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Vegetation influences desert soil arthropods and their response to altered precipitation

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ABSTRACT

Altered precipitation in the arid southwestern USA will influence both plant and soil communities, but relatively few studies explore its impact on soil arthropods who comprise an important component of soil food webs. Further, while vegetation has a well-documented influence on soil communities, it is unclear how the plant community might influence their response to altered precipitation. We altered both the size and frequency of monsoon season precipitation pulses in the Sonoran Desert and measured the resulting soil arthropod abundance, diversity, and composition. We manipulated the precipitation for two dominant shrubs representing distinctly different functional types compared to interplant spaces. Plant cover significantly influenced soil arthropods, with the deep-rooted evergreen *Larrea tridentata* increasing abundance and diversity over interplant spaces more strongly than the drought-deciduous *Ambrosia deltoidea*. Precipitation pattern altered arthropod diversity and evenness, particularly in interplant soils. While soil arthropod total abundance was resistant to altered precipitation, vegetation buffered Shannon diversity from the impacts of altered precipitation. Thus, climate-induced changes in the plant community could indirectly influence soil arthropod diversity. However, these plant-soil interactions may not be equally important under all scenarios of altered precipitation.

1. Introduction

As a result of greenhouse gas emissions and subsequent climate warming, precipitation regimes in the arid southwestern United States are expected to change. Models predict a shift in precipitation patterns, including altered timing of the summer monsoon season (Cook and Seager, 2013), increased occurrence of extreme precipitation events and severe drought (Cayan et al., 2010; Georgescu et al., 2021), and an overall increase in aridity (Seager et al., 2007; Seager and Vecchi, 2010). Increased aridity and drought conditions lead to a subsequent reduction in soil moisture (Sheffield and Wood, 2008; Cayan et al., 2010), which when combined with the hot temperatures of the desert southwest, results in the drier heat extremes recently observed in the desert southwest (McKinnon et al., 2021).

Altered precipitation in these water-limited ecosystems will inevitably influence ecological communities, including soil communities. For example, studies from several dryland ecosystems have shown that altered precipitation impacts soil microbial communities and biocrusts (e.g., Finks et al., 2021; Wang et al., 2022a; Wang et al., 2022b). Beyond microbes, soil fauna span multiple levels of the food web to influence important ecological processes such as nutrient recycling, carbon turnover and storage, and therefore plant productivity (e.g., Seastedt, 1984; Wolters, 2000; Bradford et al., 2002; Gergócs et al., 2022). Numerous studies show that altered precipitation can influence soil micro-, meso-, and macrofauna across diverse ecosystems (sensu the meta-analysis by Blankinship et al., 2011), though not all ecosystems (Blankinship et al., 2011; Eisenhauer et al., 2012). Specifically, both simulated drought and increased precipitation can alter micro- and mesofauna abundance and community composition (e.g., Lindberg et al., 2002; Holmstrup et al., 2012; Xu et al., 2012; Flórián et al., 2019), though the influence on total abundance does not always persist when considered over longer time scales (Holmstrup et al., 2012, 2013). Studies from dryland ecosystems are fewer but show that the abundance of detritivorous ground-dwelling arthropods, particularly soft-bodied taxa such as springtails, are impacted by both seasonal and long-term rainfall patterns (Kwok et al., 2016; Fischer et al., 2022). Notably, however, studies that specifically focus on soil mesofauna communities, beyond the active species able to be sampled using pitfall traps, are lacking in desert ecosystems.

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Beyond alterations in the total amount of precipitation, both the amount and frequency of precipitation pulses are important aspects of the precipitation regime. The timing and uniformity of that precipitation can have a significant impact on dryland ecosystem C and N cycling, and plant community composition and productivity (e.g., Griffin-Nolan et al., 2021; Zhao et al., 2021; Holguin et al., 2022). These studies largely focus on plants and/or soil processes, and it is unclear how the soil fauna who play a role in those processes respond to altered patterns in precipitation delivery, particularly in deserts.

In addition to climate factors, the presence and composition of the plant community can influence soil communities. Numerous studies have demonstrated that ground-dwelling soil invertebrate abundance is related to plant cover across ecosystems (e.g., Kwok et al., 2016; Pestana et al., 2020; Fischer et al., 2022). In drylands, soil fauna are more abundant beneath vegetation than in interplant spaces, given the microhabitats and availability of litter resources generated by vegetation (Santos et al., 1978; Franco et al., 1979; Kamill et al., 1985). Individual species of vegetation may harbor distinct soil communities (Wallwork et al., 1985), though perhaps only when species significantly alter soil properties such as moisture and carbon content (Wasserstrom et al., 2016). However, plant productivity and composition are also sensitive to altered precipitation, with some functional groups being more sensitive to drought than others (Munson et al., 2012; Hoover et al., 2015; Eziz et al., 2017). Given the well-documented relationship between plants and soil communities, any such climate-induced changes in plants will likely cascade to the soil food web.

It is possible that these plant-soil interactions can influence an ecosystem's response to altered precipitation. For example, drought-adapted soil microbial communities can alter the impact of reduced water availability on plant productivity (O'Brien et al., 2018; Allsup and Lankau, 2019). In one example, a ground-dwelling macroarthropod ameliorated the impact of simulated drought on plant productivity (Johnson et al., 2016). Further, drought can reduce or reverse plant-soil feedbacks compared to non-drought conditions (Kaisermann et al., 2017; Hassan et al., 2021). Thus, precipitation patterns might indirectly influence soil invertebrates through changes in plant production and community composition, setting off a multi-trophic cascade (e.g., Kwok et al., 2016; Fischer et al., 2022). This indirect effect of altered precipitation through plants may be more important than the direct effects for some taxa (Deguines et al., 2017). The presence of plants has even been shown to alleviate the effects of drought on soil fauna in a temperate grassland, particularly at the lower trophic levels (de Vries et al., 2012).

Given the important ecological role of soil arthropods in desert biogeochemistry (Sagi and Hawlena, 2021) and the lack of knowledge about their response to the altered precipitation occurring in the desert southwest U.S., we conducted a short-term field study to (1) assess how the amount and frequency of monsoon season precipitation pulses influence soil arthropod communities. We altered the precipitation regime under two dominant Sonoran Desert shrubs that represent distinctly different functional types to (2) explore the role of plant-soil linkages in the response of soil arthropod communities to altered precipitation. We hypothesized that reduced frequency of precipitation would reduce arthropod abundance and diversity, with a limited impact of pulse size alone. Further, we predicted that plant cover would buffer the arthropod community from changes in altered precipitation, given that their presence can ameliorate water and resource limitation beneath their canopies.

2. Materials and methods

2.1. Site description

The experiment was conducted at White Tank Mountains Regional Park, Maricopa County, AZ, USA (33°36′ N, 112°30′ W; elevation 450 m), at experimental plots maintained by the Central Arizona-Phoenix Long Term Ecological Research (CAP-LTER) program. Soils are Typic Haplargids, consisting of deep, well-drained soils of the Ebon and Pinamt series (Soil Survey Staff, 2022). The 5-year mean annual precipitation leading up to the study was 166.7 mm (±32.7 SE) with a mean annual temperature of 23.3 °C (±0.28 SE) (FCDMC, 2022). Average pulse size during this period was 5.03 mm (±0.58 SE) per precipitation event, with an average frequency of precipitation every 10.9 days (±1.3 SE).

2.2. Precipitation experiment

At the onset of monsoon season (July), twelve replicate individuals of two dominant shrubs, creosote (*Larrea tridentata*) and triangle-leaf bursage (*Ambrosia deltoidea*), were selected across an approx. 12,000 m^2 area. As depicted in Fig. 1, soil samples from the top 10 cm were taken from beneath the canopy of each plant, as well as twelve nearby interplant areas of unvegetated soil to represent initial conditions. Surface soils were sampled to capture the higher density of soil fauna compared to lower depths (e.g., Franco et al., 1979; Kamill et al., 1985). The selected plants and bare soil then began receiving one of four precipitation treatments: 5 mm of precipitation (representing the average pulse size received at this site) or 7.5 mm of precipitation (representing a 50% increase in pulse size) delivered either every 2 weeks (rounding up the average frequency of pulses at this site) or every 4 weeks (representing less frequent precipitation events). Thus, there were four precipitation treatments: low pulse size, high frequency (LPHF; 5mm × 2wks), low pulse, low frequency (LPLF; 5mm × 4wks), high pulse, high frequency (HPHF; 7.5mm × 2wks), and high pulse, low frequency (HPLF; 7.5mm × 4wks). These four treatments were applied to each of 3 replicates, totaling the 12 individual plants or interplant soils. Precipitation treatments were applied using a backpack sprayer, delivering 1 L (for low pulse, 5 mm) or 1.5 L (for high pulse, 7.5 mm) of deionized water evenly to the soil over a 0.5-m diameter circle centered around the plant or in an interplant space. The simulated precipitation events continued every 2 or 4 weeks until late in the monsoon season, ending in September when final soil samples were taken from beneath the canopy of each plant and the interplant spaces.

Because the research site was open to the atmosphere (i.e., not covered by a greenhouse or rainout shelter), the site also received natural precipitation throughout the study (Appendix A). Total ambient precipitation received during the study was 52 mm, with an average pulse size of 2.8 mm (FCDMC, 2022) and all but two of the pulses were below the 5 mm that is suggested to activate plant activity (Huxman et al., 2004). Therefore, ambient monsoon precipitation was relatively low during the course of the study, and it was received equally across all of the plant cover types.

2.3. Soil analyses

Soil samples were sieved to 2 mm prior to analysis. Approximately 500 g of soil was weighed into plastic 1-L bottles and saturated with 95% ethanol to preserve the invertebrates. A modified heptane flotation method was then used to extract the arthropods from the soil (Geurs et al., 1991; Winter and Behan-Pelletier, 2008). In brief, the ethanol from the preserved soil was decanted across a 38-μm mesh sieve, and the soil was then saturated with water and decanted three more times to ensure the preserved arthropods were rinsed from the soil across the sieve. The contents of the sieve (containing the arthropods) were thoroughly rinsed with water into a 2-L flask containing a stir bar, to which 20 ml of heptane was then added. The flask was sealed with a rubber stopper fitted with a hollow metal pipe that reached down into the flask below the surface of the water, ending just above the stir bar. The stir bar was spun to mix the heptane with the water containing the arthropods at 600 rpm for 20 min. The flask then settled for 5 min, allowing the heptane to float to the top carrying the arthropods. Water was drizzled through the hollow metal pipe into the bottom of the flask without disturbing the heptane layer, raising the level of the heptane so that it

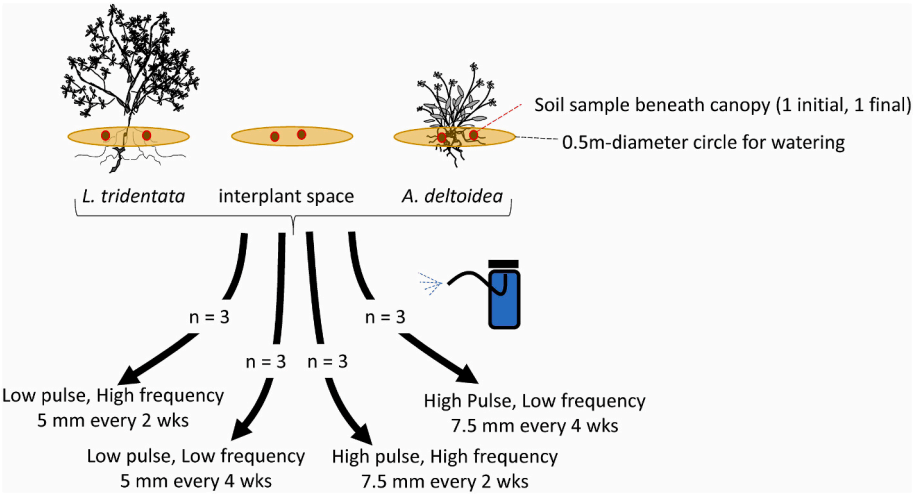

Fig. 1. Graphical depiction of the experimental design. Twelve replicate creosote shrubs (*Larrea tridentata*), triangle-leaf bursage shrubs (*Ambrosia deltoidea*), and interplant spaces were selected. Experimental precipitation treatments were added to three replicates of each plant cover type over a 0.5 m diameter circle. Soil samples were collected from each of the replicates prior to the start of the experiment (initial) and at the end of the monsoon season (final).

could be carefully removed from the flask and decanted across the sieve. The contents of the sieve were then rinsed into a sample cup using 70% ethanol. The soil and remaining water in the flask were decanted across the sieve, returned to the flask with another 20 ml of heptane to repeat this flotation process a second time, ensuring all arthropods were removed from the water. The contents of the sample cup were then identified and enumerated to the lowest possible level (Appendix B), which was Order for most taxa, as well as Class (immature Diplopoda) and Suborder (Acari). The abundance of each arthropod taxa was then expressed as the number per kg of dry soil extracted. Shannon diversity index was calculated for each sample. Because only one individual juvenile Diplopod was found, its identification at the class level would ultimately have represented one individual of its Order (had identification been possible), and therefore the Shannon index was essentially calculated at the Order/Suborder level.

Gravimetric soil water content (SWC) was estimated by drying 25 g of soil at 105 °C for 48 h. Total and inorganic C and N were measured on soils ground to a fine powder in a Spex ball mill that were either left unacidified or acidified with HCl respectively (Ball and Alvarez Guevara, 2015). Samples were analyzed on an elemental analyzer (PerkinElmer PE2400, Wattham MA). Electrical conductivity (EC; a proxy for salinity) and pH were measured on field-moist soil using a 5:1 or 2:1 water:soil dilution, respectively with an Orion 4-star pH and EC meter. Soil texture was measured using the hydrometer method (Sheldrick and Wang, 1993).

2.4. Data analyses

Data are publicly available (Ball, 2022). All statistical analyses were conducted using R (version 4.0.2, The R Foundation). To identify any differences among soils prior to the application of precipitation treatments, an Analysis of Variance (ANOVA) was used to test for the influence of plant cover type (3 levels: creosote, bursage, and bare soil) and assigned precipitation amount (2 levels: 5 mm or 7.5 mm) and precipitation frequency (2 levels: every 2 or 4 weeks) on soil biological and physicochemical properties from the July sampling. Because precipitation treatments had not yet been applied at this point, the ANOVA would identify any confounding pre-existing differences among the soils that had been assigned to each treatment. Only plant type was significant across all of these tests, and a *post hoc* Tukey test was run on a model with only Plant as a main effect to determine which plant cover types significantly differed. Further, non-metric multidimensional scaling (NMDS) was used to investigate arthropod community composition (metaMDS function in package "vegan", k = 2, stress was 0.170). A Permutational Analysis of Variance (PERMANOVA, using the adonis function of "vegan") was used to detect a significant influence of plant cover types and assigned precipitation treatments. Because, again, only plant type was a significant factor, a pairwise PERMANOVA (package "RVAideMemoire") was run on the NMDS scores to determine which plant cover types significantly differ in their position on the NMDS.

Analysis of Covariance (ANOCOVA) was used to test for a significant influence of plant cover type, precipitation amount, and precipitation frequency, with time (pre-treatment July and post-treatment September) as a continuous variable, on soil community abundance and diversity. Using time as a covariate accounts for repeated testing on the same experimental plants over time (Wan, 2019), while allowing for explicit investigation of the interaction of Time and the other main effects. All possible interactions among main effects and time were included in the model. A PERMANOVA was used to explore whether plant type, precipitation amount, precipitation frequency, or time significantly influenced community composition. Finally, a canonical correspondence analysis (CCA; function cca in "vegan") was run on the end-point September data to explore how the experimental treatments significantly altered arthropod community composition in relation to the soil physicochemical properties.

3. Results

3.1. Pre-monsoon

Prior to the experimental precipitation manipulation, creosote and bursage both hosted more abundant soil arthropod communities than interplant soils (Table 1). Arthropod communities beneath creosote and bursage only differed from each other in taxa richness, with slightly greater richness in soils beneath creosote. The NMDS and subsequent pairwise PERMANOVA also showed that plant cover types differed in their arthropod community composition, with the greatest difference between creosote and interplant soils (Appendix C). Coleoptera larvae and immature Diplopoda were only found in soils beneath creosote. Interplant soils, however, contained only Oribatid and Prostigmatid mites and occasionally ants. Compared to interplant spaces, soil beneath both creosote and bursage were also higher in electrical conductivity, % N, and both total and organic % C (Table 1). Soils beneath creosote and bursage did not differ from each other in any physicochemical properties measured. However, only soils beneath creosote had a higher SWC than interplant soils. Notably, both the ANOVAs and PERMANOVA

Table 1
Arthropod community and physicochemical properties of soil from beneath creosote (*Larrea tridentata)*, bursage (*Ambrosia deltoidea*), and interplant spaces in July, prior to the onset of the experimental manipulations. Values are means ± SE. Abundances for individual taxa are only provided for the dominant taxa, and all taxa present can be seen in Appendix B. For each metric, plant cover types with the same letter do not significantly differ from each other in a pairwise Tukey HSD test. Metrics without letters did not significantly differ according to plant cover.

	Creosote	Bursage	Interplant
Total abundance (#/kg dry soil)	279.40 ± 106.10^{a}	105.10 ± 41.70^{a}	2.43 ± 1.02^{b}
Richness	5.92 ± 0.74^{a}	4.00 ± 0.41^{b}	0.58 ± 0.19^{c}
Shannon index	1.14 ± 0.08^{a}	1.12 ± 0.08^{a}	0.11 ± 0.08^{b}
Evenness	0.69 ± 0.06^{a}	0.88 ± 0.07^{a}	0.08 ± 0.08^{b}
Oribatids (#/kg dry soil)	64.82 ± 21.98^{a}	16.72 ± 5.62^{b}	0.52 ± 0.37^{c}
Prostigmatids (#/kg dry soil)	31.72 ± 12.50^{a}	12.72 ± 2.77^{a}	1.39 ± 0.65^{b}
Mesostigmatids (#/kg dry soil)	8.66 ± 3.88^{a}	0.17 ± 0.17^{b}	0^{b}
Poduramorpha (#/kg dry soil)	107.17 ± 55.60^{a}	60.87 ± 29.89^{a}	0^{b}
SWC (% g/g)	5.10 ± 0.38^{a}	4.52 ± 0.21 ^{ab}	3.89 ± 0.23^{b}
pH	7.41 ± 0.09	7.33 ± 0.17	7.33 ± 0.09
Electrical conductivity (μS/cm)	77.98 ± 8.62^{a}	64.30 ± 6.65^{a}	31.58 ± 4.31^{b}
Total carbon (%)	0.64 ± 0.09^{a}	0.63 ± 0.09^{a}	0.26 ± 0.03^{b}
Organic carbon (%)	0.62 ± 0.09^{a}	0.50 ± 0.07^{a}	0.19 ± 0.02^{b}
Total nitrogen (%)	0.07 ± 0.01^{a}	0.06 ± 0.01^{a}	0.03 ± 0.00^{b}
Sand (%)	75.18 ± 1.56 ^{ab}	75.36 ± 1.60^{a}	71.81 ± 1.12^{b}
Silt (%)	0.86 ± 0.59	1.33 ± 0.42	0.89 ± 0.35
Clay (%)	23.97 ± 1.63 ^{ab}	23.31 ± 1.83^{a}	27.31 ± 1.10^{b}

(Appendix C) indicated that there were no pre-existing differences among soils assigned to each precipitation treatment prior to the onset of the experimental watering.

3.2. Post-monsoon treatment effects

At the end of the monsoon season after the experimental treatments, total arthropod abundance and richness were not significantly impacted by precipitation abundance or frequency (Table 2, Fig. 2). Plant cover was still a significant factor, but by September only creosote was significantly greater than interplant soils (Fig. 2a and b). This is because abundances were lower in the vegetated soils at the end of monsoon season than they were at the onset in July, while interplant soils slightly (but not significantly) increased in richness. Precipitation treatments did, however, influence Shannon diversity and evenness. Precipitation frequency caused both the Shannon index and evenness to differentiate over the course of the monsoon season (Frequency*Time, Table 2). By the end of the experiment, soils that received high-frequency precipitation had slightly but significantly greater evenness, regardless of precipitation amount (Fig. 2c). This was due to an approximate doubling of dominance by Poduromorpha springtails under creosotes and Hymenoptera (specifically, ants) under bursage and interplant soils with low-frequency precipitation pulses. Precipitation frequency interacted with precipitation amount and plant type to influence Shannon diversity (Table 2). Interplant soils had lower diversity than vegetated soils receiving the same precipitation treatment, with the exception of HPLF (Fig. 2d). Interestingly, interplant soils receiving ambient pulse size with reduced frequency (LPLF, with therefore the least amount of water) and ambient frequency with increased pulse size (HPHF, with therefore the greatest amount of water) both showed increased divergence from vegetated soils, having significantly lower diversity than all vegetated soils.

The PERMANOVA revealed that, at the end of the experiment, arthropod communities significantly differed by plant type ($P = 0.001$), but precipitation amount ($P = 0.940$) and frequency ($P = 0.259$) were not statistically significant. The CCA demonstrated that the soil communities under creosote diverged from the other cover types (Fig. 3). Soils beneath creosote had greater abundances of Oribatid mites, Diptera larvae, and Poduromorpha springtails (especially when receiving less frequent precipitation; Plant*Frequency $P = 0.012$ for Poduromorpha abundance) and were the only soils to contain Coleoptera larvae (Table 3). This community corresponds to soils that are higher in carbon content, % sand, and conductivity (Fig. 3). Communities beneath bursage diverge slightly from interplant soils. They contained a higher abundance of Oribatid mites, Poduromorpha springtails, Thysanoptera, and ants. This community corresponds with a higher carbon content and conductivity than interplant soils. Bare soils were dominated by Oribatid mites, Prostigmatid mites, and ants. Unlike vegetated soils, they contained no Mesostigmatid mites, with only rare occurrences of one individual from other taxa.

4. Discussion

Plant cover type had the greatest influence on soil arthropod communities, both before and after the experimental precipitation manipulation, in line with other studies demonstrating the influence of woody species on dryland soil community composition (Sepp et al., 2021; Xie et al., 2021). Community composition was also most strongly influenced by plant type, given that the PERMANOVA and CCA did not identify a precipitation effect. Similar to findings in the Mojave Desert, creosote impacted soil arthropods without a significant difference between different species of shrubs (Franco et al., 1979; Kamill et al., 1985). However, in our study creosote differed from interplant soils more strongly than bursage, particularly towards the end of monsoon season.

Table 2
P-values from the Analysis of Covariance (ANCOVA) exploring the effects of plant cover type and precipitation manipulations (both amount and frequency), with time as a continuous covariate, on soil arthropod communities. Factors that are significant at $\alpha < 0.05$ are in bold for emphasis.

	Total Abundance	Richness	Shannon Index	Evenness
Plant	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Amount	0.393	0.838	0.986	0.245
Frequency	0.772	0.540	**0.021**	0.147
Time	0.751	0.634	**0.006**	**<0.001**
Plant*Amount	0.912	0.745	0.821	0.063
Plant*Frequency	0.164	0.418	0.998	0.539
Amount*Frequency	0.295	0.070	0.134	0.334
Plant*Time	**0.004**	**0.015**	**0.002**	**<0.001**
Amount*Time	0.732	0.946	0.369	0.146
Frequency*Time	0.678	0.540	**0.043**	**0.037**
Plant*Amount*Frequency	0.418	0.506	**0.027**	0.067
Plant*Amount*Time	0.467	0.968	0.909	0.935
Plant*Frequency*Time	0.956	0.906	0.907	0.193
Amount*Frequency*Time	0.119	0.733	0.594	0.558
Plant*Amount*Frequency*Time	0.817	0.655	0.542	0.723

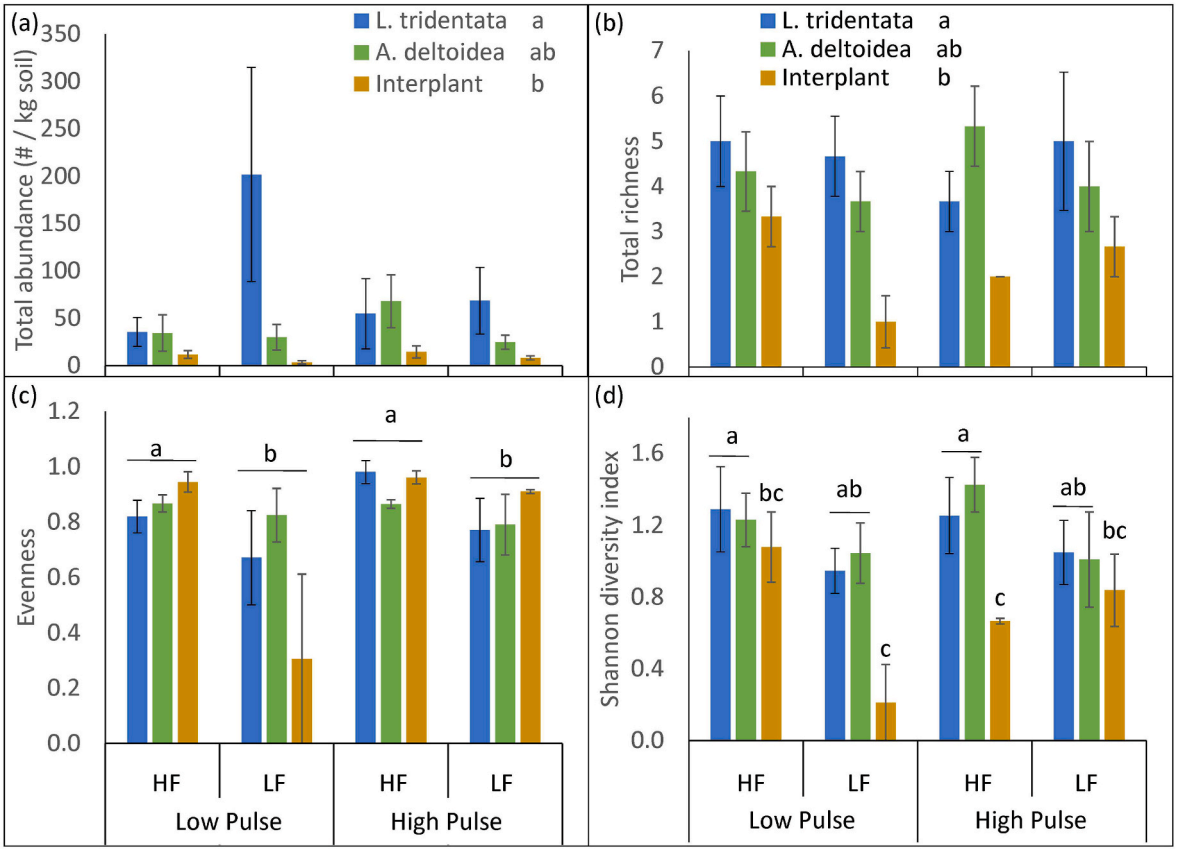

Fig. 2. Arthropod community properties at the end of the altered precipitation experiment including high frequency (HF; every 2 weeks) vs. low frequency (LF; every 4 weeks) applications of low (5 mm) and high (7.5 mm) pulse sizes. Values represent the mean, with standard error bars. For the significant main effects or interactions (Table 2), a post hoc Tukey HSD test was used to determine significant pairwise comparisons, where treatments with the same letter do not significantly differ from each other. For total abundance (a) and richness (b), plant type was the only significant factor at the end of the experiment, whereas for evenness (c) there was a significant effect of precipitation frequency, and for Shannon index (d) there was a significant interaction of plant type with precipitation amount and frequency.

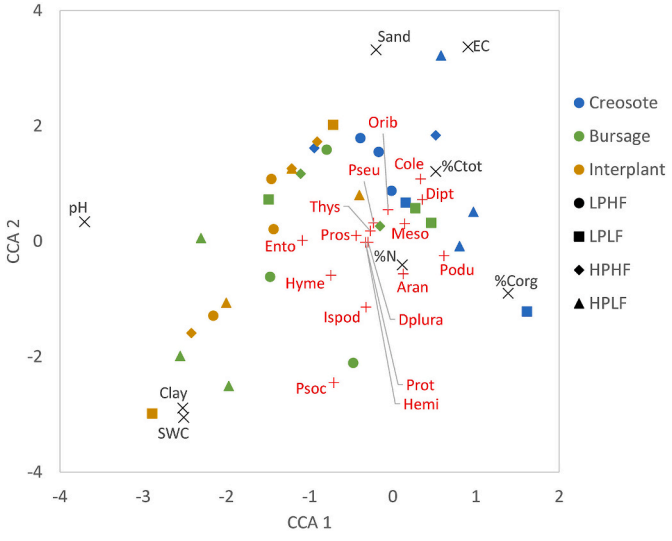

Fig. 3. Canonical correspondence analysis (CCA) of the soil arthropod community found in soil beneath three plant cover types at the end of the experimental manipulation of precipitation frequency (low and high frequency as LF and HF, respectively) and amount (low and high pulse size as LP and HP, respectively), as influenced by soil physicochemical properties. Black × marks denote soil properties, and red + marks denote arthropod taxa whose abbreviations are listed in Table 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Arthropod taxa abundance in soil (#/kg dry soil) from beneath creosote (*Larrea tridentata)*, bursage (*Ambrosia deltoidea*), and interplant spaces in September, after experimental precipitation application over monsoon season. Values are means ± SE. For the common taxa with higher abundances (i.e., not zero-inflated), an ANCOVA was used to determine significant differences among plant cover types. Plant cover types with the same letter do not significantly differ from each other in a pairwise Tukey HSD test. Metrics without letters did not significantly differ according to plant cover. The abbreviation for each taxa used in the ordination plots is included in parentheses.

	Creosote	Bursage	Interplant
Oribatid mites (Orib)	34.07 ± 20.08^{a}	6.63 ± 2.14^{b}	2.74 ± 1.27^{c}
Prostigmatid mites (Pros)	16.44 ± 8.30	8.87 ± 2.47	3.76 ± 1.00
Mesostigmatid mites (Meso)	1.54 ± 1.22	0.34 ± 0.23	0
Poduromorpha (Podu)	25.62 ± 13.03^{a}	10.72 ± 4.92^{a}	0.17 ± 0.17^{b}
Entomobryomorpha (Ento)	0	0.17 ± 0.17	0.34 ± 0.23
Diptera larvae (Dipt)	1.54 ± 0.57^{a}	0.51 ± 0.51^{b}	0.17 ± 0.17^{b}
Coleoptera larvae (Cole)	0.51 ± 0.27	0	0
Thysanoptera (Thys)	0.17 ± 0.17^{a}	2.21 ± 1.17^{b}	0.17 ± 0.17^{a}
Hymenoptera (Hyme)	2.39 ± 1.38 ^{ab}	7.86 ± 2.41^{a}	1.72 ± 0.66^{b}
Pseudoscorpion (Pseu)	0.51 ± 0.37	0.17 ± 0.17	0
Isopoda (Ispod)	0.17 ± 0.17	0.34 ± 0.23	0
Hemiptera (Hemi)	0	0.17 ± 0.17	0
Psocoptera (Psoc)	0	0.52 ± 0.52	0
Araneae (Aran)	0	0.17 ± 0.17	0.17 ± 0.17
Diplura (Dplur)	0.34 ± 0.23	0	0.17 ± 0.17
Protura (Prot)	0	0.17 ± 0.17	0

This likely reflects the different functional characteristics of these two species: Creosote is a deep-rooted, woody evergreen shrub that remains active during Sonoran Desert summers, while bursage is a smaller, drought-deciduous shrub that is largely dormant during the monsoon season. Thus, creosote provides a more reliable microhabitat throughout the monsoon season than bursage, which was leafless and not actively transporting much water during the experiment. The predominant influence of plant type suggests that any alteration in plant community composition resulting from altered precipitation could exert an indirect influence on soil community composition, more so than the direct influence of precipitation itself, as has been noted elsewhere (Kwok et al., 2016; Fischer et al., 2022). For example, decreased creosote or bursage cover with climate change (Munson et al., 2012) and an associated increase in interplant spaces could reduce soil diversity and food web complexity.

Though the altered precipitation treatments did not influence arthropod abundance or richness, they did have a statistically significant influence on Shannon diversity and evenness. Reduced frequency of precipitation (regardless of amount) decreased evenness, though the taxa responsible for the reduced evenness differed by vegetation type. Ants became more dominant with less frequent precipitation in the more exposed soils beneath the leafless bursage and interplant spaces, but interestingly the soft-bodied Poduromorpha springtails became more dominant beneath creosotes. Isotopic signatures suggest that the Poduromorpha likely feed on microbially-processed organic matter (Potapov et al., 2016), so an increase in their abundance could alter organic matter storage in the soils. Without the relatively sheltered microclimate beneath creosotes, it is the more drought and heat tolerant ants that dominate under reduced frequency of precipitation. Species of ants in the Sonoran Desert differ in their food sources, and their increased dominance could lead to increased harvesting of plant products, fungivory, and predation on other insects. This could impact other organisms competing for similar resources (e.g., rodents; Brown and Davidson, 1977), or the plant species whose seeds are preferred by these ants (Martyn et al., 2022). Both frequency and amount of precipitation influenced Shannon diversity, largely due to the response of interplant soils because vegetated soils were statistically equivalent across the treatments. This suggests that vegetation (regardless of type) buffered soil diversity from changes in precipitation amount and frequency, yielding a field response that is similar to what has also been observed by de Vries et al. (2012) in a greenhouse experiment using temperate grass species.

Further, we observed that the significant difference between vegetated and interplant soils under the typical precipitation regime (represented as LPHF) was exacerbated when soils received these pulses less frequently (LPLF) with therefore the least amount of water, but also increased precipitation pulse sizes at average frequency (HPHF) with therefore the greatest amount of water. The treatment reflecting the projected future precipitation regime (larger pulses less frequently, represented in the HPLF treatment) is the only precipitation treatment where interplant soils had equivalent diversity to the vegetated soils. Therefore, the beneficial influence of vegetation on soil arthropod diversity may not be equally important under all scenarios of altered precipitation.

The fact that soil arthropod abundance was resistant to altered precipitation may reflect the limitations of the soil food web. Blankinship et al. (2011) found in their meta-analysis that soil fauna were more sensitive to decreased precipitation in forested ecosystems than non-forested ecosystems, possibly due to greater C-limitation in the non-forested ecosystems. However, within our study, the vegetated soils with greater soil C were less sensitive to altered precipitation than the non-vegetated interplant soils, so clearly other driving factors are needed to explain the sensitivity to altered precipitation. However, no single soil physicochemical parameter measured in our study was significantly altered by precipitation treatment, so it is likely an impact of microclimate or a combination of factors that is important. Notably, only one of the precipitation studies included in the meta-analysis came from a desert ecosystem, and that study focused on microfauna, not meso- or macrofauna that were measured in the present study. Thus, the extent to which our observations are true in desert ecosystems worldwide, and the mechanism responsible, warrants further exploration. Further, this short-term study focused on only one discrete monsoon season, which does not allow us to capture the full impacts that may result from dispersal and reproduction potential of these organisms. Thus, the long-term impacts of sustained alterations in precipitation may differ (e.g., Holmstrup et al., 2013).

CRediT authorship contribution statement

Becky A. Ball: Designed the study, assisted with the field work and data collection, conducted the data analysis, and drafted the manuscript. **Kelly Bergin:** Led the field work and conducted the data collection. **Amanda Morrison:** Conducted the data collection and assisted the data analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The datasets generated during the current study are publicly available on the EDI Data Portal

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2022.104873.

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