

FINAL REPORT

Digging up Boulder's biodiversity: Buried responses to climate and land management

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Background

One of the most pressing tasks of the Anthropocene is anticipating and mitigating changes in biodiversity resulting from human influence. Much of this biodiversity has an intrinsic value – a remarkable display of form and function whose adaptation to local ecosystems is impressive and informative. However, diverse organismal groups often also play a key role in the sustained functioning of ecosystems whose services we depend on. Microarthropods are a critical taxonomic group whose abundance and diversity may not be appreciated with the naked eye, but can amaze under a microscope and drive the functioning of soils and ecosystems (Fig. 1). In this project, we took advantage of an experimental study system in Boulder’s xeric tallgrass prairie to ask: How abundant and diverse are microarthropods in Boulder’s unique grasslands, and are they likely to be impacted by anticipated climatic shifts and land management choices?

In soils, microarthropods mainly consist of springtails (subclass Collembola) and mites (subclass Acari) ranging in size from 0.1 – 2.0 mm – slightly larger than the nematodes and microbes that they commonly consume, but smaller than the macroarthropods (ants, beetles, spiders, etc.) that prey upon them (Coleman and Wall 2015). As their relative size suggests, they are a critical link in soil food webs, supporting the flow of energy through multiple trophic levels. Microarthropods have long been known to speed up litter decomposition and carbon/nutrient cycling (e.g., Gonzalez et al. 2003, Nielsen et al. 2011), as they indirectly disperse microbes and directly feed upon fungi, freeing up nutrients that further stimulate microbial activity (Lussenhop 1992). However, their influence extends beyond the soil food web. Microarthropods are active in root zones, potentially feeding upon beneficial fungi (Moore 1988). Recent studies demonstrate that they can alter the interactions between plants and soils (Kutakova et al. 2018) and ultimately influence plant productivity (Soong et al. 2016). The clear linkage of microarthropods to larger-scale ecosystem function has led to the group being explored as a key bioindicators of soil quality and properties (George et al. 2017).

Though the functional importance of these microscopic critters can be high, systems vary greatly in the diversity and abundance of microarthropods that they support. Boulder’s xeric tallgrass prairies are a unique ecosystem, supported by just enough rainfall, soil water holding capacity, and lack of agricultural development to support a diversity of plant species found from the intermountain west, shortgrass steppe, and tallgrass prairies. Reports funded by the city and county document the amazing diversity of birds, bats, reptiles, insects, and other wildlife supported by these habitats. However, our understanding of diversity in plant and wildlife communities is not matched in local soil biota. Global studies suggest that grasslands may support lower levels of microarthropod abundance and diversity than forested systems, though these metrics are ultimately tied to amounts of organic matter and soil carbon, and estimates vary (Crossley et al. 1975, Wu et al. 2011). For example, studies from tallgrass prairies in Kansas, Wisconsin, and Oklahoma suggest that grasslands could support densities ranging from 10,000 to over 70,000 individuals per m² (top 5cm of soil), and richness ranging from 28 to 81 taxonomic groups (Stepanich 1975, Lussenhop 1981, Seastedt 1984). In systems on the low end of diversity, shifts in the microarthropod community could alter ecosystem function (e.g., carbon cycling; Nielsen et al. 2011), making it critical to understand where Boulder’s grasslands fall on this spectrum.

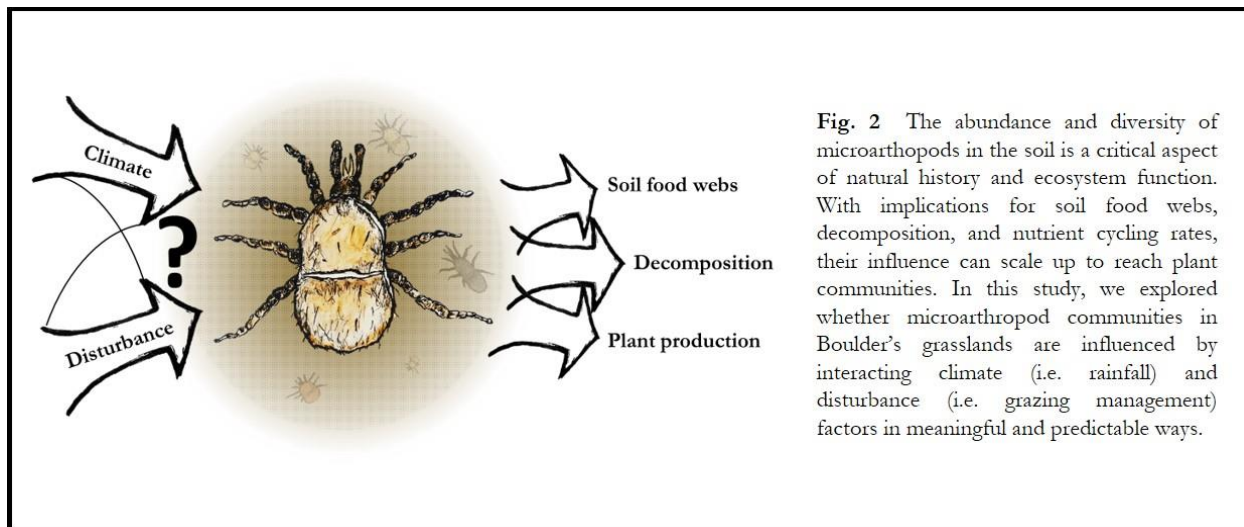


Fig. 1 Diversity of microarthropods found in Boulder’s soils. From top to bottom: cohort Astigmata, subclass Collembola, order Oribatida, order Mesostigmata, suborder Prostigmata. (Credit: J.Larson)

Although it is useful to quantify baseline microarthropod metrics in a system, understanding their temporal dynamics is of equal relevance to conservation and land management. Many types of environmental variability have been shown to affect microarthropod communities, and these responses could scale up to impact soil nutrient dynamics, plant communities, and/or other trophic levels. For example, in both alpine systems and desert grasslands, dry conditions lead to losses in microarthropod abundance and/or activity (Olear and Seastedt 1994, Whitford and Steinberger 2012, but see O'Lear and Blair 1999). Physical disturbances that affect organic matter mixing into the soil could also influence microarthropod communities. In a Wisconsin prairie, Lussenhop (1981) found that physical soil disturbance (via raking) increased microarthropod densities, and accordingly, bacterial densities and decomposition rates. However, benefits could be mediated by other costs of disturbance; in Pawnee National Grassland, only light grazing (not moderate or heavy) was associated with higher microarthropod abundances (Crossley et al. 1975). In contrast, Whitford and Steinberger (2012) found few effects of grazing in a desert grassland, where drought was the dominant driver. Although the vast majority of Boulder's grasslands are exposed to frequent grazing, the impacts of this management practice on local soil biota – especially in the context of anticipated shifts towards drier soils – is virtually unexplored.

Given the potential importance of microarthropod communities for our local ecosystems, we identified two major objectives (Fig. 2).

- 1) Qualitative: Document the abundance and diversity of soil microarthropods in Boulder's unique xeric tallgrass prairie, including specimen photographs.
- 2) Quantitative: Assess short-term responses of soil microarthropods to rainfall (extreme dry and wet scenarios) and land management (grazing impacts). *Hypothesis*: Microarthropod abundance and diversity decline under dry conditions. Grazing may support microarthropods (especially in fall, via higher soil-litter mixing), but only in favorable, wet conditions.



Methods

Study site & design. The study site was established in May 2018 in a xeric tallgrass prairie site owned by City of Boulder Open Space and Mountain Parks (OSMP) (Fig. 3). We constructed a 40m x 160m fenced grazing enclosure separated into six blocks to impose three grazing treatments (2 each): spring grazing, fall grazing, no grazing. The first fall grazing treatment was imposed from Oct-Dec 2018, but the first spring graze did not begin until June 2019, just after the sampling date for this study. We therefore reduce the grazing treatment to fall graze (2 blocks) or no graze (4 blocks)

for the current assessment. Within each grazing block, we established 12 plots (2.3m x 3m) assigned randomly to one of three watering treatments: ambient rainfall, dry (66% reduction by passive rainfall shelter), and wet (66% surplus by adding collected water). This resulted in 8 replicate plots per treatment combination (72 plots total).

In half the plots, we set up permanent sampling locations to collect soil moisture measurements every couple weeks throughout the rainfall manipulation (data included in this report are from the day of mite sampling). To do this, we used a handheld TDR soil moisture sensor calibrated to be used with two 12cm stainless steel probes (Campbell Hydrosense II). To collect repeated samples in the field, we hammered two permanent stainless steel nails of a similar size and at a similar distance into the soil in each sampled plot; by removing the manufactured probes and contacting the nails instead, we were able to capture relative changes in soil moisture to a depth of 12cm at the same locations over time. We also include a metric of vegetative cover for each plot, which was estimated visually as total percent aerial cover of live plant material in a 0.5m² subplot in the year of sampling.

Microarthropod sampling. We collected soil samples on June 4th 2019. This sampling date was selected to be late enough that water treatments had time to be effective (they are imposed annually from late April to early September), but early enough to occur within the wettest part of the year, prior to late summer heat waves and rainfall reductions which drastically reduce surficial mite populations. Prior to sampling, the most recent rainfall was on June 1st, where it rained 1.6 inches at the field site. Unfortunately, because the spring grazing period did not begin until mid-June, we were not confident in resampling mite populations after the treatment went into effect, but consider the immediate impacts of grazing on mite populations to remain an important next direction. To assess the microarthropod community, we collected one soil sample per plot (approx. 5cm diam x 5cm deep; O'Lear and Blair 1999) and kept samples cool, dark, and moist until processing in the lab within the same day. Because the soils are rocky (leading to variable soil collection volumes), we processed a standard volume of soil from each sample.

To extract microarthropods from soil samples, we used a modified Tullgren-funnel extraction method, which creates a heat/humidity gradient that forces live microarthropods to leave soil samples (following Seastedt and Crossley 1978) (Fig. 4). For each of the 72 collected soil samples, the soil sample was homogenized by breaking up the soil and removing rocks and then gently packed into 100ml cylinders created from PVC pipe. The cores were then placed in a heat

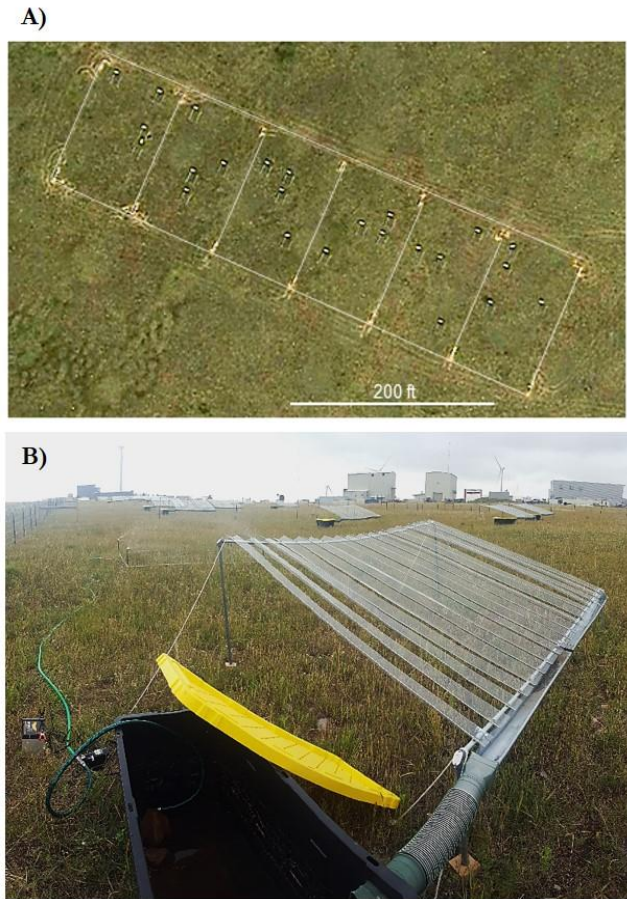


Fig. 3 A) The study site is a xeric tallgrass grass prairie in Boulder, CO. Within the larger study site, we established a grazing enclosure in 2018 with six blocks assigned to either fall, spring, or no grazing. B) Within each block, established plots are assigned to one of three rainfall treatments. Extreme dry plots are covered by passive rainfall shelters (foreground), while sprinklers add captured water to extreme wet plots (background); remaining plots are exposed to ambient rainfall.

gradient for 7 days where the temperature and light were gradually increased 3 times in order to slowly force the mites out of the soil samples and into a solution of 50% ethanol for preservation (Fig. 5). By the end of the extraction period, temperatures in the airspace above soil cores reached approx. 60°C (Fig. 5), while soil temperatures reached $47.3 \pm 1.2^\circ\text{C}$ on average. After microarthropods were extracted, we examined each sample and counted the number of mites belonging to each of five key functional groups (see next section). Although these groups occur at different taxonomic levels, they are relevant because mites within these groups share important functional roles. We also digitally photographed unique specimens found in samples, which will be compiled into an Appendix and classified down to lower levels (orders, families, or genera where possible) as a compilation of the taxonomic diversity found at the site.



Fig. 4 (left) We built a custom Tullgren-funnel extractor, which uses light and aluminum casings around soil cores to create a heat gradient that forces mites to leave the soil and collect in sample vials below.

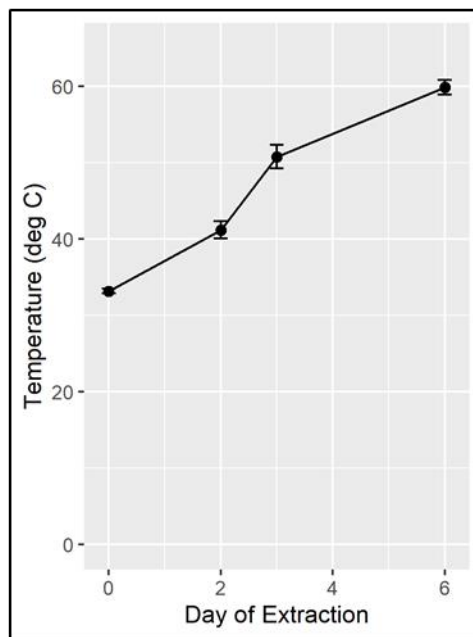


Fig. 5 (Right) Light and temperatures level were gradually increased over the 7 day extraction period. To avoid soil disturbance, we sampled the airspace between the light and soil sample from 6 randomly selected samples after each temperature increase. On the final day, we measured actual soil temperatures from 8 replicate samples.

Mite Classification. Extracted specimens were classified into five functional groups for analyses (Walter & Proctor 2013):

- 1) Subclass Collembola. Collembolans, also known as springtails, are found in soils of most grasslands and forests across the world, often in high abundance. Most species of Collembola are detritivores and play a key role in the turnover of soil nutrients, while only a few feed on live plant matter.
- 2) Cohort Astigmata (subclass Acari). Astigmatids tend to prefer moist, temperate soils high in organic matter, and feed as detritivores, grazing on fungi and algae. With shorter generation times and faster dispersal capabilities, appear to respond relatively quickly to disturbances they can be helpful as bioindicators of environmental change (Behan-Pelletier 1999)
- 3) Order Oribatida (subclass Acari). Oribatid mites are found globally in almost every soil type and system (forests, deserts, grasslands, and even tundra), but thrive in high-litter environments such as coniferous forests. Most Oribatids are detritivores and help recycle dead plant and fungi matter. Although they reproduce and move slower than Astigmatids, they also exhibit sensitivity to the environment and are used as bioindicators (Behan-Pelletier 1999).
- 4) Order Mesostigmata (subclass Acari). Mesostigmata is an order of Acari that is found globally but contains fewer species than the other orders discussed here. Because they are the primary predators of the microscopic soil mite world, they are found anywhere other

mites reside. Most are predators of other mites and their eggs, but some species feed of fungi, nematodes, or small insects.

- 5) Suborder Prostigmata (subclass Acari). Prostigmatids are diverse and found in many extreme environments, from Antarctic soils to burned prairies. Although many prostigmatids are specialized, diets are also diverse among the group, which includes predators, herbivores, and fungivores. Prostigmatids typically feed via piercing-sucking rather than particle digestion, which means they may have limited effects on decomposition and soil formation.

Analysis.

We used functional group and total mite densities across grazing treatments (control, fall) and water treatments (control, dry, wet) to describe soil mite communities and responses in Boulder's xeric tallgrass prairies. Prior to analyses, we examined data for outliers. Specifically, we identified and removed four samples that had high, outlying totals of any functional group (an order of magnitude, and more than two standard deviations above the functional group mean). These removed samples had estimated total densities ranging from 28,000 to 117,000 mites per m², while the maximum density found in retained samples was 22,000 mites per m².

Characterizing mite communities. To begin characterizing mite communities, we used means and standard errors of mite abundances within and across functional groups, as well as correlations between different functional groups. We tentatively explored other aspects of community structure – functional group richness, evenness, and Shannon-Weaver diversity – but a high number of low-density samples combined with the coarse level of current classification (samples varying from one to five functional groups represented) resulted in less meaningful metrics. However, to inform future sampling efforts, we created a species area curve at the functional group level, which shows the number sampled plots against the estimated number of functional groups expected to be found in a particular environment, and allows an estimation of sampling effort needed to fully capture diversity in the future. To create this curve, we subsetted the data to include only control plots with no grazing or rainfall manipulation (n=16), then used the 'specaccum' function from the R package 'vegan' to randomly subsample from the subsetted data (n=100 permutations per estimate).

We are currently compiling unique, documented specimens into an Appendix of digital photographs, where we will continue working with experts to identify mites to the lowest possible taxonomic levels (beyond functional groups reported here). These could provide a finer estimate of the extent of mite diversity that may be observed in Boulder's xeric grasslands.

Characterizing mite responses. To quantify treatment effects on microarthropod abundances, we use Poisson generalized linear mixed models (GLMMs), which are appropriate for testing treatment effects with count response data. We first modeled total mite densities as a function of manipulated treatments: rainfall, grazing, and their interaction (with block as a random effect). To assess whether the interaction term should be retained in the model, we used a log likelihood ratio test to compare the full model to a reduced one without the interaction term. We then repeated this approach within individual functional groups to explore whether they differed in their responses (Collembola excluded due to low frequencies).

To explore possible drivers underlying treatment effects on mite densities, we also ran separate models of total mite abundance as a function of soil moisture and vegetative cover - two continuous variables expected to be influenced by rainfall and grazing manipulations. Vegetative cover was collected for all plots (n=67), while soil moisture (i.e. volumetric water content sampled from the top 12cm of soil on the day of mite sampling) was only sampled in half of the plots (n=33). Because of this, we ran a separate model for each variable to utilize full statistical power with respect to vegetative cover, but compare these results to a combined model at the smaller sample size given some correlation between the two variables (r=0.41). All analyses were performed in R (R Core Team. 2018).

Results & Discussion

Soil mites in Boulder's xeric tallgrass prairie. Across all plots, we found densities ranging from 0 to 22,000 mites per m², with an average of 4677 ± 553 mites per m² (Fig 1). Averages among more typical samples were low compared to other studies documenting anywhere from 10,000 to 70,000 mites per m² in North American grasslands (Crossley 1975, Lussenhop 1981, Seastedt 1984). This could suggest that our effort underestimates true mite densities in the soil to some degree, potentially due to necessary sampling or extracting protocols (e.g., greater human handling of soils given our inability to take soil cores). However, there are also pathways by which our sampling could overestimate densities - because these soils can contain over 60% rock at the surface (Branson et al. 1965), the actual soil volume available for mite occupancy is likely lower on an area-basis than in our estimates. Still, these relatively low estimates are viable from a biological perspective, considering that studies in comparable grasslands occur further east, where higher levels of precipitation and plant biomass should lead to higher mite abundances than observed in these xeric, rocky grasslands. Even within the current study site, plots receiving supplemental rainfall had double the mite densities, on average (see below for details on treatment effects), demonstrating the critical impact of water.

Ultimately, these observations do suggest a need for greater spatiotemporal resolution in sampling. Although we sampled at the tail end of peak annual rainfall period, we cannot assess whether we captured mites at their peak abundances within the year, or whether sampling earlier would have also contributed to higher estimates, particularly given the observed impact of water over space. Our data also suggest a potential need for greater spatial resolution, depending on the scale of inference. Mite densities appear to be highly heterogeneous; within a given treatment, per-plot estimates ranged widely (e.g., from 0 to over 12,000 mites per m² within non-grazed, ambient rainfall plots). Although this range is suitable to assess patterns across the larger study area, no individual plot is likely void mites; obtaining high-accuracy estimates for smaller communities (e.g., individual plots) simply requires more sampling. The functional group-area curve suggests that cataloging full functional group diversity for a given environment at the site-level requires as many as 4 to 5 samples, with wide variation when only 1 sample is collected (Fig. 7). When we look more closely at the distribution of functional groups within samples, we found that Shannon-Weaver diversity indices largely tracked the number of functional groups represented in

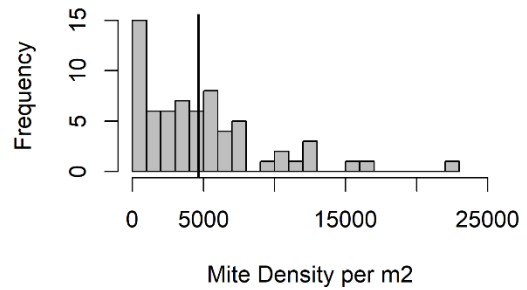


Fig. 6 Histogram of total soil mite densities found in samples across all experimental treatments (n=67). Vertical line indicates the mean (4677 mites per m²).

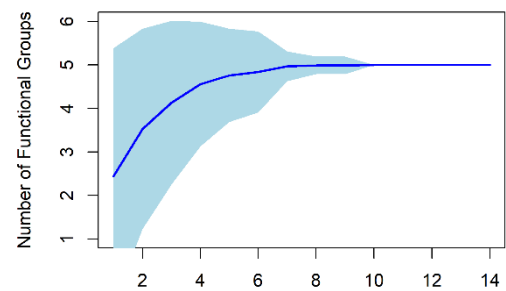
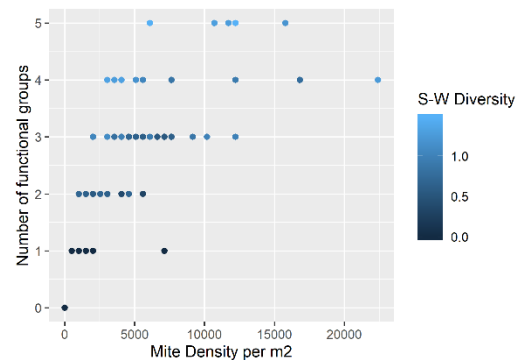


Fig. 7 (above) Accumulation curve showing the number of functional groups expected to be detecting per an increasing number of samples. Data were generated for ungrazed plots in ambient rainfall only.

Fig. 8 (below) The number of functional groups detected in a sample (out of 5 possible) increased as a function of mite density. Points are colored by another diversity metric – Shannon-Weaver Diversity – which follows the same trend, suggesting that diversity was limited by the number of mites found.



a sample, and that the latter tended to be a function of total mite abundance -- i.e. plots with more mites had higher functional group diversity (Fig 8). Because of the many low density samples (which must, by constraint, have low diversity), it is difficult to separate diversity from density, and we focus largely on densities for the remainder of the report. An expanded sampling effort would allow for a higher resolution of detection and more effective diversity estimates moving forward (see also Fig. 7). Given the potential ties between community diversity and ecosystem functioning, this remains an important aspect to assess.

Patterns across functional groups suggested a range in commonality, but some correlation in occurrence – particularly among the more common groups. Prostigmata was the most abundant mite group followed by Mesostigmata, Oribatida, Astigmata, and Collembola (springtails) (Fig. 9). Although the diverse Prostigmatid group is often very common in prairie grasslands, Oribatids are typically the most abundant (Crossley 1975, Lussenhop 1981, Seastedt 1984). However, relative abundances of the groups can change throughout the growing season, and other studies have shown typically deeper-occupying Prostigmatids being more abundant in mid-late spring – around the time that this study occurred – perhaps when soil moisture is higher (Crossley 1975). Because Oribatids are strictly detritivores, they may also be less prevalent at this particular site due to the lower plant cover in this windswept xeric tallgrass prairie relative to more mesic and productive prairies. Astigmatids and Collembolans are typically found lower abundances, as observed here, and may have been too infrequent to detect correlations with other groups. However, just as samples with higher densities tended to have higher richness, we generally saw positive correlations among the Prostigmata, Mesostigmata, and Oribatida, suggesting that common detritivorous and predatory mites generally varied in tandem.

Effects of grazing and rainfall. In addition to examining the effects of grazing and rainfall manipulations on soil mites, we also looked at effects of two potential underlying factors which could mediate mite responses to these treatments: soil moisture and vegetative cover. Specifically, we expected higher soil moisture and vegetative cover (a proxy for productivity) in the wet treatment

and lower values in the dry treatment, which should parallel expectations for treatment effects on mite densities. Interestingly, we found that drought induced a significant decrease in both cover ($t=-3.65$, $p<0.001$) and soil moisture ($t=-3.07$, $p=0.005$) relative to the control, but that the wet treatment did not significantly affect either factor (Fig. 10A & B). Although soil moisture is dynamic, and these data reflect conditions only on the day of sampling, we also did not observe any strong of an effect when averaging across May and early June soil moisture sampling days ($n=4$). We have documented significantly wetter soils in the days immediately after manipulated rain events (data not shown), but it appears that this effect is only briefly measurable at the surface. Given the more consistent and extreme effects of drought on both soil moisture and vegetative cover

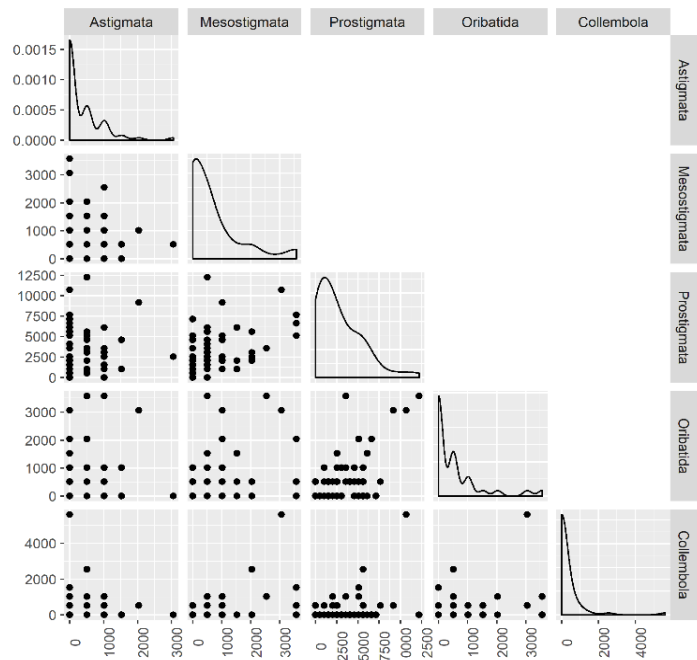


Fig. 9 (above) Distribution of density estimates for five functional groups (diagonal) and scatterplots of densities between pairs of functional groups (below the diagonal).

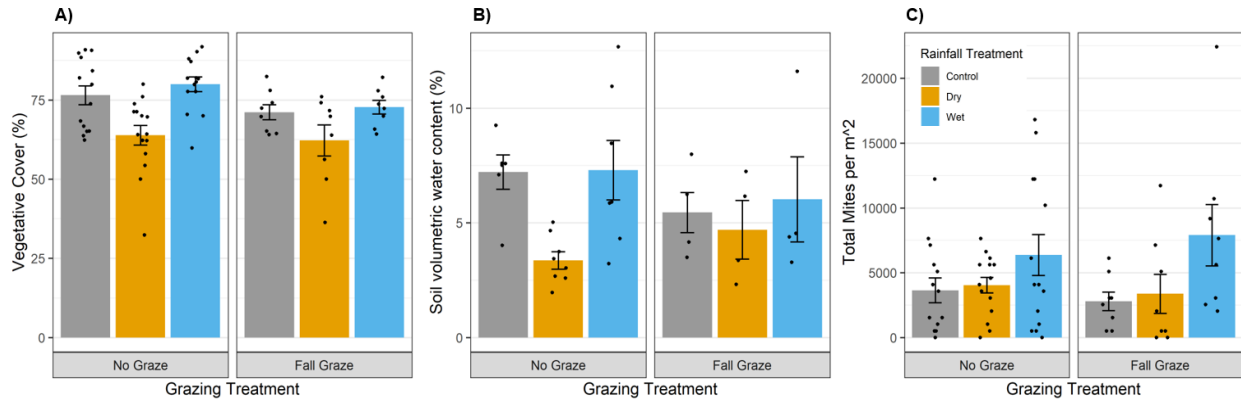


Fig. 10 A) Percent vegetative cover, B) soil moisture, and C) mite densities as a function of grazing and water treatments. Bars show means and std. errors, points are samples. Soil moisture differences should be interpreted as relative rather than absolute.

(which reflects a longer-term effect of the treatment), we might expect that drought would also elicit a stronger mite response.

As expected, soil mite densities did increase with both vegetative cover ($z=5.45$, $p<0.001$; Fig. 11A) and soil moisture ($z=3.87$, $p<0.001$; Fig. 11A); however, the two shared some correlation ($r=0.41$), and when included in a single model (with reduced sample size), soil moisture was the stronger driver. Contrary to expectations, we found a more substantial mite response to the wet treatment than the dry treatment (Fig. 10C). Rainfall and grazing treatments ultimately interacted to influence total mite densities (the model retaining an interaction term performed significantly better, $\chi^2 = 7.77$, $p = 0.02$): while densities tended to be higher under the wet treatment relative to the ambient control ($z=4.03$, $p<0.001$), the difference in densities between the control and wet treatment was larger under the fall graze scenario ($z=2.46$, $p=0.014$) (Fig. 10C).

The measurable increase in mites under water addition suggests that the treatment did have meaningful impacts on ecosystem processes that were not fully captured by soil moisture or vegetation indicators. We saw no greater response of indicators to the wet treatment when swapping them out for longer-term metrics (i.e. 3-wk averaged soil moisture [$n=4$ sampling dates]) or more direct proxies (i.e. plant biomass as a metric of plant production). Still, moisture and decomposing litter/organic matter (as a lower-level food resource) are two critical supporting factors for mite communities (evidenced also by observed positive relationships, Fig. 11). It is possible that while the water treatment does not result in higher soil moisture levels that are sustained at the surface (relative to ambient), that short-term bursts in

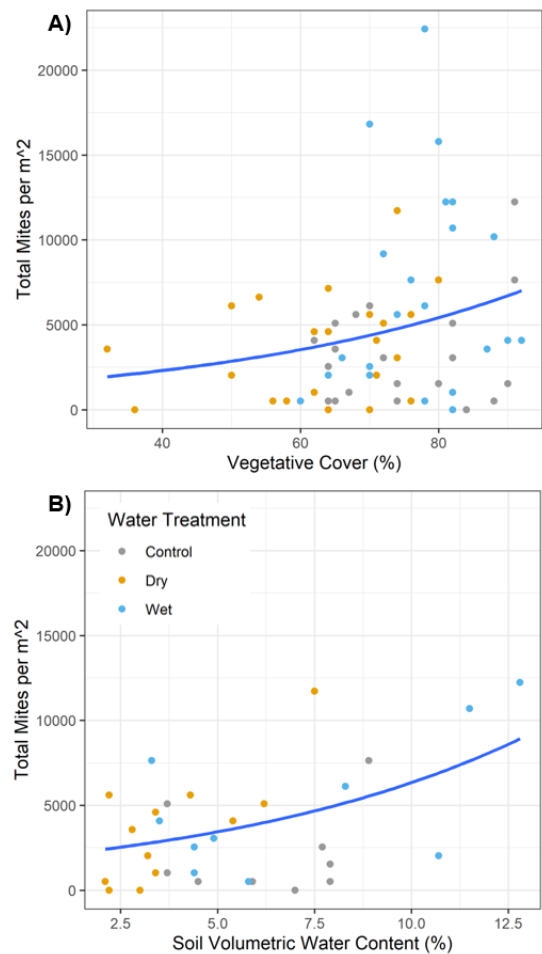


Fig. 11 Total mite densities as a function of A) percent vegetative cover and B) soil volumetric water content. Soil moisture was only measured in half of the plots (i.e. smaller sample size), and variation should be interpreted as relative changes rather than absolute.

soil moisture, along with wetter and cooler soils at depth, still attract and support higher mite numbers. There may also be a measurable increase in plant activity and organic matter belowground in response to water (e.g., greater root production, exudation, and turnover) that is not captured by vegetative cover or aboveground biomass. Because grazing has been shown to stimulate root activity in this way in more productive systems (in more mesic mixed-grass prairies, but less so in shortgrass steppe, Milchunas et al. 2008), this could explain an additive positive effect of the fall graze and water treatment relative to control conditions. Notably, most functional groups responded to water addition in some capacity, demonstrating its impact across the trophic web (Fig. 12).

The lack of mite reduction in the dry treatment – despite significant reductions in soil moisture and vegetative cover – may be related to the shape of these relationship between these factors and mite densities. In both cases, the data suggest only a gradual change in mite densities up to a certain threshold (approx. 70% cover, or 7.5% soil moisture, Fig. 11), beyond which counts were able to reach much higher levels. It may be that below these thresholds, mite densities are too low for further changes in abiotic properties to have substantial effects. Although grazing had fairly minimal effects on mite densities in this initial study, there could be more substantial effects over time if the timing, intensity, or frequency of grazing become substantial enough to influence soil moisture retention, vegetation, or belowground productivity. Effects of both drought and grazing were also minimal across functional groups (Fig. 12).

Conclusion. In this initial sampling effort, we documented several major microarthropod functional groups. Although densities were lower than expected and suggest a need for more extensive sampling efforts, we found measurable benefits of a high rainfall spring for mite

populations beyond what would be expected based on surficial soil moisture or aboveground productivity. Because mites were at such low densities, drought did not appear to further reduce mite densities (despite inducing lower cover and soil moisture levels), and the impact of a prior year fall graze was rainfall-dependent, but subtle. However, the nature of these uncovered relationships do suggest that drought and grazing effects could become stronger in more productive grasslands. Committing to further study of these groups over space and time, as well as their relationships to belowground ecosystem properties and processes (e.g., changing soil organic matter, nutrient cycling), will generate a better understanding of how belowground biota and function will respond to climate change in the context of land management choices.

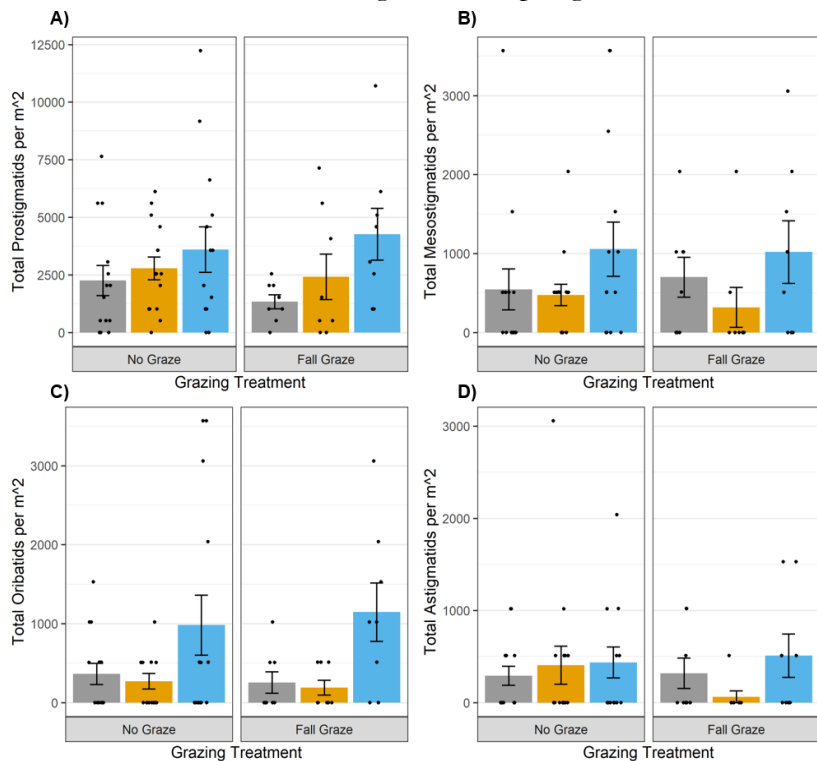


Fig. 12 Effects of grazing and rainfall and rainfall manipulations on functional group densities, including A) Prostigmatids (sig. interaction, higher wet response in fall graze, $z=2.21$, $p=0.027$), B) Mesostigmatids (sig. effect of wet treatment, $z=2.53$, $p=.011$), C) Oribatids (sig. effect of wet treatment, $z=5.07$, $p<0.001$), and D) Astigmatids (no sig differences). Springtails occurred in too few plots to assess treatment effects.

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