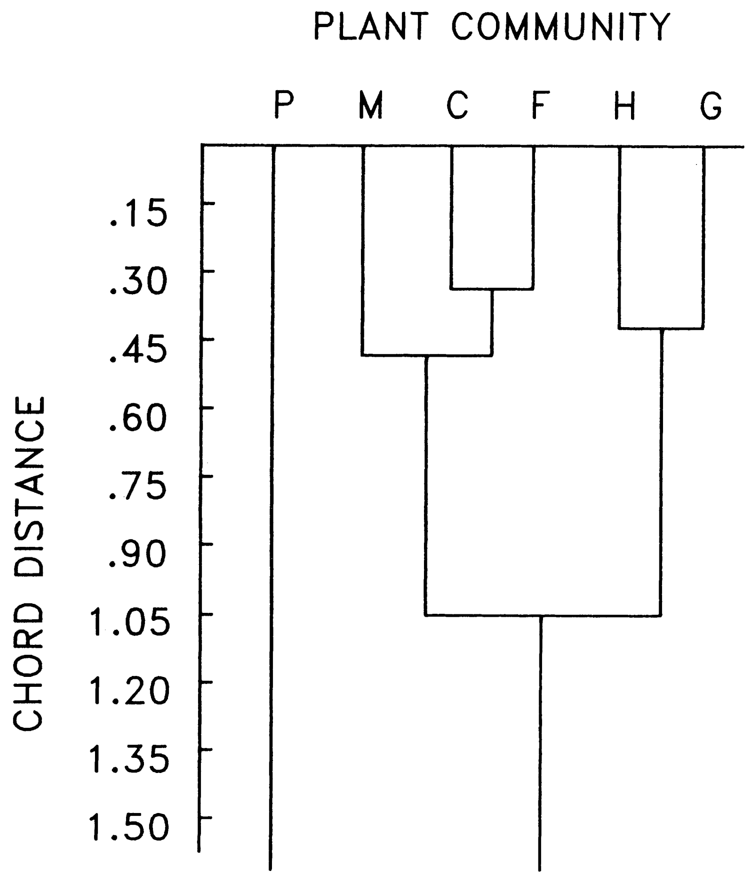

Fig. 4.—Cluster analysis of chord distances between sample sites for the warm-dry season. P = playa, M = mesquite fringe, H = herbaceous, C = creosote bush, F = fluff grass, G = black grama

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The seasonal fluctuations of community similarity may be due to the combined effect of temperature, moisture and nitrogen availability. In the warm-wet season, all of these factors are optimum, and differential nitrogen distribution and availability are most apparent. Greatest soil nitrogen contents are located in the mesquite and grama grass zones: therefore, collembolan communities in these zones are also most similar. In the other seasons, nitrogen availability is lessened, so collembolan community similarity is controlled by other factors.

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