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REVIEW ARTICLE

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Reducing tillage intensity benefits the soil micro- and mesofauna in a global meta-analysis

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Abstract

Soil fauna drives crucial processes of energy and nutrient cycling in agricultural systems, and influences the quality of crops and pest incidence. Soil tillage is the most influential agricultural manipulation of soil structure, and has a profound influence on soil biology and its provision of ecosystem services. The objective of this study was to quantify through meta-analyses the effects of reducing tillage intensity on density and diversity of soil micro- and mesofaunal communities, and how these effects vary among different pedoclimatic conditions and interact with concurrent management practices. We present the results of a global meta-analysis of available literature data on the effects of different tillage intensities on taxonomic and functional groups of soil micro- and mesofauna. We collected paired observations (conventional vs. reduced forms of tillage/no-tillage) from 133 studies across 33 countries. Our results show that reduced tillage intensity or no-tillage increases the total density of springtails (+35%), mites (+23%), and enchytraeids (+37%) compared to more intense tillage methods. The meta-analyses for different nematode feeding groups, life-forms of springtails, and taxonomic mite groups showed higher densities under reduced forms of tillage compared to conventional tillage on omnivorous nematodes (+53%), epedaphic (+81%) and hemiedaphic (+84%) springtails, oribatid (+43%) and mesostigmatid (+57%) mites. Furthermore, the effects of reduced forms of tillage on soil micro- and mesofauna varied with depth, climate and soil texture, as well as with tillage method, tillage frequency, concurrent fertilisation, and herbicide application. Our findings suggest that reducing tillage intensity can have positive effects on the density of micro- and mesofaunal communities in areas subjected to long-term intensive cultivation practices. Our results will be useful to support decision making on the management of soil faunal communities and will facilitate modelling efforts of soil biology in global agroecosystems.

HIGHLIGHTS

- Global meta-analysis to estimate the effect of reducing tillage intensity on micro- and mesofauna

- Reduced tillage or no-tillage has positive effects on springtail, mite and enchytraeid density
- Effects vary among nematode feeding groups, springtail life forms and mite suborders
- Effects vary with texture, climate and depth and depend on the tillage method and frequency

KEYWORDS

agricultural land use, conservation agriculture, conventional agriculture, soil biodiversity, soil cultivation

1 | INTRODUCTION

Soil fauna comprise a large part of the world's biodiversity and regulates crucial processes of energy and nutrient cycling (Coleman & Wall, 2015). The food web interactions of soil fauna have a large influence on the quality of crops (Ouedraogo et al., 2006), the cycling of nutrients (Evans et al., 2019), as well as pest and disease incidence (Lavelle et al., 2004). Soil microfauna (nematodes) and mesofauna (mites, collembolans, enchytraeids) are among the most important taxonomic groups of soil fauna, in terms of density and biomass (Gardi et al., 2009). Via their feeding interactions, nematodes contribute to soil functioning, specifically to carbon flow (Sohlenius, 1980), nutrient cycling (Coleman et al., 1984), regulation of soil microbial populations and ultimately plant productivity (Bardgett et al., 1999). Springtails and mites play a crucial role in the recycling of soil organic matter by affecting microbial activity and regulating fluxes between organic matter pools (Neher & Barbercheck, 2019). Enchytraeids are essential detritophages, involved in organic matter decomposition and in mineralisation through the digestion of plant residues (Pelosi & Rombke, 2016). Enchytraeids also improve soil structure, porosity and hydraulic conductivity through faecal pellet production and redistribution of mineral and organic matter (Van Vliet et al., 1995). Hence, understanding the reduced tillage effects on soil fauna is of interest not only to the scientific community but also to farmers, practitioners, policy makers and agricultural consultants.

Soil tillage represents the most influential agricultural manipulation of soil structure and one of the main agricultural practices affecting soil biodiversity (van Capelle et al., 2012), due to its repetitive application, its depth range and its influence on residues (Strudley et al., 2008). Tillage is applied to temporarily reduce bulk density, increase gas diffusion and convection, and water retention (La Scala et al., 2008). The short-term effects of tillage are slowly reversed when the soil consolidates after rainfall events, and cycles of freezing and thawing (Mapa et al., 1986). Ploughing and harrowing for a total inversion of the soil (conventional tillage) is the most common tillage practice. Conservation tillage minimises soil disturbance, leaves most of the crop residues on the soil surface and is often practised on large farms (>100 ha). The only disturbance in no-tillage systems is by seeding and during harvest (Strudley et al., 2008). The tillage techniques commonly used in arable farming (Table 1) are chosen by farmers based on the objective (i.e., preparation for a seedbed, weed control, plant protection and nutrition, and water supply) and can be classified according to depth and mechanical effects as inversion or non-inversion, mixing and fragmentation. Globally, about 9% of the arable land is under no-tillage, with higher adoption rates in the United States followed by Argentina and Brazil. South America has 42.3% of all arable land under conservation tillage, followed by the US with 34.4% (Blanco-Canqui & Ruis, 2018).

The impacts of tillage on soil fauna are quantitative (i.e., population densities) and qualitative (i.e., species composition and diversity) (Minor et al., 2004). Tillage affects soil fauna mainly via changes in the soil's physical environment and food resources (Zhang et al., 2015). In ploughed plots, residues are buried down to 25 cm, making organic matter less available. Due to anaerobic conditions, microarthropods at this depth often cannot use these residues as a food resource (Dittmer & Schrader, 2000). Also, the mechanical and physical disturbance caused by tillage destructs the habitats of some fauna groups (Ayuke et al., 2019). Under reduced or no-tillage, the litter layer stabilises soil moisture and temperature for soil fauna (Ayuke et al., 2019; House & Parmelee, 1985) and nutrient resources remain in the crop residue at the soil surface for longer time periods. The release of these nutrients takes place more slowly under reduced or no-tillage than under conventional tillage, which is perhaps more efficient in terms of nutrient

TABLE 1 Categories used in the meta-analysis for grouping tillage methods and their effects on soil

Tillage category	Terminology for tillage treatments found in the literature	Depth of soil preparation (cm)	Mechanical effect on soil	Degree of soil disturbance	Residue left on the soil surface
Full inversion tillage	Mouldboard plough, plough, ploughing, conventional plough, deep ploughing, conventional tillage, inversion and ripping, periodically mechanically disturbed, soil turning tillage, deep tillage	15–40	Inversion, mixing, fragmentation	Very high	< 15%
Deep soil loosening	Deep plough (reduced tillage), rotary tiller, harrowing, chisel plough, heavy spading, rotary tillage, ridge tillage, disk harrow, rotary hoe, chiselling, rotary machine	40–80	Fragmentation	Low	> 30%
Shallow soil loosening	Shallow tillage, rotary harrow, disking, fixed-tine cultivator (non-inversion), tine shallow cultivator, wing cultivator + rotary harrow, disk ploughing, rotary tiller, non-inverting tine subsoiler, manual tillage, manual ploughing, hand plough, hand tillage, tine cultivator, hand hoeing, sprintine cultivator, non-inversion tillage, rotovator, tooth tool, shallow cultivator, rotary cultivation, rotary digger	15–40	Fragmentation	Low - medium	> 30%
Reduced tillage	Minimum tillage, reduced frequency, strip tillage, ridge tillage, stalk puller - conservation minimum tillage, conservation tillage, minimum tillage, ridging, ploughless tillage	5–15	Mixing, fragmentation	Medium-low	15–30%
No-tillage	Direct sowing, zero tillage, surface drilling, undisturbed meadow, direct drilling, permanent green cover, direct drill	5	None	None	Undisturbed

cycling over several cropping seasons (House & Parmelee, 1985). Therefore, the effects of soil tillage on organisms depend on habitat demands and food preferences, ability to burrow and body size (D'Hose et al., 2018). For example, different tillage intensities may affect soil micro- and mesofauna by altering soil structure, as they use existing pore spaces or channels for locomotion within the soil and cannot burrow (Hassink et al., 1993).

Some global meta-analyses have been used to estimate the effects of tillage on soil fauna through the systematic analysis of studies reporting results of soil-fauna monitoring in fields with varying tillage intensity. The effects of tillage on micro- and mesofauna have been assessed in a global meta-analysis by Graaff et al. (2019), who revealed high stochasticity in responses among and within groups of soil fauna. A global meta-analysis conducted by van Capelle et al. (2012) estimated negative effects of less intensive soil cultivation on springtails and mites in sandy and loamy soil, and positive effects in silty soils. More recently, Puissant et al. (2021) reported the negative effects of conventional tillage on the maturity and structure of the nematode community and the density of omnivorous nematodes in a global meta-analysis. Nevertheless, a global quantitative assessment on the effects of tillage on soil micro- and mesofauna providing more detail on abiotic- and management-related interacting factors and a more differentiated response of taxonomic groups is still needed to explain the high stochasticity and site-specific context of the effects observed in previous meta-analysis.

The objective of this study was to estimate the effect of reducing tillage intensity on density and diversity of soil micro- and mesofaunal communities. We aimed to systematically analyse through meta-analyses the available global data collected in experimental fields under different tillage intensities on density and diversity of soil nematodes, springtails mites and enchytraeids. We also tested how the effects of reducing tillage intensity differ in soils with different properties (pH, organic matter, texture, moisture), in different climates, and in interaction with other management practices (fertilisation, pesticide application).

2 | METHODS

2.1 | Data collection

2.1.1 | Literature search

We conducted a systematic literature review in compliance with the Preferred Reporting Items for Systematic Reviews and Meta-analysis (PRISMA) framework (Figure S1) (Moher et al., 2009). We searched the literature for peer-reviewed publications reporting results on the effects of different tillage intensities on soil fauna using the Web of Science search engine. We used the following search terms: 'TOPIC: (tillage OR plough* OR chisel* OR till* OR mouldboard* OR disc* OR tine* OR rotatory OR rotary OR harrow*) AND (fauna* OR biota* OR organism* OR mesofauna* OR acari OR mite* OR enchytraeid* OR nematod* OR springtail* OR collembola*)'. After refining and removal of duplicates, we obtained 3459 results that were manually screened based on title and abstract.

2.1.2 | Inclusion criteria

After checking all the query results, a total of 133 papers published between 1981 and 2020 (Table S1) fitted our selection criteria for the meta-analysis:

1. Studies report density or biomass data, not only community composition in fields under different tillage intensities.
2. Studies report means and sample sizes in conventional tillage compared to different forms of reduced tillage. Studies with missing standard deviation or standard error were also included in the meta-analyses.
3. The data is available in the articles in the form of text, tables or figures. When the data were presented as graphs, we manually digitised the figures to estimate means and standard deviation (SD) or standard error (SE) using WebPlotDigitizer Version 4.3 (Rohatgi, 2020).
4. All tillage trials were conducted on the same site to avoid variability due to soil properties and site characteristics.
5. Applied amendments did not have high concentrations of heavy metals or cause potential toxicity to soil animals, that is, studies with untreated sewage sludge or other types of industrial residues were not selected.
6. Cropping system or vegetation cover was similar in all plots, to avoid effects of rotations or different vegetation cover.

2.2 | Data extraction and creation of database

From the selected papers and their supplementary material, we collected the mean density or biomass data of the control and treatment for the different taxonomic groups reported in the study, their replicate numbers (n) and standard deviation (SD) or standard error ($SE, SD = SE\sqrt{n}$). In the case that minimum and maximum values were reported, we estimated the sample mean and standard deviation with the methods proposed by Wan et al. (2014). Additionally, we extracted metadata related to:

1. Site characteristics: Location, longitude and latitude, mean annual precipitation,
2. Soil properties: Soil textural class; sand, silt and clay contents; pH; organic matter; organic carbon content; bulk density; moisture and water content,
3. Vegetation cover: Main crop or sequence of crop rotations when available,
4. Sampling of soil fauna: Extraction methods used in the study for each taxonomic group, sampling depth, time since the last tillage practice;
5. Management practices: type of fertiliser, application of pesticides, period of time under tillage practices, tillage frequency, tillage depth, tillage method (see Table 2).

The data and metadata were entered into a database, with each row representing one single pairwise comparison of conventional tillage and reduced forms of tillage or no-tillage. In the case of studies that reported data on long-term experiments with different sampling dates or measurements of organism density or biomass as time series, individual data for each sampling occasion was extracted as well as the measurement time and treatment duration. This was done to avoid substantial loss of data or the need to aggregate data over time. The resulting database covered 3440 pairwise comparisons (observations) of density or biomass data of nematodes, springtails, mites and enchytraeids.

Most of the studies presented total values of density or biomass of soil fauna for the entire community, for different life forms, trophic groups, or suborders. For the studies that reported species-specific data, the life form or suborder was determined based on available species descriptions, searched for in global databases (i.e., Burkhardt et al. (2014), Drilobase Project (2021), Janssens (2007)) or in scientific publications where these species have been previously classified as part of an ecological category, and also based on expert opinion. The densities of each individual species were summed to calculate the total density of each group. If species-specific standard errors or standard deviations were reported in the studies, these were used to

TABLE 2 Fixed-effects moderators of the effects of reduced tillage intensity compared to conventional tillage on soil micro- and mesofauna

Moderator	Subgroups/range
Nematode feeding group	Bacterivorous, fungivorous, herbivorous, omnivorous, predatory
Springtail life form	Epedaphic, hemiedaphic, euedaphic
Mite suborder	Oribatid, Mesostigamatid, Prostigmatid, Astigmatid
Diversity	Species richness, species diversity
Sampling methods	Nematodes: Baermann funnel, cotton-wool filter, elutriation
	Springtails and mites: Berlese-Tullgreen funnel, high gradient funnel, MacFadyen funnel, Tullgreen funnel
	Enchytraeids: Baermann funnel, hand sorting, MacFadyen funnel, wet funnel
Sampling depth	0–5 cm, 0–10 cm, 5–10 cm, 10–20 cm
Climatic zone	Koeppen classification system (Kottek et al., 2006)
Mean annual rainfall	90–3500 mm
Soil texture classes	Clay (clay and clay loam)
	Silty (silt, silty clay, silty loam, silty clay loam, silty sand)
	Loam (loam, loamy sand, loamy silt)
	Sandy (sand, sandy clay loam, sandy loam)
Soil pH	3.9–8.6
Soil organic matter	0.2–11.4%
Soil organic carbon	0.01–8.4%
Reduced tillage treatment	Deep soil loosening, shallow soil loosening, reduced tillage, no-tillage
Tillage frequency	Once a year, twice a year
Time period after tillage	0–1460 days
Herbicide application	Glyphosate, glyphosate/bialaphos, other herbicide, no herbicide
Type of fertilisation	Mineral, mineral and organic, organic, none

estimate the variances for each taxonomic group as a pooled standard deviation.

2.3 | Tillage categories and other moderating factors

We adopted the tillage categories proposed by Briones and Schmidt (2017) to group the different tillage terminology found in the literature. Based on the general description of the tillage operations reported in the studies, the tillage treatments were assigned to one of the categories described in Table 2. In our meta-analysis, all pairwise comparisons use a more intense form of tillage as a control, which usually refers to full inversion tillage to a depth of 25 cm typically using a mouldboard plough followed by secondary tillage (see Table 2). Deep soil loosening refers to tillage methods that loosen the soil to a depth greater than 15 cm without inversion. Shallow soil loosening refers to tillage methods that loosen the soil up to 15 cm depth. Reduced tillage refers to tillage methods that disturb (mix or fragment) the soil up to 15 cm depth. No-tillage refers to treatments in which the soil is only disturbed for sowing.

2.4 | Statistical modelling

2.4.1 | Calculation of effect sizes

The analysis was carried out using the log response ratio as the outcome measure ($LRR = ln(\overline{x_i}/\overline{x_c})$, where $\overline{x_i}$ and $\overline{x_c}$ are the mean density or biomass in the treatment and control, respectively). A positive effect size ($LRR > 0$) means increased faunal densities with reduced forms of tillage, and a negative effect size ($LRR < 0$) means reduced faunal densities. To facilitate the interpretation of the results, the mean effect sizes for each faunal group are also reported in the main text as a percentage change ($\%\ change = (exp(LRR) - 1) * 100$). The amount of heterogeneity (τ^2) was estimated using the restricted maximum-likelihood estimator (Viechtbauer, 2005). Studentised residuals and Cook's distances are used to identify whether studies may be outliers or influential

(Viechtbauer & Cheung, 2010). Studies with a studentised residual larger than the $100^*(1-0.05/(2k))$ percentile of a standard normal distribution are considered potential outliers (i.e., using a Bonferroni correction with two-sided $\alpha = 0.05$ for k studies included in the meta-analysis). Studies with a Cook's distance larger than the median plus six times the interquartile range of the Cook's distances are considered to be influential. The rank correlation test (Begg & Mazumdar, 1994) and the regression test (Sterne & Egger, 2005), using the standard error of the observed outcomes as predictors, were used to check for funnel plot asymmetry. The analysis was carried out using R (version 3.6.1) (R Core Team, 2019) and the metafor package (version 3.0.2) (Viechtbauer, 2010).

2.4.2 | Multiple imputation approach

Studies that reported mean values and number of replicates for experimental and control groups but were missing measures of precision (due to lack of reporting or figures with poor quality), but that still reported mean values and number of replicates for experimental and control groups were also included in our meta-analysis. Studies with missing data may still be informative and ignoring them may be a source of bias (Burgess et al., 2013). The missing variances from individual studies were imputed using multiple imputations by chain equations using the R package *mice* (Buuren & Groothuis-Oudshoorn, 2011), applying classification and regression trees as a univariate imputation method. The estimated effect sizes and variances are pooled estimates of 20 imputed datasets using the *pool* function of the *mice* package, which combines the estimates from repeated complete data analysis applying Rubin's combination rules (Rubin, 2004).

2.4.3 | Meta-analysis

The majority of the studies reported multiple outcomes (1–206 outcomes per study) that represent dependent data, that is, due to reporting of multiple taxonomic groups, in multiple follow-up times, different treatment conditions with common control, measured at different depths or different within-site locations. Becker (2000) suggests modelling the dependence of the data, which offers an accurate analysis of the effects of dependence and allows questions as to whether the effects are comparable across multiple outcomes or how explanatory variables relate differently to different outcomes. This was accounted for by following the approach by Pustejovsky and Tipton (2022), which combines dependence structures arising from a multilevel data structure (i.e., observations within studies) and correlated effect sizes within studies, using clubSandwich (Pustejovsky & Tipton, 2022) and metaphor (Viechtbauer, 2010) R packages.

Mixed-effects meta-regressions were conducted, including observation and study identifier as random-effects as well as fixed-effects moderators shown in Table 2. Soil texture was grouped into classes either as reported in the studies or calculated from the particle size distribution using an online soil texture calculator (USDA, 2016). Climate zones were determined based on the Koeppen classification system (Kottek et al., 2006), which uses five main climate categories with further subdivisions according to seasonal distribution, amount of rainfall and temperature regimes.

3 | RESULTS

3.1 | Effects on taxonomic groups

Significantly higher total density of springtails (+35%), mites (+23%) and enchytraeids (+37%) were observed under reduced tillage intensity compared to conventional tillage methods (Figure 1). When looking at different nematode trophic groups, springtail life forms and higher

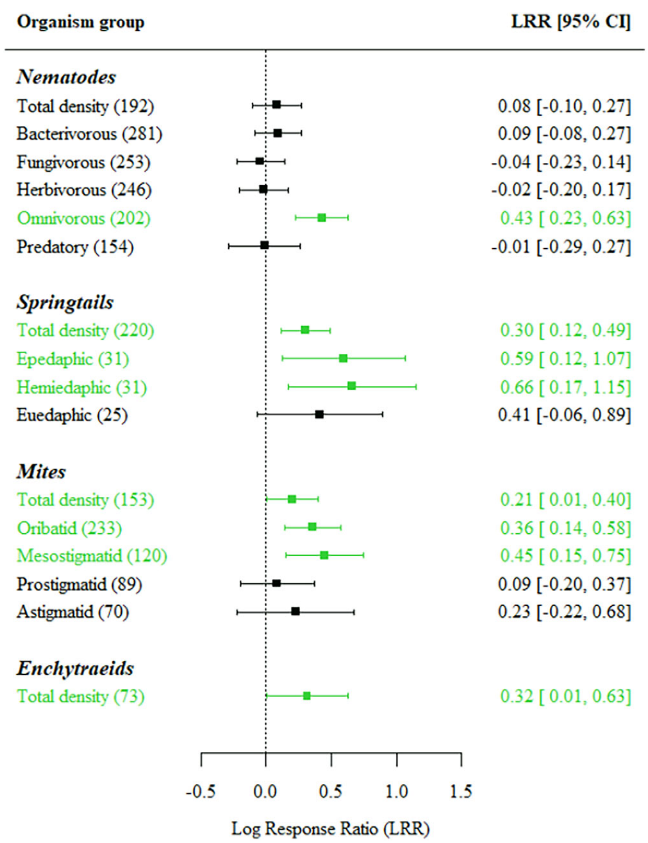

FIGURE 1 The effect of reduced tillage intensity on the density of each soil faunal group compared to (conventional tillage methods) controls. Forest plots show the mean effect, within brackets the 95% confidence intervals, and within parentheses the sample sizes for each group. Significant positive effects are shown in green. Overall effect refers to the effect of reduced tillage intensity on the total density of each taxonomic group.

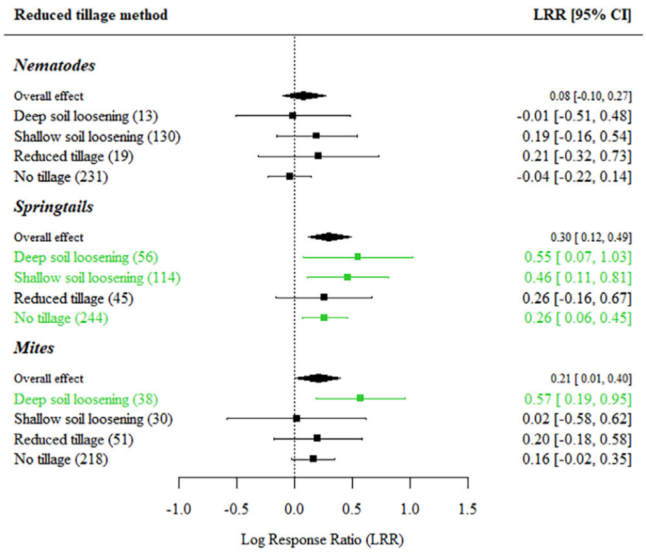

FIGURE 2 The effect of reduced tillage intensity on the density of each soil faunal group compared to (conventional tillage methods) controls for different forms of reduced tillage. Forest plots show the mean effect, within brackets the 95% confidence intervals, and within parentheses the sample sizes for each form. Overall effect refers to the effect of reduced tillage intensity on the total density of each taxonomic group.

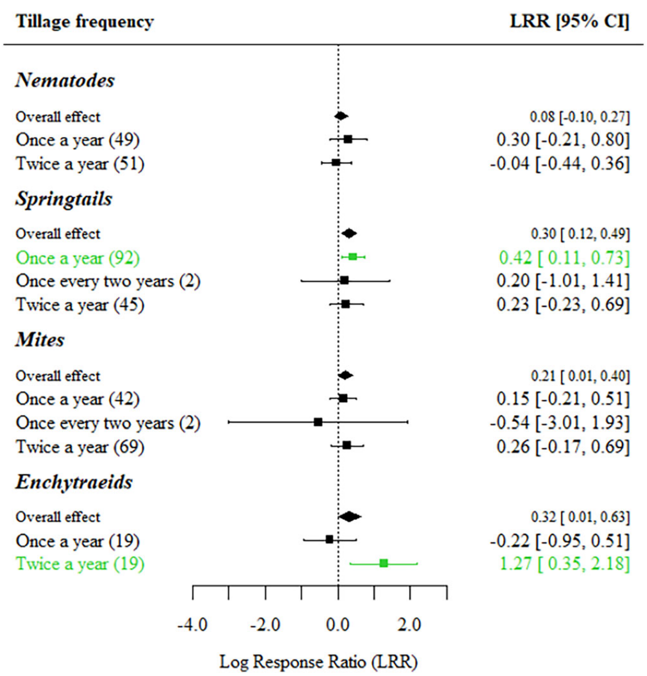

FIGURE 3 The effect of reduced tillage intensity on the density of each soil faunal group compared to (conventional tillage methods) controls for different tillage frequencies. Forest plots show the mean effect, within brackets the 95% confidence intervals, and within parentheses the sample sizes for each frequency. Overall effect refers to the effect of reduced tillage intensity on the total density of each taxonomic group.

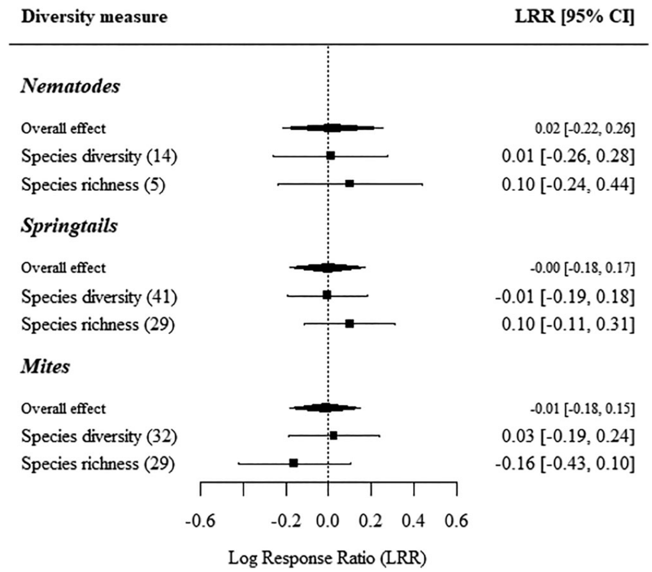

FIGURE 4 The effect of reduced tillage intensity on the density of each soil faunal group compared to (conventional tillage methods) controls at different sampling depths. Forest plots show the mean effect, within brackets the 95% confidence intervals, and within parentheses the sample sizes for each depth range. Significant positive effects are in green, significant negative effects are in red. Overall effect refers to the effect of reduced tillage intensity on the total density of each taxonomic group.

mite orders, we found significantly higher densities of omnivorous nematodes (+53%); epedaphic (+81%) and hemiedaphic (+84%) springtails; and oribatid (43%) and mesostigmatid (+57%) mites under reduced tillage intensity. However, the species richness and diversity of nematode, springtail and mite communities (Figure S2) were not significantly different under reduced tillage intensity compared to conventional tillage.

The effects of reduced tillage intensity on some taxonomic groups depend on the type of tillage method used in the experiment (Figure 2). We observed no significant differences in nematode density under reduced tillage for different tillage methods. Significantly higher springtail density was found under deep soil loosening (+73%), shallow soil loosening (+58%) and no-tillage (+30%) compared to conventional tillage. Higher mite density was observed for deep soil loosening (+77%). We observed no significant effects of different tillage frequencies on nematodes and mites. Higher springtail density was observed under reduced tillage intensity when conventional tillage operations were conducted once a year (+52%), and on enchytraeids when more intense tillage operations are conducted twice a year (+254%) (Figure 3). The time between tillage operations and faunal sampling does not significantly modulate the effects of reduced tillage intensity compared to conventional tillage (Figure S3).

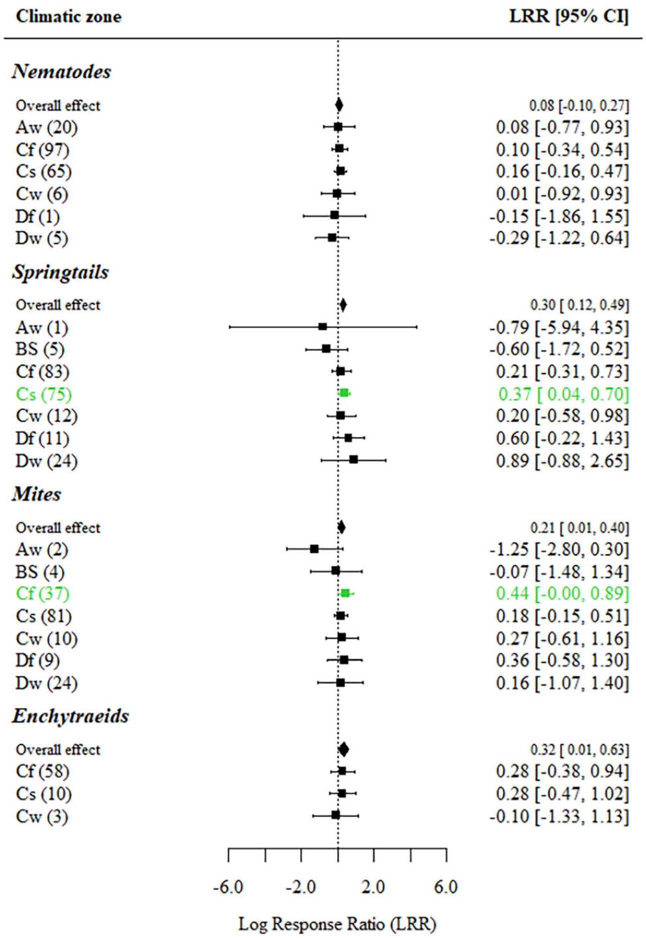

FIGURE 5 The effect of reduced tillage intensity on the density of each soil faunal group compared to (conventional tillage methods) controls in different climatic zones according to the Koeppen-Geiger classification (Kottek et al., 2006); (a): Tropical (w: Savanna, dry winter), (b): Arid (S: Steppe), (c): Temperate (w: Dry winter, f: No dry season, s: Dry summer), (d): Continental (w: Dry winter, f: No dry season). Forest plots show the mean effect, within brackets the 95% confidence intervals, and within parentheses the sample sizes for each zone. Significant positive effects in green. Overall effect refers to the effect of reduced tillage intensity on the total density of each taxonomic group.

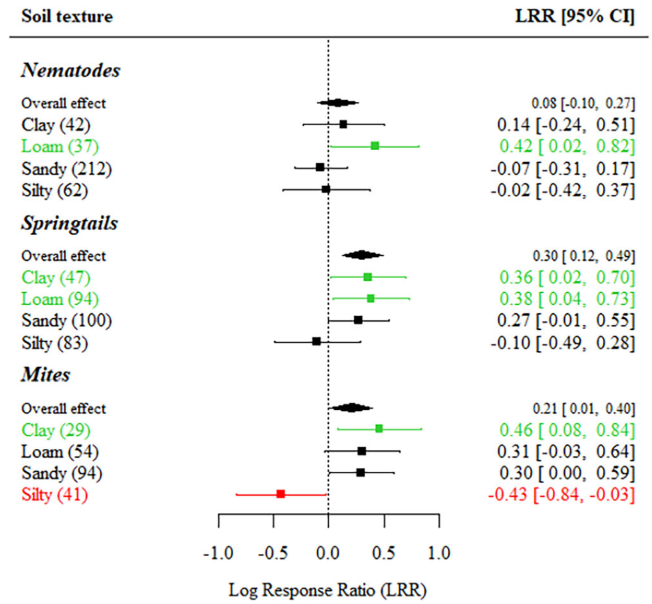

FIGURE 6 The effect of reduced tillage intensity on the density of each soil faunal group compared to (conventional tillage methods) controls in soils of different textures. Forest plots show the mean effect, within brackets the 95% confidence intervals, and within parentheses the sample sizes for each soil texture. Significant positive effects in green and significant negative effects in red. Overall effect refers to the effect of reduced tillage intensity on the total density of each taxonomic group.

Springtail and mite densities were significantly higher under reduced tillage compared to conventional when MacFadyen funnels (+46%) are used for springtail extraction and Berlese-Tullgreen funnels (+55%) for mite extraction (Figure S4). For all the other extraction methods for each taxonomic group analysed separately, no significant results were observed.

The effects of reduced tillage on soil fauna through the soil profile (Figure 4) showed significantly lower nematode density under reduced tillage compared to conventional at 10–20 cm (−36%), significantly higher springtail density at 0–5 cm (+40%) and, and significantly higher mite density at 0–10 cm (+85%). At other sampling depths, no significant effects were observed. No sufficient data was reported on enchytraeids at different depths.

3.2 | Interaction with abiotic factors

3.2.1 | Climatic variables

The effect of reduced tillage intensity compared to conventional tillage methods on the soil faunal community is not significantly modulated by the mean annual precipitation reported at the research site (Figure S5). When looking at the effect of reduced tillage intensity in sites corresponding to different climatic zones (Figure 5), we found that reduced tillage intensity has a significantly positive effect on springtail density in areas with hot-summer Mediterranean climates (Cs, +45%) and on mites in areas with humid subtropical climates (Cf, +55%).

3.2.2 | Soil properties

Higher nematode density was observed in loamy soils (+52%) under reduced tillage compared to conventional.

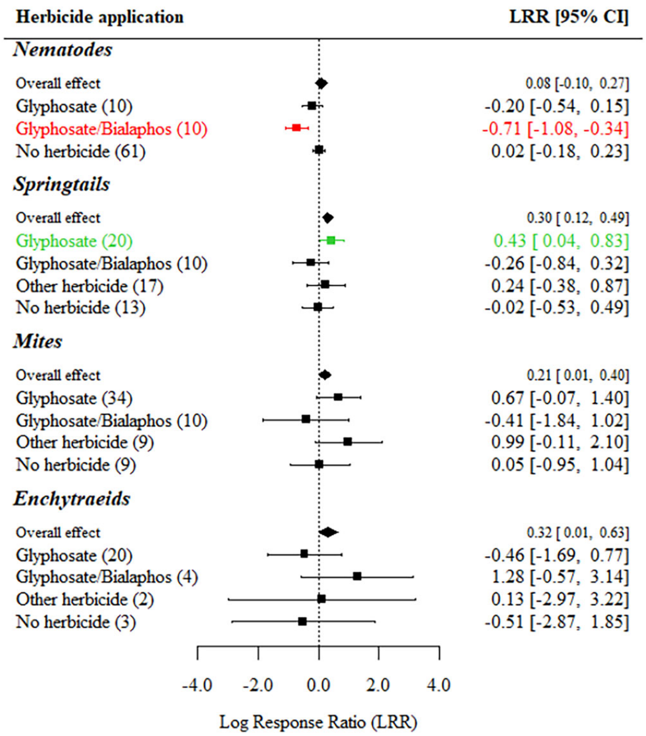

FIGURE 7 The effect of reduced tillage intensity on the density of each soil faunal group compared to (conventional tillage methods) controls with simultaneous application of herbicides. Forest plots show the mean effect, within brackets the 95% confidence intervals, and within parentheses the sample sizes for each herbicide. Overall effect refers to the effect of reduced tillage intensity on the total density of each taxonomic group.

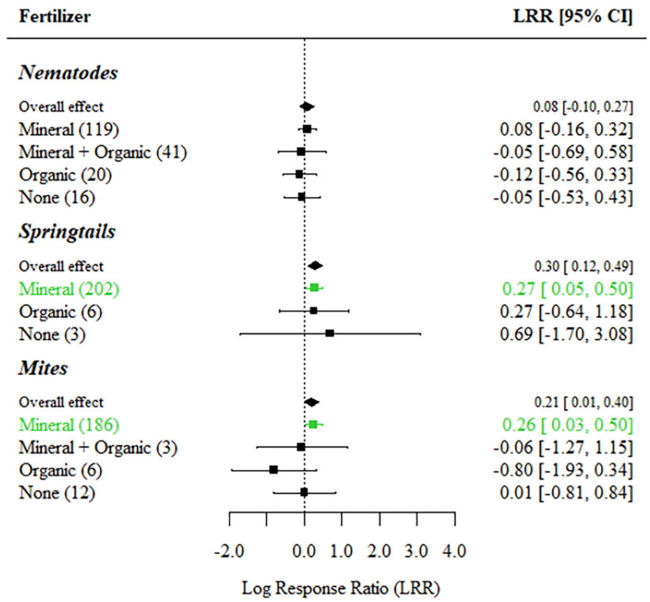

FIGURE 8 The effect of reduced tillage intensity on the density of each soil faunal group compared to (conventional tillage methods) controls for different types of fertiliser. Forest plots show the mean effect, within brackets the 95% confidence intervals, and within parentheses the sample sizes for each fertiliser type. Overall effect refers to the effect of reduced tillage intensity on the total density of each taxonomic group.

Higher springtail density was observed under reduced tillage in clay (+43%) and loamy (+47%) soils. Higher mite density under reduced tillage was observed in clay soils (+58%) and lower mite density under reduced tillage was observed in silty soils (−35%) (Figure 6). There were not enough observations for different soil textures to assess their moderating influence on the effects of reduced tillage intensity on enchytraeids. Other soil properties such as soil pH (Figure S6), organic matter content (Figure S7) and organic carbon content (Figure S8) do not significantly modulate the effects of reduced tillage intensity on soil fauna.

3.2.3 | Influence of concurrent management practices

Regarding the effect of the simultaneous application of herbicides (Figure 7), we found significant negative effects of reduced tillage intensity on nematodes when glyphosate/bialaphos is applied (−51%) and significant positive effects on springtails when glyphosate is applied (+54%). Furthermore, our meta-analysis shows significant positive effects of reducing tillage intensity on springtails (+31%) and mites (+30%) when mineral fertilisers are applied as part of the cropping calendar (Figure 8).

4 | DISCUSSION

Our results show that the density of omnivorous nematodes, springtails, mites and enchytraeids is significantly higher under reduced tillage intensity compared to conventional tillage. The results for nematodes (based on 192 observations) agreed with the recent findings of Puissant et al. (2021), who detected no significant tillage effects on total nematode density, but positive effects of reduced tillage on omnivorous nematodes. Regarding the lack of significant effects on total nematode density, Zhang et al. (2017) suggest the selection of disturbance-tolerant taxa resulting from long-term exposure to conventional farming systems, as taxa intolerant to disturbance may no longer be present in arable soils (Sanchez-Moreno et al., 2006). A higher taxonomic resolution would be needed to understand the tillage effects on nematodes as these can be genus-dependent (Sanchez-Moreno et al., 2006; Zhang et al., 2012). Additionally, Xin et al. (2018) indicate that no-tillage may cause long-term soil compaction and depth stratification of nutrient and organic matter which could influence the density of soil arthropods. Oseto and Boles (1987) also noted that some forms of cultivation accelerate the decomposition of crop residue, which may favour some taxonomic groups (particularly springtails and prostigmatid mites). In addition to the tillage method, the frequency of tillage has different effects on soil fauna. Our meta-analyses show that reduced forms of tillage have a positive effect when the more intense tillage method in the control plot is conducted once and twice a year. This suggests that reducing tillage intensity in fields where tillage is conducted less frequently (i.e., once every 2 years) may not have important effects, as faunal communities have sufficient time to recover between two successive disturbances (Dorel et al., 2010).

The results for springtails and mites contrast those reported by van Capelle et al. (2012) who concluded in their review of German data that reducing tillage intensity (conventional vs. no-tillage) has negative effects on springtails and mites. The higher springtail density observed under reduced tillage is consistent with the evidence provided by several individual studies, that is, Brennan et al. (2006) and Oseto and Boles (1987). Conventional tillage can make springtails more vulnerable to dehydration as they inhabit the plough layer (Oseto & Boles, 1987), are sensitive to changes in soil moisture, food resources (Olejniczak & Lenart, 2017) and soil disturbances (Rebek et al., 2002); effects that are reduced in reduced or no-tillage systems. A further suggested mechanism for the positive effects of reduced tillage is a shift towards a primarily fungal-based system which favours fungivorous organisms (Brennan et al., 2006; Coulibaly et al., 2017).

Regarding springtail life forms, we found higher densities of ep- and hemiedaphic springtails under reduced tillage compared to conventional. Coulibaly et al. (2017) noted that epedaphic species strongly and rapidly increased in the first 2 years, contrary to euedaphic species which needed over 4 years of reduced tillage for changes to be observed. This is probably related to the better abilities of epedaphic springtails to disperse and colonise (Chauvat et al., 2014). Olejniczak and Lenart (2017) explained the lack of consistent effects on euedaphic springtails by contrasting species-specific effects, which may favour some species and reduce others. Dittmer and Schrader (2000) noted that body size may determine the size and direction of the tillage effects: smaller euedaphic springtails may prefer smaller pores produced by reduced tillage and are less sensitive to compaction under no-tillage, while large euedaphic springtails likely require larger pores resulting from full inversion tillage.

Mite populations are on average larger under reduced forms of tillage than under conventional tillage. Soil mites (primarily, oribatid and mesostigmatid) adapted to living in highly structured environments with stable microclimates are sensitive to fluctuations when the original pore network is destroyed (Minor et al., 2004). The positive effects on mites can also be related to more available prey such as springtails, other groups of mites and enchytraeids (Hopkin, 1997; Schrader & Bayer, 2000). Additionally, springtails and mites, which are mostly fungal feeders, may increase by the shift of organic matter decomposition pathways from bacterial to fungal channels (Minoshima et al., 2007). The estimation of the effects of reduced forms of tillage on different mite suborders revealed higher densities of oribatid and mesostigmatid mites. Oribatid mites are considered highly sensitive to stress due to tillage or other types of mechanical disturbance in their habitat (Edwards & Lofty, 1975; Rieff et al., 2020). Furthermore, the positive effect on mites in the upper 10 cm may be explained by the litter layer under reduced and no-tillage, which could provide predatory mites with more abundant and diverse prey (Bedano et al., 2016; Schrader & Bayer, 2000). No significant effects were observed on prostigmatid mites, which are known to be well-adapted to cultivated agroecosystems (Coleman et al., 2017) and can reach high-density levels (Loring et al., 1981) even under conventional tillage (Oseto & Boles, 1987). Rieff et al. (2020) noted that reduced forms of tillage can lead to a shift in mite communities from species more adapted to disturbances and stress (Mesostigmata and Astigmata) to communities of groups less adaptable to disturbance (Oribatida).

We noted that various tillage methods affect springtails and mites differently. Deep soil loosening has a significant positive effect on springtails and mites, whereas no-tillage and shallow soil loosening have a significant positive effect only on springtails. This may be explained by the effects of the different tillage methods on the soil. For example, the non-inverting tine subsoiler has the strongest physical effect in deeper soil layers as the tines break the soil and the surface layers are exposed to the action of the rotary cultivator (Petersen, 2002). Our results further show positive effects of reduced forms of tillage on mites, springtails and enchytraeids in shallow layers of the soil profile, and negative effects on nematodes in deeper layers. This agrees with the consensus that positive effects of reduced intensity are more important in the shallow soil layers for mites and springtails (Miura et al., 2008; Petersen, 2002).

We found positive effects of reduced forms of tillage on enchytraeid populations. Our results for enchytraeids are comparable to those of van Capelle et al. (2012) on the effects of reduced tillage, who reported the highest enchytraeid abundances under reduced tillage intensity, compared to conventional tillage. Van Vliet et al. (1997) and Dominguez and Bedano (2016) noted that enchytraeids are more abundant in the 0–5 cm layer under no-tillage, as mulch and crop residue accumulating in the soil surface under reduced or no-tillage stimulate fungal growth, which serves as a food resource (Gizzi et al., 2009). Our results contrast several individual studies, that is, House and Parmelee (1985), Zwart et al. (1994) and Severon et al. (2010), who reported negative effects of reduced forms of tillage and no-tillage on enchytraeids. These contrasting results may be explained by the timing of the sampling, that is, contrasting results may be observed in the spring and autumn sampling following the harvest and residue incorporation by tillage. van Capelle et al. (2012) observed that enchytraeid density tends to be highest under conservation tillage and is lowest under no-tillage systems, hence no general conclusions can be derived on the response of enchytraeid density to cultivation. More research is needed to understand the effects of different tillage methods on enchytraeid density.

We found no significant effects of reduced tillage intensity on frequently reported indices of diversity of the assessed taxonomic groups. This lack of significant differences among different tillage intensities could be caused by only a few dominant taxa occurring at the study sites (Freckman & Ettema, 1993). Furthermore, individual studies (Olejniczak & Lenart, 2017) reported higher springtail diversity under conventional tillage compared to no-tillage in the first year of experiments, but the opposite result was observed in their second year. This implies that observation time may not be sufficient for changes in the diversity of soil-faunal communities to manifest (Coulibaly et al., 2017; Mondino et al., 2010; Tabaglio et al., 2009), as most experiments included in our meta-analysis are only short-term (maximum 3 years).

The effects of reduced tillage intensity compared to conventional tillage on faunal do not vary with the time between tillage operations and sampling. The time lag between changes to soil physical properties and changes in soil biology may explain why nematode density did not differ between different tillage intensities (Griffiths et al., 2002; Zhang et al., 2012). The effects of different tillage systems on nematodes may only be detected after several years of a given reduced tillage practice (Dorel et al., 2010; Griffiths et al., 2012; Okada & Harada, 2007; Zhong et al., 2017). Gizzi et al. (2009) and Coulibaly et al. (2017) noted that at least 2 years of reduced or no-tillage are needed to have a detectable impact on soil fauna. This highlights the need for more long-term experiments that measure the effects of different cultivation intensities on soil fauna.

We found higher densities under reduced tillage compared to conventional tillage of nematodes in loam soils, springtails in clay and loam soils, mites in clay soils and lower mite density in silty soil. A potential explanation for this is that tillage effects on soil physical properties largely depend on soil texture (Blanco-Canqui & Ruis, 2018), which may translate into differential effects on the different taxonomic groups of soil fauna. Soil organic matter, organic carbon and pH are the soil properties that could have a greater influence on the response of soil fauna to different tillage intensities (Bedano et al., 2016; Griffiths et al., 2012; Olejniczak & Lenart, 2017). However, we found no significant relation between the effects of reduced tillage intensity with these soil properties. This may be explained by data scarcity, as many studies did not report soil properties. Nonetheless, some individual studies also found no significant association between the effects of agricultural management, soil properties and fauna. Furthermore, Bedano et al. (2016) suggest using more specific and responsive soil properties such as pore size distribution or assessing different fractions of organic matter.

Mean annual precipitation did not moderate the effect of reduced tillage. Positive effects of reduced tillage on springtails and mites were found in areas with Mediterranean and subtropical climates. In Mediterranean zones, the seasonal variation due to spring and autumn precipitation may intensify the tillage effects (Renaud et al., 2004). Furthermore, the different species occurrence between temperate and tropical areas may account for different effects of tillage on soil fauna (Badji et al., 2007). Overall, the lack of moderating effects observed in different climatic zones and precipitation regimes suggests that the positive effects of reduced tillage intensity can be more broadly generalised.

We observed positive effects of reduced tillage intensity on springtails and mites when mineral fertilisers are applied. This could be explained by the higher number of observations (springtails: 202, mites: 186) corresponding to mineral fertilisation compared to other forms of fertilisation. Mineral fertilisation often has no effect on soil fauna (Betancur-Corredor et al., 2022); therefore, when applied concurrently, tillage may have a greater effect on soil fauna.

We observed contrasting effects of reduced tillage when glyphosate is applied. Lower nematode density was observed under reduced tillage when glyphosate/bialaphos was applied concurrently. Higher springtail density was observed when glyphosate was applied. Rieff et al. (2020) noted a higher sensitivity of springtail density to herbicide application in topsoil layers. We theorise that conventional tillage incorporates herbicide residue in the soil, which affects springtails through direct toxicity. Under reduced or no-tillage, the herbicide remains at the soil surface and is likely to leak into the subsoil through macropores (Alletto et al., 2010). Furthermore, herbicide usage is usually higher in reduced and no-tillage systems compared to plough-based cropping systems (Melander et al., 2013). Therefore, no-tillage/reduced tillage would benefit soil fauna even more if no herbicides were applied.

5 | CONCLUSION

Our global meta-analysis provides consistent quantitative evidence of generally positive effects of reduced tillage intensity on the density of omnivorous nematodes, springtails, mites and enchytraeids compared to conventional tillage methods. The size, direction and statistical significance of these effects vary among different life forms, trophic groups and suborders, and are more pronounced in finer-textured soils (i.e., clay or loam). Furthermore, the effects of reduced tillage can vary with soil depth, reduced tillage method and herbicide application. Some potential explanations for these positive effects are improved habitat conditions, reduced disturbance, more abundant and diverse prey, decreased risk of drought and more food resources. Our results will be useful to support evidence-based, informed policy-making on biodiversity preservation, and decision making on agricultural management and will facilitate modelling efforts of the effects of agricultural management on soil fauna communities.

AUTHOR CONTRIBUTIONS

All authors contributed to the study's conception and design. Material preparation, data collection and analysis were performed by Bibiana Betancur-Corredor and Birgit Lang. The first draft of the manuscript was written by Bibiana Betancur-Corredor and all authors provided their comments and edited subsequent versions of the manuscript. All authors read and approved the final manuscript.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study is openly available at the BonaRes Repository for Soil and Agricultural Research Data: https://doi.org/10.20387/bonares-eh0f-hj28.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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