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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Ecto- and endoparasitic nematodes respond differently across sites to changes in precipitation

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Abstract

Plant parasitic nematodes are among the greatest consumers of primary production in terrestrial ecosystems. Their feeding strategies can be divided into endoparasites and ectoparasites that differ substantially, not only in their damage potential to host tissue and primary production, but also in their susceptibility to environmental changes. Climate change is predicted to increase variability of precipitation in many systems, yet the effects on belowground biodiversity and associated impacts on primary productivity remain poorly understood. To examine the impact of altered precipitation on endo- and ectoparasitic soil nematodes, we conducted a 2-year precipitation manipulation study across an arid, a semiarid, and a mesic grassland. Plant parasite feeding type abundance, functional guilds, and herbivory index in response to precipitation were evaluated. Responses of endo- and ectoparasites to increased precipitation varied by grassland type. There was little response of ectoparasites to increased precipitation although their population declined at the mesic site with increased precipitation. The abundance of endoparasites remained unchanged with increasing precipitation at the arid site, increased at the semiarid, and decreased at the mesic site. The herbivory index followed closely the trends seen in the endoparasites response by stagnating at the arid site, increasing at the semiarid, and decreasing at the mesic site. Our findings suggest that altered precipitation has differing effects on plant parasite feeding strategies as well as functional guilds. This may have important implications for grassland productivity, as plant parasite pressure may exacerbate the effects of climate change on host plants.

Keywords Climate change · Drought · Grassland · Rainfall · Soil fauna

Introduction

Like many terrestrial ecosystems, grassland primary production is most limited by water availability (Sala et al. 1988). Climate change studies that assess grassland ecosystem precipitation regimes predict variation in the overall amount and increased frequency of extreme events (Melillo et al. 2014). These precipitation changes can have a major effect on the functioning of grasslands above and belowground (Sala et al. 2012; Wilcox et al. 2017), and may also impact an important driver of plant productivity—their obligate nematode parasites (Todd et al. 1999).

Plant parasitic nematodes (PPN) are affected by soil physical conditions such as soil aggregation and available water films, as well as by biological interactions including microbial pathogens, predators, host plant suitability and sensitivity, and the nutritional quality of roots (Khan 1993; Yeates and Bongers 1999). Through their feeding, PPN can directly cause considerable losses in plant growth and

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biomass to susceptible hosts (Ingham and Detling 1990; Brinkman et al. 2008; Jones et al. 2013) and in some ecosystems PPN consume more primary production that all other herbivores combined (Lauenroth and Burke 2008). PPN also have indirect ecological effects. For example, Bardgett (2005) suggests nematode herbivory not only affects many ecosystem functions, but also serves as an ecosystem connection by driving plant productivity (De Deyn et al. 2003), altering soil microbial communities (Khan 1993; Grayston et al. 2001), and exerting control on aboveground organisms by influencing plant community diversity (Van der Putten 2003; Wardle et al. 2004).

Feeding strategies of PPN determine their population responses to environmental conditions and their interactions with other organisms. Ectoparasites are more likely to be exposed to environmental fluctuations (e.g., drying), predation and pathogens, as they move freely between plant roots to feed. In contrast, endoparasites are relatively buffered from environmental variation, carrying out most of their life cycle within the root itself—with the exception of their infective, soil dwelling second stage juvenile form—and are more susceptible to plant defenses (Macguidwin and Forge 1991; Holbein et al. 2016). While both ecto- and endoparasites cause localized damage during feeding that can make hosts vulnerable to bacterial and fungal infection (Henderson and Clements 1977; Back et al. 2002), some endoparasitic species are often seen as more harmful to plants, because they enter and migrate through host tissue, causing extensive damage as well as limiting the plant host's ability to induce defense mechanisms (Bird and Bird 2001; Jones et al. 2013).

The interplay between changing precipitation and PPN feeding is an important, but poorly understood aspect of grassland responses to climate change. One field study that tested total PPN abundance to changes in precipitation found little measurable effect (Torode et al., 2016), while other studies found PPN populations to be positively affected by greater long-term mean annual precipitation (MAP) and primary productivity allowing for more basal resources in plant roots (Sylvain et al. 2014; Nielsen et al. 2014; Vandegehuchte et al. 2015) as well as being negatively affected by greater top-down control via increased predation (Franco et al. 2019).

Potential differences due to the feeding strategies were not assessed in any of these studies. The different life strategies or functional guilds of PPN are also important as this informs the duration and survivability of key nematode groups. Whether a nematode is capable of quickly establishing a base population in a disturbed environment, or is slower-reproducing, longer lived, and more sensitive to environmental fluctuations (i.e. drought), determines the assigned colonizer-persister (cp) value (Bongers 1990; Ferris et al. 2001; Preisser and Strong 2004). Identifying the feeding strategy, cp value and genus offers the potential estimate of the given impact of different PPN groups on plants and overall ecosystem productivity. Therefore, not only genera identification, but feeding and life strategy knowledge, can help to elucidate the response of PPN abundance to changing precipitation regimes.

The aim of this paper was to investigate the effects of incoming precipitation on the abundance of ecto- and endoparasites across three distinct grasslands that represent differing MAP levels across the Great Plains of North America spanning over 1000 km. We explored the patterns of PPN feeding group abundances across the arid, semiarid, and mesic grasslands, and tested two hypotheses: first, we hypothesized that PPN abundance would respond differently to the precipitation treatments based on feeding strategy. This hypothesis is based on the idea that stronger top-down forces under increasing precipitation would have greater impacts on ectoparasites vs. endoparasites (Eisenback 1993; Bird and Bird 2001). And second, we hypothesized that greater cp value nematodes would increase with increasing precipitation across sites and with water addition treatments. The first hypothesis builds from our previous results suggesting that predation with increases in precipitation over time can suppress PPN populations (Franco et al. 2019). We expected ectoparasites to be more susceptible to increased predation (in wetter treatments), since endoparasites have a more protected, within-root life cycle and are, therefore, less vulnerable to predation (Macguidwin and Forge 1991). The second hypothesis followed the logic that greater cp nematodes require more suitable microhabitats for reproduction, and that the plant damage potential expressed as an herbivory index (HI) would also increase, as there would be a greater population of the more damaging endoparasites with higher available soil water.

Materials and methods

Sites description and experimental design

This research was conducted across three distinct grassland ecosystems in North America: a desert grassland, a semiarid shortgrass steppe, and a mesic tallgrass prairie. These sites comprise an annual precipitation gradient, as well as variation in other climatic characteristics, soil types, and vegetation composition (Table 1). The desert grassland—located in the Jornada (JRN) Basin Long-term Ecological Research (LTER) in Southern New Mexico—has a long-term MAP of 245 mm, with vegetation dominated by the perennial grass *Bouteloua eriopoda* (Havstad and Schlesinger 2006). The Semiarid Grassland Research Center (SGRC) formally known as the shortgrass steppe LTER, located in northern Colorado, has a MAP of 321 mm and is dominated by the

Table 1 Site characteristics for the Jornada Basin LTER, NM (Arid), Semiarid Grasslands Research Center, CO (Semiarid), and Konza Prairie LTER, KS (Mesic)

	Arid	Semiarid	Mesic
Geographic location			
Latitude	32° 33′ N	40° 50′ N	39° 4′ N
Longitude	106° 49′ W	104° 45′ W	96° 34′ W
Ecosystem type	Chihuahuan Desert	Shortgrass Steppe	Tallgrass Prairie
Climate			
MAP (mm)[a]	245	321	835
MGSP (mm)[b]	105	204	428
MAT (°C)[c]	14.7	8.4	12.5
Soil type	Aridisols	Aridisols/Mollisols	Mollisols
Texture*	Fine sandy loam	Fine sandy loam	Silty clay loam
Rainfall treatments (relative to ambient)			
Large reduction	− 80%	− 70%	− 60%
Moderate reduction	− 50%	− 40%	− 30%
Moderate addition	+ 50%	+ 40%	+ 30%
Large addition	+ 80%	+ 70%	+ 60%
Most Abundant PPN**			
Ectoparasite	*Merlinius*	*Helicotylenchus*	*Helicotylenchus*
Endoparasite	*Ditylenchus*	*Ditylenchus*	*Ditylenchus*

*Obtained from Soil Survey USDA

**Plant parasitic nematode (https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx)

[a]Mean Annual Precipitation

[b]Mean Growing Season Precipitation

[c]Mean Annual Temperature

[a–c]Obtained from NOAA climate data from Las Cruces, NM, Nunn, CO, and Manhattan, KS

warm season perennial grass, *Bouteloua gracilis* (Lauenroth and Burke 2008). The tallgrass prairie mesic site—located in Eastern Kansas at the Konza Prairie LTER (KNZ)—averages 835 mm of precipitation annually, with *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium* as the dominant vegetation species (Knapp 1998).

Experiments at each site were established on a relatively flat area, with vegetation representative of the larger ecosystem and with the exclusion of livestock grazing. Rain-out shelters for the experiment were set-up at each site in 2016 to manipulate rainfall inputs during the growing season (Gherardi and Sala 2013); see Franco et al. (2019) for additional details. Shelters intercepted incoming precipitation, temporarily storing the water in an accompanying tank, and distributing the water through solar-powered irrigation systems (Gherardi and Sala 2013). Five levels of precipitation manipulations were determined based on long-term, site-based historical precipitation extremes. Extreme and moderate water reduction, extreme and moderate water addition, and an ambient control were randomly assigned to plots (5 × 2.5 m) based on proportional changes in precipitation specific to the site considered. We applied a drought equivalent to a 100-year drought and an irrigation equivalent to 1 in 100-year deluge at each site. For the arid, semiarid, and mesic sites, respectively, this resulted in 80%, 70%, and 60% of incoming precipitation being diverted from the extreme drought to the extreme water addition treatments, while moderate water reduction treatments diverted 50%, 40%, and 30% of incoming precipitation to the moderate water addition treatments. Eight replicates of all treatments were carried out at each site, for a total of forty plots per site. Treatments were interspersed and spaced at least 5 m apart. Rainfall manipulations were maintained for both the 2016 and 2017 growing seasons.

Soil and nematode collection

Soil samples were collected from each site in September, except for the semiarid site in 2016 that was not collected until October. Sampling was conducted using a soil corer (2.5 cm dia.) to collect four sub-samples to a depth of 10 cm directly beneath the plants of the dominant vegetation type within each experimental plot. The four sub-samples collected from each plot were combined and gently mixed in a plastic bag to form one composite sample per treatment.

The soil corer was cleaned with alcohol wipes between each plot to avoid cross-contamination. Soil samples were placed in a cooler with ice packs to prevent overheating during transportation to the lab at Colorado State University for

nematode extraction. Upon arrival at the lab, samples were stored at 4 °C and extracted within 5 days.

Nematode extraction, counting, and identification

Nematode extraction was performed with 100 g aliquots of the composite sample using Baermann funnels, from which daily samples of 20 ml solution were collected for 3 days, for a total of 60 ml, and stored at 4 °C (Hooper 1970). The nematode solution was reduced to 5 ml and poured onto counting dishes for identification of PPN at the genus level. The total number of nematodes were counted, trophic groups were identified, and PPN feeding strategies (ecto- and endoparasites) were determined based on Yeates et al. (1993) using an inverted microscope (Olympus CKX41, 200× magnification). Nematodes in the genus *Tylenchus* and *Ditylenchus*, known to be fungivores, plant parasites, or facultative plant parasites were considered to be fungivores and plant parasites, respectively (Yeates et al. 1993). Nematodes were preserved with 5% formalin (Southey 1986) and at least 100 PPN were identified to the genera level. Nematode abundances were calculated as the number of individuals per kg of dry soil (soil moisture was calculated by drying 50 g of soil for each sample at 105 °C for 72 h).

All identified PPN were classified into one of the five groups along the cp scale (Bongers 1990). The cp scale considers a range from 1 (extreme r strategists) to 5 (extreme k strategist), where nematodes assigned to group 1 are enrichment opportunists that increase their population quickly after soil disturbance and enrichment processes, nematodes belonging to cp 2 and cp 3 groups have progressively longer life cycles and are more sensitive to soil disturbances, while nematodes in groups 4 and 5 are mostly composed of k-strategists that are very sensitive and slow to recover following disturbance (Bongers and Bongers 1998). Potential nematode impacts on grass productivity were estimated via indirect means using an herbivore impact (HI) factor assigned to each genus based on evidence of known relationships of host plant damage severity by different genera (Ferris 1980; Freckman and Virginia 1989); on a scale of 1–0, where 1 is assigned to the most damaging PPN genus *Meloidogyne,* which was not found in our samples (Table 1). The herbivore impact factor was multiplied by the density of each genus and impact factors for all genera were summed for determination of the HI, interpreted as the potential feeding damage by the PPN taxa found at the three grassland sites.

Statistical analysis

Both years were combined in our analysis which allowed ten levels of received precipitation to be used as a continuous explanatory variable. Linear mixed-effect models (LME) for PPN feeding group abundances were generated using received growing-season precipitation, site, and their interaction, with plot included as a random effect to account for any interdependency of repeated measurements. The assumptions for homogeneity of variance and normality of residuals were met and no transformations to the data were necessary. The conditional r^2 was achieved by the methods of Nakagawa and Schielzeth (2013). These same LME models were applied to the cp grouping of the PPN genera and to the HI of each sample collected. Due to low abundance of cp 4 and 5 groupings these nematodes were combined in the analysis. One sample collected resulted in an exceptionally high number of endoparasites and was removed in all analyses to avoid any influence from outlier data.

To visualize if the individual site and precipitation treatments influenced the PPN community composition, we used non-metric multidimensional scaling (NMDS). As the data contained a high number of absences within genera—which is common for nematode data—Bray–Curtis was chosen as the dissimilarity metric, as it does not equate absences. Relationships of the sites and precipitation levels to the nematode genera abundances were revealed by superimposing data for one genus at a time on the NMDS plot (Ida and Kaneda 2015). The dissimilarity measure and projected distance between genera was calculated. A non-parametric multivariate statistical test of variances (npMANOVA) was used to test the effect of site and seasonal precipitation on community composition. All analyses were conducted using R software, version 3.2.2 (R Core 2018), with the following packages; vegan (Oksanen et al. 2019), nlme (Bates et al. 2015), piecewiseSEM (Bartoń 2017), and package ggplot2 was used for data visualization (Wickham 2009).

Results

Precipitation variation and nematode response

Plant parasitic nematodes were detected in all samples and PPN populations generally were lowest in the arid site and greater in the semiarid site, with the greatest populations in the mesic site. Feeding groups responded uniquely by site to precipitation treatments (Ectoparasites: $P_{\text{Interaction}} < 0.001$, $R^2 = 0.79$, Fig. 1a; Endoparasites: $P_{\text{Interaction}} < 0.001$, $R^2 = 0.39$, Fig. 1b). Both ecto- and endoparasites decreased in response to increasing precipitation in the mesic grassland (Fig. 1). However, the groups differed in their response to altered precipitation in the semi-arid site, such that endoparasites increased with precipitation, while ectoparasites displayed no trend with precipitation. Meanwhile, neither group responded to increasing precipitation at the arid site.

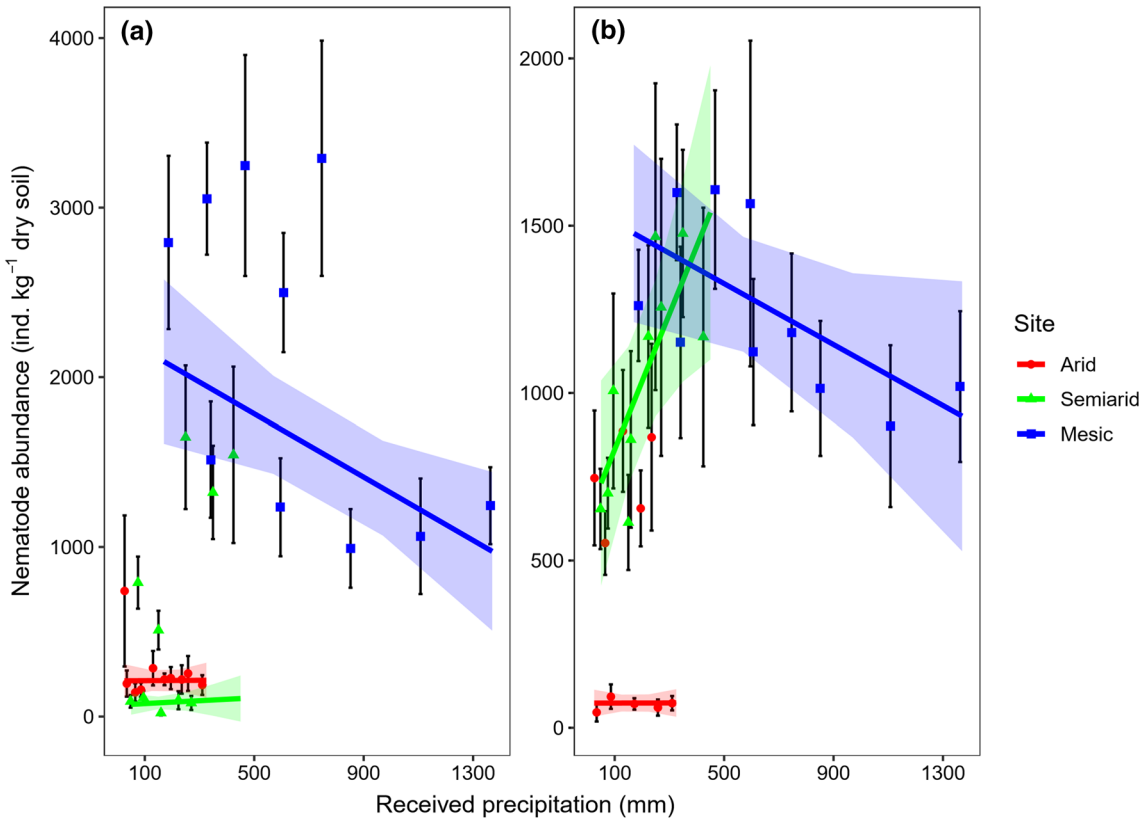

Fig. 1 Response of plant parasitic nematodes to manipulated precipitation across three ecosystem types. Color-coded trend lines represent effects of manipulated precipitation ($n=80$) predicted by mixed effects models. Shaded regions indicate 95% confidence limits. Points represent mean abundance of nematodes per precipitation level (n = 16), and error bars represent standard error of the mean. **a** Ectoparasitic abundance of nematodes ($P_{\text{Received precip.}}<0.001$, $P_{\text{Site}}<0.001$, $P_{\text{Interaction}}=<0.001$, $R^2=0.793$); **b** endoparasitic abundance of nematodes ($P_{\text{Received precip.}}<0.001$, $P_{\text{Site}}<0.001$, $P_{\text{Interaction}}=0.0154$, $R^2=0.387$). For all tests $n=238$

Nematode life history strategies

The PPN functional data (Table 2) suggested cp groups abundances had variable responses to the different precipitation regimes from each site. Abundance of genera representing cp2 life strategies decreased with increasing seasonal precipitation at the mesic site and increased in abundance at the other two sites ($P_{\text{Received precip.}}<0.001$, $P_{\text{Site}}<0.001$, $P_{\text{Interaction}}=0.491$, $R^2=0.24$, Fig. 2a). The cp3 nematodes responded to increasing seasonal precipitation differently at each site ($P_{\text{Interaction}}<0.001$, $R^2=0.22$); with abundance responses changing from positive to negative from the semiarid to mesic sites, and a very slight increase in cp3 nematodes with increased received precipitation at the arid site (Fig. 2b). The nematodes having longer life cycles and belonging to the grouped cp4–cp5 classifications decreased in abundance with increasing seasonal precipitation at the mesic and semiarid sites but increased in abundance at the arid site ($P_{\text{Interaction}}=0.003$, $R^2=0.12$, Fig. 2c). The HI followed closely the trends seen in the endoparasitic abundance response (Fig. 1b) by decreasing at the mesic site, increasing at the semiarid site, and stagnating at the arid site ($P_{\text{Received precip.}}<0.001$, $P_{\text{Site}}<0.001$, $P_{\text{Interaction}}=0.67$, $R^2=0.21$, Fig. 3).

Nematode genera at each site

The composition of the PPN community was affected by site ($P=0.001$, $R^2=0.22$, Fig. 4). Twenty-two PPN genera were found across sites. Thirteen genera (Criconema, Ditylenchus, Filenchus, Gracilacus, Helicotylenchus, Hoplolaimus, Merlinius, Paratylenchus, Pratylenchus, *Rotylenchus*, *Subanguina*, *Tylenchorhynchus*, and *Xiphinema*) were present in all sites sampled. In contrast, one genus was endemic to the semiarid site (*Longidorus*), while eight genera occurred only in the mesic site (*Basiria*, *Coslenchus*, *Hemicycliophora*, *Mesocriconema*, *Pararotylenchus*, *Paratrophorus*, *Psilenchus*, and *Trichodorus*). The arid site was associated with the greatest abundance of the genera *Merlinius*, whose species feed on many host plants globally, including those found in each grassland site (Navas and Talavera 2002). *Basiria*, *Trichodorus*, *Mesocriconema*, and *Hemicycliophora*

Table 2 Plant–parasitic nematode taxa detected in each MAP level and their potential impact on plant growth and performance based on literature values

Genera (cp value)	Impact factor	Regional gradient		
		Arid	Semiarid	Mesic
Basiria (2)	0.05			×
Coslenchus (2)	0.05			×
Criconema (3)	0.05	×	×	×
Ditylenchus (2)	0.4	×	×	×
Filenchus (2)	0.05	×	×	×
Gracilacus (2)	0.05	×	×	×
Helicotylenchus (3)	0.4	×	×	×
Hemicycliophora (3)	0.3			×
Hoplolaimus (3)	0.4	×	×	×
Longidorus (5)	0.3		×	
Merlinius (3)	0.07	×	×	×
Mesocriconema (3)	0.4			×
Pararotylenchus (3)	0.07			×
Paratrophorus (3)	0.07			×
Paratylenchus (2)	0.05	×	×	×
Pratylenchus (3)	0.5	×	×	×
Psilenchus (2)	0.05			×
Rotylenchus (3)	0.4	×	×	×
Subanguina (2)	0.5	×	×	×
Trichodorus (4)	0.5			×
Tylenchorhynchus (3)	0.05	×	×	×
Xiphinema (5)	0.07	×	×	×

Endoparasites are bolded

are endemic genera found in the mesic site, and clustered outside the polygon denoting the mesic site. *Helicotylenchus* and *Paratylenchus* were found at each grassland, but had greater abundances in our semiarid and mesic sites, respectively.

Discussion

Plant parasitic nematode differences across sites

Our findings suggest that PPN populations were lowest in the arid site and greatest in the mesic site; however, this trend was not equally observed in ecto- vs. endoparasitic nematodes. Although the mesic site did have the greatest abundances of PPN for both groups, we observed a greater abundance of ectoparasites at the arid site than the semiarid site (Fig. 1). This increase in arid ectoparasitic nematodes follows what was found in our previous study in the same site that showed an increased in community weighted mean of plant parasites body size when exposed to increasing precipitation (Andriuzzi et al. 2020). The finding of increased precipitation supporting more consumers coincides with previous studies suggesting that increased precipitation has a strong, positive effect on PPN abundances within single sites (Jordaan et al. 1989; Bardgett et al. 1999; Todd et al. 1999; A'Bear et al. 2014; Sylvain et al. 2014). There is also evidence to support that at large spatial scales across landscapes and regions, climatic characteristics have greater influences on the soil biota composition (and the local nematode community structure) than inherent soil characteristics (Ettema and Wardle 2002; Blankinship et al. 2011; Nielsen et al. 2014). This may in part explain the greater PPN populations observed at more mesic grasslands as this site had the highest MAP.

Plant parasitic nematode response to precipitation treatments

In agreement with our first hypothesis, the two feeding strategies of plant parasitic nematodes, ecto- and endoparasites, responded differently to precipitation manipulations. This was especially evident at the semi-arid site, where endoparasites responded positively to increased rainfall, while ectoparasites remained largely flat across the manipulated gradient in precipitation. Contrary to our prediction, ectoparasitic abundance did not significantly change with received precipitation at the drier sites (arid and semiarid) but decreased greatly at the mesic site (Fig. 1a). We suspected that for the more xeric sites (arid and semiarid) that increased soil moisture would allow ectoparasitic nematodes to actively move between root feeding sites, allowing for greater reproduction, and completion of the life cycle. This idea was supported by previous work reporting PPN to increase following 1 year of irrigation (Freckman et al. 1987), likely due to increased plant growth and root biomass, but little change in ectoparasitic populations were seen in the drier sites. Aligning with our hypothesis, ectoparasitic abundance was negatively affected by increased water availability in the mesic grassland. This response at the mesic site could be caused by increased top-down control by predator nematodes on ectoparasites, since the abundance of predaceous nematodes increased with increasing precipitation in this same site (Franco et al. 2019). Moreover, Franco et al (2019) found the abundance of PPN increased in drought conditions, where predators nematodes populations declined; showing a dismantling of the predator–prey balance in which PPN and lower trophic group nematodes are released by the decrease in predator populations in the mesic site.

The endoparasite response to increasing precipitation also differed from our hypothesis in that each site showed a unique outcome to the precipitation treatments rather than remaining unchanged. Endoparasitic nematodes were expected to exhibit a reduced response to environmental changes, as most of their life cycle occurs within

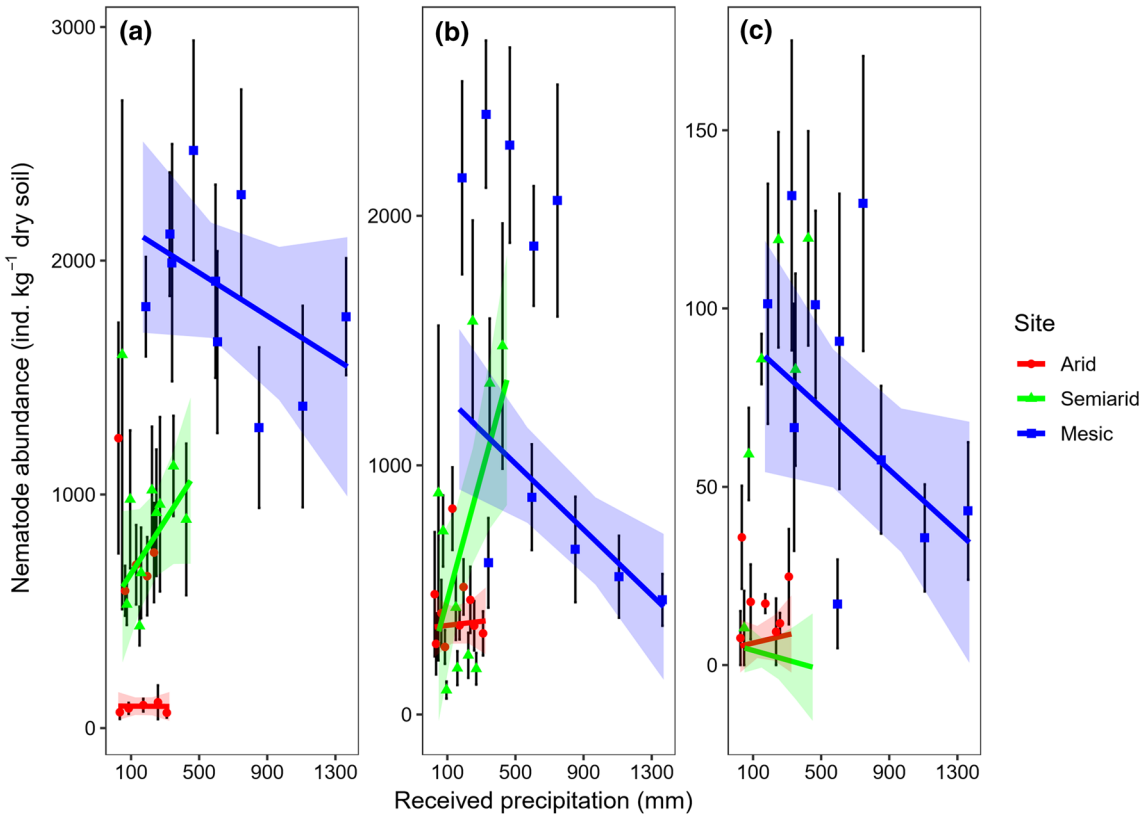

Fig. 2 Response of plant parasitic nematode life strategies as grouped by colonizer-persister scales (cp) to manipulated precipitation across three ecosystem types. Color-coded trend lines represent effects of manipulated precipitation ($n=80$) predicted by mixed effects models. Shaded regions indicate 95% confidence limits. Points represent mean abundance of nematodes per precipitation level ($n=16$), and error bars represent standard error of the mean. **a** Abundance of cp2 nematodes ($P_{\text{Received precip.}}<0.0001$, $P_{\text{Site}}<0.001$, $P_{\text{Interaction}}=0.491$, $R^2=0.242$); **b** abundance of cp3 nematodes ($P_{\text{Received precip.}}<0.001$, $P_{\text{Site}}<0.001$, $P_{\text{Interaction}}<0.001$, $R^2=0.219$); **c** abundance of cp4 and 5 nematodes ($P_{\text{Received precip.}}<0.001$, $P_{\text{Site}}<0.001$, $P_{\text{Interaction}}=0.003$, $R^2=0.121$. For all tests $n=239$

roots—providing these nematodes with shelter from environmental fluctuations and predation. The negative response of endoparasitic populations to increased seasonal precipitation seen at the mesic site could be due to increased plant chemical defenses against initial invasion and establishment of endoparasites, since increased soil water could increase plant growth and ability to invest in defensive compounds (Hakes and Cronin 2011). The findings at the semiarid site support previous work reporting a positive response of endoparasitic abundance to increased precipitation in dryland agricultural systems of South Africa (Kandel et al. 2013) as *Pratylenchus* is known to have inhibited growth in either too little or high soil moisture (Kable and Mai 1986).

Functional diversity of plant parasitic nematodes

It is important to know which genera are present and how they are affected by future precipitation patterns, as the life strategies of different PPN genera vary greatly. Some PPN complete several generations in a year (e.g., *Pratylenchus*, *Paratylenchus*, *Helicotylenchus*), others may only complete one, while still others may have generation times that exceed 12 months (e.g., *Xiphinema*, *Longidorus*). This could lead to differences between a thousand, a hundred, or a ten-fold population increase, respectively, within a growing season (Jones and Northcote 1972). Precipitation influenced the structure of the PPN communities in the grasslands studied, as the precipitation treatments significantly impacted abundance and distribution of the functional guilds of the PPN communities identified. Colonizer (*r* strategist) nematodes (cp2) as well as cp3 nematodes responded negatively to increased precipitation at the mesic site, but increased in the semiarid site, while more persistent cp4–5 nematodes were enhanced by increasing precipitation only in the arid site and decreased in the wetter grasslands. The overall decrease of the longer-lived, slower generating ectoparasitic nematodes at the higher wetter sites could be explained by increased predation pressure on these PPN genera that does not occur at our drier sites. Should the mesic grasslands become wetter in the future these persistent nematodes may become less numerous in abundance and lead to greater increases in

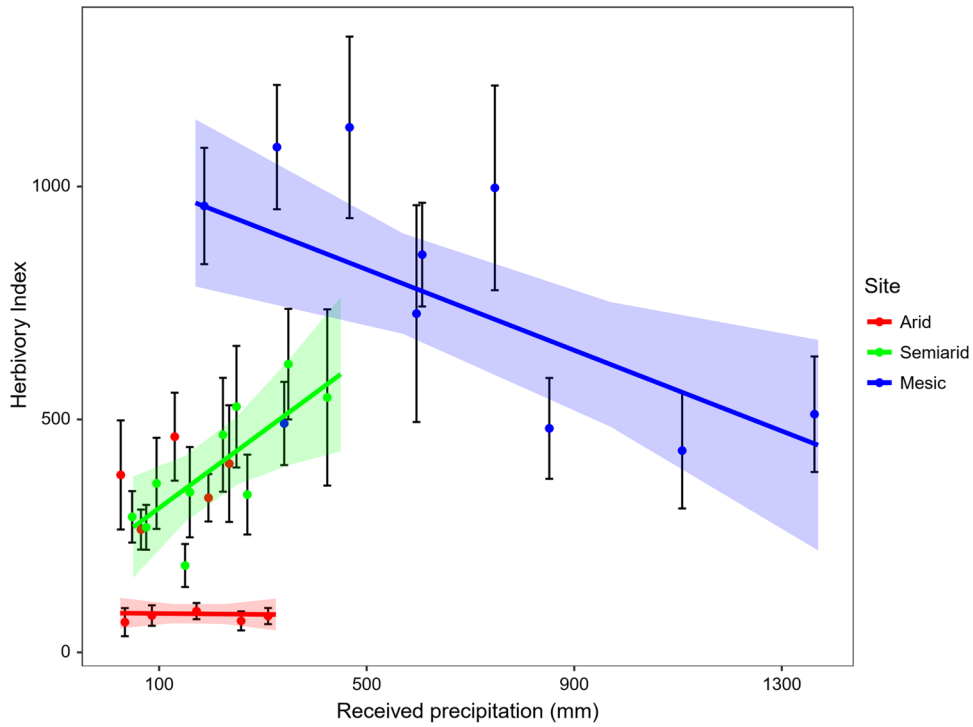

Fig. 3 Herbivory Index (an indicator of potential severity of herbivorous nematodes on plant growth) response to manipulated precipitation across three ecosystem types. Color-coded trend lines represent local effects of manipulated precipitation ($n=80$) predicted by mixed effects models. Shaded regions indicate 95% confidence limits. Points represent mean abundance of nematodes per precipitation level ($n=16$), and error bars represent standard error of the mean ($P_{\text{Received precip.}}<0.0001$, $P_{\text{Site}}<0.0001$, $P_{\text{Interaction}}=0.6645$, $R^2=0.2129$). $n=238$. The herbivory impact index was calculated as [(∑(number of nematodes/genus × impact factor)]. Impact factors for each genus are listed in Table 2 (modified from Freckman and Virginia 1989)

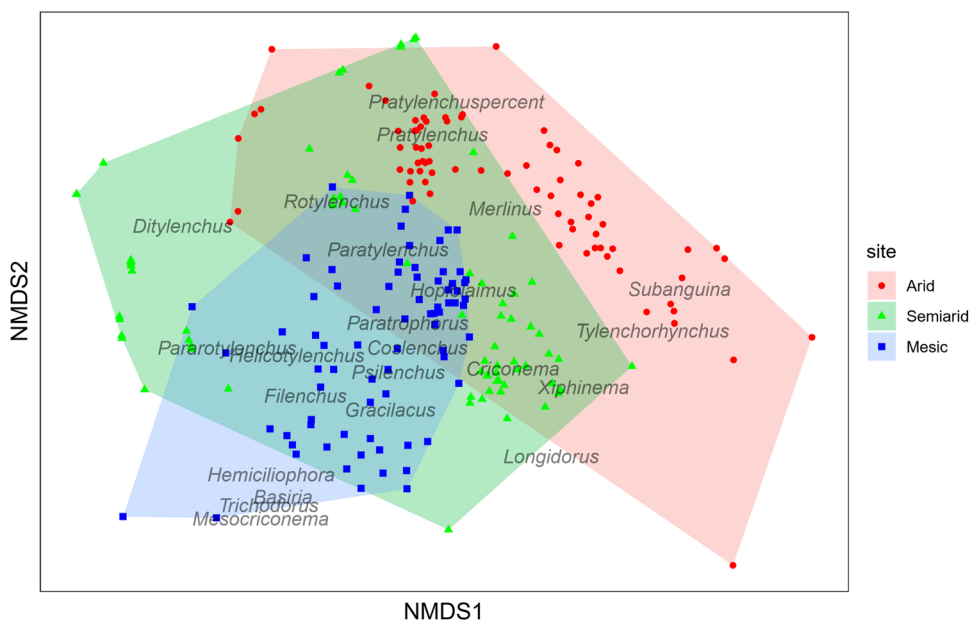

Fig. 4 Plant parasitic nematode (PPN) composition across the three grassland sites. Nonmetric multidimensional scaling plot of PPN genera as a function of received growing season precipitation ($n=239$, Bray–Curtis). The genera are grouped by site (shape and color) (npMANOVA: $F=38.86$, $R^2=0.221$, $P=0.001$)

colonizer nematodes shifting from more stable trophic structures to less structured ones.

Across our three sites, HI was affected by the precipitation treatments in a different way. While increasing precipitation did not affect HI at the arid site, opposing responses were found for the mesic and semiarid sites showing a decrease and increase, respectively. This finding suggests that in the mesic site more frequent droughts could intensify the overall severity of root herbivory, while the same is true for increasing rainfall at the semi-arid site. Previous field work on cereal cropping systems found the effects of diseases caused by nematodes were more evident under drought conditions that resulted in damaged root systems not efficiently taking in soil moisture and nutrients (Kandel et al. 2013). The increase in available soil water could potentially increase both predation and plant defenses which may offset damage caused by PPN and, therefore, reduce the impact of infestation. The negative impact of received precipitation on endoparasitic nematodes may also

help explain the observed decrease in HI as in general they cause more potential damage (Jones et al. 2013).

Community structure of plant parasitic nematodes

Plant parasitic nematode community structure was affected by site as visualized by the NMDS plot (Fig. 4). *Paratylenchus* has a drought resistant growth stage, which explains the placement closer to the arid site compared to *Helicotylenchus* which lacks such resistance and was rarely found in the arid site (Yeates and Lee 1997). The NMDS plot suggests that site can be a predictive factor in determining, where some specific genera may be found. *Ditylenchus* was the most abundant endoparasite at all three sites, but had the greatest quantity in the semiarid site, which is evident from the NMDS results placing *Ditylenchus* in the polygon signifying the semiarid site. The most abundant ectoparasite genera differed between the three sites (Table 1). Overall, there were more endoparasites present in the arid and semiarid sites and more ectoparasites at the mesic site. This confirms that ectoparasites respond positively to increased precipitation, which aligns with our initial hypothesis.

Implications for grassland ecosystems under climate change

Altered precipitation patterns as a result of climate change pose a challenge to grassland plant species diversity and productivity. If mesic grasslands do get drier as is predicted, these grasses may support a greater population of ectoparasitic nematodes. Given that our results suggest that endoparasites also increase with drought, we suspect that an overall increase in both feeding strategies could further intensify PPN damage within potentially water-stressed mesic grasslands.

Previous work suggests that, in general, endoparasites are superior competitors to ectoparasites (Eisenback 1993; Jones et al. 2013), and while PPN herbivory and plant disease may not always kill their host, they do reduce the plant's productivity compared to healthier uninfected plants (Grime 1998; De Deyn et al. 2003; Neher 2010). Plant hosts from natural ecosystems have coevolved with PPN much longer than crop-nematode systems, but under climate change endoparasites may have an advantage that could ultimately lead to changes in plant diversity and composition via selection pressure and PPN driven succession in mesic grasslands (De Deyn et al. 2003; Brinkman et al. 2008).

Conclusion

Our results show that plant parasitic nematode abundance, functional guilds, and herbivory index are influenced by seasonal precipitation differently across a regional climatic gradient in grasslands. The varying effects of seasonal precipitation on the structure of plant parasitic nematode communities highlight the vulnerability of mesic and semiarid grasslands to predicted effects of climate change. Mesic grasslands are projected to experience longer durations of drought which will increase both the abundance of the generally more detrimental endoparasitic plant parasite and, consequently, the herbivory impact on plants. Semiarid grasslands may see an increase in wet precipitation events that would lead to increased endoparasite abundance, also resulting in greater herbivory impact. Finally, our results indicate that PPN populations in arid grasslands will remain relatively unchanged despite increases in droughts or deluges. The interaction seen among precipitation treatments and site affecting plant parasitic nematodes communities by specific feeding strategy, functional guild, and herbivory index has not previously been reported. More studies focused on nematode-driven soil processes along climatic gradients with conjunction of plant data (i.e. biomass) will advance our understanding of the ecosystem-wide repercussions of altered precipitation from climate change. Plant parasitic nematode feeding is a dominant control in overall grassland biomass production (Ingham and Detling 1990; Neher 2010) and will increase with drought, thus potentially exacerbating climate change impacts on grassland productivity, more severely in mesic than arid sites.

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Author contribution statement OES and DHW designed research. ALCF, LAG, CMdT, WSA, KEA, and EAS performed research. KEA analyzed data and KEA, ALCF, SJF, and DHW wrote the paper.

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