



REVIEW

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Influence of forest thinning on the soil fauna: a systematic review of current knowledge and research gaps

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Abstract

Key message This systematic review shows that thinning effects on soil fauna abundance and species richness vary with thinning strategy and methodological approach. Positive responses are due to improved resources and favorable microclimate conditions, whereas negative responses were mainly associated with unfavorable microclimate conditions. However, current evidence remains fragmented, highlighting the need for standardized, comprehensive experiments to draw robust conclusions and generalize management recommendations.

Context As harvesting and reforestation expand to meet bio-economy and renewable energy demands, forests face increasing pressure from both unsustainable practices and climate change. Forest thinning, widely used across many regions, alters forest structure, vegetation and microclimate, leading to cascading effects on soil biodiversity. Yet, compared to microbial communities, soil fauna remains comparatively understudied despite their diversity and central role in ecosystem functioning.

Aims We conducted a systematic review to assess how forest thinning influences soil fauna.

Results Only 41 articles were identified: 27 focused on macrofauna (170 observations), 20 on mesofauna (96), and 6 on microfauna (13). These experiments varied considerably in their forest thinning strategies, sampling methods and soil fauna metrics, making it difficult to conclude whether soil fauna abundance or species richness respond to thinning in a consistent way. Both positive and negative effects were reported. Reducing forest cover can lead to less favorable microclimatic conditions with cascading negative effects on soil fauna. Conversely, the resulting increase in understory vegetation biomass and diversity caused by forest opening can create more heterogeneous microhabitats and resources with cascading positive effects on soil fauna.

Conclusion The observed variability in research approaches limits our mechanistic understanding of soil fauna response to thinning. We therefore emphasized recommendations for future research to improve methodological consistency and the robustness of findings.

Keywords Macrofauna, Mesofauna, Microfauna, Arthropod, Forest management

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1 Introduction

While harvesting and reforestation rates are increasing to meet the demands of the bio-economy and renewable energy, forests are under pressure from unsustainable practices and climate change. Therefore, management techniques are widely employed to promote forest sustainability. They not only reduce forest vulnerability but also improve resistance and resilience to a range of inter-related disturbances, including drought, insect outbreaks, and fires (Spittlehouse and Stewart 2004; Malmshiemer *et al.* 2008; Mäkipää *et al.* 2023). Thinning is a common and largely applied practice that reduces stand density while supporting timber production (Vesala *et al.* 2005; Zhang *et al.* 2018; Mäkipää *et al.* 2023). By decreasing competition for water, light, and nutrients, thinning often improves tree growth and health (Sheriff 1996; Sohn *et al.* 2016), lowers fire risk (Hurteau *et al.* 2008), enhances drought tolerance (Cotillas *et al.* 2009), and bolsters resistance to pathogens (Chmura *et al.* 2011).

By altering canopy structure, thinning also modifies resource availability and microclimatic conditions (Drever and Lertzman 2003; von Arx *et al.* 2012) and influences the development of understory vegetation (Thomas *et al.* 1999; Metlen and Fiedler 2006; Ares *et al.* 2010; Taki *et al.* 2010; Zhou *et al.* 2016). The environmental changes induced by thinning often promote plant diversity and natural regeneration (e.g., Zhu *et al.* 2003; Willms *et al.* 2017; Dang *et al.* 2018; Li *et al.* 2020) as well as vertebrate diversity (e.g., Verschuyt *et al.* 2011; Demarais *et al.* 2017). Yet, the effects of thinning on understory diversity are generally positive but can vary considerably depending on local environmental conditions and management practices. For instance, a meta-analysis by Li *et al.* (2020) found that thinning had a positive effect on understory plant diversity in China. However, another meta-analysis by Willms *et al.* (2017) revealed that, in North America, thinning had limited effects on understory richness and cover, except in the case of non-native species.

Modulating harvest levels through thinning affects not only the aboveground vegetation but also belowground communities, including microorganisms and soil fauna. Yet our knowledge of the latter remains extremely limited and incomplete (Anthony *et al.* 2023). In recent decades, research on the effect of forest thinning on soil microbial structure and activity has intensified (Wu *et al.* 2019; Zhou *et al.* 2020; Zhang *et al.* 2023). However, findings remain inconsistent, varying with thinning intensity, forest type, and biome. For example, Zhang *et al.* (2023) found that moderate thinning (30–60% reduction of stems or basal areas) increased microbial biomass and enzyme activity, likely due to the increased carbon inputs from post-harvest residues. In contrast, Zhou *et al.* (2020) reported that more intensive thinning reduced

mycorrhizal growth, which was linked to decreased fine-root biomass or increased abundance of saprophytic fungi or Gram-positive bacteria within the microbial community. Zhou *et al.* (2020) also observed that thinning increased total microbial biomass in deciduous forests but had no effect in mixed deciduous-evergreen forests.

Compared to our understanding of microorganisms, our knowledge of how thinning affects soil fauna remains extremely limited (Hartshorn 2020), despite their pronounced diversity and essential roles in ecosystem functions (Stork and Blackburn 1993; Delgado-Baquerizo *et al.* 2020). Soil fauna are key drivers of litter decomposition, nutrient cycling, and carbon storage (Hättenschwiler *et al.* 2005) and constitute a major reservoir of biodiversity (Orgiazzi *et al.* 2016). Yet, they remain poorly studied due to logistical challenges (cryptic species, time-consuming methods, approach bias) or taxonomic impediment (André *et al.* 2002; Dubois 2003; Guerra *et al.* 2020). As a result, soil biodiversity is still largely absent from biodiversity monitoring, conservation policies, or carbon models (Maréchaux *et al.* 2021; Guerra *et al.* 2024). Recent advances in environmental DNA and metabarcoding now offer promising tools to integrate belowground biodiversity in large-scale assessments (Oliverio *et al.* 2018; Ruppert *et al.* 2019).

Soil fauna is commonly classified by size (Swift *et al.* 1979). Macrofauna, invertebrates larger than 2 mm (e.g., Araneae, Diplopoda, Isopoda, Coleoptera, Formicidae, Lumbricina, Gasteropoda), contribute to litter fragmentation (Hättenschwiler *et al.* 2005) and soil structure, thereby facilitating air and water infiltration and promoting root growth and root exudation (Lavelle 1997; Vasconcellos *et al.* 2013; Lévassieur *et al.* 2025). Mesofauna, ranging from 0.2 to 2 mm, are microbial detritivore and predatory organisms, primarily represented in the taxa Collembola and Acari. They regulate microbial activity and diversity (Thakur *et al.* 2015) and are preyed upon by numerous soil organisms (Santonja *et al.* 2018; Aupic-Samain *et al.* 2021). Finally, microfauna, animals smaller than 0.2 mm, including mostly nematodes, promote nutrient cycling by consuming various soil microorganisms (Scheu *et al.* 2005), and are consumed by larger soil organisms (Wall 2012). Altogether, while our understanding of microbial responses to thinning is expanded, the effects on soil fauna remain poorly documented. This gap highlights the need to synthesize current knowledge and identify research priorities to better integrate soil fauna into forest management and ecosystem assessment. To address this issue, we conducted a systematic review aiming to clarify how forest thinning influences soil fauna (macro-, meso-, and microfauna) in forest ecosystems. Our research question was structured following the PECOS framework (Table 1). Specially, we aimed to (1) explore how forest thinning

intensity affect soil fauna abundance and species richness, and (2) identify the key environmental parameters modified by thinning (e.g., microclimate, resource availability) that influence soil fauna.

2 Material and methods

2.1 Research question and search strategy

We used the PECOS framework, i.e., a structure to organize the core elements of our research question (Table 1; Grames et al. 2019). To collect articles for this review, we conducted a literature search using the ISI Web of Science database (www.webofknowledge.com).

Soil fauna was defined as invertebrates that spend a significant proportion of their life within the soil or its annexes (e.g., tree stump, litter; Coleman et al. 2004).

To broaden the scope of this review, we also considered experiments on forest retention. While both methods reduce tree density, retention is usually applied to mature stands as a harvesting method to achieve ecological or silvicultural objectives, such as promoting biodiversity, buffering the microclimate, or securing regeneration. Given that the vast majority of the reviewed experiments pertain to traditional thinning, we used the term “thinning” throughout the paper.

During July 2024, we gathered all articles published between 1975 and 2024 that included the following combinations of search terms: [(soil OR litter) AND (fauna OR biota OR invertebrate* OR arthropod* OR insect* OR macrofauna OR earthworm* OR annelid* OR arachnid* OR spider* OR myriapod* OR chilopod* OR diplopod* OR coleoptera* OR mesofauna OR microarthropod* OR collembol* OR springtail* OR acari OR mite* OR enchytraeid* OR microfauna OR nematod* OR detritivore* OR predator*) AND (forest thinning OR thinning OR forest retention OR tree removal OR stand density)].

2.1.1 Inclusion criteria

We identified and downloaded 824 publications. To select relevant articles for this review, we screened the titles and abstracts of the 824 publications. We retained experiments that met the following eligibility criteria: (1) they involved field experiments conducted in forest ecosystems where forest thinning or tree retention was implemented, (2) they

directly examined the effects of forest thinning or forest retention as a presumed disturbance, and (3) they quantified the responses of soil fauna in terms of abundance or species richness to forest thinning or forest retention (Fig. 1; O’Dea et al. 2021). Field experiments refer to studies that included a clear management intervention in their design where canopy cover was affected by a thinning/tree retention treatment. We excluded 783 articles that did not meet these criteria (e.g., agroecological concerns, forest resistance to pest attack issues; Fig. 1; Biryol et al. 2025).

2.1.2 Data extraction and systematic map database

A total of 41 articles were retained and included in this review (see Appendix Table 2). We collected all available information from the text, tables, figures, and appendices of each publication. The following information was extracted: organisms, sampling (design, method and period; Appendix Fig. 7), site location, experimental plot information (stand characteristics, thinning methods, and implementation), and soil fauna outcome (abundance or species richness). Using these data, experiments were classified by soil fauna body size (i.e., macro-, meso-, or microfauna) and forest type (evergreen, deciduous, or mixed). The location of the experimental site was recorded to assign a Köppen-Geiger climate classification (tropical, subtropical, temperate, or continental; Peel et al. 2007). Additionally, experiments conducted under the Mediterranean climate (Csa-Csb in the Köppen-Geiger system) were treated separately from the general temperate category because of its distinctive dry-summer regime. QGIS (v. 3.16.11) was used to visualize the global distribution of the experiments. For experiments conducted at several experimental sites, a single site was selected to maintain map clarity.

3 Results

3.1 Location of experiments

To date, research on forest thinning and soil fauna has been carried out in 15 countries, mostly in Europe and North America (20 and 15 experiments respectively; Fig. 2). Macrofauna and mesofauna have been mainly studied in the USA (10 out of 27 articles), while research in Asia

Table 1 PECOS elements used in this review

| PECOS elements | Description |
|----------------|--|
| Population | Soil fauna found in forest ecosystems. We defined these as invertebrates that spend a significant proportion of their life within the soil or its annexes (e.g., litter, tree stump) |
| Exposure | Experiments that investigated the impact of forest thinning or forest retention |
| Comparison | Any comparison between forest or plantation plots where stand density has been modified. The comparison may be temporal or spatial |
| Outcomes | Abundance and/or species richness of soil fauna was retained |
| Space | Experiments carried out in the field. All types of forest and plantations are considered relevant |

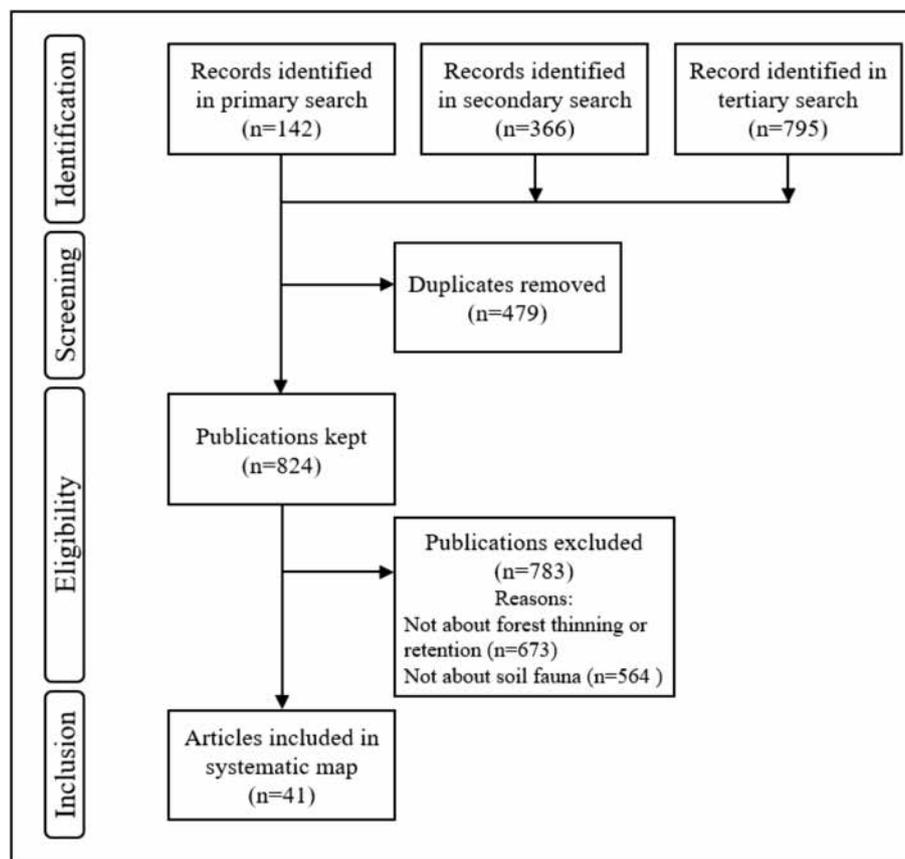


Fig. 1 Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) flowchart. Publication search was conducted in Web of Science. The number of articles retrieved and excluded are shown in each step. The search was made during January 2022 (primary search), October 2022 (secondary search) and on July 2024 (tertiary search), using progressively broader combinations of soil biota and forest thinning-related keywords

has focused more on microfauna (3 out of 6 experiments; Fig. 2). The majority of experiments have taken place in the Northern Hemisphere, between 30°N and 35°N. Only one experiment has been conducted in the Southern Hemisphere (Budiaman et al. 2020; Fig. 2).

3.2 Stand structure

The primary experimental system has been evergreen forests (31 out of 41 articles; Appendix Table 2; Fig. 3A). No experiments on microfauna response to forest thinning have been conducted in a deciduous or mixed forest. In deciduous forests, the dominant tree species were *Quercus* spp. (Henneron et al. 2015, 2017; Perry et al. 2018; Elek et al. 2018; Boros et al. 2019; Samu et al. 2021), *Acer* spp. (Shields et al. 2008; Perry et al. 2018), or *Populus* spp. (Lindo and Visser 2003, 2004). Only two experiments have been conducted in mixed forests: *Pinus sylvestris* L. and *Fagus sylvatica* L. in Spain (Herrera-Alvarez et al. 2020) and *Acer saccharum* Marsh., *Fagus grandifolia* Ehrh., *Betula allghaniensis* Britt., *Picea rubens* Sarg., and *Tsuga canadensis* L. in the USA (Ames et al. 2023). Forest age ranged from

10-year-old plantations of *Alstonia scholaris* L. (Budiaman et al. 2020) to >1000-year-old natural stands of *Pinus ponderosa* Dougl. (Peck and Niwa 2005; Appendix Table 2).

3.3 Metrics used for quantifying forest thinning

Several metrics have been used to describe stand characteristics following forest thinning, e.g., reductions in tree density (trees/ha), basal area per hectare (m²/ha), timber volume or tree retention per hectare (m³/ha), and canopy cover (%). Only five articles measured both trees density and basal area per hectare (Castin-Buchet and André 1998; Apigian et al. 2006; Herrera-Alvarez et al. 2020; Landi et al. 2020; Maccherini et al. 2021). In these experiments, control plots showed a basal area ranging from 4.8 m²/ha (Peck and Niwa 2005) to 57.2 m²/ha (Maccherini et al. 2021), or tree density ranging from 200 stems/ha (Schowalter et al. 2003) to 2500 stems/ha (Castin-Buchet and André 1998). Forest thinning has been shown to reduce tree density between 14% (Quevedo et al. 2014) and 81% (Yi and Moldenke 2005, 2008), a wide range reflecting the considerable variability in thinning strategies and initial forest structures. Numerous

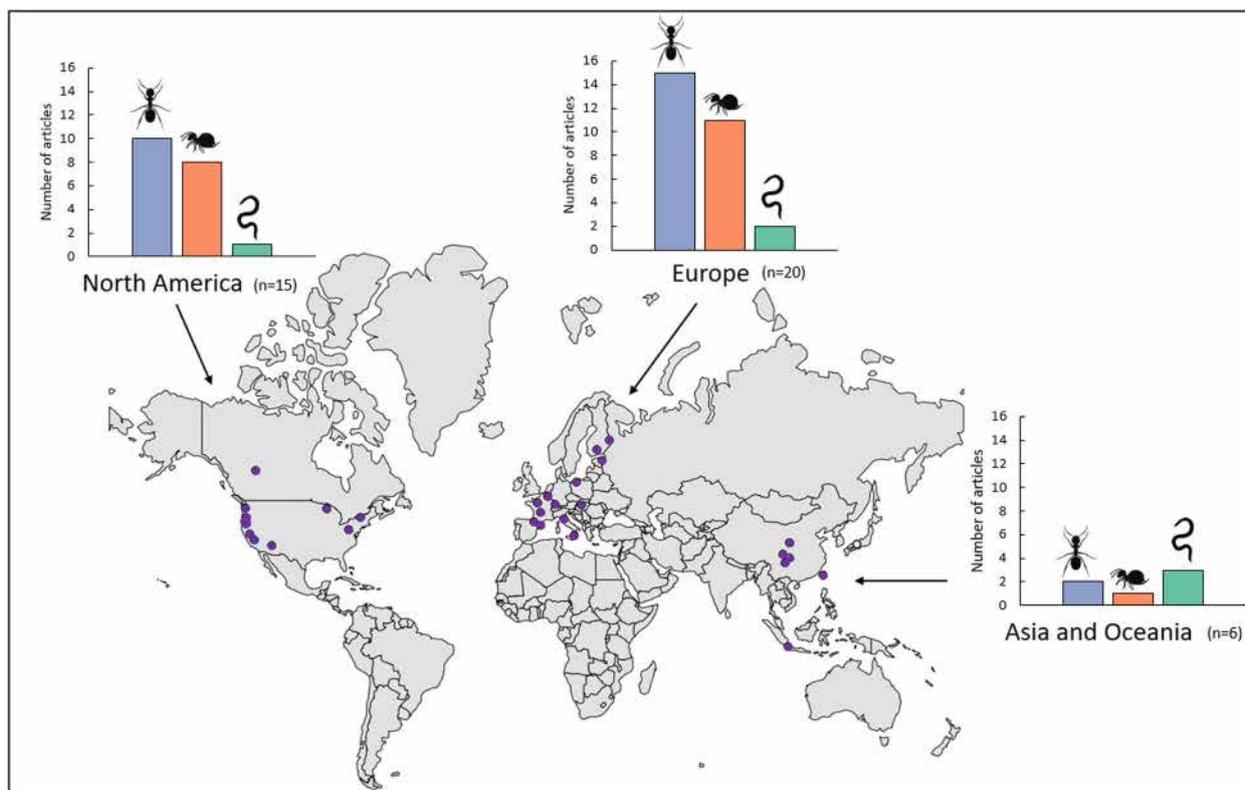


Fig. 2 Location and number of experiments included in this review according to soil fauna body size group (blue for macrofauna, orange for mesofauna, and green for microfauna). A number of articles focus on more than one biological group, resulting in a difference between the number of dots on the map and the number of experiments on the graphs

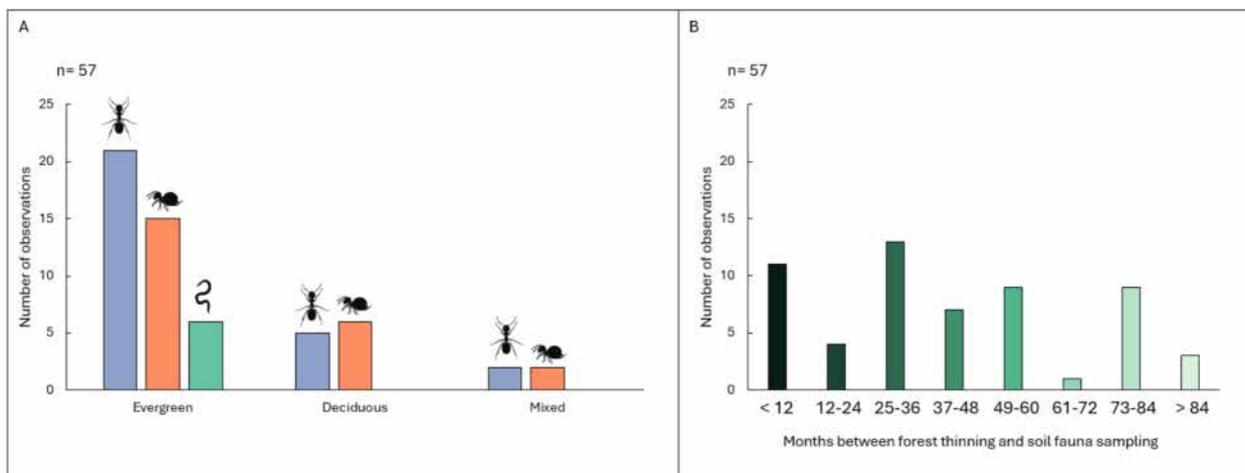


Fig. 3 Number of observations according to (A) forest type and soil fauna body size group (blue for macrofauna, orange for mesofauna, and green for microfauna) and (B) time interval between forest thinning intervention and soil fauna sampling

tree-density reduction methods have been employed: canopy opening, partial harvesting, thinning from below, selective thinning, line thinning, mechanical thinning, crop tree thinning or tree retention. These methods were often combined with additional treatments like prescribed burning,

understory clearing, or management of logging debris (e.g., mastication, removal). This methodological diversity leads to substantial differences in post-thinning stand structure, making direct quantitative comparisons between experiments challenging (Fig. 4; Appendix Table 2).

3.4 Experimental design

A wide range of experimental designs was used during the experiments. Some have focused on a single type of thinning treatment (Hyvärinen et al. 2005; Halaj et al. 2008; Halaj et al. 2009; Remm and Lõhmus 2016; Skłodowki 2021; Samu et al. 2021; Boros et al. 2019; Marra and Edmonds 2005; Peck and Niwa 2005; Maleque et al. 2007; Budiaman et al. 2020), while others have compared several treatment types (e.g., thinning from below, selective thinning; Landi et al. 2020; Maccherini et al. 2021; Siira-Pietikäinen et al. 2003, 2001; Siira-Pietikäinen and

Haimi 2009; Elek et al. 2018; Samu et al. 2021; Boros et al. 2019; Ames et al. 2023; Lindo and Visser 2003, 2004). Some experiments have applied a gradient approach to thinning, e.g., a continuous reduction in tree density or basal area up to a defined maximum (Schoy et al. 1984; Castin-Buchet and André 1998; Schowalter et al. 2003; Henneron et al. 2015, 2017; Ruppert et al. 2023) or tested multiple intensities, e.g., low, moderate, heavy thinning (Yi and Moldenke 2005, 2008; Huang et al. 2014; Yang et al. 2018; Herrera-Alvarez et al. 2020; Muscolo et al. 2021; Yin et al. 2021, 2022; Shields et al. 2008). Other

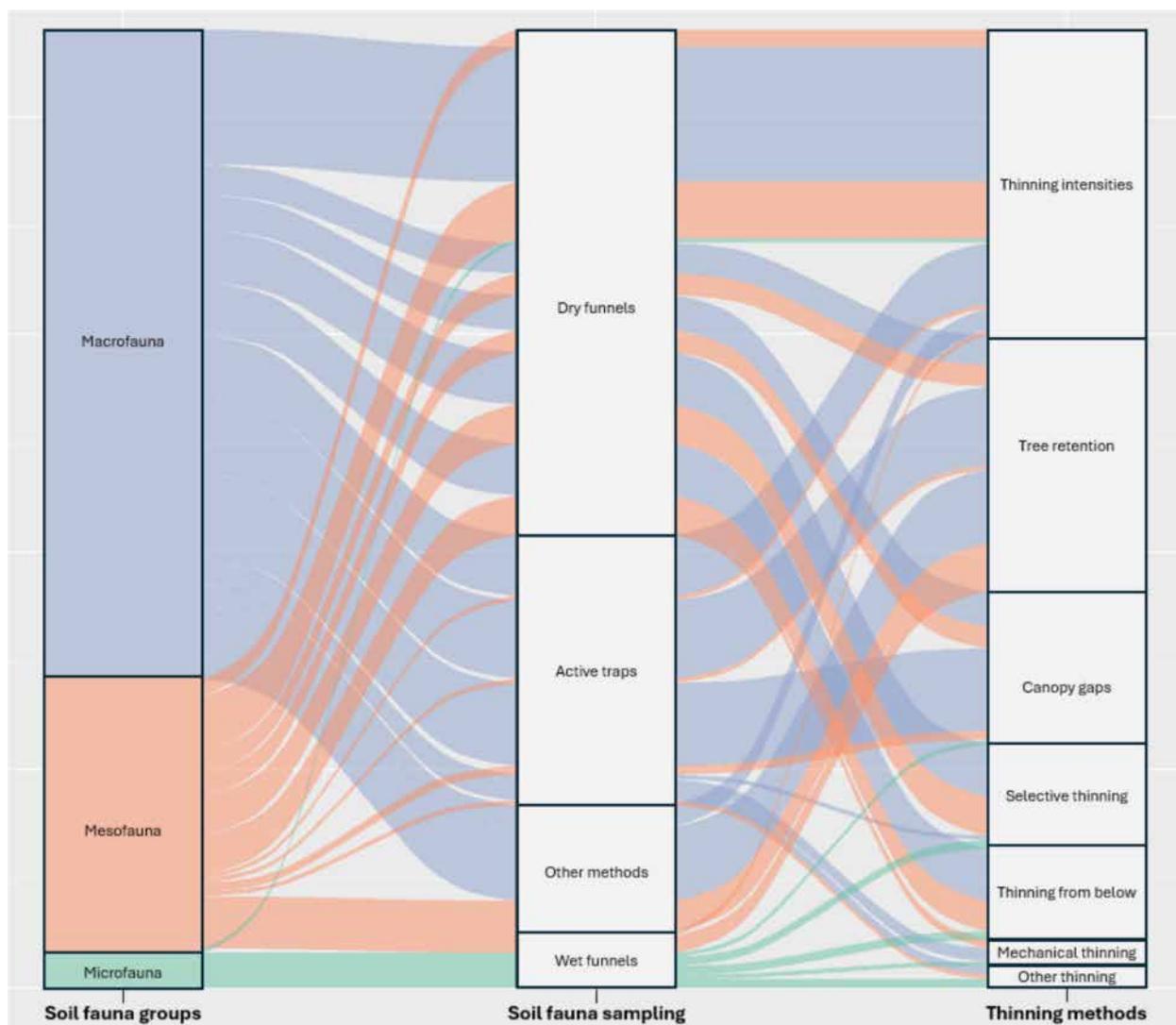


Fig. 4 Alluvial diagram illustrating the soil fauna body size groups (left bar), sampling types (middle bar), and thinning implemented (right bar) reported in the articles included in this review. Soil fauna groups are shown in blue for macrofauna, orange for mesofauna, and green for microfauna. For clarity, soil fauna sampling methods have been grouped (dry funnels included *Berlese-Tullgren funnels*, *Berlese-type funnels*, *High-gradient Berlese extractor*, *High-gradient Tullgren funnels*, *High-gradient extractor*, *Macfadyen extractors*, *Tullgren funnels* and *dry funnels*; active traps included *Pitfall traps*, *Crawl traps*, *Malaise traps*, *Window flight traps*, and *Flight-interception traps*; other methods included *agitated ethanol solution*, *eDNA metabarcoding*, *hand-sorting* and *sieve samples*, and wet funnels included *Baermann funnels*, *cotton wood filter method*, and *wet funnels*). Other thinning included the following forest thinning practices: *Crop-tree release*, *line-thinning*, *partial harvesting*, *mechanical thinning* and thinning without information in the experiments

experiments have investigated thinning in combination with other management practices, such as prescribed fires (Villa-Castillo and Wagner 2002; Apigian et al. 2006; Gibson et al. 2022), understory clearing (Quevedo et al. 2014; Perry et al. 2018), or soil harrowing (Siira-Pietikäinen et al. 2003; Appendix Table 2).

3.5 Sampling timing

Most experiments were run within 1 to 7 years following thinning (38 out of 41 articles; Appendix Table 2; Fig. 3B). Only three experiments have examined the long-term (i.e., more than 7 years) effects of this practice (Schowalter et al. 2003; Peck and Niwa 2005; Siira-Pietikäinen and Haimi 2009), while fourteen experiments included before-after design (both pre- and post-thinning sampling; Siira-Pietikäinen et al. 2001; 2003; Marra and Edmonds 2005; Hyvärinen et al. 2005, 2009; Apigian et al. 2006; Huang et al. 2014; Perry et al. 2018; Elek et al. 2018; Boros et al. 2019; Budiaman et al. 2020; Landi et al. 2020; Maccherini et al. 2021; Samu et al. 2021).

3.6 Macrofaunal responses to forest thinning

Twenty-seven experiments have investigated the effects of forest thinning on soil macrofauna (Fig. 2), mainly Araneae, Coleoptera, and Hymenoptera (Appendix Table 2; Fig. 5). The sampling methods included active trapping in 13 experiments, material collection (i.e., litter, humus, forest floor, woody debris, or epiphyte at tree base) in 11 experiments and flight-interception trapping (i.e., Malaise traps, sticky traps, or window traps) in 4 experiments (Appendix

Table 2). Although flight-interception traps are typically designed to sample aboveground flying invertebrates, we retained these 4 experiments because they focused on beetle assemblages that are strongly associated with the forest floor or decomposing substrate (e.g., saproxylic and litter-dwelling species), fitting our operational definition of soil fauna (Table 1). Soil macro-invertebrates were extracted either through manual hand sorting in 3 experiments or using a funnel and sieve (Berlese-Tullgren funnel, dry funnel, or a sieve) in 6 experiments (Fig. 4). Most experiments were conducted in coniferous forests dominated by *Pseudotsuga menziesii* Mirb. (7 out of 21 articles), *Pinus* spp. (7 out of 21), or *Picea abies* L. (4 out of 21).

Reported responses to thinning varied: some experiments found no response, others reported positive or negative responses, and several showed both positive and negative responses to forest thinning depending on the taxon (Appendix Table 2; Appendix Table 3). Fourteen experiments reported no effect of thinning on macrofauna abundance: six on Coleoptera (Villa-Castillo and Wagner 2002; Apigian et al. 2006; Halaj et al. 2009; Elek et al. 2018; Herrera-Alvarez et al. 2020; Skłodowski 2021); five on Hymenoptera (Apigian et al. 2006; Yi and Moldenke 2008; Quevedo et al. 2014; Perry et al. 2018; Herrera-Alvarez et al. 2020); four on Chilopoda (Schoy et al. 1984; Yi and Moldenke 2008; Perry et al. 2018; Herrera-Alvarez et al. 2020); three on Araneae (Schoy et al. 1984; Elek et al. 2018; Herrera-Alvarez et al. 2020) and Hemiptera (Yi and Moldenke 2008; Halaj et al. 2009; Herrera-Alvarez et al. 2020); two on Diplopoda (Schoy et al. 1984;

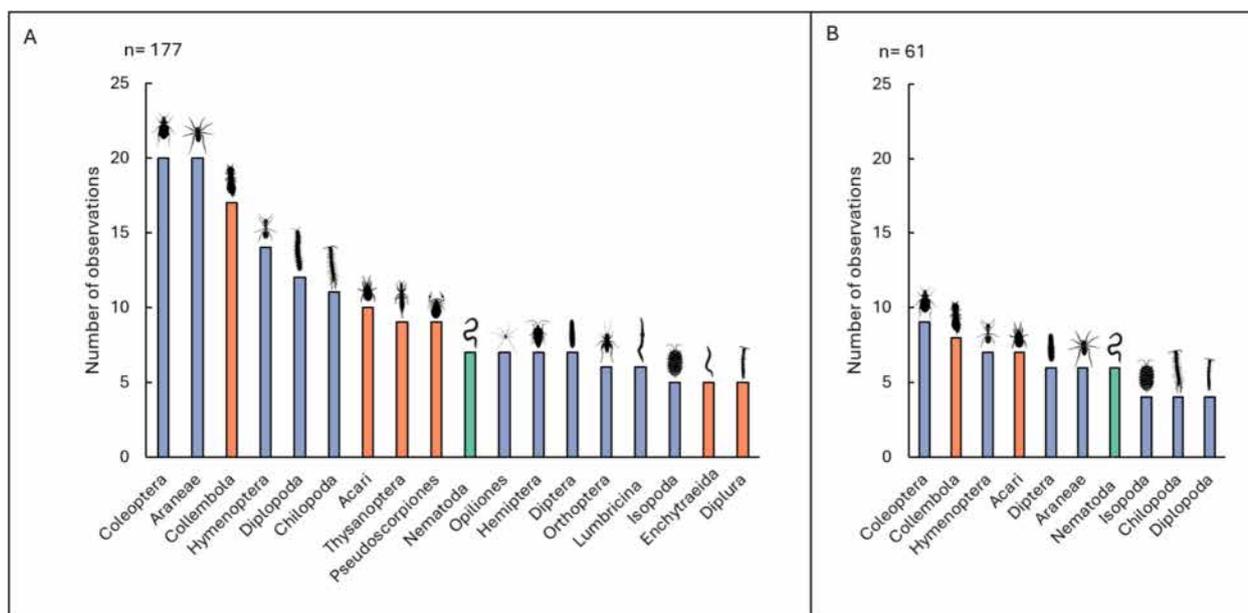


Fig. 5 Number of observations of (A) abundance and (B) species richness according to soil fauna body size group (blue for macrofauna, orange for mesofauna, and green for microfauna). Only taxa represented in at least 4 articles are shown (excluding insect larvae, snails, and slugs for abundance and Diplura, Lumbricina, Enchytraeida, Hemiptera, insect larvae, Oribionia, Pseudoscorpiones, and snails for species richness)

Halaj et al. 2009), Lumbricina (Perry et al. 2018; Herrera-Alvarez et al. 2020), Orthoptera (Yi and Moldenke 2008; Halaj et al. 2009), Gastropoda (Remm and Löhms 2016; Perry et al. 2018); and finally, only one on Diptera (Herrera-Alvarez et al. 2020), Isopoda (Henneron et al. 2015), and Opiliones (Perry et al. 2018).

Regarding macrofauna species richness, eight experiments reported a neutral effect of forest thinning: five for Coleoptera (Villa-Castillo and Wagner 2002; Siira-Pietikäinen et al. 2003; Herrera-Alvarez et al. 2020; Muscolo et al. 2021; Ruppert et al. 2023), four for Hymenoptera (Quevedo et al. 2014; Herrera-Alvarez et al. 2020; Muscolo et al. 2021; Ruppert et al. 2023), two for Araneae (Herrera-Alvarez et al. 2020; Ruppert et al. 2023), for Chilopoda (Herrera-Alvarez et al. 2020; Ruppert et al. 2023), Diptera (Herrera-Alvarez et al. 2020; Ruppert et al. 2023), Diplopoda (Ruppert et al. 2023), Lumbricina (Herrera-Alvarez et al. 2020), Hemiptera (Herrera-Alvarez et al. 2020), Isopoda (Henneron et al. 2015), Opiliones (Ruppert et al. 2023), and Gastropoda (Remm and Löhms 2016).

In contrast, thinning impacted macrofauna, with 10 experiments reporting positive effects on various taxa. These included shifts in Araneae abundance (Muscolo et al. 2021; Halaj et al. 2008, 2009; Samu et al. 2021) and species richness (Elek et al. 2018; Samu et al. 2021), Coleoptera abundances (Shields et al. 2008; Muscolo et al. 2021) and species richness (Hyvärinen et al. 2005; Elek et al. 2018), as well as the abundances of Annelida (Schohy et al. 1984; Castin-Buchet and André 1998; Henneron et al. 2015), Hymenoptera (Muscolo et al. 2021; Halaj et al. 2009), Lumbricina (Schohy et al. 1984; Castin-Buchet and André 1998), Diptera (Muscolo et al. 2021; Halaj et al. 2009), Diplopoda (Muscolo et al. 2021), Hemiptera (Muscolo et al. 2021), and Orthoptera (Perry et al. 2018). The researchers stated that thinning increased resource quantities and environmental heterogeneity, creating microhabitats and refuges for macrofauna (Yi and Moldenke 2005; Maleque et al. 2007; Huang et al. 2014; Muscolo et al. 2021).

That said, the positive effects of thinning on macrofauna were influenced by several factors, including time since treatment (Huang et al. 2014; Perry et al. 2018), season (Yi and Moldenke 2005; Muscolo et al. 2021), study site characteristics (Schowalter et al. 2003; Maleque et al. 2007), and interactions with fire (Apigian et al. 2006; Hyvärinen et al. 2009). For example, Yi and Moldenke (2005) found that, in a *P. menziesii* forest in the USA, thinning positively influenced the abundances of Araneae, Orthoptera, and Polydesmida during the wet season, but no effect during the dry season. Similarly, Huang et al. (2014) observed that, in a *Cryptomeria japonica* (Thunb.) D. Don forest of Taiwan, the abundance of ground hunter spiders and sheet web weaver spiders was greater in thinned versus control plots one year after the treatment. However, 2 years later, only

ground hunter spiders remained more abundant in plots with 50% thinning intensity.

Conversely, five experiments found negative effects of thinning on macrofauna. These included reductions in Araneae abundance (Siira-Pietikäinen et al. 2003; Siira-Pietikäinen and Haimi 2009), Coleoptera abundance (Halaj et al. 2008; Yi and Moldenke 2008; Siira-Pietikäinen and Haimi 2009), and species richness (Halaj et al. 2008), Diplopoda abundance (Yi and Moldenke 2008) and species richness (Henneron et al. 2015), and Opiliones abundance (Yi and Moldenke 2008). These declines were attributed to changes in soil moisture, notably greater litter dryness, as thinning increased levels of radiation and wind (Apigian et al. 2006; Yi and Moldenke 2005, 2008; Herrera-Alvarez et al. 2020). Again, responses were context-dependent, shaped by season (Yi and Moldenke 2005, 2008; Muscolo et al. 2021), site-specific characteristics (Schowalter et al. 2003), time since intervention (Halaj et al. 2008), and interactions with fire (Apigian et al. 2006). For example, Apigian et al. (2006) showed that thinning had a negative effect on the abundance of Carabidae (predatory Coleoptera) and Lycosidae (Aranea) when followed by fire, while there was a positive effect on guilds of wood-boring beetles.

3.7 Mesofaunal responses to forest thinning

Twenty experiments focused on soil mesofauna, mainly Acari and Collembola (Appendix Table 2; Fig. 5). Most used Berlese-Tullgren-type funnel (12 articles), while others employed MacFadyen extractor (2 articles), wet funnels (4 articles), or pitfall trapping (3 articles; Appendix Table 2; Fig. 4). As with macrofauna, research was mainly conducted in evergreen forests (12 out of 20 articles including 5 in *Pinus* spp. forests), although eight experiments took place in deciduous forests (3 in *Acer* spp. forests and 3 in *Quercus* spp. forests).

No article reported a positive effect of thinning on mesofauna species richness (Fig. 6B; Appendix Table 3). Besides this lack of positive effects, thirteen experiments reported no significant response of mesofauna to forest thinning. Specifically, no response was reported on Acari abundance (Herrera-Alvarez et al. 2020; Gibson et al. 2022) and species richness (Herrera-Alvarez et al. 2020; Maccherini et al. 2021; Ruppert et al. 2023), Collembola abundance (Siira-Pietikäinen et al. 2001, 2003; Peck and Niwa 2005; Siira-Pietikäinen and Haimi 2009; Halaj et al. 2009; Budiaman et al. 2020; Herrera-Alvarez et al. 2020) and species richness (Herrera-Alvarez et al. 2020; Muscolo et al. 2021; Ruppert et al. 2023), Thysanoptera abundance (Yi and Moldenke 2008) and species richness (Herrera-Alvarez et al. 2020; Ruppert et al. 2023), Pseudoscorpiones abundance (Perry et al. 2018; Herrera-Alvarez et al. 2020) and species richness (Herrera-Alvarez et al. 2020), Diplura abundance (Yi

and Moldenke 2008), and Enchytraeida abundance (Siira-Pietikäinen and Haimi 2009).

Six experiments reported a direct negative effect of forest thinning on mesofauna, i.e., on Enchytraeida abundance and species richness (Elek et al. 2018; Boros et al. 2019), on Acari abundance and species richness (Marra and Edmonds 2005), on Collembola species richness (Henneron et al. 2017), as well as on the abundances of Pseudoscorpiones (Yi and Moldenke 2008) and Thysanoptera (Herrera-Alvarez et al. 2020). Another six experiments reported interactive effects with other factors, i.e., thinning outcomes depended on soil layer (Peck and Niwa 2005), study site characteristics (Landi et al. 2020), time period (Landi et al. 2020; Muscolo et al. 2021), Collembola life-form studied (Henneron et al. 2017), or forest stand composition (Lindo and Visser 2003, 2004). For example, in a US coniferous forest, thinning negatively affected Acari abundance in the forest floor but not in the topsoil (Peck and Niwa 2005). In addition, within the forest floor, thinning affected Acari differently regarding the groups (Peck and Niwa 2005): it had a negative effect on Oribatid (mainly detritivore mites) and Prostigmatid (mainly predatory mites), and no effect on Astigmatid Acari (either microbivores-detritivores or opportunistic).

Only one experiment reported a direct positive effect of thinning on mesofauna abundance (Collembola, Diplura, and Pseudoscorpiones; Muscolo et al. 2021). In other cases, positive responses were context-dependent, influenced by time since the forest intervention (Siira-Pietikäinen et al. 2001; Maccherini et al. 2021), the season (Muscolo et al. 2021), the soil layer studied (Gibson et al. 2022), and the Collembola life-form studied (Henneron et al. 2017). For example, in a *Pinus nigra* subsp. *laricio* stand in Italy, Acari

and Protura abundances were higher in thinned plots compared to controls, but only during summer (Muscolo et al. 2021). Likewise, in a *P. ponderosa* forest in the USA, thinning increased the abundance of soil-dwelling Collembola, while litter-dwelling Collembola showed no response (Gibson et al. 2022). Additionally, Collembola functional groups responded differently in younger forest stands (<90 years old): epiedaphic (r-strategist) Collembola showed increased abundance and species richness, while hemiedaphic and euedaphic (K-strategists) groups experienced declines in species richness. Collembola functional groups, which differ in their vertical distribution and ecological strategy, may reflect distinctive pattern of Collembola response to thinning. Epiedaphic species inhabit litter layer and can rapidly colonize new habitats, while hemiedaphic and euedaphic species live deeper in the soil and may be more sensitive to habitat disruption (Henneron et al. 2017).

Across these 20 articles, mesofauna responses to thinning, both in terms of abundance and species richness, were shaped by other experimental factors. For instance, time since thinning mattered and ranged widely from just 1 week to 41 years (Peck and Niwa 2005; Budiaman et al. 2020), and site-specific conditions also played an important role (Landi et al. 2020; Maccherini et al. 2021). Research in a mixed forest in Spain showed a non-significant trend toward reduced mesofauna abundance and species richness (Acari and Collembola) following thinning, likely due to decreased soil humidity (Herrera-Alvarez et al. 2020). Forest thinning can affect microclimatic conditions, notably soil temperature and humidity, which are likely the key variables determining mesofaunal responses (Marra and Edmonds 2005; Peck and Niwa 2005). Differences among experiments in thinning

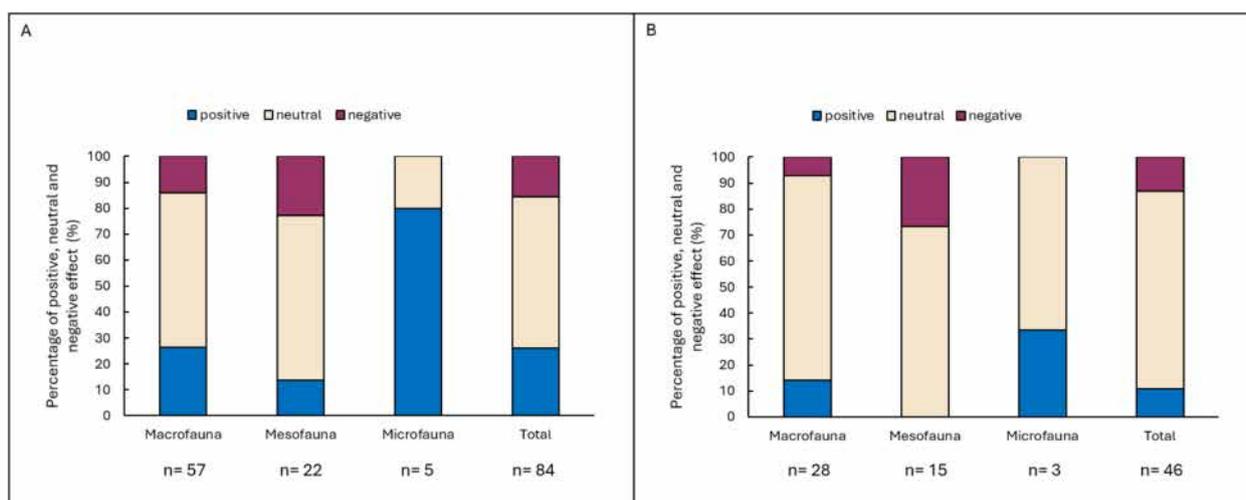


Fig. 6 Percentage of experiments with positive (dark blue), neutral (cream), and negative (purple) effect on (A) abundance and (B) species richness according to soil fauna body size group. Soil fauna responses related to other design factors (i.e., interactive effect in Appendix Table 2) are excluded. Only the response of the whole group was considered if an article divided the response of a taxa into groups (e.g., different taxonomic resolutions for Coleoptera, trophic groups for Nematoda, life-forms for Collembola or behavior for Lumbricina)

intensity, tree species composition, and stand structure (e.g., mean basal area, age, tree dimensions), likely lead to distinct microenvironmental outcomes. These context-dependent factors may thus explain the variability reported in soil mesofauna responses to thinning across experiments. Indeed, the effects of thinning could be driven by a change in the understory plant community. For example, Muscolo et al. (2021) observed that the positive effect of thinning on Collembola and Pseudoscorpionida abundance in intensively thinned plots was largely related to an increase in understory plant richness, which promoted microhabitat and resource availability. Similarly, in a temperate area with young to mature oak forests (<90 years old), Henneron et al. (2017) reported that Collembola community composition shifted after thinning. This shift decreased the abundance of euedaphic (K-strategist) and hemiedaphic Collembola and, conversely, increased the abundance and species richness of epiedaphic (r-strategist) Collembola. The rise in epiedaphic species was mainly mediated by the increase in understory plant richness, while the decline in euedaphic species was linked to microclimatic changes caused by forest cover removal. These functional shifts suggest that thinning primarily benefits opportunistic surface-dwelling species, while reducing the abundance of soil-dwelling species. Similarly, in a *P. ponderosa* forest in the USA, ground cover influenced the impact of forest thinning, and, notably, the grass cover was positively associated with soil Collembola abundance (Gibson et al. 2022).

3.8 Microfaunal responses to forest thinning

Six articles investigated how nematode abundance and taxa richness responded to thinning (Fig. 5). Most used wet funnels (5 articles) and one used dry funnel (Appendix Table 2; Fig. 4). As nematodes are typically extracted using wet funnel methods that rely on their active movement in water, this detail is reported here for descriptive purposes only and was not further considered in the study (Herrera-Alvarez et al. 2020). All were conducted in coniferous forests (Appendix Table 2; Fig. 3A).

Five experiments reported that thinning had a positive effect on total nematode abundance (Yang et al. 2018; Landi et al. 2020; Yin et al. 2021, 2022; Gibson et al. 2022) and taxonomic richness (Maccherini et al. 2021; Yin et al. 2021, 2022). In some cases, these positive effects depended on the time since thinning and study site characteristics (Landi et al. 2020; Maccherini et al. 2021), while in others, the composition of forest stand played a key role (Yin et al. 2022). Yin et al. (2022) observed that thinning enhanced total nematode taxonomic richness in *Pinus massoniana* Lamb. and *Cupressus funebris* Endl. plantations but not in fir plantations. The authors attributed this to fir plantations having lower understory vegetation cover and diversity, along with fewer food resources. Non-linear relationships

between thinning intensity and total nematode abundance were observed in the two experiments that applied three thinning intensities: low, intermediate, and high (Yang et al. 2018; Yin et al. 2021). Total nematode abundance was the highest in response to intermediate thinning (Yang et al. 2018; Yin et al. 2021). Both experiments suggested that the intermediate disturbance hypothesis might explain these patterns, linking the positive response of nematodes with changes in soil physicochemical properties and the understory vegetation.

The same authors also observed both positive and negative effects when the results were analyzed by trophic group. Yang et al. (2018) observed that, in a *Picea asperata* Mast. plantation, the abundance of plant parasitic nematodes increased in thinned versus control plots. This was the opposite for predatory and omnivorous nematodes. The authors hypothesized that omnivorous and predatory nematodes are more sensitive to environmental change (Yang et al. 2018). Similarly, Yin et al. (2021) reported that, in a *P. massoniana* plantation, thinning reduced the proportion of fungivorous nematodes but increased the proportion of herbivorous nematodes. Lastly, soil depth also mediated the influence of thinning. Yin et al. (2021) observed that the abundance of omnivorous and predatory nematodes increased at a depth of 0–10 cm but decreased at a depth of 10–20 cm following thinning, emphasizing the need to consider soil vertical variation when examining the impacts of thinning on the nematode community.

4 Research perspectives and knowledge gaps

The 41 articles included in this review employed a broad range of forest thinning strategies, sampling methods, and soil fauna assessment methods, making it difficult to draw general conclusions about the overall impact of thinning on soil fauna. Briefly, we observed no negative effect of forest thinning on microfauna ($n=6$ articles), no positive effect on mesofauna species richness ($n=10$ articles), and mainly neutral effects (abundance and richness) on macrofauna and mesofauna (Fig. 6). Moreover, when thinning had negative effects, they were mainly explained by a decreased forest cover and, consequently, modifications of the microclimate and resources availability at ground level. In contrast, positive effects were attributed to increases in the abundance and diversity of understory plant species, which enhanced microhabitat and resource availability.

These contrasting results primarily reflect a strong heterogeneity in experimental design and environmental context. Forest structure was described using various metrics, notably in terms of decreased basal area (m^2/ha) or decreased tree density (trees/ha). These two variables are not directly interchangeable but rather complementary: basal area provides an integrative measure of stand volume and reflects resource acquisition (e.g., light transmission and water

consumption), while tree density reflects stem abundance and spatial distribution. Ideally, both should be reported in order to capture different aspects of forest structure that can influence soil fauna communities. However, as most experiments only used only one of these variables, meaningful comparisons remain limited, particularly when experiments also varied significantly in both thinning intensity, thinning type (e.g., selective thinning, thinning from below, crop tree thinning) and the application of additional treatments such as prescribed fire, understory clearing, or management of logging debris (mastication, removal, stacking). However, methodological variability extends beyond forest metrics: soil fauna measurements differed in terms of sampling depth, recording duration after forest thinning intervention (1 to 63 years post-treatment), sampling season, often without information on climate conditions or site descriptors (e.g., topography, geology). Standardization of these parameters, as well as reporting biodiversity metrics (absolute, relative abundance, richness, or functional indices), is crucial for improving reproducibility and comparability.

To facilitate cross-study comparisons, study site descriptions are needed and must include the composition of the dominant, overstory vegetation (broadleaf, coniferous, evergreen, or deciduous) and of the understory vegetation (e.g., dominant species and cover). Furthermore, pre- and post-thinning basal area measurements are essential to characterize the intensity of thinning area before and after the treatment is applied. The use of contrasting sampling methodologies might lead to contrasted results (e.g., soil monoliths or pitfall traps) and limits our ability to understand the responses of soil fauna to thinning. Therefore, adopting standardized approaches, as emphasized by recent research (e.g., Gonzalez *et al.* 2021; Potapov *et al.* 2022) is crucial. For example, soil macrofauna can be directly sampled in the field via manual hand sorting of soil blocks (i.e., TSBF method), while mesofauna and microfauna can be obtained in the laboratory using Berlese-Tullgren and Baermann funnels, respectively. Because soil fauna is extremely sensitive to pedoclimatic conditions (notably to organic matter availability and season), the timing of sampling—and associated weather before and during the sampling—must be clearly reported. Ideally, several sampling campaigns should be carried out across seasons. Additionally, information must be provided about litter thickness and soil sampling (layers and depth). Finally, we strongly encourage researchers to systematically add raw taxonomic data in appendices to enhance our knowledge of the dynamics and distributions of soil organisms worldwide.

Beyond methodological issues, this review highlights conceptual and biogeographical gaps. Only one experiment was conducted in tropical forests, revealing that these forests are markedly under-represented among articles that examine soil fauna response to forest thinning.

As tropical forests host unique communities and are specifically vulnerable to factors such as land use change (e.g., Chiappero *et al.* 2024), extrapolating pattern risks missing region-specific responses. Moreover, much of the existing research is taxonomically descriptive, and could consider the functional aspects of soil fauna. For instance, future studies could integrate functional traits (e.g., life-history traits for Collembola, ecological groups for earthworms) to better understand how thinning alters soil fauna community and its cascading effects on ecosystem functioning. For instance, our synthesis suggests that large-bodied groups, such as macro- and mesofauna may be more negatively affected by canopy opening than microfauna, likely due to their higher sensitivity to microclimatic fluctuations and habitat disruption. Furthermore, distinguishing between changes in density and diversity will also be necessary to clarify whether thinning primarily alters species turnover, community composition or overall biomass.

Taxonomic resolution significantly influenced observed effects, with finer scales revealing more nuanced patterns, underscoring the importance of careful interpretation in this field. Taxonomic resolution, limited by methodological and human constraints (e.g., sampling challenges, the Linnean shortfall, and declining expertise), is now advancing due to technologies like high-throughput sequencing. The analysis of environmental DNA (eDNA), for instance, nowadays allows identifying of all life forms from soil samples (Taberlet *et al.* 2018; Calderon-Sanou *et al.* 2024). While these DNA-based methods still require referencing and cannot fully substitute traditional approaches based on specimen collection, they can provide a unique opportunity to reconcile several sub-disciplines of soil sciences that have historically operated in isolation and help establish a shared ontology for biodiversity descriptors and metrics (Le Guillarme *et al.* 2023). Indeed, instead of studying the soil food web as a whole, these sub-disciplines have focused on diverse soil taxa of different body sizes (i.e. bacteria, fungi, micro-, meso-, and macrofauna), have developed distinct tools, knowledge and research dynamics over the last decades (Geisen *et al.* 2019).

Finally, an interdisciplinary approach is needed to connect soil biodiversity with key ecosystem functions, as well as forest resilience following a thinning intervention. As soil fauna plays pivotal roles in litter decomposition, carbon cycle, soil fertility, and soil structure (Bardgett and van der Putten 2014; Griffiths *et al.* 2021), understanding how they respond to forest thinning and how this influences these processes will be essential for developing adaptive forest management strategies that account for the belowground component of biodiversity. Integrating soil ecology with silviculture, biogeochemistry, and forest modeling will represent a decisive step toward more sustainable forest cover management under changing climatic conditions.

Appendix

Table 2 Reported effect of thinning on soil fauna body size groups (macrofauna, mesofauna, and microfauna) from selected articles. BA refers to the basal area. The values represent averages when several plots were present

| Organisms studied— Collecting method | Site localisation— Climate | Forest type (Dominant species) Stand age | Factors - Experimental plot | Thinning implementation (T) Sampling time (S) | Effect of thinning on soil fauna | Reference |
|--|-------------------------------|---|---|--|--|---|
| Macrofauna/Meso-fauna Soil and litter samples | Belgium Temperate | Evergreen forest <i>Picea abies</i> | Thinning//Soil depth (litter vs. mineral layer) A (1960 trees/ha) B (1420 trees/ha) C (1060 trees/ha) D (840 trees/ha) E (660 trees/ha) | T: 1970–1979 S: 1980 | No effect on Chilopoda, Diplopoda and Araneae abundances Positive effect on earthworm abundance — Interactive effects No effect on enchytraeids abundance in litter layer Positive effect on earthworm abundance | Scohy et al. (1984) Castin-Buchet and André (1998) |
| Macrofauna Soil samples | France Temperate | Evergreen forest <i>Pseudotsuga menziesii</i> 9-year-old or <i>Picea abies</i> 19-year-old | Thinning Control (1140 or 2500 stems/ha) Thinning (from –70 to –24% of stems/ha) | T: 1986 or 1989 S: 1994 | Positive effect on earthworm abundance | Castin-Buchet and André (1998) |
| Macrofauna Pitfall trap | USA Continental | Evergreen forest (<i>Pinus ponderosa</i>) ~125-year-old | Thinning//Fire Control (BA = 29.73 m ² /ha) Thinned (BA = 18.74 m ² /ha) Thinned + burned (BA = 15.36 m ² /ha) Wildfire burned (BA = 0 m ² /ha) | T: 1987–1993 S: 1998, 1999 and 2000 | No effect on Coleoptera (Carabidae) abundance and species richness | Villa-Castillo and Wagner (2002) |
| Macrofauna/Meso-fauna Soil samples | Finland Continental | Evergreen forest (<i>Picea abies</i>) 100-year-old | Thinning//Harrowing Control (310 m ² /ha) Selection felling (70% stand volume retained) Gap felling (0.1 to 0.2 ha gaps, 50% stand volume retained) Retention felling (10% stand volume retained) Clear felling | T: 1996 S: 1995 (before), 1996, 1997 and 1998 | No effect on total predator, herbivore, Collembola abundances and on beetle species richness Negative effect on Araneae abundance | Siira-Pietikäinen et al. (2003) |

| Organisms studied— Collecting method | Site localisation— Climate | Forest type (Dominant species) Stand age | Factors - Experimental plot | Thinning implementation (T) Sampling time (S) | Effect of thinning on soil fauna | Reference |
|---|-------------------------------|--|---|--|---|--------------------------|
| Macrofauna Pitfall trap | USA Mediterranean | Evergreen forest (<i>Pseudotsuga menziesii</i>) | Thinning//Site Control (200 trees/ha) Thinned variable density (from – 18 to – 34 m ³ /ha of trees) | T: 1937 (Site 1), 1979–1981 (Site 2) S: 2000 and 2001 | Positive effect on Coleoptera (Aleocharinae) and on Gasteropoda (<i>Ancotrema sportella</i>) abundances Interactive effects Positive effect of thinning on Araneae (<i>Neon</i> sp., <i>Xysticus</i> sp. and <i>Zelotes fratris</i>), Coleoptera (<i>Harpalus cautus</i> , <i>Stenus</i> sp., Immature staphylinids), Hymenoptera (<i>Camponotus novboracensis</i>), Oligochaeta and Orthoptera (<i>Pristoceuthophilus</i> sp.) abundances depending on the study site considered Negative effect of thinning on Coleoptera (<i>Pterostichus inopinus</i> , <i>Scaphinotus angusticollis</i> , <i>Zacatus matthewsii</i> , <i>Tachinus</i> sp.) abundance depending on the study site considered Positive effect of thinning on Chilopoda abundance in one study site and negative effect in another one | Schowalter et al. (2003) |
| Macrofauna Window trap | Finland Continental | Evergreen forest <i>Pinus sylvestris</i> , <i>Picea abies</i> 150-year-old | Thinning//Fire Control (287.9 m ³ /ha) 50-m³ retention trees/ha 10-m³ retention trees/ha 0-m³ retention trees/ha | T: 2000–2001 S: 2000 (before) and 2001 | Positive effect on saproxylic, non-saproxyllic and red-listed species richness | Hyvärinen et al. (2005) |
| Macrofauna Pitfall trap | USA Mediterranean | Evergreen forest (<i>Pseudotsuga menziesii</i>) 40–60-year-old trees | Thinning//Season Control (wet vs. dry) (649 trees/ha) Light thin with gaps (271 trees/ha) Heavy thin (123 trees/ha) | T: 1993–1994 S: 2000 and 2001 | No effect on arthropod species richness Positive effect on total arthropod abundance Interactive effects No effect of thinning on Hymenoptera (Formicidae) abundance in wet season and on Araneae abundance, Coleoptera (Carabidae) abundance, Orthoptera (Gryllacrididae) abundance and Polydesmida abundance in dry season Positive effect of thinning on Hymenoptera (Formicidae) abundance in dry season and on Araneae, Orthoptera (Gryllacrididae) and Polydesmida abundances in wet season Negative effect of thinning on Coleoptera (Carabidae) abundance in wet season | Yi and Moldenke (2005) |

| Organisms studied— Collecting method | Site localisation— Climate | Forest type (Dominant species) Stand age | Factors - Experimental plot | Thinning implementation (T) Sampling time (S) | Effect of thinning on soil fauna | Reference |
|--|-------------------------------|---|---|--|---|---------------------------|
| Macrofauna Pitfall trap | USA Mediterranean | Evergreen forest (<i>Pseudotsuga menziesii</i> , <i>Pinus lambertiana</i> , <i>Pinus ponderosa</i> , <i>Abies concolor</i> , <i>Calocedrus decurvens</i> and <i>Quercus kelloggii</i>) | Thinning//Fire Control (BA = 56.4 m ² /ha; 1109.5 trees/ha) Mechanical (BA = 40.9 m ² / ha; 428.7 trees/ha) Fire (BA = 47.8 m ² /ha; 441.5 trees/ha) Mechanical followed by fire (BA = 39.3 m ² /ha; 238.9 trees/ha) | T: 2001–2002 S: 2001 (before) and 2003 | No effect on total Coleoptera and total Hymenoptera (Formicidae) abundances Negative effect on Coleoptera (preda- tors) abundance — Interactive effects Positive effect of thinning on Coleop- tera (wood-borers) abundance in burned plots Negative effect of thinning on Coleop- tera (Carabidae) and Araneae (total and Lycosidae) abundances in burned plots Positive effect on Coleoptera (Curculio- nidae) abundance | Apigian et al. (2006) |
| Macrofauna Townes-type white Malaise trap | Japan Subtropical | Evergreen forest (<i>Cryptomeria japonica</i>) 35-year-old trees | Thinning//Site (2) Control (NA) Line-thinned (~25 and ~29% of trees) | T: 2000 S: 2004 | Positive effect on Coleoptera (Curculio- nidae) abundance — Interactive effects Positive effect of thinning on total Coleoptera (total), Cantharidae, Carabidae, Cerambycidae, Chrysomelidae, Erotyli- dae, Lycidae, Nitidulidae, Oedemeridae, Scarabaeidae, Staphylinidae and Ten- ebrionidae) abundances depending on the study site considered Positive effect on ground-dwelling arthropods richness Positive effect on Buprestidae abun- dance — Interactive effects Negative effect of thinning on Curculio- nida abundance in small opening | Maleque et al. (2007) |
| Macrofauna/Meso- fauna Pitfall trap and sticky trap | USA Continental | Deciduous forest (<i>Acer saccharum</i> and <i>A. rubrum</i>) | Tree retention//Time (June vs. August) Control Small opening (320 m ²) Large opening (1217 m ²) | T: 2004 S: 2005 | Positive effect on ground-dwelling arthropods richness Positive effect on Buprestidae abun- dance — Interactive effects Negative effect of thinning on Curculio- nida abundance in small opening | Shields et al. (2008) |
| Macrofauna Pitfall trap | USA Mediterranean | Evergreen forest <i>Pseudotsuga menziesii</i> | Thinning//Year Control (BA = from 36 to 87) 40% aggregated retention 40% dispersed retention 15% aggregated retention 15% dispersed retention | T: 1998 S: 2003–2004 | Positive effect on spider abundance Negative effect on carabid abundance and species richness — Interactive effects Negative effect on Opiliones abun- dance in 2003 | Halaj et al. (2008) |
| Macrofauna Litter and humus samples | USA Mediterranean | Evergreen forest (<i>Pseudotsuga menziesii</i>) ~40–60-year-old | Thinning//growing season (early-, mid-, late-growing) Control (649 trees/ha) Light thin (271 trees/ha) Light thin with gaps (271 trees/ha) Heavy thin (123 trees/ha) | T: 1993–1994 S: 2000 and 2001 | No effect on total herbivore abundance Negative effect on total predator, total detritivore, on Coleoptera (Pselaphidae, Staphylinidae, Tenebrionidae), Opiliones, Geophilomorpha, Pseudoscorpionida and Diplopoda abundances | Yi and Moldenke (2008) |

| Organisms studied— Collecting method | Site localisation— Climate | Forest type (Dominant species) Stand age | Factors - Experimental plot | Thinning implementation (T) Sampling time (S) | Effect of thinning on soil fauna | Reference |
|---|-------------------------------|--|--|---|--|------------------------------------|
| Macrofauna Window traps | Finland Continental | Evergreen forest <i>Pinus sylvestris</i> , <i>Picea abies</i> 150-year-old | Thinning//Fire Control 50-m ³ retention trees/ha 10-m ³ retention trees/ha 0-m ³ retention trees/ha | T: 2000–2001 S: 2000 (before) and 2001–2002 | — Interactive effects Positive effect on thinning on beetle species richness in burned plots | Hyvärinen et al. (2009) |
| Macrofauna/ Meso-fauna Soil samples | Finland Continental | Evergreen forest <i>Picea abies</i> 100-year-old | Thinning//Site preparation Control (310 m ² /ha) Selection felling (70% of the stand volume retention) Gap felling (50% of the stand volume retained) Retention felling (10% of the stand volume retained) Clear felling | T: 1996 S: 2005 | No effect on enchytraeid abundance, Collembola abundance and species richness Negative effect on macroarthropods abundance | Siira-Pietikäinen and Haimi (2009) |
| Macrofauna Crawl traps | USA Mediterranean | Evergreen forest <i>Pseudotsuga menziesii</i> | Thinning Control 40% aggregated retention 40% dispersed retention 15% aggregated retention 15% dispersed retention | T: 1998 S: 2003–2004 | Positive effect on total insects and spider abundance | Halaj et al. (2009) |
| Macrofauna Pitfall trap | Taiwan Subtropical | Evergreen forest <i>Cryptomeria japonica</i> Established in 1971 | Thinning//Year (1 or 2 years after thinning)// Intensity Control (950–1500 trees/ha) Moderate thinning (- 25% of trees) Heavy thinning (- 50% of trees) | T: 2006–2007 S: 2005 & 2006 (before) and 2007–2009 | No effect on Araneae (space web weavers and sensing web weavers) abundance — Interactive effects Positive effect of thinning the first year after thinning on Araneae (ground hunter, sheet web weavers) abundance Positive effect of thinning on Araneae (ground hunter) abundance in heavy thinning plots the second year after thinning | Huang et al. (2014) |
| Macrofauna Pitfall trap | Spain Mediterranean | Evergreen forest <i>Arbutus unedo</i> Resprouted after fire 1994 | Thinning//Year Control (1265 trees/ha) Thinning (1082 trees/ha) Thinning and understorey clearing (1122 trees/ha) | T: 2006–2007 S: 2008, 2009, 2010 | No effect on total ant abundance and species richness | Quevedo et al. (2014) |
| Macrofauna Soil sample | France Continental | Deciduous forest <i>Quercus petraea</i> 18- to 174-year-old | Thinning//forest age (< 90-year-old vs. > 90-year-old) Gradient of canopy tree BA from 2.5 to 43.7 m ² /ha | T: 1991–2008 S: 2012 and 2013 | No effect on Isopoda and epigeic earthworm abundance Positive effect on endogeic earthworm abundance Negative effect Diplopoda and anecic earthworm abundances | Henneron et al. (2015) |

| Organisms studied—Collecting method | Site localisation—Climate | Forest type (Dominant species) Stand age | Factors - Experimental plot | Thinning implementation (T) Sampling time (S) | Effect of thinning on soil fauna | Reference |
|--|---------------------------|---|--|---|--|-------------------------------|
| Macrofauna Soil and litter samples | Estonia Continental | Evergreen forest (<i>Pinus sylvestris</i> and <i>Picea abies</i>) | Thinning Control Retention cut (median 15 trees/ha) Clear-cut | T: 1989–2005 S: 2008–2009 | No effect on snail abundance and species richness | Remm and Lõhmus (2016) |
| Macrofauna/ Mesofauna Pitfall traps | USA Continental | Deciduous forest (<i>Acer</i> spp., <i>Quercus</i> spp., <i>Fagus</i> spp., <i>Liriodendron tulipifera</i> and <i>Carya</i> spp.) | Thinning//Understorey management (understorey present or removed) Control (BA: 58.5 m ² /ha) Canopy gaps (10 to 15% canopy openness) | T: 2014 S: 2013 (before), 2014 and 2015 | No effect on Annelida, Snail, Slug, Chilopoda (Geophilomorpha, Lithobiomorpha and Scolopendromorpha), Diplopoda (Abacionidae, Julidae, Parajulidae, Spirobolidae, Polydesmidae, Choctellidae), Opiliones, Pseudoscorpiones, Collembola (Neanuridae, Hypogastruridae, Entomobryidae) and Insecta (Formicidae, Rhaphidophoridae, Scolytinae, Elateridae, Histeridae, Phalacridae, Ptiliidae, Geotrupidae, Trogidae, Silphidae) abundances Positive effect on total invertebrate abundance and species richness | Perry et al. (2018) |
| Macrofauna/Meso-fauna Soil samples and pitfall traps | Hungary Continental | Deciduous forest (<i>Quercus petrae</i> , <i>Q. cerris</i> , <i>Fagus sylvatica</i> and <i>Prunus avium</i>) 80-year-old | Thinning Control Preparation cutting Gap cutting (314 m ²) Retention tree group Clear-cut | T: 2014–2015 S: 2014 (before), 2015 and 2016 (after) | Interactive effects Positive effect on Collembola (Dicyrtomidae, Katiannidae) and Curculionidae, Nitidulidae and Staphylinidae abundances in 2014 and on Diplopoda (Paradoxosomatidae), Isopoda, Araneae, Collembola (Isotomidae, Tomoceridae), Gryllidae, Carabidae and Scarabaeidae abundances in 2015 No effect on spider and ground beetle abundance Positive effect on spider and ground beetle species richness Negative effect on enchytraeid abundance and species richness | Elek et al. (2018) |
| Macrofauna/Meso-fauna Pine woody debris samples | Spain Mediterranean | Mixed forest (<i>Pinus sylvestris</i> and <i>Fagus sylvatica</i>) ~60-year-old | Thinning//Canopy type Control (1456 trees/ha) Intermediate thinning (–20% of BA; 1125 trees/ha) Intense thinning (–40% of BA; 1078 trees/ha) | T: 1999 and 2009 S: 2015 | No effect on macrofauna and mesofauna abundances and species richness Negative effect on Thysanoptera abundance | Herrera-Alvarez et al. (2020) |

| Organisms studied— Collecting method | Site localisation— Climate | Forest type (Dominant species) Stand age | Factors - Experimental plot | Thinning implementation (T) Sampling time (S) | Effect of thinning on soil fauna | Reference |
|--|-------------------------------|---|---|--|--|-----------------------|
| Macrofauna/ Mesofauna Soil samples | Italy Mediterranean | Evergreen forest (<i>Pinus laricio</i>) ~60-year-old | Thinning//Season (summer vs. winter) Control (1 935 trees/ha) Moderate thinning (– 25% of BA; 1354 trees/ha) Intense thinning (– 45% of BA; 780 trees/ha) Clear-cut (– 100% of BA; 0 trees/ha) | T: start in 2010 S: 2014–2015 | No effect on Diptera, Rhaphidioptera and Symphyla abundances and Colembola, Coleoptera and Hymenoptera species richness Positive effect on Araneae (Araneidae), Collembola, Collembola, Diplopoda, Diptera, Hemiptera, Hymenoptera and Pseudoscorpionida abundances — Interactive effects Positive effect of thinning on Psocoptera abundance in summer and on Isopoda and Thysanoptera abundances in winter Positive effect of thinning on Acari and Protura abundances in summer and negative effect in winter No effect on Chilopoda abundance in winter | Muscolo et al. (2021) |
| Macrofauna Pitfall traps | Poland Continental | Evergreen forest <i>Pinus sylvestris</i> | Tree retention Control Large (0.07 ha) Medium (0.05 ha) Small (0.02 ha) | T: X S: X+1, 2, and 3 years | No effect on total carabid abundance and small zoophagous carabid proportion Positive effect on hemizoophage carabid proportion Negative effect on large zoophagous, generalist and forest carabid proportion | Skłodowski (2021) |
| Macrofauna Pitfall traps | Hungary Continental | Deciduous forest (<i>Quercus petraea</i>) | Thinning Control Preparation cutting (– 30% of BA) Gap cutting (circular gap of 20 m diameter clear-cut) Retention tree (circular area of 20 m diameter with untouched trees) Clear-cut | T: 2014–2015 S: 2014 (before), 2015, 2016, 2017, and 2018 | Positive effect on Araneae abundance and species richness | Samu et al. (2021) |
| Macrofauna Litter samples | Germany Temperate | Evergreen forest (<i>Picea abies</i> and <i>Abies alba</i>) > 60-year-old | Harvesting intensity index from 0 to 0.335 | T: 2017 S: 2021 | No effect on leaf litter arthropod OTU richness | Ruppert et al. (2023) |
| Macrofauna/ Mesofauna Epiphyte samples | USA Continental | Mixed forest (<i>Acer saccharum</i> , <i>Fagus grandifolia</i> , <i>Betula alleghaniensis</i> , <i>Picea rubens</i> and <i>Tsuga canadensis</i>) | Thinning//Epiphyte type (basal vs. bole vs. lichen) Corridor reserve (BA= 26 m ² /ha) Shelterwood (BA= 8 m ² /ha) | T: 2016–2018 S: 2020 | — Interactive effects Negative effect of thinning on microarthropod density and richness in basal bryophyte sample No effect of thinning on microarthropod density in lichen and bole-associated bryophyte sample | Ames et al. (2023) |

| Organisms studied— Collecting method | Site localisation— Climate | Forest type (Dominant species) Stand age | Factors - Experimental plot | Thinning implementation (T) Sampling time (S) | Effect of thinning on soil fauna | Reference |
|--|-------------------------------|---|---|---|--|---------------------------------|
| Mesofauna Soil samples | Finland Continental | Evergreen forest (<i>Picea abies</i>) 100-year-old | Thinning//Site preparation//Time Control (3.10 m ³ /ha) Selection felling (70% of the stand volume retention) Gap felling (50% of the stand volume retained) Retention felling (10% of the stand volume retained) Clear felling | T: 1996 S: 1995 (before), 1996, 1997, and 1998 | No effect on Collembola abundance — Interactive effects Positive effect on enchytraeid abundance and Collembola species richness in September 1997 | Siira-Pietikäinen et al. (2001) |
| Mesofauna Soil samples | Canada Continental | Deciduous forest (<i>Populus tremuloides</i> , <i>P. balsamifera</i>) & 140-year-old Evergreen forest (<i>Picea glauca</i>) 80-year-old | Thinning//Forest composition (deciduous vs. coniferous) Control Partial-cut patch (33% tree removal) Partial-cut corridor (100% tree removal) Clear-cut | T: 1998–1999 S: 2001 | — Interactive effects No effect on Collembola abundance in conifer stands Negative effect on Collembola abundance in partial-cut corridor in deciduous stands Negative effect on Acari abundance in partial-cut corridor in deciduous stands | Lindo and Visser (2003) |
| Mesofauna Soil samples | Canada Continental | Deciduous forest (<i>Populus tremuloides</i> , <i>P. balsamifera</i>) & 140-year-old Evergreen forest (<i>Picea glauca</i>) 80-year-old | Thinning//Forest composition (deciduous vs. coniferous) Control Partial-cut patch (33% tree removal) Partial-cut corridor (100% tree removal) Clear-cut | T: 1998–1999 S: 2001 | No effect on Mesostigmata, Prostigmata and Astigmata Acari, Arthropleona and Symphypleona Collembola abundances — Interactive effects No effect on Acari and Collembola abundance in conifer stands Negative effect on Acari abundance in partial-cut corridor in deciduous stands | Lindo and Visser (2004) |
| Mesofauna Soil samples | USA Temperate | Evergreen forest (<i>Abies magnifica</i> , <i>Abies concolor</i>) | Thinning Control/Closed canopy (BA = 42.7 m ² /ha) Shrub Canopy gap (~ 25% of canopy cover) | T: 2000 S: 1998 (before) and 2000 | Negative effect on Acari abundance and species richness | Marra and Edmonds (2005) |
| Mesofauna Forest floor and soil samples | USA Mediterranean | Evergreen forest (<i>Pinus ponderosa</i>) ~ 1000-year-old or older | Thinning//Layer (forest floor vs. soil layers) Control (BA from 4.8 to 9.5 m ² /ha) Thinned (BA from 3.7 to 6.4 m ² /ha) | T: 1958–1991 S: 1999 | No effect on Collembola abundance — Interactive effects Negative effect of thinning on Acari (Oribatid, Mesostigmatid, Prostigmatid and Astigmatid) abundance in the forest floor layer | Peck and Niwa (2005) |

| Organisms studied— Collecting method | Site localisation— Climate | Forest type (Dominant species) Stand age | Factors - Experimental plot | Thinning implementation (T) Sampling time (S) | Effect of thinning on soil fauna | Reference |
|---|-------------------------------|--|---|--|---|--------------------------|
| Mesofauna Forest floor and soil samples | France Continental | Deciduous forest (<i>Quercus petraea</i>) 18- to 174-year-old | Thinning/forest age (< 90-year-old vs. > 90-year-old) Gradient of canopy tree BA from 2.5 to 43.7 m ² /ha | T: 1991–2008 S: 2012 and 2013 | Positive effect on Collembola (epedaphic) abundance and species richness Interactive effects Negative effect of thinning on Collembola (total, hemiedaphic and euedaphic) abundance and on Collembola (hemiedaphic) species richness in < 90-year-old forest | Henneron et al. (2017) |
| Mesofauna Soil samples | Hungary Continental | Deciduous forest (<i>Quercus petraea</i> , <i>Q. cerris</i> , <i>Fagus sylvatica</i> and <i>Prunus avium</i>) 80-year-old | Thinning/Year/Layer (0–4 cm vs 4–8 cm vs 8–12 cm) Control Preparation cutting (-30% BA) Gap cutting (314 m ²) Retention tree group Clear-cut | T: 2014–2015 S: 2014 (before), 2015 and 2016 (after) | Negative effect on enchytraeids abundance and species richness Interactive effects Negative effect of thinning on enchytraeids abundance and species richness in the 0–4 cm, 4–8 cm, and 8–12 cm | Boros et al. (2019) |
| Mesofauna Pitfall trap | Indonesia Tropical | Evergreen forest (<i>Akstonia scholaris</i>) 14-year-old | Thinning Before thinning After thinning (-45% of trees) | T: 2019 S: 2019 (before and a week after thinning) | No effect on Collembola (Entomobryomorpha) abundance | Budiaman et al. (2020) |
| Mesofauna/Micro- fauna Soil samples | Italy Mediterranean | Evergreen forest (<i>Pinus nigra</i>) ~60-year-old or ~45-year-old | Thinning/Year (2016, 2017 and 2018)/ Site (2) Control (BA = 51.4 m ² /ha; 924 trees/ha) Thinning from below (-33.15% of trees/ha) Selective thinning (-33.15% of trees/ha) | T: 2015 S: 2015 (before), 2016, 2017 and 2018 | Interactive effects Positive effect of thinning on nematode abundance in 2018 at one study site Negative effect of thinning on nematode abundance in 2016 at one study site and on microarthropod abundance in 2017 at both study sites | Landi et al. (2020) |
| Mesofauna/Micro- fauna Soil samples | Italy Mediterranean | Evergreen forest (<i>Pinus nigra</i>) ~60-year-old or ~45-year-old | Thinning/Year (2016, 2017, 2018)/ Site (2) Control (BA = 57.2 m ² /ha; 1021 trees/ha) Thinning from below (BA = 45.1 m ² /ha; 685 trees/ ha) Selective thinning (BA = 39.7 m ² /ha; 684.5 trees/ ha) | T: 2015 S: 2015 (before), 2016, 2017 and 2018 | No effect on microarthropod species richness Interactive effects Effect of thinning x site x year on nematode richness Positive effect of thinning on microarthropods species richness in 2017 | Maccherini et al. (2021) |
| Mesofauna/Micro- fauna Soil samples | USA Continental | Evergreen forest (<i>Pinus ponderosa</i>) ~70–80-year-old | Thinning/Fire/Layer (litter vs soil) Control (300 trees/ha) Thinned (60 trees/ha) Burned (60 trees/ha) | T: 2014 S: 2016 | No effect on Acari abundance Positive effect on nematode abundance Interactive effects Positive effect of thinning on soil Collembola abundance | Gibson et al. (2022) |

| Organisms studied— Collecting method | Site localisation— Climate | Forest type (Dominant species) Stand age | Factors - Experimental plot | Thinning implementation (T) Sampling time (S) | Effect of thinning on soil fauna | Reference |
|---|-------------------------------|---|--|--|--|---------------------|
| Microfauna Soil samples | China Continental | Evergreen forest (<i>Picea asperata</i>) ~30-year-old | Thinning Control Small sized gap (74 m ²) Medium sized gap (109 m ²) Large-sized gap (196 m ²) | T: 2008 S: 2014 | No effect on nematode (bacterivores and fungi feeders) abundance and on nematode species richness Positive effect on nematode (total and plant parasites) abundance Negative effect on nematode (predator-omnivore) abundance | Yang et al. (2018a) |
| Microfauna Soil samples | China Continental | Evergreen forest (<i>Pinus massoniana</i>) Established in 1982 | Thinning//Soil depth (0–10 cm vs. 10–20 cm) Control (1250 trees/ha) Low (100 crop tree release t/ha) Medium (150 CTR/ha) High (200 CTR/ha) | T: 2015 S: 2016–2017 | Positive effect on total nematode abundance and species richness — Interactive effects Positive effect of thinning on nematode (omnivore-predator) abundance at 0–10 cm depth and on nematode (plant feeders) proportion at the 10–20 cm depth Negative effect of thinning on nematode (fungal feeder) proportion at the 0–10 cm depth and nematode (omnivore-predator) proportion at the 10–20 cm depth | Yin et al. (2021) |
| Microfauna Soil samples | China Continental | Evergreen forest (<i>Pinus massoniana</i> or <i>Cunninghamia lanceolata</i> or <i>Cupressus funebris</i>) Established in 1982 | Thinning//Plantations type (Pine vs. Chinese fir vs Cypress) Control (1537 trees/ha) Crop-tree thinning (1233 trees/ha) | T: 2015 S: 2018 | Positive effect on total nematode abundance — Interactive effects Positive effect of thinning on nematode species richness in pine and Cypress plantations No effect of thinning on nematode species richness in Chinese fir plantation | Yin et al. (2022) |

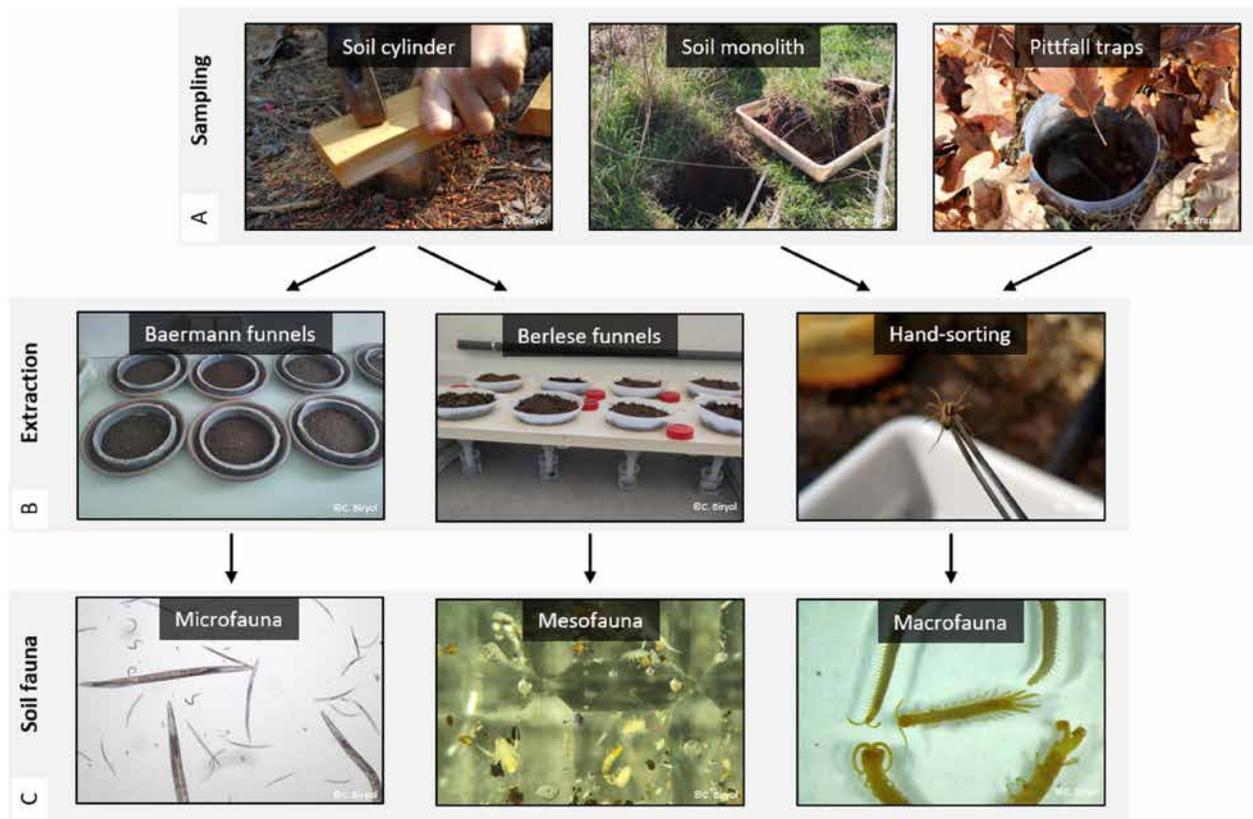


Fig. 7 Overview of common sampling methods (A) and extraction techniques (B) categorized by (C) soil fauna group

Table 3 Number of observations of positive, neutral or negative effects according to taxa included in this review. Taxa reported in less than 3 articles are excluded (i.e., Diplura, Isopoda, insect larvae, Opiliones, Orthoptera, and Gastropoda). Soil fauna responses related to other design factors (i.e., interactive effect in Appendix Table 2) are excluded. Only the response of the whole group was considered if an article divided the response of a taxa into groups (e.g., different taxonomic resolutions for Coleoptera, trophic groups for nematodes, life-forms for Collembola, or behavior for Lumbricina). The color gradient indicates the number of experiments, with more intense color representing a higher number of observations. ($n = 114$)

| | Positive effect | | Neutral effect | | Negative effect | | Total |
|------------------|-----------------|------------------|----------------|------------------|-----------------|------------------|-------|
| | Abundance | Species richness | Abundance | Species richness | Abundance | Species richness | |
| Acari | 0 | 0 | 2 | 4 | 1 | 1 | 8 |
| Araneae | 4 | 2 | 3 | 2 | 2 | 0 | 13 |
| Chilopoda | 0 | 0 | 4 | 2 | 0 | 0 | 6 |
| Coleoptera | 2 | 2 | 6 | 5 | 3 | 1 | 19 |
| Collembola | 1 | 0 | 7 | 3 | 0 | 1 | 12 |
| Diplopoda | 1 | 0 | 2 | 1 | 2 | 1 | 7 |
| Diptera | 2 | 0 | 1 | 2 | 0 | 0 | 5 |
| Lumbricina | 2 | 0 | 2 | 1 | 0 | 0 | 5 |
| Enchytraeida | 0 | 0 | 1 | 0 | 2 | 2 | 5 |
| Hemiptera | 1 | 0 | 3 | 1 | 0 | 0 | 5 |
| Hymenoptera | 2 | 0 | 5 | 4 | 0 | 0 | 11 |
| Nematoda | 4 | 1 | 1 | 2 | 0 | 0 | 8 |
| Pseudoscorpiones | 1 | 0 | 2 | 1 | 1 | 0 | 5 |
| Thysanoptera | 0 | 0 | 1 | 3 | 1 | 0 | 5 |

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Authors' contributions

C. Bi: Conceptualization, Methodology, Investigation, Data curation, Writing-Original draft preparation, Visualization. V. B.: Conceptualization, Methodology, Writing-Original draft preparation, Writing-Reviewing and Editing, Visualization, Supervision. B. P.: Writing-Reviewing and Editing, Visualization. J. T.: Writing-Reviewing and Editing, Visualization. E. F.: Writing-Reviewing and Editing, Visualization. L. P.-I.: Writing-Reviewing and Editing, Visualization. C. Ba.: Writing-Reviewing and Editing, Visualization. T. G.: Writing-Reviewing and Editing, Visualization. M. S.: Conceptualization, Methodology, Investigation, Data curation, Writing-Original draft preparation, Writing-Reviewing and Editing, Visualization, Supervision, Project administration, Funding acquisition. The authors read and approved the final manuscript.

Data availability

Published peer reviewed articles are used as a data in this study and the data are available at Biryol et al. 2025.

Declarations

Competing interests

The authors declare no competing interests.

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