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Abiotic factors and plant biomass, not plant diversity, strongly shape grassland arthropods under drought conditions

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Abstract. Arthropod abundance and diversity often track plant biomass and diversity at the local scale. However, under altered precipitation regimes and anthropogenic disturbances, plant–arthropod relationships are expected to be increasingly controlled by abiotic, rather than biotic, factors. We used an experimental precipitation gradient combined with human management in a temperate mixed-grass prairie to examine (1) how two drivers, altered precipitation and biomass removal, can synergistically affect abiotic factors and plant communities and (2) how these effects can cascade upward, impacting the arthropod food web. Both drought and hay harvest increased soil surface temperature, and drought decreased soil moisture. Arthropod abundance decreased with low soil moisture and, contrary to our predictions, decreased with increased plant biomass. Arthropod diversity increased with soil moisture, decreased with high surface temperatures, and tracked arthropod abundance but was unaffected by plant diversity or quality. Our experiment demonstrates that arthropod abundance is directly constrained by abiotic factors and plant biomass, in turn constraining local arthropod diversity. If robust, this result suggests climate change in the southern Great Plains may directly reduce arthropod diversity.

Key words: *climate change; drought; hay harvest; invertebrate; prairie; precipitation.*

Introduction

Experimentally increased plant biomass or diversity often increase arthropod abundance and diversity (Siemann 1998, Haddad et al. 2001, Crutsinger et al. 2006, Haddad et al. 2009, Burkle et al. 2013). In contrast, decreasing plant richness can decrease arthropod diversity (Haddad et al. 2000). Global climate change—including increased temperature and atmospheric CO_2, and altered precipitation patterns (de Sassi et al. 2012, Jamieson et al. 2012, Lee et al. 2014)—may also reshape plant–arthropod relationships. This is especially true in grasslands, an ecosystem covering ~37% of Earth's surface that provides many ecosystem services from livestock forage to carbon sequestration (White et al. 2000). Although many grassland organisms are accustomed to limited (and variable) precipitation (Knapp et al. 2002), climate models predict increased precipitation variability in grasslands (Maurer et al. 2020). Reduced precipitation decreases plant biomass (Heisler-White et al. 2009), but increased precipitation variability and soil water content can promote plant diversity (Knapp et al. 2002). Global climate change is co-occurring with anthropogenic disturbances such as hay harvesting, with expected repercussions for both primary producers and arthropods (Xu et al. 2013, Shi et al. 2016). Arthropods comprise the majority of animal biodiversity and provide critical ecosystem services, thus understanding their responses to these multiple stressors is an important step towards maintaining healthy ecosystems (Tscharntke and Greiler 1995, Whiles and Charlton 2006). Here we explore the synergy of changing precipitation and hay removal on the abundance and diversity of grassland arthropods, using a novel experiment to test three, non-exclusive hypotheses.

Drought can affect arthropod communities via its effects on two master regulators: water and temperature.

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Drought can indirectly affect arthropods by reducing plant turgor pressure and hence foliar water availability (Huberty and Denno 2004). Lower soil moisture can directly reduce both arthropod abundance and diversity by increasing desiccation risk (Harrison et al. 2012). Likewise, hay removal can expose soil to more insolation, thus increasing surface temperatures and filtering for heat-tolerant species (de Sassi et al. 2012). Combined, drought and hay harvest may result in higher surface temperatures and less moisture than found with drought or hay harvest alone, filtering arthropods and reducing both arthropod abundance and diversity. The abiotic constraint hypothesis (H1) predicts that decreased moisture availability and higher temperatures select for more stress-tolerant arthropods (Greenslade 1983, Chase 1996).

Drought can also reduce primary production (Heisler-White et al. 2009) and alter plant nutrient quality, indirectly affecting arthropod communities. In grasslands, reduced precipitation can increase the productivity of drought-resistant C_4 grasses at the expense of C_3 forbs (Heisler-White et al. 2009) leading to ecosystem-level decreases in plant quality via higher lignin and lower nitrogen content (Caswell et al. 1973, Tscharntke and Greiler 1995). Drought can thus directly reduce the amount of food for herbivores to eat and digestibility at the ecosystem level. However, drought can also increase the concentration of nutrients in individual plants experiencing water stress (Franzke and Reinhold 2011, Grant et al. 2014) while decreasing plant defenses. This may result in increased chewing herbivory on drought-stressed plants (Mattson and Haack 1987, Gutbrodt et al. 2011, Jamieson et al. 2012). Hay removal, by definition, reduces the amount of food for plant consumers. The more individuals hypothesis (H2) predicts that decreases in quantity and quality of forage should also reduce insect abundance, and through doing so, reduce insect diversity (Srivastava and Lawton 1998, Kaspari et al. 2003). Decreases in plant quality may also erode the common positive correlation between plant biomass and arthropod abundance (Siemann 1998, Haddad et al. 2000).

Finally, drought can affect arthropod diversity via changes to their host-plant diversity. The resource heterogeneity hypothesis (H3) predicts increasing plant diversity should directly increase arthropod diversity (Hutchinson 1959, Southwood et al. 1979, Borer et al. 2012). Drought can reduce plant diversity by favoring drought-resistant plant species, filtering out the arthropod species for which host plants become locally extinct (Haddad et al. 2001, Haddad et al. 2009, Borer et al. 2012). In contrast, management such as hay harvest may result in increased plant diversity because it results in more light and space for growth, increasing arthropod diversity despite water stress (Collins et al. 1998).

Here we report results from a novel multiyear factorial field experiment where we manipulated precipitation with rainfall shelters and mimicked management through yearly clipping (hereafter hay harvest). We test the preceding three hypotheses (see Table 1 and Fig. 1A) detailing how direct and indirect effects of drought and hay harvest work synergistically to affect the plant and arthropod assemblages in a mixed-grass prairie with implications for future climatic scenarios.

Methods

Study site

We studied the arthropod community in 2017 and 2018 from June through August at Kessler Atmospheric and Ecological Field Station (KAEFS), a mixed-grass prairie in central Oklahoma, USA (34.59° N, 97.31° W), last farmed >45 yr ago. KAEFS has Nash-Lucien complex soil (Xu et al. 2013) and is dominated by *Schizachyrium scoparium*, *Sorghastrum nutans*, *Dichanthelium oligosanthes*, *Ambrosia psilostachya*, and *Solidago nemoralis*. Mean annual rainfall is 914 mm and average temperature in July is 27.7°C (Appendix S1: Fig. S1).

Experimental design

To determine the response of arthropods to a precipitation gradient and human management, we used rain shelters to establish a gradient of precipitation and vegetation clipping to mimic hay harvesting. This experimental study is part of Drought-Net, a coordinated global network examining terrestrial ecosystem sensitivity to drought. We used a randomized block split-plot design with seven precipitation treatments (five water exclusion levels [−20%, −40%, −60%, −80%, and −100%], water addition [+50%], and control [0% change in precipitation]) replicated three times for a total of 21, 2 × 2 m plots. Rain-out shelters were established in Spring 2016 and reduced rain but not sunlight. We combined precipitation treatments with two clipping treatments (clipped or unclipped subplot) to mimic hay harvest, initiated in

Table 1. Proposed hypotheses regulating arthropod abundance and diversity in grasslands.

No.	Hypothesis name	Definition
H1	Abiotic constraint hypothesis	Abiotic factors (moisture availability and temperature) select for a subset of stress-tolerant/intolerant arthropods[1,2]
H2	More individuals hypothesis	Increasing primary producer biomass increases consumer abundance, which in turn increases consumer diversity[3,4]
H3	Resource heterogeneity hypothesis	Increasing plant diversity should increase arthropod diversity because of increased niches and diet variety[5,6,7]

Notes: References are given by the numbers in the table: [1]Greenslade (1983), [2]Chase (1996), [3]Srivastava and Lawton (1998), [4]Kaspari et al. (2003), [5]Hutchinson (1959), [6]Southwood et al. (1979), and [7]Borer et al. (2012).

September 2016. Clipping occurred in the same subplot each fall, with biomass clipped down to 10 cm and removed (see Appendix S1: Fig. S2 for experimental layout).

Microclimate sampling

To determine how our manipulations affected abiotic factors, we measured soil moisture and surface temperature. Soil probes (Decagon 5TM, ICT International) were installed at a depth of 10 cm in each clipped and unclipped subplot and continuously measured percent volumetric water content (VWC) from May 2017 to September 2018. For each arthropod sampling event (n = 6), we averaged the VWC from the 2 weeks prior to sampling to determine how the precipitation and clipping treatments affected soil moisture. We used temperature loggers (iButton®, Maxim Integrated) to measure soil surface temperature continuously from May 2017 to September 2018 and averaged the data to obtain monthly mean surface temperature for each subplot. We excluded August 2017 data because rodents disrupted the temperature loggers.

Plant sampling

To determine the effects of a precipitation gradient and land management on plant communities, we measured plant foliar cover and Shannon's diversity each year in May and August using a modified Braun-Blanquet scale (Braun-Blanquet 1932, Castillioni et al., *in review*). We estimated aboveground net primary productivity (ANPP) at the end of each growing season (September) by clipping plants, sorting to functional groups, drying, and weighing them. Plant %N was measured in 2018 using combustion analysis at the OSU Soil, Water, and Forage Lab (http://soiltesting.okstate.edu/). We calculated average plant quality (%N) per plot for each functional group weighted by group proportion present using the formula: plant quality = ((%N C_3 plants * % C_3 plants/plot) + (%N C_4 plants * % C_4 plants/plot))/2). To see if water stress affected arthropod herbivory, we measured plant herbivory on four plant species per plot (*S. nutans*, *S. scoparium*, *Chamaecrista fasciculata*, and *A. psilotachya*) in August 2018 following the Nutrient Network herbivory protocol. See Appendix S2 for detailed plant sampling protocols.

Arthropod sampling

To measure the arthropod response to our manipulations, we sampled arthropods once per month from June–August 2017 and 2018 on clear days preceded by at least two dry days (n = 6; Appendix S1: Table S1). We waited at least 1 d between sampling clipped and unclipped subplots to minimize disturbance effects. To sample arthropods, we used an inverted leaf-blower (Husqvarna 125BVX) for 50 s per plot. Samples were put on ice in the field and kept frozen until sorting. We counted and identified all arthropods to family or major taxonomic group and recorded the number of unique species or morphospecies per taxonomic group (Appendix S3). We calculated arthropod abundance and diversity for each plot and month (taxon-level; Shannon's H) except August 2017, when did not have corresponding surface temperature data.

Statistical analysis

All statistics were performed using R version 3.6.1 (R Development Core Team 2016). We used a piecewise structural equation model (SEM) (1) to examine which hypotheses regulate arthropod abundance and diversity under drought and hay harvest conditions and (2) to examine the direct and indirect effects of a precipitation gradient and hay harvest on arthropod abundance and diversity. In comparison with traditional SEM, piecewise SEMs are less restricted by the number of links per sample size, and Fisher's C is used as the goodness-of-fit statistic (Shipley 2013, Lefcheck 2016). Analogous to traditional SEM, a nonsignificant P value indicates a well-fit model. In our *a priori* model (Fig. 1A), we predicted drought and hay harvest would indirectly affect arthropod abundance and diversity through their effects on surface temperature, soil moisture, ANPP, plant quality, and plant diversity. We kept precipitation treatment as a numerical variable and log-transformed arthropod abundance and ANPP to meet normality assumptions. In order to resolve pseudo-replication due to repeated sampling, we included plot as a random variable in all model regressions. We used a single piecewise SEM model based on our a priori model and did not remove nonsignificant links. Piecewise SEMs were conducted using the piecewise SEM (Lefcheck 2016) and nlme (Pinheiro et al. 2013) packages in R.

Results

Abiotic responses to drought and hay harvest

Both drought and hay harvest treatments changed the abiotic environment. Soil surface temperature increased linearly with drought and was about 2.5°C higher on 100% drought plots relative to control plots. Hay harvest led to an average temperature increase of 1.1°C (Fig. 1B; Appendix S1: Fig. S3). The drought gradient linearly decreased soil moisture. Moisture on 100% drought plots was 14% lower than control plots, and soil moisture on water addition treatments was 7% higher (Fig. 1B; Appendix S1: Fig. S4).

Plant responses to drought and hay harvest

Total ANPP on the 100% drought plots was 65% lower than controls. Biomass of C_4 plants decreased by 59% with drought (Appendix S1: Fig. S5). Surprisingly, biomass of C_3 plants was highest on three disparate

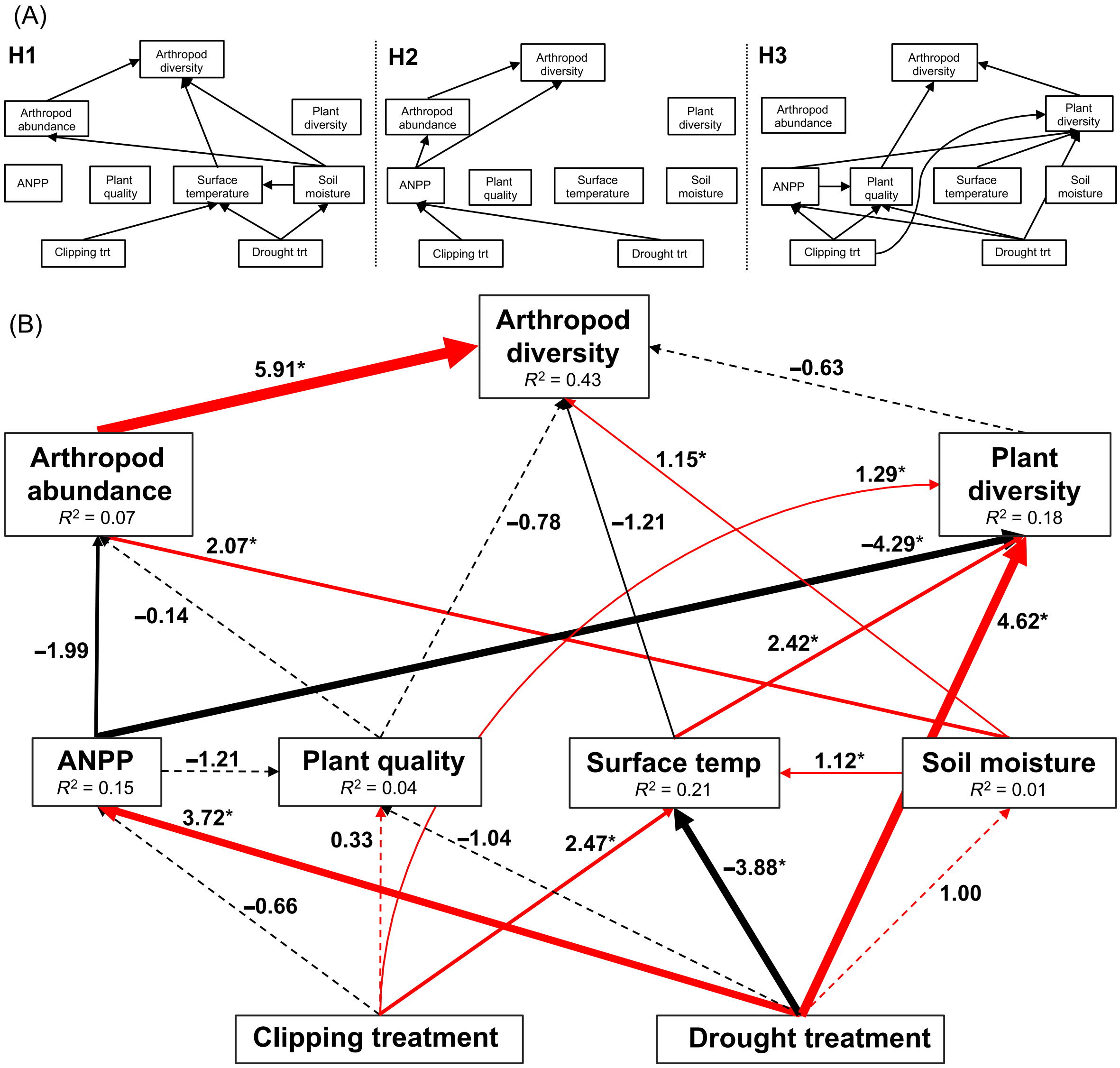

Fig. 1. Piecewise structural equation model (SEM) depicting the direct and indirect effects of drought and clipping on arthropod abundance and diversity. (A) Conceptual a priori models for each of the three hypotheses examined within our piecewise SEM (see Table 1 for hypotheses descriptions). (B) Piecewise SEM based on our a priori model. The piecewise SEM fit our data well: Fisher's C = 31.58, AIC_c = 141.84, P = 0.207. Partial R^2 values are under each predicted variable, and standardized path estimates are provided next to each path with line thickness scaled based on the magnitude of the estimate (see Methods for variable descriptions). Red and black arrows indicate positive and negative relationships, respectively. Dashed arrows represent nonsignificant paths (P > 0.05). Asterisks (*) indicate significance (P < 0.05). Model estimates, standard errors, and P values are provided in Appendix S1: Table S2.

treatments: 100% drought, control, and water addition plots (Appendix S1: Fig. S5). Hay harvest had no significant effect on ANPP, declining on average by 10% (Fig. 1B; Appendix S1: Fig. S5). Neither drought intensity nor hay harvest significantly affected plant %N (Fig. 1B; Appendix S1: Fig. S6).

We recorded 28 plant species in 2017 and 29 plant species in 2018. Plant diversity was 8% lower on 100% drought plots relative to control. Water addition increased plant diversity by 7.6% relative to control plots (Fig. 1B; Appendix S1: Fig. S7). Hay harvest increased plant diversity by 5.7% (Fig. 1B; Appendix S1: Fig. S7).

Arthropod abundance

Arthropod abundance varied 100-fold among plots in both years. We collected 3,431 arthropods in 2017 (excluding 865 in August—see Methods) and 10,153 arthropods in 2018. In 2017, the number of arthropods varied from 1 to 96 per plot (mean ± SE; 28.9 ± 1.7); in 2018 the number varied from 3 to 335 (83.1 ± 5.5). Our a priori piecewise SEM had a good fit (Fisher's C = 31.58, Akaike's information criterion, corrected [AIC_c] = 141.84, P = 0.207) and accounted for between 7% (arthropod abundance) and 43% (arthropod diversity) of the variation in the arthropod community response (Fig. 1B; Appendix S1: Tables S2 and S3). The abiotic environment and plant biomass drove arthropod abundance. Consistent with the abiotic constraint hypothesis (H1), higher soil moisture increased arthropod abundance (Fig. 1B; Appendix S1: Fig. S8). Contrary to the more individuals hypothesis (H2), increased plant biomass reduced arthropod abundance (Fig. 1B; Appendix S1: Fig. S8).

Arthropod diversity

In both years, arthropod diversity (Shannon's H) varied threefold across plots. In 2017, arthropod diversity per plot varied from 0.4 to 1.7 (1.2 ± 0.02); in 2018 the diversity varied from 0.58 to 1.9 (1.4 ± 0.03). Arthropod diversity changed with abiotic drivers and arthropod abundance. First, consistent with the abiotic constraint hypothesis (H1), increasing soil moisture increased arthropod diversity while increasing surface temperatures reduced diversity (Fig. 1B; Appendix S1: Fig. S9). Second, consistent with the more individuals hypothesis (H2), arthropod diversity increased with arthropod abundance. Plots added one species on average for every 16 more individuals (Fig. 1B; Appendix S1: Fig. S10). Third, contrary to the resource heterogeneity hypothesis (H3) plant and arthropod diversity were uncorrelated and plant quality did not increase either arthropod abundance or diversity (Fig. 1B; Appendix S1: Figs. S6 and S10).

Discussion

Our experiment demonstrated that arthropod abundance responded strongly to changes in plant productivity and soil moisture caused by drought. Arthropod diversity at the 2 × 2 m grain tracked changes in arthropod abundance and increased with higher soil moisture but decreased with temperature. Surprisingly, arthropod diversity did not track plant diversity. As current climate change predictions for the Great Plains include increased frequency and duration of severe droughts, our experimental results suggest future declines in arthropod diversity.

Our results suggest precipitation amount regulates arthropod abundance and diversity while temperature regulates arthropod diversity. Both precipitation reduction and human management (hay harvest) increased ground-level light penetration and surface temperature, a result similar to other studies (Collins et al. 1998, Xu et al. 2013). Drought increased surface temperatures more than simulated haying. Higher surface temperatures reduced arthropod diversity, suggesting high temperatures may have filtered for species that could tolerate hot patches, while not reducing overall arthropod abundance (Barton and Schmitz 2009, de Sassi et al. 2012). Increasing soil moisture promoted both higher arthropod abundance and diversity. Because of the high desiccation risk with arthropods' high surface-to-volume ratio (Harrison et al. 2012), we would expect soil moisture to filter both the species present and their abundance. Arthropods can deal with reduced moisture by relocating, burrowing in the soil, or building shelters (Berridge 2012). At the spatial scale of our experiment, arthropods likely emigrated from or avoided low moisture plots, options not available at the larger spatial scale of continental droughts.

As predicted, we found that drought conditions decreased overall plant biomass. Contrary to other studies, we found lower abundance of all arthropod trophic guilds at higher levels of plant biomass (i.e., on plots with less water reduction; Lee et al. 2014, Torode et al. 2016). There may be several reasons for this unexpected relationship. First, on plots with less water reduction (−40% to +50%) we saw a higher proportion of C_4 warm-season grasses. C_4 grasses are less palatable to arthropods than C_3 plants (Caswell et al. 1973, Heisler-White et al. 2009), likely reducing both herbivore abundance and the abundance of predators tracking prey abundance on plots with slight water reduction (Appendix S1: Fig. S11). Second, water reduction can lower plant turgor pressure, increasing the difficulty of sucking arthropods to feed (Huberty and Denno 2004). However, we did not see a change in sucking damage with plant biomass (Appendix S1: Fig. S12). Third, drought can increase the concentration of nutrients in plants experiencing water stress while decreasing plant defenses, resulting in increased chewing herbivory on drought-stressed plants (Mattson and Haack 1987, Franzke and Reinhold 2011, Gutbrodt et al. 2011). In fact, we saw a decrease in chewing damage as ANPP increased (correlated with less soil moisture; Appendix S1: Fig. S12). However, we saw no significant change in plant quality with reduced precipitation, nor did plant quality significantly affect arthropod abundance or diversity. The specific mechanism driving the increase in arthropod abundance with reduced plant biomass remains unclear, but as drought and ANPP are negatively correlated it deserves further exploration.

Plant diversity, which varied twofold (1.3 to 2.7) across our 30 plots, was uncorrelated with arthropod diversity (Fig. 1B; Appendix S1: Fig. S10). This could be due to low overall plant diversity, as both reduced precipitation and plant biomass had strong negative effects on plant diversity (Fig. 1B). Alternatively, if the abundance of C_4 plants continues to increase at the expense of C_3 plants on plots with medium water reduction, we may see a larger decrease in plant diversity and a corresponding reduction in arthropod diversity. Additionally, other studies reporting a positive relationship between plant and arthropod diversity either experimentally increased plant diversity (Crutsinger et al. 2006, Haddad et al. 2009, Burkle et al. 2013, Welti et al. 2017) or ran their experiment over a longer period, that is, 10+ yr (Siemann 1998, Haddad et al. 2009). Although we had interannual variation in our response variables, we sampled our plots after 1–2 yr of treatment, a period perhaps too short to detect a substantial change in plant diversity, which experiences a slower turnover rate than arthropod diversity. Our hay harvesting treatment increased plant diversity because of higher ground surface light, but the comparative effect was not large. Our results demonstrate that under drought conditions, plant diversity may not be as important at constraining arthropod diversity as abiotic factors and arthropod abundance.

Conclusions and Future Directions

Experiments examining the response of arthropods to precipitation manipulation typically use only one or two levels of rainfall reduction or addition (e.g., Suttle et al. 2007, Lee et al. 2014, Griffith and Grinath 2018, Tamburini et al. 2018), or look at combinations of rainfall frequency (Suttle et al. 2007, Grant et al. 2014, Mariotte et al. 2016, Torode et al. 2016). Because climate projections are inexact, our experiment utilized a seven-level precipitation manipulation gradient in combination with hay harvest. This experimental design led to insights relevant to multiple possible future precipitation regimes. As our pulse experiment transitions into a press experiment over the next years, we will see if some of the strongest effects in our results (e.g., decreases in insect abundance with increases in plant biomass) are transitory. Although we documented no effect of drought or hay harvest on %N (our measure of plant quality), other nutrients such as P, K, or micronutrients could be changing with our treatments. A better understanding of the plant above- and belowground stoichiometry across treatments will further address shifts in the dynamics of plant–arthropod interactions under future climates. Here we show evidence for the importance of moisture and temperature in regulating community abundance and diversity among arthropods, an abundant taxon (Bar-On et al. 2018) in one of Earth's dominant ecosystems (White et al. 2000).

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3033/suppinfo