Title: Meta-analysis reveals that the effects of precipitation change on soil and litter fauna in forests depends on body size

Authors and affiliations

Authors: Philip A. Martin[1*], Leonora Fisher[2*], Leticia Pérez-Izquierdo[1], Charlotte Biryol[6], Bertrand Guenet[3], Sebastiaan Luyssaert[4], Stefano Manzoni[5], Claire Menival[6], Mathieu Santonja[6], Rebecca Spake[7], Jan C. Axmacher[2], Jorge Curiel Yuste[1, 8]

*Joint lead authors

[1]BC3 - Basque Centre for Climate Change, Scientific Campus of the University of the Basque Country, 48940 Leioa, Spain

[2]UCL Department of Geography, University College London, Gower Street, London WC1E 6BT, UK.

[3] Laboratoire de Géologie, Ecole normale supérieure, CNRS, IPSL, Université PSL, 24 Rue Lhomond, 75005 Paris, France

[4]Amsterdam Institute for Life and Environment (A-LIFE), Section Systems Ecology, Vrije Universiteit Amsterdam, the Netherlands

[5] Department of Physical Geography and Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden

[6]Aix Marseille Univ, Avignon Univ, CNRS, IRD, IMBE, Marseille, France

[7]School of Biological Sciences, University of Reading, RG6 6EX, Reading, UK

[8]IKERBASQUE, Basque Foundation for Science, Bilbao, Bizkaia, Spain

Contact details of lead author: phil.martin.research@gmail.com

Abstract

Anthropogenic climate change is altering precipitation regimes at a global scale. While precipitation changes have been linked to changes in the abundance and diversity of soil and litter invertebrate fauna in forests, general trends have remained elusive due to mixed results from primary studies. We used a meta-analysis based on 352 comparisons from 30 primary studies to address associated knowledge gaps, (i) quantifying impacts of precipitation change on forest soil and litter fauna abundance and diversity, (ii) exploring reasons for variation in impacts, and (iii) examining biases affecting the realism and accuracy of experimental studies. Precipitation reductions led to large decreases in soil and litter fauna abundance, with the opposite trend observed for precipitation increases, while diversity impacts were smaller. A statistical model containing an interaction between body size and the magnitude of precipitation change showed that mesofauna (e.g. mites, collembola) responded most to changes in precipitation. Changes in taxonomic richness were related solely to the magnitude of precipitation change. Our results suggest that body size is related to the ability of a taxon to survive under drought conditions, or to benefit from high precipitation. We also found that most experiments manipulated precipitation in a way that aligns better with predicted extreme climatic events than with predicted average annual changes in precipitation and that the experimental plots used in experiments were likely too small to accurately capture changes for mobile taxa. The relationship between body size and response to precipitation found here has far-reaching implications for our ability to predict future responses of soil biodiversity to and will help to produce more realistic mechanistic soil models which aim to simulate the responses of soils to global change.

Introduction

Anthropogenic climate change is altering global precipitation patterns (Seager et al., 2018) and increasing the frequency and severity of extreme drought and precipitation events (Sun et al., 2007). Understanding the consequences of precipitation changes is particularly vital for forests, given their critical roles in the global carbon cycle (Walker et al., 2021) and in supporting global biodiversity (Benton et al., 2022). Impacts of precipitation changes on forests include increased tree mortality (Anderegg et al., 2019) and consequent increases in CO_2 emissions (Doughty et al., 2015; Yang et al., 2018), and mixed effects on aboveground forest biodiversity (Fleming et al., 2021). However, the effects of precipitation changes on belowground forest biodiversity remain poorly known (Fierer et al., 2009), despite its importance in regulating organic matter decomposition, nutrient cycling, and plant health among other ecosystem functions (Handa et al., 2014; Nielsen et al., 2015).

Precipitation changes may threaten the processes that soil and litter fauna contribute to because soil moisture is a key limiting factor to the fitness and behaviour of many taxa (Coyle et al., 2017). Precipitation reductions and associated lower soil moisture can reduce water films, restricting the movement of microfauna such as nematodes or reduce the humidity in pores which represent the habitat of mesofauna such as Collembola (Coyle et al., 2017; Erktan et al., 2020). Conversely, increased soil moisture as a result of precipitation increases can facilitate the mobility of fauna such as nematodes, potentially leading to increases in abundance due to increased ability to access food sources (Erktan et al., 2020). These changes can alter reproduction and mortality of a wide range of soil and litter fauna (Kardol et al., 2011; Singh et al., 2019; Wang et al., 2022). For example, extreme drought conditions can increase mortality for taxa such as Collembola (Wang et al., 2022) and Enchytraeidae (Maraldo et al., 2009). Nonetheless, while some studies have reported biodiversity losses as a result of precipitation reduction (Aupic-Samain, Santonja, et al., 2021; Chikoski et al., 2006; Lindberg et al., 2002) others have reported increases (Homet et al., 2021; Lensing et al., 2005), with similarly mixed results for studies of precipitation increases (Chikoski et al., 2006; Frew et al., 2013; Landesman et al., 2011) making generalisation challenging.

One obvious reason for heterogeneity among studies measuring soil faunal responses to precipitation change is the magnitude of the precipitation change itself. Most studies of precipitation change represent manipulative experiments often using rain exclusion devices for reduction treatments or irrigation for precipitation increases, with ambient conditions used as a control. Meta-analyses have failed to find a consistent relationship between the magnitude of precipitation changes and changes in either the abundance or taxonomic richness of soil fauna (Peng et al., 2022). This could in part reflect diverging responses in taxonomic groups to precipitation changes (Coyle et al., 2017). Functional traits, morphological, physiological or phenological features measurable at the individual level (Violle et al., 2007), might offer a tractable way to disentangle some of these differences.

There are many traits that could influence soil faunal responses to precipitation change. Here we focus on three. First, taxa that inhabit the litter layer are likely to be more exposed to extreme fluctuations in moisture, and thus to respond more strongly than taxa inhabiting deeper, more buffered soil horizons (Fraser et al., 2012). Second, the presence of an exoskeleton and a cuticle layer that helps to reduce water loss and may hence render arthropods less prone to desiccation than soft-bodied annelids such as Enchytraeidae (Evans, 2008; Singh et al., 2019). Third, body size relates to microhabitat preferences and therefore dependence on water availability. For example, microfauna, such as nematodes, inhabit water films, so may be particularly vulnerable as they are essentially aquatic organisms (Vandegehuchte et al., 2015), mesofauna, such as Collembola, are sensitive to changes in soil moisture because they are confined to existing air-filled pore spaces (Wang et al., 2022) while macrofauna can create their own pore spaces (Lavelle et al., 2002) and are more capable of avoidant behaviour such as burrowing to deeper depths (Gerard, 1967). Therefore, increasing body size likely yields greater resistance to changes in precipitation. Integrating information on these functional traits into research syntheses should allow for a mechanistic understanding as to why soil faunal responses to precipitation are heterogeneous.

Alongside a lack of understanding of between-study variability, it is also unclear how study design impacts study results. Meta-research in ecology has shown that differences in experimental and sampling designs can have large impacts on the accuracy of estimates of biodiversity change (Christie et al., 2019, 2020; Spake, Mori, Beckmann, Martin, et al., 2021). But methodological robustness is rarely assessed in ecological meta-analyses (Pullin et al., 2022). As well as methodological robustness, it is also unclear if experimental studies employ realistic future precipitation scenarios. This is a particularly serious issue, given existing concerns about the use of unrealistic precipitation manipulations in global change experiments which may result in under- or over- estimations of impact (Korell et al., 2020; Kröel-Dulay et al., 2022).

To address these knowledge gaps, we carried out the first meta-analysis of the effects of precipitation changes on soil and litter fauna in forests. In this study, we address three questions: (1) What are the impacts of precipitation changes on the abundance and diversity of forest soil and litter invertebrate fauna? (2) What are the major determinants of the impacts of precipitation changes on abundance and diversity? (3) What are the major biases in studies of the impacts of precipitation change on forest soil and litter invertebrate fauna?

For question 1, we hypothesised that precipitation reductions cause declines in the abundance and diversity of soil and litter fauna, whereas additional precipitation causes an increase in abundance and diversity (H1, Figure 1a). For question 2, we tested four hypotheses: (i) an increased magnitude of changes in precipitation amplifies changes in abundance and diversity (H2, Figure 1b); or that the effect of precipitation magnitude is further amplified for organisms found in litter compared to soil dwellers (H3, Figure 1c), for organisms without an exoskeleton compared to those with en exoskeleton (H4, Figure 1d), or for organisms with smaller body sizes (H5, Figure 1e). There were no hypotheses for question 3.

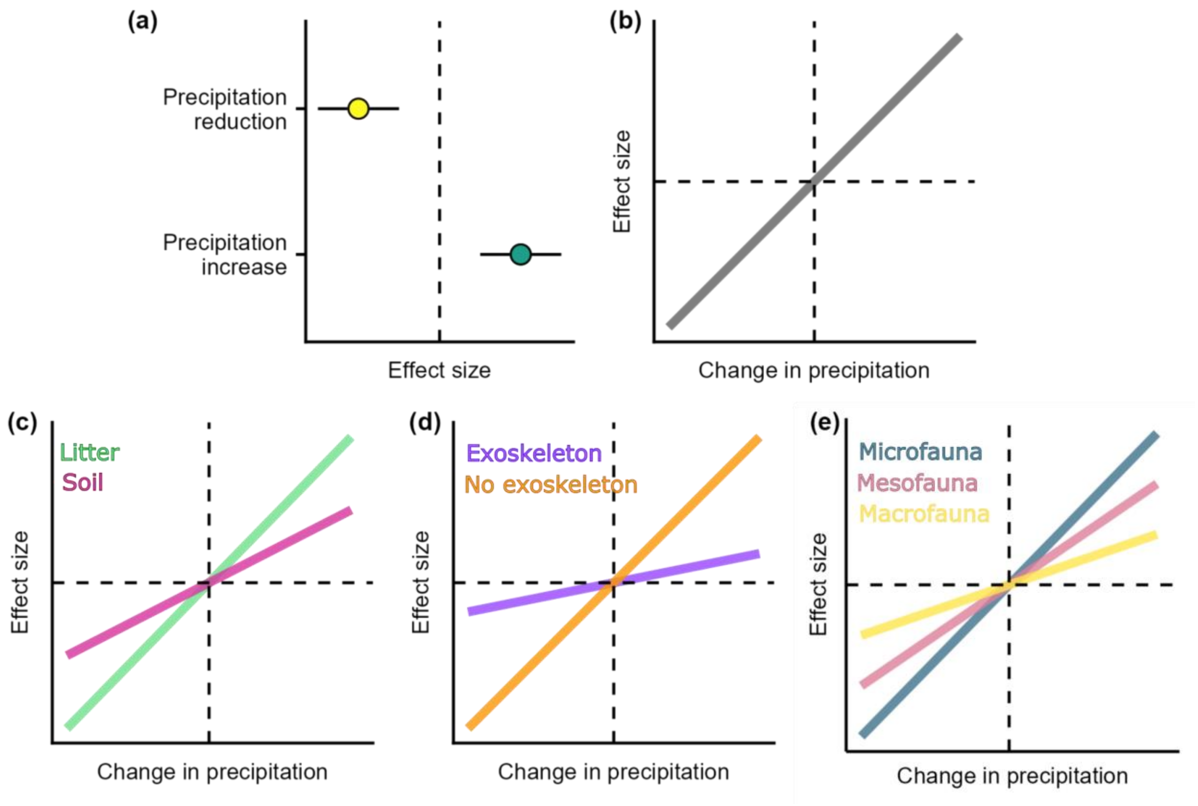

Figure 1 - Conceptual diagram of the hypotheses we test in this study - (a) precipitation reductions negatively affect soil fauna abundance and diversity, while precipitation increases have positive impacts; (b) abundance and diversity changes with respect to control plots are driven by the magnitude of precipitation changes; (c) the effects of changes in precipitation depend on whether invertebrate fauna are found in the soil or the litter; (d) the effects of changes in precipitation depend on whether invertebrate fauna have an exoskeleton or not; (e) the effects of changes in precipitation depend on the body size of invertebrate fauna. Dashed lines represent points at which there is no change in precipitation or no change in effect sizes relating to soil and litter fauna biodiversity. Effect size refers to the differences in abundance or biodiversity between control and treatment groups, with positive changes representing increases in abundance or biodiversity and decreases representing a loss in abundance or biodiversity. For all of these hypotheses we assume that abundance and diversity did not change for the control groups.

Material and Methods

Searches and screening

This study focuses on the impacts of precipitation changes on forest soil and litter invertebrate fauna in field settings. We formally defined these as PECOS elements (Table 1, Grames et al., 2019). More precise definitions of these elements can be found in the Supplementary methods. This study follows guidelines for synthesis in environmental management (Collaboration for Environmental Evidence, 2018), for more details of this see the completed ROSES checklist (Supplementary file 1).

Table 1 - Different PECOS elements used to define the scope of the meta-analysis

PECOS element	Description
Population	Soil and litter fauna found in forest ecosystems. We defined these as invertebrates which spend a significant proportion of their life in litter and/or soil, excluding ants. Details of the selected taxonomic groups are in Table S1.
Exposure	Reductions and increases in precipitation.
Comparison	Any comparison between forests that vary in the frequency or intensity of precipitation that they are subject to. This comparison may be spatial or temporal.
Outcomes	Abundance, biomass, and diversity of soil and litter fauna.
Space	Studies carried out in the field. All types of forest and woodland are considered relevant.

The searches for this study were carried out on 25/11/2021 as part of a systematic map on the impacts of natural disturbances on forest soil and litter fauna (Martin et al., 2021). To identify search terms, we used Grames et al’s (2019) method by creating search terms, using the R package litsearchr to suggest useful terms, and refining final search terms based on these suggestions (see supplementary methods for more details). Once search terms were identified, we searched four bibliographic platforms: Web of Science, Scopus, Google Scholar, and Open Access Theses and Dissertations. Since different bibliographic platforms and databases have different rules for the formatting of searches, we developed platform-specific searches (see Table S2). When searching Google Scholar, we used the R package gsscraper (Haddaway, 2020) to download the first 1000 relevant references we found. By searching for unpublished grey literature as well as published, peer-reviewed literature, we aimed to minimise the risk of publication bias which could lead inaccurate estimates of disturbance impacts (Konno & Pullin, 2020). In addition to formal searches, we contacted expert researchers to help identify potentially relevant studies and included references from primary studies that met our inclusion criteria using the R package citationchaser (Haddaway, Grainger & Gray 2021).

Once searches were complete, we downloaded all references found as .bib or .ris files and used the R package synthesisr to remove duplicate articles (Westgate & Grames, 2020). The bibfix package (Haddaway et al., 2021) was used to repair bibliographic files with incomplete data. Files were then uploaded to sysrev (Bozada et al., 2021) - an online tool that allows for screening and data extraction by review teams (see Martin, 2021). Article titles and abstracts were screened for relevance, and articles that met inclusion criteria were retained and their full text reviewed. To meet our eligibility criteria studies needed to: (1) Relate to soil and litter fauna in forests; (2) Address the impact of changes in precipitation; (3) Be field-based (i.e. not be carried out in greenhouses or mesocosms); (4) Quantitatively assess soil fauna biomass, abundance, or diversity; (5) Have a comparison between sites that vary in the intensity or frequency of the precipitation that they were exposed to; (6) Be written in English; (7) Report measures of centrality (mean or median) for relevant litter or soil fauna outcomes.

At the title and abstract screening stage, in order to be retained, articles needed to be likely to meet criteria 1-3 and criterion 5. At the full-text stage criteria 1-7 needed to be met in order for an article to be retained. At the full-text screening stage, we provided reasons for the exclusion of all articles that did not meet our inclusion criteria in accordance with ROSES guidelines (Haddaway et al., 2018; Figure S2). Despite being a multilingual team, we focussed only on English-language literature because the inclusion of non-English language literature would have made carrying out consistency checks between reviewers challenging. We acknowledge that excluding literature written in non-English languages is a shortcoming that may lead to biases (Amano et al., 2021; Konno et al., 2020).

To ensure consistency, a random sample of 10% of titles and abstracts were screened by two team members, using our inclusion criteria. Any disagreements between the two people were discussed, and eligibility criteria were revised where appropriate. Cohen's Kappa scores were calculated to test the agreement between the two people (Cohen, 1960). If Kappa scores were below 0.6, another 10% of titles and abstracts were screened by the same two team members with the process repeated until Kappa scores were >0.6. The same process was repeated for the full texts of publications that met inclusion criteria. After screening of titles and abstracts, inter-reviewer agreement was 96.6% and the Kappa score was 0.84. For full text screening agreement was 96.6% and the Kappa score was 0.92. We found 19296 papers during searches, 1020 of which were retained after screening of titles and abstracts, and 30 of which were used for critical appraisal and data extraction. We used 352 comparisons between control and treatment groups extracted from these studies. This process is summarised in more detail in Figure S1.

Critical appraisal

Critical appraisal of studies to assess their methodological robustness is a vital part of synthesis (Collaboration for Environmental Evidence, 2018). We did this by assessing the following threats to the internal validity of a study based on Martin et al. (2020) (i) selection bias: when selection of study sites leads to a result that is systematically different to the target population; (ii) confounding: where systematic distortion of the effect of a treatment caused by mixing of the treatment of interest with other disturbances (e.g. plots where precipitation was manipulated were in plantations while control plots were in natural forests); and (iii) performance bias, differences that occur due to knowledge by researchers about treatment allocation. We therefore determined whether studies (i) consisted of both spatial and temporal comparisons, (ii) used randomisation to assign treatment and control units, (iii) avoided confounding factors, and (iv) whether studies were manipulative experiments that allow determination of causality. We assigned studies an overall score of low, medium, or high validity depending on the fulfilment of a priori criteria (see Table S5). These scores were later used in statistical analyses.

Data extraction and coding

We extracted data on the means, measures of variation, and sample sizes for each relevant biodiversity measure both in control and treatment groups. When data for more than one time period or site was presented in the same study we extracted all available data. When variation around the mean was presented as standard errors we converted it to standard deviation using the equation $SD = SE \times \sqrt{n}$ where SE refers to the standard error and n refers to the sample size. Where data was presented in the form of figures we extracted this using the R package metadigitise (Pick et al., 2018). In total 16% of studies lacked data on variation and 14% lacked data on sample sizes and so to avoid problems associated with excluding studies with missing data (Nakagawa & Freckleton, 2008) we chose to impute these values using the method of Nakagawa et al. (2022). Using these data we then calculated the log response ratio and its variance (Hedges et al., 1999) as implemented by Nakagawa et al. (2022) for use as an effect size, which improves the accuracy and precision of meta-analyses especially when sample sizes are small.

Regarding explanatory variables and contextual data, we extracted information on the geographic location of studies, the perturbation type (precipitation reduction or precipitation increase), the magnitude of precipitation change (% change compared to control), the relevant taxonomic groups reported in a study, the size class of fauna (microfauna, mesofauna, and macrofauna) based on Nielsen (2019), the kind of outcome measured (abundance, diversity, or species richness), the sampling design of the study based on Christie *et al.* (2019, 2020), the sampling method (e.g. soil core, soil monolith, pitfall trap), the duration of study, the time after the beginning of perturbation in precipitation at which fauna was sampled, and whether the fauna sampled possessed an exoskeleton. For more detail and definitions of each data element that was extracted see the supplementary methods.

Statistical analyses

We used multilevel meta-analytical models with inverse variance weighting as implemented in the R package metafor (Viechtbauer, 2010). To examine the impacts of precipitation reduction or increase on soil and litter fauna abundance, taxonomic richness, and Shannon-Wiener diversity index (Figure 1a), we built models with no modifiers that included study and site as nested random effects to account for the lack of independence between observations from the same study and site (Nakagawa et al., 2023). We chose not to combine the different outcomes for diversity as doing so can blur responses and limit interpretability of results (Liu et al. 2023). We calculated the I^2 statistic to estimate the percentage of the total variability in effect size values that was due to real heterogeneity. At this stage we also performed two sensitivity analyses to test (i) the impact of removing studies that failed Geary's test of normality (Nakagawa et al., 2022); (ii) the impact of removing studies that we classified as having low validity in our critical appraisal.

To test our hypotheses about how precipitation change alters soil and litter fauna biodiversity, we ran models that included the percentage change in annual precipitation (Figure 1b). All of our other hypotheses involved interactions between changes in precipitation and other variables, and so we also ran models including interactions with the traits: (i) microhabitat (litter or soil, Figure 1c), (ii) presence of an exoskeleton (Figure 1d); and (iii) body size of study taxon (Figure 1e). To account for the potential impacts of publication bias, we included a model parameter representing the square root of the inverse of effective sample size (Nakagawa et al., 2021), to test the impact of the small-study effect, in which smaller studies have different - often larger - effect sizes when compared to larger studies. We also tested the potential of a decline effect, in which the effect sizes reported by studies declines over time (Koricheva & Kulinskaya, 2019; Nakagawa et al., 2021). Model selection was carried out using Akaike's Information Criterion adjusted for small sample sizes (AICc) with models with a ΔAICc<2 considered to have similar support. We carried out model-averaging for models with a ΔAICc<2 using the 'zero method' (Grueber et al., 2011) in the R package MuMIn (Barton, 2015) in order to produce model coefficients and associated statistics.

We assessed three different types of bias that may undermine the realism and accuracy of estimates of biodiversity changes as a result of precipitation change. To determine geographic biases we plotted study locations on a map. We derived annual precipitation and temperature data from the geographic coordinates of the sites and used the R package plotbiomes to assess biases in the forest biomes that have been studied (Ștefan & Levin, 2018). Next we assessed the similarity of the precipitation changes simulated in experiments to future projections of precipitation change in the same location. To do this we calculated the change in precipitation imposed by experiments and compared this to projected values for the same location using the HadGEM3-GC31-LL climate model for the period 2041-2060 for pathway ssp245 - a medium carbon emissions scenario. We compared the precipitation rate for experiments to those projected to occur under our selected emissions scenario by calculating the log response ratio of the two. We then ran a linear mixed effects model with a random term for each study to assess whether experiments that reduced or increased precipitation were similar in precipitation rates to predicted changes. Finally, given the importance of spatial scale when estimating biodiversity changes (Chase & Knight, 2013; Spake, Mori, Beckmann, & Martin, 2021) we assessed the plot size at which treatments were applied in experiments for fauna with different body sizes to identify where there may be a mismatch between the mobility of taxa and the scale of experiments.

Results

Impacts of precipitation change

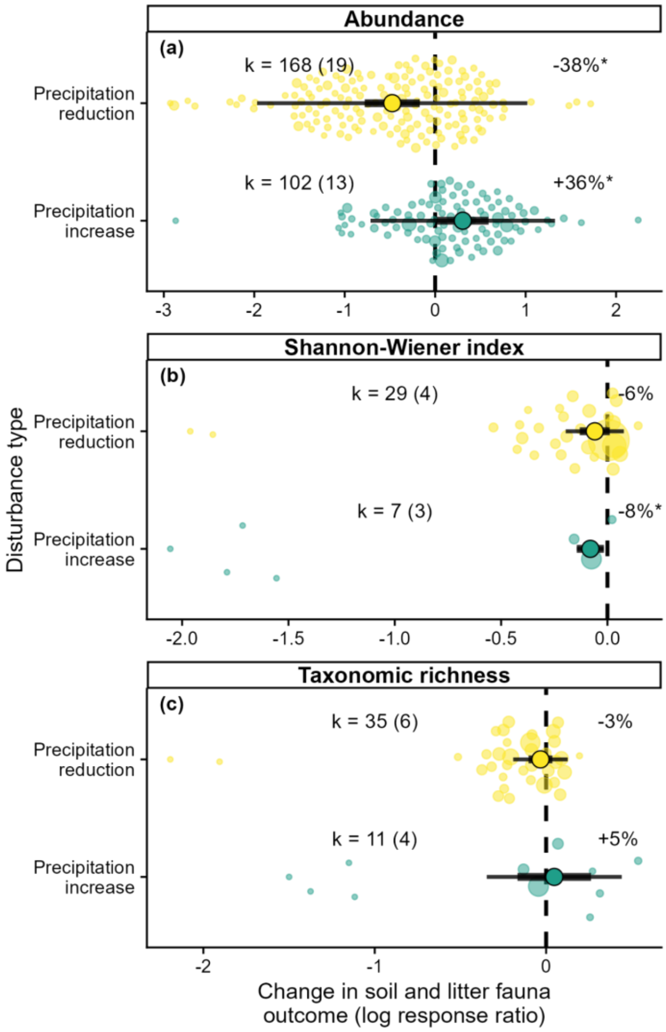

Figure 2 - Changes in the (a) abundance (b) Shannon-Wiener diversity index, and (c) taxonomic richness of soil and litter fauna in forests as a result of precipitation change. Large points refer to the summary effect size, thicker bars around them representing the 95% confidence intervals, and the thinner bars the 95% prediction intervals. Smaller, semi-transparent points represent individual comparisons. Differences in their size refer to the weight they supply to each analysis. The vertical dashed line represents where the effect size is equal to zero (i.e. where there is no difference between control and treatment groups). Annotations on the left of the plot refer to the number of comparisons in each analysis (k) and, in parentheses, the number of studies they are taken from. Annotations on the right of the plot refer to the mean weighted percentage change for each analysis and asterisks (*) indicate when effect sizes are significantly different from zero.

Precipitation reductions led to a 38% reduction in soil and litter fauna abundance (Figure 2a, coefficient = -0.48, confidence intervals = -0.78, -0.17, p-value = 0.002, k = 170). There was significant between-study heterogeneity (Q = 1059, p-value = <0.001) and the proportion of this heterogeneity that was due between-study differences was high (I^2 = 84%). Precipitation increases led to a 35% increase in abundance in soil and litter fauna (Figure 2a, coefficient = 0.31, confidence intervals = 0.19, 0.59, p-value = 0.037, k = 105). Variation in effect size was again significant (*Q* = 1542, p-value = <0.001) and a large amount of this was due to real heterogeneity (I^2 = 82). For both precipitation reduction and increases, removing effect sizes that failed Geary's test of normality did not qualitatively alter the results (Table S5). However, in the case of precipitation reduction, removing studies with low validity markedly reduced the summary effect size (Table S6). Further investigation revealed that this was likely to be due to higher validity studies reducing precipitation in a more extreme manner.

The impacts of precipitation changes on both taxonomic richness and Shannon-Wiener diversity were less pronounced than those seen for abundance. Precipitation reduction reduced taxonomic richness by 3%, but this effect was not statistically significant (Figure 2c, coefficient = -0.03, confidence intervals = -0.10, 0.04, p-value = 0.352, k = 37). Precipitation increase caused an increase in taxonomic richness of 5%, but this effect was again not statistically significant (Figure 2c, coefficient = 0.05, confidence intervals = -0.17, 0.26, p-value = 0.664, k = 11). Shannon-Weiner diversity showed a non-significant reduction with decreased precipitation (Figure 2b, coefficient = -0.06, confidence intervals= -0.13, 0.02, p-value = 0.097, k = 31) but a significant decrease with increased precipitation (Figure 2b, coefficient = -0.08, confidence intervals = -0.14, -0.02, p-value = 0.014, k = 9). Although most of these models indicated significant variability in effect sizes, the proportion of heterogeneity due to between-study differences was much lower than for the analyses of abundance (I^2 = 0-56%, Table S6). Removing effect sizes that failed Geary's test of normality did not qualitatively alter the results but again removing studies with low validity tended to lead to more extreme summary effect sizes (Table S6).

Drivers of precipitation change impact

When investigating the reasons for differences in the impact of precipitation changes on abundance, the most parsimonious models included an interaction between the magnitude of precipitation change and organism body size as well as moderators to account for study size and whether effect sizes change over time (Table S6). Model-averaging suggested that mesofauna abundance responded to changes in the magnitude of precipitation, while this was not the case for microfauna and macrofauna (Figure 3). Of the moderators only the interaction between mesofauna and the magnitude of precipitation change was statistically significant (coefficient = 0.005, SE = 0.002, p-value = 0.026), while for microfauna and macrofauna the slopes were much less steep and not statistically significant (Table S6). The effects of study size and publication year were not statistically significant either. We tested whether the impact of precipitation change differed between two of the most well-studied taxonomic groups, Collembola and Acari (Figure S4). While we found that both groups showed a response to changes in precipitation magnitude, there was no statistically significant difference between the responses (Table S9).

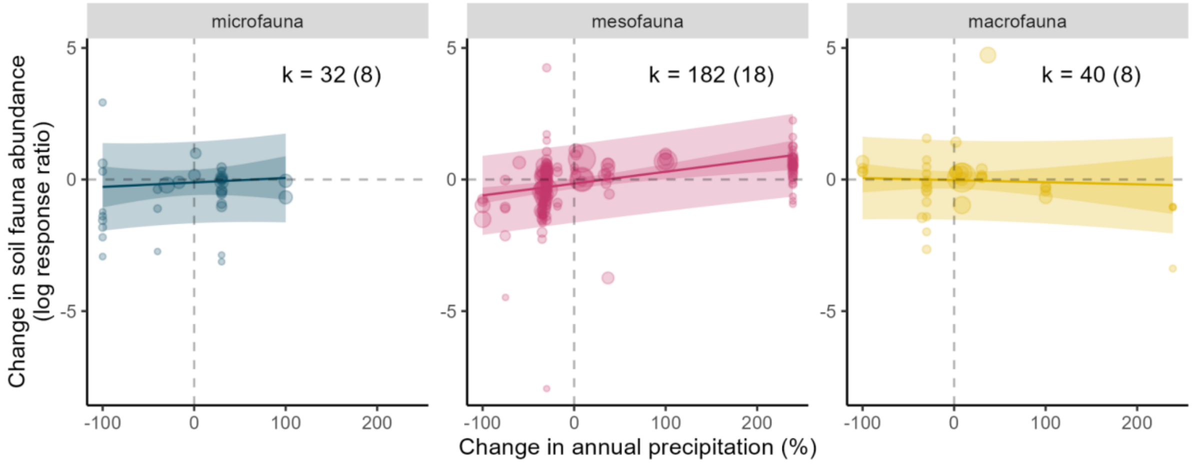

Figure 3 - Changes in the abundance of soil and litter fauna in forests relative to changes in precipitation for different faunal size classes. Points represent individual comparisons with different point sizes representing the different weights of comparisons to the analysis. Solid lines represent predictions from the most parsimonious model (R^2=0.13), with darker coloured bands representing the 95% confidence intervals, and the lighter bands the 95% prediction intervals. Dashed lines represent points at which there is no change in precipitation (x equal to zero) or in effect size (y equal to zero). Annotations on the plot refer to the number of comparisons in each analysis (k) and, in parentheses, the number of studies they are taken from.

The most parsimonious models for changes in taxonomic richness included only the magnitude of precipitation change or the year of publication (Table S11). Model-averaging showed a non-significant positive relationship with precipitation change (coefficient = 0.002, SE = 0.002, p-value = 0.349, Figure 4, Table S12), indicating weak support for the impact of precipitation change magnitude. Similarly, for Shannon-Wiener diversity the most parsimonious models included different combinations of the magnitude of precipitation change and/or the year of publication (Table S13). Model averaging showed a non-significant negative effect of precipitation magnitude on Shannon-Wiener diversity (coefficient = -0.002, SE = 0.004, p-value = 0.703, Figure S5, Table S14).

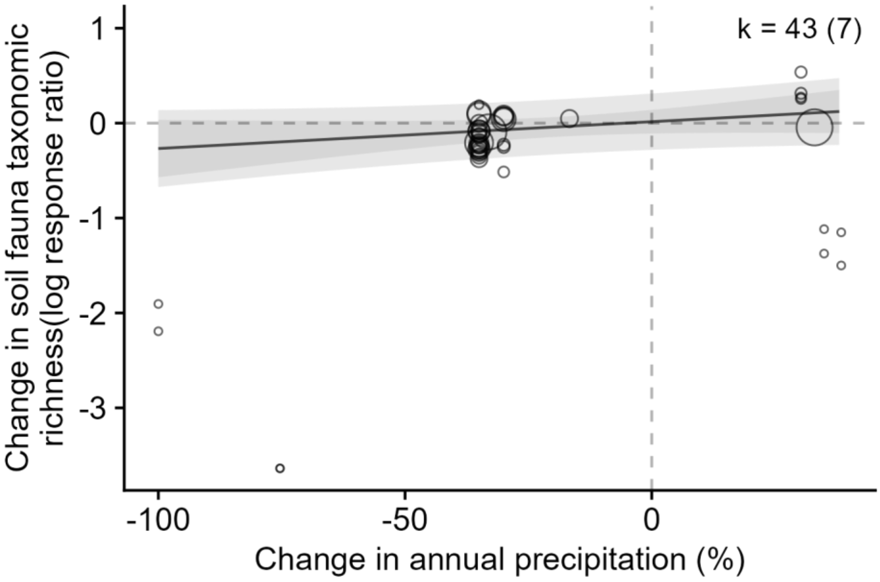

Figure 4 - Changes in taxonomic richness relative to changes in precipitation. Points represent individual comparisons with different point sizes representing the different weights of points in the analysis. The solid line represents predictions from the most parsimonious model (R^2=0.26), with darker coloured bands representing the 95% confidence intervals, and the lighter bands the 95% prediction intervals. Dashed lines represent points at which the x and y axes are equal to zero. Annotations on the plot refer to the number of comparisons in the analysis (k) and, in parentheses, the number of studies they are taken from.

Study biases

There are clear biases in the geographic distribution of studies, with a large number of studies carried out in western Europe and the USA, but relatively few in South America and Asia, and no studies found for Africa (Figure 5a). This translates to an underrepresentation of tropical forest biomes, with most studies carried out in temperate seasonal forests or woodland/shrubland biomes found in mediterranean climates (Figure 5b). In addition to geographic biases, there were also a number of biases that could impact the validity of study results. First, studies of the effects of precipitation reduction reduced precipitation by 92% more than projected changes for the same location (Figure 6a, coefficient = -2.59, SE = 0.64, p-value = 0.002), while studies of precipitation increase increased precipitation by 204% more than projected changes, although this difference was not statistically significant (Figure 6a, coefficient = 1.11, SE = 0.805, p-value = 0.197). Second, the plots used for experimental manipulations tended to be small for studies of micro-, meso-, and macrofauna (Figure 6b), with median areas of 460 m^2, 300 m^2, and 36 m^2 respectively.

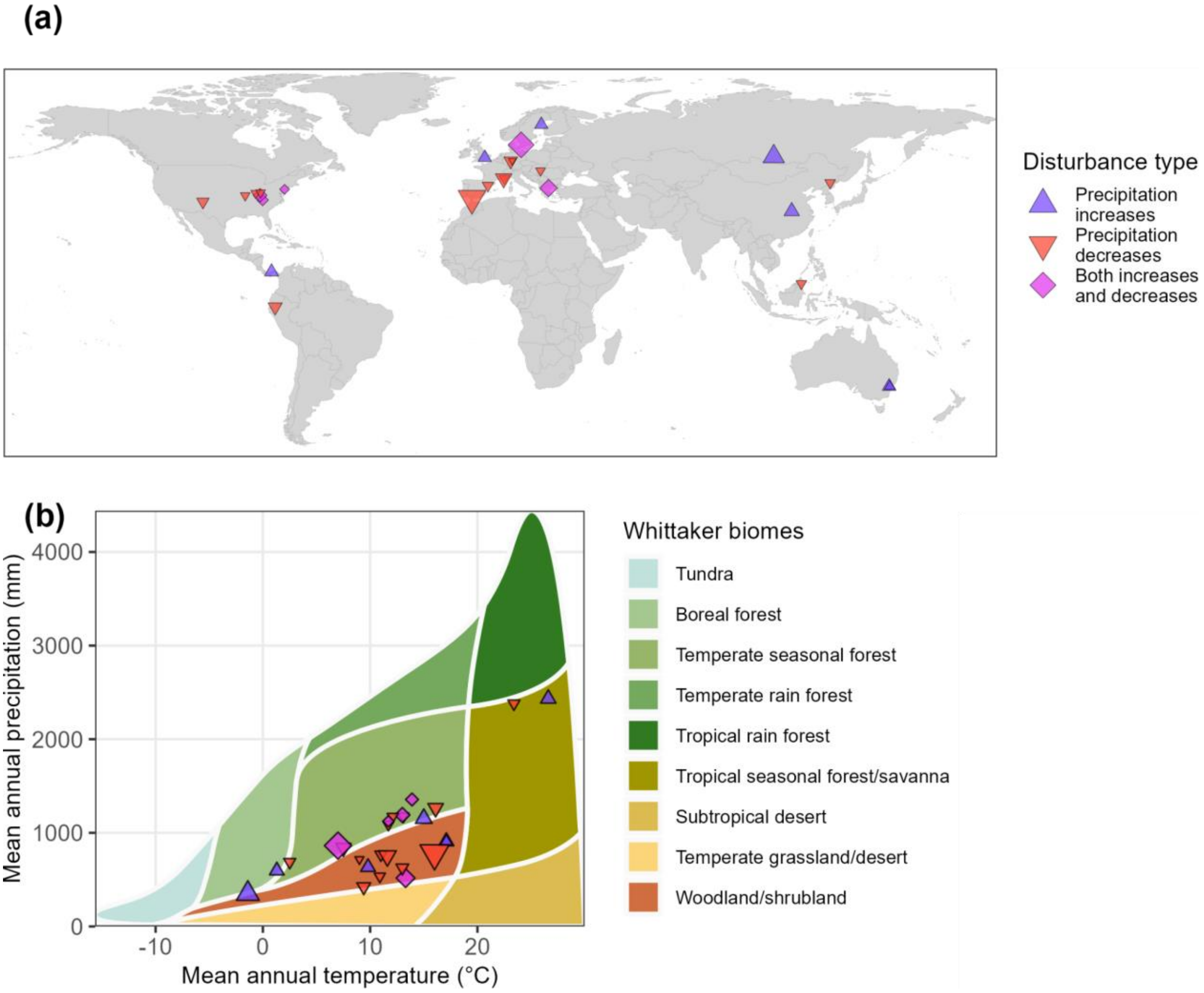

Figure 5 - (a) The location of study sites and (b) distribution within biomes. Studies of precipitation increase are shown by blue upward-pointing triangle symbols, studies of precipitation decrease by red downward-pointing triangles, and studies that investigated both increases and decreases are shown by purple diamonds. The size of the symbols indicates the number of comparisons made at each location (minimum: 1, maximum: 88). In (b) the location of each site in a Whittaker biome diagram is defined by mean annual temperature and mean annual precipitation.

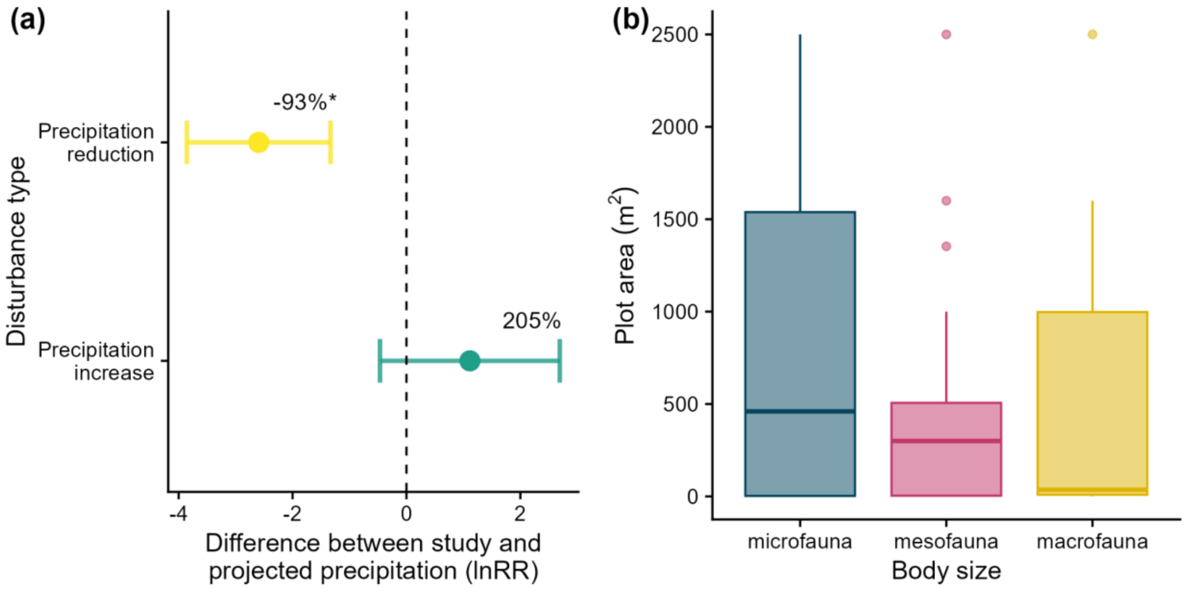

Figure 6 - Biases that affect the validity of study results: (a) Differences in precipitation changes investigated in studies compared to projected precipitation changes based on Hadlee climate model projections for 2041-2060; (b) Sizes of plots used in experimental studies of precipitation changes effects on the differing body size groups of invertebrate soil and litter fauna. In (a) points represent mean values for each group and error bars the 95% confidence intervals. The dashed vertical line represents the point at which there is no difference between projected and studied level of precipitation change. Annotations on the right of the plot refer to the mean percentage change for each analysis and asterisks (*) indicate when effect sizes are significantly different from zero.

Discussion

Our findings partially supported Hypothesis 1, indicating that reductions in precipitation generally cause large decreases in the abundance of soil and litter fauna in forests, while precipitation increases have the opposite effect. However, impacts on taxonomic richness and Shannon-Wiener diversity were typically less pronounced. Changes in abundance depended on the magnitude of precipitation changes and taxa body size: mesofauna abundance changes were positively correlated with changes in precipitation, but there was little detectable effect of body size for either micro- or macrofauna. We found weak support for a positive correlation between changes in precipitation and changes in taxonomic richness but no support of this correlation for Shannon-Wiener diversity. Thus, the best supported of our hypotheses regarding the variability in response to precipitation changes was Hypothesis 5, that the impacts of precipitation change depended on taxa body size. However, there was only weak support for Hypothesis 2, that increased magnitude of changes in precipitation amplifies changes in abundance and diversity, and little support for the effects of fauna occupying litter or soil (Hypothesis 3) or possessing an exoskeleton (Hypothesis 4) regarding the modification of impacts of precipitation changes.

Impacts of precipitation change

Our results broadly agree with those of the meta-analysis by Peng et al. (2022), who found that impacts of precipitation change on the abundance of soil fauna in forests were much larger than for richness. However, our meta-analysis included more than three times as many primary studies relating to forests, and over twice as many effect sizes, indicating that our results represent an important advance in robustness. Our results also broadly mirrored those found by the recent meta-analysis of Bristol et al. (2023) who focussed solely on nematodes and showed a non-significant increase in abundance as a result of precipitation increases and a non-significant decrease as a result of precipitation reductions. However, unlike previous meta-analyses (Blankinship et al., 2011; Peng et al., 2022), we found important evidence for nuanced effects of precipitation change.

The lack of pronounced changes in either taxonomic richness or Shannon-Wiener diversity was surprising, but one intriguing finding was that species richness changed little as a result of precipitation change, while Shannon-Wiener diversity was significantly reduced following precipitation increases. This hints that, as suggested by others, some Oribatida and Collembola species become increasingly dominant when soil moisture is increased, reducing evenness (Meehan et al., 2020). In contrast with our findings for changes in abundance, we found relatively little support for the effect of changes in precipitation magnitude or species traits on taxonomic richness or Shannon-Wiener diversity. This could result from changes in local diversity as a result of perturbations often not reflecting those in community composition (Hillebrand et al., 2018; Zajicek et al., 2021). This occurs when there is turnover in the identity and abundance of species but no systematic change in the number of species (Hillebrand et al., 2018) as appears to be common for numerous human-impacted ecosystems (Dornelas et al., 2014; Vellend et al., 2013). However, it is also possible that the apparent lack of effect is actually a result of different responses to precipitation changes across taxonomic or functional groups that we were unable to capture due to a lack of data.

Drivers of precipitation change impact

Our findings for changes in abundance suggest that water availability is a key constraint for many forest soil taxa (Aupic-Samain, Baldy, et al., 2021), but that impacts of soil moisture vary depending on organism body size. The effect of intense precipitation changes on mesofauna abundance is consistent with previous studies that suggested that this group can be particularly sensitive to environmental changes (Wu & Wang, 2019) and that high-intensity disturbances can have an enduring effect on ecological processes and hinder recovery (Nielsen & Ball, 2015). This could lead to reductions in the incorporation of leaf litter into soil, given that litter forms a major part of the diet for taxa such as Collembola and Oribatida (Potapov et al., 2022). The apparent lack of significant impact of precipitation change on micro- and macrofauna, while contradicting our expectations, could have a variety of causes.

Our results suggest that there is a hump-shaped relationship between the body size of soil and litter fauna and their sensitivity to precipitation changes, with micro- and macrofauna being relatively insensitive and mesofauna being highly sensitive. We hypothesise that this sensitivity is caused by three factors. First, differences in the ability to avoid predation. Under drier conditions, microfauna, such as nematodes, can become restricted to small pores (Erktan et al., 2020) that act as refuges from predatory mesofauna such as mites (Potapov et al., 2022) which are unable to access them. Mesofauna are confined to larger, air-filled pores (Erktan et al., 2020). In contrast to nematodes, this confinement does not protect them against predation, because meso- and macrofauna predators can move between soil layers in search of prey (Potapov et al., 2022). Thus, mesofauna remains subject to predation even in dry conditions. Second, physical adaptations to dry conditions. Both micro- and macrofauna possess physical adaptations which aid them in drier conditions. Microfauna, such as nematodes, can go into anhydrobiosis when under drought stress (Landesman et al., 2011; Watanabe, 2006). Many macrofauna, such as spiders or millipedes, have thick exoskeletons which protect them against desiccation as well as being highly mobile, thus allowing them to move more easily to wetter soil patches. In contrast, many mesofauna, such as Collembola or Protura, have few physical adaptations to drought conditions and have limited mobility within the soil. As a consequence, they are likely subject to greater drought-induced mortality than micro- or macrofauna. Third, availability of food sources. While reductions in the food sources for all soil and litter fauna seem likely in dry conditions, mesofauna may be more severely impacted than the other groups. For example, drier conditions reduce saprotrophic fungi abundance (Sanders et al., 2024) and, in the long-term, litter inputs (Deng et al., 2021) both of which serve as important sources of food for Collembola (Potapov et al., 2022). However, many micro- and macrofauna groups have relatively diverse diets, potentially providing a buffer when some sources of food are scarce (Potapov et al., 2022).

Under increased precipitation, the hump-shaped relationship between size and abundance appears to be reversed. This implies that mesofauna is more sensitive to increases in water resources than either micro- or macrofauna. Mesofauna appear to be more easily affected by seasonal changes than macrofauna due to their smaller body size and shorter life cycles (Wu & Wang, 2019), thus explaining their increase in abundance with increased precipitation. Mesofauna may also be less affected by predation under wetter conditions (Aupic-Samain, Baldy, et al., 2021). Meanwhile, for microfauna such as nematodes, increased precipitation may reduce the abundance of some fungi, reducing populations of fungivorous nematodes (T. Liu et al., 2020).

The effect of body size seen in our meta-analysis represents an advance in our understanding of the responses of soil biota to changes in precipitation associated with climate change. However, the mechanisms that regulate this response to changes in water availability are currently unclear and further research could substantially improve our ability to predict the future impact of climate change on the resilience of soils and their functioning in the face of climate change. One such potential impact is that loss of mesofauna could cause a reduction in the rate of litter decomposition (Song et al., 2020) resulting in a reduction in the incorporation of organic matter into soils and a reduction in the complexity of soil structure. Equally, such a reduction in soil mesofauna could lead to increases in the abundance of taxa belonging to other size groups that also feed on litter (e.g. earthworms) resulting in a change in the structure of soil food webs, which may potentially buffer the impacts of precipitation changes on soil functioning. However, this replacement could entail major changes in the physical structure of the soil, since earthworms are ecosystem engineers which can alter soil porosity (Flores et al., 2021). Therefore, although our explanations for the observed patterns are grounded in theory and empirical evidence from the literature new experiments and observations are needed to test them.

Study biases

Our study identified a need for changes in studies of precipitation change impacts on forest soil and litter fauna. The proposed changes may be difficult to implement, and we acknowledge that decisions about study practicalities are the result of a mixture of factors such as socioeconomics (Llorente-Culebras et al., 2023) and the obsession with academic productivity (Fischer et al., 2012). First, linked to our finding that many experiments use precipitation regime alterations that are much more extreme than projected future changes, we advocate for researchers to clearly distinguish between experiments which aim to simulate changes in mean annual precipitation and those that aim to simulate extreme events such as droughts and extreme rainfall (Korell et al., 2020). Second, this study shows that the scale of experimental manipulations in many studies may be too small to capture changes in more mobile macrofauna taxa, and so larger-scale studies are needed that allow for a wider range of organisms and processes to be studied (Hanson & Walker, 2020). Third, we found strong geographic biases, with few studies found outside of temperate and mediterranean forest biomes, and thus suggest the greater need for studies outside of these regions.

While there is a need for changes in how primary studies are conducted, the same is true for syntheses relating to soil fauna. Our study represents one of most methodologically robust meta-analyses to date in soil ecology, collating more studies than previous similar meta-analyses (Blankinship et al., 2011; Peng et al., 2022) and thus providing greater statistical power. We encourage more researchers to strive for more robust evidence syntheses and familiarise themselves with existing guidance for evidence synthesis in ecology (Collaboration for Environmental Evidence, 2018; Haddaway et al., 2018, 2020). In our study we used the log response ratio as an effect size metric, due to differences between studies in the units of abundance. Because the log response ratio measures proportionate change in biodiversity relative to a control or baseline value, there is a loss of information that can render meta-analyses vulnerable to possible inferential errors when baselines vary across studies (Spake et al., 2023). In addition, existing meta-analyses on the impacts of global change on soil fauna (Beaumelle et al., 2023; This study; Blankinship et al., 2011; Bristol et al., 2023; Peng et al., 2022; Phillips et al., 2023) use biodiversity metrics related to abundance and alpha diversity, meaning we know little about impacts on more complex aspects of biodiversity such as community composition and functional diversity. We advocate for researchers to collate and use raw data from field studies to allow for more nuanced 'full data' analyses which can avoid issues associated with the use of effect sizes (Spake et al., 2023) and that are becoming the gold standard in other fields, such as medicine (Culina et al., 2018; Spake et al., 2022). Finally, we recognise that we were unable to explicitly examine the impact of study scale (e.g., grain, extent) on observed changes in soil fauna biodiversity as a result of precipitation changes. However, given the general importance of scale for observations in ecology (Spake, Mori, Beckmann, & Martin, 2021) and the findings that precipitation change experiments have scale-dependent effects on other taxa (Korell et al., 2021) we encourage researchers to address this topic in future syntheses.

Conclusion

Overall, our results suggest that forest soil and litter fauna abundance is sensitive to changes in precipitation, and that for mesofauna this impact depends on the magnitude of precipitation change. Meanwhile, alpha diversity appeared to be relatively insensitive, with little evidence that changes were related to the magnitude of precipitation change. Given soil mesofauna affect soil functions, such as litter decomposition, changes in the abundance of this group may result in changes in the soil physical structure, soil nutrients, and soil carbon. In turn, changes in mesofauna abundance will also alter the trophic structure of belowground food webs. Our results provide new insights into belowground biodiversity change in forests that can inform more realistic soil models in the future (Deckmyn et al., 2020; Flores et al., 2021). In addition, we call on global change researchers to conduct more realistic studies of changes in mean annual precipitation, droughts, and extreme precipitation in future, in line with representative concentration pathways (RCPs; van Vuuren et al., 2011) as well as larger scale experiments to capture impacts on soil fauna more fully.

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Supplementary materials

Supplementary methods

The topic and research questions were developed as part of the HoliSoils project (holisoils.eu), which focuses on holistic management practices, modelling, and monitoring for European forest soils. The topic was defined in a series of meetings with researchers who form the Holisoils consortium and feedback via email on proposed topics. Following this, a series of questions were proposed and feedback from consortium members was included. As a result of these meetings a review team (the authors of this study) was defined who to guide the development of synthesis during the project. During scoping of the project searches that included soil microbes as a population of interest indicated that their inclusion would produce a very large literature that would have taken a large amount of time to screen (Haddaway & Westgate, 2019). As a result of this and because there have already been a large number of syntheses on the impacts of natural disturbances on soil microbes, the review team decided to exclude soil microbes from the study. We also excluded ants because we found that including them massively increased the number of papers we found in searches, which would have led to an unfeasible workload.

To identify the search terms, we used the methodology suggested by Grames et al. (2019). This involved the identification of 'naive' search terms based on the different PECO elements of our questions and scoping of these terms using the Web of Science and Scopus platforms. We decided to restrict our search terms to those related to the population and exposure elements of our PECO because we were concerned that articles may not give details of the outcome and comparison elements in their titles or abstracts. Once our search terms returned all our benchmark studies (see below) all references were downloaded and duplicates removed using the R package revtools (Westgate, 2019). We then used the R package litsearchr to identify potentially useful additional keywords based on those found in the articles during the literature search (Grames et al., 2019). PM manually reviewed suggested keywords and those considered to be useful were added. Table S2 gives details of the different keywords and associated PECO elements for this study. We then followed the recommendations of Foo et al. (2021) to estimate the number of relevant studies returned by our searches. To do this searched the Web of Science and Scopus platforms and randomly selected 500 of the returned references. We screened the references against our inclusion criteria to determine the percentage that met our inclusion criteria. Further details of this process can be found in Supplementary file 2. Since different bibliographic platforms and databases have different rules for the formatting of searches, we developed specific searches for each search system. Details of these search terms for each of the four bibliographic platforms can be found in Supplementary file 2.

To estimate the comprehensiveness of our search the review team developed a benchmark list of articles. These represent articles that we feel our searches needed to capture in order to be considered comprehensive - as recommended by guidelines for environmental evidence synthesis (Collaboration for Environmental Evidence, 2018). We supplemented this list with relevant English-language articles mentioned by reviews and meta-analysis of the impacts of disturbances on belowground organisms and soil conditions (Blankinship et al., 2011; Bouget & Duelli, 2004; Certini et al., 2021; Kristensen et al., 2020; Neary et al., 1999; Pressler et al., 2019; Zhou et al., 2020). Table S3 gives a summary of the benchmark studies.

Table S1 - Taxonomic groups of soil fauna which we included in our study. Size classification is based on Nielsen (2019).

Taxonomic group	**Common name**	**Size classification**
Nematoda	Nematodes	Microfauna
Protozoa	Protozoans	Microfauna
Protista	Protists	Microfauna
Tardigrada	Tardigrades	Microfauna
Rotifera	Rotifers	Microfauna
Acari	Mites	Mesofauna
Collembola	Springtails	Mesofauna
Protura	Proturans	Mesofauna
Diplura	Diplurans	Mesofauna
Symphyla	Pseudocentipedes	Mesofauna
Enchytraeidae	Potworms	Mesofauna
Chelonethi	Pseudoscorpions	Mesofauna
Isoptera	Termites	Macrofauna
Isopoda	Isopods	Macrofauna
Opiliones	Harvestman	Macrofauna
Amphipoda	Amphipods	Macrofauna
Chilipoda	Centipedes	Macrofauna
Diplopoda	Millipedes	Macrofauna
Megadrilacea	Earthworms	Macrofauna
Coleoptera	Beetles	Macrofauna
Araneida	Spiders	Macrofauna
Mollusca	Molluscs	Macrofauna

Table S2 - Terms associated with different PECO elements. Note that the search was broader than solely precipitation changes as it was performed as part of a systematic map on the impacts of natural forest disturbances.

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, Windthrow, Fire, Extreme rainfall, Insect pests, Tree pathogens	Drought, Fire, Wind, Typhoon, Cyclone, Hurricane, Storm, Rain, Precipitation, Disturbance, Global change, Bark beetle, Pest, Insect herbivore, Pathogen

Table S3 - Searches for different platforms. Note that searches included a wide range of natural forest disturbances as they were performed as part of a broad systematic map.

Platform	**Search string**
Open Access Theses and Dissertations	all of these words= forest, any of these words=soil belowground, any of these words=drought fire burn wind typhoon cyclone hurricane storm rain precipitation irrigation disturbance pest pathogen, all of these words= soil fauna. Searched at abstract level
Google Scolar	Google Scholar queried using gscraper R package; save_and_scrapeGS(and_terms = c('forest', 'soil', 'fauna'),or_terms=c('drought', 'fire','wind','storm','precipitation','bark beetle','pathogen'), pages = 100,backoff=TRUE,incl_cit=FALSE,incl_pat=FALSE)
Web of Science Core Collection	TS=((forest* OR woodland* OR plantation* OR clearcut OR logg* OR timber) AND (soil* OR below$ground OR root*) AND (drought* OR *fire* OR burn* OR wind* OR typhoon* OR cyclone* OR hurricane* OR *storm* OR "canopy gap*" OR rain* OR precipitation OR irrigat* OR disturb* OR “bark beetle*” OR pest OR “insect herbivore*” OR "insect infestation" OR "insect outbreak" OR "beetle outbreak" OR “pathogen*”) AND (“soil biodiversity” OR “below$ground biodiversity” OR “soil divers*” OR “below$ground divers*” OR biodiversity OR biota OR fauna OR organism* OR micro$fauna OR macro$fauna OR meso$fauna OR animal* OR arthropod* OR invert* OR insect OR detritivore* OR macroarthropod* OR micro-arthropod* OR microarthropod* OR protozoa* OR ciliat*OR protist* OR rotifer* OR tardigade OR mite* OR orbatid* OR acari* OR nematod* OR mesostigmata* OR prostigmata*OR protura* OR diplura* OR symphyla OR enchytrae* OR potworm OR oligochaet* OR annelid* OR collembol* OR springtail* OR earthworm* OR lumbricid* OR woodlice OR woodlouse OR isopod* OR termite* OR isoptera* OR millipede* OR diplopoda* OR centipede* OR chilopoda* OR beetle* Or coleoptera* OR araneida OR archnid* OR spider* OR mollusc* OR snail* OR slug OR chelonethi OR opilones OR harvestmen OR amphipod*)
Scopus	TITLE-ABS-KEY((forest* OR woodland* OR plantation* OR clearcut OR logg* OR timber) AND (soil* OR below?ground OR root*) AND (drought* OR *fire* OR burn* OR wind* OR typhoon* OR cyclone* OR hurricane* OR *storm* OR "canopy gap*" OR rain* OR precipitation OR irrigat* OR disturb* OR “bark beetle*” OR pest OR “insect herbivore*” OR "insect infestation" OR "insect outbreak" OR "beetle outbreak" OR “pathogen*”) AND (“soil biodiversity” OR “below?ground biodiversity” OR “soil divers*” OR “below?ground divers*” OR biodiversity OR biota OR fauna OR organism* OR micro?fauna OR macro?fauna OR meso?fauna OR animal* OR arthropod* OR invert* OR insect OR detritivore* OR macroarthropod* OR micro-arthropod* OR microarthropod* OR protozoa* OR ciliat* OR protist* OR rotifer* OR tardigade OR mite* OR oribatid* OR acari* OR nematod* OR mesostigmata* OR prostigmata* OR protura* OR diplura* OR symphyla OR enchytrae* OR potworm OR oligochaet* OR annelid* OR collembol* OR springtail* OR earthworm* OR lumbricid* OR woodlice OR woodlouse OR isopod* OR termite* OR isoptera* OR millipede* OR diplopoda* OR centipede* OR chilopoda* OR beetle* Or coleoptera* OR araneida OR archnid* OR spider* OR mollusc* OR snail* OR slug OR chelonethi OR opilones OR harvestmen OR amphipod*))

Table S4 - Details of benchmark studies used to assess the comprehensiveness of our search strategy.

Reference	**Focal taxa**	**Disturbance(s)**
Landesman, Treonis, & Dighton (2011)	Mesofauna	Precipitation reduction
Lindberg et al. (2002)	Oribatida, Mesostigmata, Collembola, Macroarthropod predators, Enchytraeidae	Precipitation reduction, Precipitation increases
Sohlenius and Wasilewska(1984)	Nematoda	Precipitation increases
Santonja et al. (2017)	Mesofauna	Precipitation reduction
Xu et al. (2012)	Mesofauna	Precipitation reduction
Lindberg & Bengtsson (2006)	Mesofauna	Precipitation reduction
Homet et al. (2021)	Mesofauna	Precipitation reduction
Wehne et al. (2021)	Oribatida	Precipitation reduction
Sun et al. (2013)	Nematoda	Precipitation increases

Table S5 - Criteria for study validity assessment (Martin et al., 2020). Any studies for which the answer to any of the questions is ‘no’ or ‘unclear’ were 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**
	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

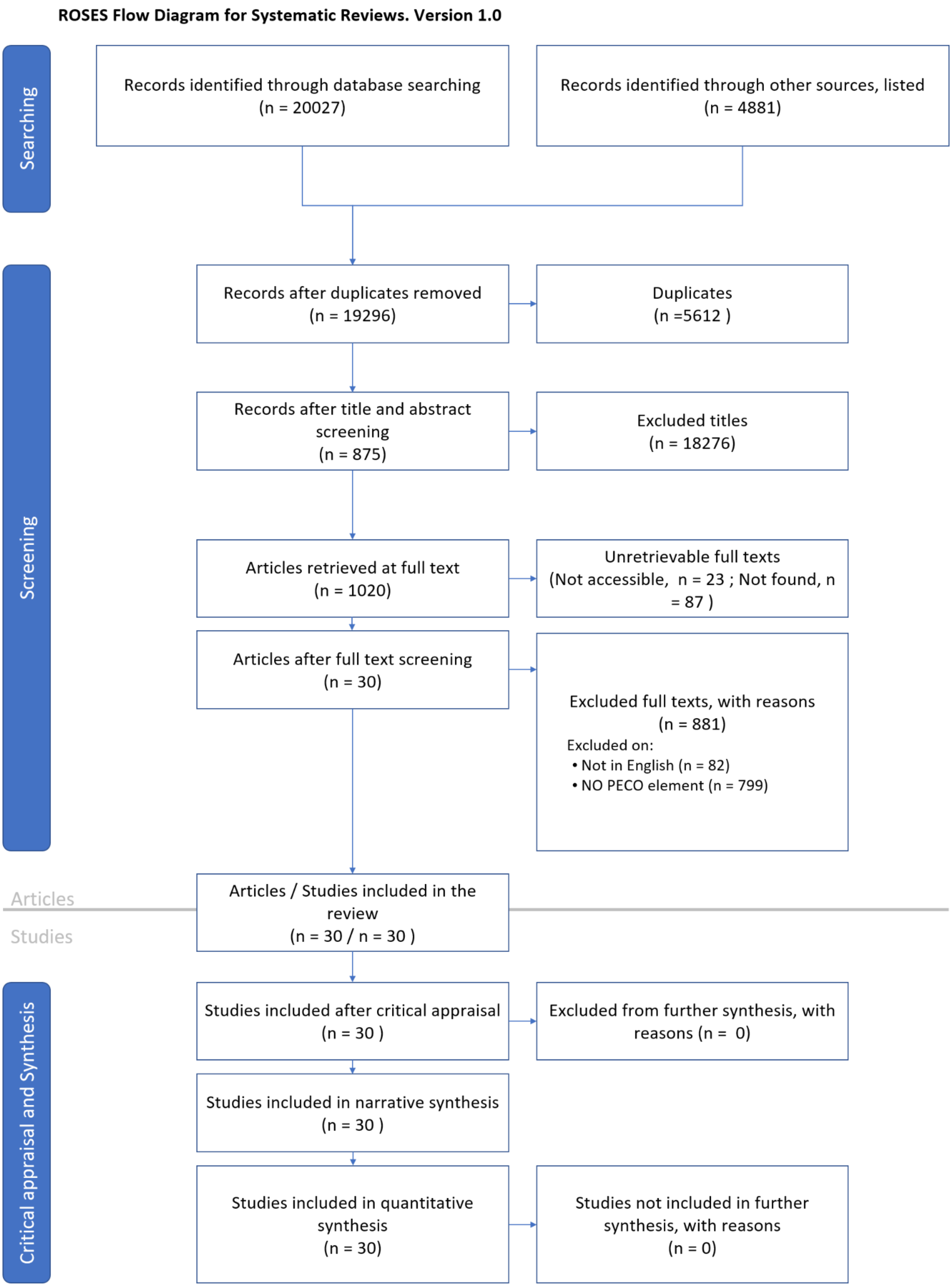

Figure S1 - ROSES flow diagram showing the process of selection and synthesis of studies used in the meta-analysis

Table S6 - Statistics from summary meta-analyses and sensitivity analyses

Disturbance	Outcome	Model type	Coeff	SE	T-statistic	P value	K	Q	Q p-value	I2
Precipitation reduction	Abundance	Null model	-0.48	0.16	-3.05	0.002	170	1059	<0.001	84
Precipitation reduction	Abundance	Failed Geary test	-0.41	0.16	-2.53	0.011	146	1034	<0.001	86
Precipitation reduction	Abundance	Low validity removed	-0.62	0.20	-3.05	0.002	62	683	<0.001	91
Precipitation increase	Abundance	Null model	0.31	0.15	2.09	0.037	105	1542	<0.001	82
Precipitation increase	Abundance	Failed Geary test	0.30	0.15	2.08	0.037	95	1536	<0.001	84
Precipitation increase	Abundance	Low validity removed	0.26	0.20	1.29	0.199	83	1402	<0.001	85
Precipitation reduction	Taxonomic richness	Null model	-0.03	0.04	-0.93	0.352	37	95	<0.001	42
Precipitation reduction	Taxonomic richness	Failed Geary test	-0.03	0.04	-0.93	0.352	37	95	<0.001	42
Precipitation reduction	Taxonomic richness	Low validity removed	-0.13	0.02	-5.62	0.000	24	59	<0.001	5
Precipitation increase	Taxonomic richness	Null model	0.05	0.11	0.43	0.664	11	10	0.400	56
Precipitation increase	Taxonomic richness	Failed Geary test	0.05	0.11	0.43	0.664	11	10	0.400	56
Precipitation increase	Taxonomic richness	Low validity removed	-0.04	0.03	-1.41	0.159	7	3	0.797	0
Precipitation reduction	Shannon-Wiener	Null model	-0.06	0.04	-1.66	0.097	31	91	<0.001	42
Precipitation reduction	Shannon-Wiener	Failed Geary test	-0.06	0.04	-1.66	0.097	31	91	<0.001	42
Precipitation reduction	Shannon-Wiener	Low validity removed	-0.11	0.02	-5.29	0.000	24	63	<0.001	0
Precipitation increase	Shannon-Wiener	Null model	-0.08	0.03	-2.47	0.014	9	3	0.927	0
Precipitation increase	Shannon-Wiener	Failed Geary test	-0.08	0.03	-2.47	0.014	9	3	0.927	0

Precipitation increase	Shannon-Wiener	Low validity removed	-0.55	0.73	-0.76	0.446	8	3	0.918	84

Table S7 - Model selection for models of change in the abundance of soil and litter fauna in forests as a result of precipitation changes. In the variables column ‘Precipitation change’ refers to the magnitude of precipitation change relative to baseline conditions, Body Size refers to the classification of taxonomic groups as either micro-, meso-, or macrofauna, ‘Decline effect’ the year in which a study was published to assess whether observed effect sizes change over time as seen in other literatures, ‘Small study effect’ a variable to assess whether smaller studies vary in their reported effect size.

Variables	df	logLik	AICc	delta
Precipitation change * Body size + Decline effect + Small study effect	11	-330.90	684.89	0.00
Precipitation change * Body size + Small study effect	10	-332.11	685.11	0.22
Precipitation change * Body size + Decline effect	10	-332.62	686.15	1.26
Precipitation change * Above/belowground + Small study effect	8	-335.17	686.93	2.04
Precipitation change*Above/belowground + Decline effect + Small study effect-	9	-334.10	686.93	2.04
Precipitation change * Body size	9	-334.13	687.00	2.11
Precipitation change * Above/belowground + Decline effect	8	-335.57	687.73	2.84
Precipitation change * Above/belowground	7	-336.70	687.86	2.97
Precipitation change * Exoskeleton + Decline effect + Small study effect	9	-335.52	689.77	4.88
Precipitation change * Exoskeleton+Small study effect	8	-336.60	689.79	4.90
Precipitation change + Decline effect + Small study effect	7	-337.70	689.86	4.97
Precipitation change + Small study effect	6	-338.81	689.95	5.06
Precipitation change * Exoskeleton + Decline effect	8	-337.39	691.37	6.48
Precipitation change + Decline effect	6	-339.61	691.55	6.66
Precipitation change * Exoskeleton	7	-338.72	691.90	7.01
Precipitation change	5	-340.90	692.05	7.16

Table S8 - Model averaged coefficients for models of changes in faunal abundance with an AICc delta <2

Variable	Estimate	SE	z value	p value
Precipitation change	-0.0008	0.0022	0.3792	0.7046
Macrofauna	0.1429	0.2479	0.5762	0.5645
Mesofauna	0.0164	0.2112	0.0777	0.9380
Microfauna	0.0413	0.3809	0.1084	0.9137
Decline effect	0.0052	0.0088	0.5899	0.5553
Small study size	-0.4051	0.4519	0.8965	0.3700
Mesofauna:Precipitation change	0.0053	0.0024	2.2266	0.0260
Microfauna:Precipitation change	0.0026	0.0040	0.6515	0.5147

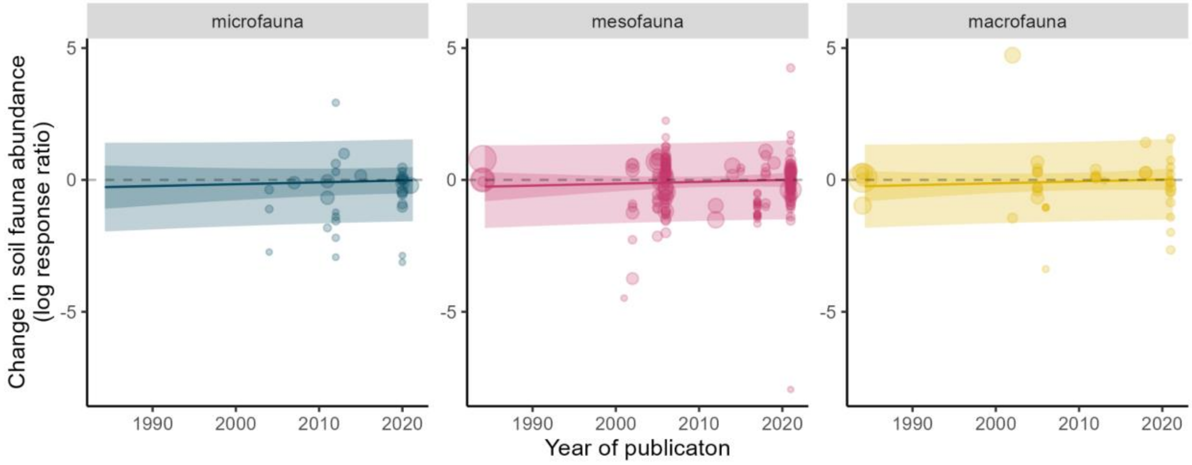

Figure S2 - Change in effect of precipitation changes over time since publication

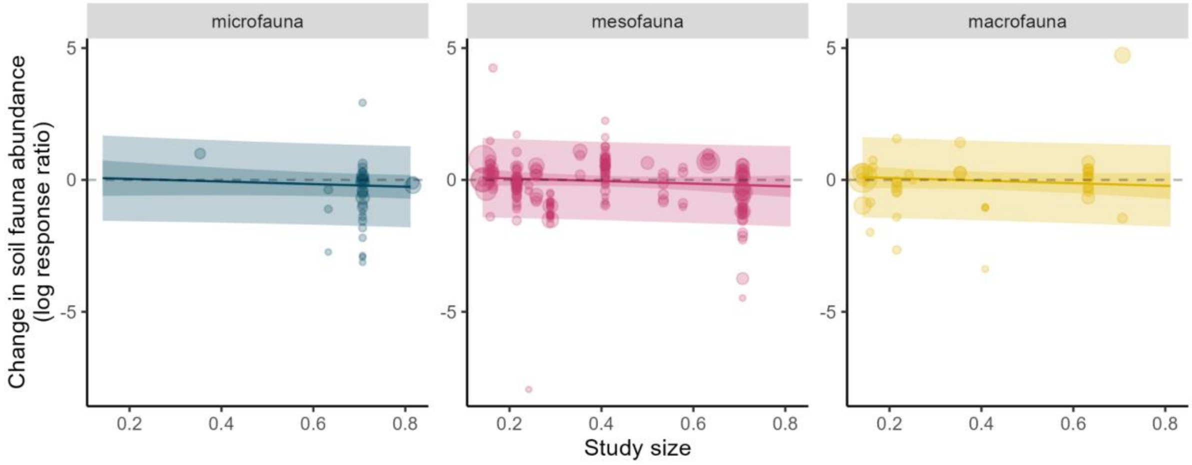

Figure S3 - Impact of study size on change in effect of precipitation on invertebrate abundance

Table S9 - Model selection for models of change in the abundance of soil and litter fauna in forests as a result of precipitation changes. In the variables column ‘Taxonomic group’ refers to a variable specifying whether abundance was related to Acari or to Collembola. See Table S1 for description of all other variables.

Variables	df	logLik	AICc	delta
Change in precipitation * Taxonomic group + Small study effect	8	-164.12	345.19	0.00
Change in precipitation * Taxonomic group + Decline effect +Small study effect	9	-163.30	345.79	0.60
Change in precipitation * Taxonomic group + Decline effect	8	-164.66	346.27	1.08
Change in precipitation * Taxonomic group	7	-165.88	346.49	1.30
Change in precipitation	5	-168.16	346.70	1.51

Table S10 - Model averaged coefficients for models of changes in faunal abundance for Acari and Collembola with an AICc delta <2

Variable	Estimate	SE	z value	p value
Precipitation change	0.0059	0.0015	3.8441	0.0001
Acari	-0.0338	0.2560	0.1319	0.8951
Collembola	0.0920	0.2577	0.3568	0.7212
Small study size	-0.2936	0.5435	0.5402	0.5891

Collembola:Precipitation change	0.0003	0.0009	0.3281	0.7428
Decline effect	0.0018	0.0094	0.1925	0.8473
Intercept	-0.0165	0.0625	0.2645	0.7914

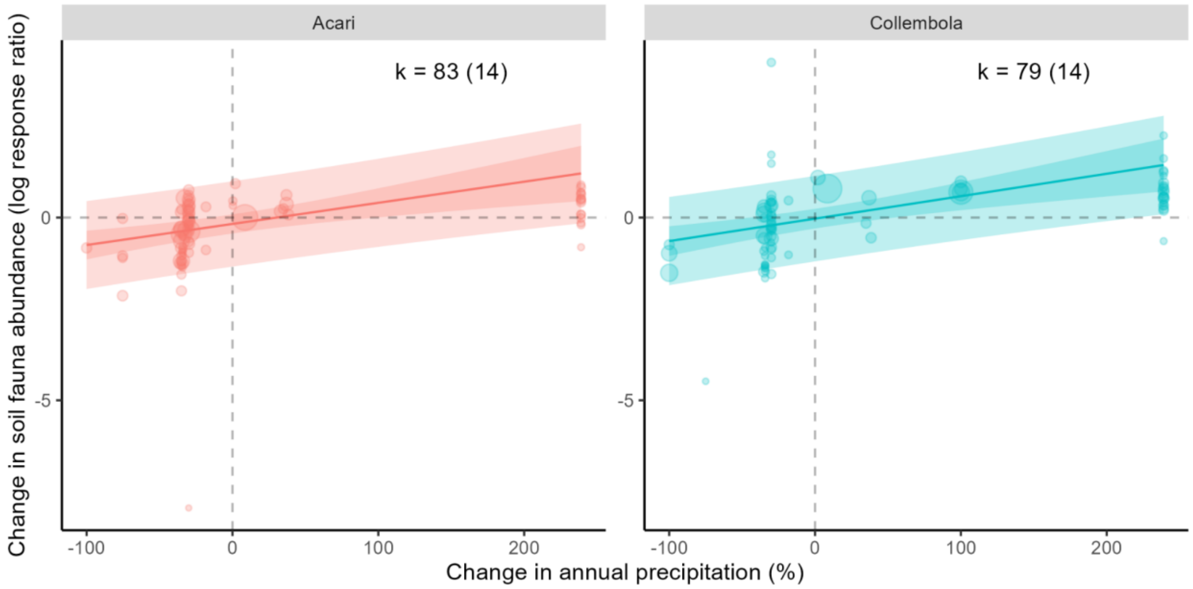

Figure S4 - Changes in the abundance of Acari and Collembola in forests relative to changes in precipitation. Points represent individual comparisons with different point sizes representing the different weights of comparisons to the analysis. Solid lines represent predictions from the most parsimonious model, with darker coloured bands representing the 95% confidence intervals, and the lighter bands the 95% prediction intervals. Dashed lines represent points at which the x and y axes are equal to zero. K signifies the number of comparisons for each taxonomic group and the number in brackets represents the number of studies.

Table S11 - Model selection for models of change in the taxonomic richness of soil and litter fauna in forests as a result of precipitation changes. See Table S1 for description of variables.

Variables in model	df	logLik	AICc	delta
Precipitation change	5	-6.41	24.46	0.00
Decline effect	5	-7.06	25.74	1.28
Small study effect	5	-7.46	26.54	2.09
Precipitation change + Decline effect	6	-6.23	26.80	2.34
Precipitation change*Above/belowground	7	-5.01	27.22	2.77
Decline effect + Small study effect	6	-6.46	27.24	2.79
Precipitation change + Small study effect	6	-6.68	27.70	3.24
Precipitation change + Decline effect + Small study effect	7	-5.30	27.80	3.35
Precipitation change * Above/belowground + Small study effect	8	-3.90	28.03	3.57
Precipitation change * Exoskeleton	6	-7.09	28.52	4.06
Precipitation change * Above/belowground + Decline effect	8	-4.51	29.26	4.80
Precipitation change * Exoskeleton + Decline effect	7	-6.67	30.54	6.08
Precipitation change * Above/belowground + Decline effect + Small study effect	9	-3.58	30.62	6.17
Precipitation change * Exoskeleton + Small study effect	7	-7.07	31.33	6.88
Precipitation change * Exoskeleton + Decline effect + Small study effect	8	-6.15	32.53	8.07
Precipitation change * Body size	8	-6.27	32.77	8.31
Precipitation change *Body size + Decline effect	9	-5.44	34.34	9.89
Precipitation change * Body size + Small study effect	9	-5.80	35.05	10.60
Precipitation change * Body size + Decline effect + Small study effect	10	-4.88	36.62	12.17

Table S12 - Model averaged coefficients for models of changes in faunal taxonomic richness with an AICc delta <2

Variable	**Estimate**	**SE**	**z value**	**p value**
Intercept	-0.0018	0.0788	0.0226	0.9820
Precipitation change	0.0019	0.0020	0.9365	0.3490
Decline effect	0.0027	0.0093	0.2962	0.7671

Table S13 - Model selection for models of change in the Shannon-Wiener diversity of soil and litter fauna in forests as a result of precipitation changes. See Table S1 for description of variables.

Variables	**df**	**logLik**	**AICc**	**delta**
Decline effect	5	-12.40	36.68	0.00
Precipitation change	5	-12.49	36.85	0.18
Precipitation change + Decline effect	6	-11.21	37.14	0.46
Small study effect	5	-13.46	38.79	2.11
Precipitation change + Small study effect	6	-12.44	39.59	2.91
Decline effect + Small study effect	6	-13.19	41.09	4.41
Precipitation change * Above/belowground	7	-11.98	41.70	5.02
Precipitation change + Decline effect + Small study effect	7	-12.00	41.74	5.06
Precipitation change * Body size	7	-12.63	43.01	6.33
Precipitation change * Exoskeleton	7	-12.64	43.01	6.33
Precipitation change*Above/belowground + Decline effect	8	-11.36	43.68	7.00
Precipitation change*Above/belowground + Small study effect	8	-11.38	43.71	7.03
Precipitation change*Exoskeleton + Decline effect	8	-11.39	43.74	7.06
Precipitation change*Body size + Decline effect	8	-11.39	43.74	7.06
Precipitation change *Body size + Small study effect	8	-11.82	44.61	7.93
Precipitation change * Body size + Decline effect + Small study effect	9	-10.73	45.88	9.20
Precipitation change * Exoskeleton + Decline effect + Small study effect	9	-10.73	45.88	9.20
Precipitation change * Above/belowground + Decline effect + Small study effect	9	-10.77	45.97	9.29

Table S14 - Model averaged coefficients for models of changes in faunal Shannon-Wiener diversity with an AICc delta <2

Variable	Estimate	SE	z.value	p_value
Intercept	-0.1842	0.1435	1.2842	0.1991
Decline effect	0.0069	0.0062	1.1237	0.2611
Precipitation change	-0.0016	0.0043	0.3810	0.7032

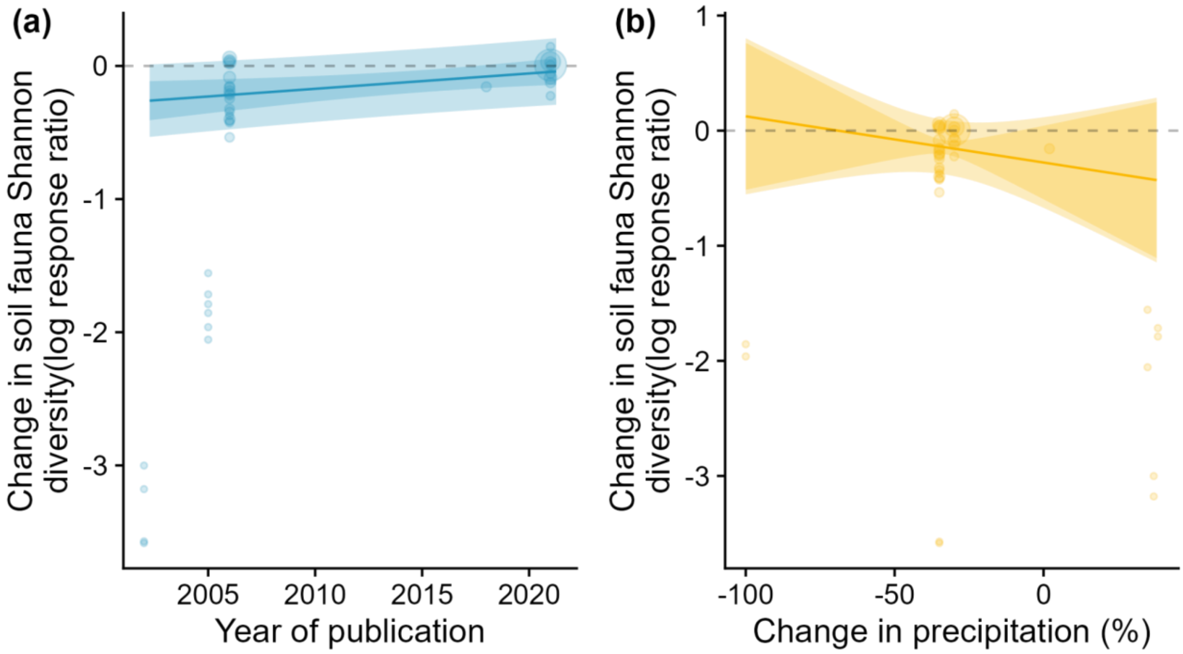

Figure S5 - Changes in Shannon-Wiener diversity relative (a) year of publication and (b) changes in precipitation. Points represent individual comparisons with different point sizes representing the different weights of comparisons to the analysis. Solid lines represent predictions from the most parsimonious model, with darker coloured bands representing the 95% confidence intervals, and the lighter bands the 95% prediction intervals. Dashed lines represent points at which the y axes are equal to zero.

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