# Abstract

The increased frequency of precipitation extremes under climate change is expected to profoundly affect forest ecosystems both aboveground and belowground. However, understanding of responses in belowground communities remains limited due to complex and contrasting results. Soil fauna regulate key ecosystem processes and disturbances would have implications on the global carbon cycle. Here, to address this knowledge gap, a meta-analysis is carried out of over 350 observations from 36 globally distributed forest sites to investigate patterns in the effect of precipitation increases and decreases on soil fauna. Variations in responses were investigated with regard to body size, feeding behaviour, treatment magnitude and duration, local climate, and ecosystem type. Soil fauna abundance and diversity present a correlation with the magnitude of water alteration that depends on body size. Mesofauna and microfauna abundance decrease with intensified water loss and increase under water addition while the opposite is found for macrofauna. The positive effect of precipitation on soil fauna abundance also depends on disturbance duration; the effect of water addition on mesofauna decreases with time but increases with time for macrofauna. Overall, soil biota abundance responded more to precipitation decreases whereas soil biota diversity responded more to precipitation increases. The effect of precipitation alteration on soil fauna biodiversity was of a smaller magnitude and did not depend on body size. Responses of abundance and diversity to precipitation change were consistent across forest biomes and local climate. Assessment of realism and the methodological quality of experimental studies provides explicit suggestions for improving the internal and external validity of future studies. This meta-analysis suggests that the responses of soil biota to global change are predictable by the intensity of precipitation alteration **and therefore initiatives to include soil fauna in models of carbon cycling should include the duration and magnitude of precipitation changes as moderators.**

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# Introduction

Soil is the largest reservoir of biodiversity on Earth, home to one quarter of all living species (FAO, 2020). Soil fauna are integral to maintaining the threatened carbon sink in forests through their role in organic matter mineralisation, regulating primary production, and developing the soil structure (Verhoef, 2004). Therefore, scientific research and public discourse have become increasingly aware of the potential ability of soil communities to contribute to tackling the major environmental crisis of our time **(Monbiot, 2022).** However, forest soil communities are threatened by both physical habitat degradation and the adverse effects of global change (Tibbett et al., 2020). Changes in the hydrological cycle, driven by climate change, will increase the frequency and magnitude of extreme precipitation and dry events experienced by forest soils (**IPCC, 2019**). Due to the contribution of soil biota to providing key ecosystem services, interest in threats to soil biota has grown and is an increasingly active scientific field. This research project conducts a meta-analysis of soil fauna literature to investigate whether there are general patterns in the response of forest soil biota to extreme precipitation increases and decreases and what variables influence the impact of precipitation alteration. Section 1 details the context and rationale of the study and Section 2 describes the methodology. The results are presented in Section 3 and discussed in Section 4. Section 4 also includes study limitations, knowledge gaps in the literature and recommended research priorities for understanding the consequences of changing precipitation regimes for soil communities.

## Environmental change

Greenhouse gas emissions from human activities have caused unprecedented changes in the global climate (IPCC, 2019). Projected alterations of global atmospheric circulation and hydrological processes will modify mean annual precipitation and precipitation variability (IPCC, **REF**). Changes manifest as expansions of arid regions (Seager et al., 2018) and increased frequency and severity of extreme precipitation events (Y. Sun et al., 2007). The altered precipitation regimes are anticipated to profoundly alter the functioning and structure of terrestrial ecosystems (Knapp et al., 2008) and consequently influence the terrestrial carbon cycle, with potential feedbacks on future global scale change. This has promoted extensive research intro the consequences of precipitation changes, particularly in forests due to their significant role in carbon cycling and storage (Friedlingstein et al., 2020; Walker et al., 2021). In addition to sequestering approximately 12% of anthropogenic carbon emissions, forests also provide vital ecosystem services at local, regional and global scales(Thompson et al., 2011). Disturbances are important drivers of forest ecosystem dynamics (Franklin et al., 2002; Kuuluvainen & Aakala, 2011), and thus changing disturbance regimes could considerably alter the structure and functioning of these ecosystems. However, while the impacts on forest structure, tree mortality, and aboveground biodiversity are relatively well understood, the impact on soil biological communities is less well known.

## Role of soil biota.

Threats to soil biota is important as these communities play a key role in regulating biogeochemical cycling, providing essential ecosystem services through nutrient and carbon cycling. While bacteria and fungi carry out nearly 90% of decomposition (Swift et al., 1979) the larger soil fauna play an important role in the initial stages of decomposition, providing fragmented plant material in useful forms for microbial mineralisation (DeLuca et al., 2019). Soil fauna also regulate nutrient cycling by feeding directly on organics matter or distributing nutrients by grazing on or transporting microbes through adhesion or their digestive tracts (Paul et al., 2015). Biodiversity is understood to be particularly good indicator for the performance and health of any ecosystem and this holds for below-ground ecosystems (van Straalen, 1998). Hugely diverse and complex biological communities exist in the soil, promoted by the vast number of niches that are available in such a physiochemically heterogenous environment (Tiedje et al., 2001; Ettema and Wardle, 2002). Below-ground biodiversity is intimately linked to above-ground functioning (Fierer et al., 2009; Wardle et al., 2004). Ecosystem multifunctionality, including plant diversity, decomposition, nutrient retention, and nutrient cycling, is greatly enhanced with increased soil biodiversity (Wagg et al., 2014). Soil species play an integral role in determining soil properties, for example, aeration, hydrology, and gaseous components (Hole, 1981). Soil biodiversity has also been shown to improve plant resilience to disturbance (Márquez et al., 2007; Redman et al., 2002). Despite the importance of soil biota scarce taxonomic knowledge, technical challenges associated with the inaccessibility of soil, and the small size of most soil organisms means scientific understanding of soil organisms and diversity remains limited (Bardgett, 2002; Wardle et al., 2002).

## Threat to forest carbon sink

Any changes to the soil biota will have widespread implications for the ecosystem services they provide (Haines-Young & Potschin, 2012; Yang et al., 2018). The global budget for carbon depends on soil biodiversity (Nielson et al., 2010), so understanding the impact of high and low precipitation extremes on soil communities is vital, particularly in forest ecosystems which are major carbon sinks (Piao et al., 2019). The threat of precipitation change to the forest carbon sink remains uncertain. Evidence shows that precipitation reduction can stimulate changes in soil biota and trophic structure that indirectly cause an increase in carbon litter loss (Homet et al., 2021; Tsiafouli et al., 2018), which has the potential for unfavourable positive feedbacks with climate change. On the other hand, Santonja et al. (2017) show a decrease in carbon loss under low precipitation conditions. Threats to soil biodiversity are of particular concern since biodiversity loss is a major driver of change in ecosystem function (Bardgett & van der Putten, 2014; Fanin et al., 2018; Hautier et al., 2015). However, huge biodiversity of soils results in considerable functional redundancy in some cases (**Walker, 1992**, Wellnitz and LeRoy Poff, 2001), clearly demonstrated by the 89 species of nematodes identified in one Cameroon forest soil core (Bloemers et al., 1997). Low responsiveness of some ecosystems to extreme events indicates a high buffering capacity (Kreyling et al., 2008). Thus, the threat to soil functional diversity is complex and a subject of some debate.

## Conflicting results from experimental studies

Despite a large amount of research on the impacts of precipitation increases and decreases on soil fauna, generalising about their impact is difficult due to conflicting results. Empirical studies on the effects of precipitation reduction on forest soil fauna show decreased abundances in a range of soil fauna, from Nematodes and Collembola (Landesman, Treonis and Dighton, 2011; C. Wang et al., 2021; Pflug and Wolters, 2001; Kuperman, Potapov and Sinitzina, 2002) to Oribatid mites and beetles (Lindberg and Bengtsson, 2005; Williams et al., 2014). However, other studies show increases in termites (Ashton et al., 2019), microarthropods (R. S. Williams et al., 2014) and Acari (Lensing et al., 2005), and negligible impacts on mesofauna (A. R. Taylor et al., 2004). Elevated precipitation tends to increase soil fauna abundance and diversity as organisms are positively related to soil moisture, particularly arthropods, such as Collembola, Acari and Isopoda (Chikoski et al., 2006; S. N. Johnson et al., 2018). However, precipitation increases tend to affect the abundance and composition of soil biota less than decreased precipitation, implying an asymmetrical response to precipitation changes (Lindberg et al., 2002; R. S. Williams et al., 2014). For instance, in some studies Collembola and Oribatida do not respond to increased precipitation, indicating some inbuilt resilience (Lindberg & Persson, 2004). For smaller organisms such as Nematodes, there is evidence of a decline in abundance in the mineral layer, but increases at deeper depths (Liu et al., 2020), although this is inconsistent with other observations of negligible response to precipitation extremes (Sohlenius & Wasilewska, 1984). Larger organisms may also be less affected by water addition (Riutta et al., 2012).

The reasons for the variation between studies is not clear but may be linked to differences in the traits of different soil fauna taxa, variations in local climate and ecosystem type and/or differences in the characteristics of disturbance (e.g., magnitude of precipitation alteration, or duration of disturbance) (Blankinship et al., 2011; Fierer et al., 2009). These factors will affect the resistance (the impact of a disturbance) and the resilience (the speed of recovery to pre-disturbance level) of soil communities.

## Body size

The focus on single taxonomic groups in experimental studies has led to a limited general understanding of soil organisms’ resilience to disturbance and what leads to disparities between or within different taxonomic groups. The focus on a single or limited amount of soil taxonomic groups is predominantly due to practical constraints and the large heterogeneity of relevant spatial scales that comes with the huge variance in body size among organisms (macrofauna can be 1000 times the size of microfauna) (**Berg, in Hall et al., 2012).** To overcome the difficulties in drawing general conclusions about the soil community, soil biota are commonly classified according to size (body width) into three main groups: macrofauna (500 μm– 50 mm, e.g., earthworms, termites), mesofauna (80 μm– 2 mm, e.g., Collembola, Acari), and microbiota (1–120 μm, e.g. bacteria, fungi, protozoa, nematodes) (Figure 1). While body size cannot be unequivocally connected with function, it is a pragmatic solution to categorisation based on several key concepts. For instance, body width relates to their microhabitats: microfauna inhabit water films, mesofauna inhabit existing air-filled pore spaces, and macrofauna, as ecosystem engineers, are able to create their own pore spaces and contribute to soil structure development. Body size is also related to an organism’s adaptive capacities (**Lavelle and Spain, 2001**), dispersal characteristics (**Berg, 2012;** Ettema and Wardle, 2002), position in the food web (Petchey et al., 2008; R. J. Williams & Martinez, 2004), and rate of reproduction, all of which are regulators of biota resistance to disturbance (Scheu & Schulz, 1996; Siepel & van de Bund, 1988). Alternative groupings, such as trophic levels, become increasingly difficult to apply with increasing size as the trophic structure becomes more fluid with organisms operating on several separate trophic levels (**Swift et al., 1979**).

Diagram

Description automatically generated

Figure 1 Size classification according to body width (from Swift et al., 1979 in Nielsen, 2019)

The importance of body size in explaining the response of soil biota to changing precipitation patterns remains unclear. Resistance to reduced precipitation is associated with an organism’s dependence on free water in soil, with resistance to desiccation generally increasing with decreasing size (Lavelle and Spain, 2001). However, smaller organisms can access resources in small pore spaces unavailable to larger organisms (Strong et al., 2004). Furthermore, microfauna recover relatively rapidly from drying events (Fierer et al., 2003), whereas larger organisms such as microarthropods recover more slowly, if at all (Lindberg et al., 2002). Differing responses could reflect differences in reproduction rates or reproductive strategies (Moore et al., 1988), with fast-reproducing species, like microfauna, able to show larger responses to favourable conditions more likely to recover quickly from negative impacts (Jernelöv & Rosenberg, 1976; Morecroft et al., 2002). This suggests possible interactions with the severity and duration of precipitation alteration.

## Trophic levels

Trophic dynamic theory (e.g., Hairston, Smith and Slobodkin, 1960) indicates that trophic levels experience different limitations, so will exhibit specific responses to changes in precipitation. Trophic levels are a basic abstraction of the food web and describe the hierarchical levels in a food chain which are comprised of organisms that are functionally equivalent and share the same feeding habits (Reichle, 2020). However, the influence of trophic levels is complex. For example, a greenhouse study found that while lower trophic levels were decreased by drought, the higher trophic levels showed a mix of positive and negative responses (de Vries et al., 2012). Dry conditions have been shown to amplify top-down effects of predatory soil invertebrates (Lang et al., 2014), which interacts with low soil moisture content to negatively affect detrivorous and fungivorous mesofauna (Santonja et al., 2017). Few studies have looked at the effect of irrigation on soil food web structure, but results from a temperate forest experiment show increased precipitation suppressed bacterivorous and fungivorous nematodes (Liu et al., 2020). Indirect effects on soil fauna include trophic cascades from the strongly affected microbes (Peguero et al., 2021).

## Strength and duration of disturbance

Only a few soil biota studies have considered the impact of variations in the magnitude or frequency of precipitation disturbance (Nielsen & Ball, 2015). Intensification of precipitation is expected to modify the activity and metabolic rates of soil biota (Whitford, 1989) and affect the carbon and nutrient pool of the soil (Nielsen & Ball, 2015). Empirical results suggest the effects of a disturbance (both water addition and reduction) depend more on the duration than severity (Flórián et al., 2019). However, the intensity and duration of water reduction might interact, with evidence that the effects of elevated drought intensity are strongest for long term drought compared to brief time scales (Gao et al., 2019), while for a less severe reduction in precipitation the long-term resilience within soil biota was high (Holmstrup et al., 2017). Organisms may be well adapted to survive occasional severe drought episodes but be reduced in abundance during a prolonged dry period (Holmstrup et al., 2012). Tree mortality is also more sensitive to prolonged precipitation reductions than short-term drought (DeSoto et al., 2020), which would likely impact below-ground sensitivity to drought duration. Previous meta-analysis suggests the positive effect size of precipitation on abundance intensified with time but did not consider the impact of disturbance strength (Blankenship et al., 2011). Disturbance intensity and duration interactions likely fluctuate with ecosystem type and the context of climate (F. Sun et al., 2020).

## Background climate and ecosystem type

Soil organisms are adapted to survive under dry conditions (Waagner et al., 2011), especially in arid and semi-arid areas where drought is a common climatic feature (Petersen, 2011).

Physiological and phenological adaptations of arthropods to water level fluctuations have been observed in the Amazon and Central European floodplains (Adis & Junk, 2002; Junk, 1997), including high reproduction rates, dispersal and reimmigration (Marx et al., 2012). Therefore, the precipitation regime of a region may determine the response of soil biota to precipitation disturbance (Nielsen & Ball, 2015; Petersen, 2011).

Soil and ecosystem factors also affect the resilience of soil biota (Bachar et al., 2010), where changes in pH result in changes in Acari and Collembola abundance and their interactions with other organisms (Verhoef & Dorel, 1988). Physical properties, such as texture and bulk density, have a strong influence on soil resilience and resistance to disturbance (Miller & Baharuddin, 1987). The effect of disturbance also differs between forest types (Seidl et al., 2017). Certain plant-soil interactions can increase the resilience of soil biota through enhanced root biomass and plant supplementation of nutrients (F. Sun et al., 2016, 2018), and above-ground biodiversity tends to drive below-ground diversity, particularly in the rhizosphere (Kowalchuk et al., 2002).

## Using meta-analysis

A quantitative synthesis of results across studies will enlighten us to the general effects of precipitation decreases and increases on soil fauna and identify the sources of variations (Gurevitch et al., 2018). The need for generalisations and exploring variability between studies has been emphasised in recent years (Birkhofer et al., 2012) and meta-analyses provides an effective way to achieve this goal if used correctly. Meta-analysis is a statistical method now used extensively in ecology and has made a significant contribution to the field, for example through developing theories, examining covariates, and assessing the impact of global change. However, meta-analyses are often carried out without recognition of key methodological pitfalls, including the violation of statistical assumptions. A large literature exists on these pitfalls, but the quality of ecology meta-analysis remains mixed (Gates, 2002; Koricheva & Gurevitch, 2014; Stewart, 2010). The use of checklists such as those developed for ecologists by Koricheva and Gurevitch (2014) and Nakagwa et al. (2017), and for other disciplines such as PRISMA (<https://prisma-statement.org/PRISMAStatement/>) are useful for ensuring quality standards of a meta-analysis and appropriately interpreting results. This includes overcoming difficulties resulting from missing data, publication bias, non-independence among observations, and data exclusion (Gurevitch et al., 2001). Investigating the quality of primary studies is particularly overlooked, and involves assessing both the internal validity, the reliability of the results, and the external validity, the generalisability and realism of results (Gates, 2002). For instance, here the internal validity would be the extent to which a study represents a trustworthy causal relationship between a precipitation change treatment and an effect on soil biota. For a global change meta-analysis, the external validity of the studies can be understood as the comparability of hypothetical and actual environmental changes. Precipitation changes in disturbance experiments generally surpass mean rates of projected changes (Korell et al., 2020) due to a focus on short-term extreme events. Extreme events affect ecosystem functioning more than average changes (Smith, 2011), so these experiments are pertinent, but for longer term experiments there are a shortage of experiments that reflect the site-specific changes projected by General Circulation Models (de Boeck et al., 2020; Korell et al., 2020).

## Research questions and aims

Over the last decade, several meta-analyses have focused on the effect of global change on soil biota abundance and diversity (Blankinship et al., 2011; Manzoni et al., 2012; H. Wang et al., 2021; Peng et al., 2022). The results show a general decrease in abundance and diversity with reduced precipitation and increases with elevated precipitation. However, these studies were limited in scope and did not compare decreases and increases in precipitation in the same study (except Peng et al., 2022). In addition, most of these studies used search methods that were not comprehensive (i.e., solely dependent on bibliographic platforms), potentially leading to unreliable estimates of the impacts of changes in precipitation (Konno & Pullin, 2020).

This study aims to answer the following research questions:

1. **To what extent do precipitation extremes, including increases and decreases, effect the abundance and diversity of soil fauna in forests?**

This study hypothesizes that precipitation extremes effect the abundance and diversity of soil biota. Due to the positive relationship of soil biota to soil moisture, I expect that precipitation decreases will decrease abundance and diversity whereas precipitation will lead to increases. The effect of precipitation decreases is expected to be of a larger magnitude than precipitation increases.

1. **To what extent do disturbance effects depend on body size?**

I hypothesise that the disturbance effect on abundance and diversity depends on the body size of the measured organism. Due to the strong relationship between body size and an organism’s adaptive capacity, I consider that larger organisms will be more resilient to disturbance compared to smaller, less mobile organisms.

1. **Do the varied responses among organisms of a similar body size depend on disturbance intensity, disturbance length, forest type, soil factors, and background climate?**

I hypothesise that non-uniform responses among body size groups depend on disturbance intensity, disturbance length, forest type, soil factors, and background climate.

1. **Does the trophic level of an organism impact resilience to disturbance?**

I consider that the trophic level of an organism will impact the resilience to disturbance due to differing limitations.

# Methods

## Data acquisition

This meta-analysis was conducted from a set of filtered studies that had been selected according to the systematic review process outlined in full by Martin et al. (**2022**). The search was conducted using four bibliographic platforms (Scopus, Web of Science Core Collection, and Open Access Theses and Dissertation) and internet searches (Google Scholar) and was limited to include only English language publications. The search terms were defined by the different Population, Exposure, Comparison, Outcomes, and Space (PECOS) elements of the studies’ interest following Grames et al. (**2019**). Therefore, the following eligibility criteria for studies to be included in the meta-analysis were used: 1) the studies must measure the response of one or more soil fauna organism to precipitation increases or decreases in a forest ecosystem; 2) the studies must consider either a spatial or temporal comparison between the frequency or intensity of forest disturbance; 3) measured outcomes must include the quantitative assessment of either abundance, biomass, trophic interactions or diversity (e.g., Shannon-Weiner Index, Simpsons Diversity Index) of soil fauna; 4) studies must be field based. Here soil fauna is defined as invertebrates which spend a significant portion of their life in litter and/or soil. Ants were excluded from this definition due to the very large literature on this group, meaning reviewing impacts on all taxa would have been difficult. Table 1 gives details of the different keywords and associated PECO elements for this study. Given the large number of syntheses on the impact of natural disturbances on soil microbes, they were considered outside of the scope of this study.

After filtering the initial study set with the above eligibility criteria, the search yielded 30 studies: 5 studies which considered both precipitation decreases and increases; 14 precipitation decrease studies; and 11 precipitation increase studies.

## Critical appraisal

Critical appraisal of studies considered suitable for quantitative synthesis is an important part of the systematic review process (Pullin et al., 2018). Doing this assesses the methodological robustness of a study by considering the threats to the internal validity of a study. Appraisal was carried out with the criteria in Appendix 1, following the protocol in Martin et al. (2020). The key biases considered are: (1) selection, (ii) confounding, and (iii) performance bias. Studies are assigned as ‘low validity’, ‘medium validity’, and ‘high validity’ depending on the fulfilment of criteria (Appendix 3). Sensitivity analysis was performed by examining how summary effect sizes are altered by excluding studies considered low validity Appendix 4.

## Data coding and extraction

For data extraction, response data were taken directly from tables, figures, and written text. Data were extracted from figures using the R package metaDigitise (Pick et al., 2019). Within this package, axis scales were defined, and data point locations were defined by hand. Means, measures of variability (standard deviations (SD) or standard errors (SE)) and sample sizes for treatment and control groups were extracted. When SEs were reported, the SDs were calculated as: , where is the number of replicates. Additional information extracted from the studies is summarised in Table 2 and included: response parameter, units, disturbance type (precipitation increase or decrease), time since disturbance started, trophic level of soil organism, method of soil biota sampling, quantitative characterisation of disturbance severity, forest type (e.g., temperate seasonal forest, boreal forest, tropical forest), size of plot and sampling area, depth of sampling, soil characteristics (pH, soil texture, soil organic matter, soil moisture), page number, table or figure number. The disturbance severity and associated units were extracted from the study as reported and converted into a percentage of annual precipitation change if needed. To ensure some degree of independence between measurements, if a study reported several taxonomic resolutions, the species or trophic groups were recorded as subsets of the lowest taxonomic resolution and were treated as such in subsequent statistical analysis.

Table 1 Terms associated with different PECO elements (Martin et al., **2022**)

|  |  |  |
| --- | --- | --- |
| **PECO element** | **PECO elements for this study** | **Search terms related to PECO element** |
| Population | Forest soil fauna | Forest synonyms = Forest, Woodland, Plantation  Soil synonyms = Soil, Belowground, Root  Soil fauna terms = Soil biodiversity, Belowground biodiversity, Soil diversity, Belowground diversity, Biodiversity, Biota, Fauna, Microfauna, Mesofauna,  Macrofauna, Animal, Arthropod, Invertebrate, Detritivore, Macroarthropod, Microarthropod, Protozoa, Ciliate, Nematode, Nematoda, Protist, Rotifer, Rotifera, Tardigrade, Acari, Oribatid, Mite, Collembola, Springtail, Protura, Diplura, Symphyla, Chelonethi, Opiliones, Harvestmen, Ispotera, Termite, Isopoda, Woodlice, Amphipoda, Megadrilacea, Oligochaete, Annelid, Enchytraeus, Enchytraeidae, Potworm, Lumbricidae, Earthworm, Chilopoda, Centipedes, Diplopoda, Millipedes, Coleoptera, Beetles, Araneida, Spiders, Mollusca,  Snails, Slugs |
| Exposures | Drought, Extreme rainfall | Drought, Storm, Rain, Precipitation, Disturbance, Global change, Hurricane |

## Trophic level

The dataset was modified to include trophic group information to test for common changes in trophic structure among certain taxa. Species were categorised according to the following broad behaviour: species that are parasitic (parasites), or consume detritus (detritovores), consume plant roots (herbivores), bacteria (bacterivore), fungi (fungivores), or soil fauna (predators). Species were placed into trophic categories using author defined trophic descriptions where available as authors are considered in the best position to describe the role of species within their study system. Where descriptions were not included, trophic levels were defined from general patterns in the literature. Araneae, Chilipoda, and Mesostigmata were defined as predators (Koehler, 1999; Lewis et al., 2006; Samiayyan, 2014), and Thysanoptera were defined primarily as herbivores, although some are known to be fungivores (**Mound, 2009**). Collembola were defined as primarily fungivores (Bengtsson, Hedlund and Rundgren, 1994; **Coleman et al., 2017**), despite occasional ingestion of soil fauna, or decomposing plant or animal debris (Coleman, 2008; Gilmore & Potter, 1993; Gunn & Cherrett, 1993). However, the omnivorous feeding habits of Acari, Coleoptera, Enchytraeidae, Nematoda and other macroarthropods precludes categorisation from the literature (Dash, Senapati and Mishra, 1980; Yeates et al., 1993; Brussaard, 1998; Halaj, Peck and Niwa, 2005; Schmelz et al., 2013, O’Connor, 1967).

This meta-analysis includes 639 observations, 364 of which are not subsets of lower taxonomic resolutions and thus used in main analysis. Of these 364, 221 were related to precipitation decreases (147 abundance and 71 diversity observations) and 236 were related to precipitation increases (105 abundance and 36 diversity observations).

## External data extraction

Missing and extra data was obtained using the raster and hwsdr package in R (Wieder et al., 2014; **Hufkens, 2021**). Mean annual temperature and precipitation data were extracted from [worldclim.org](http://www.worldclim.org) and soil properties (silt, sand, and clay content, pH, available water storage capacity (WSC), organic carbon, and bulk density) were extracted from the Harmonised World Soil Database (HWSD) (Fischer et al., 2006). The site locations were plotted on a Whittaker biome diagram (**Stefan and Levin, 2022**) using the plotbiomes R package and on terrestrial ecoregions using ArcGIS 10.3.1. (Dinerstein et al., 2017).

Table 2. Meta-data extracted from each study considered suitable for quantitative synthesis

|  |  |
| --- | --- |
| **Metadata Extracted** | **Detailed description** |
| Response parameter | Density/abundance, richness, other diversity metrics, evenness, community composition. |
| Disturbance type | Precipitation increases or decreases. |
| Taxonomic group | Taxonomic group of organism. |
| Trophic group | The trophic of the taxonomic group the data refers to. If not detailed in study, defined from literature. |
| Latitude and Longitude | The latitude and longitude of the site. |
| Mean Annual Precipitation | The mean annual precipitation in mm as reported in the study. |
| Mean Annual Temperature | The mean annual temperature in °C as reported in the study. |
| Month sampling was done | The calendar month in which sampling was undertaken. |
| Season sampled | The season in which sampling was undertaken. |
| Forest biome | Ecosystem classified as boreal forest, temperate seasonal forest or tropical forest. |
| Coniferous/deciduous | Whether the dominant species in the forest site studied was coniferous or deciduous. |
| Managed/unmanaged | Whether a site was managed for forestry or not. |
| pH | Soil pH as reported in the study. |
| Soil moisture | Soil moisture as reported in the study. |
| Soil type | Broad soil classification. |
| Depth of sampling | The depth to which soil was sampled. Method such as pitfall traps or active searching is ‘NA’. |
| Size of plot | Area of plot used for treatment or control in m2. |
| Size of sampling unit | Area of sampling unit used in cm2. |
| Strength of treatment during disturbance | The percentage change in precipitation as a result of rainfall exclusion or addition during the period of disturbance. |
| Average annual strength of disturbance | The percentage change in precipitation over an entire year. The magnitude of this change will be lower when the disturbance is imposed for less than one year. |
| Time after disturbance was imposed | Time since the beginning of the disturbance. |
| Time after disturbance has finished | Time since the disturbance finished. If the disturbance is ongoing enter ‘NA’. |
| Active/passive sampling | Is the sampling active (e.g. baited traps or mustard extraction of earthworms) or passive (e.g. removal of soil cores). |

## Statistical Analyses

For each comparison, the response ratio of abundance or diversity was calculated between the altered precipitation site (treatment group) and the control site:

where is the mean abundance or diversity of the disturbed site and is the mean abundance or diversity of the control site. To be useful for statistical analysis, the natural logarithm of the response ratio (lnRR) was employed following Hedges, Gurevitch and Curtis (1999):

If and are normally distributed and is unlikely to be negative (true for this study), then will be approximately normally distributed with mean approximately equal to the true log response ratio (Hedges et al., 1999; D. W. Johnson & Curtis, 2001). For ease of interpretation when presented in text, the logarithmic response ratio and confidence intervals of treatments were back-transformed to a linear measure of percentage change after disturbance as follows:

where is the model estimate. As with most ecological meta-analyses, a random effects model was used with the assumption that differences among studies within a group are due to both sampling error and random variation (Gurevitch & Hedges, 1999). Meta-analyses commonly weight study effect sizes by the inverse of within-group variance to raise the power of studies with lower variation and therefore improve the precision of the estimate of overall mean effect (Gurevitch & Hedges, 1999; Koricheva & Gurevitch, 2014). However, in this study approximately 25% of the studies did not report estimates of variation. To include as many studies as possible and avoid biases introduced by deleting missing data (Kambach et al., 2020; Nakagawa & Freckleton, 2008) absent effect size variances were imputed based on the median effect size variance (Weir et al., 2018).

All meta-analysis computations were done in R using the metafor package (Viechtbauer, 2010). While two studies are considered the minimum requirement for meta-analysis (Valentine et al., 2010), this study only conducts a meta-analysis or sub-group analysis when there are three or more studies.

A linear mixed-effect model was applied to test whether the responses of abundance and diversity to precipitation treatments differed from zero. To account for possible pseudoreplication at the study scale, each model included study and site as a random factor. Heterogeneity was estimated using the I2 statistic, which estimates the proportion (from 0 to 100) of the variance in study estimates that is due to true between study heterogeneity (Higgins & Thompson, 2002)). Datasets that show high I2 values (>50%) indicate substantial heterogeneity deriving from true between study variance which should be explored through further analysis.

Possible causes of true between-study variance heterogeneity were explored by conducting mixed effects meta-regressions with study and site as the random effect and various moderators. Many variables, outlined in Table 3, were considered in this subgroup analysis to provide a broad overview. This analysis was performed on the dataset including only observations where the disturbance duration and strength is defined (90% of full dataset). Analysing many subgroups can inflate Type I errors (**Berry, 1990**), so the occurrence of these errors should be considered when interpreting results. These explanatory variables were assessed for collinearity to ensure that modelled variables could be estimated independently. The distribution and shape of data for each moderator was assessed for evenness to inform the robustness of subsequent analysis.

To investigate the effect of trophic level on the response of soil biota to disturbance, the original dataset was reduced to include only observations with trophic level information. The dataset was also reduced to include only nematode observations for a sub-analysis of nematodes due to the high number of nematode observations. Mixed effects meta-regressions were also conducted on this data. Whenever fewer than three comparisons per grouping remained, the category was excluded from further analysis.

## Model selection

The Akaike information criterion for small sample sizes (AICc), an estimator of prediction error, was used to provide support for each model (Burnham & Anderson, 2004). The model with the lowest AICc was considered the most parsimonious, best model. Models with AIC ≥7 are considered to have no support. The goodness of fit of each model was estimated by calculating a psuedo R2 for each model as presented by Raudenbush **(1994, 2009)**:

where the residual heterogeneity, , is the difference in total variance, , after adding one or more predictors to the model. This can provide a negative estimate, which is truncated to zero (López-López et al., 2014).

Means were considered to be significantly different from one another if their 95% confidence intervals (CIs) were nonoverlapping and were significantly different from zero if the 95% CI did not overlap with zero (Gurevitch & Hedges, 1999). All statistical analysis was performed in R, with meta-analysis carried out using the metafor package (Viechtbauer, 2010) and figures drawn using ggplot2 and orchardplot packages (Wickman, 2016; Nakagawa et al., 2017).

Table 3. Description and range of predictor variables used in the models

|  |  |  |  |
| --- | --- | --- | --- |
| **Variable in models** | **Description** | **Range** | **Reference** |
| Body size | Microfauna, mesofauna, or macrofauna | - | - |
| ***Disturbance*** |  |  |  |
| Duration | Time since the disturbance began (years) | 0 – 17 | - |
| Strength | Change in mean annual precipitation applied to plot (%) | -100 – 239 | - |
| ***Environment*** |  |  |  |
| Forest biome | Temperate seasonal forest, tropical forest, boreal forest | - | - |
| Temperature | Mean annual temperature in \*C | 1.2 – 28.9 | Primary studies and WorldClim |
| Precipitation | Mean annual precipitation (mm) | 383 – 4500 | “ |
| ***Soil parameters*** |  |  |  |
| pH |  | 3.6 – 7 | Wieder et al. (2014) |
| Total carbon | Topsoil organic carbon % weight | 2.1 – 22.3 | ” |
| Available WSC | Available water storage capacity (coded values; 1 = 150mm water per m of the soil, 6 = 15mm | 1 – 6 | ” |
| Bulk density | Topsoil bulk density (kg dm-3) | 1.1 – 1.54 | ” |
| Sand | Topsoil sand fraction (% weight) | 17 – 85 | ” |
| Silt | Topsoil silt fraction (% weight) | 10 – 44 | ” |
| Clay | Topsoil clay fraction (% weight) | 4 – 51 | ” |
| ***In sub models*** |  |  |  |
| Trophic level | Bacterivore, detritivore, fungivore, fungivore/detritivore, herbivore, mixed, omnivore, predator | - | Primary studies and literature |
| ***Robustness*** |  |  |  |
| Year | Year of publication | 1984 - 2021 | - |
| Plot scale | Area of the plot to which treatments were applied (m2) | 2.19 - 2500 | - |
| Sample scale | Area of the sample (cm2) | 4.15 - 7854 | - |

## Bias and Sensitivity Analysis

Publication bias occurs when studies that found non-statistically significant results are missing due to a lower likelihood of publication (Jennions & Møller, 2002a; Lortie et al., 2007; Marks-Anglin & Chen, 2020). Bias may be suspected if small positive effect sizes are present without small negative effect sizes (Newton et al., 2009), and will lead to biased estimates of weighted effect sizes. The publication bias was assessed using a regression test for funnel plot asymmetry of the linear mixed effects model when including effect size standard error as a moderator (Egger et al., 1997; Sterne & Egger, 2006). Analyses were considered significantly biased if the intercept differed from zero at p=0.1 (Egger et al., 1997). Additionally, the magnitude of effect sizes reported for the same topic have been shown to change over time due changes in methodology, publication bias, or real biological changes in the magnitude of effect (Jennions & Møller, 2002b; Leimu & Koricheva, 2005). To test for the significance of temporal changes, publication year was included as a moderator in the analysis as in Zvereva, Toivonen and Kozlov (2008).

Meta-analyses are vulnerable to outliers and influential data points. For example, a study with very low variance will have a high weight and can result in skewed averages. Therefore, Cook’s Distance was calculated for each observation to examine the effect of observations with large residuals and/or high leverage on fitted model results (**Cook and Weisberg, 1984**). The sensitivity of analysis was reasonably high (i.e., summary effect sizes changed after exclusion), so values with Cook’s distances greater than three times the average cook’s distance were excluded for subsequent analysis (5.6% of observations)(Viechtbauer & Cheung, 2010)**.**

Scale dependence is a central issue in ecology (Levin, 1992) and can obscure relationships or produce relationships by artefact in cross-study synthesis (Spake et al., 2021). Scale dependence in this meta-analysis was tested by conducting meta-regressions of plot and sampling size against effect size.

Table 4. Summary table of articles included in this meta-analysis. Precipitation changes indicate increases (+) or decreases (-) relative to the mean annual precipitation at each site.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Article** | **Country** | **Precipitation change** | **Experimental design** | **Soil organism** | **Response parameter** | **Forest biome** | **No. of observations** |
| Ashton et al., 2019 | Malaysia | – | BA | Isoptera | Abundance | Tropical rainforest | 1 |
| Aslam et al., 2015 | Australia | + | CI; R; B | Mesostigmata, Nematoda, Oribatida | Abundance | Temperate seasonal forest | 7 |
| Aupic-Samain et al., 2021 | France | – | CI | Acari, Collembola | Abundance | Temperate seasonal forest | 7 |
| Bakonyi et al., 2007 | Hungary | – | CI | Nematoda | Diversity | Temperate seasonal forest | 68 |
| Chikoski, Ferguson and Meyer, 2006 | Canada | + | CI; R | Acari, Araneida, Chilipoda, Coleoptera, Collembola, Diplura, Diptera, Hempitera | Abundance | Temperate seasonal forest | 43 |
| Ferguson and Joly, 2002 | Canada | + | CI; R | Collembola | Abundance | Temperate seasonal forest | 1 |
| Frew et al., 2013 | Australia | + | CI | Nematoda, Scarabaeidae | Abundance | Temperate seasonal forest | 2 |
| Homet et al., 2021 | Spain | – | CI; B | Mesofauna | Abundance, Diversity | Temperate seasonal forest | 109 |
| Johnson et al., 2018 | Australia | + | CI | Acari, Coleoptera, Collembola, Diptera, Isopoda, Nematoda, Thysanoptera | Abundance, Diversity | Temperate seasonal forest | 7 |
| Krashevska et al., 2012 | Ecuador | – | CI; R; B | Testate amoebae, Collembola | Abundance | Tropical rainforest | 11 |
| Kuperman, Potapov and Sinitzina, 2002 | USA | – | O | Collembola | Abundance | Temperate seasonal forest | 4 |
| Landesman, Treonis and Dighton, 2011 | USA | – + | CI | Nematoda | Abundance | Temperate seasonal forest | 33 |
| Lensing, Todd and Wise, 2005 | USA | – + | CI; R | Araneidae, Collembola | Abundance | Temperate seasonal forest | 32 |
| Lindberg and Bengtsson, 2005 | Sweden | – | CI; R; B | Collembola, Macroarthropods, Oribatida | Abundance, Diversity | Boreal forest | 60 |
| Lindberg and Persson, 2004 | Sweden | + | CI; R; B | Collembola, Macroarthropods, Oribatida | Abundance, Diversity | Boreal forest | 8 |
| Lindberg, Engtsson and Persson, 2002 | Sweden | – + | CI; R; B | Collembola, Enchytraidae, Macroarthropods, Mesostigmata, Oribatida | Abundance, Diversity, Evenness | Boreal forest | 26 |
| Liu et al., 2020 | China | + | CI; R; B | Nematoda | Abundance | Temperate seasonal forest | 54 |
| Peguero et al., 2021 | Spain | – | CI; R | Arthropods, Collembola, Mesostigmata, Oribatida | Abundance | Temperate seasonal forest | 4 |
| Pflug and Wolters, 2001 | Germany | – | CI | Collembola | Abundance | Temperate seasonal forest | 1 |
| Riutta et al., 2012 | United Kingdom | + | BACI; P | Diploda, Oniscidea | Abundance, Diversity | Temperate seasonal forest | 8 |
| Santonja et al., 2017 | France | – | CI | Entomobryomorpha, Mesostigmata, Neelipleona, Oribatida, Poduromorpha, Prosigmata, Symphypleona | Abundance | Temperate seasonal forest | 23 |
| Sohlenius and Wasilewska, 1984 | Sweden | + | CI; B | Nematoda | Abundance, Diversity | Boreal forest | 21 |
| Sun et al., 2013 | China | + | CI; R | Nematoda | Abundance, Diversity | Temperate seasonal forest | 7 |
| Sun et al., 2020 | China | + | CI; B | Nematoda | Abundance | Tropical rainforest | 5 |
| Taylor et al., 2004 | Germany | – | CI; R | Nematoda | Abundance | Temperate seasonal forest | 3 |
| Tsiafouli et al., 2005 | Greece | – + | CI | Collembola, Oribatida | Abundance, Diversity | Temperate seasonal forest | 24 |
| Tsiafouli, Monokrousos and Sgardelis, 2018 | Greece | – | CI | Acari, Collembola | Abundance | Temperate seasonal forest | 4 |
| Wang et al., 2021 | China | – | CI; R | Nematoda | Abundance, Diversity | Temperate seasonal forest | 5 |
| Williams et al., 2014 | USA | – + | CI | Acari, Coleoptera | Abundance, Diversity, Evenness | Temperate seasonal forest | 12 |
| Wise and Lensing, 2019 | USA | – | BACI; R | Acari, Araneidae, Arthropods, Collembola, Mesofauna | Abundance | Temperate seasonal forest | 49 |

Experimental design: Before After Control Impact (BACI) Before After (BA); Control Impact (CI); Randomised (R); Blocked (B); Paired (P)

# Results

## Characterising the literature

In total, the meta-analysis presented here includes 16 precipitation increase studies at 16 sites and 19 precipitation decrease studies at 26 sites. While the studies were generally distributed across different sizes of soil biota, precipitation decrease studies investigating mesofauna responses were more common (65% of sites) than sites investigating microfauna (27% of sites) and macrofauna (27% of sites). Percentages do not equal 100% as some studies measured more than one body size. Precipitation increase studies were more evenly distributed in their consideration of microfauna, mesofauna and macrofauna (50%, 56%, and 50%, respectively). The spatial distribution of studies is centred in Europe and north-eastern United States, with several studies in Asia, Ecuador, and Australia but no studies in the African continent (**Figure 2**). The majority (76%) of the studies included in the meta-analysis focused on temperate seasonal forests, while a smaller percentage considered boreal (12%) and tropical rainforests (12%). Most sites were natural forests, although precipitation increase sites had a larger proportion of plantation studies, 37.5% compared with 12% of drought sites. All studies bar two precipitation decrease studies had an experimental design. Sampling depth is mostly consistent across studies, while the soil biota quantification methods varied widely across all studies.

## Bias and scale dependence

A publication bias towards more negative effect sizes was detected in the reported effect of precipitation decrease on diversity (p=0.0029) and a positive skew (bias) was detected for the effect of precipitation increases on diversity (p=0.0001). No publication bias was detected for abundance observations under either precipitation changes. The publication date was found to have no effect, showing no significant temporal changes in effect sizes (Table 5). Evidence of moderate scale dependence was found for the plot and sample size (Table 5).

Table 5. Pearson's product-moment correlation of effect size with variables possibly contributing to bias.

|  |  |  |
| --- | --- | --- |
| **Variable** | **Pearson’s correlation** | **p value** |
| Publication year | -0.0854 | 0.227 |
| Sample area | -0.271 | 0.000561 |
| Plot area | 0.336 | 9.80E-07 |

**A**

A map of the world

Description automatically generated with medium confidence

**B**

Chart, diagram

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**Figure 2. (A)** Geographic location of relevant studies and the global Whittaker forest biomes. Precipitation decrease studies are shown by triangle symbols, precipitation increases by squares, and studies that investigated both disturbance types are shown by circles. Opacity of the symbols indicates the number of studies at each location. **(B)** Location of each study in a Whittaker biome diagram defined by mean annual temperature and mean annual precipitation.

## Responses to disturbance

Overall, both soil fauna abundance and diversity decreased with precipitation reduction and increased with elevated precipitation (Figure 3, Table 6). Abundance measures responded more to precipitation reduction than increases (–37.3±10.4%, p <.0001; 34.9±11.4%, p= 0.0053, respectively) whereas diversity responded more to precipitation increases than precipitation decreases (14.7±3.76%, p=0002; –6.70±3.31%, p=0.0335, respectively). The high I2 values for these models (all values except diversity under increased precipitation are greater than 60%) indicate high between-study heterogeneity to be explored through further analysis. Initial explorations revealed varied responses in abundance of body width groups: significant reductions after precipitation decreases are observed in macrofauna

**Diagram

Description automatically generated**

**Figure 3 (A&B) Response (lnRR, loge(control/treatment)) of soil fauna abundance (A) and diversity (B) to precipitation alterations.** Black circles represent fitted means conditioned to a model including the disturbance type (i.e. precipitation increases or decreases) as a moderator and study and site as random variables.Positive values for the response ratio indicate an increased abundance relative to the control treatment. Confidence in estimates is indicated by the horizontal lines, with the bold line representing 95% confidence intervals and the non-bold line represents the 95% prediction intervals. Coloured circles represent individual effect sizes, and k = number of effect sizes (observations), with the number of grouping levels (study sites) for each level of the moderator shown in brackets

(41.3±20.9%, p=0.005) and mesofauna (-39.3±16.6%, p=0.0011) while for precipitation increases, macrofauna decrease (-24.7±17.7%, p=0.063) and mesofauna increase substantially (78.2±14.8%, p<0.0001) ) (Figure 3, Appendix 2). The decrease in microfauna abundance with precipitation reductions, and the smaller change with precipitation increases, is statistically non-significant. Only mesofauna had >3 diversity observations for precipitation reduction, with significant decreases (-9.66±4.38%, p=0.018) (Appendix 2). All body size groups increased diversity significantly for precipitation.

**Table 7.** Variables included in models of abundance change after precipitation disturbance.Models are ranked by ∆AIC, with the smaller the ∆AIC representing the most parsimonious models. Interaction effects are shown by \* symbol. Results are not presented for ‘both disturbances’ under ‘duration’ as this wasn’t considered to make theoretical sense given the difference in the range of durations between disturbance types. Full comparisons of models with all variables included in Appendix.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Both disturbances** | | | **Precipitation decreases** | | | **Precipitation increases** | | |
| Variables included in model | df | R2 | ∆AIC | df | R2 | ∆AIC | df | R2 | ∆AIC |
| size | 5 | 0.016 | 249.5 | 5 | 0.0549 | 34.4 | 5 | 0.350 | 5.57 |
| size\*duration | 8 | 0.025 | 249.3 | 8 | 0.125 | 21.4 | **8** | **0.409** | **0** |
| size\*strength | **8** | **0.374** | **0** | **8** | **0.201** | **0** | 8 | 0.398 | 2.28 |
| duration | - | - | - | 4 | 0.0240 | 41.0 | 4 | 0.00473 | 77.0 |
| strength | 4 | 0.235 | 91.1 | 4 | 0.0155 | 43.4 | 4 | 0.0288 | 71.9 |
| duration\*strength | 6 | 0.250 | 84.7 | 6 | 0.0536 | 37.0 | 6 | 0.0496 | 72.0 |

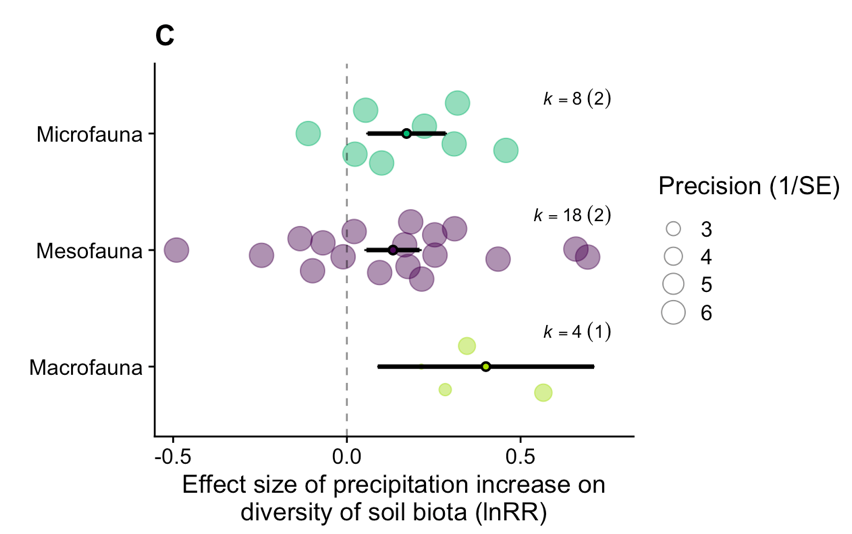
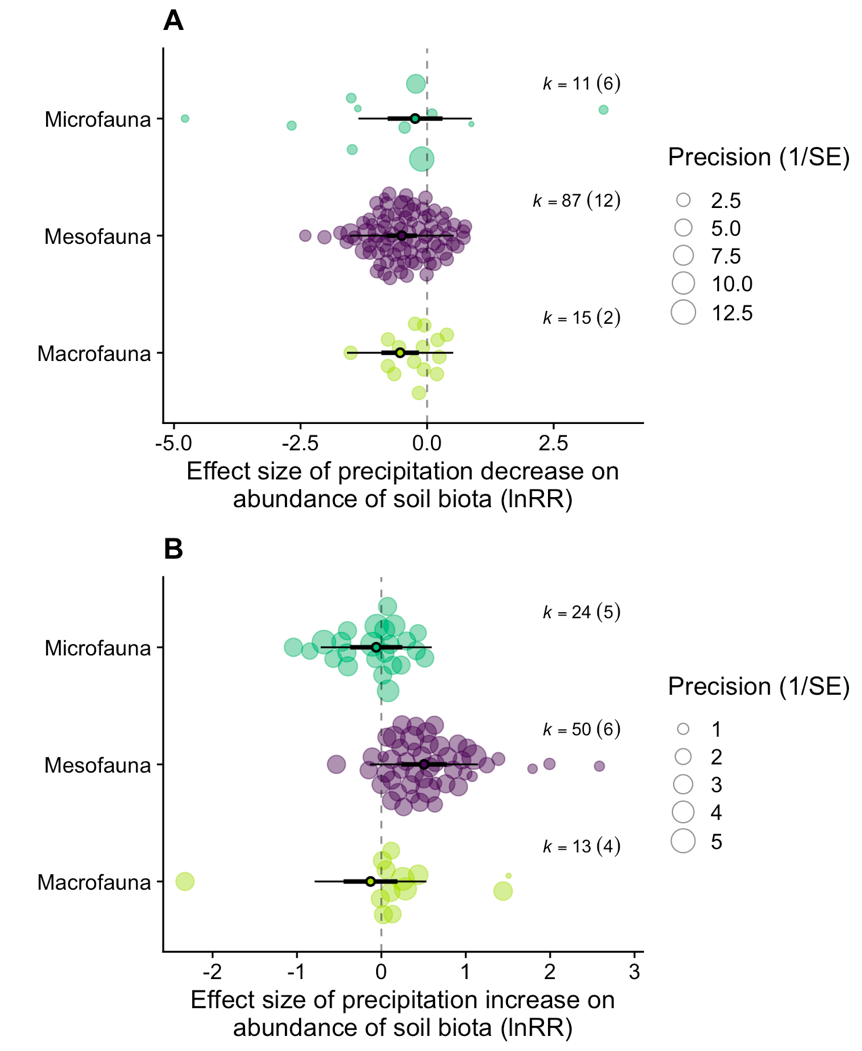
**Table 6.** Linear mixed-effect models summary table of the impact of precipitation alteration on soil biota abundance and diversity parameters. I 2 ranges from 0-100%, and I 2>50 is high heterogeneity.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Precipitation treatment** | **Soil biota parameter** | **k** | **Mean** | **95% Confidence Interval** | **p value** | **I2 (%)** |
| Decrease | Abundance | 114 | -0.5391 | -0.7243 to -0.3539 | <.0001 | 81.2 |
|  | Diversity | 52 | -0.0694 | -0.1333 to -0.0054 | 0.0335 | 62.9 |
| Increase | Abundance | 88 | 0.4053 | 0.2134 to 0.5972 | <.0001 | 72.2 |
|  | Diversity | 26 | 0.1368 | 0.0645 to 0.2091 | 0.0002 | 42.1 |

## Model selection

Model selection (Table 7, Appendix 5) suggested that the best model describing soil biota changes after decreased precipitation included both the body width of the organism and the strength of the disturbance, with an interaction between the two. This model predicted that as the intensity of water reduction, represented by the percentage change relative to annual precipitation, increased, the abundance of microfauna and mesofauna declined, whereas the abundance of macrofauna increased (Figure 5). This model had an R2 of 0.20. The slope of the relationship was the highest and the most precise with mesofauna, showing a decrease of –44.0% after a water reduction intensity of 50% and – 62.7% at 100% intensity. Macrofauna abundance increases by 65.6% with complete exclusion of water (-100%). However, the negative trend observed with macrofauna abundance should be interpreted with caution given the relatively few data points and a low spread of precipitation decrease intensities. The relationship between organism abundance and strength of reduced precipitation was much more important than forest type, background climate and soil characteristics (Appendix 5).

**Figure 4. (A and B)** Response of soil fauna abundance of different body widths after precipitation decrease (**A**) and precipitation increase (**B**). (**C**) Diversity response of soil fauna of different body widths to precipitation increases. Means for all figures are conditioned to a model including the body width size as a moderator and study and site as random variables. Positive values for the response ratio indicate an increased abundance or diversity relative to the control treatment. Confidence in estimates is indicated by the horizontal lines, with the bold line representing 95% confidence intervals and the non-bold line represents the 95% prediction intervals. Coloured circles represent individual effect sizes, and k = number of effect sizes (observations), with the number of grouping levels (study sites) for each level of the moderator shown in brackets



**Chart

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**Figure 5 Effect of the duration of precipitation increase treatment on the abundance of microfauna (A), mesofauna (B) and macrofauna (C).** lnRR (loge(control/treatment) is the estimated effect size from the meta-regression model, lnRR > 0 indicates increased abundance. Red lines are meta-regression model fits to data points including the duration of treatment as a moderator and study and site as random variables. Grey error bands represent the upper and lower 95% confidence intervals. The size of the symbols corresponds to the inverse variance or weight of the study in the model

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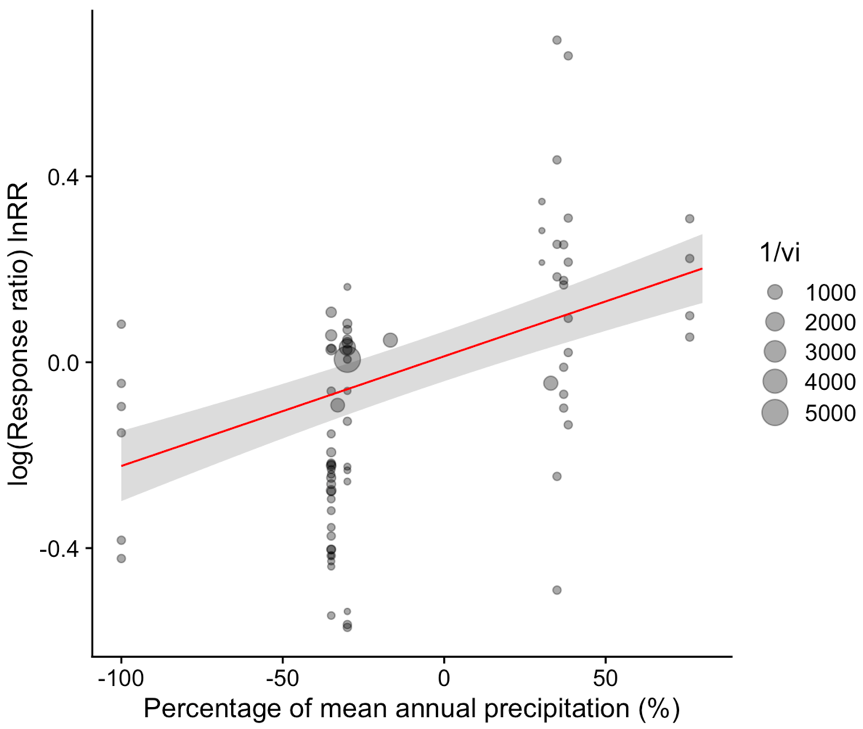
**Figure 6 Effect of the magnitude of precipitation reduction on microfauna (A), mesofauna (B) and macrofauna (C) abundance.** lnRR (loge(control/treatment) is the estimated effect size from the meta-regression model, lnRR<0 indicates reduced abundance. Red lines are meta-regression model fits to data points including the magnitude of precipitation as a moderator and study and site as random variables. Grey error bands represent the upper and lower 95% confidence intervals. Here an intensity of –100% is a complete exclusion of rainfall, and –50% excluded 50% of the mean annual precipitation at each site. The size of the symbols corresponds to the inverse variance or weight of the study in the model.

Under increased precipitation, the soil biota abundance was more strongly related to the duration of disturbance than the severity of disturbance. The most parsimonious model included the size of biota and the duration of disturbance as moderators, with an interaction between the two (Figure 6). This model has an R2 of 0.409. Here, an extended duration of experimental treatment decreases the effect on mesofauna but increases the effect on macrofauna. Initially macrofauna are negatively affected by water addition, –45.6% at 0 years, whereas after 1 year of treatment abundance increases by 127%. Excluding the mesofauna observations with extremely long duration to test the sensitivity of the model strengthens the magnitude of relationship, from a line of to . Therefore, mesofauna abundance increases by 85% at the start of water addition, but only increases by 10.4% after a year of treatment. Intensity of water addition with body size and only body size were also important in explaining differences between control and disturbed sites (∆AICc ≤7, R2 values of 0.35 to 0.40).

Diversity parameters after reduced or enhanced precipitation showed very weak relationships with all variables, all R2 <0.1. However, models with both precipitation disturbances observations did show that diversity is related to the strength of disturbance, with an R2 of 0.291 (Figure 4). Diversity decreases with enhanced severity of water reduction and increases with more intense water addition. An 80% reduction in water addition leads to a diversity decrease of -16.6% while an increase in water addition of 80% increases diversity by 22.6%. The lack of interaction with body size in the most parsimonious model is either a result of low numbers of micro- and macrofauna diversity observations or indicates that a similar response is expected across all body group sizes.

Combining observations from both disturbance types showed a linear response of soil biota to altered precipitation regimes (Figure 5). The size of biota and the annual strength of disturbance had the highest explanatory power (R2 0.37) for abundance. As the amount of added (excluded) water relative to the annual average increased, the abundance of microfauna and mesofauna increased (decreased). The slope of this relationship is highest and the most significant with mesofauna: with a 100% decrease in mean annual precipitation, mesofauna abundance is expected to decline by 59.4%, and at a 100% increase, abundance increases by 62.5%. Macrofauna have an opposite relationship with strength of disturbance, with 56.9% increases in abundance expected with 100% decrease in precipitation and a 41.9% increase in abundance with the opposing change, i.e., a 100% increase in precipitation.

***Figure 7. Response (lnRR, loge(control/treatment)) of soil biota diversity to the intensity of precipitation reduction****. lnRR < 0 indicates decreased abundance. Here an intensity of 100% represents a doubling of mean annual precipitation (MAP). -100% is a complete exclusion of rainfall, and –50% excludes 50% of MAP. The size of the symbols corresponds to the inverse variance (1/vi) or weight of the study in the model.*



**Chart, scatter chart

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**Figure 8. Continuous response (lnRR, loge(control/treatment)) of microfauna (A), mesofauna (B) and macrofauna (C) to the intensity of precipitation alteration**. lnRR > 0 indicates increased abundance. The size of the symbols corresponds to the inverse variance (1/vi) or weight of the study in the model.

## Environmental effects

In general, environmental variables, including temperature, precipitation, soil texture (sand, silt and clay content), and forest biome type, were not significant explanatory variables (Appendix 5).

## Trophic grouping

From observations where the information is available, trophic levels play a role in determining soil fauna abundance response to precipitation alteration. The most parsimonious model for both precipitation increases and decreases comprised the trophic level and the duration of treatment (Figure 6). Model fit for precipitation increases was better than those for precipitation decreases, with an R2 of 0.6 and 0.33, respectively. For precipitation decreases, models including the body width of biota and the strength of disturbance had similar parsimony, but the explanatory power of these models was lower than those with trophic levels (APPENDIX). The greatest average responses to precipitation reduction and precipitation increase are seen in the abundance of fungivores (-44.7%, p=0.0014 and 67%, p=0.0023, respectively) and predators (-40.9%, p=0.002 and -41.4%, p=0.065, respectively). As duration of experiment increases, the magnitude of change for all trophic groups tends towards 0. These trends should be interpreted with caution given the relatively few data points and a low spread of duration lengths - particularly trends for detritivores under decreased precipitation and predators under precipitation increases.

A

Chart, diagram

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B

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**Figure 9. Response of trophic levels of soil biota to the duration of precipitation decreases (A), and precipitation increases (B).** lnRR > 0 indicates increased abundance. The size of the symbols corresponds to the inverse variance (1/vi) or weight of the study in the model. Variance does not vary for mixed and fungivore/detritivore effect sizes as these values have been assigned from the mean variance.

## Nematodes

The majority of microfauna included in this analysis were nematodes, which decreased with both precipitation increases (ns) and water reduction (–68%, p = 0.081). Nematoda observations were assessed, and the most parsimonious model was found to include both length of disturbance and strength of disturbance as predictors, but with low explanatory value (R2 = 0.01). Although trophic information was given in many studies of nematodes, the trophic level was not found to be an important moderating variable in model comparisons.

## Robustness checks

Pearson’s correlation robustness checks on the accuracy of external data showed that the mean annual temperature and precipitation data from WorldClim.org were significantly correlated with the figures given by the studies, but that the USDA sand and silt percentages had a significantly negative relationship with the reported sand and silt in studies, indicating a very poor representation of true site conditions (Table **8**). While clay has a statistically significant positive relationship, the correlation remains low.

## External validity

The magnitude of experimental precipitation manipulation ranged from –100% to about 150% relative to mean annual precipitation, while worst–case scenarios from CMIP5 models predicted precipitation changes from –26% to +24% in the regions these experiments were conducted in. The correlation between experimental disturbance and climate projection was very weak regardless of the time period considered (2050 and 2070 scenarios are shown in Figure 9). This mismatch indicates that precipitation manipulations on soil biota generally do not match model projections. The comparison is not completely accurate as the experiments represent extremes of shorter durations whereas projections represent average annual changes.

**Table 8. Pearson’s correlation coefficient** between study values and externally sourced data. Correlation coefficients >0.65 indicate a fairly strong positive relationship and good agreement with figures from literature. Coefficients<0.5 indicate a weak or negative correlation and poor agreement with study values.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **External data** | **Clay** | **Sand** | **Silt** | **Temperature** | **Precipitation** |
| HSWD Clay | **0.467** | – | – | – | – |
| HSWD Sand | – | **–0.182** | – | – | – |
| HSWD Silt | – | – | **–0.505** | – | – |
| WorldClim Temperature | – | – | – | **0.934** | – |
| WorldClim Precipitation | – | – | – | – | **0.673** |

Bold values indicate significant correlations (p<0.05)

**Chart

Description automatically generated**

***Figure 10*** *Percentage change from mean annual precipitation conditions in experimental manipulations plotted against mean proportional change in precipitation between current and future conditions projected by CMIP5 models. Projections are given for 2050 (A) and 2070 (B) under the RCP8.5 worst case scenario. Solid lines show the 1:1 line between experiment and projection. Studies fall on this line if the experimental manipulation of precipitation matches that of the projections. Dashed lines show the respective zero line for experimental and projected values. Shaded areas indicate that the direction is correct, but the magnitude is different from projected values. Each shaded circle represents a unique experimental manipulation in a study included in this meta-analysis.*

# Discussion

This study is the first to assess the effect of both precipitation increases and decreases across a large number of global forest sites. These results indicate that disturbance intensity is key to understanding the response of soil biota to precipitation alterations. Mesofauna abundances decline by about 60% with a complete exclusion of precipitation, whereas macrofauna abundance increases by about 65%. An extended duration of treatment decreases the positive effect of elevated precipitation on mesofauna, from an increase of 85% at the start of water addition, to only 10% increases after one year. For macrofauna, the duration of water addition impacts the direction of change: initially abundance decreases, but after a year abundance more than doubles. The positive relationship with water addition on biodiversity does not appear to depend on body size, with declines of 16% with 80% water reduction and increases of about 20% with 80% water addition. The background climate, forest biome and soil types were largely unimportant in determining soil fauna response, perhaps implying more universality in the system that previously thought. The following section will discuss (1) the general impact of precipitation alteration, (2) the impact of body size on responses to changing precipitation, (3) the impacts of intensity of precipitation manipulation on soil fauna, and finally, (4) the limitations of this study and recommendations for future research.

## Precipitation alteration

This analysis revealed that disturbance had non-uniform effects on soil biota abundance and diversity, with predominantly positive effects from precipitation increases, and negative effects with precipitation reduction. Results fit with the hypothesis that the negative effect of precipitation reduction on abundance would be of greater magnitude than the effect of precipitation increases, supported by previous observations of an asymmetrical response to precipitation changes seen in soil biota (Lindberg et al., 2002; R. S. Williams et al., 2014) and in soil ecosystem and carbon processes (Luo et al., 2017; Zhang et al., 2018). Contrary to expectations, diversity parameters present an opposite asymmetry to water additions.

## Importance of body size

Understanding the capacity of different organisms to cope with disturbance will help identify which organisms and soil ecosystem functions are most at risk. This meta-analysis supports the hypothesis that the effect of precipitation alteration on abundance would depend on the body size of the organism, but not that diversity is significantly impacted by the size of an organism.

While organisms of all body size were limited by precipitation reduction, the average magnitude of change differed, likely due to morphological and biological differences affecting their resilience (J. Bengtsson, 2002). Microfauna was affected the least by precipitation reduction despite dependence on water filled pore space and water films around soil particles for their activities (Young et al., 1998); Eo et al., 2007). This fits with previous meta-analysis results showing a minor negative response to drought for nematodes, the predominant microfauna species (Zhou et al., 2022). Moreover, nematode response to drought is particularly low in forests (Zhou et al., 2022), perhaps because of significant resistance that comes with enhanced tree cover (Barros et al., 2018; de Keersmaecker et al., 2015), which could further explain greater resistance to precipitation reduction. On the other hand, the effect of precipitation decreases is seen clearly in declines of mesofauna abundance. These results align with expectations from literature that soil mesofauna can be particularly sensitive to environmental change (Hopkin, 1997; Jucevica and Melecis, 2006). This positive association with soil moisture has been demonstrated across multiple taxa and many ecosystems, from mites (Badejo, 1990; Badejo & Akinwole, 2006; Wallwork, 1983) to Collembola (Jucevica & Melecis, 2006; Kardol et al., 2011; Pflug & Wolters, 2001). Macrofauna appear to be the least resilient to precipitation reductions, perhaps due to longer generation times and larger microhabitats (Birkhofer et al., 2017). These results indicate that macrofauna’s greater agility and dispersal capabilities, which are thought to enable populations to persist through distribution shifts and re-colonisation (Perry et al., 1990; **Grubb, 1987)**, may not be sufficient to overcome sensitivities to soil moisture reduction. Perhaps this is due to restrictions in the ability of macrofauna to recolonise after disturbance (Zaitsev et al., 2014).

With enhanced precipitation, body size impacted the direction of change, with macrofauna abundance declining and mesofauna increasing in abundance. Similarly to precipitation decreases, microfauna showed no significant changes in abundance. The increase in mesofauna abundance is consistent with previous meta-analysis results (Blankinship et al., 2011) although the magnitude of change is about 25% less pronounced. This meta-analysis here includes more than twice the number of observations for mesofauna and gives more precise confidence intervals so is more likely to represent the true effect size. Significant declines in macrofauna abundance contrasts previous meta-analysis (Blankinship et al., 2011), which suggested moderate (non-significant) increases in abundance. These differences result from the inclusion of a greater number of observations for macrofauna (24 observations in this study compared to their 3). As a result of additional statistical power, the findings of this meta-analysis are more likely to represent the true effect size. Previous work does suggest that while the abundance of macrofauna can be promoted by moderate water additions, excessive soil water can lead to losses, in part due to low oxygen availability (Korobushkin et al., 2019; Radford et al., 2001; Tuf et al., 2008). Another possible explanation for declining populations is an increase in predator populations. One potential predator of Araneida, one of the taxon negatively affected, is centipedes (Lewis, 1981), known to preferentially select microsites with high humidity (Albert, 1983) and increase abundance with water addition (Chikoski et al., 2006). Similar negative relationships with soil moisture have been found for earthworms (Talavera et al., 2020). However, the average effect size for macrofauna is heavily influenced by negative observations from one study, Lensing, Todd and Wise (2005), and the vast majority of macrofauna studies do show increased populations with precipitation increases as hypothesised.

## Intensity of precipitation disturbance

Although previous research indicates that the effect of global change on soil fauna depends on aboveground vegetation (Blankinship et al., 2011) and background climate (Meehan et al., 2020), this study, in line with recent meta-analysis (Peng *et al.* 2022), finds that these factors are largely unimportant in determining soil fauna response. Instead, this synthesis indicates that, as well as the body width of taxa, the effect of precipitation manipulation experiments on soil fauna are strongly driven by the duration and severity of the disturbance.

### Precipitation reduction

The magnitude of precipitation reduction explained the most variance in the response of soil biota abundance to decreases in precipitation (Figure 2). Very few experiments have compared multiple intensities of precipitation reduction (Flórián et al., 2019), so a quantitative synthesis of primary studies provides novel insight into soil fauna response to altered intensity. The greater decline in micro- and mesofauna at high intensities suggests that while these organisms can be adapted to survive under dry conditions for a certain period (Waagner et al., 2011), pronounced intensity could permanently influence the ecological functioning of organisms and reduce recovery (Nielsen & Ball, 2015). These results are broadly consistent with the recent meta-analysis by (Peng *et al.*, 2022), which found a non-significant negative impact of the magnitude of drought on soil biota density. However, the opposite trend is observed for macrofauna abundance, showing increased abundance with severe precipitation exclusion and a negative effect of milder precipitation reduction. Results could possibly be attributed to either a decline in abundance of more moisture sensitive predators with severe precipitation reductions (Lensing et al., 2005), the temporary movement out of small experimental plots at high severities and subsequent re-colonisation, or omnivorous feeding habits allowing for increased survival as prey resources become limiting (Moore et al., 1988). Resistance of macrofauna may result in an increase in top-down pressure on smaller organisms. However, this trend should be interpreted with caution as it could be an artefact of the low spread of precipitation severities and relatively few data-points. Furthermore, the possible food-web context and cascading effects remains poorly studied so the implications of resistant macrofauna for top-down controls on smaller organisms remains speculative.

### Precipitation increases

Varied responses to precipitation increases were found within different body width groups (Figure 4). Previous meta-analysis found effects of precipitation alteration increased with treatment duration but did not determine if this varied between size groups (Blankinship, Niklaus and Hungate, 2011; Peng *et al.*, 2022). This is important because while macrofauna support the positive relationship in Blankinship, Niklaus and Hungate (2011), mesofauna populations, in contrast, show more pronounced increases with short-term elevations in precipitation. These results fit with the idea of a response hierarchy to resource pulses, where precipitation response thresholds are determined by the ability of organisms to utilise water pulses of different durations (Schwinning & Sala, 2004). Smaller mesofauna respond to brief period of irrigation due to faster growth and reproduction and a greater resistance to wet-dry oscillations, whereas larger soil animals may benefit from continually elevated soil water potentials at depth. Longer events will disproportionately increase the abundance of higher animals, compared to the activities of mesofauna. One possible implication is that predation pressure on mesofauna will increase with disturbance duration. Furthermore, prolonged precipitation increases could fill soil pore spaces and restrict the movement of mesofauna, increasing the likelihood of unsuitable anaerobic conditions (**El-Gayar, 2014**).

### Continuous response to precipitation alteration

As the first meta-analysis to compare both precipitation increases and decreases on soil fauna across body width groups, this analysis provides evidence of a continuous response to precipitation alteration across both decrease and increases in precipitation. This result provides a useful synthesis of precipitation alteration studies that has not been shown before and aligns with previous evidence that intense drought does tend to have a greater magnitude of impact than a similar severity of increased precipitation (Lindberg et al., 2002; R. S. Williams et al., 2014).

## Diversity

The positive relationship of biodiversity with water addition does not depend on body size, suggesting that the effect is consistent across body width sizes. This is surprising given the profound body size variation. However, the majority of diversity observations were for mesofauna, so the dataset does not lend itself to an in depth consideration of differing impacts across body sizes.

The synthesis of both increases and decreases in precipitation is particularly useful for diversity, as the strength of precipitation alteration had a much greater explanatory power when both precipitation increases and decreases impacts were included. Previous meta-analysis did not include sufficient diversity observations for rainfall increases to assess the response to changing magnitude, so the correlative response to water additions is interesting (Peng *et al*., 2022).

## Trophic grouping

The effect of precipitation alteration on abundance is related to trophic structure, as expected, and explained more of the variance in response to the duration of precipitation increases than body size.

However, the relatively small number of data points and low spread in durations means some trends are likely an artefact of a few precise, highly weighted observations and additional research is needed to validate these trends. Briefly, the positive relationship of fungivores with water additions is in line with previous meta-analysis results (Blankinship et al., 2011) and expectations that lower trophic levels decrease with drought (de Vries et al., 2012). Declines of predators with precipitation reduction indicates a bottom-up trophic response to decreasing water availability. However, contrary to expectations (Blankinship et al., 2011), water addition decreases predators and organisms with mixed feeding habits. In general, as the duration of precipitation alteration increases, the impact on the different trophic levels decreases.

## Limitations

This analysis is subject to limitations of the literature used in analysis. Critical appraisal of the methodology of literature revealed about a third of studies did not explicitly account for spatial heterogeneity through appropriate randomisation. While this is a high proportion of studies, sensitivity analysis showed that the summary effect sizes did not alter direction and remained statistically significant when these low validity studies were excluded (Appendix 4). Publication bias, where papers that report significant results are more likely to be published (Jennions & Møller, 2002a; Lortie et al., 2007; Marks-Anglin & Chen, 2020), is also a potential problem in all meta-analyses and could overstate the effect of precipitation alteration. This was addressed, and measures of diversity were found to be more biased than abundance, perhaps due to the smaller number of observations and imputed variances. Diversity observations were also limited for micro- and macrofauna and included a limited range of durations and precipitation intensities. Therefore, conclusions regarding diversity under precipitation disturbance should be treated with some caution. In addition, data extraction was not duplicated by another independent individual, which increases the chance of mistakes or biases (K. S. Taylor et al., 2021). A standardised data extraction form was used to minimise this risk. It is also possible that relevant studies were not captured from the searches undertaken, although all reasonable efforts were made to ensure the majority were included.

Considerable variance remained for all models of soil biota change, perhaps indicating important moderating variables that have not been considered. The studies have substantial between-study heterogeneity and a low proportion have generalisable results due to variations in different sampling techniques, quantification of disturbance intensity, measures of abundance, and site history. Furthermore, the detail provided on the disturbance severity and soil characteristics was inconsistent and sometimes difficult to interpret, particularly for the studies of real drought events. These factors, among others, may have a bearing on this meta-analysis.

## Knowledge gaps and research priorities

This synthesis has shown how important both the severity and duration of precipitation disturbances are for predicting the response of soil biota. While several studies did consider temporal trends, the number of studies with a range of severities was very limited. Therefore, more multi-severity and duration experiments are needed to test these results and consider the biotic mechanisms by which these factors interact with different soil biota.

A major knowledge gap is the way in which soil food webs are influenced by precipitation alteration. Understanding shifts in ecosystem function requires considering interactions between different trophic levels (Cragg & Bardgett, 2001). However, few studies provided detailed information on the trophic levels of organisms and most studies only considered one type of soil organism without integrating results into changes in community structures. A key remaining challenge is connecting quantitative changes in abundances and diversity of soil biota to decomposition, carbon storage, regulation of aboveground diversity, and nutrient cycling. A few more recent studies did include functional information, and there are concerted efforts to quantify the effect of disturbances on soil functioning, which will elucidate the overall impact of results presented here (Cimpoiasu et al., 2021).

As with much of ecology (L. J. Martin et al., 2012), there is an overrepresentation of studies in North America, Europe and temperate woodlands, probably influenced by physical, financial, and institutional constraints (Evans & Foster, 2011). This narrow geographical distribution limits the representativeness of the results and affects the robustness of conclusions drawn about the significance of climate and forest biomes on soil biota responses. Furthermore, an investigation into the external validity of primary studies revealed no relationship between the disturbances applied and the projected changes in the hydrological state at each site. While the CMIP5 model projections are long-term changes in annual precipitations and many of the studies are relatively short-term manipulations, this relates to concerns raised by Korell et al. (2020) that unrealistic manipulations of climate do not provide a mechanistic understanding of the effect of climate change on ecology. Thus, this requires more globally distributed and realistic experiments to facilitate a better predictive understanding of future ecosystems.

The majority of the studies included in this meta-analysis only considered the effect of precipitation extremes but future changes in precipitation regimes are unlikely to act in isolation to other global changes (e.g. warming, fires, nitrogen deposition) (see Peng et al., 2022 for a meta-analysis on multiple drivers). Consequently, more multi-factor experiments are necessary. In particular, deforestation and forest degradation are currently the biggest threats to forests worldwide so understanding the interactions of soil biota in degraded soils with precipitation change is vital.

# Conclusion

Extreme precipitation and changing hydrological patterns under climate change pose a significant threat to forest soil fauna and the essential services they provide. This study is the first meta-analysis of this scope to quantify the effect of both extreme precipitation increases and decreases on forest soil fauna. Soil fauna abundance and diversity present a positive correlation with the magnitude of water addition, decreasing with water loss and increasing with water application. These results suggest that the intensity, i.e., the magnitude and duration, of precipitation change is particularly important for the resilience and resistance of soil organisms. The effect of altered precipitation on abundance also depends on trophic structure and body size, whereas biodiversity mostly depends on magnitude of precipitation change. Several mechanistic constraints emerged from this synthesis. First, the abundance and diversity of soil biota is generally limited by water. Second, in line with the response hierarchy to resource pulses (Schwinning & Sala, 2004), larger organisms are more resilient to extreme, prolonged water alteration while smaller organisms take advantage of shorter-term water pulses. Notably, this analysis indicates that the abundance and diversity of soil fauna decrease with water reduction and increase with water addition in a consistent way across forest biomes and climatic conditions. Therefore, there may be more general global patterns in soil fauna responses than previously thought, which will help predictions of changes in soil biota.

Through critical appraisal and assessment of publication biases, the results of this meta-analysis are found to be reasonably robust to potential biases. However, soil fauna experiments should prioritise randomisation and methodological quality as this has led to low validity of many studies. To consolidate the trends revealed by this meta-analytical approach, future studies should cover a wider range of precipitation intensities, focus on macro- and microfauna diversity, and include details on trophic structure. A continued effort into quantifying the impact of changes in soil fauna on soil carbon storage and nutrient cycling will be important for policies aiming to sustain the provision of forest ecosystem ecosystems, such as REDD+ and the new EU Forest Strategy for 2030. Calls for realism in climate change ecological research means including more realistic disturbance treatments and multi-factor experiments as interactions between different global change factors can induce responses not predicted by single-factor experiments (Peng *et al*., 2022).

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Appendix 1. Criteria for study validity assessment (P. A. Martin et al., 2020). Any studies for which the answer to any of the questions is ‘no’ or ‘unclear’ will be assigned as having low validity; remaining studies will be assigned as having medium validity if any of the answers are ‘partially’ and high validity if all the answers are ‘yes’.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Question/criterion** | **Response to question** |  |  |  | **Type of bias addressed** |
|  | **Yes** | **Partially** | **No** | **Unclear** |
| Did the study consist of both temporal and spatial comparisons? | Before-after-control-impact study | Before-and-after study or Controlled study | N/A as study is not eligible for inclusion based on inclusion criteria | Lacking sufficient information to judge | Selection bias |
| Did the study use randomization? | Study accounts for spatial heterogeneity by using appropriate randomisation of samples | N/A as study was either randomized with respect to the management intervention or not (e.g. random site selection but not random allocation of treatments/controls) | Study does not attempt to randomize sampling | Lacking sufficient information to judge | Selection bias |
| Did the study avoid confounding factors? | Confounding factors were likely to be minimal as a result of blocking/pairing or stated attempts to match samples | Some confounding factors present, likely to have a moderate impact on outcome | Study was subject to confounding factors that could have a major impact on the outcome | Lacking sufficient information to judge | Selection bias and performance bias |
| Can study determine causality? | Experimental study in which comparator samples were selected prior to the management intervention being used | Correlative study in which comparators are selected after the management intervention has already been implemented, thereby limiting the ability of researchers to determine the similarity of comparators prior to management intervention use. | N/A - Studies with no comparator will be excluded | Lacking sufficient information to judge | Selection bias and performance bias |

Appendix 3. Results of study validity assessment

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Article** | **Did the study consist of both temporal and spatial comparisons?** | **Did the study use randomization?** | **Did the study avoid confounding factors?** | **Can study determine causality?** | **Validity** |
| Ashton et al. 2019 | Partially | No | Yes | Yes | Low validity |
| Aslam et al. 2015 | Partially | Yes | Yes | Yes | Medium validity |
| Aupic-Samain et al. 2021 | Partially | Yes | Partially | Yes | Medium validity |
| Bakonyi et al. 2007 | Partially | No | Partially | Yes | Low validity |
| Chikoski et al. 2006 | Partially | Yes | Partially | Yes | Medium validity |
| Ferguson and Joly, 2002 | Partially | Yes | Partially | Yes | Medium validity |
| Frew et al. 2013 | Partially | No | Yes | Yes | Low validity |
| Homet et al. 2021 | Partially | No | Yes | Yes | Low validity |
| Johnson et al. 2018 | Partially | No | Yes | Yes | Low validity |
| Krashevska et al. 2012 | Partially | Yes | Yes | Yes | Medium validity |
| Kuperman et al. 2002 | Partially | Yes | Yes | Partially | Medium validity |
| Landesman et al. 2011 | Partially | No | Partially | Yes | Low validity |
| Lensing et al. 2005 | Partially | Yes | No | Partially | Medium validity |
| Lindberg and Bengtsson, 2006 | Partially | Yes | Yes | Yes | Medium validity |
| Lindberg and Persson, 2004 | Partially | Yes | Yes | Yes | Medium validity |
| Lindberg et al. 2002 | Partially | Yes | Yes | Yes | Medium validity |
| Liu et al. 2020 | Partially | Yes | Yes | Yes | Medium validity |
| Peguero et al. 2021 | Partially | Yes | Yes | Yes | Medium validity |
| Pflug and Wolters, 2001 | Partially | Yes | Yes | Yes | Medium validity |
| Ruitta et al. 2012 | Yes | No | Yes | Yes | Low validity |
| Santonja et al. 2017 | Partially | No | Partially | Yes | Low validity |
| Sohlenius and Wasilewska, 1984 | Partially | Yes | Yes | Yes | Medium validity |
| Sun et al. 2013 | Partially | Yes | Partially | Yes | Medium validity |
| Sun et al. 2020 | Partially | No | Yes | Yes | Low validity |
| Taylor et al. 2004 | Partially | No | No | Yes | Low validity |
| Tsiafouli et al. 2005 | Partially | Yes | Partially | Yes | Medium validity |
| Tsiafouli et al. 2018 | Partially | Yes | Partially | Yes | Medium validity |
| Wang et al. 2021 | Partially | Yes | Partially | Yes | Medium validity |
| Williams et al. 2014 | Partially | Yes | Partially | Yes | Medium validity |
| Wise and Lensing, 2019 | Yes | Yes | Yes | Yes | High validity |

Appendix 4. Summary effect size comparison without the studies found to have low validity

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Abundance |  |  |  | Diversity |  |  |  |
|  |  | n (k) | Mean | 95% CI | p value | n (k) | Mean | 95% CI | p value |
| All studies | Decrease | 114 | -0.5391 | -0.7243 to -0.3539 | <.0001 | 52 | -0.0694 | -0.1333 to -0.0054 | 0.0335 |
| Increase | 88 | 0.4053 | 0.2134 to 0.5972 | <.0001 | 26 | 0.1368 | 0.0645 to 0.2091 | 0.0002 |
| Excluding studies with low validity | Decrease | 98 | -0.5024 | -0.7243 to -0.2804 | <.0001 | 36 | -0.1209 | -0.1814 to -0.0604 | <.0001 |
| Increase | 81 | 0.4696 | 0.2353 to 0.7039 | <.0001 | 23 | 0.1021 | 0.0390 to 0.1651 | 0.0015 |

Appendix . Response (ln(RR)) of different body width sizes to precipitation decreases and increases. Categories with k<3 are not considered.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Body width size** |  | **Precipitation decreases** | | | | | **Precipitation increases** | | | | |
|  | **k** | **ln(RR)** | **% Change** | **95% CI** | **p value** | **k** | **ln(RR)** | **% Change** | **95% CI** | **p value** |
|  |  |  |  |  |  |  |  |  |  |  |  |
| Macrofauna | Abundance | 11 | -0.533 | -41.3 | -0.905 to -0.161 | **0.005** | 24 | -0.2835 | -24.7 | -0.582 to 0.0157 | 0.0633 |
|  | Diversity | 1 | - | - | - | - | 4 | 0.4001 | 49.2 | 0.0889 to 0.7114 | **0.0117** |
| Mesofauna | Abundance | 90 | -0.50 | -39.3 | -0.801 to -0.199 | **0.0011** | 54 | 0.5778 | 78.2 | 0.314 to 0.842 | <.0001 |
|  | Diversity | 48 | -0.101 | -9.66 | -0.186 to -0.0175 | **0.0178** | 30 | 0.1327 | 14.2 | 0.0562 to 0.209 | **0.0007** |
| Microfauna | Abundance | 19 | -0.237 | -21.1 | -0.781 to 0.307 | 0.393 | 17 | -0.0498 | -4.86 | -0.380 to 0.281 | 0.7679 |
|  | Diversity | 2 | - | - | - | - | 8 | 0.1718 | 18.7 | 0.0598 to 0.2838 | 0.0026 |

Appendix 5. Model results

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Abundance** | | | | | | **Drought** | | | | | | **Precipitation increases** | | | | | |
|  | **All** | | | **Diversity** | | | **Abundance** | | | **Diversity** | | | **Abundance** | | | **Diversity** | | |
| **Model** | **df** | **R2** | **∆ AIC** | **df** | **R2** | **∆ AIC** | **df** | **R2** | **∆ AIC** | **df** | **R2** | **∆AIC** | **df** | **R2** | **delta AIC** | **df** | **R2** | **∆AIC** |
| Null model | 3 | 0 | 257 | 3 | 0 | 59.3 | 3 | 0 | 45.6 | 3 | 0 | 4.06 | 3 | 0 | 75.9 | 3 | 0 | 2.82 |
| Body size | 5 | 0.0158 | 249 | 5 | 0.0039 | 63.0 | 5 | 0.0549 | 34.4 | 5 | 0 | 13.7 | 5 | 0.350 | 5.57 | 5 | 0 | 9.33 |
| Duration | 4 | 0.00377 | 256 | 4 | 0.0002 | 61.5 | 4 | 0.0240 | 41.0 | 4 | 0 | 7.35 | 4 | 0.00473 | 77.0 | 4 | 0.0016 | 5.49 |
| Annual strength | 4 | 0.235 | 91.1 | 4 | 0.2826 | 1.58 | 4 | 0.0155 | 43.4 | 4 | 0 | 7.60 | 4 | 0.0288 | 71.9 | 4 | 0.0356 | 4.50 |
| Disturbance strength | 4 | 0.247 | 82.4 | 4 | **0.2901** | **0** | 4 | 0.0127 | 44.2 | 4 | 0.0299 | 4.43 | 4 | 0.0284 | 72.0 | 4 | 0.181 | 0.308 |
| Size \*Strength | 8 | **0.374** | **0** | 8 | 0.2709 | 13.8 | 8 | **0.2006** | **0** | 6 | 0 | 17.2 | 8 | **0.398** | **2.28** | 8 | 0.0203 | 19.8 |
| Duration \*Size | 8 | 0.0251 | 249 | 8 | 0.0044 | 70.3 | 8 | 0.1250 | 21.4 | 6 | 0 | 14.9 | 8 | **0.409** | **0** | 8 | 0.0698 | 18.4 |
| Duration \*Strength | 6 | 0.250 | 85 | 6 | 0.2902 | 4.7 | 6 | 0.0536 | 37.0 | 6 | 0.0253 | 9.93 | 6 | 0.0496 | 72.0 | 6 | 0.0983 | 9.10 |
| Temperature | 4 | 0.00351 | 256 | 4 | 0.0 | 61.9 | 4 | 0.0064 | 46.0 | 4 | 0.0316 | 4.32 | 4 | 0.0103 | 75.8 | 4 | 0.0840 | 3.11 |
| Precipitation | 4 | 0.00634 | 254 | 4 | 0.0313 | 54.9 | 4 | 0.0073 | 45.7 | 4 | 0 | 8.00 | 4 | 0.0110 | 75.7 | 4 | 0.107 | 2.44 |
| Forest type | 5 | 0.0103 | 253 | 4 | 0.0012 | 61.3 | 5 | 0.0387 | 39.0 | 4 | 0.0624 | 2.25 | 4 | 0.00642 | 76.7 | 4 | 0 | 5.78 |
| pH | 4 | 0.00296 | 257 | 4 | 0.0017 | 61.2 | 4 | 0.0232 | 41.2 | 4 | 0.00425 | 6.16 | 4 | 0.0194 | 73.9 | 4 | 0 | 6.44 |
| Organic Carbon | 4 | 0.00680 | 254 | 4 | 0.0010 | 61.3 | 4 | 0.0218 | 41.6 | 4 | 0.0118 | 5.65 | 4 | 0.00640 | 76.7 | 4 | 0 | 5.62 |
| Available WSC | 4 | 0.00625 | 254 | 4 | 0.0000 | 63.2 | 4 | 0.0090 | 45.2 | 4 | 0 | 8.63 | 4 | 0.00877 | 76.2 | 4 | 0.0580 | 3.86 |
| Clay | 4 | 0.00288 | 257 | 4 | 0.0065 | 60.1 | 4 | 0.0191 | 42.4 | 4 | 0.0715 | 1.64 | 4 | 0.00638 | 76.7 | 4 | 0.0564 | 3.90 |
| Sand | 4 | 0.00546 | 255 | 4 | 0.0138 | 58.6 | 4 | 0.0206 | 42.0 | 4 | 0.0516 | 2.97 | 4 | 0.00812 | 76.3 | 4 | 0.192 | 0 |
| Silt | 4 | 0.00835 | 253 | 4 | 0.0000 | 62.8 | 4 | 0.0101 | 44.9 | 4 | 0 | 7.99 | 4 | 0.00947 | 76.0 | 4 | 0.122 | 2.01 |
| Bulk density | 4 | 0.00465 | 255 | 4 | 0.0000 | 61.8 | 4 | 0.0111 | 44.6 | 4 | 0.0958 | 0 | 4 | 0.01945 | 73.9 | 4 | 0.102 | 2.58 |

df Degrees of freedom

Appendix 6 Relationships between the effects of drought and precipitation on the abundance and diversity of soil biota lnRR and four continuous variables

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Treatment** |  | **Variables** | **Intercept** | **Slope** | **P value** |
| Precipitation increases | Abundance | Mean annual temperature | 0.4242 | -0.0189 | ns |
|  |  | Mean annual precipitation | -0.0414 | 0.0003 | ns |
|  |  | Magnitude of treatment (% average) | 0.1043 | 0.0023 | **0.0664\*** |
|  |  | Duration of treatment | 0.1266 | 0.0001 | ns |
|  | Diversity | Mean annual temperature | 0.1261 | -0.0068 | ns |
|  |  | Mean annual precipitation | 0.2232 | -0.0002 | ns |
|  |  | Magnitude of treatment (% average) | -0.0434 | 0.0036 | ns |
|  |  | Duration of treatment | 0.1452 | 0 | ns |
| Drought | Abundance | Mean annual temperature | -0.9099 | 0.0363 | ns |
|  |  | Mean annual precipitation | -0.4782 | 0 | ns |
|  |  | Magnitude of treatment (% average) | -0.0363 | 0.0069 | **0.0831\*** |
|  |  | Duration of treatment | -0.7581 | 0.0002 | **0.0013\*\*** |
|  | Diversity | Mean annual temperature | -0.1913 | 0.0101 | ns |
|  |  | Mean annual precipitation | 0.0531 | -0.0001 | ns |
|  |  | Magnitude of treatment (% average) | -0.0087 | 0.002 | ns |
|  |  | Duration of treatment | -0.1349 | 0 | ns |

Results are from 16 separate random-effects models using Metafor and include soil biota from all taxa, body width, and forest biomes; p values are from model results

ns Not significant

\* significant at an alpha level of 0.1

\*\* significant at an alpha level of 0.05

Appendix 6 Relationships between the effects of drought and precipitation on the abundance and diversity of soil biota lnRR and four continuous variables

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Treatment** |  | **Variables** | **Intercept** | **Slope** | **P value** |
| Precipitation increases | Abundance | Mean annual temperature | 0.4242 | -0.0189 | ns |
|  |  | Mean annual precipitation | -0.0414 | 0.0003 | ns |
|  |  | Magnitude of treatment (% average) | 0.1043 | 0.0023 | **0.0664\*** |
|  |  | Duration of treatment | 0.1266 | 0.0001 | ns |
|  | Diversity | Mean annual temperature | 0.1261 | -0.0068 | ns |
|  |  | Mean annual precipitation | 0.2232 | -0.0002 | ns |
|  |  | Magnitude of treatment (% average) | -0.0434 | 0.0036 | ns |
|  |  | Duration of treatment | 0.1452 | 0 | ns |
| Drought | Abundance | Mean annual temperature | -0.9099 | 0.0363 | ns |
|  |  | Mean annual precipitation | -0.4782 | 0 | ns |
|  |  | Magnitude of treatment (% average) | -0.0363 | 0.0069 | **0.0831\*** |
|  |  | Duration of treatment | -0.7581 | 0.0002 | **0.0013\*\*** |
|  | Diversity | Mean annual temperature | -0.1913 | 0.0101 | ns |
|  |  | Mean annual precipitation | 0.0531 | -0.0001 | ns |
|  |  | Magnitude of treatment (% average) | -0.0087 | 0.002 | ns |
|  |  | Duration of treatment | -0.1349 | 0 | ns |

Results are from 16 separate random-effects models using Metafor and include soil biota from all taxa, body width, and forest biomes; p values are from model results

ns Not significant

\* significant at an alpha level of 0.1

\*\* significant at an alpha level of 0.05

**Figure 11. (A and B)** Response of soil fauna abundance of different body widths after precipitation decrease (**A**) and precipitation increase (**B**). (**C**) Diversity response of soil fauna of different body widths to precipitation increases. Means for all figures are conditioned to a model including the body width size as a moderator and study and site as random variables. Positive values for the response ratio indicate an increased abundance or diversity relative to the control treatment. Confidence in estimates is indicated by the horizontal lines, with the bold line representing 95% confidence intervals and the non-bold line represents the 95% prediction intervals. Coloured circles represent individual effect sizes, and k = number of effect sizes (observations), with the number of grouping levels (study sites) for each level of the moderator shown in bracketsAppendix 6 Relationships between the effects of drought and precipitation on the abundance and diversity of soil biota lnRR and four continuous variables

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Treatment** |  | **Variables** | **Intercept** | **Slope** | **P value** |
| Precipitation increases | Abundance | Mean annual temperature | 0.4242 | -0.0189 | ns |
|  |  | Mean annual precipitation | -0.0414 | 0.0003 | ns |
|  |  | Magnitude of treatment (% average) | 0.1043 | 0.0023 | **0.0664\*** |
|  |  | Duration of treatment | 0.1266 | 0.0001 | ns |
|  | Diversity | Mean annual temperature | 0.1261 | -0.0068 | ns |
|  |  | Mean annual precipitation | 0.2232 | -0.0002 | ns |
|  |  | Magnitude of treatment (% average) | -0.0434 | 0.0036 | ns |
|  |  | Duration of treatment | 0.1452 | 0 | ns |
| Drought | Abundance | Mean annual temperature | -0.9099 | 0.0363 | ns |
|  |  | Mean annual precipitation | -0.4782 | 0 | ns |
|  |  | Magnitude of treatment (% average) | -0.0363 | 0.0069 | **0.0831\*** |
|  |  | Duration of treatment | -0.7581 | 0.0002 | **0.0013\*\*** |
|  | Diversity | Mean annual temperature | -0.1913 | 0.0101 | ns |
|  |  | Mean annual precipitation | 0.0531 | -0.0001 | ns |
|  |  | Magnitude of treatment (% average) | -0.0087 | 0.002 | ns |
|  |  | Duration of treatment | -0.1349 | 0 | ns |

Results are from 16 separate random-effects models using Metafor and include soil biota from all taxa, body width, and forest biomes; p values are from model results

ns Not significant

\* significant at an alpha level of 0.1

\*\* significant at an alpha level of 0.05

Appendix 6 Relationships between the effects of drought and precipitation on the abundance and diversity of soil biota lnRR and four continuous variables

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Treatment** |  | **Variables** | **Intercept** | **Slope** | **P value** |
| Precipitation increases | Abundance | Mean annual temperature | 0.4242 | -0.0189 | ns |
|  |  | Mean annual precipitation | -0.0414 | 0.0003 | ns |
|  |  | Magnitude of treatment (% average) | 0.1043 | 0.0023 | **0.0664\*** |
|  |  | Duration of treatment | 0.1266 | 0.0001 | ns |
|  | Diversity | Mean annual temperature | 0.1261 | -0.0068 | ns |
|  |  | Mean annual precipitation | 0.2232 | -0.0002 | ns |
|  |  | Magnitude of treatment (% average) | -0.0434 | 0.0036 | ns |
|  |  | Duration of treatment | 0.1452 | 0 | ns |
| Drought | Abundance | Mean annual temperature | -0.9099 | 0.0363 | ns |
|  |  | Mean annual precipitation | -0.4782 | 0 | ns |
|  |  | Magnitude of treatment (% average) | -0.0363 | 0.0069 | **0.0831\*** |
|  |  | Duration of treatment | -0.7581 | 0.0002 | **0.0013\*\*** |
|  | Diversity | Mean annual temperature | -0.1913 | 0.0101 | ns |
|  |  | Mean annual precipitation | 0.0531 | -0.0001 | ns |
|  |  | Magnitude of treatment (% average) | -0.0087 | 0.002 | ns |
|  |  | Duration of treatment | -0.1349 | 0 | ns |

Results are from 16 separate random-effects models using Metafor and include soil biota from all taxa, body width, and forest biomes; p values are from model results

ns Not significant

\* significant at an alpha level of 0.1

\*\* significant at an alpha level of 0.05

**Figure 4. (A and B)** Response of soil fauna abundance of different body widths after precipitation decrease (**A**) and precipitation increase (**B**). (**C**) Diversity response of soil fauna of different body widths to precipitation increases. Means for all figures are conditioned to a model including the body width size as a moderator and study and site as random variables. Positive values for the response ratio indicate an increased abundance or diversity relative to the control treatment. Confidence in estimates is indicated by the horizontal lines, with the bold line representing 95% confidence intervals and the non-bold line represents the 95% prediction intervals. Coloured circles represent individual effect sizes, and k = number of effect sizes (observations), with the number of grouping levels (study sites) for each level of the moderator shown in bracketsAppendix 6 Relationships between the effects of drought and precipitation on the abundance and diversity of soil biota lnRR and four continuous variables

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Treatment** |  | **Variables** | **Intercept** | **Slope** | **P value** |
| Precipitation increases | Abundance | Mean annual temperature | 0.4242 | -0.0189 | ns |
|  |  | Mean annual precipitation | -0.0414 | 0.0003 | ns |
|  |  | Magnitude of treatment (% average) | 0.1043 | 0.0023 | **0.0664\*** |
|  |  | Duration of treatment | 0.1266 | 0.0001 | ns |
|  | Diversity | Mean annual temperature | 0.1261 | -0.0068 | ns |
|  |  | Mean annual precipitation | 0.2232 | -0.0002 | ns |
|  |  | Magnitude of treatment (% average) | -0.0434 | 0.0036 | ns |
|  |  | Duration of treatment | 0.1452 | 0 | ns |
| Drought | Abundance | Mean annual temperature | -0.9099 | 0.0363 | ns |
|  |  | Mean annual precipitation | -0.4782 | 0 | ns |
|  |  | Magnitude of treatment (% average) | -0.0363 | 0.0069 | **0.0831\*** |
|  |  | Duration of treatment | -0.7581 | 0.0002 | **0.0013\*\*** |
|  | Diversity | Mean annual temperature | -0.1913 | 0.0101 | ns |
|  |  | Mean annual precipitation | 0.0531 | -0.0001 | ns |
|  |  | Magnitude of treatment (% average) | -0.0087 | 0.002 | ns |
|  |  | Duration of treatment | -0.1349 | 0 | ns |

Results are from 16 separate random-effects models using Metafor and include soil biota from all taxa, body width, and forest biomes; p values are from model results

ns Not significant

\* significant at an alpha level of 0.1

\*\* significant at an alpha level of 0.05

Appendix 6 Relationships between the effects of drought and precipitation on the abundance and diversity of soil biota lnRR and four continuous variables

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Treatment** |  | **Variables** | **Intercept** | **Slope** | **P value** |
| Precipitation increases | Abundance | Mean annual temperature | 0.4242 | -0.0189 | ns |
|  |  | Mean annual precipitation | -0.0414 | 0.0003 | ns |
|  |  | Magnitude of treatment (% average) | 0.1043 | 0.0023 | **0.0664\*** |
|  |  | Duration of treatment | 0.1266 | 0.0001 | ns |
|  | Diversity | Mean annual temperature | 0.1261 | -0.0068 | ns |
|  |  | Mean annual precipitation | 0.2232 | -0.0002 | ns |
|  |  | Magnitude of treatment (% average) | -0.0434 | 0.0036 | ns |
|  |  | Duration of treatment | 0.1452 | 0 | ns |
| Drought | Abundance | Mean annual temperature | -0.9099 | 0.0363 | ns |
|  |  | Mean annual precipitation | -0.4782 | 0 | ns |
|  |  | Magnitude of treatment (% average) | -0.0363 | 0.0069 | **0.0831\*** |
|  |  | Duration of treatment | -0.7581 | 0.0002 | **0.0013\*\*** |
|  | Diversity | Mean annual temperature | -0.1913 | 0.0101 | ns |
|  |  | Mean annual precipitation | 0.0531 | -0.0001 | ns |
|  |  | Magnitude of treatment (% average) | -0.0087 | 0.002 | ns |
|  |  | Duration of treatment | -0.1349 | 0 | ns |

Results are from 16 separate random-effects models using Metafor and include soil biota from all taxa, body width, and forest biomes; p values are from model results

ns Not significant

\* significant at an alpha level of 0.1

\*\* significant at an alpha level of 0.05

**Figure 11. (A and B)** Response of soil fauna abundance of different body widths after precipitation decrease (**A**) and precipitation increase (**B**). (**C**) Diversity response of soil fauna of different body widths to precipitation increases. Means for all figures are conditioned to a model including the body width size as a moderator and study and site as random variables. Positive values for the response ratio indicate an increased abundance or diversity relative to the control treatment. Confidence in estimates is indicated by the horizontal lines, with the bold line representing 95% confidence intervals and the non-bold line represents the 95% prediction intervals. Coloured circles represent individual effect sizes, and k = number of effect sizes (observations), with the number of grouping levels (study sites) for each level of the moderator shown in bracketsAppendix 6 Relationships between the effects of drought and precipitation on the abundance and diversity of soil biota lnRR and four continuous variables

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Treatment** |  | **Variables** | **Intercept** | **Slope** | **P value** |
| Precipitation increases | Abundance | Mean annual temperature | 0.4242 | -0.0189 | ns |
|  |  | Mean annual precipitation | -0.0414 | 0.0003 | ns |
|  |  | Magnitude of treatment (% average) | 0.1043 | 0.0023 | **0.0664\*** |
|  |  | Duration of treatment | 0.1266 | 0.0001 | ns |
|  | Diversity | Mean annual temperature | 0.1261 | -0.0068 | ns |
|  |  | Mean annual precipitation | 0.2232 | -0.0002 | ns |
|  |  | Magnitude of treatment (% average) | -0.0434 | 0.0036 | ns |
|  |  | Duration of treatment | 0.1452 | 0 | ns |
| Drought | Abundance | Mean annual temperature | -0.9099 | 0.0363 | ns |
|  |  | Mean annual precipitation | -0.4782 | 0 | ns |
|  |  | Magnitude of treatment (% average) | -0.0363 | 0.0069 | **0.0831\*** |
|  |  | Duration of treatment | -0.7581 | 0.0002 | **0.0013\*\*** |
|  | Diversity | Mean annual temperature | -0.1913 | 0.0101 | ns |
|  |  | Mean annual precipitation | 0.0531 | -0.0001 | ns |
|  |  | Magnitude of treatment (% average) | -0.0087 | 0.002 | ns |
|  |  | Duration of treatment | -0.1349 | 0 | ns |

Results are from 16 separate random-effects models using Metafor and include soil biota from all taxa, body width, and forest biomes; p values are from model results

ns Not significant

\* significant at an alpha level of 0.1

\*\* significant at an alpha level of 0.05

Appendix 6 Relationships between the effects of drought and precipitation on the abundance and diversity of soil biota lnRR and four continuous variables

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Treatment** |  | **Variables** | **Intercept** | **Slope** | **P value** |
| Precipitation increases | Abundance | Mean annual temperature | 0.4242 | -0.0189 | ns |
|  |  | Mean annual precipitation | -0.0414 | 0.0003 | ns |
|  |  | Magnitude of treatment (% average) | 0.1043 | 0.0023 | **0.0664\*** |
|  |  | Duration of treatment | 0.1266 | 0.0001 | ns |
|  | Diversity | Mean annual temperature | 0.1261 | -0.0068 | ns |
|  |  | Mean annual precipitation | 0.2232 | -0.0002 | ns |
|  |  | Magnitude of treatment (% average) | -0.0434 | 0.0036 | ns |
|  |  | Duration of treatment | 0.1452 | 0 | ns |
| Drought | Abundance | Mean annual temperature | -0.9099 | 0.0363 | ns |
|  |  | Mean annual precipitation | -0.4782 | 0 | ns |
|  |  | Magnitude of treatment (% average) | -0.0363 | 0.0069 | **0.0831\*** |
|  |  | Duration of treatment | -0.7581 | 0.0002 | **0.0013\*\*** |
|  | Diversity | Mean annual temperature | -0.1913 | 0.0101 | ns |
|  |  | Mean annual precipitation | 0.0531 | -0.0001 | ns |
|  |  | Magnitude of treatment (% average) | -0.0087 | 0.002 | ns |
|  |  | Duration of treatment | -0.1349 | 0 | ns |

Results are from 16 separate random-effects models using Metafor and include soil biota from all taxa, body width, and forest biomes; p values are from model results

ns Not significant

\* significant at an alpha level of 0.1

\*\* significant at an alpha level of 0.05