

EDAPHIC COLLEMBOLA (COLLEMBOLA) AS INDICATORS OF THE CHEMICAL CHARACTERISTICS OF SOIL IN A PEACH ORCHARD (*PRUNUS PERSICA* (L.) BATSCH) IN MICHOACÁN, MEXICO

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Abstract. Edaphic collembola are abundant in agricultural soils and can be used as bioindicators of the condition of the soils they inhabit. We study the composition, diversity, and phenology of the collembola community in a peach orchard (*Prunus persica* (L.) Bach) located in Zitácuaro, Michoacán, Mexico. We evaluated the effect of physical and chemical characteristics of the orchard's soil on the edaphic collembola community. Collembola were extracted by Berlese funnels from samples of leaf litter and soil obtained monthly, from September 1993 to August 1994. Fallen leaves were not removed from the ground for the duration of the study. Sixty-nine species were registered: 58 in leaf litter and 53 in soil. Collembola density varied from 248 to 15,889 ind m⁻² in leaf litter and 419 to 7,286 ind m⁻² in soil. The layer of fallen leaves exhibited the highest density, species richness and diversity of collembola. The edaphic variables that altered collembola density were organic matter content, cationic exchange capacity (CEC) and carbon-to-nitrogen ratio. Richness was affected by organic matter and total nitrogen. Diversity was affected by pH, total nitrogen, calcium, and carbon-to-nitrogen ratio. The density of dominant species was negatively affected by phosphorus and calcium content, as well as CEC.

Keywords: *Hemisotoma thermophila*, collembola, soil fauna, soil ecology, organic matter, competition

Introduction

In agrosystems, the study of euedaphic, hemiedaphic and epiedaphic collembola is relevant due to its high abundance and numerous functional roles within the supporting, regulating, and maintaining ecosystem services. Thus, these arthropods can represent up to 75% of the total abundance of edaphic fauna (Scheunemann et al., 2015). Their activity contributes to soil respiration and aggregation, dissolved organic carbon leaching, organic matter decomposition and nitrogen mineralization (Siddiky et al., 2012; Coleman et al., 2018). Collembola are also part of trophic chains as the prey of other arthropods (Potapov

et al., 2020), and by feeding principally on fungi and decomposing plant material (Castaño-Meneses et al., 2004; Palacios-Vargas, 2014).

Some species can promote plant growth and exert a positive influence on agricultural production as a biological control against plant-pathogens (Shiraishi et al., 2003; Friberg et al., 2005; Meyer-Wolfarth et al., 2015); they also benefit the association between plants and mycorrhizae (Gange, 2000; Innocenti and Sabatini, 2018) and stimulate increased root biomass (Ngosong et al., 2014).

Collembola play an important part in edaphic trophic chains. Although their low biomass limits their decomposition of materials that fall to the ground, collembola are particularly important in agricultural soils because they mobilize a great amount of nutrients (Filser, 2002; Coulibaly et al., 2017). They also affect the biomass and activity of soil microorganisms through selective consumption and are thus able to change the structure of fungi and bacteria communities in soil (Anslan et al., 2016; Coulibaly et al., 2019).

These hexapods are affected by biotic and abiotic factors. Soil temperature and water content are known to affect their activity, fecundity, and mortality (Sengupta et al., 2017; Xie et al., 2023). Likewise, populations of edaphic collembola are known to be limited by food availability (Salamon et al., 2004; Ngosong et al., 2009), though other authors, such as Kustec (2018), call this into question. Since the density (Brennan et al., 2006) and diversity of edaphic collembola (Scheu and Schaefer, 1998; Jøergensen and Scheu, 1999; Cutz-Pool et al., 2007) increase when food resources and water enter the soil, leaf litter, fertilizers and irrigation are expected to increase their diversity.

Soil pH and water content affect collembola abundance because they favor the development of the microbiota on which these arthropods feed. Collembola feed on both the organic matter entering the soil and the microorganisms that colonize such matter (Muturi et al., 2009). Also, their abundance is scarcely affected by herbicides applied (Mohamed et al., 2017).

In agroecosystems, different types of management are commonly implemented to improve the conditions and/or quality of the species of commercial interest. However, collembola communities are particularly sensitive to these types of management because such handling usually modifies food availability and the physicochemical conditions of the habitat (Salamon et al., 2004; Ngosong et al., 2009); for example, humus and/or seedlings growing near plants of commercial interest are usually removed, whereas fertilizers and different types of irrigation are often utilized. Research has reported that communities of edaphic collembola are affected by the type of humus, the time it has lain on the ground (Fuji and Takeda, 2012) and its functional characteristics (Raymond-Léonard et al., 2018). When humus is not removed, the oxidative environment is reduced and soil quality is enhanced (Tabaglio et al., 2009).

Studies report that the use of fertilizers in agroecosystems increases the abundance of certain species of collembola (Schütz et al., 2008; Wang et al., 2015). Moreover, it has been found that microarthropod abundance is positively related with the carbon and nitrogen content in soil and negatively related with pH (Wang et al., 2015). Prior studies conducted in several ecosystems have found that reduced rainfall decreases soil humidity and increases its temperature, which has a negative effect on the abundance, diversity, and biomass of edaphic collembola (Tsiafouli et al., 2005; Kardol et al., 2011; Xu et al., 2012; Santonja et al., 2017). However, such effects are not found in certain types of soil (e.g., Xu et al., 2012).

Although increasingly more studies are conducted on collembola communities in agroecosystems, at present few works simultaneously analyze their euedaphic and epiedaphic communities in such systems. However, these works have found that the compositions of euedaphic and epiedaphic collembola communities differ from each other and that the abundance and biomass of the latter tend to be greater (Fuji and Takeda, 2012).

Much has been learned on the behavior of edaphic collembola communities in different crops, such as corn and wheat (Mendoza et al., 1999; Muturi et al., 2009; Greenslade et al., 2010; Gimenes et al., 2020; Chassain et al., 2023). Studies have been performed on a variety of crops, such as apple orchards grown traditionally and organically (Doles et al., 2001), papaya orchards managed traditionally and integrally (Culik et al., 2006), alfalfa crops fertilized with biosolids (Flores-Pardavé et al., 2011), fields in which only potatoes have been sown over the past 90 years and different soil fertilizers have been used (Twardowski et al., 2016), olive orchards managed organically, integrally and conventionally (Ruano et al., 2004; Gkisakis et al., 2015), mango orchards with minimal and technified management (Cabrera-Mireles et al., 2019), as well as vineyards, almond and olive orchards, alfalfa crops, and pastures (Sisterson et al., 2020).

The objectives of this research were (i) to discover the density, composition, diversity and phenology of the community of euedaphic, hemiedaphic and epiedaphic collembola in a peach orchard (*Prunus persica*) in Zitácuaro, Michoacán (Mexico) subjected to management with a particular use of fertilizers and irrigation, and (ii) to evaluate the influence of the physical and chemical characteristics of the edaphic collembola community.

Materials and methods

Study area

The study was conducted in a peach orchard located in Polvorín Valley (*Figure 1*), 3 km to the east of Zitácuaro, Michoacán, Mexico (19° 26' N, 100° 20' W, 1950 m a.s.l.). The 1.4-hectare orchard in Polvorín is slanted less than 10% and has an irrigation channel at its northern end. The fully productive orchard trees were 6 years old and equally distanced from each other at 4-meter intervals. The soil was a humic andosol (Soil Survey Staff, 1999).

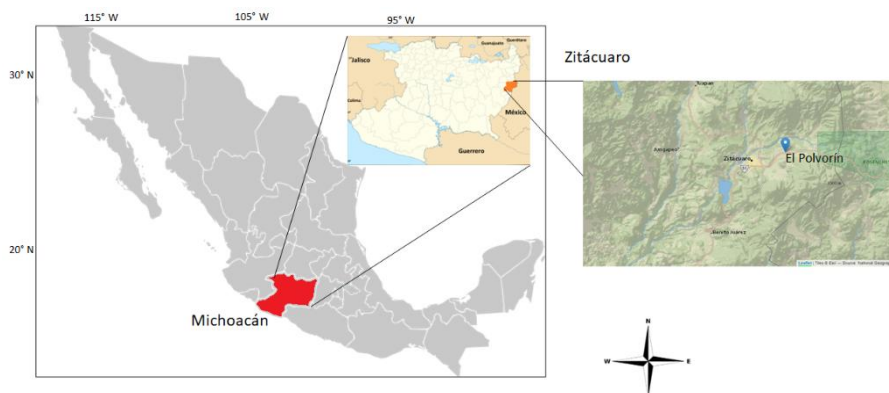


Figure 1. Localitation of the study area in Zitácuaro, Michoacán, Mexico

The land in the study area was originally a pine forest that had been cleared out approximately 76 years ago. It was an open pasture for the first 30 years and has been

used to grow peaches for the past 46 years. The climate is temperate subhumid with summer rainfall [noted as C(w2)(w)b(i')g, according to the Köppen classification, amended by García (2004)], with a mean monthly temperature of 19.2 °C (Figure 2).

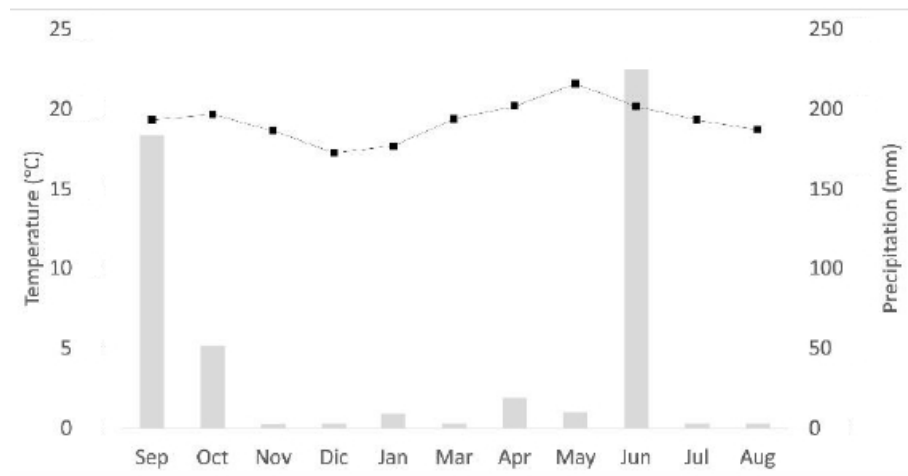


Figure 2. Accumulated precipitation (mm) and mean temperature (°C) per month during the study, provided by the meteorological station at Zitácuaro, Michoacán, Mexico

During this study, the orchard was watered, and a number of fertilizers were applied: ammonium sulfate, calcium and ash in November, January and February; urea, ammonium nitrate, potassium, superphosphate and ammonium sulfate in March; amounts of urea in June; and poultry manure in May. The orchard was watered in January, February, and March. Before the study began, the orchard had typically been weeded and the leaves that fell under the trees had been removed. For the duration of this study, the soil was kept uncovered except for the leaves and small branches that fell from the peach trees.

Data collection

In the orchard, 100 trees were chosen as a square measuring 10 × 10 trees (*ca.* 1,500 m²). One sample of leaf litter and one sample of soil were collected each month from beneath 17-19 randomly selected trees, from September 1993 through August 1994 (except February 1994). Samples were collected 30 cm away from the trunk, under the canopy of each tree. If a sample was collected twice under the same tree (during the same month), the second was collected opposite from the first sample (180°). Leaf litter was collected in 8 × 8 cm (64 cm²) squares reaching the depth of the mineral soil; this layer was never more than 1 cm deep. A sample of soil was then collected in a circular area measuring 8 cm in diameter (50.3 cm²) and 10 cm in depth.

Samples were processed in a laboratory on the same day they were collected. The Berlese-Tullgren method was then applied for 14 days: the first 7 days with no heat source and the last 7 days with a heat source (a 40-watt light bulb; 45°C). Collected specimens were separated, quantified, and mounted in Hoyer's solution for later identification. Mounted specimens were identified to the species using the keys proposed by Richards (1968), Christiansen and Bellinger (1994) and Bellinger et al. (2016-2023).

Community structure

A two-way analysis of variance was performed to study how month and edaphic layer affect collembola density. The discrete data were transformed as $\sqrt{(x + 0.5)}$ because they were normalized. The analyses were run in STATISTICA ver. 8 software (StatSoft, 2007).

The diversity in the collembola community was calculated using the Shannon diversity index (H') with a natural logarithm (Magurran, 2004). Layer diversity was compared using the t test to compare the Shannon diversity indexes.

In order to analyze overall changes in the diversity values corresponding to each month and layer (soil-leaf litter), true diversity was estimated between 0 and 1 (Jost, 2006), corresponding to species richness and the Shannon index exponential, respectively. Also, the expected maximum richness and diversity for each month and layer were calculated using the ACE non-parametric estimator (Chao and Lee, 1992; Chao and Shen, 2003). Calculations were made using SPADE software (Chao and Shen, 2010).

Furthermore, the Sørensen similarity index was calculated for collembola communities in both layers for each of the eleven sampled months.

A canonical correspondence analysis was made of the abundances of each Collembola species in the soil and of their evaluated parameters from nine collection dates. The highest number of soil variables was analyzed between November 1993 and August 1994. We used XLSTAT-Premium ver. 20.3.1 software (Addinsoft, 2020) for this purpose.

Predictors of collembola abundance, richness, and diversity

Multiple regressions were performed using the “backward” method between specific richness (S) and diversity (H') in the collembola community, and between the abundance of dominant species *Hemisotoma thermophila* (Axelson, 1900) and the edaphic variables, applying average monthly values (Draper and Smith, 1966; Zar, 1984).

The abundance values were corrected to $\sqrt{(x + 0.5)}$ for this purpose, since they were discrete. Edaphic variables, such as organic matter, total nitrogen, and carbon, were expressed in percentages and transformed as: arc sine $\sqrt{(x/100)}$ (Sokal and Rohlf, 2012).

Soil analysis

Collembola were extracted from 5-10 randomly selected soil samples (10 samples from September to October 1993 and five from November 1993 to August 1994). The samples were then dried and sieved using a 2-mm screen, and the following edaphic analyses were conducted: pH in water using a potentiometer Corning 340 model 7 and a soil-to-water ratio of 1:2; organic matter percentage by the Walkley and Black method; phosphorus by the Bray-1 method; potassium, extracted in ammonium acetate 1N at pH 7 (1:5 ratio), by flame emission spectroscopy Corning (Corning Incorporated, New York, USA); magnesium and calcium in the same solution by extraction in ammonium acetate 1 N at pH 7.0 (1:5 ratio) and EDTA volumetry; nitrogen by the Kjeldahl method; and cationic exchange capacity (CEC) in ammonium acetate 1 N at pH 7.0 by centrifugation (Chapman and Pratt, 1961; Hesse, 1971; Jackson, 1976; Page, 1982; Hanlon, 2000).

Potassium and magnesium were only evaluated in the samples taken in September and October, whereas CEC and C/N ratio were evaluated starting in November. Linear corrections were made between the evaluated edaphic variables (Zar, 1984).

Temperature and precipitation

Temperature and precipitation data from the study period were obtained from the meteorological station at Zitácuaro, Michoacán, provided by Mexico's National Meteorological Service (*Servicio Meteorológico Nacional de México*).

Results

Collembola community

We collected 10,214 specimens from 69 species, of which 7,985 belonged to 58 species living in leaf litter and 2,229 to 53 species found in soil (*Table 1*). Forty-one species were found in both layers, whereas 12 were exclusively found in soil and 17 in leaf litter. The Sørensen similarity index between layers was 0.759 (*Figure 3*). Pooling the entire year's data, the Shannon diversity index (H') of soil was 2.88, which was significantly higher than that of leaf litter (2.33; t test: $t = 20.31$, $df = 4689$, $P < 0.001$).

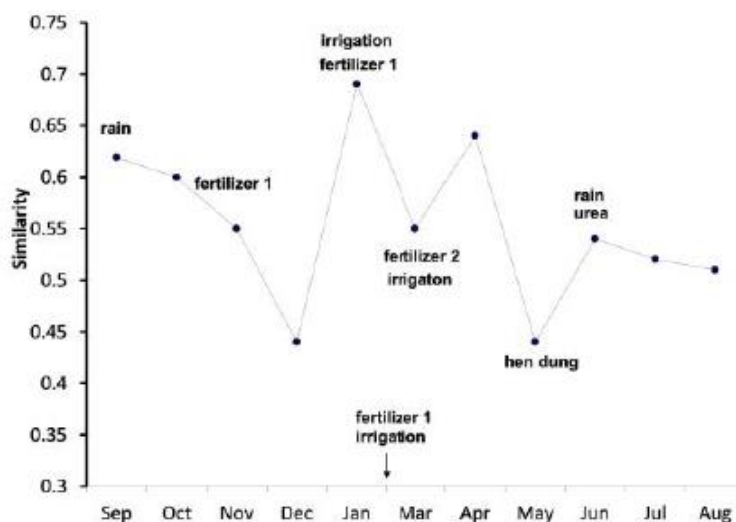


Figure 3. Monthly variation in the Sørensen similarity index for the springtail community in leaf litter and soil

The species with the highest relative abundance in leaf litter were: *Hemisotoma thermophila* (Axelson, 1900) (37.6%), *Ceratophysella denticulata* (Bagnall, 1941) (17.6%), *Desoria ca. flora* (6.1%), *Mesaphorura macrochaeta* Rusek (1976) (5.3%) and *Seira ca. purpurea* (4.5%), i.e., 71.1% of the collembola found (*Table 1*). On the other hand, the dominant species in the soil were: *Hemisotoma thermophila* (16.5%), *Desoria ca. flora* (12.8%), *Sphaeridia serrata* Folsom & Mill. (1938) (11.8%), *Lepidocyrtus ca. cinereus* (8.0%) and *Ceratophysella denticulata* (7.8%), which comprised 56.9% of the collembola in this layer (*Table 1*). The dominant species in the entire edaphic habitat were: *Hemisotoma thermophila* (33.1%), *Ceratophysella denticulata* (15.5%), *Desoria ca. flora* (7.6%) and *Mesaphorura macrochaeta* (4.7%).

Table 1. Relative and absolute abundance of the edaphic collembolan species in litter (L), soil (S), and both strata (L + S) in a peach orchard in Zitácuaro, Michoacán, Mexico

Species	Absolute abundance			Relative abundance (%)		
	L	S	L+S	L	S	L+S
<i>Brachystomella stachi</i> Mills, 1934	11	13	24	0.14	0.58	0.24
<i>Brachystomella parvula</i> (Schäffer, 1896)	330	105	435	4.13	4.71	4.27
<i>Ceratophysella denticulata</i> (Bagnall, 1941)	1403	173	1576	17.57	7.76	15.46
<i>Ceratophysella armata</i> (Nicolet, 1842)	15	23	38	0.19	1.03	0.37
<i>Ceratophysella succinea</i> (Gisin, 1949)*	7	0	7	0.09	0	0.07
<i>Desoria ca. flora</i>	485	286	771	6.07	12.83	7.56
<i>Desoria ca. marissa</i>	19	76	95	0.24	3.41	0.93
<i>Parisotoma ca. notabilis</i>	24	55	79	0.3	2.47	0.77
<i>Desoria ca. trispinata</i>	33	35	68	0.41	1.57	0.67
<i>Desoria</i> sp.	8	17	25	0.1	0.76	0.25
<i>Dicyrtoma aurata</i> ‡ (Mills, 1934)	0	2	2	0	0.09	0.02
<i>Dicyrtoma mithra</i> ‡ Wray, 1949	0	2	2	0	0.09	0.02
<i>Dicyrtomina rossi</i> † Wray, 1952	3	0	3	0.04	0	0.03
<i>Calvatomina quadrangularis</i> ‡ (Mills, 1934)	0	2	2	0	0.09	0.02
<i>Entomobrya confusa</i> Christiansen, 1958	206	43	249	2.58	1.93	2.44
<i>Entomobrya willosia</i> †	5	0	5	0.06	0	0.05
<i>Entomobrya ca. triangularis</i> (Schött)	15	7	22	0.19	0.31	0.22
<i>Entomobrya ca. bicolor</i> † Guthrie, 1903	1	0	1	0.01	0	0.01
<i>Entomobrya ca. comparata</i> Folsom, 1919	36	13	49	0.45	0.58	0.48
<i>Entomobrya ca. sinelloides</i> † Christiansen, 1958	2	0	2	0.03	0	0.02
<i>Folsomides parvulus</i> Stach, 1922	124	27	151	1.55	1.21	1.48
<i>Folsomides oculatus</i> †	5	0	5	0.06	0	0.05
<i>Hemisotoma thermophila</i> (Axelson, 1900)	3004	369	3373	37.62	16.55	33.08
<i>Isotomurus palustris</i> (Muller, 1776)	83	61	144	1.04	2.74	1.41
<i>Isotomurus tricolor</i> † (Packard, 1873)	4	0	4	0.05	0	0.04
<i>Lepidocyrtus ca. cinereus</i>	207	179	386	2.59	8.03	3.79
<i>Lepidocyrtus ca. pallidus</i>	283	74	357	3.54	3.32	3.5
<i>Lepidocyrtus floridensis</i> Snider, 1967	40	9	49	0.5	0.4	0.48
<i>Lepidocyrtus cyaneus</i> † Tullberg, 1871	39	0	39	0.49	0	0.38
<i>Lepidocyrtus ca. lanuginosus</i>	20	7	27	0.25	0.31	0.26
<i>Lepidocyrtus floridanus</i> †	18	0	18	0.23	0	0.18
<i>Lepidocyrtus finus</i> ‡	0	1	1	0	0.04	0.01
Christiansen and Bellinger, 1980						
<i>Lepidocyrtus cyaneus</i> Tullberg, 1871	3	9	12	0.04	0.4	0.12
<i>Mesaphorura macrochaeta</i> Rusek, 1976	422	57	479	5.28	2.56	4.7
<i>Mesaphorura ca. clavata</i>	41	12	53	0.51	0.54	0.52
<i>Mesaphorura ca. granulata</i>	13	27	40	0.16	1.21	0.39
<i>Mesaphorura ca. yosiii</i> †	22	0	22	0.28	0	0.22
<i>Mesaphorura ca. latens</i> †	11	3	14	0.14	0.13	0.14
<i>Mesaphorura krausbaueri</i> ‡ Börner, 1901	0	4	4	0	0.18	0.04
<i>Mesaphorura silvicola</i> ‡ (Folsom, 1932)	0	3	3	0	0.13	0.03
<i>Mesaphorura ruseki</i> † Christiansen and Bellinger, 1980	2	0	2	0.03	0	0.02
<i>Amaritulla hades</i> ‡ (Christiansen & Bellinger, 1980)	0	1	1	0	0.04	0.01
<i>Polykatianna intermedia</i> † Snider, 1978	2	0	2	0.03	0	0.02
<i>Polykatianna polygonia</i> † Snider, 1978	1	0	1	0.01	0	0.01
<i>Proisotoma bulba</i> † Christiansen & Bellinger, 1981	27	0	27	0.34	0	0.26
<i>Thalassaphorura encarpata</i> (Denis, 1931)	267	101	368	4.61	4.53	3.61

Species	Absolute abundance			Relative abundance (%)		
	L	S	L+S	L	S	L+S
<i>Protaphorura parvicornis</i> (Mills, HB, 1934)	11	8	19	0.14	0.36	0.19
<i>Protaphorura churchiliana</i> (Hammer, 1953)	0	5	5	0	0.22	0.05
<i>Pseudosinella octopunctata</i> † Börner, 1901	4	0	4	0.05	0	0.04
<i>Pseudosinella ca. vita</i> †	2	0	2	0.03	0	0.02
<i>Ptenothrix quadrangularis</i> † (H.B. Mills, 1934)	8	0	8	0.1	0	0.08
<i>Schoettella distincta</i> ‡ (Denis, 1931) Bonet, 1931	0	6	6	0	0.27	0.06
<i>Seira dubia</i> Christiansen & Bellinger, 1980	33	2	35	0.41	0.09	0.34
<i>Seira ca.purpurea</i>	358	9	367	4.48	0.4	3.60
<i>Seira ca. bipunctata</i>	33	20	53	0.41	0.9	0.52
<i>Sinella ca. vita</i>	3	5	8	0.04	0.22	0.08
<i>Sminthurides</i> sp. 2 ‡	0	2	2	0	0.09	0.02
<i>Sminthurides</i> sp. 1 ‡	0	2	2	0	0.09	0.02
<i>Sminthurides ca. occultus</i> ‡	0	2	2	0	0.09	0.02
<i>Sminthurinus ca. elegans</i>	106	48	154	1.33	2.15	1.51
<i>Sminthurinus latimaculosus</i> Maynard, 1951	8	8	16	0.1	0.36	0.16
<i>Sminthurus butcheri</i> † Snider, 1969	2	0	2	0.03	0	0.02
<i>Sminthurus fitchi</i> ‡ Folsom, 1896	0	1	1	0	0.04	0.01
<i>Sminthurus ca. incisus</i>	11	19	30	0.14	0.85	0.29
<i>Sminthurus ca. Sylvestris</i>	0	30	30	0	1.35	0.29
<i>Sminthurus ca. elegans</i> †	15	0	15	0.19	0	0.15
<i>Sphaeridia serrata</i> Folsom et Mills, 1938	61	264	325	0.76	11.84	3.19
<i>Sphaeridia pumilis</i> (Krausbauer, 1898)	27	2	29	0.34	0.09	0.28
<i>Willowsia cf. Buski</i>	5	0	5	0.06	0	0.05
Total	7985	2229	10214	100	100	100

†Exclusive species in litter; ‡Exclusive species in soil. The dominant species (relative abundance > 5% at least one stratum) are highlighted with boldfaced print

Seasonal variation pattern

Temperature and precipitation. The average temperature registered during the study period was 19.2°C (sd = 1.1°C). Minimum monthly average temperature was recorded in December (17.3 °C), while maximum monthly average temperature was 21.6 °C, recorded in May (Figure 2).

An accumulated precipitation of 516 mm was registered during this period, most of which took place in two months: September 1993 (183.7 mm) and June 1994 (225 mm). Dry conditions prevailed during the remaining months.

Similarity. The Sørensen similarity indexes between collembola communities in leaf litter and in soil varied throughout the year between 0.44 and 0.69 (Figure 3). The highest similarity values were associated to the months in which the orchard was watered or had rainfall.

Density. Collembola density in leaf litter varied from 248 ind m⁻² in December to 15,889 ind m⁻² in September, and collembola in soil varied from 418 ind m⁻² in May and July to 7,286 ind m⁻² in September (Figure 4). According with the ANOVA test (Table 2) Collembola density varied significantly according to the collection month ($F_{10,386} = 11.371$, $P < 0.0001$), layer ($F_{1,386} = 54.044$, $P < 0.0001$) and month x layer interaction ($F_{10,386} = 2.537$, $P = 0.006$). Collembola density was 2.8 times higher in the fallen leaves (6,084 ind m⁻²) than in the soil (2,149 ind m⁻²).

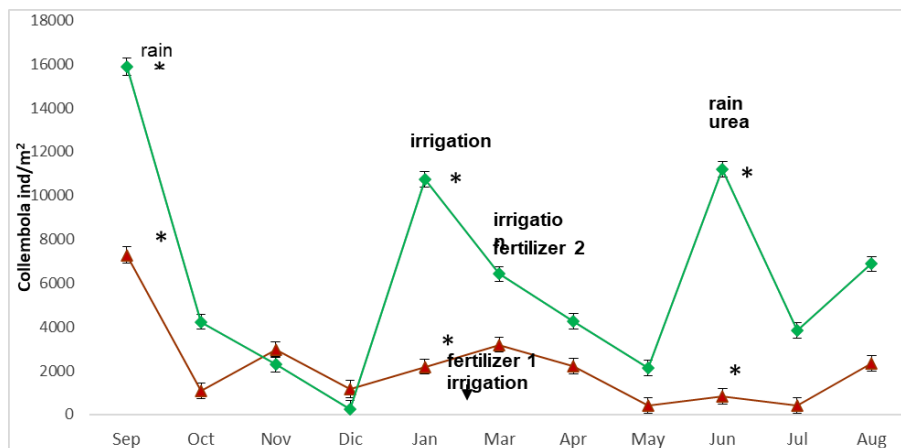


Figure 4. Variation in springtail density (No./m² ± e.e.) in leaf litter (diamonds) and soil (triangles) in a peach orchard in Zitácuaro, Michoacán, Mexico (N = 17-19). Months with significant differences between layers with P < 0.05 (Tukey's test) are indicated with asterisks

Table 2. Effect of collection month, layer, and interaction between both parameters on density of Collembola in a peach orchard of Zitácuaro, Michoacán, Mexico

Source	d.f. source	d.f. error	F	P
Collection month	10	386	11.371	0.0001
Layer	1	386	54.044	0.0001
Collection month x layer interaction	10	386	2.537	0.006

The monthly pattern of variation in density data for soil and leaf litter was as follows: September (11,457 ind m⁻²) > January, June, March, August and April (3,234-6,337 ind m⁻²) > May and December (709-1,274 ind m⁻²) (Tukey's test: P<0.05; Figure 5). Irregular variation was recorded in the changing density values throughout the year, most of which are related to land irrigation or the frequency of rainfall (Figures 4 and 5).

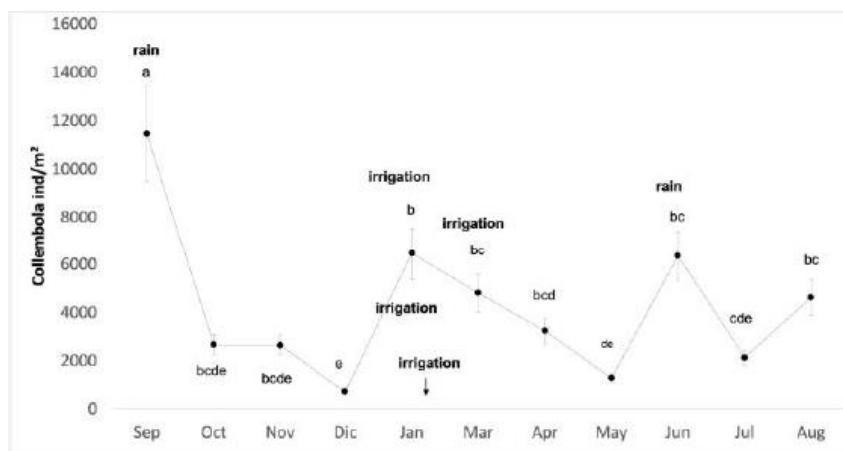


Figure 5. Monthly variation in the density of edaphic springtail (No./m² ± e.e.) in a peach orchard in Zitácuaro, Michoacán, Mexico. Pooled data from soil and leaf litter (N = 34-38). Different letters denote significant differences between months with P < 0.05 (Tukey's test)

Species richness. The highest values of specific richness were recorded for leaf litter, except in the months of September and December (Figure 6). The accumulated data from both layers show a trend similar to the dynamics in the layer of dead leaves (Figure 6). Leaf litter presented five units more than soil (Figure 7). Sample coverage was between 81.4 and 100% for true richness. Estimated true richness in leaf litter was 48.4 (99% sample coverage), 3.6 units higher than the estimated true richness in soil (95.9% sample coverage).

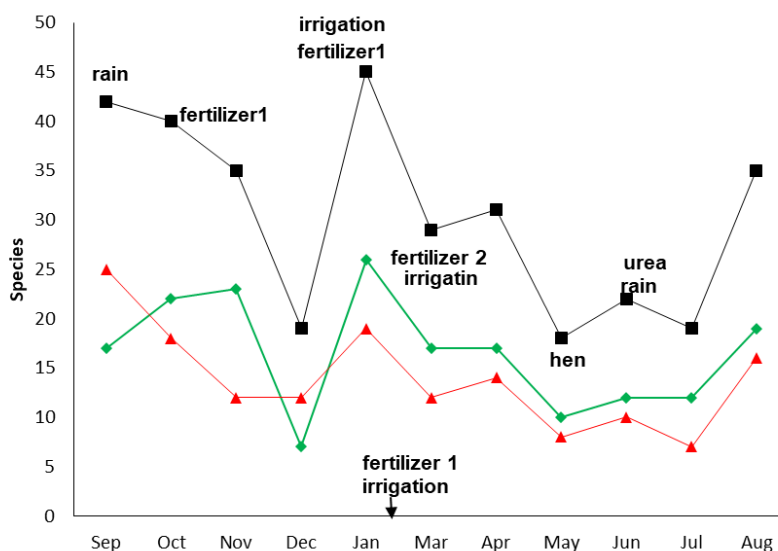


Figure 6. Monthly variation in *Collembola* species richness in leaf litter (diamonds) and soil (triangles), and in both layers (squares) in a peach orchard in Zitácuaro, Michoacán, Mexico. Accumulated data from both layers are shown in squares

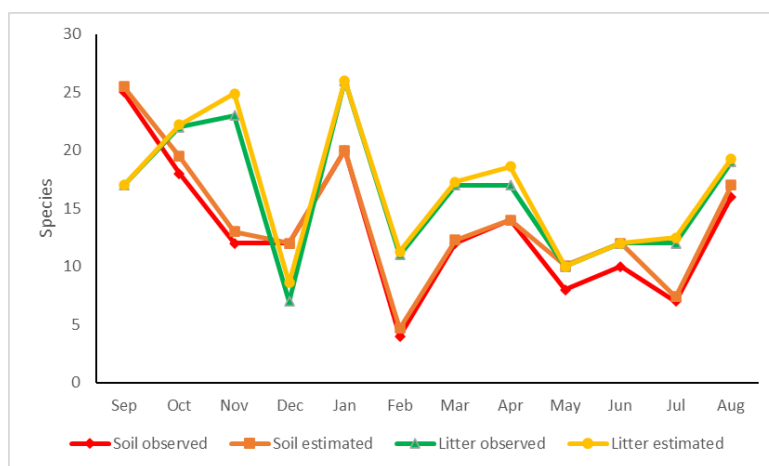


Figure 7. True richness in leaf litter and soil estimated and observed values

Diversity. The H' values in leaf litter progressively increased from September (1.99) to November (2.67). They then dropped, to rise again in January (2.65). A downward trend was subsequently observed for the rest of the study period. The H' value in soil peaked in September (2.76) and then progressively fell the rest of the study period, except

for an increase in January (2.52) (Figure 8). These values were significantly higher in the soil collected in September (2.76), December (2.38) and June (1.26) than in leaf litter (1.99, 1.65 and 0.54 respectively; *t* tests: $P < 0.05$). Conversely, this parameter was significantly higher in leaf litter during November (2.54 vs. 1.65 in soil, *t* test: $P < 0.05$). Soil was 59% more diverse than leaf litter. Sample coverage of the observed diversity went from 84.7% to 99.8% (Figure 9). Estimated true diversity was 17.59 (98.7%) in soil and 10.31 (99.9%) in leaf litter.

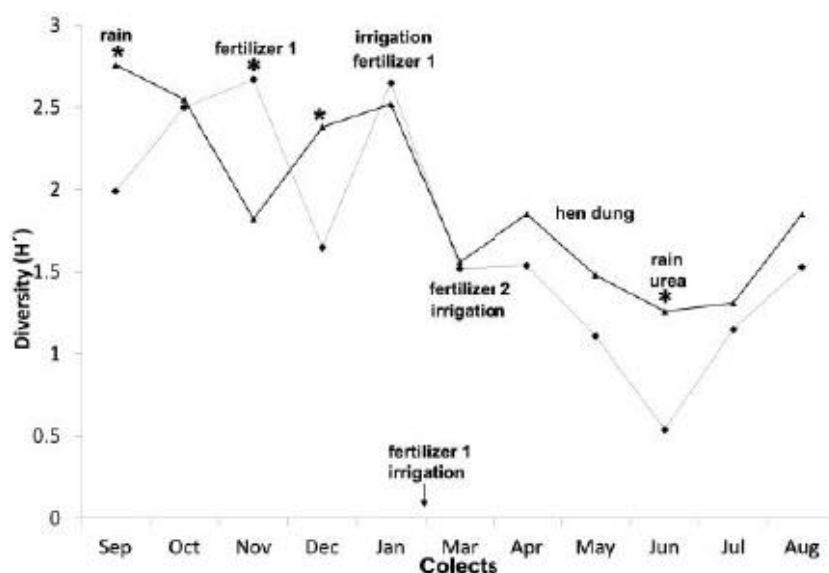


Figure 8. Monthly variation in the Shannon diversity index for springtails in leaf litter (diamonds) and soil (triangles) in a peach orchard in Zitácuaro, Michoacán, Mexico. Months with significant differences between layers with $P < 0.05$ (*t* test) are indicated with asterisks

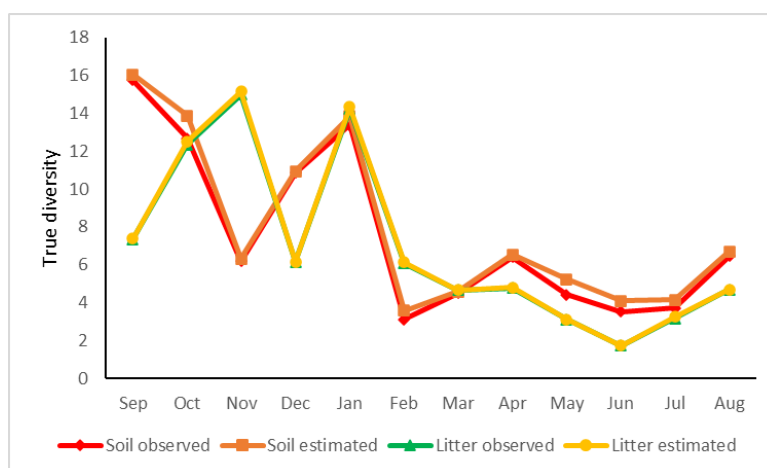


Figure 9. True diversity in leaf litter and soil, observed and estimated values

As for the effective number of species, 10.30 were observed and 10.31 (99.9%) estimated in total leaf litter, whereas 17.37 were observed and 17.59 (98.7%) estimated in total soil. This indicates that collembola diversity was higher in soil than in leaf litter (Figure 9).

Soil characteristics and monthly variation

We found $222 \pm \text{SE } 28$ ppm (range: 36-474 ppm) of magnesium and 520 ± 24 ppm (range: 301-704 ppm) of potassium in the soil of the peach orchard ($n = 20$). According with the ANOVA (Table 3), the sampling month had a significant effect on organic matter content, total nitrogen, calcium, and carbon-to-nitrogen ratio ($P < 0.01$). Soil pH tended to be acid (3.8-6.5). The monthly differences between the remaining edaphic parameters are shown in Table 4.

Table 3. Mean values (\pm e.e., range) and results of the ANOVA to determine the effect of the date on the edaphic parameters of a peach orchard of Zitácuaro, Michoacán, Mexico between September 1993, and August 1994

Parameter	Mean \pm ee	Range	N	d.f.	F	P
pH	5.18 ± 0.06	3.80-6.50	65	10,54	1.721	0.100
OM (%)	7.26 ± 0.10	4.71-9.57	65	10,54	3.270	0.002
N _{total} (%)	0.31 ± 0.01	0.22-0.42	65	10,54	12.110	<0.001
P (ppm)	15.3 ± 1.4	4.0-72.0	65	10,54	1.30	0.25
Ca (ppm)	760 ± 87	138-3367	65	10,54	15.374	<0.001
CEC	24.14 ± 1.03	6.91-32.79	45	8,36	0.960	0.47
C/N	14.70 ± 0.28	11.23-20.29	45	8,36	2.735	0.018

OM, organic matter content; N_{total}, Nitrogen total content; P, Phosphorus content, Ca, Calcium content; CEC, cationic exchange capacity; C/N, carbon/nitrogen ratio. Significant values of P are highlighted with boldfaced print

Table 4. Monthly variation (1993-1994; mean \pm e.e.) of edaphic traits in a peach orchard of Zitácuaro, Michoacán, Mexico; $n = 5$ (except Sep. and Oct., when $n = 10$)

Month	OM (%)	N _{total} (%)	Ca (ppm)	C/N
Sep	7.6 ± 0.2^a	0.36 ± 0.01^a	1998 ± 218^a	ND
Oct	7.0 ± 0.1^{ab}	0.36 ± 0.01^a	1182 ± 168^b	ND
Nov	7.8 ± 0.5^a	0.32 ± 0.01^{ab}	501 ± 112^{bc}	13.94 ± 0.32^{ab}
Dec	7.8 ± 0.3^a	0.29 ± 0.02^{bc}	462 ± 86^{bc}	15.56 ± 0.85^a
Jan	6.0 ± 0.2^b	0.29 ± 0.01^{bc}	412 ± 40^c	11.92 ± 0.33^b
Mar	7.2 ± 0.3^{ab}	0.29 ± 0.01^{bc}	540 ± 126^{bc}	14.44 ± 0.23^{ab}
Apr	7.1 ± 0.2^{ab}	0.26 ± 0.01^c	294 ± 49^c	15.68 ± 0.51^a
May	6.9 ± 0.1^{ab}	0.26 ± 0.01^c	261 ± 40^c	15.45 ± 0.90^a
Jun	8.0 ± 0.2^a	0.30 ± 0.01^{bc}	391 ± 54^c	15.60 ± 0.66^a
Jul	7.4 ± 0.2^{ab}	0.27 ± 0.01^{bc}	404 ± 67^c	14.66 ± 0.47^{ab}
Aug	7.0 ± 0.7^{ab}	0.27 ± 0.01^{bc}	262 ± 37^c	15.26 ± 1.64^{ab}

Means with different letters were significantly different ($P < 0.05$; Tukey tests). OM, organic matter; N_{total}, Nitrogen total content; Ca, Calcium content; ND, no data available. The significant highest values are highlighted with boldfaced print

Significant positive correlations were registered in organic matter between total nitrogen (N_{total}) and C/N ratio, as well as between calcium content and total nitrogen, phosphorous and pH. Only one significant negative correlation was registered between C/N ratio and total nitrogen (Table 5).

Table 5. Correlation indices between edaphic variables of a peach orchard (*Prunus persica*) of Zitácuaro, Michoacán, Mexico; d.f. = 63 (except for CEC and C/N, where d.f. = 43)

	OM	N _{total}	P	Ca	CEC	C/N
pH	0.143	0.054	-0.189	0.426***	0.148	0.135
	OM	0.350**	0.121	0.189	-0.051	0.637***
		N _{total}	0.189	0.703***	0.063	-0.382**
			P	0.275*	-0.029	-0.075
				Ca	-0.030	-0.077
					CEC	-0.126

OM, organic matter; CEC, cationic exchange capacity; C/N, carbon:nitrogen ratio. Significant values are highlighted with boldfaced print. *P < 0.05, **P < 0.01, ***P < 0.001

Collembola and soil features

According to the following equation, organic matter content (OM), cationic exchange capacity (CEC) and nitrogen-to-carbon ratio (C/N) significantly affected collembola density (D_C) in the soil, the first one positively and the last two negatively:

$$D_C = 3.53 + (6.76) OM - (0.042) CEC - (0.18) C/N$$

$$(r^2 = 0.152, F_{3,44} = 5.27, P = 0.002)$$

The richness of the edaphic collembola community (S_C) was significantly affected by organic matter content (OM) and total nitrogen in the soil (N). Both affected it directly, as shown by the equation 1:

$$S_C = -41.09 + 20220.61 (OM) + 5669.82 (N_{total})$$

$$(r^2 = 0.426, F_{2,44} = 3.34; P = 0.005) \quad (\text{Eq.1})$$

The diversity index of the edaphic collembola community (H'_C) was significantly affected by pH (pH), total nitrogen content (N), calcium content (Ca) and carbon-to-nitrogen ratio (C/N); the first one negatively and the other edaphic variables positively, according to equation 2:

$$H'_C = -12.5885 - 0.61 (pH) + 784.13 (N) + 0.0012 (Ca) + 1.21 (C/N)$$

$$(r^2 = 0.488, F_{4,44} = 4.28, P = 0.001) \quad (\text{Eq.2})$$

The density of *Hemisotoma thermophila* (D_{Ht}) was significantly and negatively influenced by phosphorus (P) and calcium (Ca) content, as well as by cationic exchange capacity (CEC), as illustrated by equation 3:

$$D_{Ht} = 41.51 - (0.072) P - 0.003 (Ca) - 0.05 (CEC)$$

$$(r^2 = 0.73, F_{3,16} = 3.25, P = 0.08) \quad (\text{Eq.3})$$

Canonical correspondence analysis

The CCA analysis showed that, in conjunction, canonical axes 1 and 2 explained 54.2% of the variance in composition, with nitrogen best explaining axis 1 ($r = 0.59$) together with OM ($r = 0.31$), and calcium ($r = 0.90$) best correlated to axis 2. The Monte-Carlo significance test showed $p = 0.02$ with 500 permutations. The species most closely

related to axis 1 were *Desoria ca. flora*, *Sphaeridia serratus*, *Lepidocyrtus ca. floridensis* and *Mesaphorura krausbaueri*, whereas those closest to axis 2 were *Lepidocyrtus cf. cinereus* and *Mesaphorura macrochaeta* (Figure 10).

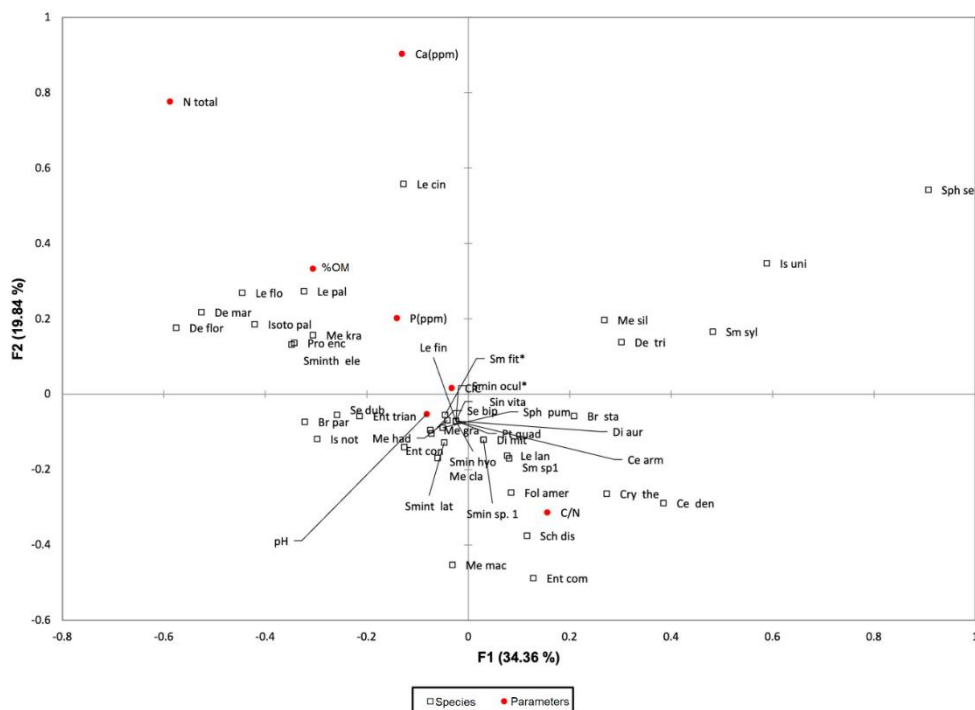


Figure 10. Relationship between soil variables and the diversity of the springtail community in soil. Circles indicate the edaphic variables. Axes 1 and 2 explain 54.2% of variance; see text

Discussion

The role played by irrigation and rainfall

In both layers, seasonal variations in the density (Figure 4), richness (Figure 6) and, to a lesser degree, diversity (Figure 7) of the collembola community were irregular during the study period. This could be explained by the intense rainfall that occurred in September 1993 and June 1994, as well as the first irrigation that took place well into the dry season, in January 1994. These events had an explosive effect on the abundance and richness of the edaphic collembola community. Also, the rain in September and irrigation in January explain the high diversity registered in these months. Different authors, such as Anslan et al. (2018), Badejo et al. (1998), Doles et al. (2001) and Muturi et al. (2009), have recorded a positive correlation between humidity content and the abundance of collembola in soil.

Rain also favors certain species, helping them exploit their medium. Thus, we found that in September, *C. denticulata* provided 27.9% of similarity, *Desoria ca. flora* 17.6% and *M. macrochaeta* 10.4%. In January, *Seira dubia* provided 16.1%, whereas *C. denticulata* and *H. thermophilla* accounted for 12.1%, respectively. In April, *H. thermophilla* contributed 53.4% of similarity, *C. denticulata* 10.2% and *M. macrochaeta* 6%. In June, *H. thermophilla* provided 88.4% (Figure 3). It would seem that water favors species that are able to inhabit a layer other than the one where they usually grow; we believe this should be studied further.

Despite the above, the effect of irrigation and rain was not always positive. Although the intense rainfall in June favored the abundance of collembola in leaf litter (*Figure 4*), it had an adverse effect on their diversity in both layers (*Figure 7*). This was due to the dominance of *H. thermophilla*, since the highest number of individuals of this species was registered in June, both in leaf litter and in soil. More studies are needed to know more on the biology of this species.

Water in soil creates conditions that favor the end of the quiescent period (Hopkin, 1997) and the rupture of the chorion (Vegter, 1987). Collembola are known to heavily depend on levels of soil humidity for survival and reproduction, either directly or indirectly, as their amount of food may increase by way of plant, animal, or fungi tissue (Lindberg et al., 2002; Palacios-Vargas et al., 2007a; Seeger and Filser, 2008). Several epiedaphic collembola feed on algae and protozoa (Dunger et al., 2002; Ngosong et al., 2014), which is why water availability is key to the presence of these food resources. However, soil saturated with water can produce adverse effects when soil micropores become flooded, causing mortality in microfauna (Hallam et al., 2020). On the other hand, the dry season is known to be a factor that causes some populations of collembola to dwindle and migrate from leaf litter to mineral soil (Miranda and Palacios-Vargas, 1992).

It is even more crucial for collembola to be in a humid habitat when one considers that most feed on fungi (Ruess et al., 2004; Chahartaghi et al., 2005; Caravaca and Ruess, 2014). Many fungivorous species were recorded in this study, which is why soil humidity is so relevant. For example, *Hemisotoma thermophila* feeds on the conidia of *Alternaria* sp. and plant material and fungi mitospores from corn crops (Castaño-Meneses et al., 2004), whereas *Morulina alata* Yosii 1954 consumes spores from *Cortinarius anomalus* (Fr ex Fr) Fr, *Inocybe fastigiata* (Schaeff.) Quél. and *Mycena pura* (Pers.) P. Kumm (Nakano et al., 2017). This coincides with Kustec (2018), who states that epiedaphic collembola are principally saprotrophs.

Temperature

Temperature also played a role in the dynamics of the edaphic collembola community because it is a determining factor for their physiology and affects the time it takes to reach sexual maturity, the time span of their life cycle, the size of individuals and the number and duration of instars (Snider and Butcher, 1973). Thus, the temperatures registered during our study fall within the optimum temperature range indicated by Sengupta et al. (2017) and Snider and Butcher (1973) for the populations in the collembola community to reach their highest fecundity.

Carbon and nitrogen release, nitrification and the decomposition rate of edaphic organic matter are likely to increase during the months with higher temperature (Kustec, 2018). The above may imply a boost to the ascending forces in the orchard soil and leaf litter. This increase was exploited by collembola, since its population density was higher in September, March and June, accumulated density was higher in March and June, richness values were highest in March, April and July, and diversity was greater in September and August.

Fertilizers and manure

Our results do not show a clear pattern of the effect that fertilizers have on the density, richness, or diversity of collembola (*Figures 5, 6 and 8*). However, since an overall decrease in collembola density was recorded in both layers, it would be interesting to use controlled experiments to test the possible negative effect of fertilizer no. 1 (ammonium

sulfate, calcium, and ash). A decrease in richness and diversity was also recorded in leaf litter the month after this fertilizer was applied, namely in November, January, and February. The same could be done with poultry manure because the values for density, richness and diversity fell the month it was applied (May), compared to values from the previous month (April) (Figures 5, 6 and 8). This pattern of reduced diversity following the application of manures and fertilizers coincides with the findings of Song et al. (2016) and Pommeresche et al. (2017).

Our results differ from those of Ngosong et al. (2009), who found that mineral fertilization with NH_4NO_3 increased the populations of some edaphic collembola, and from those of King et al. (1980), who detected an increase in the populations of mites and collembola after applying superphosphate. This contrasting response to fertilizers may be related to the fact that they affect the microbial biomass in different ways, as found by Jøergensen and Scheu (1999). The results also coincide with those recorded by Machado et al. (2019), who found that the edaphic collembola community varies when manures are applied to the soil. Soil eutrophication with nitrogen has been found to lower richness and diversity in collembola communities because nitrogen can be toxic in soil. This occurs because it raises soil acidity and may form nitric acid, which affects the microorganisms that serve collembola as food. Phosphorus has the most significant influence on the structure of the edaphic collembola community.

The application of manures and fertilizers to soil and leaf litter alters the conditions of both strata. Such changes trigger pressure that acts on the populations of collembola, which may induce changes to the structure of their community (Kustec, 2018). Thus, the ascending forces in soil and leaf litter may increase with greater nutrient availability. These forces may be exploited by some populations. This was the case with *H. thermophila* and *C. denticulata*, whose abundance increased substantially in March and April both in leaf litter and soil, and *Lepidocyrtus* cf. *cinereus* and *Sphaeridia serratus* in soil.

Dominant species

We observed that *Hemisotoma thermophila* did not appear in either layer when the first sample was collected but started to appear in October with 11 individuals in leaf litter and 6 in soil. Then 12 were found in November and 5 in December, both times in the fallen leaves. Six were found in the soil in December. When the fifth sample was collected in January, the population size remained large, and it became the dominant species in both layers and the most abundant in leaf litter. This species was not detected by Lytton-Hitchins et al. (2015), whose work covered several months in cotton fields that were watered and had rainfall. Cutz et al. (2007) found a similar condition in a corn and alfalfa crop that was watered using clean water, but *H. thermophila* was very abundant at the site next to it, which was watered with wastewater from Mexico City.

In Mexico, *H. thermophila* is widely distributed throughout the Trans-Mexican Volcanic Belt and in the states of Chiapas, Guerrero, Durango, and Jalisco (Palacios-Vargas, 2000; Palacios-Vargas et al., 2007b; Magaña-Martínez and Palacios-Vargas, 2010). This species is also known to tolerate heavy metals and to be quite abundant in urban areas that have been polluted with industrial waste (Fiera, 2009). *H. thermophila* is highly capable of colonizing different media that contain food, such as leaf litter. On the other hand, the rises in the population of this species could be attributed to a high reproduction rate.

Leaf litter in orchard management

When fallen leaves were not removed from under the orchard trees, resources used by collembola became highly available. This created new microhabitats in the layer that were exploited by several populations of collembola that lived there, as has also been recorded by Scheu and Schaefer (1998). The positive effect of leaving leaf litter on the ground (under each tree) suggests the existence of a strong ascending force that favors the collembola populations, as has been recorded by Filser (2002) and Wardle et al. (1999). However, our results differed from those of Kustec (2018) since he did not observe any effect of medium enrichment on the edaphic collembola community.

It may be that several species, such as *Ceratophysella denticulata*, *Desoria flora* and *Mesaphorura macrochaeta*, already lived in the mineral soil and colonized and exploited the leaf litter when it became an available habitat, as has been observed in other systems (Badejo et al., 1998; Das and Joy, 2009). It is recommended for orchard management to consider keeping leaf litter on the ground as a mechanism to improve and fertilize the soil through the activity of the edaphic fauna living there. This soil management used in the orchard was similar to that of agrosystems with non-tilled land, since all the fertilizers were applied on top of the ground. This reduced the oxidative environment and improved the quality of the soil, as recorded by Tabaglio et al. (2009) in a corn crop.

pH

The pH of the studied soil was acid despite the seasonal variation in the structure of the collembola community. Soil acidity can cause (a) lowered ability to absorb phosphorus (Scheu and Setälä, 2002), (b) stimulated development of important fungi that degrade organic matter (Ruess et al., 2004), and (c) diminished development of macrofauna and increased density in fungivorous collembola (Scheu, 2002).

This study found that increased soil pH led to lower collembola diversity values. This matches the findings of Machado et al. (2019), who observed that changes in pH affected edaphic collembola communities. Added materials also caused variations in pH: it rose with ash (Qin et al., 2017) and fell with NO_3NH_4 . Also, as mentioned above, permanent soil acidity limits its phosphorus content, which would have repercussions on the structure of the edaphic collembola community.

Density, species richness and diversity

The collembola density we obtained (leaf litter: 248 to 15,889 ind m^{-2} , soil: 167 to 7,286 ind. m^{-2}) showed maximum values higher than those observed by De la Rosa and Negrete-Yankelevich (2012) in pasture leaf litter (100 ind m^{-2}), secondary forest (200 ind m^{-2}) and montane cloud forest (700 ind m^{-2}); by Cutz-Pool et al. (2010) in *A. religiosa* forest (1,362 ind m^{-2}); and by Paul et al. (2011) in agroecosystems (1,289 ind m^{-2}) and forests (2,558 ind m^2). Our findings were similar to those of Cutz-Pool et al. (2007) in corn crops watered with wastewater (8,479 ind m^{-2}) and clean water (1,989 ind m^{-2}). Only Culik et al. (2002) found higher values than ours in agroecosystems (46,731-103,656 ind m^{-2}).

We found that Collembola density was higher in leaf litter than in soil, as had previously been reported by Culik et al. (2002), Addison et al. (2013) in vineyards, Hendrix et al. (1986) at non-tilled sites and Badejo et al. (1998) at a series of agroforestry sites. Leaf litter make a habitat that is easily accessed and that provides highly available resources to fungivorous species (Kaneda and Kanuko, 2008). This layer is expected to

contain greater fungi biomass and a slower decomposition rate than mineral soil (Kaneda and Kanuko, 2008).

The richness found in the orchard (69 species) was greater than what Cutz-Pool et al. (2010) observed in a forest of *A. religiosa* (8-11 species) and Cutz-Pool et al. (2007) in a corn crop with two different irrigation systems (wastewater: 29 species, clean water: 19 species), as well as what was found in a seminatural forest (13) and a plantation of *Abies religiosa* (6) (Luque et al., 2011). On the other hand, the Shannon diversity indexes found in this study (2.33 in leaf litter and 2.88 in soil) were greater than those obtained by De la Rosa and Negrete-Yankelevich (2012) in mature cloud forest (leaf litter: 2.2, soil: 2.1), secondary forest (leaf litter: 1.4, soil: 2.4) and mature forest glade (leaf litter: 1.0, soil: 1.4); Cutz-Pool et al. (2010) in *A. religiosa* forest (leaf litter: 1.28); Culik et al. (2002) in agroecosystems with organic fertilization (1.28-2.14); and Cutz-Pool et al. (2007) in cornfields watered with wastewater (2.02) and clean water (1.85). The high richness and diversity values we recorded could be a result of the exhaustive sampling work that was performed.

The density, richness, and diversity of the edaphic collembola community are linked to soil calcium content and pH. We also found that calcium and total nitrogen are highly correlated. It was difficult to show the causal relationships within the studied system due to the orchard soil management. Calcium is amply used (Vincent et al., 2018) as a constituent of the Collembola exoskeleton (Adejuyigbe et al., 2006), yet this element still leaches when collembola forage on fungi (Ineson et al., 1982). The abundance of several Collembola species has been observed to be related to calcium, magnesium, and manganese saturation (Salmon and Ponge, 1999). Moreover, it may be that collembola in the studied orchard help mobilize nitrogen from leaf litter and regulate nitrogen dynamics within the layer by consuming fungi (Beare et al., 1992).

The multivariate analysis corroborates the results obtained by means of regressions. Nitrogen, calcium, and organic matter are fundamental for the preservation of collembola communities (Figure 10), either because they serve as a direct food source for certain populations or because they help fungi grow that can become food or pH reducers in a stressful environment. Such populations can also be used as bioindicators of the conditions of the medium (Cutz-Pol et al., 2007).

Conclusions

The collembola community in the peach orchard responded to orchard management. The populations showed that they were regulated by the availability of food and refuge provided by the leaf litter on the ground (ascending forces). This is observed in the fact that most specimens were found in this layer. The most important factor that affects abundance and richness is water availability, either by irrigation or rainfall, although the density and richness of collembola are favored by organic matter content. We found that the dominant species in the orchard was *Hemisotoma thermophila*. Nevertheless, sampling were taken 30 years ago, our results can important patterns than can be compared to actually conditions in the same studied area.

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Author contributions. Andrés Miranda-Rangel: Conceptualization; formal analysis; investigation; methodology; funding acquisition, visualization; writing original draft. Zenón Cano-Santana: Methodology, visualization, writing review & editing. Gabriela Castaño-Meneses: Formal analysis, investigation, methodology, visualization, writing review & editing; José G. Palacios-Vargas: Conceptualization, resources, supervision, writing review & editing. Paulina Corona-Tejeda: Investigation.

Conflict of interest. The authors have no conflicts of interest to disclose.

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