Received: 2 August 2022 | Accepted: 26 August 2022

DOI: 10.1002/ecs2.4364

ARTICLE

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Responses of nematode abundances to increased and reduced rainfall under field conditions: A meta-analysis

Dylan Bristol[1] | **Kamrul Hassan**[1,2] | **Joseph C. Blankinship**[3] | **Uffe N. Nielsen**[1]

[1]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia

[2]Department of Entomology, Sylhet Agricultural University, Sylhet, Bangladesh

[3]Department of Environmental Science, University of Arizona, Tucson, Arizona, USA

Correspondence
Dylan Bristol
Email: d.bristol2@westernsydney.edu.au

Funding information
Australian Research Council, Grant/Award Numbers: DP190101968, DP150104199

Handling Editor: Grizelle Gonzalez

Abstract

Ecosystems are projected to experience altered precipitation patterns associated with climate change, with some areas becoming wetter and others drier. Both above- and belowground communities will be impacted by such rainfall changes, yet research has predominantly focused on the flora and fauna aboveground. Still, there is a growing body of literature for the effects of altered precipitation on soil fauna. Nematodes are diverse and abundant in most soils, represent multiple trophic levels, and influence essential soil processes, making this group a good proxy for broader impacts on soil food webs. Hence, we assessed the effects of increased and reduced rainfall amount on total and trophic-level abundances of nematodes using a meta-analytical approach based on 46 independent observations from 37 field studies and tested whether effects differed among ecosystem types and with treatment duration (<1 year, short term; >1 year, long term). Overall, total and trophic group's abundances, except fungal feeders, were negatively impacted by reduced rainfall irrespectively of treatment duration. Increased rainfall had a positive effect on total abundances and plant parasitic nematodes, but only in longer term studies (>1 year). The impacts of altered rainfall were consistent across the ecosystems studied; however, most studies focus on grasslands and deserts, making it difficult to draw broad generalizations. Reductions in rainfall are therefore likely to decrease soil nematode abundance, with less pronounced effects on fungal feeders. Increased rainfall, on the other hand, may favor plant parasites, likely due to increased plant productivity. Hence, projections of reduced rainfall will have significant negative impacts on nematode abundances, at least in grasslands and deserts, with cascading effects on soil processes.

KEYWORDS

ecosystem function, ecosystem process, experimental duration, nematode trophic groups, rainfall regime

INTRODUCTION

Global circulation models predict significant changes in precipitation amount and frequency, with reduced rainfall expected in most nonpolar regions, which will impact flora and fauna, both above- and belowground, in most biomes (Singh et al., 2019). The effects of altered rainfall amount on vegetation, and to a lesser degree fauna, have been studied widely aboveground while less attention has been given to belowground responses (Blankinship et al., 2011; Liu et al., 2016). In recent years, however, there has been increasing interest in belowground biotic responses given their importance to ecosystem functions (Kojima et al., 2014; van den Hoogen et al., 2019). Among soil biota, nematodes are an ideal study group as they are very abundant, highly diverse, represent multiple trophic levels, and regulate soil processes through their interactions with plants, microbes, and other soil fauna (Guan et al., 2019). Understanding how nematodes are impacted by climate change is therefore important to predicting changes in ecosystem functions under future conditions (Papatheodorou et al., 2012).

Soil nematodes are semiaquatic animals that rely on water films or water-filled soil pores for movement; hence, changes in water availability are likely to affect their activity in the short term and nematode abundances and community composition in the longer term (Nzogela et al., 2020). A recent global survey of nematode trophic groups showed that nematode abundances are positively correlated with mean annual precipitation, at least when other factors, such as soil carbon (C) and nutrients, are not limiting abundances (van den Hoogen et al., 2019). Moreover, physical and chemical properties as well as biotic interactions may moderate responses to changes in rainfall, for example, warming and changes in rainfall may interact to influence nematode abundances given the effect of temperature on physiological processes (Nielsen et al., 2015). Hence, it is expected that reduced and increased rainfall amount will have negative and positive effects on nematode abundances, respectively, unless other factors are limiting abundances (A'Bear et al., 2014), with particularly large effects where nematodes are limited by water availability (Stott, 2016).

Nematodes are generally grouped by feeding preferences, including bacterivores, fungivores, herbivores, omnivores, and predators (Xiaoming et al., 2013), that affect soil processes differently and are likely to show contrasting responses to climate changes given their resources may be differentially impacted (Dong et al., 2013). For example, plant parasitic nematodes could benefit more than other trophic groups where increased rainfall results in greater plant productivity but has limited effects on other resources, such as microbial biomass (Olusanya et al., 2019). Conversely, plant parasitic nematodes may be the most impacted trophic group in drought-affected soils due to the lack of plant growth. Similarly, fungivore and bacterivore nematodes are likely to be impacted differently by altered rainfall given that bacteria and fungi show contrasting relationships with soil water availability. Fungi appear to be more desiccation resistant than bacteria (Barnard et al., 2013) and would therefore be less impacted by drought. Hence, fungivore nematodes may not be as severely impacted by reduced water availability compared with other trophic groups (Bouwman & Zwart, 1994; Jones et al., 1969). Furthermore, increases or reductions in plant parasites and microbial grazers may impact predatory nematode abundances due to resource availability and could have cascading effects throughout the soil food web (Chiew et al., 2011). In general, due to the consensus that decreased precipitation increases the survival stresses on organisms (Diakhaté et al., 2016), it can be predicted that the response ratios for decreased precipitation will be significantly greater than the increased rainfall responses (Ilieva-Makulec & De Boeck, 2013).

Experimental studies in both the field and laboratory have shown that nematode abundances typically respond negatively to reduced water availability while responses to increased water availability are more inconsistent (Cesarz et al., 2017; Pengfei et al., 2018). Still, some studies found limited effects of reduced rainfall on nematode abundances (Sylvain et al., 2014; Vandegehuchte et al., 2015). Moreover, a few notable studies have found contrasting responses across nematode trophic groups to altered precipitation (Andriuzzi et al., 2020; Ankrom et al., 2020). Noticeably, plant parasites typically show a stronger response to increased rainfall than other nematode trophic groups (Guogang et al., 2020). Two meta-analyses assessing soil biotic responses to global changes provide strong evidence that altered rainfall regimes influence nematode assemblages. Blankinship et al. (2011) found that reduced rainfall was more likely to reduce nematode abundances in colder and drier ecosystems. Treatment effect sizes were variable but largely depended on ecosystem type, given differences in temperature and rainfall, suggesting that nematode responses are governed by contemporary environmental conditions. Another meta-analysis similarly found mostly negative responses to decreased precipitation and mostly positive responses to increased precipitation (A'Bear et al., 2014). This meta-analysis furthermore found that nematode trophic groups showed contrasting responses to rainfall manipulations while responses generally were stronger in experiments of longer duration (A'Bear et al., 2014). This could potentially be due to the trophic groups having different tolerances to rainfall and potentially increased rainfall having a relatively slower response rate compared with reduced rainfall, where the impact is felt immediately. Thus, it is critical to understand in what ways differing experimental lengths impact response ratios for both rainfall changes, to contextualize and refine experimental designs in the future.

Since the most recent meta-analysis in 2014, 25 new studies have manipulated rainfall to test effects on soil nematode abundances under field conditions (e.g., Feng et al., 2019; Guogang et al., 2020; Quanhui et al., 2018), making it possible to evaluate the effects across studies in different ecosystem types, across rainfall gradients, and of different duration. Here, we present the results of a meta-analysis of how altered rainfall amounts impact total nematode and trophic group's abundances with the aim of addressing the following three questions: (1) How does reduced and increased rainfall affect nematode total and trophic group's abundances? (2) Are responses consistent across rainfall gradients and ecosystem type? (3) Are responses affected by experimental duration?

METHODS

Literature search and paper selection

We collected relevant papers through an online search of the Web of Science Core Collection database focusing on the effect of altered rainfall regimes, specifically reduced and increased rainfall amount relative to ambient conditions at a site, on total and/or trophic group's abundances of nematodes. Nematode trophic groups were categorized as plant parasites, bacterial feeders, fungal feeders, and omnivores–predators. The "topic search" keyword filter included variations of the following words: "nematode" and "function" and "rainfall" and "precipitation" and "increased" OR "flood" and "drought" and "decreased." References of the papers used in the analysis were also checked for relevant studies that did not come up using the search terms. Papers of any publication year were included within the analysis when they were completed using a robust experimental design. Specifically, experiments included had to experimentally manipulate rainfall under field conditions and include an appropriate ambient rainfall control, include at least three replicates, and treatments must be imposed for more than 1 month.

Data collection and extraction

If a paper matched the criteria (as described above), we recorded total nematode abundance and abundance of nematode trophic groups including corresponding standard deviation (±SD) and sample sizes (N) for ambient, increased, and reduced rainfall. If SD was not available, we calculated SD by multiplying standard error and square root of the sample size ($SE = SD/\sqrt{N}$). The X_E, SD_E, and N_E represent the experimental group (E) mean, SD, and sample size while X_C, SD_C, and N_C represent the control group (C) mean, SD, and sample size (Blankinship et al., 2011; Hedges et al., 1999). Meta-data were prepared directly from tables or extracted from figures using WebPlotDigitizer v. 4.1 (Rohatgi, 2012) where possible or obtained directly from the author. Data were organized as total nematode abundance and nematode trophic group's abundances under ambient, increased, and/or decreased rainfall. We obtained 46 independent observations of nematode responses to altered rainfall amounts from 37 relevant papers. We also included unpublished observations from six dryland sites (Nyngan, Cobar, Broken Hill, and Milparinka in New South Wales, and Charleville and Quilpie in Queensland) across eastern Australia where rainfall was manipulated for 4 years (Bristol et al., unpublished data). Our meta-analysis included a total of 227 individual measures of nematodes (total and trophic group) under ambient and altered rainfall (increased and decreased). Treatment size ranged from −20% to −80% reduction and 15%–300% increased rainfall relative to ambient conditions at the sites. In studies with multiple time points or treatments, only data from the last year were collected to use balanced sampling across studies and avoid concerns of pseudo-replication, which would lead to some experiments carrying greater weight in the analysis.

Calculation of effect size and interpretation

We calculated ratio of means (ROM) to represent mean effect sizes, given the large variation of measurements between papers, using the metacont function from metaphor package in R (Viechtbauer, 2020). We did not present effects size as Hedges' d/standardized mean difference (SMD) due to similar results between treatment groups (data not present). ROMs are calculated using the natural logarithm of mean abundance of nematodes in experimental groups (i.e., increased or decreased rainfall) to that of the control group (ambient rainfall) with corresponding SD and sample size (N) of individual observations. ROM values >1 and <1 represent positive and negative treatment effects on nematode abundances, respectively. ROM values that do not differ from 1 indicate no treatment effects on nematode trophic group's abundances. We tested for publication bias by producing a histogram of effect size to check the data of depression around zero (Begg & Mazumdar, 1994).

Meta-analysis

All meta-data were analyzed using R version 4.0.3 (R Development Core Team, 2020). We chose random-effects models to quantify effects of increased and decreased rainfall relative to ambient rainfall on individual response variables (i.e., the relative abundance of nematode trophic groups). Due to the high variation in each treatment effect in the papers collected, and the sampling variation, the random-effects model was chosen to be best suited for this analysis (Rosenberg et al., 2000). Multiple subcategories were used to demonstrate the effects of altered rainfall regimes on total nematode abundance and nematode trophic groups across all studies and whether these differ among ecosystem types, experimental duration, and precipitation at the site (Appendix S1: Tables S1 and S2). Additionally, we used linear regressions to test whether response ratios of total or trophic groups were related to mean annual precipitation or treatment size across the studies to assess whether treatment effects are moderated by local conditions or experimental design, respectively.

RESULTS

Total and trophic group responses to altered rainfall

The effect of altered rainfall varied across total and trophic group's abundances (Figure 1). Total nematode abundances were 45.4% lower in the decreased rainfall treatments across all studies (ROM = 0.546, $n = 27$, $p = 0.008$), while there was no effect of increased rainfall. The abundance of plant parasites was 46.0% lower in the decreased rainfall treatments (ROM = 0.5399, $n = 19$, $p = 0.04$), but no effect of increased rainfall was observed across all observations (Figure 1). The abundance of omnivores and predators was 59.8% lower in the decreased rainfall treatment (ROM = 0.4019, $n = 19$, $p < 0.001$), but was not affected by increased rainfall (ROM = 1.1012, $n = 22$, $p = 0.6782$). Fungivores were not significantly different under reduced or increased rainfall. Bacterivores showed a significant reduction of 35.9% under decreased rainfall conditions (ROM = 0.6403, $n = 20$, $p < 0.0001$).

There was no correlation between nematode total or trophic group's abundance response ratios and mean annual rainfall of individual studies, except for a negative correlation between the effect size of increased rainfall for omnivores/predators with increased precipitation and the effect size of decreased rainfall for fungivores with decreased precipitation (Appendix S1: Figure S1). Similarly, there was no correlation between nematode abundances and treatment size for reduced or increased rainfall treatments. Hence, treatment size was not included as a variable in the meta-analysis.

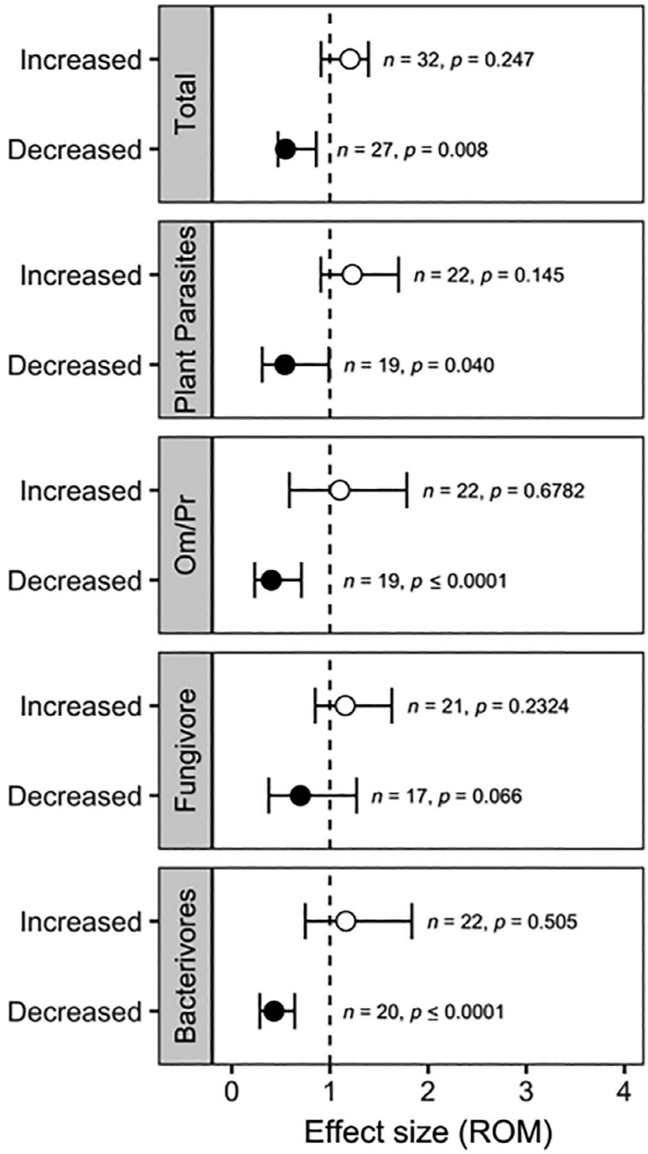

FIGURE 1 Mean response ratio (± bootstrapped 95% CI) of increased and decreased rainfall treatments relative to ambient rainfall for total and nematode trophic group's abundances: Plant parasites, omnivores and predators (Om/Pr), fungivores, and bacterivores. Ratio of means (ROM), which measures the response ratio; the dotted line represents no response, ROM values >1 represent positive treatment effects on nematode abundances, and ROM values <1 represent negative treatment effects on nematode abundances; n = number of observations included in each treatment, p value indicates the level of significance.

Effects of altered rainfall across ecosystem types

The effects of altered rainfall regimes on nematode abundances varied among ecosystem types (Figure 2). Nematode abundances were 39.2% lower in desert ecosystems under decreased rainfall conditions (ROM = 0.608, $n = 11$, $p = 0.041$), 54.9% in grasslands (ROM = 0.451, $n = 10$, $p = 0.004$), and 54.9% in other ecosystems (ROM = 0.451, $n = 6$, $p = 0.048$) under decreased rainfall conditions. However, no effect was observed for increased rainfall (Figure 2).

Effects of experimental duration on nematode responses

The effect of altered rainfall differed among short-term and longer term studies (Figure 3). Reduced rainfall had a negative effect on total abundances both in short-term (<1 year) (ROM = 0.4094, $n = 11$, $p = 0.004$) and long-term (>1 year) studies (ROM = 0.6300, $n = 16$, $p = 0.006$; Figure 3). By contrast, increased rainfall only had a significant positive effect on total abundances (ROM = 1.1831, $n = 18$, $p = 0.027$) and plant parasitic nematodes (ROM = 1.6401, $n = 13$, $p = 0.010$) in the longer term studies. Likewise, fungivores showed a tendency to increased abundances (47.2%) in longer time studies (ROM = 1.4722, $n = 13$, $p = 0.059$; Figure 3). By contrast, bacterivores were only significantly negatively impacted by reduced rainfall condition irrespective of experimental length (short term; ROM = 0.2670, $n = 8$, $p = 0.0018$; long term; ROM = 0.6204, $n = 12$, $p = 0.024$; Figure 3).

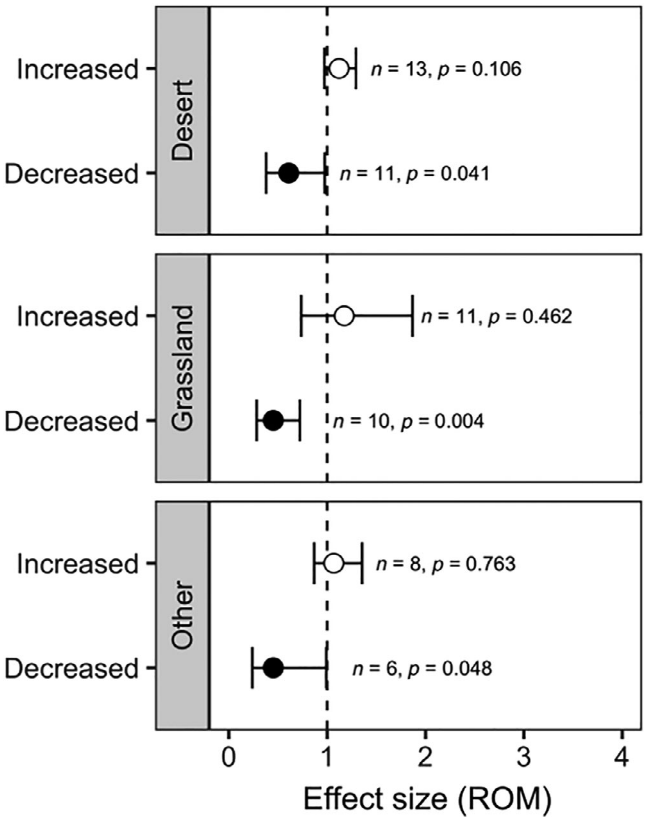

FIGURE 2 Mean response ratio (± bootstrapped 95% CI) of decreased and increased rainfall treatments on nematodes in different ecosystem types: Desert, grassland, others (which include subtropical forests, temperate forests, coniferous forests, wetland forests, boreal forests, and evergreen forests; $n = 14$); ratio of means (ROM), which measures the response ratio; dotted line represents no response, ROM values >1 represent the treatment positively impacting nematode abundances, and ROM values <1 represent the treatment negatively impacting nematode abundances; n = number of data sets included in each treatment, with the associated p value.

DISCUSSION

Our results show strong evidence that projected changes in rainfall will have significant consequences for nematode communities, but that the effects differ among trophic groups, ecosystems, and with experimental duration. Overall, we found that nematode abundances were 45% lower in reduced rainfall treatments across all studies, whereas increased rainfall had no effect on total or trophic group's abundances. All trophic groups, except fungivores, showed a negative response to rainfall reductions, although the effect was particularly pronounced for omnivores and predators (59.8% reduction relative to ambient). However, our results suggest that the effect of increased rainfall may take longer to manifest, with a 9% increase in total nematode abundances, driven by a strong increase in plant parasites, in longer term studies (i.e., >1 year). Reduced rainfall resulted in a 39.2% reduction of nematodes in deserts and a 54.9% reduction in grasslands—the two main ecosystems studied. The observed changes in nematode abundances are likely to have cascading repercussions on essential soil processes, including nutrient mineralization and primary productivity.

Nematode trophic group responses to altered rainfall amounts

As expected, our meta-analysis supports the notion that nematodes are sensitive to rainfall reductions despite many nematodes thought to be quite resilient to drought (Dima et al., 2015; Zhang et al., 2019). However, the impacts of reduced rainfall differed considerably across trophic groups, with very pronounced effects in most feeding types, except fungal-feeding nematodes. Omnivorous and predatory nematodes rely on the

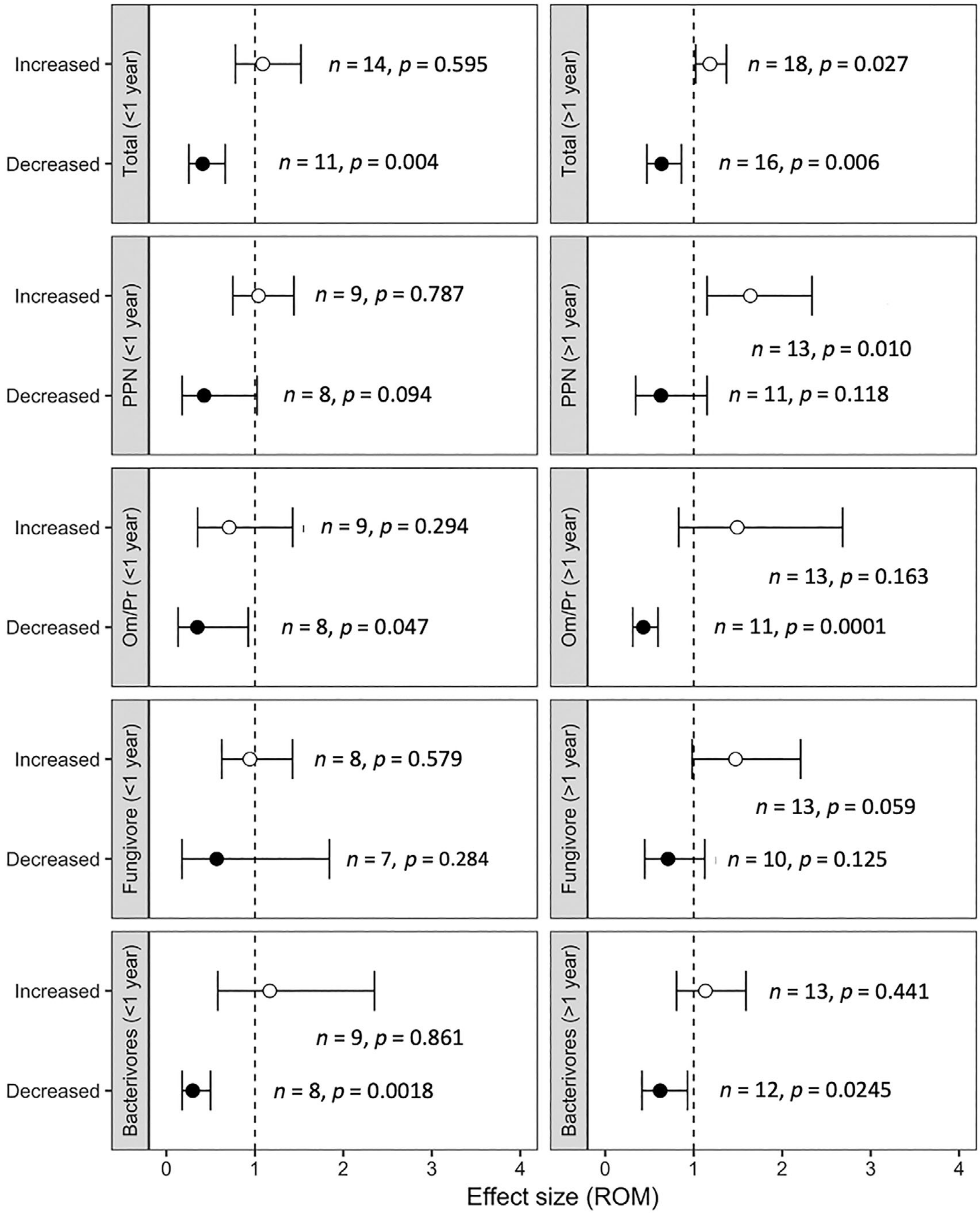

FIGURE 3 Mean response ratio (± bootstrapped 95% CI) of increased and decreased rainfall treatments in different experimental time periods (<1 year and >1 year), for total and nematode trophic group's abundances: Plant parasitic nematodes (PPN), omnivores and predators (Om/Pr), fungivore, and bacterivores. Ratio of means (ROM), which measures the response ratio; the dotted line represents no response, ROM values >1 represent positive treatment effects on nematode abundances, and ROM values <1 represent negative treatment effects on nematode abundances; n = number of observations included in each treatment, with the associated p value.

availability of resources that may be affected by water limitation and appear to be more sensitive to disturbance compared with other trophic groups (Krashevska et al., 2019), perhaps explaining why this group is so heavily impacted. Fungi are considered more drought resistant than bacteria (Barnard et al., 2013), which would suggest that resource availability for fungal feeders would be less impacted by reduced rainfall than other trophic groups (Guan et al., 2019), even if there are some direct negative effects of water stress (Wagner et al., 2015). However, few studies have assessed the effects on fungal feeders and fungal biomass simultaneously, making it difficult to test this assumption. Plant parasites were somewhat less impacted by reduced rainfall compared with the other trophic groups, except fungivores, possibly because plants provide a more favorable habitat (Olusanya et al., 2019). Given that nematodes are largely dependent on precipitation as all soil fauna are constrained by water availability, at least below certain threshold values (Fehmi & Kong, 2012), we expected a negative correlation between nematode abundances and drought treatments, with greater effect sizes where reduced rainfall results in water limitation. However, response ratios were not related to mean annual rainfall across the study sites, except for a weak albeit significant negative correlation between omnivore–predator effect sizes and rainfall, indicating that the impact of reduced rainfall is relatively consistent and therefore predictable.

It was generally expected that rainfall would have positive impacts on both above- and belowground fauna, particularly in water-limited systems. Surprisingly, total and trophic group's abundances showed no response to increased rainfall across all studies, with individual studies ranging from negative (e.g., Feng et al., 2016; Maranhão et al., 2018) to neutral (e.g., Papatheodorou et al., 2012) and positive (e.g., Andriuzzi et al., 2018; Cesarz et al., 2017) effects. However, it appears that the benefit of increased rainfall may take longer to manifest given the higher total abundances and more plant parasitic nematodes observed in the longer term experiments only. This is likely because reductions in rainfall have more immediate impacts on nematodes due to increased stress as well as longer term indirect effects through changes in resource availability, whereas increased water availability is more likely to predominantly have longer term impacts due to enhanced resource availability (Golluscio et al., 1998; Guan et al., 2019). However, the effects of rainfall changes will also be moderated by antecedent rainfall conditions at the study site irrespective of longer term rainfall (Nielsen & Ball, 2015).

The positive response of plant parasites to increased rainfall in longer term studies (>1 year) may be due to a more rapid increase in plant growth relative to changes in other resources (e.g., microbial biomass, prey for predatory nematodes) (Bardgett & van der Putten, 2014). For example, bacteria and fungi primarily utilize resources derived from plants through rhizodeposition, root growth, and litter inputs, indicating that these organisms will respond to increased plant growth but may not be strongly limited by water per se (Fisher et al., 2013). Similarly, microbial grazers will respond to the increase in bacterial and fungal biomass and activity in the longer term, but this relationship may take longer to manifest. However, increased abundances of plant parasitic nematodes would lead to heightened feeding on plant roots, which could reduce plant growth and thereby suppress effects at higher trophic levels (Guan et al., 2019). Similarly, an increase in feeding activities of microbial grazers could suppress microbial biomass and activity, resulting in weaker responses to increased rainfall (Nielsen, 2019). Furthermore, an increase in predators may cause a decrease in overall nematode abundance (Freckman et al., 1987; Maranhão et al., 2018). Our results hence suggest that climate change may result in altered soil food web composition given observed trophic-group-specific responses.

While climate change is expected to cause increased and decreased precipitation depending on location (Singh et al., 2019), our results show that decreased rainfall will have the strongest and most substantial effects on nematode communities. This trend is consistent with individual studies finding that drought affects abundances more than increased rainfall (e.g., Andriuzzi et al., 2018; Feng et al., 2013). The previous meta-analysis by A'Bear et al. (2014) similarly found negative effects of drought on both plant feeders and bacterial feeders, whereas we also observed negative effects on omnivores–predators. A'Bear et al. (2014) also found that increases in precipitation had a positive effect on nematode abundances across all available studies at that time, while we only observed positive effects in studies of longer duration (i.e., >1 year). Focusing solely on field studies may change the outcome, whereby effects of longer duration studies may simply take longer to manifest compared with a greenhouse where an isolated environment could speed up the process. As plant parasites were seen to only increase in longer term studies, it is critical that we assess the effects of climate change over realistic timelines to more accurately represent changes in our ecosystems. The observed responses to changes in rainfall are well supported in the literature currently, with a few exceptions, which is not surprising as water is well known to be a major driver of the interactions between aboveground and belowground systems (Nielsen & Ball, 2015).

Effect across ecosystem types and with experimental duration

Most ecosystems studied were drylands and grasslands where primary productivity is already water-limited (Knapp et al., 2020; Maranhão et al., 2018) and the abundance of soil fauna communities is expected to be similarly constrained by resource availability (Guan et al., 2019). While nematodes are generally considered relatively drought tolerant (Nielsen & Ball, 2015), our meta-analysis shows that soil nematodes in drylands and grasslands will be severely negatively impacted by a further reduction in water availability, likely because resource availability is further exacerbated or due to stress-driven mortality. Dryland systems are broadly expected to experience reduced rainfall reduction (Zhang et al., 2019), indicating that nematode abundances and ecosystem functions may be severely affected in these widespread ecosystems under future climates. Few papers have manipulated rainfall in forest systems likely because water is not considered a key limiting factor to most forests and because water is difficult to manipulate effectively in deep-rooted plants (Feng et al., 2013). While decreased rainfall did impact nematode abundances in forest ecosystems, the correlation was weaker than in deserts and grasslands.

Conversely, it is expected that an increase in precipitation in ecosystems where water is the limiting factor would alleviate resource constraints, thus facilitating plant growth and microbial activity (Nielsen & Ball, 2015), which in turn would promote nematode abundances. However, organisms that occur naturally in water-limited ecosystems are typically well adapted to drought conditions, which might limit their capacity to quickly respond to increased water availability, for example, due to slow growth rates and longer reproductive cycles (Golluscio et al., 1998). Similarly, in ecosystems with abundant water availability, increased rainfall did not appear to alleviate resource constraints. Nematodes may be more tolerant to reductions in resources such as rainfall; however, they are still semiaquatic organisms, meaning they are not comfortable with reductions in rainfall across space and time regardless of their drought tolerance.

Our results show that experimental duration has a strong impact on the outcome of manipulative studies. Specifically, reduced rainfall has immediate impacts on nematode abundances, whereas increased rainfall takes longer to manifest, with correlations not statistically significant across short-term studies (<1 year). Hence, it may be impractical to reach conclusions about the effects of increased rainfall on soil biota in short experiments (Freckman et al., 1987; Maranhão et al., 2018). However, as discussed above, in the longer term, enhanced resource availability will likely result in increased nematode numbers and shifts in community composition. Similarly, the consequences of reduced rainfall may not be persistent in the long term. For example, over time, species that can survive in water-limited conditions are likely to become more prominent or more drought-tolerant species may colonize, thus the impacts of reduced rainfall could be less severe over a longer period (Diakhaté et al., 2016). This could suggest that the effects observed initially may be ameliorated over time but may also result in changes in community composition as more water-stress-tolerant species become more abundant. Such changes in community composition may impact the ecosystem more broadly over a larger time that we have not yet observed. Finally, it is worth noting that primary production shows a stronger relationship with mean annual precipitation than with interannual rainfall variability (Golluscio et al., 1998), indicating that the effect of altered rainfall regimes through changes in resource availability and quality may take considerable time to manifest (Nielsen et al., 2015).

CONCLUSION

Climate change projections predict less rainfall in most nonpolar regions (Singh et al., 2019). Our results show that such reductions in rainfall will have substantial consequences for soil nematodes globally (45% decrease on average), although fungal feeders may not be impacted. By contrast, increases in rainfall will have weaker impacts on nematode abundances, at least initially favoring plant parasitic nematodes, potentially resulting in cascading impacts on plant growth due to greater root herbivory. Our results therefore suggest predominantly negative effects of climate change on nematodes in most ecosystems, which is expected to impact important soil processes, such as nutrient cycling and decomposition.

AUTHOR CONTRIBUTIONS

Dylan Bristol and Uffe N. Nielsen conceived and designed the meta-analysis. Dylan Bristol collected the data directly from authors and online databases with input from Kamrul Hassan. Dylan Bristol conducted all formal analyses with input from Uffe N. Nielsen and Kamrul Hassan. Dylan Bristol wrote the first draft with direct supervisions from Uffe N. Nielsen, Kamrul Hassan, and Joseph C. Blankinship. All authors reviewed the manuscript critically and approved the final version for publication.

ACKNOWLEDGMENT

The work was supported by funding from the Australian Research Council awarded to Uffe N. Nielsen (DP150104199 and DP190101968).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study and code associated with data visualization and analysis (that are not novel but standard for meta-analysis; Bristol et al., 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.20417526.v1.

ORCID

Dylan Bristol https://orcid.org/0000-0001-7356-3152
Kamrul Hassan https://orcid.org/0000-0002-4921-8313

Joseph C. Blankinship https://orcid.org/0000-0001-5154-7354
Uffe N. Nielsen https://orcid.org/0000-0003-2400-7453

REFERENCES

A'Bear, A. D., T. H. Jones, and L. Boddy. 2014. "Potential Impacts of Climate Change on Interactions among Saprotrophic Cord-Forming Fungal Mycelia and Grazing Soil Invertebrates." *Fungal Ecology* 10(1): 34–43.

Andriuzzi, W. S., B. J. Adams, J. E. Barrett, R. A. Virginia, and D. H. Wall. 2018. "Observed Trends of Soil Fauna in the Antarctic Dry Valleys: Early Signs of Shifts Predicted under Climate Change." *Ecology* 99(2): 312–21.

Andriuzzi, W. S., A. L. C. Franco, K. E. Ankrom, S. Cui, C. M. de Tomasel, P. Guan, L. A. Gherardi, O. E. Sala, and D. H. Wall. 2020. "Body Size Structure of Soil Fauna along Geographic and Temporal Gradients of Precipitation in Grasslands." *Soil Biology and Biochemistry* 140(140): 107638.

Ankrom, K. E., A. L. C. André, S. J. Fonte, L. A. Gherardi, C. M. de Tomasel, W. S. Andriuzzi, E. A. Shaw, O. E. Sala, and D. H. Wall. 2020. "Ecto- and Endoparasitic Nematodes Respond Differently across Sites to Changes in Precipitation." *Oecologia* 193(3): 761–71.

Bardgett, R. D., and W. H. van der Putten. 2014. "Belowground Diversity and Ecosystem Functioning." *Nature* 515: 505–11.

Barnard, R. L., C. A. Osborne, and M. K. Firestone. 2013. "Responses of Soil Bacterial and Fungal Communities to Extreme Desiccation and Rewetting." *The ISME Journal* 7(11): 2229–41.

Begg, C. B., and M. Mazumdar. 1994. "Operating Characteristics of a Rank Correlation Test for Publication Bias." *Biometrics* 50(4): 1088–101.

Blankinship, J. C., P. A. Niklaus, and B. A. Hungate. 2011. "A Meta-Analysis of Responses of Soil Biota to Global Change." *Oecologia* 165(3): 553–65.

Bouwman, L. A., and K. B. Zwart. 1994. "The Ecology of Bacterivorous Protozoans and Nematodes in Arable Soil." *Agriculture Ecosystems & Environment* 51(1–2): 145–60.

Bristol, D., K. Hassan, J. Blankinship, and U. Nielsen. 2022. "Bristol et al. Meta-Data Figshare.xlsx." Figshare Dataset. https://doi.org/10.6084/m9.figshare.20417526.v1.

Cesarz, S., M. Ciobanu, A. J. Wright, A. J. Wright, A. Ebeling, A. Vogel, W. W. Weisser, and N. Eisenhauer. 2017. "Plant Species Richness Sustains Higher Trophic Levels of Soil Nematode Communities after Consecutive Environmental Perturbations." *Oecologia* 184(3): 715–28.

Chiew, F. H., W. J. Young, W. Cai, and J. Teng. 2011. "Current Drought and Future Hydroclimate Projections in Southeast Australia and Implications for Water Resources Management." *Stochastic Environmental Research and Risk Assessment* 25(4): 601–12.

Diakhaté, S., N. Y. Badiane-Ndour, H. Founoune-Mboup, S. Diatta, A. Fofana Fall, R. R. Hernandez, L. Cournac, R. Dick, and L. Chapuis-Lardy. 2016. "Impact of Simulated Drought Stress on Soil Microbiology, and Nematofauna in a Native Shrub + Millet Intercropping System in Senegal." *Open Journal of Soil Science* 6(12): 189–203.

Dima, C., C. Junhui, C. Pengfei, H. Shuijin, X. Yichun, T. Indree, and B. Yongfei. 2015. "Regional-Scale Patterns of Soil Microbes and Nematodes across Grasslands on the Mongolian Plateau: Relationships with Climate, Soil, and Plants." *Ecography* 38(6): 622–31.

Dong, Z., R. Hou, Q. Chen, Z. Ouyang, and F. Ge. 2013. "Response of Soil Nematodes to Elevated Temperature in Conventional and No-Tillage Cropland Systems." *Plant and Soil* 373(1): 907–18.

Fehmi, J. S., and T. M. Kong. 2012. "Effects of Soil Type, Rainfall, Straw Mulch, and Fertilizer on Semi-Arid Vegetation Establishment, Growth and Diversity." *Ecological Engineering* 44: 70–7.

Feng, S., P. Kaiwen, Z. Akash, L. Zhang, X. Sun, Z. Li, S. Wang, Q. Xiong, D. Song, and O. A. Olatunji. 2016. "The Response of the Soil Microbial Food Web to Extreme Rainfall under Different Plant Systems." *Scientific Reports* 6: 37662.

Feng, S., P. Kaiwen, O. A. Olusanya, Z. Li, W. Chen, A. Zhang, D. Song, X. Sun, D. Huang, and X. Tan. 2019. "Specific Legumes Allay Drought Effects on Soil Microbial Food Web Activities of the Focal Species in Agroecosystem." *Plant and Soil* 437(1): 455–71.

Feng, X., A. Porporato, and I. Rodriguez-Iturbe. 2013. "Changes in Rainfall Seasonality in the Tropics." *Nature Climate Change* 3(9): 811–5.

Fisher, J. B., Y. Malhi, I. C. Torres, D. B. Metcalfe, M. J. van de Weg, P. Meir, J. E. Silva-Espejo, and W. H. Huasco. 2013. "Nutrient Limitation in Rainforests and Cloud Forests along a 3,000-m Elevation Gradient in the Peruvian Andes." *Oecologia* 172(3): 889–902.

Freckman, D. W., W. G. Whitford, and Y. Steinberger. 1987. "Effect of Irrigation on Nematode Population Dynamics and Activity in Desert Soils." *Biology and Fertility of Soils* 3(1): 3–10.

Golluscio, R. A., O. E. Sala, and W. K. Lauenroth. 1998. "Differential Use of Large Summer Rainfall Events by Shrubs and Grasses: A Manipulative Experiment in the Patagonian Steppe." *Oecologia* 115(1): 17–25.

Guan, P., X. Zhang, Y. Cheng, H. Zheng, and W. Liang. 2019. "Biocrust Regulates the Effects of Water and Temperature on Soil Microbial and Nematode Communities in a Semiarid Ecosystem." *Land Degradation & Development* 31(11): 1335–43.

Guogang, Z., S. Xin, L. Yang, M. Jia, Z. Wang, G. Han, and L. Wang. 2020. "The Response of Soil Nematode Fauna to Climate Drying and Warming in *Stipa breviflora* Desert Steppe in Inner Mongolia, China." *Journal of Soils and Sediments* 20(4): 2166–80.

Hedges, L., J. Gurevitch, and P. Curtis. 1999. "The Meta-Analysis of Response Ratios in Experimental Ecology." *Ecology* 80(4): 1150–6.

Ilieva-Makulec, K., and H. J. De Boeck. 2013. "Changes in Soil Nematode Community Structure Following Warming and Drought Manipulations in a Grassland Mesocosm Experiment." *Polish Journal of Ecology* 61(1): 157–63.

Jones, F. G. W., D. W. Larbey, and D. M. Parrott. 1969. "The Influence of Soil Structure and Moisture on Nematodes, Especially *Xiphinema*, *Longidorus*, *Trichodorus* and *Heterodera* spp." *Soil Biology and Biochemistry* 1: 153–65.

Knapp, A. K., A. Chen, R. J. Griffin-Nolan, L. E. Baur, C. J. W. Carroll, J. E. Gray, A. M. Hoffman, et al. 2020. "Resolving the Dust Bowl Paradox of Grassland Responses to Extreme Drought." *Proceedings of the National Academy of Sciences of the United States of America* 117(36): 22249–55.

Kojima, Y., J. L. Heitman, G. N. Flerchinger, J. L. Heitman, G. N. Flerchinger, T. Ren, R. P. Ewing, and R. Horton. 2014. "Field Test and Sensitivity Analysis of a Sensible Heat Balance Method to Determine Soil Ice Contents." *Vadose Zone Journal* 13(9): 1–10.

Krashevska, V., A. A. Kudrin, R. Widyastuti, and S. Scheu. 2019. "Changes in Nematode Communities and Functional Diversity with the Conversion of Rainforest into Rubber and Oil Palm Plantations." *Frontiers in Ecology and Evolution* 7: 9–13.

Liu, T., X. Chen, F. Hu, W. Ran, Q. Shen, H. Li, and J. K. Whalen. 2016. "Carbon-Rich Organic Fertilizers to Increase Soil Biodiversity: Evidence from a Meta-Analysis of Nematode Communities." *Agriculture, Ecosystems and Environment* 232: 199–207.

Maranhão, S. R. V. L., E. M. R. Pedrosa, L. M. P. Guimaraes, A. Chaves, D. A. H. S. Leitão, and T. F. S. Vicente. 2018. "Nematode Abundance and Diversity in Sugarcane Fields in Brazil." *Tropical Plant Pathology* 43(6): 485–98.

Nielsen, U. N. 2019. *Soil Fauna Assemblages – Global to Local Scales*. Cambridge: Cambridge University Press.

Nielsen, U. N., and B. A. Ball. 2015. "Impacts of Altered Precipitation Regimes on Soil Communities and Biogeochemistry in Arid and Semi-Arid Ecosystems." *Global Change Biology* 21(4): 1407–21.

Nielsen, U. N., D. H. Wall, and J. Six. 2015. "Soil Biodiversity and the Environment." *Annual Review of Environment and Resources* 40: 63–90.

Nzogela, Y. B., S. Landschoot, A. L. Kihupi, D. L. Coyne, and G. Gheysen. 2020. "Pathogenicity of the Root-Lesion Nematode, *Pratylenchus zeae*, on Rice Genotypes under Different Hydro-Ecologies in Tanzania." *Nematology* 22(2): 221–33.

Olusanya, O. A., S. Gong, A. Tariq, K. Pan, X. Sun, W. Chen, L. Zhang, M. A. Dakhil, D. Huang, and X. Tan. 2019. "The Effect of Phosphorus Addition, Soil Moisture, and Plant Type on Soil Nematode Abundance and Community Composition." *Journal of Soils and Sediments* 19(3): 1139–50.

Papatheodorou, E. M., H. Kordatos, T. Kouseras, N. Monokrousos, U. Menkissoglu-Sprioudi, J. Diamantopoulos, and M. D. Argyropoulou. 2012. "Differential Responses of Structural and Functional Aspects of Soil Microbes and Nematodes to Abiotic and Biotic Modifications of the Soil Environment." *Applied Soil Ecology: A Section of Agriculture, Ecosystems & Environment* 61: 26–33.

Pengfei, W., Z. Hongzhi, C. Liwei, K. Wickings, S. Fu, and C. Wang. 2018. "Author Correction: Impacts of Alpine Wetland Degradation on the Composition, Diversity and Trophic Structure of Soil Nematodes on the Qinghai-Tibetan Plateau." *Scientific Reports* 8(1). https://doi.org/10.1038/s41598-017-00805-5.

Quanhui, M., Y. Hongying, L. Xiaodi, Z. Xu, G. Zhou, and Y. Shi. 2018. "Climatic Warming Shifts the Soil Nematode Community in a Desert Steppe." *Climatic Change* 150(3–4): 243–58.

R Development Core Team. 2020. *R Studio Version 3.6. RStudio: Integrated Development Environment for R*. Boston, MA: Rstudio, Inc.

Rohatgi, A. 2012. "WebPlotDigitizer. Version 4.5." https://automeris.io/WebPlotDigitizer.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. *MetaWin: Statistical Software for Meta-Analysis*. Sunderland, MA: Sinauer Associates.

Singh, R. K., J. Arrighi, E. C. de Perez, O. Warrick, P. Suarez, B. Koelle, E. Jjemba, et al. 2019. "International Conference on Climate Risk Management, Inputs for the Intergovernmental Panel on Climate change's Sixth Assessment Report." *Climate and Development* 8(11): 655–8.

Stott, P. 2016. "Climate Change. How Climate Change Affects Extreme Weather Events." *Science* 352(6293): 1517–8.

Sylvain, Z. A., D. H. Wall, K. L. Cherwin, D. P. C. Peters, L. G. Reichmann, and O. E. Sala. 2014. "Soil Animal Responses to Moisture Availability Are Largely Scale, Not Ecosystem Dependent: Insight from a Cross-Site Study." *Global Change Biology* 20(8): 2631–43.

van den Hoogen, J., S. Geisen, D. Routh, H. Ferris, W. Traunspurger, D. A. Wardle, R. G. M. de Goede, et al. 2019. "Soil Nematode Abundance and Functional Group Composition at a Global Scale." *Nature* 572(7768): 194–8.

Vandegehuchte, M. L., Z. A. Sylvain, L. G. Reichmann, C. M. de Tomasel, U. N. Nielsen, D. H. Wall, and O. E. Sala. 2015. "Responses of a Desert Nematode Community to Changes in Water Availability." *Ecosphere* 6(3): 44.

Viechtbauer, W. 2020. "Automated Report Generation for Meta-Analyses Using the R Package Metafor, 'Metafor Version 2.4'." *Meta-Analysis Package for R*. Evidence Synthesis Technology Webinar, Environmental Evidence Summit.

Wagner, D., N. Eisenhauer, and S. Cesarz. 2015. "Plant Species Richness Does Not Attenuate Responses of Soil Microbial and Nematode Communities to a Flood Event." *Soil Biology and Biochemistry* 89: 135–49.

Xiaoming, S., X. Zhang, S. Zhang, G. Dai, S. Han, and W. Liang. 2013. "Soil Nematode Responses to Increases in Nitrogen Deposition and Precipitation in a Temperate Forest." *PLoS One* 8(12): e82468.

Zhang, W., G. Villarini, and G. A. Vecchi. 2019. "Impacts of the Pacific Meridional Mode on Rainfall over the Maritime Continent and Australia: Potential for Seasonal Predictions." *Climate Dynamics* 53(12): 7185–99.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Bristol, Dylan, Kamrul Hassan, Joseph C. Blankinship, and Uffe N. Nielsen. 2023. "Responses of Nematode Abundances to Increased and Reduced Rainfall under Field Conditions: A Meta-Analysis." *Ecosphere* 14(1): e4364. https://doi.org/10.1002/ecs2.4364