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Does logging affect soil biodiversity and its functions? A review

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Abstract

Silvicultural practices affect over 30% of the global forest area and are a major driver of forest degradation. Logging is a forest management practice that is becoming increasingly widespread, since it is an important source of income for developing countries. Despite the expanding body of research on aboveground communities, little is known about the effects of logging on belowground communities. We conducted a qualitative systematic literature review to assess the current state of knowledge about the impact of logging on soil biodiversity and ecosystem functions. We addressed the effects of logging operations (e.g., clear-cutting, selective logging) on i) soil organisms (from microorganisms to soil fauna) and ii) soil functions mediated by soil biota. In general, the reviewed articles reported a negative effect of logging operations on abundance and diversity of microorganisms. Regarding soil fauna, most studies focus on insect taxa, with the impact on other soil fauna taxa remaining poorly understood. Decomposition was the most commonly studied ecosystem function. In general, the literature has reported negative effects of logging on soil functions; however, some studies found neutral or positive responses. This review highlights that logging operations have detrimental effects on a variety of different groups of organisms (e.g., microorganisms and insects) and functions (e.g., decomposition, microbial activity, bioturbation). However, on the basis of the evidence to date, low-intensity logging operations can be a beneficial practice for the conservation of soil organisms and ecosystem functions.

Keywords Silvicultural practices | Selective logging | Clear-cutting | Soil fauna | Ecosystem functioning | Macrofauna | Microorganism

1. Introduction

The global forest area is estimated at 4.6 billion ha and harbors approximately two thirds of the world's terrestrial biodiversity (Hansen et al. 2013, Watson et al. 2016). More than 30% of this forest area is primarily managed for the production of wood and non-wood forest products (FAO 2020). These economic activities have drastically reduced biodiversity (Jaureguiberry et al. 2022), with negative consequences for ecosystem functioning. While there are many reviews on the effects of forest management on aboveground communities (Duguid & Ashton 2013, Basile et al. 2019), little is known about belowground communities and the soil ecosystem functions that they control (but see Tomao et al. 2020).

Silvicultural management strategies usually differ among forest biomes. For example, clear-cutting, which involves the removal of all trees in a forest area, is the most common example of silvicultural management in temperate and boreal forests (Fedrowitz et al. 2014), and has been criticized because it simplifies the forest structure (Rosenvald & Lõhmus 2008). Therefore, in recent decades, variable retention has emerged as a silviculture alternative to traditional clear-cutting in these types of forests. Variable retention implies the long-term retention of dispersed individual trees,

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aggregated groups of trees, and small areas of intact forests (Gustafsson et al. 2012). Compared to traditional silviculture, variable retention has been found to maintain biodiversity and ecological cycles (Martinez-Pastur et al. 2009). On the other hand, conventional selective logging is the most common practice in tropical forests; it involves the removal of a single or a small group of mature trees, leaving the rest intact (Günter et al. 2011). However, even at low intensity (e.g., <5 trees removed per hectare), this technique damages the soil. Over the past two decades, reduced impact logging techniques have emerged to mitigate these deleterious effects (Putz et al. 2008). Reduced impact logging implies the implementation of techniques that reduce the environmental impact on forest stands and soils (Putz et al. 2008).

Soil supports a large portion of biodiversity, including microorganisms (e.g., bacteria and fungi), and micro- (e.g., nematodes), meso- (e.g., mites and springtails), and macrofauna (e.g., insects, myriapods, and earthworms) (Orgiazzi et al. 2016; Tab. 1). These soil communities play an essential role in regulating multiple ecosystem functions, such as plant productivity, nutrient cycling decomposition and soil structure maintenance (Brussaard 2012, Bardgett & van der Putten 2014). Logging operations may have direct and indirect negative consequences on soil organisms (e.g., composition, abundance, biomass, diversity) and the ecosystem processes they mediate (Fig. 1). Several studies have provided evidence that intense logging operations simplify tree strata and alter the understory vegetation, significantly modifying micro-environmental soil conditions (e.g., increase in temperature and decrease in soil moisture; Fimbel et al. 2001, Franklin et al. 2002, Putz et al. 2008, Huang et al. 2011). These soil conditions can strongly affect the small and ectothermic groups of soil fauna (da Silva Santana et al. 2021). In addition, the technology and infrastructure necessary to manage the forest can affect soil ecosystems by increasing soil erosion (Wenger et al. 2018, Haas et al. 2020; Fig. 1). Empirical evidence from tropical dry forests (Barreto-Garcia et al. 2021) and tropical/subtropical forests (Ross et al. 2018, Azevedo et al. 2021) suggests that the effects of logging operations on soil organisms and functions may depend on the type of organisms and functions involved. For example, there is evidence that soil fungal communities are resistant to forest management, with a neutral response having been reported (Pereira et al. 2018). Moreover, other studies have shown that these fungal communities are negatively affected by selective logging, but that they may recover after repeated logging operations (i.e., re-logging before or after the end of the designated cutting cycle; Li et al. 2020). In addition, the effects of forest management on soil fauna remain controversial. Some authors demonstrated a decrease in abundance and richness in managed forests compared with primary forests (Osawa et al. 2005, Martínez-Falcón et al. 2015), whereas others did not find changes in those parameters (Matos et al. 2019).

The impact of forest management activities on soil organisms and ecosystem functions can vary depending on the specific management approach, re-entry cycle, time since management and ecosystem type, as well as on the taxonomic composition of the soil organisms affected. Furthermore, while there is a review that assess the impact of deforestation on soil ecosystem functions in topical forest (Veldkamp et al. 2020) to our knowledge, no literature review has been performed on belowground communities (from microorganisms to macrofauna) and their ecosystem functions in different biomes. We conducted a scientific literature review to

Table 1. Estimated biomass, abundance (individuals/m^2) and diversity (number of described species) of main soil biota groups.

	Taxon	Biomass* or Abundance	Diversity
Microorganism	Bacteria	4–20 billion /cm^3	> 15000
	Fungi	100 mg[1]	≈ 150000
Microfauna	Nematodes	1000–100,000 ind.m^{-2}	50000
Mesofauna	Acari	≈ 500.00 ind.m^{-2}	54000
	Collembola	1000–100,000 ind.m^{-2}	9000
Macrofauna	Lumbricidae	≈ 500 ind.m^{-2}	7000
	Isopoda	≈ 300 ind.m^{-2}	4000
	Coleoptera	300–3000 ind.m^{-2}	400,000
	Diplopoda	≈ 500 ind.m^{-2}	8000
	Chilopoda	≈ 600 ind.m^{-2}	3300

* Biomass is indicated only for fungi. Numbers are approximate, since most soil species have still not been described, especially in under-represented regions (e.g., Africa, South America). Sources: Micro-, meso- and macro-fauna: Potapov et al. 2022a; bacteria and fungi: Bardgett & van der Putten (2014), Orgiazzi et al. (2016), Precott et al. (2023).

assess the current state of knowledge about the effects of forest management on belowground organisms and the soil functions they mediate. Specifically, we aimed to highlight the available evidence of logging operations (e.g., clear-cutting, selective logging) on i) soil organisms (from microorganisms to soil micro-, meso-, and macrofauna) and ii) soil functions mediated by soil biota.

2. Literature selection and data processing

We performed an exhaustive systematic literature search in Scopus and Web of Science database in October 2021. We used the following combination of keywords that related logging to soil organisms: ['selective logging' OR 'selective harvesting' OR 'selective cutting' OR 'timber

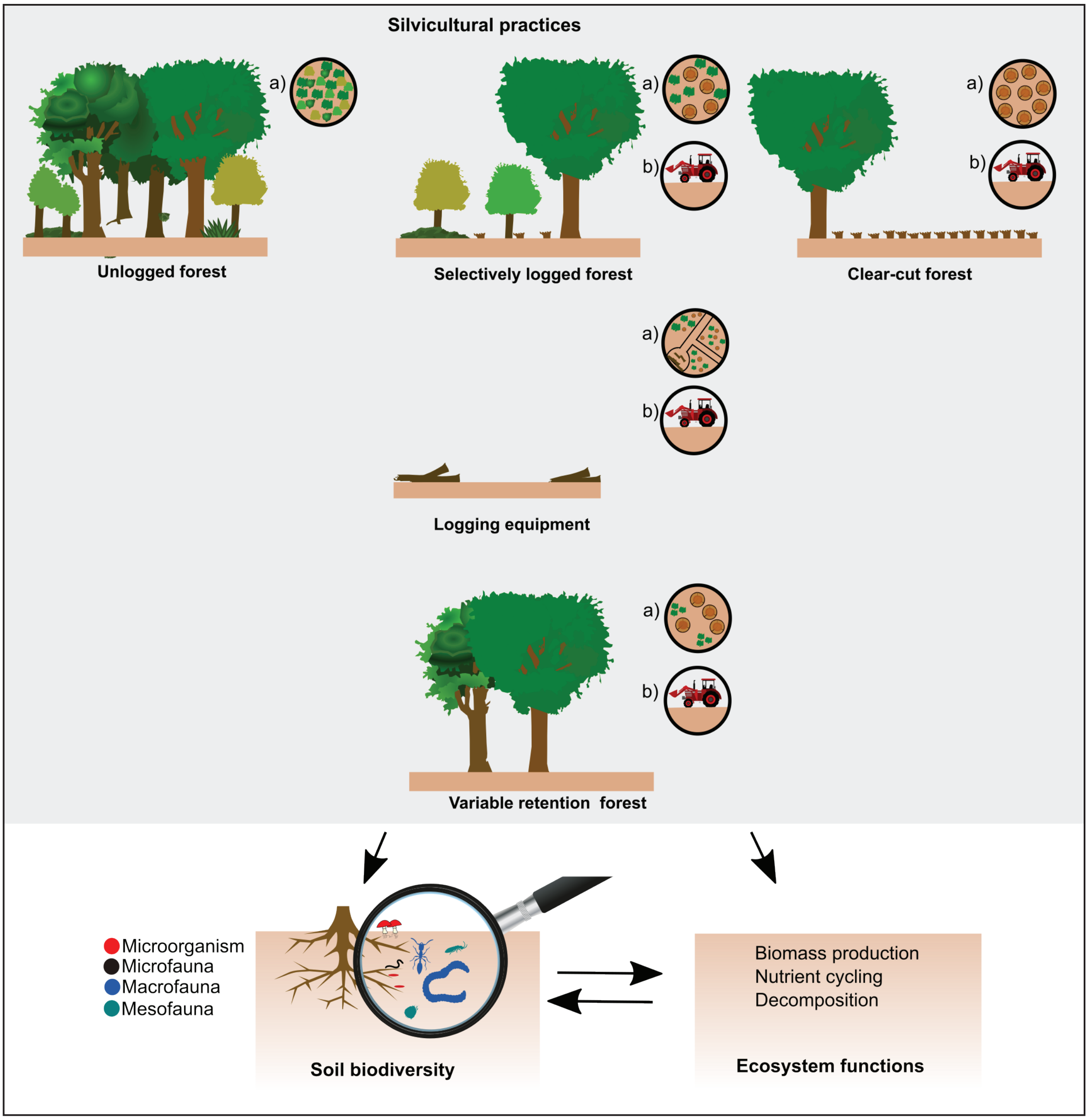

Figure 1. General overview of this synthesis review. Silvicultural practices, which can affect soil biodiversity and ecosystem functioning driven by soil organisms, can be categorized into two main aspects: (**a**) alterations in tree strata and understory vegetation, as silvicultural practices often lead to the simplification of tree strata and bring about changes in the composition of understory vegetation. It is important to note that logging equipment also involves the utilization of temporary roads, trails, and log collection points as integral components of this practice, and (**b**) technology and infrastructure: the incorporation of technology and the development of infrastructure play a crucial role in shaping the effects of silvicultural practices on soil organisms and the overall functionality of ecosystems.

harvesting' OR 'clear-cut harvesting'] and [microfauna OR mesofauna OR macrofauna OR microarthropod* OR macroarthropod* OR mesoarthropod* OR 'soil fauna' OR 'soil organisms' OR 'soil biota' OR collembola OR acari OR termite* OR earthworm* OR invertebrate* OR coleoptera OR beetle* OR formicidae OR isopoda OR microbes OR bacteria OR fungi OR microorganism* OR microbiome OR nematode* OR insect]. We also used the following combination of keywords that related logging to soil functions: ['selective logging' OR 'selective harvesting' OR 'selective cutting' OR 'timber harvesting' OR 'clear-cut harvesting'] and ['nutrient cycling' OR decomposition OR 'som dynamic*' OR 'som formation' OR 'soil structure' OR 'water infiltration' OR aggregate*]. We found 552 articles that address logging in relation to soil organisms and 305 to soil functions. We screened the articles by reading the title, abstract and full text. We included articles that studied soil organisms and/or soil functions and satisfied the following criteria: (2) compared different logging operations between managed forests and unlogged forests; or (3) analyzed the time since logging operations in managed forests compared or not with unlogged forests; or (4) analyzed different logging re-entries (cycle) to managed forests compared or not with control (unlogged) forests; or (5) compared different logging intensities; or (6) analyzed managed forests with different logging equipment. Studies that evaluated above-ground arthropods (e.g. Lepidoptera, Diptera) were excluded. We also excluded studies that focused on soil organisms or ecosystem functions in estuaries or that used fire for forest management.

3. Results and Discussion

3.1 Distribution of the literature

We identified 54 studies evaluating the effects of logging operations on soil organisms and 29 studies on ecosystem functions; about half of them were published between 2015 and 2021 (Fig. 2, Tab. 2). Studies that related logging to soil organisms were carried out in 19 countries and those relating logging to soil functions were conducted in 15 countries, with Brazil and Indonesia presenting the highest number of articles on both topics (Fig. 3). Moreover, soil organism and ecosystem function data are not evenly distributed across global biomes (Fig. 4). Tropical forests concentrate 56% of the data on soil organisms and 48% of the data on ecosystem functions, followed by temperate forests.

Table 2. Number of articles addressing main research questions.

Research questions	Number of articles
1) Characterization of soil biodiversity in logged forests.	**54**
a) Effects of different logging operations on soil microorganisms	20
Effects of different logging operations in managed forests compared to unlogged forests	15
Effects of time since logging operations in managed forests compared to unlogged forests	1
Effects of logging re-entries in managed forests compared with unlogged forest	2
Effects of different logging re entries	2
b) Effects of different logging operations on soil fauna	34
Effects of different logging operations in managed forests compared to unlogged forests	19
Effects of time since logging operations in managed forests compared to unlogged forest	5
Effects of time since logging	3
Effects of logging intensities in managed forests compared to unlogged forest	1
Effects of logging intensities	1
Effects of logging re-entries in managed forests compared with unlogged forest	3
Effects of logging equipment (e.g., skid trails, logging roads) compared with unlogged forest	2
2) Characterization of soil functions in logged forests.	**29**
Effects of different logging operations in managed forests compared to unlogged forest	19
Effects of time since logging operations in managed forests compared to unlogged forest	3
Effects of logging intensities in managed forests compared to unlogged forest	1
Effects of logging intensities	4
Effects of logging re-entries compared with unlogged forest	1
Effects of logging equipment (e.g., skid trails, logging roads) compared with unlogged forest	1

Concerning soil organisms, most studies (68 %) included in our review focused on meso- or macrofauna (e.g., arthropods), whereas a much smaller proportion (32 %) considered microorganisms (e.g., bacteria, fungi). Regarding soil functions, the decomposition process was the most widely addressed topic (30 % of the publications), followed by soil nutrient storage capacity, with 26 % of the studies.

3.2 Effects of logging on soil microorganisms

Fungi is an extremely diverse group of microorganisms that is highly dependent on forest attributes, playing a vital role in forest ecosystems (Tomao et al. 2020). For example, mycorrhizae are fungi that engage in symbiotic associations with plant roots, and are important in the uptake and transfer of nutrients to plants, in the

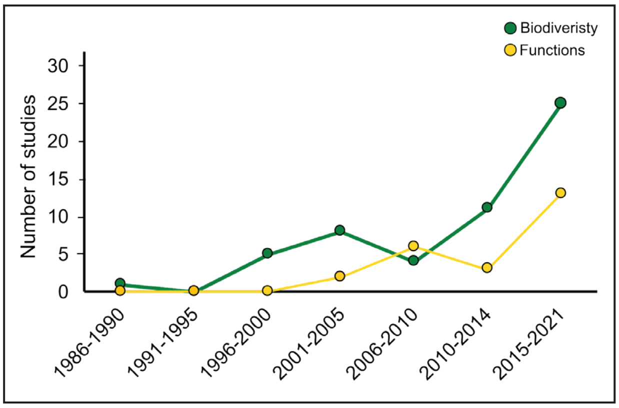

Figure 2. Number of studies focusing on soil organisms (—) and ecosystem functions (—) from 1986 to 2021.

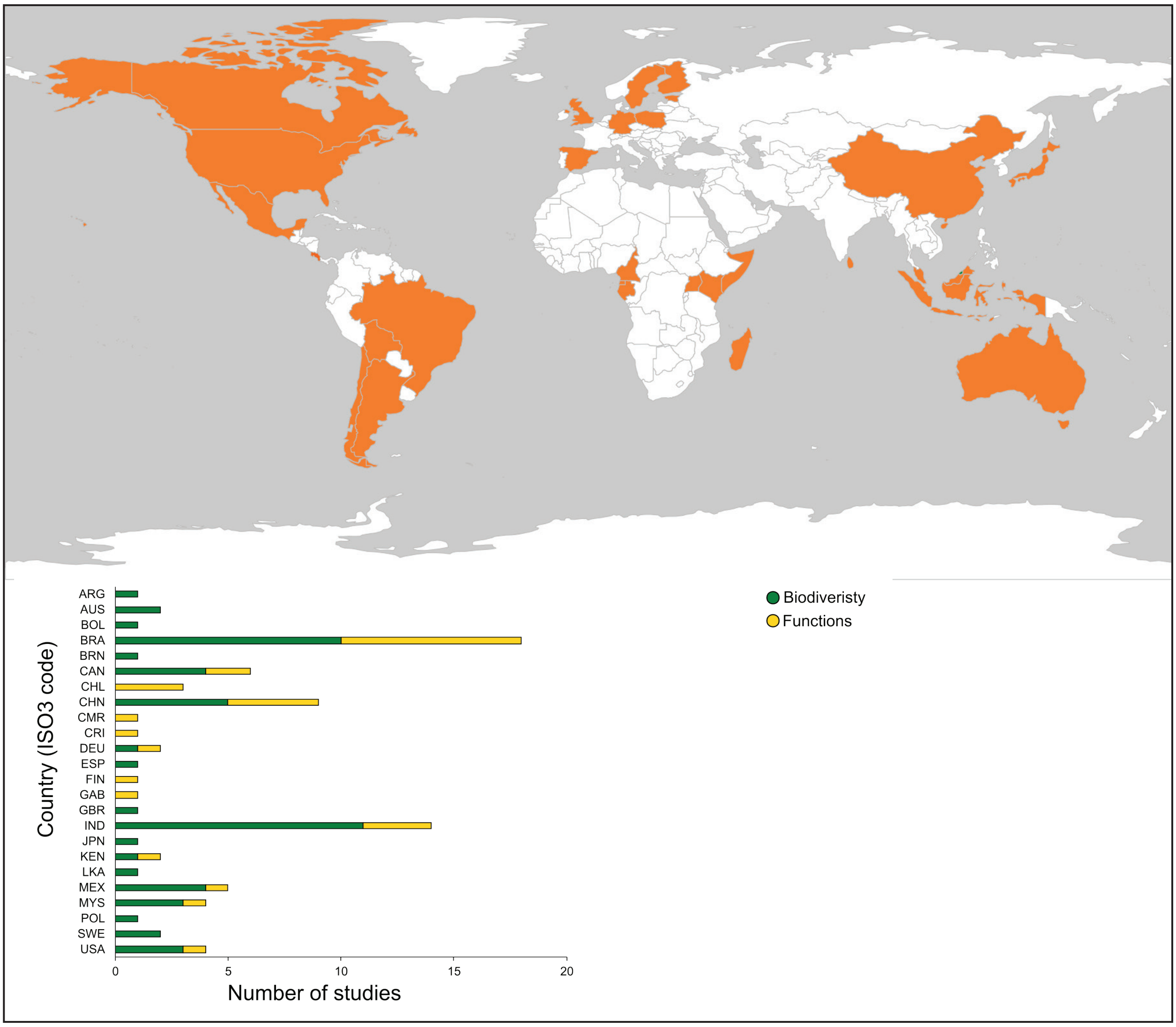

Figure 3. Worldwide distribution of logging studies included in this review. The bar chart represents the number of articles in each country (■).

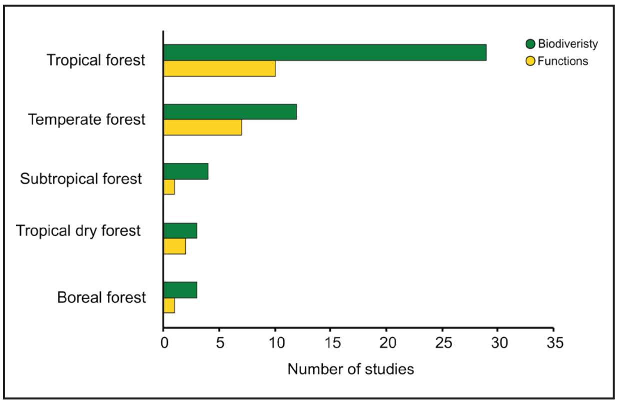

Figure 4. Number of reviewed studies on soil biodiversity and functions conducted in different biomes.

modification of the physical soil environment (e.g., aggregation), in the stimulation of microbial activity, and in soil carbon storage (Powell & Rillig 2018). Logging operations may have negative consequences on soil microorganisms (e.g., composition, abundance, biomass, diversity), which in turn can affect ecosystem functions.

In this review, most studies on the abundance, biomass, and diversity of soil microorganisms addressed the effects of different logging operations (clear-cutting, selective cutting, and variable retention) compared to unlogged forests (75 %), whereas only 10 % of articles evaluated the effects of logging re-entries, and 10 % focused on the effect of re-entries compared to unlogged forest (Tab. 2). Some of the reviewed studies pinpointed one particular group of microorganisms, such as fungi (55 %) or bacteria (25 %), whereas others used a multi-taxon approach (e.g., studying fungi and bacteria together, 20 %). The metrics used to measure abundance or biomass were ugCg-1, PLFA biomass, colonization percentage, and spore count, whereas for diversity, the studies used OTUS diversity, Shannon index, or species richness. Regarding to the effects of logging on multi-taxon approach studies reported negative (50 %), neutral (25 %) and both negative and neutral responses (25 %) on abundance and diversity parameters (Fig. 5).

Concerning the effects of logging on soil fungi, some studies reported changes in fungal composition due to different logging operations (Purahong et al. 2015, Varenius et al. 2016, Sterkenburg et al. 2019, Li et al. 2020). Nevertheless, there is evidence that fungal community composition is similar in logged and unlogged forests (Kerfahi et al. 2014, Tripathi et al. 2016). With respect to soil fungi abundance and diversity, the articles showed negative (63 %), neutral (27 %), or both responses (10 %) (Fig. 5). Negative effects were mainly observed when comparing different logging operations (e.g., selective logging, variable retention) compared with unlogged forest in different biomes (e.g., tropical, subtropical, temperate, boreal forests).

In logged forests, changes in forest structure caused by logging operations cause damage to root systems and modify soil properties (e.g., temperature, moisture, and organic matter) compared to unlogged forests (Andrew et al. 2016, Schappe et al. 2017). These changes may be the main factors explaining the negative effects of logging operations on soil fungi, particularly the mycorrhizal fungal community. However, in subtropical forests Li et al. (2020) found a negative effect in the short term after three re-entry cycles, but in the long-term a subsequent recovery of fungal diversity after logging operations is observed. This result suggests that in some systems, fungal communities can recover even after 3 re-entries. Moreover, other reviewed studies demonstrated that selective logging in temperate forests, may negatively impact mycorrhizal fungi, but this response depend on the percentage of trees retained (Hewitt et al. 2018). These authors demonstrated that richness and colonization of mycorrhizal fungi was lower in logged forests that retained 20 % of standing tree basal area (e.g., for seed trees or conservation purposes) than in unlogged patches of primary or secondary forest. However, other studies conducted in different types of biomes (e.g., tropical dry forest: Pereira et al. 2018, boreal forest: Varenius et al. 2016 and tropical forest: da Silva et al. 2020) have shown that logging operations (e.g., selective logging, clear cutting) have neutral effects on fungal diversity when compared with unlogged forest. Plausible mechanisms that could explain these results could be attributed to the ability of different spores of mycorrhizal fungi to persist in the soil or to re-establish from colonization of the surrounding forest after forest management (Jones et al. 2003, Sterkenburg et al. 2019, Policelli et al. 2020).

Regarding the effects of logging on soil bacteria, all studies showed that bacterial biomass or diversity may be negatively affected by forest management (Fig. 5). These studies have evaluated different logging operations (Purahong et al. 2015, Song et al. 2015, Chen et al. 2021), different re-entries of logging (Li et al. 2020), and time since logging intervention (Jin et al. 2019) in tropical, subtropical and temperate forests. These responses may be a consequence of changes in soil properties after logging operations. For example, in subtropical forests, the lower bacterial biomass in logged than in unlogged forests may be a consequence of lower soil N content, since bacteria may be limited by the amount of soil N (Song et al. 2015). Moreover, Li et al. (2020) showed that different re-entries of logging indirectly affected bacterial diversity through changes in stand density and soil properties (e.g., pH and soil moisture). In addition, there is evidence that bacterial responses to forest management may depend on the sampling season (Entry et al. 1986). Interestingly, in subtropical forests, Jin et al. (2019) found that bacterial diversity was lower in regenerated forests after 5, 10, and 25 years of selective logging as compared to unlogged forests, but did not change when comparing among regenerated forests.

3.3 Effects of forest management on soil fauna

Most studies (61 %) aimed to identify the effects of different logging operations on forests (e.g., clear-cutting, selective cutting) compared with unlogged forests, whereas 20 % addressed the effects of time since logging operations compared to unlogged forests, and only three (8 %) focused on the effects of re-entry cycles of logging compared with unlogged forests (Tab. 2). Most of these studies targeted a particular taxon (e.g., dung beetles, ants, 79 %), whereas other studies had a multi-taxon approach on macro- or mesofauna (21 %). Abundance of meso- and macrofauna was typically measured by calculating the number of individuals per unit and diversity was calculated using Shannon index or species richness.

Regarding soil mesofauna, only 8 % of the studies in our review focused on this group (Fig. 5). Springtails and mites are the most abundant soil mesofauna groups and play important roles as decomposers, scavengers, and predators in soil food webs (Potapov 2022a). Evidence suggests that in tropical forests, reduced impact logging, conventional logging operations (Hasegawa et al. 2014), and different re-entries of logging (Edwards et al. 2014) have neutral effects on springtail abundance and diversity compared with unlogged forests. However, in a temperate forest, clearcutting had a negative effect on mite abundance compared to unlogged forest (Lindo & Visser 2003). Even more interesting is the fact that these results found by Lindo & Vissser (2003) seem to depend on the type of forest. While in coniferous forests clear-cutting reduced abundance, in deciduous forests there were neutral effects, indicating that the latter could be rapidly recolonized by trees, herbs, and grasses vegetation allowing the recovery of the soil habitat for different organisms.

Considering the multi-taxon approach, 16 % of the studies on soil macrofauna focused on all macrofaunal communities or at least two groups. In tropical forests, they showed that soil macrofauna abundance decreased in logged forests compared to primary forests (Negrete-Yankelevich & Fragoso 2007, Martínez-Falcón et al. 2015) or did not change between logged and unlogged forests (Hasegawa et al. 2014). Interestingly, the negative effects of logging occur shortly after logging (i.e., 2 months; Negrete-Yankelevich & Fragoso 2007). Furthermore, Oliver et al. (2000) reported in temperate forests that coleopteran families and ant morphospecies richness did not change in logged forests.

Most studies that focused on a specific taxonomic group of macrofauna evaluated the effects of logging operations on Coleoptera (e.g., Scarabaeoidea and Carabidae) (45 %; Fig. 5). Coleoptera are the most diverse group of soil animals and are involved in multiple ecosystem functions. They play key roles in nutrient cycling, bioturbation, and secondary seed dispersal (Nichols et al. 2008). For example, dung beetles are typically used as indicators to evaluate and monitor the effects of habitat change on decomposition in tropical forests (Gardner et al. 2008). Carabids are usually used as bioindicators in

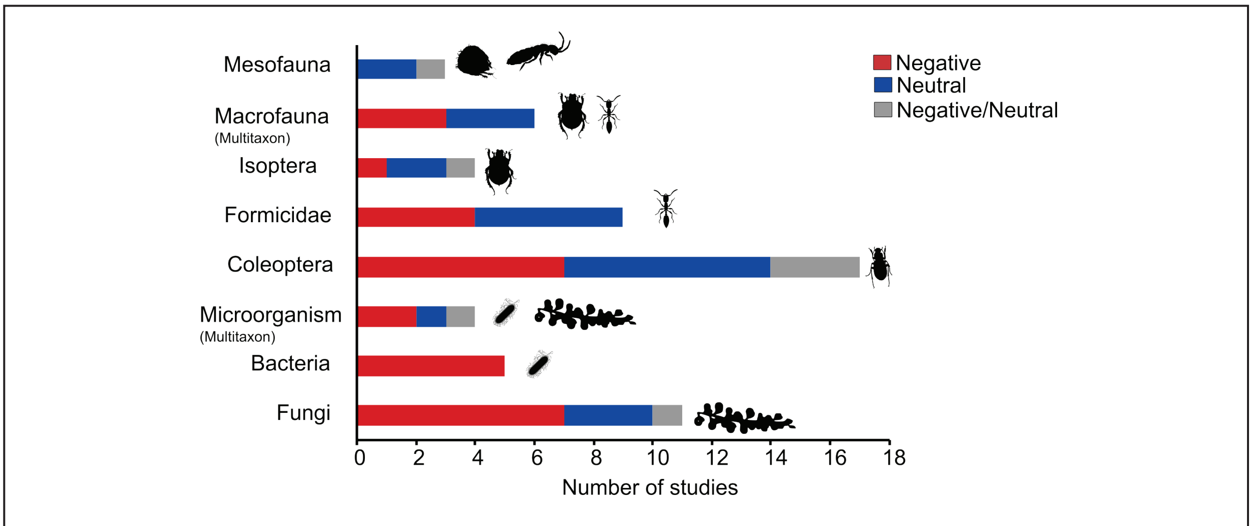

Figure 5. Number of reviewed studies showing positive, neutral, negative or neutral/negative effects of logging on soil organisms. Note that Microorganism (Multitaxon) refers to studies that do not distinguish between bacterial and fungal organisms.

temperate or boreal forests (Rainio & Niemela 2003), and are considered an important predator group in soil food webs. Logging operations are expected to affect dung beetles and carabids through different mechanisms. For example, dung beetles are mainly affected by environmental changes, such as increased canopy openness, soil moisture and reduced litter depth (Hosaka et al. 2014). Furthermore, carabids are particularly affected by changes in forest structure, especially as they relate to their food resources, such as herbivorous insects (Lövei & Sunderland 1996). In addition, different traits such as highly specialized groups and those at higher trophic levels such as carabids should be more sensitive to forest management.

We found that 50 % of the studies reported changes in Coleoptera species composition among logging operations (e.g., selective logging, once-twice re-entries logged forests, temperate forest: Masís & Marquis 2009; tropical forest: Edwards et al. 2012, 2014; subtropical forest: Yu et al. 2017, Osawa et al. 2005), different logging intensities (tropical forest: França et al. 2017), and clearings for logging (e.g., skid trails, logging roads, log yards; subtropical forest: Hosaka et al. 2014). However, some studies that compared Coleoptera species composition among different type of forests under different logging operations found subtle changes (boreal forest: Atlegrim et al. 1997; temperate forest: Latty et al. 2006; tropical forest: Slade et al. 2011) or no changes (tropical forest: Davis 2000; Scheffler 2005).

Concerning the effects of forest management on the abundance and diversity of Coleoptera, almost 44 % of the reviewed articles showed negative effects, whereas 37 % showed neutral responses, and the remaining 18 % found both negative and neutral effects (Fig. 5). Negative effects were mainly observed in tropical forests. For example, studies that compared primary vs. logged forests showed that the diversity of dung beetles decreased in logged forests (Slade et al. 2011, Edwards et al. 2012, França et al. 2018). Forest canopy and micro-environmental changes in logged forests did not seem to be the major drivers of this pattern. In addition, subtle changes in micro-environmental variables may be observed in low-intensity managed forests compared with unlogged forests. Interestingly, when comparing the gradient of logging intensity in tropical forests, França et al. (2017) showed that dung beetle diversity decreased with increasing logging intensity up to a threshold of 18–20 m^3 ha^{-1}, above which there was no clear additional response. Furthermore, selective logging produce forest clearings when drastic changes in vegetation occurs as a consequence of logging equipment on skid trails, roads, and log yards. There is evidence that in tropical forests, abundance and diversity of beetles decrease drastically in these clearings (Hosaka et al. 2014, Yamada et al. 2014). Interestingly, and contrary with to the results found by França et al. (2018) with in selective logged forests, when drastic changes in vegetation occurs as a consequence of logging equipment, canopy openness is the most important environmental factor affecting dung beetle assemblages. Finally, in a wide range of ecosystem types (e.g. tropical, subtropical, temperate and boreal forests) abundance and diversity of Coleoptera were found to be similar in intact forests and selectively logged forests (carabids: Atlegrim et al. 1997, Moore et al. 2004, dung beetles: Scheffler 2005, Slade et al. 2011; ground-dwelling beetles: Yu et al. 2017). The authors attributed these results to some characteristics of the managed forests. For example, in most cases, logged forests are surrounded by a matrix of intact forest, which permits the recolonization of individuals. In addition, there is evidence that a few years after selective logging (< 10 years), habitat conditions for dung beetles could be similar to those of unlogged forests (Scheffler et al. 2005). Moreover, Yu et al. (2017) highlight the importance of considering feeding habitat when studying the effects of logging on Coleoptera. These authors found that while the total abundance of ground-dwelling beetles did not change in logged compared to unlogged forests, the abundance of saproxylic beetles was lower in selectively logged forests and frugivorous species showed the opposite pattern. These results show that the responses of different functional groups to silvicultural practices may be masked if feeding habitats are not considered in the studies.

Formicidae is another macrofaunal group usually studied in the context of logging operations (25 %; Fig. 5). It has been estimated that their biomass represents up to 20–50 % of the total arthropod biomass in tropical forests (Dial et al. 2006). Ants are present in almost all functional groups, including predators, scavengers, herbivores, and granivores (Potapov et al. 2022a). Therefore, the negative effects of logging operations on this insect group could affect both above- and belowground ecosystem processes. In our review, almost 62 % of the studies reported changes in ant species composition due to different logging operations (e.g., selective logging, once-twice-logged forest: Kalif et al. 2001, Gunawardene et al. 2010, Edwards et al. 2014, Miranda et al. 2017). However, no changes in ant species composition were reported in some studies that compared different logging operations (Vasconcelos et al. 2000, Woodcock et al. 2011) or forests selectively logged recently vs forests that have been historically logged (Ross et al. 2018). Regarding the effects of forest management on ant abundance and diversity, 50 % of the articles showed negative effects, whereas the remaining 50 % found neutral effects (Fig. 5). Negative effects were observed in tropical and temperate forests under recent selective logging (Ross et al. 2018) or twice-logged forests (Woodcock et al. 2011). Furthermore, in tropical forests, low-intensity management has been shown to minimize the negative impact of logging on ant communities (Vasconcelos et al. 2000, Miranda et al. 2017). It has been suggested that ant communities need at least 8 years to recover from changes induced by logging (Gómez & Abril 2011).

In addition, about 11 % of the studies on soil fauna focus on Isoptera (e.g., termites). Termites are highly abundant in tropical and subtropical forests and play a key role in the decomposition of plant organic matter (Potapov et al. 2022a). Regarding the effects of forest management on termite abundance or diversity, the articles showed negative (25 %), neutral (50 %), or both responses (50 %) (Fig. 5). The evidence provided in those studies suggests that this insect group is minimally affected by the time spanned between the last forest management intervention and termite sampling (Eggleton et al. 1999, Azevedo et al. 2021) or by the period when the forest was under selective logging management (Bourguignon et al. 2018). Finally, it is important to note that there is some evidence that logging affects some feeding guilds of termites more than others. For example, the abundance of soil-feeding termites was negatively affected by logging operations compared to unlogged forest (Eggleton et al. 1999, Jones et al. 2003).

Articles focusing on the effects of silvicultural practices on soil fauna show a strong limitation in terms of the taxonomic groups of soil fauna evaluated. In most cases, the studies included in our review focused mainly on Formicidae and Coleoptera (76 %) and only three studies focused on mesofauna (e.g., Acari and Collembola) and none on microfauna (e.g., Nematoda). In turn, soil fauna represents a highly diverse group of organisms that play key roles in multiple ecosystem processes (e.g. nutrient cycling, decomposition, pest control, Soliveres et al. 2016). Therefore, knowledge of the functional traits of soil fauna is key to understand the impact of forest management on ecosystem functioning (Vandewalle et al. 2010). However, the use of feeding groups appears in only 20 % of the studies. In summary, these studies highlight that, at least for beetles (Yu et al. 2017), carabids (Osawa et al. 2005), ants (Gomez & Abril 2011) and termites (Eggleton et al. 1999, Jones et al. 2003) feeding guilds can be more informative than general assemblages.

In terms of the effect of logging operations, the articles analyzed showed that soil fauna had both negative and neutral responses to forest operations, and this trend was observed for the three main ecosystems where 92 % of the studies were conducted. Interestingly, no positive responses were reported. Selective logging was the most studied silvicultural practice, with neutral responses dominating, suggesting that this practice may not imply profound changes in the habitat characteristics for soil fauna. There is evidence that at least for insects, forests that have been logged for less than 10 years are likely to have habitat conditions similar to those of unlogged forests (Scheffler et al. 2005). In addition, the landscape configuration and composition may be an important factor modulating the effects of logging operations on soil fauna. For example, there is evidence that logged forest surrounded by intact forest allows recolonization of individuals (Scheffler et al. 2005). It is important to note that these results are likely to be masked by differential responses of feeding guilds to forest management, as suggested by the results of Yu et al. (2017). These authors showed that when the abundance of beetles is pooled together, abundance does not change with logging, but by analyzing for feeding guilds saproxylic beetles decreased under logged forest. The inability to detect a significant difference in these field experiments can also arise from a combination of low sample size and small or moderate effect sizes.

Finally, this review shows that we do not have many of the pieces of the puzzle needed to provide robust evidence on the effects of forest management on soil fauna. Some soil macrofauna taxa are missing from the literature, and the lack of representation of meso- and microfauna groups may reflect the lack of scientific expertise in these soil faunal groups, particularly in underrepresented regions (Guerra et al. 2020). To fill this knowledge gap, as soil ecologists, we first need to improve local and global scientific networks to share research facilities and taxonomic expertise. Soil Biodiversity Observation Network (Soil BON) is an ongoing global initiative that offers standardized sampling protocols for microorganisms and micro-, meso- and macrofauna (Guerra et al. 2020, Potapov et al. 2022b). Second, future studies on this topic should focus on trait-based approaches, which have been pivotal in understanding changes in biota in managed forests and the consequent effects on ecosystem functioning (de Bello et al. 2010). Trait-based approaches are in their infancy in soil ecology; their future implementation will increase our knowledge and reduce the uncertainty of the effects of forest management on soil fauna. For example, in a meta-analysis, Mc Cary & Schmitz (2021) showed that traits of invertebrate communities that can be easily measured (e.g., size and feeding habitat) are useful for detecting the impact of land use change and have an effect on ecosystem functioning. Moreover, we found that the distribution of studies worldwide is concentrated in certain biomes; i.e., 82 % of the studies were carried out in tropical forests.

In relation to this biome imbalance, it is also the biome where a higher proportion of forest area remain (45 %), followed by boreal and temperate forests (adding up to 43 % of the world forest area, FAO 2020).

3.4 Effects of logging on soil functions

Most studies (65 %) dealing with the effects of logging on soil functions addressed the effects of different logging operations (e.g., clear-cutting and selective logging), followed by 15 % of studies that explored the effects of logging intensities compared to unlogged forest (Tab. 2). Concerning the effects of forest logging on soil functions associated with soil organisms, 14 % of the articles evaluated the role of soil fauna (e.g., presence, abundance, and activity) in decomposition or the role of microorganisms in C and N cycling. Moreover, two studies evaluated the effects of belowground diversity on multiple ecosystem functions in different forest management systems (Jin et al. 2019, Huang et al. 2020).

Few articles have evaluated the biomass of understory vegetation (e.g., leaf litter, wood, and root biomass, 17 %; Fig. 6). In forests, carbon stocks are stored in five pools: aboveground biomass, leaf litter, dead wood, roots, and soil organic carbon (IPCC 2003). Carbon stocks can play an important role in climate regulation (Chapin 2002). It has been estimated that tropical forests harbor 45 % of terrestrial carbon stocks (Bonan 2008), and that forest management is a key factor influencing carbon sequestration. The studies included in this review have shown that logging operations may have neutral (Ibrahima et al. 2010, Almeida et al. 2015) or negative effects on litter or root biomass (Lindo & Visser 2003). In addition, two articles reported an increase in deadwood stocks in logged forests compared with undisturbed forests (Keller et al. 2004, Carlson et al. 2017; Fig. 6). Soil C stocks were evaluated in 20 % of the papers (Fig. 6). In general, 33 % of the studies on C stocks reported negative effects on logged forests with respect to unlogged forests (i.e., Christophel et al. 2013) or on forests subjected to low-intensity logging operations (i.e., Rozak et al. 2018). Furthermore, almost another 33 % showed neutral effects on C stocks (Panichini et al. 2017, Bomfim et al. 2020), and a similar proportion found negative/positive responses to logging operations (Alice-Guier et al. 2020, Huang et al. 2020). These different responses may be due to the lower changes in C stocks in managed forests than in unlogged forests. For example, Panichini et al. (2017) showed that forests at different times since the last selective logging entry (e.g., 10 and 50 years) exhibited less than 10 % change in the level of soil C, which is not sufficient to cause significant differences. Interestingly, Huang et al. (2020) showed that C stocks increased or decreased, depending on the number of times (from 1 to 5) the forest was logged.

Decomposition processes (e.g., decomposition of leaf litter, wood, and dung) were the most widely studied ecosystem processes (31 %). These processes are the main source of soil organic matter and nutrients required for plant growth (Wardle et al. 2002). Studies on decomposition reported negative, neutral and positive effects (approximately 44 %, 33 % and 22 %, respectively) of logging (Fig. 6). For example, litter decomposition was found to decrease in logged forests (Pérez et al. 2009, Yeong et al. 2016, Both et al. 2017), mainly because of changes in forest structure. Regarding the articles that evaluated the role of soil fauna in decomposition process, Both et al. (2017) showed that, while the inclusion of mesofauna in litterbags increased

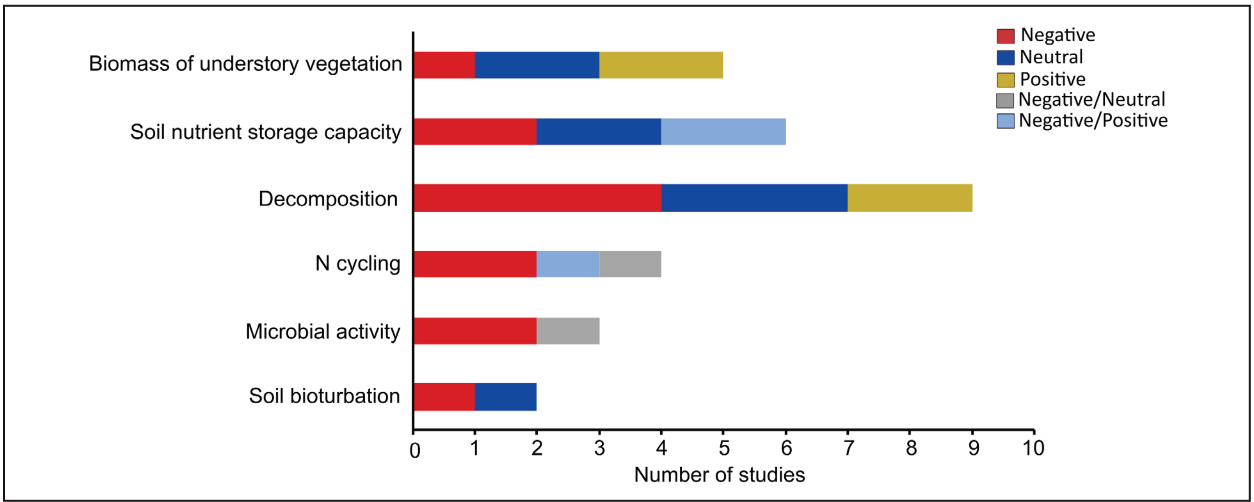

Figure 6. Number of reviewed studies showing positive, neutral, negative, neutral/negative or negative/positive effects of logging on soil functions.

leaf litter decomposition, the effect was independent of logging operations. However, there is evidence that a diverse litter fauna community increases decomposition in unmanaged forests in comparison with logged forests (at least in the first 120 days of incubation; Martinez-Falcon et al. 2015). Nevertheless, logging intensity did not affect leaf litter decomposition, and macrofauna had neutral effects on this process (Schleuning et al. 2011). Furthermore, there is evidence that wood decomposition increases in logged forests as a consequence of higher soil temperatures than in unlogged forests (Finér et al. 2016). Contrary to the number of studies evaluating dung beetles, only two studies have focused on dung decomposition. In tropical forests, dung decomposition decreases with canopy openings resulting from logging road networks, as shown by the pattern observed in the abundance of dung beetles (Hosaka et al. 2014). However, neutral responses have been observed in logged forests, supporting the hypothesis that low-intensity selective logging can retain some ecosystem processes (França et al. 2018).

Almost 14 % of the studies evaluated N cycling; half of them found negative responses, whereas the other half found both negative and positive responses (Fig. 6). This ecosystem function contributes to the conversion of N to a usable form for plants (Zhu et al. 2015). For example, Pérez et al. (2009) found that forests subjected to conventional selective logging had lower N mineralization rates than unlogged forests. Furthermore, there is evidence that damage during conventional selective logging increases N turnover (Feldpausch et al. 2009). In addition, only 11 % of the articles evaluated microbial activities in the context of logging operations. Microbial activity is a potential indicator of the microbial function (Schotler et al. 2018). On the one hand, Barreto-Garcia et al. (2021) showed that logging negatively influenced the activity and C transformation of the soil microbial biomass. On the other hand, there is evidence that logged and unlogged forests have similar respiration rates (Liu et al. 2006) or that increasing the chronosequence of logging affects enzymatic activities, but the pattern depends on the metabolites studied (Jin et al. 2019).

Finally, approximately 8 % of the articles evaluated the effects of dung beetles on soil bioturbation (Fig. 6). Interestingly, the pattern found depended on the methods used for data analysis. For example, soil bioturbation decreases with logging intensity (França et al. 2017). However, a neutral relationship was observed when pre- and post-logging operations were compared (França et al. 2018).

4. Conclusions

In this article, we present evidence that soil ecologists have addressed the effects of forest logging on soil organisms and, to a lesser extent, on ecosystem functions, with a clear increment in the last two decades. The studies addressed different silvicultural practices (e.g., clear-cutting, selective logging), logging intensities, re-entry cycles of logging and logging equipment (e.g., skid trails, logging roads). In general, the effects of logging on the abundance and diversity of soil organisms was found to be negative or neutral, with no reports of positive effects. It is noteworthy that this negative effects of logging have been observed across a range of intensity levels, from clear-cutting to selective logging and variable retention. The pattern from negative to neutral responses was also observed for soil ecosystem functions, with only 10 % of the papers reporting positive effects. These patterns may reflect the heterogeneity of logging operations and re-entry cycles.

Further studies should be conducted to propose silvicultural practices that minimize negative effects on soil organisms and functions. For example, in our review, we found that low-intensity logging (5 m^3 ha^{-1}) minimizes the negative impact of logging on soil fauna and ecosystem functions. However, the scientific evidence on this topic is limited in comparison to studies on aboveground organisms (Duguid & Ashton 2013, Basile et al. 2019). More scientific effort is needed to determine the effects of different logging operations on soil organisms and functions that are underrepresented in the literature (e.g., nematodes, springtails, mites, earthworms, bioturbation). The study of the effects of silvicultural practices on soil biota and ecosystem functions is an emerging research topic. To preserve multifunctional forests and ensure the provision of multiple ecosystem services, such as lumber provision, climate regulation, and soil fertility, future research should focus on identifying the direct and indirect effects of forest management on soil multifunctionality. For this purpose, it is essential to integrate soil biota in studies on biodiversity–ecosystem functioning relationships.

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