A systematic map of forest disturbance impacts on soil and litter fauna: knowledge gaps and a roadmap for future research

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Abstract
Anthropogenic climate change is increasing the frequency and severity of natural disturbances such as fires, droughts, wind damage, and insect and pathogen outbreaks in forests. The impacts of these disturbances on aboveground biodiversity are relatively well known, but this is not true for belowground biodiversity, particularly soil fauna. While a number of syntheses exist summarising the impacts of these different disturbances, it is unclear which topics have been well or poorly studied, or what biases affect the literature. To fill this knowledge gap and provide a road map to guide future research, we undertook a systematic map with the aims of characterising the literature on the impacts of natural forest disturbances on soil and litter fauna. We found 307 primary studies of 24 taxonomic orders of soil and litter fauna from 48 different countries. Our results show that studies of fire impacts were vastly more common than studies of other disturbances, while there were very few studies on the impacts of insect pests and pathogens or the impacts of multiple combined disturbances. Most studies focussed on meso- and macrofauna such as springtails or beetles, with relatively few studies on microfauna such as nematodes. Biodiversity metrics often measured abundance or local diversity, with few studies examining more complex outcomes like food webs. There were clear geographic biases, with many studies conducted in Europe and North America, but few in Africa and South America, leaving gaps in our knowledge of impacts outside of Temperate and Mediterranean forests. Study design robustness was highly variable, but was typically low for studies of fire, windthrow, and pests and pathogens, while it was high for studies of precipitation change. Studies tended to be short, often lasting for less than 2 years. Reporting of the intensity of disturbances was common for studies of precipitation change but for other disturbances was relatively rare. Our results indicate that while much progress has been made in understanding the impacts of forest disturbances on soil and litter fauna, there is a need to study: (i) a wider range of disturbances and especially the effects of multiple disturbances, (ii) a wider range of taxonomic groups, (iii) field sites in boreal and tropical forests, especially in the wet tropics, and (iv) there is a pressing need for longer-term studies with more robust methodologies.

Keywords: Soil fauna; evidence synthesis; fire; precipitation change; insect pests; plant pathogens; windthrow

Introduction

The frequency, extent, and intensity of natural disturbances in forests, such as fires (Pechony & Shindell, 2010), droughts (Clark *et al.*, 2016; Feldpausch *et al.*, 2016), wind damage (Patacca *et al.*, 2023), and insect and pathogen outbreaks (Ju *et al.*, 2015) are increasing in many forest biomes. This increase in disturbance is largely attributable to anthropogenic climate change and altered land-use practices. For example, warmer and drier conditions lead to more intense droughts and fires, while intensification in land use can promote accidental fires (Barlow *et al.*, 2020; Lapola *et al.*, 2023). Warmer drier conditions can also promote insect outbreaks, while warmer and wetter conditions are linked to increased wind and pathogen disturbance (Seidl *et al.*, 2017). Increases in disturbance intensity can drastically alter forest structure (Jacquet, Orazio & Jactel, 2012), reduce carbon storage (Seidl *et al.*, 2014), and alter biodiversity (Viljur *et al.*, 2022), representing a major challenge for forest management (Patacca *et al.*, 2023; Lecina-Diaz *et al.*, 2024). Therefore, understanding the impacts of these disturbances on forest biodiversity and ecosystem services is crucial for developing strategies to reduce their negative impacts (Lecina-Diaz *et al.*, 2024).

While the impacts of natural disturbances on aboveground forest biodiversity are well documented (Viljur *et al.*, 2022; Lecina-Diaz *et al.*, 2024), our understanding of threats to belowground biodiversity remains limited (Phillips *et al.*, 2017). Much of the research on the impacts of global change and disturbances on belowground communities has focussed on microorganisms, while soil and litter invertebrate fauna have been studied less frequently. For instance, studies investigating global change impacts on soil microbes outnumber those on soil fauna by a factor of five (Zhou, Wang & Luo, 2020; Peng *et al.*, 2022). This disparity is particularly striking given the extraordinary abundance and diversity of soil fauna. Just three taxa, nematodes (van den Hoogen *et al.*, 2019), springtails (Potapov *et al.*, 2023), and earthworms (Phillips *et al.*, 2019) - have a combined global biomass 28 times higher than that of all wild terrestrial vertebrates (Bar-On, Phillips & Milo, 2018), and represent more than 30 times as many species (Pillay *et al.*, 2022; Anthony, Bender & van der Heijden, 2023).

As well as being highly abundant and diverse, soil and litter invertebrate fauna perform a wide range of roles in forest ecosystems, many of which are key in determining soil properties with consequent impacts on plant communities. One of their most fundamental roles is in facilitating decomposition, both by physical breakdown of dead plant material and the biological mineralisation of litter, thereby converting relatively recalcitrant compounds into simpler forms and enhancing nutrient availability to plants (Wardle, 1999; Griffiths *et al.*, 2021; Njoroge *et al.*, 2022). While microorganisms carry out much of the decomposition seen in forests, experimental exclusions of invertebrate fauna indicate that they account for around 31% of total litter decomposition, underlining their significant contribution (Zeng *et al.*, 2024; but see Kampichler & Bruckner, 2009). Soil fauna, particularly macrofauna such as termites and earthworms, also reshape the physical characteristics of soils by building networks of galleries and burrows that promote water infiltration, aeration, and root penetration (Bardgett & van der Putten, 2014; Nielsen, Wall & Six, 2015; Zeng *et al.*, 2024). The ecological functions performed by soil fauna differ by region with macrofauna, such as termites and earthworms, dominating decomposition processes in tropical forests, while in boreal and temperate forests soil microbes and mesofauna are more important (Zeng *et al.*, 2024).

However, the lack of research on how they respond to natural disturbances in forests hampers our ability to predict how these ecosystem functions will change in the near future and how this may vary by context. This knowledge gap is particularly concerning given that forest soils serve as major carbon sinks (Georgiou *et al.*, 2022; Mo *et al.*, 2023), and because increases in disturbance frequency and severity may disrupt water and biogeochemical cycles vital for carbon sequestration through the incorporation of leaf litter into soil. Improving our predictions of how altered disturbance regimes will affect forest soil processes therefore requires a thorough understanding of the impacts on soil and litter fauna.

Despite the relative lack of attention paid to the impacts of natural forest disturbances to soil and litter fauna, several meta-analyses have synthesised how they are impacted by fire (Pressler, Moore & Cotrufo, 2019; Viljur *et al.*, 2022), precipitation change (Peng *et al.*, 2022; Bristol *et al.*, 2023; Goncharov *et al.*, 2023; Martin *et al.*, 2024), and insect pests (Kristensen, Rousk & Metcalfe, 2020). While these studies provide valuable insights, few of them systematically assess which topics are well studied or poorly studied (hereafter knowledge clusters and knowledge gaps, respectively) or the biases that affect the literature (although see Martin *et al.*, 2024). The existing literature hints at three major topics relating to this: (i) *what* is studied - imbalances in the amount of research on different natural disturbances (Seidl *et al.*, 2017; Montagné-Huck & Brunette, 2018; Viljur *et al.*, 2022), and taxonomic or functional groups of soil and litter fauna (Pressler *et al.*, 2019; Martin *et al.*, 2024); (ii) *where* it is studied - an overrepresentation of studies from Europe and North America, with other regions lacking studies (Cameron *et al.*, 2018; Martin *et al.*, 2024); and (iii) *how* it is studied - a reliance on simple biodiversity metrics that limit our ability to predict ecosystem functioning (Gongalsky *et al.*, 2021) and methodological weaknesses in study design (Christie *et al.*, 2019, 2020). Despite indications of these issues in the literature, to date, there has been no systematic attempt to quantify them.

To address these knowledge gaps we used systematic mapping: an approach that aims to identify, collate, catalogue, and describe the evidence related to a particular topic (James, Randall & Haddaway, 2016). This methodology is similar to systematic review, but rather than attempting to answer questions relating to impacts of stressors or management, it instead aims to identify research clusters and gaps to guide future field-based and synthesis research (James *et al.*, 2016). Here we used this methodology to address two research objectives:

1. Identify knowledge clusters and knowledge gaps related to the impacts of natural forest disturbances on soil and litter fauna.
2. Explore the robustness and characteristics of methodologies used by primary studies.

Methods

Searches and screening

Our systematic map focused on primary studies that assess the impacts of natural disturbances on soil and litter invertebrate biodiversity in forest ecosystems in field settings. To guide the scope of the work we formally defined five important PECOS elements: Population, Exposure, Comparison, Outcomes, Space (Table 1, Grames *et al.*, 2019a). Our study methods follow existing guidelines (Collaboration for Environmental Evidence, 2018; Haddaway *et al.*, 2018) and our preregistered protocol (Martin *et al.*, 2021). We highlight any deviations from the protocol here and discuss them in more detail in the supplementary materials.

The searches for this study were carried out on 25/11/2021. To identify search terms, we created an initial list, then used the R package litsearchr to suggest additional terms, and refined final search terms based on these suggestions (Grames, Stillman & Tingley, 2019b; see supplementary methods for more details). We aimed to balance search sensitivity (i.e. the retrieval of all relevant studies) and specificity (i.e. the retrieval of only relevant documents) by following the recommendations of Foo et al. (2021) and developing a benchmark list of articles deemed essential to be included in our searches (Collaboration for Environmental Evidence, 2018). Once final search terms were identified, we performed platform-specific searches in Web of Science, Scopus, Google Scholar, and Open Access Theses and Dissertations. When searching Google Scholar, we used the R package gsscraper (Haddaway, 2020) to download the first 1000 relevant references we found, which should encompass the majority of relevant studies (Haddaway *et al.*, 2015). Searching for unpublished grey literature as well as published, peer-reviewed literature, minimised the risks associated with publication bias (Konno & Pullin, 2020). In addition to formal searches, we contacted five 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).

Table 1 - Different PECOS elements used to define the scope of the systematic review

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.
Exposure	Reductions in precipitation, increases in precipitation, insect pests, plant pathogens, fire, and windthrow.
Comparison	Any comparison between forests that vary in the frequency or intensity of a disturbance of interest that they are subject to. This comparison may be spatial or temporal.
Outcomes	Abundance, biomass, and diversity of soil and litter fauna, as well as interactions between different soil fauna.
Space	Studies carried out in the field. All types of terrestrial forest and woodland were included, including savannas.

Once searches were completed, we downloaded all references found as .bib or .ris files and used the R packages synthesisr to remove duplicate articles (Westgate & Grames, 2020) and bibfix (Haddaway *et al.*, 2021) 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, fire, windthrow, insect pests, or plant pathogens; (3) Be field-based (i.e. not be carried out in greenhouses or mesocosms); (4) Quantitatively assess soil fauna biomass, abundance, diversity, or interactions between soil fauna; (5) Have a comparison between sites that vary in the intensity or frequency of the disturbance that they were exposed to; (6) Be written in English. At the title and abstract screening stage, we retained articles that met criteria 1-3 and criterion 5. At the full-text stage, criteria 1-6 needed to be met 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). Despite being a multilingual team, we focussed only on English-language literature to simplify consistency checks between reviewers. We acknowledge that excluding literature written in non-English languages is a shortcoming that may lead to biases (Konno *et al.*, 2020; Amano *et al.*, 2021).

To ensure consistency, a random sample of 10% of titles and abstracts were screened by two team members (PM and LPI), 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 also 96.6% but the Kappa score was 0.92. We found 19,295 papers during searches, 1,020 of which were retained after screening of titles and abstracts, and 307 of which were used for data extraction. We did not perform formal critical appraisal of studies as this is considered an optional component of systematic mapping (James *et al.*, 2016), but we did collect information about study designs during data extraction.

Data extraction and coding

Our data extraction attempted to collate site-scale information from each publication. We considered sites to be separate when different experimental designs were used or when the different locations were separated by at least 10 km. Where information was not presented separately for different sites, we considered studies to represent a single site. We extracted contextual data to identify knowledge and gaps, biases, and methodological issues. To do this we extracted the following variables: geographic location, disturbance type, taxa of all soil and litter fauna recorded, the body size class of organisms studied (macrofauna, mesofauna, microfauna), the biodiversity outcomes recorded, whether studies were experimental or observational, the study design used, sampling methods, time after disturbance, and whether studies reported the intensity of disturbances. In a deviation from the preregistered protocol, we did not extract information on the season in which sampling was conducted or the scale at which measurements were made as these details were often missing from primary studies.

Analysis

Our analyses had two major aims: (i) the identification of themes that have been well-studied, those that have been studied rarely, and any biases present in the literature on the effects of forest disturbances on soil and litter fauna and (ii) an assessment of the study designs used in primary studies on the effects of forest disturbances on soil and litter fauna. Themes that have been well-studied, referred to as knowledge clusters, represent opportunities for in-depth synthesis such as systematic review and meta-analysis, whereas those that have been studied relatively rarely, referred to as knowledge gaps, represent potentially useful topics for future primary research (James *et al.*, 2016).

Our analyses of knowledge clusters, gaps, and biases concentrated on the geographic distribution of studies, the taxonomic and size class groups of fauna that were investigated, and the metrics of biodiversity that had been used. To identify regions that had been studied we produced maps of the distribution of study sites for each different disturbance. Following this we characterised the geographic biases associated with the study of each of the different disturbances. In order to do this we assessed whether the distribution of studies differed from the distribution of the disturbances we were interested in, namely fire, precipitation changes, windthrow, and pests and pathogens. Since we were interested in forest disturbances and their potential impacts on soil and litter fauna, we aimed to identify locations where the intensity of forest disturbances has been great enough to cause tree mortality. We compiled global datasets on fire impacts (Tyukavina *et al.*, 2022), wind speeds (University of East Anglia Climatic Research Unit & Harris, 2019), the Standardised Precipitation-Evapotranspiration Index (SPEI) as an index of precipitation extremes (Beguería *et al.*, 2024), and datasets of insect damage for Western North America (Berner *et al.*, 2017) and Europe (Forzieri *et al.*, 2023). There were no global datasets of insect damage and acknowledge the limitation of this element of the analysis.

The datasets on fire impacts and insect damage already included information on tree mortality, so no further calculations were required. However, for the datasets of wind speed and precipitation extremes, we set a threshold of 12 metres per second for wind speed, considered intense enough to cause windthrow (ref for this), and an SPEI value of <-2 or >2, which is considered to be extremely dry or wet (Pyarali *et al.*, 2022). For each dataset we then calculated the maximum intensity of disturbance for each pixel at a resolution of 0.5 degrees over the period 2001-2020. Following this, we masked the datasets so that they represented the distribution of disturbances within forests that could potentially cause tree mortality. We plotted the distribution of each of the disturbances along with the distribution of corresponding study sites to highlight areas where disturbances had occurred but there were few studies. Similarly, we assessed this in climate space by summing the number of pixels found within bins of 1℃ of mean annual temperature of each other and 10 mm of mean annual precipitation and overlaying this with the distribution of sites within climate space.

Aside from geographic biases we also assessed the taxonomic and size class groups of fauna that were investigated, and the metrics of biodiversity that had been used. We assessed which taxonomic groups had been studied for each of the different disturbances of interest by summing the number of sites at which each taxonomic group was studied for the different disturbances, which we summarised in the form of a heatmap. To assess whether there was a bias in the research attention each taxonomic group had received relative to their global abundance, we used estimates of global biomass for taken from Rosenburg et al (2023), Potapov et al (2023), van den Hoogen et al (2019), and Bar-on et al (2018) for springtails, mites, termites, millipedes, centipedes, earthworms, potworms, spiders, and scorpions. We then calculated the percentage of sites at which each taxonomic group was studied for each of the disturbances and subtracted the percentage of global biomass represented by the same group. This data was summarised in the form of a heatmap. Following this, we also assessed the number of taxonomic groups and body size classes that had been investigated at each site and produced histograms to show the distribution of this data. Finally, we assessed the different metrics of soil and litter fauna biodiversity that have been used to assess the impacts of the different disturbances.

To assess methods used in primary studies, we concentrated on the use of different study designs, the length of studies, the size of areas sampled in each study, and the depth to which samples were taken. These elements are key determinants of the robustness and scope of studies. We classified study designs based on the definitions and assessment of methodological robustness provided by Christie et al (2019). More details of this can be found in Table 2. It should be noted that many of the different elements of study design are not mutually exclusive. To examine how study robustness varied by disturbance type, we produced plots of each combination of study design elements we found in primary studies, divided by disturbance type. In addition, we assessed important aspects of study methods like the time after disturbance at which samples were taken, area of plots used for sampling, and the depth to which samples were taken. To assess the potential for synthesis studies to examine the impacts of different disturbance intensities on soil and litter fauna we calculated the percentage of studies for each disturbance type that reported this information. We also produced a bar chart showing the frequency with which different sampling/processing methods were used.

All analyses were carried out in R version 4.2.2 and we used the packages Tidyverse (Wickham *et al.*, 2019), terra (Hijmans, 2024), sf (Pebesma & Bivand, 2023), cowplot (Wilke, 2024), and lemon (Edwards, 2024). Fully reproducible code for all analyses can be found in the Zenodo repository associated with this article.

Table 2 - Classification of field study design elements used in this study

Study method element	**Description**
Observational	A study in which no manipulation is made and where researchers take advantage of the occurrence of a disturbance (e.g. study assessing the impacts of a spontaneous wildfire)
Experimental	A study in which the disturbance of interest is manipulated (e.g. exclusion of precipitation to simulate precipitation change)
After (A)	A study where change in biodiversity is assessed only after a disturbance
Before-After (BA)	A study where biodiversity is assessed both before and after a disturbance
Control-Impact (CI)	A study in which a comparison is made between an area in which a disturbance has occurred and an area where it has not
Randomised (R)	A study in which the manipulation of a disturbance is randomly distributed within a study area
Blocked	A study in which different treatments are applied in spatially contiguous areas (Blocks)

Results and discussion

Our systematic map summarises information from 307 primary studies of the impacts of natural forest disturbances on soil and litter fauna, representing 387 study sites. Of the disturbances we considered, fire was studied much more (286 sites, 79%) than precipitation change (47 sites, 13%), windthrow (38 sites, 10%), and pests or pathogens (16 sites, 4%). There were roughly equal numbers of study sites in broadleaf forests (177 sites, 45.7%) and needleleaf forests (175 sites, 45.2%), with few studies carried out in mixed forests (6 sites, 1.6%) and a number of sites where no details of forest type were given (29 sites, 7.5%). Most sites were located in naturally occurring forests (258 sites, 66.7%), with a relatively small number of studies carried out in plantations (26 sites, 6.7%), and a large number of studies where no detail was provided if forests were plantations or not (103 sites, 26.6%).

Knowledge clusters, knowledge gaps, and biases

Geographical knowledge clusters, gaps, and biases

Study sites were found in Europe (Figure 1a, c, e, g, 161 sites) and North America (104 sites) with fewer sites in Oceania (43 sites), Asia (38), Africa (24) and South America (17). Temperate broadleaf forests were the most studied biomes (126 sites, 35.6% of all sites), Boreal (51 sites, 14.4%) and Mediterranean forests (42 sites, 13%). In contrast, Tropical coniferous forests and dry forests were barely studied at all with only three sites between them. Temperate broadleaf forest was the most studied biome for each individual disturbance with 81 sites for fire, 7 for pests and pathogens, 23 for precipitation change, and 15 for windthrow. However, while this information clearly demonstrates there has been more research effort in biomes found in Europe and North America, it is insufficient to identify whether this represents a bias.

To evaluate potential biases, we quantified the number of sites in each biome relative to the area affected by disturbances. Overall, this indicated boreal and tropical forests received less attention than would be expected given the area affected by different disturbance (Figure 1b, d, f, h). However, this pattern varied by disturbance. For fires, Mediterranean forests were by far the most well studied with 46.7 sites per million km^2 affected by fire (Figure 1b), followed by temperate savanna and shrubland (15.3 sites per million km^2) and temperate broadleaf forests (8.6 sites per million km^2). Meanwhile, fire in boreal forests and moist and dry tropical forests was relatively understudied relative to its distribution with just 2.4, 1.4, and 0.6 sites per million km^2 affected by fire respectively (Figure 1b). This is particularly worrying for boreal and tropical moist forests, where large areas have been affected by fire (Figure 1a).

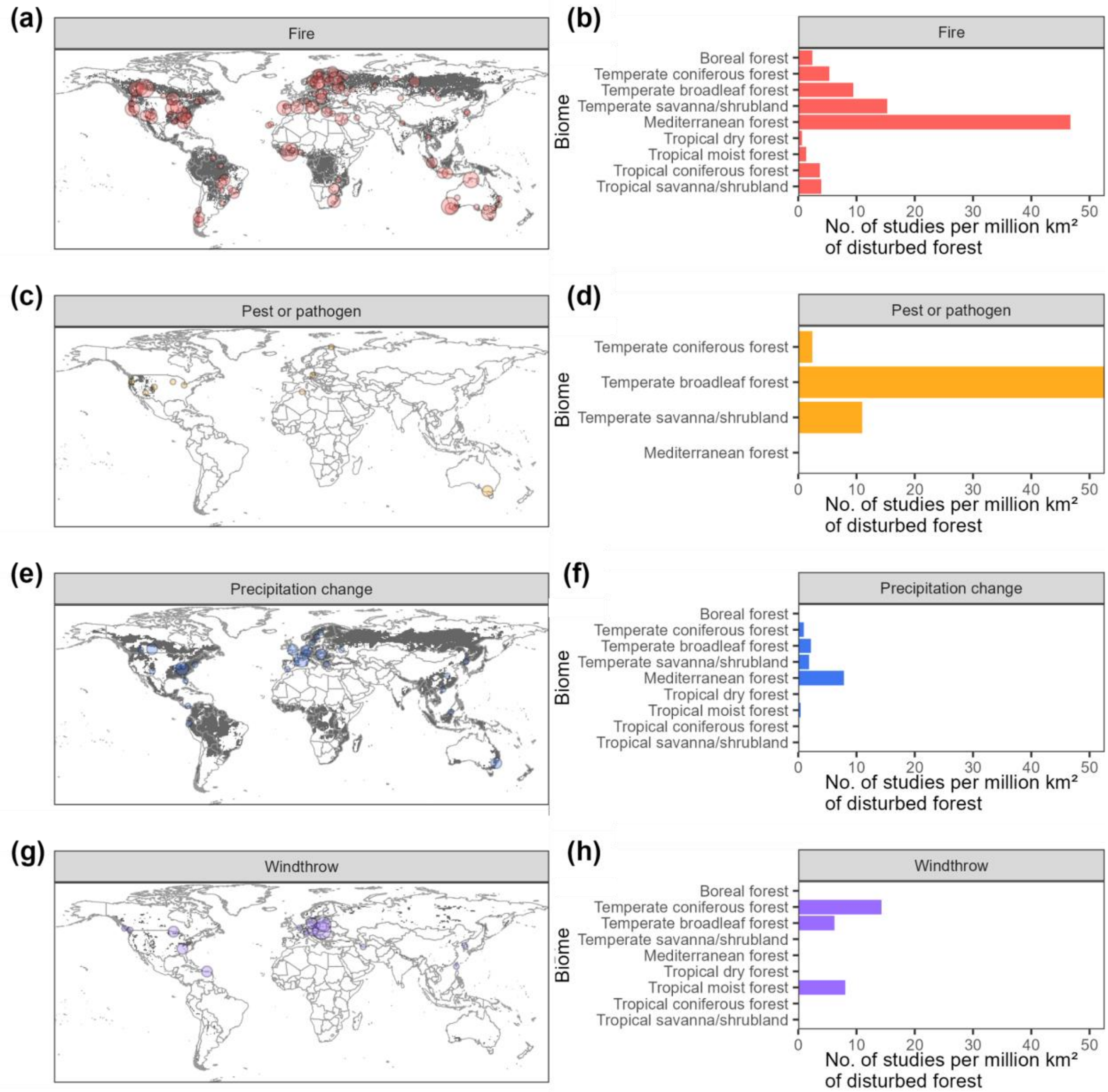

Figure 1 - The geographic distribution of sites where impacts of natural disturbances on soil and litter fauna have been assessed for (a) fire, (c) pest or pathogens, (e) precipitation change, or (g) windthrow and the number of sites within different biomes relative to the area of forest disturbed for (b) fire, (d) pest or pathogens, (f) precipitation change, and (h) windthrow). For plots a,c,e, and g the gray area represents the forest area affected by disturbances at a resolution of 0.5 degrees that were sufficiently intense to cause tree mortality and point size represents the number of study sites within an area. Axis labels in the right hand panels are only included for biomes where the corresponding disturbance was detected.

The lack of data on the distribution of perturbations caused by pests and pathogens to forests limited our analysis of bias to biomes found in Europe and western USA (Figure 1c). However, our results showed that temperate broadleaf forest was by far the most well studied biome (52.6 sites per million km^2 of forest disturbed), while there were relatively few studies in temperate savanna and shrubland, temperate coniferous forest, and no studies in Mediterranean forest.

In the case of precipitation changes, Mediterranean forests were the most well studied relative to the area of forest disturbed (Figure 1f, 7.8 sites per million km^2 of forest disturbed), followed by temperate broadleaf forests (2.1 sites per million km^2), and temperate savannas (1.9 sites per million km^2). Meanwhile, there were very few studies in boreal forests (0.1 sites per million km^2) and no sites in tropical moist and dry forests or savannas (Figure 1f). For windthrow, there were relatively few studies in total, but the most well studied biome relative to the area affected by this perturbation was temperate coniferous forest (Figure 1h, 14.3 sites per million km^2), followed by tropical moist forests (8.1 sites per million km^2) and temperate broadleaf forest (2.4 sites per million km^2). Meanwhile there were no studies in Mediterranean, boreal, tropical coniferous, and tropical dry forests or temperate or tropical savannas. The lack of studies in boreal forest is a particular concern, where we estimate that 2.3 million km^2 of forest - an area equivalent to the size of Greenland - are impacted by windthrow.

Our results reveal an imbalance in research effort on the impacts of natural forest disturbances on soil and litter fauna, a substantial amount of work conducted in temperate, boreal, and Mediterranean forests. Tropical forest biomes meanwhile have received relatively little attention. When adjusting for the area affected by different disturbances, this pattern shifts slightly: while tropical forest biomes remain understudied, boreal forests also emerge as understudied due to the vast areas impacted by precipitation changes and fire.

These geographic biases limit our ecological understanding in several key ways. First, it means that we lack evidence from some forest ecosystems where the biomass of soil fauna such as nematodes and earthworms is especially high - namely boreal forests and tropical peatlands (van den Hoogen *et al.*, 2019; Phillips *et al.*, 2019). Disturbances that reduce the abundance of soil fauna in these ecosystems could have disproportionately large impacts on processes such as nutrient cycling and carbon sequestration, but we are currently poorly equipped to quantify these risks and predict resulting outcomes. Second, in regions such as tropical moist forests, which have historically experienced low rates of disturbance from fires and droughts (Feldpausch *et al.*, 2022), soil and litter faunal communities may be more sensitive to these disturbances due to a lack of evolutionary exposure (Balmford, 1996). The increasing frequency of natural forest disturbances under climate change (Dale, Hughes & Hayes, 2016; Seidl *et al.*, 2020; Patacca *et al.*, 2023) raises serious concerns about the resilience of soil and litter fauna ecosystem resilience, yet the biases identified in our study mean that empirical data on faunal responses remain scarce - particularly in the case of precipitation change. Third, the underrepresentation of tropical forest means that particular taxonomic groups, such as termites, which play a key role in nutrient cycling in these regions, are also likely to be underrepresented.

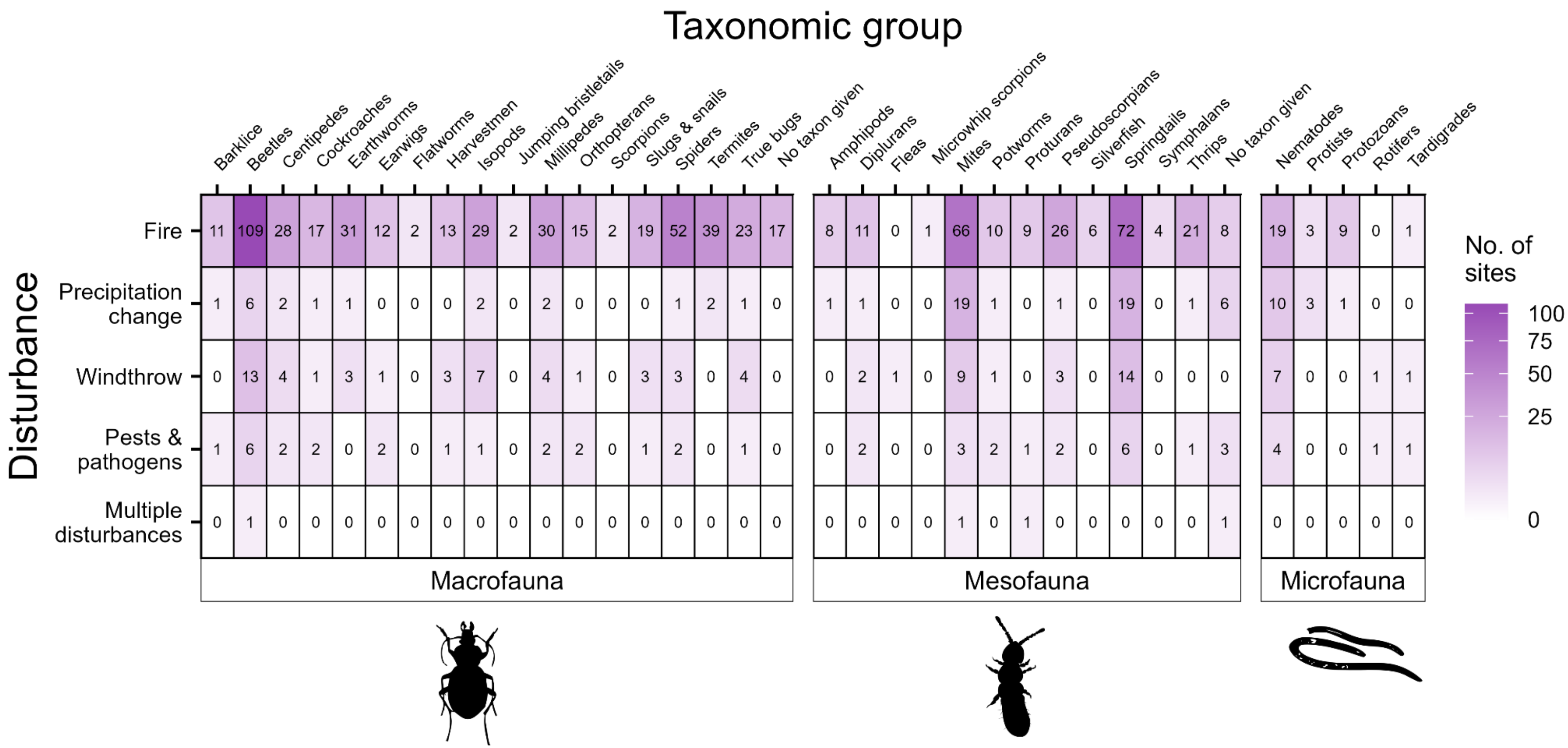

Figure 2 - Number of sites at which the impacts of natural forest disturbances on soil and litter fauna have been assessed for different combinations of taxonomic groups and disturbances. Labels at bottom refer to different size classes of soil and litter fauna, while those at the top refer to more detailed taxonomic groups.

Biases in taxonomic groups and biodiversity metrics

Some taxa were studied more than others but this varied by disturbance
Some soil and litter taxa were clearly studied more than others, but this varied by disturbance type (Figure 2). For example, beetles were studied at 39% of sites where fire, windthrow, or pests and pathogens had been investigated, but only studied at 14% of sites where precipitation change was investigated. Springtails and mites were also heavily studied, especially for precipitation change where they were both studied at 44% of sites. However, for other disturbances, springtails were more commonly studied than mites. Regarding microfauna, the most frequently investigated group was nematodes, although, relative to the number of sites where fire was studied, this group received relatively little attention. Focusing solely on fire, there were also a large number of sites at which spiders, termites, and earthworms were investigated. There were few sites that investigated disturbance impacts on Fleas, Rotifers, or Tardigrades (Figure 2). There were also few sites that examined the impacts of multiple disturbances. More broadly, for all disturbances, macro- and mesofauna were more commonly studied than microfauna.

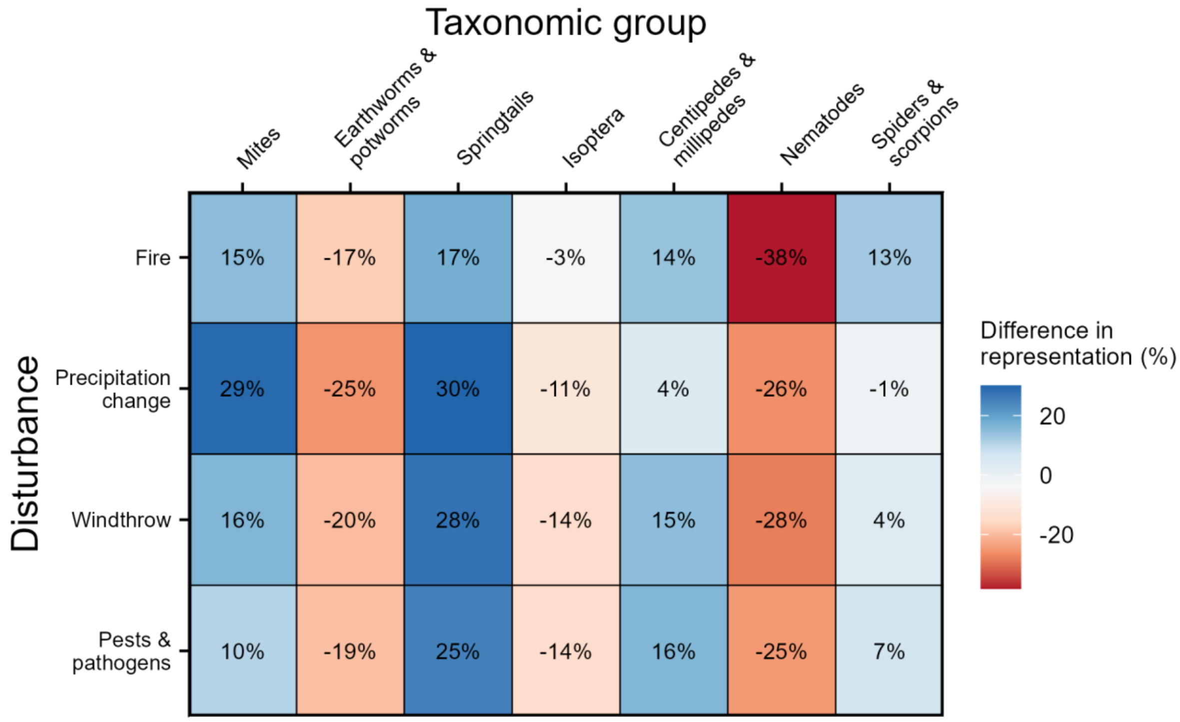

Figure 3 - Bias in study effort for different taxonomic groups, shown by the difference between the percentage of sites at which they were investigated for each disturbance type and the percentage of total global biomass that each group represents

Although our analyses showing the number of sites where different taxonomic groups have been studied was informative, it did not reveal whether there is a bias in which groups are studied. To assess this, we accounted for global estimates of biomass for a subset of taxonomic groups, showing that nematodes, earthworms, potworms, and termites are understudied (Figure 3). While nematodes were neglected for all disturbances, this was particularly true for fire. Meanwhile groups such as mites and springtails were studied at a greater percentage of sites than represented by their global biomass, indicating a bias towards studying these groups, especially in studies of precipitation change (Figure 3). There were smaller positive biases towards studying centipedes, millipedes, spiders, and scorpions.

Deciding what constitutes a good study organism is complex (Dietrich *et al.*, 2020). However, when studying the impacts of forest disturbances on soil and litter fauna, we hypothesise that researchers have prioritised two factors: the sensitivity of the group to disturbance and the ease of studying that group. For example, beetles are the amongst the most studied group for most disturbances, especially fire, probably because extensive taxonomic knowledge means they can be identified easily and because most studies focus on beetles found in the litter layer, meaning that sampling methods are less labour-intensive than those needed for sampling soil organisms. Ground beetles, in particular, are considered fire-sensitive and have been proposed as bioindicators for the wider impacts of fires (Gerlach, Samways & Pryke, 2013). Similarly, spiders and termites were heavily studied in sites where forest fires had occurred, likely for similar reasons as seen for beetles (Gerlach *et al.*, 2013). In contrast, beetles were used relatively infrequently in studies of precipitation change. This is probably because their high dispersal capacity means they can move easily between smaller experimental plots, such as those used in precipitation exclusion or addition experiments, diminishing the impacts of changes in precipitation (Martin *et al.*, 2024).

In contrast to beetles, springtails and mites have been studied more intensively in precipitation change experiments. This is likely because the groups are particularly sensitive to changes in soil moisture (Aupic-Samain *et al.*, 2021; Martin *et al.*, 2024) and have relatively low dispersal ability, making them good study organisms for this context. Our findings that mesofauna, as a whole, have been more intensively studied than microfauna is aligns with the previous findings of reviews on the impacts of natural disturbances on soil fauna (Pressler *et al.*, 2019; Martin *et al.*, 2024) suggesting that the relative ease of sampling and taxonomic identification drives this research focus.

Our analyses of biases clearly show that nematodes, earthworms, and potworms are understudied relative to their global biomass. This presents an interesting contrast with earlier reviews on soil biodiversity, which found a much greater focus on nematodes and earthworms (Guerra *et al.*, 2020; Beaumelle *et al.*, 2021). This difference is, in part, likely to be due to the differences in the contexts of these reviews which did not focus on forest ecosystems, meaning that they included agricultural areas, where taxa such as earthworms are commonly used as indicators of soil quality (Fründ, Graefe & Tischer, 2011; Demetrio *et al.*, 2020). Interestingly, springtails and mites have received much more research attention, relative to their global biomass, likely due to the less labour intensive methods needed to sample and identify them relative to earthworms and nematodes. More generally, as Potapov *et al.* (2020) state, the knowledge gaps and biases we observed in the study of soil and litter fauna are likely to be impacted by a lack of taxonomic expertise for the understudied groups.

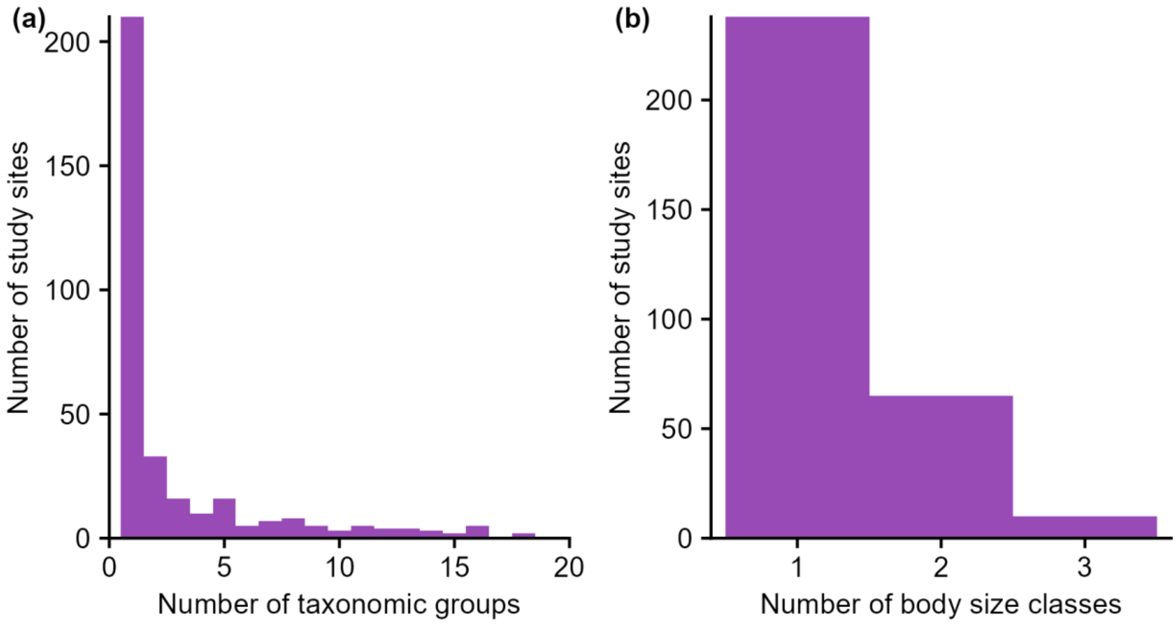

Figure 4 - The number of sites for which (a) different numbers of taxonomic groups were studied and (b) different body size classes were studied

At the vast majority of sites only a small number of taxonomic groups were sampled (Figure 4a, mean = 2.97, median = 1). Researchers only investigated more than five taxonomic groups at 15.7% of sites and more than 10 taxonomic groups at 7.3% of sites. This picture was mirrored when considering the number of body size classes (i.e. micro-, meso-, and macrofauna) that researchers sampled at different sites, which was typically low (Figure 4b, mean=1.27, median=1). Two or more size classes were sampled at 24.0% of sites and three size classes were investigated at only 3.2% of sites.

Studies mostly focussed on relatively simple biodiversity metrics such as abundance and alpha diversity (Figure 5). However, research on fire impacts examined a broader range of outcomes such as changes in community composition, evenness, and network interactions, compared to other disturbances (Figure 5). Studies on both precipitation change and windthrow assessed community composition at a moderate number of sites, whereas studies of the impacts of pests and pathogens or of multiple disturbances, rarely did so. Overall, disturbances that received more research attention tended to have a greater diversity of biodiversity outcomes investigated (Figure 5). This could be driven by the increased incentivisation of novelty in ecological research (Ottaviani *et al.*, 2023), meaning that once basic effects of disturbances have been shown researchers seek to find impacts on more complex biodiversity outcomes.

The tendency to favour simpler metrics is common in disturbance ecology (Marshall *et al.*, 2020; Davison, Rahbek & Morueta-Holme, 2021) and is largely due to the logistical difficulty and resource needs of measuring more complex variables such as species interactions (Morales-Castilla *et al.*, 2015; Harvey *et al.*, 2017; Moreno-Mateos *et al.*, 2020). These challenges are particularly pronounced in soil ecology, where the opaque nature of soil makes direct observation of feeding interactions difficult, unlike in aboveground ecosystems. However, methods such as gut content analysis and stable isotope analyses can be used to infer diet (Potapov *et al.*, 2020). Investigating the impacts of disturbances on soil and litter food webs is particularly important given their potential for assessing the stability of multiple ecosystem functions and services (de Vries *et al.*, 2013; Barnes *et al.*, 2018). However, in order to do this there is a need for more multi-taxon studies, which as we have shown, are sorely lacking. Similarly, there is a distinct lack of studies that assess the impacts of disturbances on organisms of differing body size. This limits a more holistic view of the impacts of disturbances on soil and litter organisms.

Figure 5 - The number of sites at which different outcome measures have been assessed for each of the different natural disturbance types considered by our study.

Implications of knowledge clusters, gaps, and biases for future studies

Our knowledge of the impacts of natural disturbances on soil fauna has increased markedly over the past two decades. As our analysis shows we now possess quantitative estimates of impacts of disturbances for 37 different taxonomic groups, and, in the case of fire, have information from every major forest biome in the world. We have deep knowledge about the impacts of forest fires on groups like beetles, springtails, and mites. However, there are also a number of important gaps that future primary studies should aim to fill. First, given the widespread nature of precipitation extremes, there are relatively few studies of prescription change on forest soil and litter fauna. Second, important groups like nematodes and earthworms are understudied in the context of forest disturbances. Third, we need more multi-taxa and multi-body size studies that will enable more meaningful metrics that can be linked to soil function be measured.

Focusing on evidence syntheses, the current study suggests that there is sufficient primary literature to allow for meta-analyses of the impacts of fire, precipitation change, and potentially windthrow on soil and litter fauna in forests. These meta-analyses should predominantly focus on meso- and macrofauna, due to the relative lack of information about microfauna, and could investigate biodiversity in the form of abundance, alpha diversity, evenness, and community composition. Since most study sites were found in North America and Europe, the ability of any such analyses to generalise effects of disturbance outside of these regions is questionable. As such we urge any future quantitative synthesis on this topic to fully consider constraints on generality that may result from this, as well as other biases and to test how well studies generalise (Spake *et al.*, 2022).

Based on our findings, key priorities for future primary research include an increase in research on tropical forest biomes, particularly relating to the impacts of fire and precipitation change. There is also a greater need for research in boreal regions for most disturbances. In addition, for our analyses of pests and pathogens we constructed a spatial dataset that covered the western USA and Europe. This indicates the need for greater efforts to build large-scale datasets of pest and pathogen impacts in forests in order to identify potential risks posed by these disturbances.

Characteristics and robustness of study methods

In most sites observational methodologies were used (277, 69%) as opposed to experimental methods (126 sites, 31%). For most disturbances, study designs were dominated by observational control-impact studies (also known as space-for-time studies) which have relatively low robustness (Figure 4). For studies of fire, windthrow, and pests and pathogens, a majority of sites (64%, 80%, and 73% respectively) were studied using observational control-impact designs. However, only 2% of sites where precipitation change was investigated used this methodology. Precipitation change studies tended to use more robust experimental methodologies (Figure 4), including blocked, randomised control-impact designs (12 sites, 22%) and randomised control-impact designs (8 sites, 15%). Before-after-control impact (BACI) studies were rare, with these methods used in 30 sites (11%) where fire impacts were studied and 3 sites (5%) where precipitation change was studied. No studies on pest and pathogen impacts or windthrow used BACI methods.

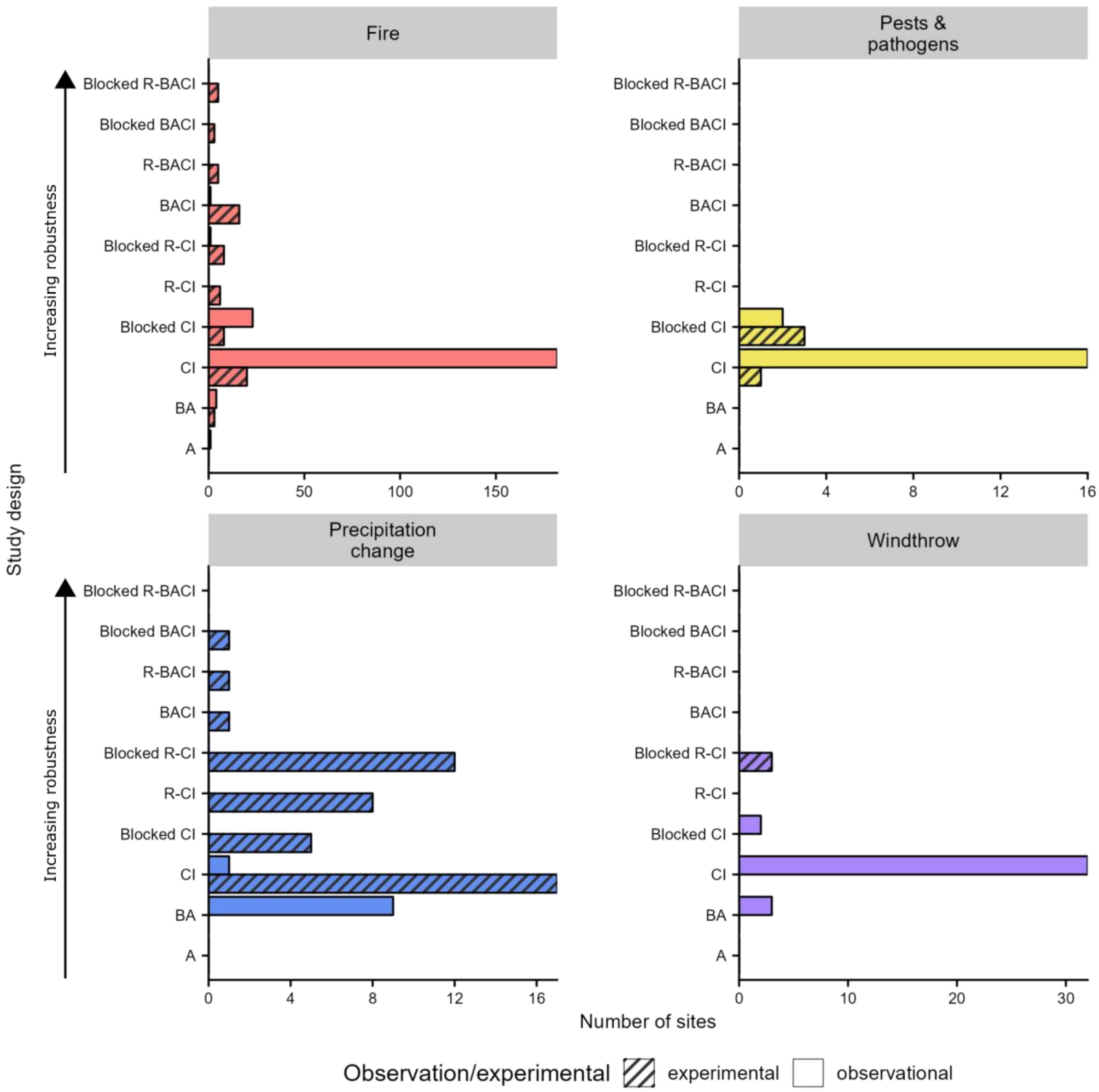

Figure 6 - Prevalence of different study designs for sites included in the systematic map. Design names follow Christie *et al* (2019, 2020): A - After; BA - Before-and-after; CI - Control-Impact; BACI - Before-after-control-impact; Blocked - studies where blocking was used to reduce variation between locations where different treatments were used; R - randomised. Study designs are organised on the y-axis based on their ability to accurately infer the impacts of disturbances on soil and litter fauna and are based on Christie *et al* (2019, 2020) as well as Frampton et al (2022). Note the differences in scale on the x axes.

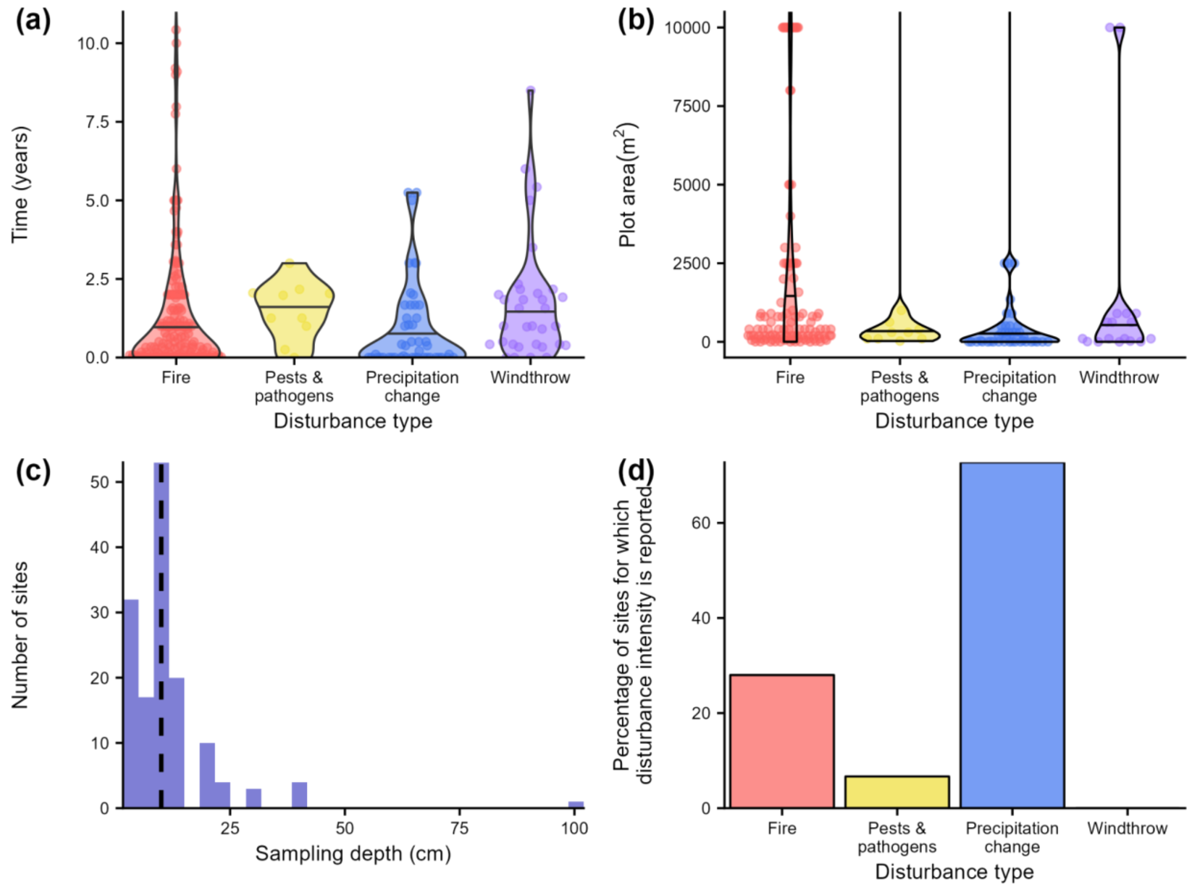

Figure 7 - Details of methods and reporting by studies for each different disturbance: (a) Study length and (b) plot area for each natural disturbance, (c) the sampling depth at each study site, and (d) the frequency with which the intensity of disturbance was reported for sites for each different disturbance type. The violin plots in (a) and (b) show the distribution of values for each disturbance, with horizontal lines representing the median for each disturbance type. Each point represents a value from an individual primary study. In (c) the vertical dashed line represents the overall median depth to which samples were taken.

Studies tended to be relatively short, with a median difference between first and last sampling time of 7.9 months. This varied between disturbances, with precipitation change (median = 1.9 months), and fire (7.8 months) having the shortest study lengths (Figure 7a). Studies on windthrow (15.4 months) and pests and pathogens (19.4 months) tended to be longer (Figure 7a). The median plot size used for studies was 400 m^2, although this was higher for studies of fire (Figure 7b, 800 m^2), and lower for studies of precipitation change (150 m^2), windthrow (100 m^2), and pests and pathogens (250 m^2). The median depth to which samples were taken was 10 cm and this was very consistent across all disturbance types (Figure 7c). Finally, the intensity of disturbance was rarely reported for most of the disturbances we investigated (Figure 7d) with only 27% of sites reporting fire intensity, 6% of sites reporting intensity of pest or pathogen disturbances, and 0% of studies of windthrow reporting intensity. Studies of precipitation change on the other hand, reported the intensity of these disturbances 73% of the time (Figure 7b).

The current study clearly demonstrates a bias towards observational studies and space-for-time substitution, especially for primary studies of the impacts of fire, windthrow, and pests and pathogens. This method represents the quickest and usually cheapest method for comparing biodiversity under different conditions by comparing sites that differ in their exposure to a disturbance, but are otherwise similar (De Palma *et al.*, 2018). While such designs can produce high precision estimates of biodiversity change, they are not necessarily accurate because differences in sites other than exposure to disturbance (e.g. soil type or slope) often occur because disturbance occurrence is non-random in space (De Palma *et al.*, 2018). This typically means that control-impact designs incorrectly estimate biodiversity change and that these estimates are less accurate than those provided by more complex study designs (Christie *et al.*, 2019, 2020). On the other hand, studies on precipitation impacts were, in general, likely to be considerably more robust than studies on other disturbances. Precipitation change studies were almost exclusively experimental in nature which have a much greater ability to determine causality than observational studies (De Palma *et al.*, 2018; Christie *et al.*, 2019). In addition, the use of study design elements such as blocking, where different treatments (e.g. control and precipitation reduction) are replicated in blocks to ensure that comparisons are valid, and randomisation were much more common for studies of precipitation change than for other disturbances.

Although experimental studies can allow for highly accurate assessments of the impacts of forest disturbances, space-for-time studies offer a number of advantages. One of these is that they investigate disturbances that have occurred in the real world, rather than simulated disturbances, such as when rainfall is restricted in a precipitation change experiment. This means that the intensity of the disturbance is potentially more representative of real-world conditions than those where experimental manipulations have been carried out (Korell *et al.*, 2020; Martin *et al.*, 2024). In addition, the use of space-for-time approaches allow for chronosequences to be used, where differently aged forest patches are measured to infer long-term dynamics, which would be impossible to do using experimental methods (Walker *et al.*, 2010). Given the pros and cons of different methodologies, we argue that researchers should aim to increase the number of studies using methodologies that are underrepresented for each disturbance type. In the cases of fire, pest and pathogens, and windthrow we encourage more experimental work to allow causality to be more clearly characterised. In the case of precipitation change, we recommend the establishment of long-term monitoring programs which could be used to examine the effect of droughts or large precipitation events in a more realistic manner. Such varied methods would allow for testing of the impacts of different methodologies on observed results (França *et al.*, 2016).

We found that most studies were relatively short term, typically lasting for less than 3 years, although there were some studies on fire impacts that were more long-term. Consequently, we lack a good understanding of the long-term impacts of natural forest disturbances on soil and litter fauna, such as the recovery of populations and communities (Malmström, 2010). This is concerning, because the little information we have suggests that recovery of soil organisms after fire is very limited (Pressler *et al.*, 2019). This reflects a common issue in ecology: the logistical challenges of long-term research, short-term funding, and the pressure for quick results. Additionally, most studies did not report the intensity of disturbance that soil fauna were exposed to, although many studies of precipitation change did report this - likely because changes in precipitation are easy to quantify and studies of precipitation were often controlled experiments. This lack of data on the intensity of disturbances other than precipitation change hinders our ability to generalise about the impacts of varying disturbance intensity, which is perceived as being one of the key determinants of disturbance impact (Malmström, 2010; Zaitsev *et al.*, 2016; Pressler *et al.*, 2019). While the availability of this information for studies of precipitation change has allowed for more nuanced analyses of how impact varies as the magnitude of precipitation change is altered (Goncharov *et al.*, 2023; Martin *et al.*, 2024) similar analysis for fire, windthrow, and insect pests and pathogens are unlikely to be possible. As such, we urge primary researchers to report indicators of disturbance severity where possible and for researchers working on syntheses to contact primary authors directly to gain more details about disturbance severity.

(3) Future directions for primary studies and evidence synthesis

Our study has broad implications for both primary studies and evidence synthesis of the impacts of natural disturbances on soil and litter fauna. From the perspective of primary studies, given their importance as a driver of forest disturbance in Europe (Patacca *et al.*, 2023), there is a clear need for further studies on the impacts of insect pests and pathogens on soil and litter fauna in forests. Additionally, since disturbances rarely occur in isolation (Bowler *et al.*, 2020) and the impacts of multiple disturbances are challenging to predict, further research on the impacts of multiple disturbances is essential. Regarding what organisms should be considered a priority, researchers should consider collecting data for a wider range of taxonomic groups, especially for microfauna such as nematodes, and important functional groups such as earthworms. For some disturbances such as pests and pathogens we still lack basic information relating to resulting changes in the abundance and diversity of soil and litter fauna and so research should concentrate on this, while for other disturbances, such as fire and precipitation change, we possess a relatively large amount of information about basic biodiversity metrics and so research should aim to focus on the potential impacts of fires on community and ecosystem functioning by investigating trophic networks. We also recommend that researchers attempt to undertake more studies outside of North America and Europe, particularly when studying topics such as precipitation change and fire which is likely to affect a wide range of forests globally.

From the perspective of improving study designs, studies of fire, pests and pathogens, and windthrow should aim to move away from observational studies towards more robust experimental methods that incorporate design elements such as randomisation. At the same time, it would also be useful to increase the number of observational studies of precipitation change, since an overreliance on experimental studies may come at the cost of realistic treatments and thus results. If the diversity of study types was increased for the different disturbances it would allow for the impacts of different study designs to be assessed and accounted for in analyses. In addition to more robust study designs, there is also a clear need for longer studies, especially for disturbances other than fire. This would allow us to study the long-term impacts of these disturbances. Finally, we recommend that authors report the intensity of disturbances that they have studied. Doing this would allow for a more nuanced assessment of disturbance impacts.

In addition to the implications for primary research, we also identify a number of implications for evidence syntheses. First, fire, precipitation change, and windthrow are likely ready for quantitative synthesis in the form of meta-analysis. However, due to gaps in the taxonomic groups and metrics that have been measured in the field, any synthesis will have to largely focus on meso- and macrofauna abundance, alpha diversity, or evenness. In addition, due to the large geographic biases we found, studies should be careful not to overgeneralise about impacts. Syntheses of fire impacts should be able to add valuable insight to changes over time, but that meta-analyses of other disturbances will be limited to relatively short-term impacts. Finally, a lack of contextual information from studies about the intensity of disturbances, means that authors of syntheses should routinely contact primary authors to supply this information.

Study limitations

Our study represents one of the very few systematic maps relating to soil ecology (Envall *et al.*, 2023; Ouédraogo *et al.*, 2024) and by following best-practice guidelines (James *et al.*, 2016; Collaboration for Environmental Evidence, 2018) and the publication of an a priori protocol (Martin *et al.*, 2021) we have ensured that it is methodologically highly robust. However, there are still a number of limitations that, if addressed, would have increased the robustness of our work further. The most important limitation of our systematic map is that only studies that were written in English were considered for inclusion. Although this practice is common (Hannah *et al.*, 2024), excluding literature written in non-English languages may lead to biases (Konno *et al.*, 2020; Amano *et al.*, 2021). In the case of our study, the lack of consideration of major languages such as Chinese, Spanish, and Portuguese (Amano, González-Varo & Sutherland, 2016) is likely to have further reduced the number of relevant studies we found from tropical biomes. Methods to overcome this barrier include the use of review teams with increased linguistic diversity and the prudent use of automated translation to help screening and data extraction (Hannah *et al.*, 2024).

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