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The effect of alternative agricultural practices on soil biodiversity of bacteria, fungi, nematodes and earthworms: A review

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ABSTRACT

Life in soil is a key driver of important ecosystem processes, such as the recycling of carbon and nutrients. In current intensive agricultural soils, however, richness and abundance of many groups of soil organisms are often reduced, which may threaten soil health and sustainable agriculture in the long run. Therefore, a switch to alternative agricultural practices (e.g., minimal tillage) that are less detrimental or even stimulate soil life has been suggested as a way to increase sustainable food production. Although we understand how some of these practices impact specific species or functional groups in soils, it is necessary to get a more complete overview to understand which practices can be used in agriculture to improve soil biodiversity. Here, we present a systematic literature review identifying which practices are studied as alternatives to current, intensive practices for four soil taxonomic groups encompassing a range of trophic groups and functions in the soil ecosystem: nematodes, earthworms, bacteria and fungi. Further, we review how these alternative practices impact the abundance and diversity of these four taxonomic groups, as well as for the 14 functional groups identified and retrieved from the review. We found that a total of 23 alternative agricultural practices, grouped into 10 groups of practices, were studied for the four target taxonomic groups. Three groups of practices, 'fertilization', 'soil cover' and 'tillage' were studied for all taxa. In general, alternative agricultural practices had positive impacts on the species richness in the four taxonomic groups and on the abundance of organisms in the functional groups. However, there were some exceptions. For example, organic fertilizers reduced the abundance of epigeic earthworms, while enhancing the abundance of endogeic and anecic earthworms. There was only one alternative practice, i.e., the use of cover crops, that was neutral to positive for the abundance of all functional groups across all taxa. Our review revealed that there are gaps in the literature, as practices that are commonly studied for aboveground biodiversity, such as field margins or flower strips, are not studied well across taxonomic and functional groups and need to be further studied to improve our understanding of the impact of alternative practices on soil life. We conclude that alternative agricultural practices are promising to enhance soil biodiversity. However, as some practices have specific impacts on taxonomic groups in the soil, we may require careful application and combinations of alternative agricultural practices to stimulate multiple groups.

1. Introduction

Most species on the planet are known to live in the soil (Anthony et al., 2023). In both natural and agricultural ecosystems, this soil life is driving key ecosystem processes (Nielsen et al., 2015; Wall et al., 2015; Bender et al., 2016) such as carbon and nutrient cycling (Nielsen et al., 2011; de Graaff et al., 2015), carbon storage (Hartmann and Six, 2023) and disease suppression (Brussaard et al., 2007), which are essential for supporting biodiversity below- and aboveground (Lehmann et al., 2020). Hence, soil biodiversity is a crucial aspect of ecosystems and their

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functioning (Jones et al., 2001; Delgado-Baquerizo et al., 2020) and is underlying sustainable food production in agroecosystems (Rillig et al., 2018, 2023; El Mujtar et al., 2019). Intensive agriculture, however, has strongly reduced soil biodiversity (De Vries et al., 2013; Tsiafouli et al., 2015; Plaas et al., 2019, Bender et al., 2023), via soil carbon depletion, mechanical soil disturbances, addition of mineral fertilizers, and vegetation changes (Zhang et al., 2007; Campbell et al., 2017). This has resulted in reduced soil functioning (Papendick and Parr, 1992). There is a growing awareness that we need to protect and even regenerate soil biodiversity in agricultural soils in order to maintain sustainable agricultural production in the future (Lal, 2008; Schreefel et al., 2020; FAO, 2020; Hartmann and Six, 2023).

To enhance soil biodiversity in agricultural systems, a shift towards alternative management practices that are less intensive is commonly seen as a potential part of the solution (Bengtsson et al., 2005, Chen et al., 2020; Morugán-Coronado et al., 2020). Such management practices generally imply a reduction in soil disturbances, both chemically and mechanically, as well as diversification of crop rotations and field margins and the use of organic instead of mineral fertilizer (Papendick and Parr, 1992; Tsiafouli et al., 2015; Chen et al., 2020). Using such agricultural practices, referred to as alternative practices in our review, might be a promising way forward to protect and enhance soil biodiversity (Tsiafouli et al., 2015; Beckmann et al., 2019; Cozim-Melges et al., 2024). For instance, the application of organic fertilizers has been shown to enhance the abundance of earthworms, bacteria and fungi (Bengtsson et al., 2005; Briones and Schmidt, 2017; Cozim-Melges et al., 2024), which in turn may also favor natural disease suppression (Clocchiatti et al., 2020). Also, a reduction in tillage depth or frequency can favor earthworms and fungi (Briones and Schmidt, 2017; Chen et al., 2020). Finally, the use of wider crop rotations, or the inclusion of cover crops into the rotation, are known to also enhance earthworms and fungi (Bengtsson et al., 2005; Briones and Schmidt, 2017) and favor disease suppression (Peralta et al., 2018). These examples show that we have some understanding of the impact of alternative practices on soil communities. Yet, most previous studies focused on the impact of specific practices, and/or on specific taxonomic groups (De Graaff et al., 2019; Chen et al., 2020; Morugán-Coronado et al., 2020) or on farming systems as a whole (van Rijssel et al., 2022). Therefore, we still lack an overview of which practices are studied, and how those different practices impact soil biodiversity.

The impact of agricultural practices on soil biodiversity may differ between species and taxonomic groups (Brussaard et al., 2007; Thiele-Bruhn et al., 2012; De Graaff et al., 2019; Houšková et al., 2021) and between functional groups (Wang et al., 2019; Geisen et al., 2019). Functional groups may play specific roles in ecosystem functioning. For example, losses in the abundance of certain saprophytic fungi may result in a lower capacity of soil communities to degrade recalcitrant organic inputs (Šnajdr et al., 2011; Li et al., 2022a; van der Wal et al., 2013) and can harm disease suppression (Clocchiatti et al., 2020). In contrast, a higher abundance of pathogenic fungi, more commonly found in croplands (Labouyrie et al., 2023), may lead to plant diseases and reductions in yield (Ellingboe, 1980). Likewise, practices that enhance the biodiversity or abundance of nematodes, might be positive if they enhance omnivorous or predator nematodes, which would help with predation of potential pests (Van der Putten et al., 2006; Steel and Ferris, 2016), while an increase in herbivorous nematodes could reduce crop yields (Putten et al., 2006; Khan & Kim, 2007). As a result, how alternative practices impact the abundance of certain functional groups can have important functional consequences for agroecosystems (Fitter et al., 2005; Crowther et al., 2019; Delgado-Baquerizo et al., 2020; Li et al., 2022b). Therefore, to understand the impacts of alternative practices on soil communities, it is key to look beyond impacts on the total number of species present in soils, and also focus on impacts on the abundance of functional groups. Soil biodiversity comprises a wide and complex net of taxa, making it difficult to encompass them all in a study or review. Nevertheless, some of these groups are known to be well studied and with a potentially higher abundance of literature. Obtaining a comprehensive overview of how agricultural practices affect both taxonomic diversity (e.g., species richness) of some of the key and broader groups in the soil food web, i.e., earthworms, nematodes, bacteria and fungi (Pulleman et al., 2012; Bardgett & Van der Putten, 2014, Anthony et al., 2023; Fonte et al., 2023), as well as the abundance of their functional groups is essential to sustainable agriculture.

The aim of this literature review is to explore (i) what alternative agricultural practices have been studied so far to assess impacts of agriculture on soil biodiversity, specifically on the taxonomic groups of earthworms, nematodes, bacteria and fungi; and (ii) what is the impact of these agricultural practices on the richness of these taxonomic groups, as well as on the abundance of their functional groups. With this review we will be able to understand how well studied the taxonomic and their retrieved functional groups are. In addition, we will provide an overview of how the agricultural practices studied in the literature impact the diversity and abundance of the taxonomic and functional groups, respectively. Together, this review will shed light on the potential gaps in our knowledge and will allow us to start understanding which alternative practices can be used to enhance soil biodiversity in agroecosystems.

2. Methods

2.1. Literature review

We performed a systematic literature review using SCOPUS and Web of Science. This study was performed as a follow up from a previous literature review (see Cozim-Melges et al., 2024). The search queries were last run on the 12th of February, 2022. The search query used was formulated to retrieve studies that tested the impact of alternative practices on soil biodiversity in arable land and production grasslands, and this literature review focussed on retrieving data on soil taxa and their functional groups studied in the literature. We used separate search queries for the four taxonomic groups (Table 1). Each search query started with the broad terms of “agricultural” and/or “grazing” (and derived terms) together with “practices”, to capture all potential alternative practices studied both in arable land and in grasslands. Then, these terms were followed by the name of the taxonomic groups targeted, i.e. bacteria, fungi, nematodes, and earthworms. Finally, the search term was ending with the two biodiversity indicators used in our review, i.e. richness or abundance (Table 1.). The four taxa targeted were chosen, because they cover multiple trophic levels in the soil food

Table 1
Search queries and search engines used in the literature review.

Taxa	SCOPUS	Web Of Knowledge (all databases)
Nematodes	TITLE-ABS-KEY (((agric* AND graz*) OR agric* OR graz*) AND practice AND soil AND nematod* AND (richness OR abundance))	You searched for: TOPIC: (((agric* AND graz*) OR agric* OR graz*) AND practice AND soil AND nematod* AND (richness OR abundance))
Earthworms	TITLE-ABS-KEY (((agric* AND graz*) OR agric* OR graz*) AND practice AND soil AND earthworm AND (richness OR abundance))	You searched for: TOPIC: (((agric* AND graz*) OR agric* OR graz*) AND practice AND soil AND earthworm AND (richness OR abundance))
Bacteria	TITLE-ABS-KEY (((agric* AND graz*) OR agric* OR graz*) AND practice AND soil AND bacteri* AND fung* AND ratio AND biomass)	You searched for: TOPIC: (((agric* AND graz*) OR agric* OR graz*) AND practice AND soil AND bacteri* AND fung* AND ratio AND biomass)
Fungi	TITLE-ABS-KEY (((agric* AND graz*) OR agric* OR graz*) AND practice AND soil AND bacteri* AND fung* AND ratio AND biomass)	You searched for: TOPIC: (((agric* AND graz*) OR agric* OR graz*) AND practice AND soil AND bacteri* AND fung* AND ratio AND biomass)

web (Yeates et al., 1993; Neher, 2001; Veen et al., 2010; Lu et al., 2020), are known to play key roles in the functioning of agricultural soils and are often used as reference groups for soil health in agro-ecosystems (Pulleman et al., 2012).

Studies were selected based on inclusion and exclusion criteria (Fig. 1). For each study we recorded the location of the study (latitude, longitude), the scale of the study (field, farm), the practices studied (i.e., type of reference and type of alternative practice; taxonomic and functional groups considered (the latter only when available); class of indicator used for measurement (categorized as i. richness, when measuring number of species; ii. abundance -count or biomass-; or iii. compound, i.e., an indicator that is based on combining a ratio of both richness and abundance, e.g. Shannon); and finally, the impact of the alternative practice on biodiversity recorded as positive or negative, when significant results were observed in either direction, or as "no observed effect" when no significant effects were found. Functional groups of the taxa were not determined a-priori, but resulted from the studies that were retrieved. The full list of studies selected can be found in supplementary material A.

2.2. Mapping of practices and analysis

The data was organized in single data records, where every impact of a given retrieved practice on a given group corresponded to a single data record. Alternative agricultural practices were retrieved from the literature into common definitions either based on their nature and/or intensity. Since agricultural practices were retrieved from the papers reviewed (rather than predefined), these are reported in the results section. A study could have multiple data records on the effect of practices, i.e., multiple practices for a given group, multiple groups for a given practice, or both, as well as a practice could be tested by multiple intensity levels, despite grouped in a same practices (e.g. varying fertilization rates of organic fertilizer). The software R (v. 4.0.3 - R Core Team, 2023) was used for organizing and analyzing data. First, we identified the practices, functional groups and type of indicators used in the literature. Afterward, we counted the total records for each combination of alternative agricultural practices-taxonomic/functional group and the respective indicators used. Then we analyzed the impacts of practices on soil biodiversity, focusing on data records using richness indicators for taxonomic groups, and abundance or biomass indicators for functional groups. This was done to avoid the use of compound indicators, such as Shannon, and standardize the biodiversity aspect assessed by taxonomic and functional groups. We focus on (1) richness for taxonomic groups to represent the quantification of proper diversity of species and because this a commonly used biodiversity measure across taxonomic groups and the idea is often that higher species richness improves stability of systems (Ives et al., 2000, Fischer et al., 2016). For functional groups (2) we focus on abundance, the majorly and almost exclusively used metric in studies, because it can tell us something about the quantitative changes in the soil community and potential impacts on functions and quantify changes in the presence of specific functional characteristics in the system, better representing potential changes in function than richness would.

For each data record we then noted down/scored whether the impact of the alternative on the richness of the taxonomic and the abundance of the functional groups was positive, negative or whether there was no effect observed. The data was used to calculate the percentage of data records that were positive, negative or had no impact per taxonomic and functional group for each alternative practice. In our literature review, practices were considered to have a positive influence more than 50 % of the data records reported a positive impact or if the sum of positive and 'no observed effects' was higher than 50 %. When the highest proportion of data records was positive, but not over 50 %, and the second-highest negative, or vice-versa, we considered results to be inconsistent. We report the percentage of effects of practices across both taxonomic and functional groups, and hence cannot be used for quantification of impacts.

CRITERIA OF INCLUSION	CRITERIA OF EXCLUSION
(I1) English text and;	(E1) no methods in the study to calculate statistical significance or;
(I2) Published and peer-reviewed and;	(E2) Greenhouse or laboratory studies or;
(I3) with discriminated agricultural practices and;	(E3) no explicit methodology and a varying control object (e.g. crops, taxa, functional groups or;
(I4) with discriminated effects on the target taxonomic groups and;	(E4) no control group established for effects or relatable to our reference or;
(I5) on a scale ranging from farm to landscape and;	(E5) no discrimination between practices effects on taxonomic/functional groups
(I6) focussed on the biodiversity of ecosystems and;	
(I7) sampled date from real life agroecosystems	

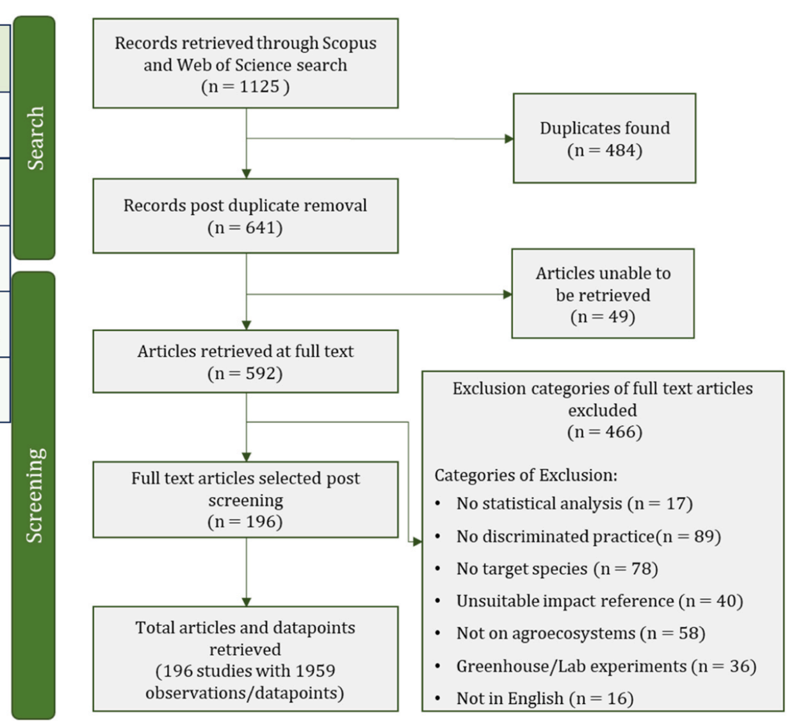

Fig. 1. Depiction of the criteria of inclusion and exclusion used to determine which studies were selected (left) and the diagram of the search and screening procedures as well as the studies in each part (right).

3. Results

3.1. Number of studies and observations

In our literature review we found 196 studies that met our selection criteria (supplementary material A). A total of 23 alternative agricultural practices have been studied. The alternative and intensive agricultural practices retrieved from the literature are categorized under common definitions (supplementary material B). In short, the practices studied were then further clustered into 10 groups based on the nature of their application and scope for comparison with their intensive counterpart: (1) enhancing crop diversity, both in space and time ("crop diversity"); (2) altering fertilization regimes and types ("fertilization"); (3) absence of grazing ("grazing"); (4) related to irrigation ("irrigation"); (5) absence of pesticide use to control pests ("no pesticide use"); (6) creating surrounding zones as habitat/foraging area for biodiversity ("planned biodiversity interferences"); (7) generating soil cover to protect the soil ("soil cover"); (8) less intensive or no tillage ("tillage"); (9) absence of GMOs ("no GMO"); and (10) a mix of diverse practices that do not fit with any particular category above ("miscellaneous").

In total, there were 1959 data records relating to the effect of alternative practices, which were distributed unevenly across the four taxonomic groups and their respective functional groups (Fig. 2, supplementary material C, D). We found most data records (Fig. 1) for nematodes (840 data records), followed by earthworms (453), bacteria (429), and lastly fungi (373). The four taxonomic groups represented could be subdivided into 14 functional groups. We combined nematodes that were classified as omnivores or predators into omnivores-predators, because some studies only reported this as one group. Algivorous nematodes were grouped with herbivores (Fig. 2, supplementary material D). Finally, when studies classified all free-living nematodes as one group, we did not include these into our data analyses on functional groups.

Overall, the most used metric to study soil biodiversity was abundance (or biomass for microbes) (1675 data records), followed by compound indicators that combine species richness and abundance metrics (e.g., Shannon diversity) (166) and species richness (118), with most richness data records found for taxonomic groups (Fig. 2; supplementary material D). Some studies use a combination of two or more indicators (42 studies, 21 %), but most studies only use one indicator to assess the impact of agricultural practices on taxonomic and/or functional groups (154 studies, 79 %). At the level of the taxonomic groups, abundance was the most used indicator, yet species richness and compound indicators were also used frequently, i.e. 72,1 %, 12,5 % and 15,4 % respectively. In contrast, for functional groups, abundance was used most frequently and the use of species richness or compound indicators was rare, i.e., 84.7 % abundance, 8,8 % compound and 6,3 % richness. For few functional groups, species richness or compound indicators were used, exclusively for herbivorous nematodes and those of earthworms.

3.2. Practices studied per taxonomic group

No single practice was studied for all taxonomic or functional groups (Fig. 3). We found that around 50 % of all possible combinations of alternative practices with functional groups was studied, i.e., just over half of the cells in Fig. 3 are filled. Fertilization, crop diversity, soil cover, tillage, no pesticide use and fertilization where the groups of practices most comprehensively studied, with fertilization covering over 83 % of the combinations between practices and taxonomic groups/ functional groups (Fig. 3). At the level of individual practices, 'zero tillage' and the 'use of solid manure/organic fertilizer' were the most studied practices. In addition, 'no fertilizer use', was also studied often. In contrast, the use of 'natural buffer areas', was the least studied practice for soil biodiversity and for some practices we only found studies assessing nematodes, such as the ones in the groups 'grazing',

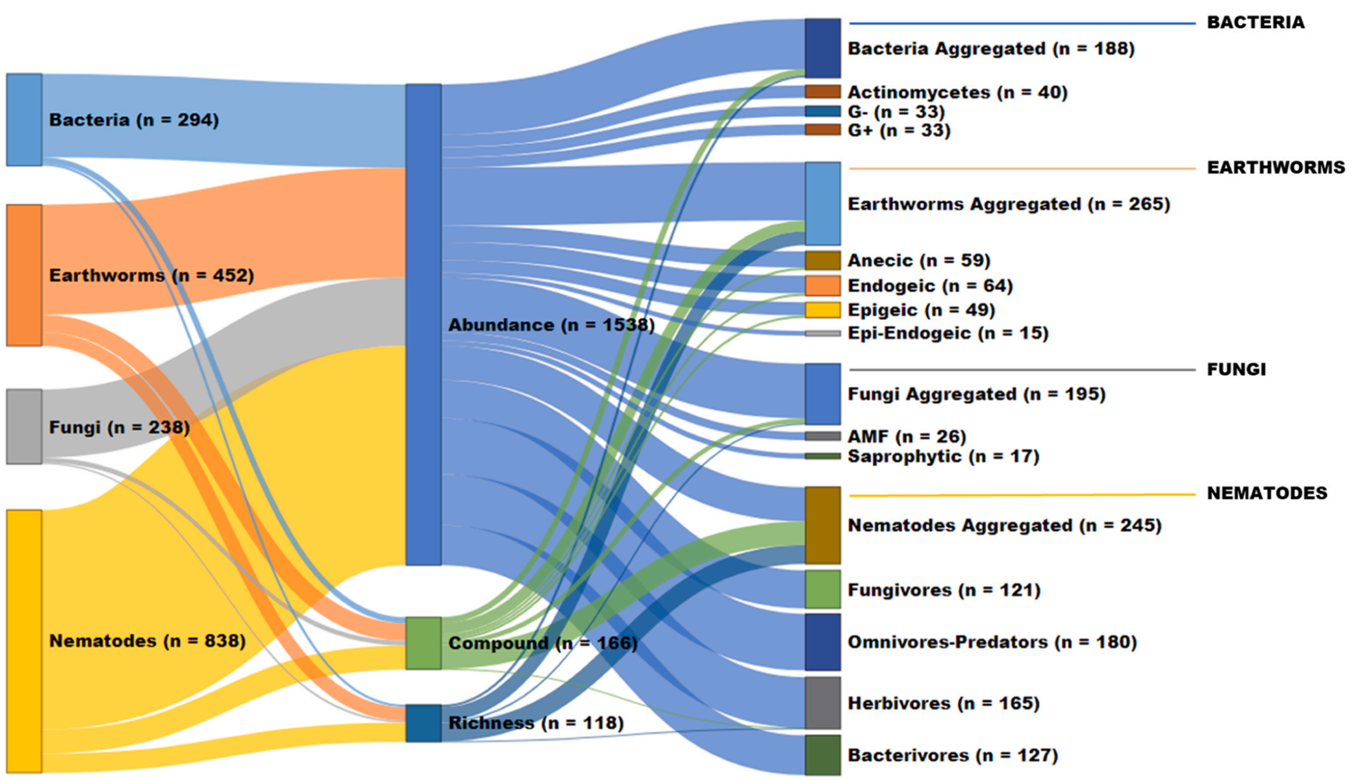

Fig. 2. Distribution of data records retrieved from the literature in terms of the taxonomic groups, the indicators found and the functional groups. AMF, G+ and G- refers to arbuscular mycorrhizal fungi, gram positive bacteria and gram negative bacteria respectively. The term "aggregated" means that the data records targeted the taxonomic group instead of a functional group.

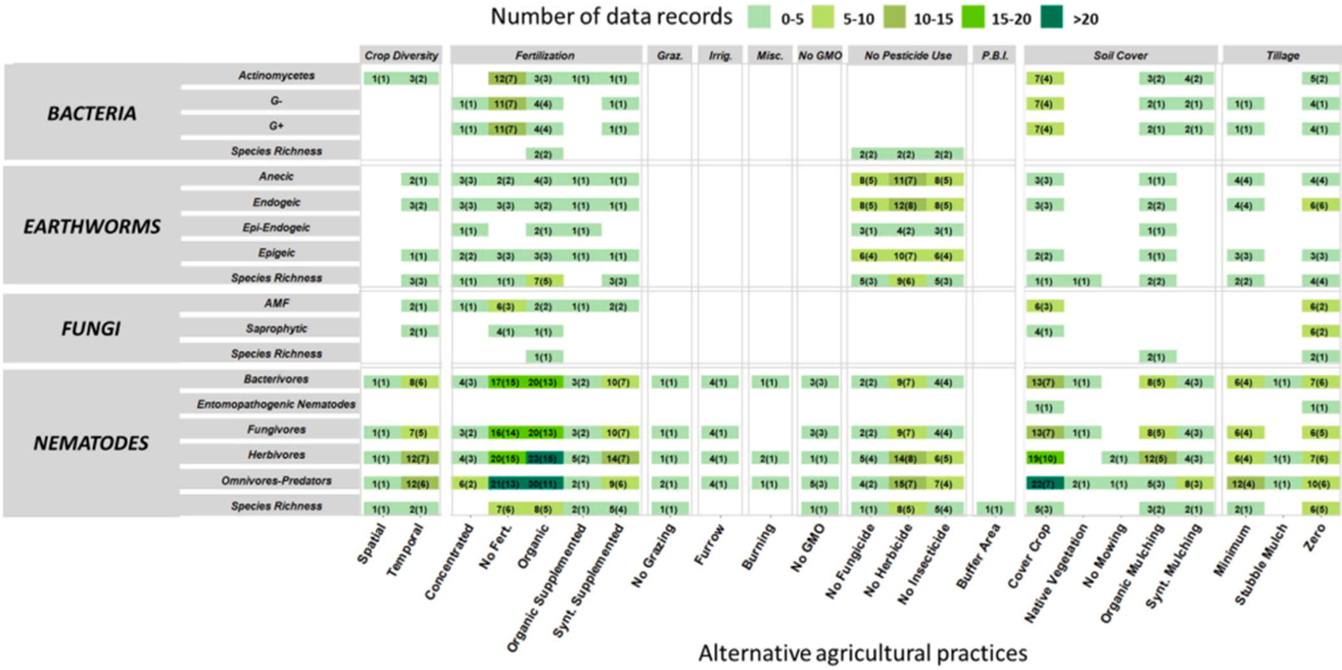

Fig. 3. Number of data records found for each alternative practice for all functional groups and taxonomic groups, represented as species compiled. The number of studies is displayed between parentheses. Colours range from blue (low records) to green (high records). Empty fields indicate no data records were found for that practice for that taxonomic groups/functional group. In the groups of practices, the terms Graz. refers to grazing, Irrig. refers to irrigation, Misc. refers to miscellaneous, and P.B.I. refers to planned biodiversity interferences.

'irrigation', 'no GMO', 'planned biodiversity interferences' and 'miscellaneous' (Fig. 3).

From the perspective of taxonomic groups, we found that nematodes were the most comprehensively studied group, where 18 out of the 23 practices were studied. Meantime, the impact of practices was least studied on bacteria (15 of the 23), particularly in terms of species richness of the taxonomic group (4 of the 23).

3.3. The impact of practices

For species richness of the taxonomic groups, we found that most practices either had a positive effect or no observed effect on species richness. There were however two instances where the impact of alternative practices on species richness was predominately negative for a taxonomic group: both organic matter mulching and inorganic fertilizer supplemented by organic fertilizer reduced species richness of earthworms (Fig. 4). For abundance of functional groups, most alternative practices (over 70 %) had a majorly positive impact (Fig. 4). For both taxonomic richness and abundance there were a large number of practices where the majority of records indicated "no effect observed". Nevertheless, there was considerable variation on which and how functional groups were affected across practices. For example, zero tillage enhanced abundance of most functional groups, and still reduced the abundance of fungivorous nematodes.

For some groups of practices, we found that individual alternative practices within that group had contrasting impacts on the taxonomic richness and/or abundance of functional groups. For example, within the group "soil cover" synthetic mulching enhanced nematode species richness and abundance of most functional groups, while organic matter mulching had no effect on any of the taxonomic or functional groups and even reduced species richness of earthworms (Fig. 4 & supplementary material G). Another example is the group of fertilization practices, where we found that practices with more easily accessible nitrogen such as 'concentrated organic', 'synthetic fertilizer supplemented' and 'supplemented with inorganic'. These practices had no effect on species richness and also variable (negative to positive) effects on the abundance of functional groups cancelling each other out. Meanwhile, the practice with more recalcitrant compounds, i.e. 'solid manure', generally enhanced taxonomic species richness and the abundance of most taxonomic groups, except for epigeic earthworms. Also, within the group of practices 'no pesticide use' alternative practices generally enhanced taxonomic species richness and abundance in functional groups, with the exception of 'no fungicide use' which had a negative effect on the abundance of omnivorous-predatory nematodes. Finally, as mentioned above, 'zero tillage' had overall majorly positive impacts on the species richness of all taxonomic groups, for which it was studied, and the abundance of functional groups, but only reduced the abundance of fungivore nematodes (Fig. 4). This suggests that "generic" nomenclatures of practices (e.g. fertilization, soil cover or no pesticide use) may not be accurate enough to effectively understand their impact on soil biodiversity.

4. Discussion

The overall aim of our literature review was to understand how well studied alternative practices are across the taxonomic groups of earthworms, nematodes, bacteria and fungi as well as their retrieved functional groups, and how these alternative practices impacted on both the diversity of taxonomic groups and the abundance of functional groups. Our literature review showed that not all practices are studied for all taxonomic groups and their respective functional groups, indicating gaps in our understanding. For example, even the most well studied group of practices, i.e., 'fertilization', was not studied for all functional groups. Furthermore, some practices that are known to have key impacts on aboveground biodiversity, e.g., 'pesticide use' and 'planned biodiversity interferences' (Bengtsson et al., 2005; Jones et al., 2021), were not studied extensively for microbes or for all taxonomic groups, respectively. All in all, we found that the alternative practices retrieved generally enhanced species richness of the taxonomic groups and abundance of the functional groups. However, the impact of practices was variable, ranging from negative to positive effects with a substantial number of observations showing 'no effect' and depended on the

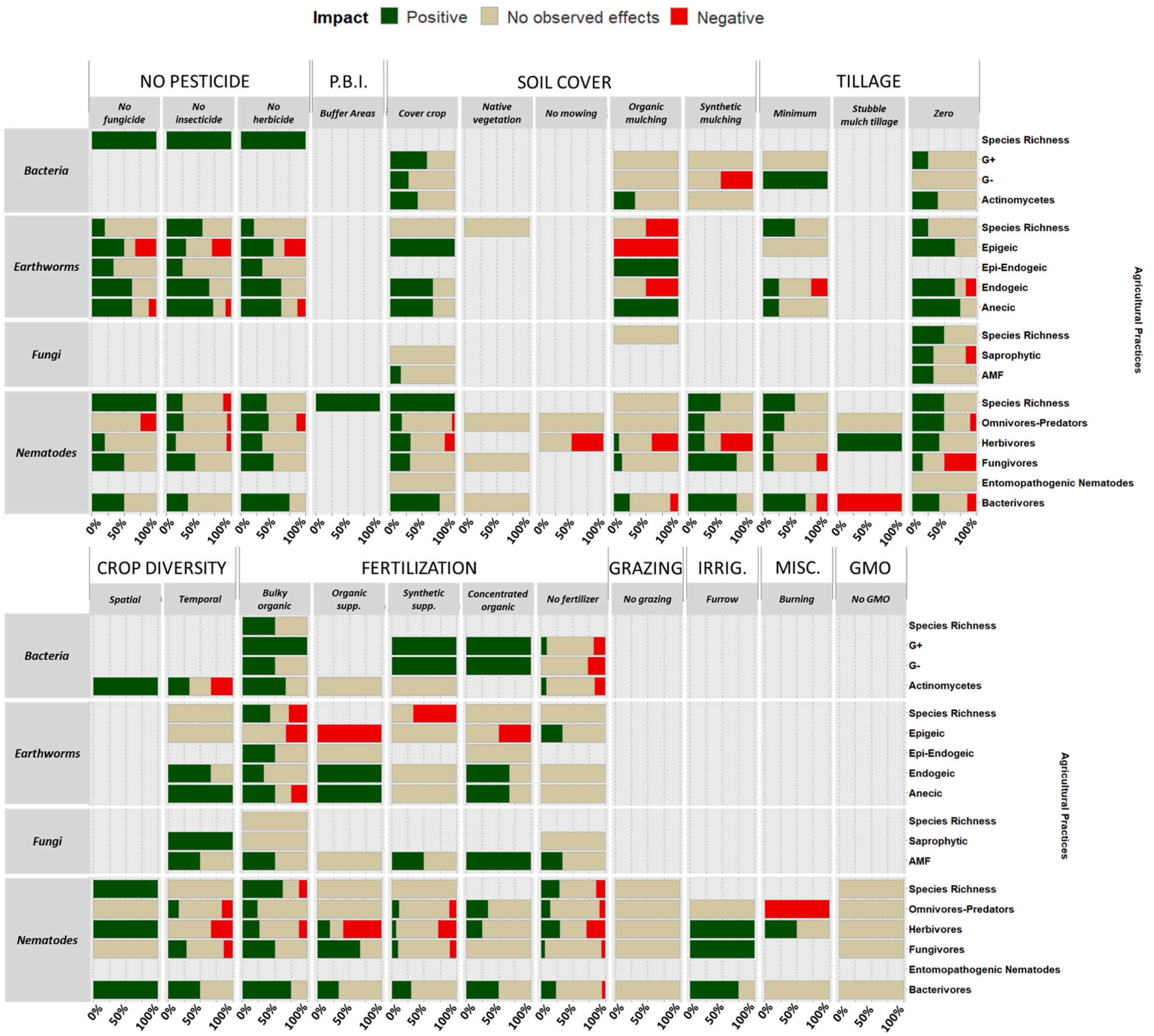

Fig. 4. Distribution of effects of the retrieved agricultural practices found in the studies on both species richness of taxonomic groups (first row for each taxonomic group) and abundance of their functional groups. Green bars represent the percentage of positive effects, red bars represent the percentage of negative effects and beige, no observed effects – effects are based on the comparison with conventional, intensive practices, found in supplementary material B. Supp. is an abbreviation for supplemented. 'P.B.I.', refers to Planned biodiversity interferences, 'IRRIG' to Irrigation, and 'MISC.' Miscellaneous, respectively. Practices definitions and the groups of practices can be found in supplementary material B.

taxonomic or functional group under consideration. In this section, we discuss our findings.

4.1. The practices studied for soil biodiversity

Overall, the most well studied practices were directly interfering with soil, be it chemical (i.e., 'fertilization') or mechanical (i.e., 'tillage' and 'soil cover'). Nevertheless, we found gaps across all taxonomic/functional groups, with alternative practices mostly being studied for specific taxonomic or functional groups. As a result, there was no single practice studied for all taxonomic or functional groups and some groups of the practices were hardly studied at all, i.e., grazing, irrigation and planned biodiversity interferences. Many of those practices are applied to affect biodiversity aboveground, such as vascular plants, (Elliott et al., 2023) or insects (Albrecht et al., 2010; Kleijn et al., 2019), and hence those practices might be understudied for soils (Van der Putten, 2001; Wardle and Van der Putten, 2002; Wardle et al., 2004). In addition, some practices are known or applied for their specific impacts on species or groups of soil organisms, which are then targeted in the research. For example, we know that tillage practices affect the structure of soils and can directly break fungal hyphae or impact earthworms (Jansa et al., 2003; Kabir, 2005; Peigne et al., 2009; Briones and Schmidt, 2017). However, it will be important to fill these gaps to understand the full impact of alternative practices. For example, the use of natural buffer areas or reductions in pesticide use, often targeting restoration of aboveground biodiversity (Bengtsson et al., 2005; Geiger et al., 2010; Cozim-Melges et al., 2024), may also influence soil communities directly or indirectly via plant-soil interactions (Van der Putten, 2001; Wardle and Van der Putten, 2002; Wardle et al., 2004; Kumar et al., 2021).

Concomitant to our findings on alternative practices, we also found that some taxonomic groups received more attention in the literature than others. We retrieved most studies for nematodes and least for bacteria and fungi. That nematodes were the most studied group is not surprising because they can be identified using a microscope, they are linked to a broad range of functions in the soil as they cover a range of trophic levels (Yeates et al., 1993; Neher, 2001; Yeates, 2003; Veen et al., 2010; Lu et al., 2020), and they include some well-known agricultural pests (Verschoor, 2002; Van der Putten et al., 2006). Nematodes have been used as targets for control in agriculture already for decades (Biswal, 2022). Although current methodological advancements in the field of soil science, such as molecular techniques, have allowed for an increased focus on microorganisms and their functional groups in the literature, we still did not find many studies/data records concerning microorganisms (i.e. bacteria and fungi in this review), particularly for practices related to 'crop diversity' and 'pesticide use'. Although, this may partly result from our search query, it also is still challenging to identify microorganisms and classify them based on the functions they perform (O`Donnell et al., 1994; Bohannan et al., 2003; Bloem et al., 2004; Malaterre et al., 2013; Geisen et al., 2019). Instead, microbial community composition or the abundance of specific groups that are known as relevant for agriculture may be more frequently used to assess impacts of alterative practices. This is for instance reflected in our database in the number of studies focusing on arbuscular mycorrhizae fungi (AMF; Smith and Read, 2010; Šnajdr et al., 2011; Li et al., 2022b). Better understanding how functional groups in soils, particularly the ones more directly connected to expected ecosystem functions and (dis) services, such as herbivore nematodes, predator nematodes and AMF, respond to a range of management practices will be essential to understand how functions such as carbon and nutrient cycling may be affected (Strickland et al., 2010; Nielsen et al., 2011; Waring et al., 2013; Wagg et al., 2014). It will be important for future work to close the gaps identified in this literature review, particularly on the taxonomic/functional groups that are studied less well, to gain a more complete understanding of the impact of alternative practices on soil biodiversity.

4.2. *The effects of alternative practices on soil biodiversity*

Our second aim was to identify the impact of the retrieved agricultural practices on both the species richness of taxonomic groups and the abundance of functional groups. We found that alternative practices generally had positive effects on species richness of the taxonomic groups and also on the abundance of functional groups. These findings are in line with previous reviews and meta-analyses (de Graaff et al., 2015; Briones and Schmidt, 2017; Zhang et al., 2017; Chen et al., 2020; Morugán-Coronado et al., 2020; Cozim-Melges et al., 2024) and may be explained by higher availability or diversity of organic matter to soil organisms (Haddaway et al., 2017) or to less chemical and mechanical disturbance of the soil (Jansa et al., 2003; Kabir, 2005). In addition, higher diversity of crops or inputs of organic matter can also facilitate more niches in the soil (Langlois et al., 2020; Guzman et al., 2021). Overall, this suggests that alternative practices are less intensive and disturbing than conventional ones, which favors soil biodiversity (Newbold et al., 2015, Tsiafouli et al., 2015).

Even though effects of alternative practices were generally positive, we also found a substantial amount of data records indicating no effects of an alternative practice on biodiversity. Although it could be that many of the practices indeed have limited impacts on soil biodiviersity, we also know that many of the studies in testing alternative practices are not set up to test one practice versus the other, but are set up to test different levels or intensities of a certain practice. When some of the intensity levels are close to business as usual practices, or when the impact of alternative practices only significantly impacts soil biodiversity at an optimal intensity, this may lead to a relative large number of 'no effects', which we observe in the case of our review. Additionally, it may take time before alternative practices affect soil biodiversity and for some studies the duration of experiments may not be long enough to detect effects. Alternatively, sampling may have taken place in seasons or moments where effects of practices were harder to observe, e.g., due to weather conditions (Joos, 2023). Finally, some practices may truly not have strong impacts on soil biodiversity or on the abundance of functional groups. It will be essential to untangle in future work to what extent methodological or sampling constraints drive the observation that relatively many practices had limited impacts on soil biodiversity.

In some occasions, we observed contrasting effects of practices on functional groups within a same taxonomic group. For example, for earthworm responses to 'organic matter mulching' a reduction in the overall species richness and the abundance of epigeic and endogeic earthworms, while the abundance of epi-endogeic earthworms was enhanced. It is hard to explain this finding ecologically, as the epi-endogeic groups is functionally overlapping with both other groups, but our finding could result from the limited use of the classification 'epi-endogeic' earthworms. These contrasting effects might also arise from indirect consequences, such as changes in community composition, caused by these practices or changes such as presence of higher abundance of higher trophic levels associated with lower intensity land-use (Tsiafouli et al., 2015), which might cause on itself changes in biodiversity. Another example showed that the abundance of bacterivorous nematodes was enhanced by 'synthetic fertilizer supplemented', while the abundance of herbivorous nematodes decreased. This practice may have resulted in easily available carbon and nutrients, which can stimulate bacteria and hence bacterivores (Mayrhofer et al., 2021). It is however less clear why this type of fertilization would reduce herbivores and whether this is a general response. Further research is needed for a more conclusive definition, yet that could actually be a positive consequence, as herbivorous nematodes can be potential pests to crops (Bernard et al., 2017). For species richness of the taxonomic groups, the impact of alternative practices is more consistent, i.e., there was less variation in responses. This might be driven by a lower number of studies, and hence lower number of retrieved data records, compared to those for the abundance of functional groups.

An important next step will be to test how interactions between promising alternative practices impact on biodiversity, because they are often not applied in isolation. It could be that practices applied simultaneously further impair biodiversity (Pardo et al., 2024) or could enhance it by providing better conditions. Also, it will be essential to understand long-term effects and gain knowledge on how the environmental context is modifying effects of practices on soil life (Guerra et al., 2020, Köninger et al., 2023). Moreover, future research could use the overview of functional abundance metrics related to soil biodiversity in this review and correlate them to ecosystem functioning effects found in the literature. Admittedly, to correlate functional abundance with ecosystem functioning, it is necessary to incorporate this research question to field experiments themselves first. This is crucial to understand how to steers soil biodiversity with agricultural management for multiple soil functions (Thiele-Bruhn et al., 2012). In the meantime, adding assessments on community composition or effects on endemic/specific species could also be explored. Additionally, the knowledge on practices affecting biodiversity in this review should be linked with their potential effects on ecosystem services in future research (in line with Balvanera et al., 2006), and tailored to management practices that more broadly account for impact on ecosystems in its complexity. This is a crucial aspect in the enhancement of biodiversity in agroecosystems and to balance the multiple demands on agroecosystems, connecting the functions affected by biodiversity to the services expected for food production and for provision of a wide range of other ecosystem services. Finally, it will be essential to further quantify the how the intensity and duration of practices impacts on soil biodiversity, as this can help implementation.

5. Conclusions

We found knowledge gaps in our understanding on impacts of alternative practices on soil biodiversity. Particularly, some well-known alternative practices that are applied to enhance aboveground biodiversity (i.e., not using pesticides or implementing field margins) are not commonly studied for soil biodiversity. At the same time, biodiversity of some groups, such as microbes, is not studied for a wide range of practices. Generally, we conclude that alternative agricultural practices have positive effects on soil biodiversity, both in terms of species richness of taxonomic groups and abundance of functional groups. Still, for most of the retrieved alternative practices impacts are variable and depend on the taxonomic or functional group under consideration. Therefore, those practices will not improve biodiversity of all groups simultaneously. Nevertheless, there are some practices that have positive effects on the richness and abundance of most groups of soil organisms and hence have the potential to enhance overall belowground biodiversity in agroecosystems: 'no insecticide use', 'no herbicide use', 'crop diversity – temporal and spatial', 'minimum tillage', 'cover crop', 'no fertilizer'. For many of these practices we know that they are also beneficial for aboveground biodiversity of agroecosystems (Bengtsson et al., 2005; Cozim-Melges et al., 2024) and that effects may even positively impact biodiversity beyond the farm boundary (Tscharntke et al., 2012; Willett et al., 2019).

CRediT authorship contribution statement

G. F. (Ciska) Veen: Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Conceptualization. **Wim H. van der Putten:** Writing – review & editing, Methodology. **Hannah H.E. van Zanten:** Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization. **Philipp Oggiano:** Writing – review & editing, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Raimon Ripoll-Bosch:** Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization. **Felipe Cozim-Melges:** Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109329.

Data availability

Data will be made available on request.

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Further reading

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