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Abstract

The adoption of less intensive soil cultivation practices is expected to increase earthworm populations and their contributions to ecosystem functioning. However, conflicting results have been reported on the effects of tillage intensity on earthworm populations, attributed in narrative reviews to site-dependent differences in soil properties, climatic conditions, and agronomic operations (e.g., fertilization, residue management and chemical crop protection). We present a quantitative review based on a global meta-analysis, using paired observations from 215 studies performed over 65 years (1950-2016) across 40 countries on five continents, to elucidate this long-standing unresolved issue. Results showed that disturbing the soil less (e.g., no-tillage and Conservation Agriculture) significantly increased earthworm abundance (mean increase of 137% and 127%, respectively) and biomass (196% and 101%, respectively) compared to when the soil is inverted by conventional ploughing. Earthworm population responses were more pronounced when the soil had been under reduced tillage for a long time (>10 years), in warm temperate zones with fine-textured soils, and in soils with higher clay contents (>35%) and low pH (<5.5). Furthermore, retaining organic harvest residues amplified this positive response to reduced tillage, whereas the use of the herbicide glyphosate did not significantly affect earthworm population responses to reduced tillage. Additional meta-analyses confirmed that epigeic and, more importantly, the bigger-sized anecic earthworms, were the most sensitive ecological groups to conventional tillage. In particular, the deep burrower *Lumbricus terrestris* exhibited the strongest positive response to reduced tillage, increasing in abundance by 124% more than the overall mean of all 13 species analysed individually. The restoration of these two important ecological groups of earthworms and their burrowing, feeding and casting activities under various forms of reduced tillage will ensure the provision of ecosystem functions such as soil structure maintenance and nutrient cycling by “nature’s plough”.

Conventional tillage decreases the abundance and biomass of earthworms and alters their community structure in a global meta-analysis

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Introduction

Land use and soil management are major drivers of global change, exerting pressures on soils and the ecosystem services they provide (Smith *et al.*, 2016). The foremost factor that determines the direct impacts of human activities on agricultural soils is the intensity of land use, in terms of harvest frequency, usage of agro-chemicals, animal stocking rates, irrigation and tillage. Effects of tillage intensity on soil biological properties and soil biodiversity are also of great interest because firstly, many soil functions are mediated by biological activities and secondly, soil organisms are often used as indicators of the status or 'health' of soils (Doube & Schmidt, 1997; van Capelle *et al.*, 2012; Briones, 2014). In the case of arable land, much research has focussed on the type, depth, frequency and intensity of soil cultivation practices as drivers of environmental impacts, especially in relation to greenhouse gas balances (Six *et al.*, 2004; Lugato *et al.*, 2014; Zhao *et al.*, 2016).

In agricultural soils, earthworms are the key agents in providing essential ecosystem services (Lee, 1985). Earthworms are nature's plough according to Darwin (1881) who first recognised this in his last book by indicating that our lands have been ploughed many times, and still are, well before this human implement was invented more than 4000 years ago.

Directly or indirectly, earthworms play a role in improving soil structure and soil porosity, nutrient cycling, plant growth and plant health. Under conservation tillage systems, earthworms play a more important role than under conventional tillage in the functioning of the farming systems since intensive cultural practices are often associated with decreases in their populations (e.g. Cuendet, 1983; Boström, 1988; Buckerfield & Wiseman, 1997; Curry *et al.*, 2002; van Capelle *et al.*, 2012; Tsiafouli *et al.*, 2015). However, the adoption of more sustainable managed systems does not always result in an increase of earthworm abundance and diversity (Chan, 2001; Berner *et al.*, 2008). This conflicting picture might be the result of failing to examine the effects of conventional tillage under a broader scheme including the levels of tillage, agrochemical inputs, crop residue management, soil factors (texture, pH, soil moisture) and climate (Chan, 2001; Bertrand *et al.*, 2015).

Conventional inversion tillage has not significantly changed since its inception and is usually performed with a mouldboard plough that prepares a clean seedbed by burying all surface residues down to a depth of 20-40 cm, which is aimed at preventing weed, pest and disease proliferation and giving the crop the optimum germination conditions (Gajri *et al.*, 2002). However, when the soil is turned over, earthworms are injured and killed directly, they become exposed to harsh environmental conditions and predators and, in the case of anecic worms (vertical burrowers), their biogenic structures (pores and tunnels) are destroyed and their food sources buried. These actions also bring other undesirable side-effects such as depletion of soil organic matter (Lal, 2013), the deepening of the soil organic layer (Briones & Bol, 2003; Piccoli *et al.*, 2016), plough-pan formation and soil compaction, as well as soil erosion, especially when extreme events (heavy rain, drought and strong winds) hit the bare exposed soil (El Titi, 2003; Vršič, 2011). In addition, the number (secondary tillage/surface tillage after mouldboard tillage) and frequency of the tillage operations (per annum or per seasons) are also known to influence earthworm populations (e.g. Ivask *et al.*, 2007; Capowiez *et al.*, 2009a).

Alternative tillage practices, such as reduced, minimum and zero tillage, reduce the level and intensity of mechanical soil disturbance (Derpsch *et al.*, 2010; Soane *et al.*, 2012; Lal, 2013). They range from reducing the ploughing depth (shallow or superficial tillage), to loosening the soil without turning it (non-inversion tillage), to direct seeding without any soil tillage (no-till). Finally, in recent years conservation tillage/agriculture has been increasingly adopted in which the soil is covered throughout the year, either by a cover crop or by the crop residues from the previous crop (Kassam *et al.*, 2009). However, this is not always the case and sometimes crop residues are used somewhere else or superficially incorporated during seedbed preparation, when machinery for direct seeding is not available. Keeping the soil covered not only helps to prevent erosion but also sustains soil moisture and restores soil organic matter in the root zone (Lal, 2013).

However, soil texture has a substantial influence on the overall benefits of these less soil-disturbing practices. For example, some unstructured light sandy soils might not be suitable for non-inversion tillage because the soil aggregates tend to form a compact structure that prevents air and water flow (Morris *et al.*, 2010). However, since organic matter improves aggregate stability (Ramos *et al.*, 2003), combining non-inversion tillage with practices that increase residue retention helps to reduce soil vulnerability to compaction (Zang *et al.*, 2007) and to encourage earthworms (Baker *et al.*, 1998; Kladivko *et al.*, 1997; Bittman & Kowalenko, 2004).

Furthermore, earthworm abundance and activities are also directly influenced by other soil factors including clay content (Baker *et al.*, 1998) and pH (Edwards & Bohlen, 1996; Lee, 1985), but most importantly by food availability (Curry, 2004). Interestingly, the nature of the organic amendments applied to cultivated soils (e.g. farmyard manures, livestock slurries, composts, biochar, straw, green residues or even stubble retention) has produced contradictory results due to the paucity of the data (Bertrand *et al.*, 2015). Thus, whereas a supply of additional food sources usually promotes earthworm populations (Schmidt *et al.*, 2003; Leroy *et al.*, 2008; Crittenden *et al.*, 2014; Blanchet *et al.*, 2016; D'Hose *et al.*, 2016), other recent studies did not find any significant effect (e.g. Bamminger *et al.*, 2014; Stroud *et al.*, 2016).

Other agricultural inputs such as insecticides, fungicides and herbicides can also affect earthworm populations in different ways (for a comprehensive review on the effects of different pesticides on earthworm species see Datta *et al.*, 2016). In particular, the world's number one herbicide for weed control, glyphosate (N-(phosphonomethyl) glycine), has become of special concern at European scale. It acts through enzyme inhibition in the Shikimate pathway, which is unique in plants, fungi and bacteria for producing aromatic amino acids (Herrmann & Weaver, 1999) and therefore, it was expected to have little or no impact on animals. However, there have been some reports of harmful effects on microorganisms, insects and frogs, which has prompted increased interest in investigating its potential adverse effects on field populations of earthworms (e.g. Givaudan *et al.*, 2014; García-Torres *et al.*, 2014; Gaupp-Berghausen *et al.*, 2015; Garcia-Perez *et al.*, 2014, 2016) and to date, the results vary from negative to no effect.

Finally, the effects of tillage practices on earthworms can also be modulated by climatic factors. While at the global scale temperature and rainfall regimes determine the structure and composition of earthworm communities (Brussaard *et al.*, 2012; Rutgers *et al.*, 2016), at regional and local scales they also have a direct influence on the size of their populations and on their responses to agricultural inputs (e.g. Boudiaf *et al.*, 2015; Velki & Ecimovic, 2015). However, tillage practices can override earthworms' environmental tolerance limits (Nieminen *et al.*, 2011), making it difficult to disentangle the relative significance of each driver on the overall response.

Earthworms are, arguably, the most readily recognised and widely known group of soil animals. Therefore, the effects of tillage practices on earthworms are of very wide interest not only to scientists studying soils, cropping systems and biodiversity, but also to farmers, agronomists and agricultural advisors (Doube & Schmidt, 1997). Since Chan (2001) published his highly cited narrative review paper on the effects of tillage on earthworm communities, more empirical evidence has accumulated on the topic, including studies from under-reported regions, studies on specific effects of tillage systems and/or agronomic practices, and studies that have reported results on individual species rather than total earthworm numbers or biomass. Recent narrative reviews include Bertrand *et al.* (2015) and Datta *et al.* (2016). Considering the variety of interacting factors described above that can alter the overall effect of tillage operations on earthworm populations, a quantitative assessment is urgently needed to provide a more objective and clearer picture than previous reviews based on expert opinion or vote-counting methods (e.g. van Capelle *et al.*, 2012).

Meta-analysis (after Rosenberg *et al.*, 1997) offers a robust methodology for combining data from multiple studies by weighing individual results (by replication and associated error term) and calculation of a standardised metric (effect-size). The objective of the present study was to compile the available experimental field data on tillage and earthworms, and to use meta-analysis to globally quantify the magnitude of the response variable (here, earthworm population sizes) with regard to reduced tillage practices. We also tested whether principal soil characteristics (clay and soil organic C, soil texture and pH) or environmental variables (rainfall) could modulate population responses. In addition, since different degrees of tolerance to soil tillage have been reported depending on the species, ecological groupings (epigeic, anecic and endogeic; *sensu* Bouché, 1977) and maturity stages, we also performed a quantitative analysis of the effects of reduced tillage practices on the species composition and ecological and age structure of earthworm populations.

Materials and Methods

Databases

In our literature survey we attempted to include all available published studies that compared earthworm communities under conventional tillage (our control treatment) and any other forms of "reduced tillage" (experimental group) and that reported earthworm data obtained by using quantitative sampling methodologies (i.e. quadrats, soil cores or blocks). However, we excluded papers based solely on indirect population assessment methods such as earthworm surface casts, middens, macropoes, etc. (e.g. Miura *et al.*, 2008; Singh *et al.*, 2015). Studies were collected from peer-reviewed journals, as well as other sources such as book chapters, PhD dissertations, project reports and conference papers, as a recommended approach to reduce publication bias (McAuley *et al.*, 2000).

We compiled information from each of these papers (sometimes from related sources cited in the papers) on site location (longitude and latitude), year(s) of the study, method for earthworm collection, soil texture class (categorical variables); depth of hand sorting, years of cultivation, % clay, % organic C and soil pH (all continuous variables). In addition, we extracted information on tillage operations, organic amendments and other agronomic practices (details in the following sections; see also Table 1). When the soil properties were reported per soil layer the averaged value of all soil layers was used. Importantly, where a publication failed to report key information, such as soil properties, we either contacted authors/co-authors directly to obtain the missing details, or we used other published literature or data sources from the same site to gather site and soil descriptions and precipitation.

To account for different sampling efforts, all animal census data reported as numerical or graphical data were converted to individuals m^{-2} and g m^{-2} for abundance and biomass data, respectively. In the case of biomass data reported as dry weights or ash-free dry weights (e.g. Haukka, 1988; Parmelee *et al.*, 1990; Jordan *et al.*, 1997a; Hubbard *et al.*, 1999) we used the conversion factor 10 given by Peter & Luxton (1982). Data presented only in graphic format was extracted using DataThief III software (Tummers, 2006).

We selected 215 potential papers published from 1950 to 2016, but only 165 could be included in the analyses due to missing essential data (e.g. errors and/or sample sizes) or lack of a sound treatment comparison (e.g. absence of a true control). Data and metadata from the selected papers that met the criteria were inserted into datasets (Microsoft Excel), with each row representing an 'individual record', i.e. containing earthworm data for tillage comparisons collected from a specific site, soil type and/or crop rotation or fertilisation management. When results from the same experiment were reported in different papers by the same or different authors, the most complete source of information, containing the longest investigated period, was selected (e.g. Hendrix *et al.*, 1992 and Parmelee *et al.*, 1990; Eichhorn & Tebrügge, 1990 and Henke, 1994; Söchtig, 1992 and Söchtig & Larink, 1992; Radford *et al.*, 1995 and Wilson-Rummenie *et al.*, 1999; Jordan *et al.*, 1997a,b; Pothoff, 1999 and Potthoff & Beese, 1998; Emmerling, 2001 and Webber & Emmerling, 2005; Fortune *et al.*, 2003, 2005 and Kennedy *et al.*, 2013; Riley *et al.*, 2008 and Pommeresche & Loes, 2009; Laszlo, 2007 and Birkas *et al.*, 2010; Joschko *et al.*, 2009, 2012, Severon *et al.*, 2012 and Schirrmann *et al.*, 2016). Similarly, if two papers reported results from the same experiment, but with sampling being performed in different seasons of the same year(s) or two consecutive years, the results from those samplings were averaged to produce one record for each experimental site (e.g. Krabbe *et al.*, 1993, 1994; Tan *et al.*, 1998, 2002; Stancevicius *et al.*, 2003 and Jodaugiene *et al.*, 2005). The only exceptions to this were when separate publications based on the same field experiment were the only source for building one of our specific databases (e.g. total biomass or abundances of single species, ecological groupings; see section dealing with earthworm data). In these cases, the publication was used to build that specific database irrespective of the length of the investigated period; in any case, two papers reporting the same study never contributed to the same dataset. Table S1 (supplementary material) shows a summary of the publications that contributed to each of the databases.

Reporting of results from a study with an associated error term (standard error, standard deviation, 95% confidence limits, percentiles or CV), together with the sample size (N), enabled the ready incorporation of these data into the databases. Furthermore, in the case of longstanding and well-documented studies, N was calculated as the number of replicate plots/sites × number of study years, only if sampling was done repeatedly over years, to give more weight to these longer-term studies in the analyses. This was done to avoid the ambiguity associated with extracting a single data point per measurement time series (Curtis *et al.*, 2013) and to enable the comparisons between shorter and longer duration studies.

If the errors were reported as SED or LSD (i.e. the error value was associated with a difference between two means (pooled error estimate)) or if the type of error was not specified, we chose to calculate a new error for each treatment by averaging sampling times or rotations (see Table S1). However, in some cases, this was the only way to include these papers: Ellis *et al.* (1977); Barnes & Ellis (1979) (sites B clay winter wheat, Berkshire and Oxfordshire); Mallet *et al.* (1987); Karlen *et al.* (1994); Radford *et al.* (1995); Aslam *et al.* (1999); Hutcheon *et al.* (2001) (single species dataset); Carter *et al.* (2002); Pekrun *et al.* (2003); Zida *et al.* (2011) and Kennedy *et al.* (2013). Similarly, if a particular study totally failed to report the error associated to the mean, but showed data separately for several sampling dates (months, seasons), crop rotations, different sites, fertilization rates or soil types, the average value and associated error was calculated. This was a compromise to be able to include a number of these studies in the meta-dataset; however, in these particular cases, in order to decrease their weight in the analyses, the sample size was considered to be the number of values used to calculate the mean and SD. There were a few articles in which, although errors were reported, the image quality of the figure provided in the paper did not allow for an accurate extraction of the essential data (mean and error) and hence, as before, the individual means for each sampling occasion were averaged to obtain the mean and the associated SD and N values. In addition, a small number of studies provided multiple tillage comparisons but without errors. In this case, when the two most intensive and the two most reduced interventions rendered similar earthworm results, we paired and averaged them to get an SD for each combined tillage treatment (N=2). Finally, because a number of studies (especially in the ‘grey literature’) only reported one single record (N=1), they could not be used for meta-analysis purposes.

As a result, three studies, despite reporting earthworm abundance data and meeting the meta-analysis criteria (see above), had to be removed from the meta-dataset due to mean and variance values of either control or experimental groups being equal to zero, which impeded the calculation of the effect size metric (LnR). The final number of articles that contained useable earthworm abundance and biomass information (145 and 85, respectively) contributed with 284 and 157 observations, respectively, to these two databases used in the subsequent analyses.

Mean annual rainfall (MAR) values for each study site were obtained from each publication, if provided. When MAR was not reported in the original paper, or could not be obtained through personal communication, values were obtained from the Meteorological Office Tables (1982) and from Müller (1982) for the nearest location at similar altitude. Climate zones were established using the Köppen classification system (Köppen, 1923, 1931), which divides the Earth into five main climate categories (A=tropical rain climate without cool season, B=dry climates, C=warm temperate climates, D=snow climates and E=ice climates) and with further sub-divisions according to the seasonal distribution and amount of rainfall and to the winter and summer temperature regimes (f=sufficient moisture in all months; s=dry season in the summer of the respective hemisphere; w=dry season in the winter of the respective hemisphere).

Tillage categories, food inputs and crop protection factors

In his review, Chan (2001) pointed out that it is virtually impossible for a reader to understand all the regional differences in terminology and characteristics of all the tillage implements reported in the literature. Furthermore, many authors did not properly report the tillage operations (primary and secondary) performed for different cultivation treatments, or the type, dosage and timing of agrochemicals applied and/or how the crop residues were treated (i.e. intact/shredded/chopped, left on the surface/incorporated into the soil, burnt or not, etc.). Therefore, in order to avoid random exclusion/inclusion decisions, we adopted a pragmatic attitude and compared some form of 'intensive/conventional' tillage implemented in the local area or region against a 'reduced/minimal' version.

Accordingly, five categories of reduced tillage were defined (Table 1), as compared to “Conventional tillage” (**CT**), the Control, which usually refers to inversion tillage down to a depth of 25 cm or more and typically using a mouldboard plough, as follows: 1) “Reduced tillage” (**RT**), which involves shallow ploughing (usually less than the top 15 cm gets turned over); 2) “Deep soil loosening non-inversion tillage” (**DSL**), defined as vertical tillage where the soil is loosened, broken or lifted to a depth greater than 15 cm but not inverted (typically by using a chisel plough or other tined tools); 3) “Shallow soil loosening non-inversion tillage” (**SSL**), as a tillage operation where the soil is loosened to a depth of no more than 15 cm; 4) “No-tillage” (**NT**), with minimum or no soil disturbance other than a small incision for placing the seed (usually called “direct drilling”, “direct seeding”, “no-till) and 5) “Conservation agriculture” (**CA**), defined in the literature as those systems with hardly any soil disturbance and a permanent cover of the soil surface (usually by leaving at least >30% of the previous crop’s residue or by having the ground surface covered with dead or living mulch). However, we also decided to include in this last category those NT treatments where crop residues were left on the surface, but removed from the CT treatments. This allowed us to differentiate these studies from most reported cases where residues were removed from both CT and NT.

In addition, we also included a very small number of other studies, which did not compare tillage treatments specifically, but different ploughing depths (e.g. 15 cm vs. 25 cm; Söchtig, 1992; Söchtig & Larink, 1992; Bakken *et al.*, 2009). In this case, the most intense tillage treatment was selected as CT and the other treatments with minimum or zero loading were classified as CA in the meta-dataset.

Studies that included additional organic matter applications (e.g. straw, organic or green manures, mulching and cover crops) or specific residue management practices (e.g. burning) were only included in the meta-dataset if they were applied in a comparable fashion to both the CT and the other form(s) of reduced tillage investigated. For example, when different fertilisation inputs were superimposed onto the main tillage treatments, they were computed as two different records (e.g. CT+mineral fertiliser was compared to NT+mineral fertiliser and CT+organic fertiliser to NT+organic fertiliser). These subsets of studies were also used for additional meta-analyses to enable the distinction between the effects of the level and/or frequency of disturbance (i.e. tillage) and those derived from the amount and/or quality of food (i.e. linked to organic residues) added. Accordingly, we established a new grouping variable called ‘food inputs factor’ to distinguish between those studies where the organic material retained in the CT and NT treatments either came from a secondary crop and was incorporated as ‘green’ material (=cover crop, green manure, catch crop etc.) or if they were true ‘harvest residues’ derived from the main crop (i.e. straw, stubble etc.), which are not green and low in N and that could be burnt or not (stubble), or whether they were supplied in the form of ‘animal manure’ (i.e. derived from cattle or poultry) that are high in N. This enabled us to compare systems that included food addition with those where the crop residues were exported (‘removed’).

Similarly, in order to have a measure of the effects of agrochemical inputs on earthworm populations we also created another grouping factor called ‘crop protection’. In this case, we aimed to compare the effect of tillage in relation to the use different types of pesticides and herbicides, with special attention to the use of glyphosate, a broad-spectrum herbicide at the centre of current debate (see Introduction).

Other studies on earthworm populations that compared farming systems (e.g. conventional *vs.* organic farming systems) or agronomic treatments where only one tillage form had cover or catch crops, as well as those comparing land-use conversions (e.g. from tilled plots to grassland) were not included. In a few cases, data from the published literature originated from factorial experiments (i.e. tillage regimes × cropping systems × fertilization regimes) and, in these cases, the data inputted in the meta-dataset for tillage represents a combination of the other factors (e.g. Rovira *et al.*, 1987; Reeleder *et al.*, 2006; Marchão *et al.*, 2009).

Earthworm species, age and ecological groups

The available literature data are presented variably as populations of different species, a few species or for the whole community (see Table S1). This issue was resolved through the construction of two separate subsets of data: (1) total numbers and biomass of earthworms and (2) abundances of every single species. However, when only one species was identified and it was highly dominant (i.e. representing >80-90% of the total population) then the collated data contributed to the total numbers meta-dataset and also to the subsidiary species-specific one. This was the case of Tanck *et al.* (2000) (*Amynthas* spp. only); Clapperton *et al.* (1997), Clapperton (1999) and Rosas-Medina *et al.* (2010) (*Aporrectodea caliginosa*); Hubbard *et al.* (1999) (*A. trapezoides*); Reeleder *et al.* (2006) (*A. turgida*); Errouissi *et al.* (2011) and Mallett *et al.* (1987) (*Lumbricus terrestris*); Zida *et al.* (2011) (*Dichogaster affinis*); Brito-Vega *et al.* (2009) (*Phoenicodrilus taste*); Domínguez & Bedano (2016) (*Microscolex phosphoreus*). Subsequently, we analysed the abundances of the most reported species in the literature to test if certain species were more sensitive than others to reduced tillage practices.

In addition, a small number of papers also provided information about the age and the ecological structure of the earthworm communities which allowed us to build two additional meta-datasets: (3) abundances of mature (adults and subadults) and immature individuals and (4) numbers of worms in the epigeic, anecic and endogeic ecological group. Since juvenile earthworms usually constitute the majority of the individuals in these agricultural soils (e.g. Marwitz *et al.*, 2012; Domínguez & Bedano, 2016) and since they can be very sensitive to tillage (e.g. Ulrich *et al.*, 2010), it is important to determine the effects of management practices on this seldom measured component of earthworm populations. Similarly, because the ecological classification of earthworms clearly reflects where they preferentially feed and burrow (*sensu* Bouché, 1977), the effect of tillage practices is expected to have a stronger effect on those species linked to the surface layers (i.e. epigeics and anecics) that are more exposed to disturbance than on those building horizontal burrows in the deeper mineral layers (i.e. endogeics).

2.3. Grouping variables

In the case of some categorical and numerical variables, pre-grouping is needed before conducting meta-analyses in order to achieve maximum in-group homogeneity (Jeffery *et al.*, 2011). Accordingly, soil texture was grouped into three broad classes: clayey, sandy and loamy/silty, either as it was reported in the paper or as estimated from the particle size distribution using an online calculator (http://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/?cid=nrcs142p2_054167). Earthworm extraction methods were classified into five groups: hand-sorting, chemical extraction (formalin, mustard or permanganate), chemical+hand-sorting (i.e. combination of the two previous methods), electrical (octet method) and 'other methods' which included the less commonly used techniques for collecting earthworms (Berlese, wet-sieving, and the combination of electrical and hand-sorting).

In the case of continuous variables (such as rainfall, soil clay and soil organic C contents, soil pH, ploughing depth and years of cultivation), the use of ungrouped data would have led to a substantial loss of information. This can be related to the high precision of their measurements, which typically results in an insufficient number of records within each group (see for example, Jeffery *et al.*, 2011). To group variables uniformly across studies and to avoid subjective intervals, the groupings were established according to criteria used in well referenced world databases. For example, MMR values are typically plotted in 100, 200 or 500 mm intervals (e.g. http://www.ncdc.noaa.gov/cag/time-series/global) and here they were classified into three groupings: <500, 500-1000 and >1000 mm. Similarly, following the codesets proposed in the Harmonized World Soil database (Nachtergaele *et al.*, 2008), we classified the clay content values across studies by grouping the data according to three simplified topsoil textural classes: 'coarse textured soils' <18% clay, 'medium textured'

18%-35% clay and ‘fine textured’ >35% clay. Equally, we also followed this recommended classification for grouping organic C contents: <0.6%, 0.6-1.2%, 1.2-2.0% and >2.0%. Finally, in the case of soil pH, three categories were used: ‘very acid soils’ pH <5.5 ‘acid to neutral’ pH = 5.5-7.2 and ‘carbonate rich soils’ pH>7.2, to take into account the pH dependence of aluminium solubility and possible toxic effects (Haynes & Mokolobate, 2001; Nachtergaele *et al.*, 2008).

In addition, the ploughing depth varies with effective root zone of the crop and has important implications for water storage and nutrient availability (Riley & Ekeberg, 1998). We therefore grouped the information about depth of ploughing in the CT treatment into three classes: ‘shallow ploughing’ (<20 cm), ‘normal mouldboard ploughing’ (20-25 cm) and ‘deep ploughing’ (>25 cm), according to the definitions found in the published literature (e.g. Kouwenhoven *et al.*, 2002; Bakken *et al.*, 2009; Parvin *et al.*, 2014).

In the case of food inputs, due to the paucity of the data, we classified the selected studies into just two categories: ‘with organic matter (OM) additions’, including all those papers where *any* kind of organic material was added to all the tillage treatments compared (see above), and ‘without OM additions’ referring to all those papers in which no organic materials were added to the experimental plots and all crop residues were removed from the fields. Similarly, we established three classes for the agrochemical grouping variable: ‘P’ when standard pesticides were applied to the experimental treatments, ‘HnoG’ when herbicides was used but glyphosate was not one of them, and ‘G’ when glyphosate was included in the crop protection management practices.

Finally, the studies reported in the selected papers included in our meta-analyses showed great variability in relation to the numbers of years of controlled cultivation, ranging from <1 year to 48 years, with the majority being cultivated for fewer than 10 years. It is known that long- and short-term cultivations can have different effects on soil properties (Mubarak *et al.*, 2005). Therefore, in order to examine the effects of agricultural history and length of field experiments on the responses of earthworm communities we established three categories for the duration of cultivation: <10 years, 10-20 years and >20 years.

2.4. Meta-analyses

We used meta-analysis techniques (Rosenberg *et al.*, 2000) to determine the effect of tillage on earthworm populations. Calculations were based on random effects models (Hedges *et al.*, 1999; Rosenberg *et al.*, 2000). In the categorical random effects model, groups with fewer than two valid studies were excluded from each analysis. Resampling tests were generated from 999 iterations.

We defined the "control" group in the meta-analyses to be the conventional treatment and the "experimental" groups all five other tillage practices (RT, DSL, SSL, NT and CA) in which densities were expected to be higher than under conventional, more intensive agricultural cultivation. We calculated the mean effect size using MetaWin Version 2 statistical software (Rosenberg *et al.*, 2000) as a weight cumulative effect size based on the variance of the sample and expressed as the natural logarithm of the Response Ratio (R):

$$LnR = Ln\left(\frac{\overline{X}^{E}}{\overline{X}^{C}}\right)$$

where $\overline{X}^{E}$ is the mean earthworm abundance or biomass in the experimental treatment and $\overline{X}^{C}$ is the mean earthworm abundance or biomass in the control treatment (CT). The reason for using the natural logarithm is that it linearizes the metric and reduces the skewness of the sampling distribution of R (Hedges *et al.*, 1999).

To test the effects of publication bias (Rothstein *et al.*, 2005), we used the Fail-safe N technique (Rosenthal & Rosnow, 1991). This involved computing the combined P value for all of the studies included, and calculating the number of additional studies showing no effect (i.e. average Z value of 0) that would be needed in order to change the P value from significant to non-significant at P = 0.05. Therefore, the robustness of the findings of the meta-analysis is directly correlated with the size of the Fail-safe N number.

All graphical outputs are forest plots showing the effect size (LnR) calculated from each group. On the X-axis, the ‘effect size’ was exponentially transformed and reported as the percentage change in earthworm populations (abundance or biomass) (i.e. [R − 1] × 100; Jeffery *et al.*, 2011). Therefore, each point represents the mean effect size for each grouping, with the horizontal error bar lines indicating the 95% confidence intervals (CIs). All graphs display the grand mean effect at the top and then in decreasing order of effect size values, except in the case of continuous variables, where the categorical groups were defined according to intervals (i.e. rainfall, % clay, % C, soil pH, ploughing depth and years of cultivation; see above) which are shown sequentially.

Finally, we used meta-regressions (Borenstein *et al.*, 2009) under random model effects to assess the relationship between the effect size (LnR; dependent variable) and each of the six continuous independent variables (rainfall, clay and organic C contents, soil pH, ploughing depth and years of cultivation). The significance level of the heterogeneity of the model (Q_M), i.e. the variation in the effect sizes that is explained by the model, was tested against a χ^2 distribution with 1 degree of freedom which is equivalent to calculating the significance level of the slope against a normal distribution (Rosenberg *et al.*, 2000). From this, a significant Q_M means that the independent variable explains a significant amount of the variability in effect sizes and a significant Q_E (amount of residual error heterogeneity) implies that there is still heterogeneity among the effect sizes that is not explained by the model.

Results

Total earthworm abundance and biomass

From the larger abundance dataset, it can be seen that although the majority of the investigations were performed in Europe and America (in particular, North America), studies from Africa (Tunisian Republic, Burkina Faso and the Republics of Cameroon, Kenya, Malawi, Zambia, Zimbabwe, South Africa and Madagascar), Oceania (5 studies from Australia and 4 from New Zealand) and Asia (Iran, India, China, Japan) also contributed to the meta-analysis (Fig. 1).

Rosenthal's Fail Safe N for the abundance data ranged from 1,024 to 25,171 and in the case of biomass, from 200 to 13,779, with the lowest values obtained for those grouping classes that only included very few studies due to the paucity of data (e.g. food inputs and crop protection grouping factors). Nonetheless, even in those cases, a minimum number of 200 observations with an average Z value of zero would have been needed to significantly change the outcome of the meta-analyses of these two datasets. In contrast, a much larger number of these observations (>13,000) would have been needed to reach different conclusions for tillage treatments, rainfall and climate zone, sampling method, soil texture and years of cultivation. Consequently, we can conclude confidently that publication bias in our literature survey was highly unlikely to have a significant effect on the interpretations and conclusions.

Influence of sampling methods

The percent response to a change in tillage practices (i.e., "conventional" *vs.* "other forms of reduced" tillage) calculated separately for earthworm sampling methods showed that with the exception of the octet method, all collection techniques detected significantly greater abundance and biomass in soils under reduced tillage than under conventional treatments (Fig. 2). The sample means of the different techniques were not significantly different between them ($p > 0.05$), reflecting that hand-sorting (the most commonly used method by researchers), chemical expulsion using formalin or mustard and the combination of these two methods seem to be similarly efficient in estimating earthworm populations (both abundance and biomass) in agricultural soils (Fig. 2). In the two earthworm datasets, the 'other methods' category, encompassing a small number of studies with miscellaneous methods, such as wet sieving, Berlese extractors and the combination of hand-sorting with electrical or soil sieving, had variable results, but recorded a greater treatment effect than the other sampling techniques (Fig. 2).

Influence of tillage and other management practices

Significantly larger earthworm populations, in terms of abundance and biomass, were observed with decreasing intensity in agricultural management ($p < 0.05$; Figs. 3a,b). No-tillage and conservation agriculture resulted in the greatest percentage of change in earthworm populations compared to conventional controls (abundance: 137% and 127% and biomass: 196% and 101% under NT and CA, respectively). With other tillage categories, the more the soil was disturbed, the less beneficial the effects on earthworms were, with deep soil loosening (non-inversion tillage) and reduced (inversion) tillage having similar effects to the conventional practices (Figs. 3a,b).

The depth of ploughing during conventional tillage practices also affected earthworm populations, although the overall effect of this classification factor was not significant. However, for both data sets working depths less than 20 cm tended to have the greatest positive effect size, reflecting a larger increase in earthworm biomass and abundance with reduced tillage (Figs. 4a,b).

The importance of how deep soil is conventionally ploughed in controlling earthworm populations was also partially evidenced by a negative relationship between the effect size metric and this variable, with the model being statistically significant for earthworm numbers but not biomass (Fig. 5). Furthermore, although the meta-regression model for abundance data showed the best goodness of fit, in both cases there was a significant amount of heterogeneity in the data, which was not explained by the model (Fig. 5).

Another important effect agricultural management had on earthworm populations was related to the availability of organic materials (OM). The presence of a catch crop, of crop residues from the previous year (either left on the soil surface or incorporated into the soil) and/or the addition of organic amendments (such as animal manures) provide food and habitat space for earthworms in these cultivated soils. Consequently, a greater positive effect of reduced tillage intensity on earthworm populations was observed when any of those supplementary food materials were provided in field studies compared to when they were removed (Figs. 4c,d), with the results being significant for the abundance data only ($p = 0.020$; Fig. 4c).

Surprisingly, the effects of reduced tillage intensity on earthworm population sizes, categorised by the use of crop protection substances, were not statistically significant ($p > 0.05$) and with the outcome of using pesticides showing the more variable results (Figs. 4e,f). However, when herbicides were added, a positive effect on earthworms was observed, with glyphosate having the greatest positive effect (Figs. 4e,f).

Finally, earthworm population sizes tended to show a greater response to reduced tillage over time (Figs. 4g,h). This effect was significantly greater for studies with cultivation treatments in place for at least 10-20 years (126% and 137% change in abundance and biomass, respectively) compared to studies with cultivation duration of fewer than 10 years (64% and 73% positive effect for abundance and biomass, respectively). Because the number of studies that included sites cultivated for more than 20 years was low, the response ratio for this categorical class showed a much greater variability (Figs. 4g,h).

These results for duration of experimental treatments were borne out further by the outcome of the meta-regression analyses (Fig. 6), indicating that the slope in both regression models (abundance and biomass) was probably not zero, which suggests that the longer the duration of reduced cultivation, the larger earthworm population will be (Fig. 6). Even though both meta-regression models were significant, there was an important amount of heterogeneity in the two data sets that was not fully explained by the number of years the land had been under cultivation.

Influence of climatic factors

The response ratio of earthworm abundance and biomass to change in tillage practices was significantly affected by annual rainfall amounts ($p = 0.022$ and $p = 0.008$, respectively; Figs. 7a,b). Although there was a positive response for each of the three categories, a significantly greater response in earthworm abundance and biomass was observed in more humid areas (>1000 mm per annum) compared to study sites where the mean annual precipitation ranged between 500 and 1000 mm (Figs. 7a,b). In addition, low rainfall (<500 mm) values were also associated with positive increases in earthworm populations in the less intensively tilled soils (Figs. 7a,b). These results were borne out further when the data were categorised according to climate zones ($p = 0.002$ and $p = 0.008$ for abundance and biomass, respectively; Figs. 7c,d), with the largest effect on earthworm populations being observed in cold climates with a dry season in the winter (Cw). Significantly lower, but still positive effects, were also found in C (dry) and D (snow) climates with sufficient moisture all months (Cf and Df). Even warm tropical rain climates, with monthly temperatures $>18^{o}$C all year round, promoted earthworm abundances under reduced tillage operations, but only if a dry period occurred in the winter (Figs. 7c).

This positive response of earthworm populations under all rainfall categories explains the absence of a significant regression relationship between the response ratio of earthworm numbers and biomass and rainfall amounts when analysed as a continuous variable ($p > 0.05$; results not shown).

Influence of soil factors

Earthworm numbers and biomass responses to changes in agricultural management also varied with soil texture, although the overall effect of this grouping variable was not statistically significant, likely due to large variance of the few studies conducted on sandy soils (Figs. 8a,b). However, all soil textural classes analysed here showed a positive effect on earthworm population sizes. In the case of abundance, a statistically significant increase was observed for clayey soils compared to loamy textures (Fig. 8a), whereas these two soil textures rendered similar results for the biomass data (Fig. 8b).

By contrast, when grouping the response ratios by percentage clay classes (Figs. 8c,d), there was a significant effect of soil clay content on earthworm abundance ($p = 0.011$), and the result for earthworm biomass was marginally significant ($p = 0.07$). In both cases, the highest clay content was associated with the largest effect on earthworm populations (on average, 167% and 209% change when soils contained >35% clay; Figs. 8c,d), with the differences to the soils with least clay content (<18%) being significant.

This positive relationship between the response ratio of earthworm populations (numbers and biomass) and soil clay content was also confirmed by the results from the meta-regression analyses (Fig. 9), indicating that significant increases in earthworm communities under less intensive cultivation occurred on soils with finer textures. However, in the case of the biomass data, although the clay content explained a significant amount of variation in the response ratio, there was still heterogeneity not being fully explained by the model (Fig. 9b).

There was no statistically significant effect of reduced tillage practices on earthworm abundance and biomass when the soils were classified according to their organic C contents (Figs. 8e,f). All four analysed intervals showed positive effects, but larger effect size trends relative to the control tillage treatment were observed for the lower organic C contents (<0.6% in the case of abundance data and less than 1.2% for biomass). There were no significant differences between the four categories tested (i.e. <0.6%, 0.6-1.2%, 1.2-2.0% and >2.0%) and accordingly, the meta-regression analyses also failed to produce a significant relationship between Ln(R) and the soil C contents reported in the literature ($p > 0.05$; results not shown).

Finally, the response ratio of earthworm abundance and biomass to less intensive cultivation was significantly affected by soil pH ($p = 0.005$ and $p = 0.027$, respectively; Figs. 8g,h). Even though there was a positive response for the three categories tested, a statistically significant increase in earthworm populations was observed in the acidic soils (pH < 5.5), despite the fact that the studies comprising this category showed the greatest variance. This result was also confirmed by the negative relationships, albeit not significant, between the response of earthworm populations to reduced tillage and the soil pH values recorded at the investigated sites $p > 0.05$; results not shown).

Community structure

Sixty papers provided information about abundances of different earthworm species under conventional and "other reduced forms of tillage"; however, only 51 studies met the meta-analyses criteria and contributed with 260 records for a total number of 31 species. Unfortunately, just over a third of these species were only reported in single published articles (i.e. N = 1), which did not allow the calculation of the response ratio. In addition, a small number of species were recorded in 2-3 studies, which resulted in their associated variance values being, in some cases, up to 20 times higher than for the rest. Therefore, Fig. 10a only shows the response ratio of the 13 most frequently reported species to reduced tillage intensity. It can be seen that grouping the data according to earthworm species composition showed a statistically significant effect of reduced tillage on earthworm species' abundances ($p = 0.001$). Furthermore, significant increases in the abundances occurred for the majority of the species reported in the literature, with the largest effects being observed for *Lumbricus terrestris* and *L. rubellus*. Only three species (recorded in a small number of studies) showed no statistical significant response to changes in tillage, namely *Aporrectodea icterica*, *A. trapezoides* and *A. turgida* (Fig. 10a).

Age structure

A limited number of papers (29) reported data on the numbers of mature and immature worms collected from each of the tillage treatments, but after removing all those studies that did not meet the meta-analysis criteria, only 23 papers contributed to the metaset providing 76 records on age classes.

The meta-analyses of this much smaller dataset revealed that applying other forms of reduced tillage had a slightly stronger effect on adult worms than on the immature ones (Fig. 10b), but the difference between these two life cycle stages of earthworm was not significant.

Functional groups

Among the literature reviewed, 43 papers included information about the responses of the three well recognised earthworm ecological groupings (epigeic, anecic and endogeic worms, *sensu* Bouché, 1977). After a thorough checking for their suitability for meta-analysis purposes, 39 studies were included in the metaset, contributing 174 records.

The result of this meta-analysis highlighted the significantly stronger responses of the epigeic and anecic worms to reduced forms of tillage than those exhibited by the endogeics, although all three groups showed a significant positive response ($p = 0.001$; Fig. 10c). Indeed, the former two ecological groups showed an overall increase greater than 100% (117% and 123%, respectively) when tillage was reduced.

Discussion

Overall, the results of this meta-analysis demonstrate that earthworm population sizes increase when tillage intensity is reduced, reaching the highest values when the least intensive practices, i.e. no-till and conservation agriculture, are applied. This effect was consistent across the two databases analysed (abundance and biomass); however, besides tillage, other agronomic and environmental factors (e.g. organic matter additions, climatic conditions and soil characteristics) modulated the observed responses.

General effects of reducing tillage intensity on earthworm abundance and biomass

From our extensive global review it is clear that, besides the direct effects of the different tillage implements used to prepare the soil for planting (mouldboard plough, chisel, disk, harrows, etc.), the intensity (i.e. how deep is the soil disturbed) and other agronomic practices (e.g. handling of crop residues) also have strong influences on earthworm populations (Edwards, 1983; Lee, 1985; Ivask *et al.*, 2007). Consequently, the entire ‘cropping calendar’ (encompassing tillage operations, planting, fertilising, adding crop protection substances, harvesting and handling the crop residues) determines the overall outcome of the impact of tillage on earthworms and could explain the inconsistent results reported in the literature (see for example Chan, 2001 for a general overview of these conflicting views).

Furthermore, in agreement with several individual studies (Gerard & Hay, 1979; Bogužas *et al.*, 2010), we found a significant negative relationship between ploughing depth and earthworm abundance. Interestingly, our meta-analyses also confirmed that the shallower the soil inversion is, the greater the chance that the resilient populations would recover and build larger numbers under reduced tillage (Gerard & Hay, 1979), also possibly helped by less alterations in water stable aggregates (Bogužas *et al.*, 2010) and organic matter distribution along the soil profile (Briones & Bol, 2003; Piccoli *et al.*, 2016).

Regarding how frequently the soil is ploughed, among the studies included in our meta-analyses, only eight trials specified that ploughing was performed only once a year (usually in autumn/fall period), another four papers indicated that this operation took place in spring and one that the soil was ploughed in both seasons. However, the vast majority of the published papers merely stated 'annual ploughing', 'conventional ploughing' or 'mouldboard ploughing' without specifying when exactly this operation took place. It has been noticed that this lack of detailed descriptions of tillage practices in the published reports is also to blame for the contrasting findings reported by the different authors (Chan, 2001). Despite some studies reporting that spring ploughing was particularly negative for immature worms (De St. Remy & Day-Nard, 1982; Marinissen, 1992), their results were inconclusive probably because of the confounding effects of samplings at specific times when favourable climatic conditions and organic applications took place.

Another interesting aspect that contributes to the conflicting picture of the effects of tillage on earthworms is the land use history, i.e. how many years the soil has been cultivated, what the previous use of the land was and how much time has passed since its last conversion to arable land. This is important because the ability of earthworm communities to adapt to a soil environment that has been ploughed once or several times every year is expected to increase over time, as the more resilient species will remain in the community. Therefore, soon after land use conversion, mortality rates are expected to be higher than in those soils that have been cultivated for many years, but food supply can also be higher temporarily for instance after grassland conversion (Edwards, 1983), and individual fields will differ in their suitability for recolonization by earthworms from field margins (Roarty & Schmidt, 2013). Therefore, the available literature offers contrasting responses, ranging from prompt recoveries after a few months (e.g. Marinissen, 1992) to population numbers remaining very low after many years of cultivation (25-30 years; e.g. Barley, 1959; Low, 1972), but also either increases and decreases at time intervals of just a few years (<10 years; see also Chan, 2001 for detailed descriptions).

In our quantitative survey, we found a very strong positive response of earthworm populations to reduced tillage operations when the soil had been under reduced tillage for a long time (>10 years) and significant percentages of change in both earthworm numbers (117-126%) and biomass (75-137%) were observed. The limited number of long-term studies (>20 years) did not allow us to reach a clear conclusion on earthworm population recovery from conventional tillage in the long-term. However, the fact that the two means (abundance and biomass) for this effective class were greater than the grand mean suggest that a similar trend is expected, although it will need to be confirmed in future research. The discrepancy with those studies reporting rapid recoveries after conversion to reduced tillage can be explained by the confounding effects of other factors besides tillage; for example, by having legumes as a catch crop (Boström, 1995), the application of manures (Marinissen, 1992), the presence of large, species-rich earthworm communities in field margins and/or the use of unrealistically small plots in experiments that can be recolonised quickly (Roarty & Schmidt, 2013) or by more favourable weather conditions for earthworm reproduction at the time of the sampling (e.g. Curry, 2004; see also above).

Leaving the crop residues after crop harvest instead of removing them from the fields in preparation for the next cropping season is another major factor that likely explains the contrasting observations in earthworm responses to tillage in the literature (Curry, 2004; Schmidt et al., 2003). Crop residue retention provides a protective layer that prevents soil water evaporation and supplies additional food for earthworms (Curry, 2004). It also increases cation exchange capacities over time due to the accumulation of organic carbon in the top soil. Certain management practices, such as burning the straw residues after harvest, have negative effects on carbon sequestration, with 36% losses in the top after 100 years of annual burning compared with areas that were not burned (Spagnollo, 2004). In spite of the ecological importance of residue handling, very few studies across our literature survey provided detailed descriptions of how the harvest residues were managed and whether other organic materials such as green residues and/or animal manures were added in the control and experimental treatments under comparison. However, the information provided by the studies available allowed us to confirm that adding a potential food source for earthworms amplifies their response to reduced tillage, in other words, reduced disturbance combined with larger food supply increases earthworm populations greatly (Schmidt *et al.*, 2003). The results from our meta-analyses for residue additions were significant for earthworm numbers but not for biomass, possibly due to the difference in the number of observations included in each data set (69 vs. 31) and hence, in the number of degrees of freedom. It should also be pointed out that in our meta-study we included in the “conservation agriculture” category all those experimental designs in which the no-till treatments retained the crop residues but that were removed from the control plots, with the aim of counteracting for the change in another important factor besides the tillage. However, the dataset also contained a few studies that compared conventional agriculture with other forms of reduced tillage (shallow and deep soil loosening) in which crop residues were used as mulch, which makes it very difficult to separate the effects of each factor.

Intensive agricultural production systems often involve the application of various chemical substances with the aim of protecting the growing crop against damage by pests and diseases. Even in less intensive systems the use of synthetic pesticides is widespread and of environmental concern due to their long persistence in the soil (Srimurali *et al.*, 2015). Their toxic effects could reach non-target organisms such as earthworms and decrease their survival and reproduction rates and affect their behaviour (see review by Datta *et al.*, 2016). However, the results of our meta-analyses showed an enormous variability in the responses of earthworms to pesticides, likely due to the fact that more than one type of chemical compound were involved and that very often cocktails of herbicides, fungicides and insecticides are applied to the soils or as seed dressings. Specifically, we did not find any significant effect of the use of glyphosate on earthworm populations and both abundance and biomass tended to be even greater when this herbicide was used in the fields (on average 35% increase compared with the overall mean). Other studies did not observe any detrimental effects of this broad-spectrum herbicide on earthworm populations (Fusilero *et al.*, 2013) and in some occasions the response was species dependent (Givaudan *et al.*, 2014) or being modulated by other factors such as a reduction in root colonization by arbuscular mycorrhizal fungi (Zaller *et al.*, 2014). Different herbicide dosages, combinations with other agrochemicals and the fact that this kind of research has been usually performed under laboratory conditions might explain the differences and highlights the need for more field research to clarify whether the observed increases are the result of direct or indirect effects.

The modulating effects of abiotic factors

Across all five continents and all climates, the response of earthworm populations to decreasing tillage intensity was greater in warm temperate climates with a dry season in the winter and warm/hot summers (i.e. with at least 4 months of mean temperatures above 10^{o}C) according to the Köppen classification system (1923, 1931). This highlights the important role of temperature and moisture gradients on earthworm population dynamics and their seasonal variations across the globe (e.g. Lavelle & Spain, 2001; Moron-Rios *et al.*, 2010; Najar & Khan, 2011; Redmond *et al.*, 2014; Hackenberger & Hackenberger, 2014; Kanianska *et al.*, 2016). Accordingly, seasonal mortality rates have been attributed to water shortages, but high rainfall conditions have also been linked to earthworm declines due to the low nutrient status of these moist soils (Fragoso & Lavelle, 1992). However, the optimum values for earthworm activities and reproduction might vary for different species and ecological groups (Curry, 2004). This might explain why our meta-analyses results showed the contrasting result of having more positive responses of earthworms to reduced tillage either in rainy areas (>1000 mm on average per year) or in regions with low annual precipitation values (<500 mm). Furthermore, wet cultivated soils are more prone to soil compaction (tillage-pan formation) and several studies have reported earthworm avoidance of and higher mortality rates in soils degraded by compaction and tillage-pans (Radford *et al.*, 2001; Birkas *et al.*, 2004; Capowiez *et al.*, 2009b). Therefore, the recovery of the earthworm populations (or more specifically, of the resilient species/ecological groupings) might be encouraged by drier conditions. On the other hand, positive responses in dry climates can also be expected because reduced tillage conserves water (Blevins *et al.*, 1983), prolonging active periods for earthworms.

In addition, previous studies have found that the negative impacts of intensive tillage on earthworm populations are also greater in finely textured soils (i.e. with a high percentage of clay) due to the fact that these light particles dry out very quickly when they are turned over (Chan, 2001). In agreement with these findings, the greatest change in earthworm populations to reductions in tillage intensity was observed in clayey soils (123%). Furthermore, the results from our meta-regression analyses indicated that earthworms showed the largest positive response to reduced tillage with higher soil clay contents (>35%). It is known that heavy clay soils usually support higher population numbers due to their higher water retention, which are important factors for earthworm survival (Gerard & Hay, 1979; Baker *et al.*, 1998; Curry, 2004). Also, in relation to this, clay soils tend to retain organic matter more tightly than coarse textured soils. The reasons can be found in the chemical bonds that are formed on the surface of clay particles that hold organic matter and slow down its decomposition, together with a greater tendency for the clay soils to form aggregates, which protect the organic matter from microbial attack (Rice, 2002).

Indeed, the positive relationship between soil organic carbon and earthworm density has also been observed previously (Hendrix *et al.*, 1992). The studies included in this review, which covered a good range of carbon contents (from 0.18% in some African sandy soils to around 12% in Mexican clay soils) showed that, on average, higher carbon contents were linked to higher population numbers. While the meta-regression analyses did not reveal a significant response of earthworm populations to reduced tillage in relation to the carbon content of the soils as a single factor, it did show that the largest percentage of change in earthworm densities (≈132%) in response to reduced tillage occurred in those soils with the lowest organic content (<0.6%). Agricultural managements leading to lower soil carbon contents generally support fewer earthworms (e.g. Curry, 2004; Ayuke *et al.*, 2011). It is therefore plausible that reduced tillage leading to higher soil C contents (Blevins *et al.*, 1983) is most beneficial for earthworms in soils with the lowest soil C baseline values. Overall, the amount of carbon present in the soil might not be a good sole predictor of tillage impacts on soil invertebrate communities because other factors such as rainfall patterns and previous land use history could be masking the overall effects (Guo & Gifford, 2002). For example, some studies have observed that soil carbon content in the top soil tends to increase in the more conservative agricultural operations because of a greater accumulation of crop residues on the surface and the absence of a disturbed soil profile compared to the ploughed soils (Kibet *et al.*, 2016; Piccoli *et al.*, 2016). However, these effects seem to be climatic dependent, with a maximum in soil C occurring after a wet preceding year and minimum after a dry preceding year (e.g. Conyers *et al.*, 2015).

Similarly, other studies have reported an increase in soil organic matter concomitant with a decrease in soil pH; for instance, Gillman (1985) indicated that for 1% increase in soil carbon, soil pH declines by 1 unit. Consequently, in the long-term soil organic matter accumulation under reduced tillage might result in soil acidification especially in low pH buffering capacity soils (Conyers *et al.*, 2015) and when high N fertilizers are used (Blevins *et al.*, 1983). In relation to this, the results of our meta-analyses also indicated that although there was a negative relationship between the earthworms' response ratio and soil pH, they responded significantly more positively to reduced tillage operations in the most acidic soils category (pH <5.5). It is generally assumed that earthworms can withstand strong acidic conditions (pH <4; Bouché, 1972), with some species being described as eurytopic (e.g. *Aporrectodea caliginosa*; Räty, 2004), but their burrowing activities will greatly increase at pH values above 5.4 (Auclerc *et al.*, 2011). On the other hand, it is known that soils with high clay and organic matter content also have a greater cation exchange capacity than sandy soils (Bot & Benites, 2005), as a result of clay and humus having electrostatic surface charges that attract and hold ions. This improves nutrient availability for plants and soil organisms, including earthworms and a significant positive relationship has been previously found between CEC and earthworm biomass (Reich *et al.*, 2005). Together, these findings imply that organic matter accumulation and the chemical bonding of organic substrates onto clay particles clearly benefit earthworm populations, especially in soils with low carbon contents and low pH buffering capacities.

Effects of reducing tillage intensity on taxonomic richness, age structure and functional groupings

Besides abundance and biomass, the structure of the earthworm communities can also be profoundly altered by soil cultivation (Edwards, 1983). However, while some authors have not detected any significant changes in earthworm species diversity in response to soil management (e.g. Gerard & Hay, 1979; Reddy *et al.*, 1997), others have reported a drastic reduction in the taxonomic richness in tilled soils. For instance, Curry *et al.* (2002) observed a decline in species richness from 9 to 1 species after intensive destoning and cultivation for a potato crop. Some differentiated effects, on species or ecological groups, have been reported consistently; for example, the bigger-sized worms (anecics), such as *L. terrestris* and *A. longa*, were more sensitive to tillage than the shallow burrowing and small endogeic species such as *Allolobophora chlorotica*, *A. caliginosa* and *A. icterica* (Wyss *et al.*, 1992; Edwards

& Lofty, 1982). Our global meta-analysis presents the first comprehensive, quantitative review of the responses of earthworm species and the three ecological groups to reduced tillage practices.

Many agronomically or tillage-focussed studies report total earthworm numbers (and less frequently, biomass) as one of several commonly measured indicators of the biological effects of tillage practices. Our meta-analysis provides compelling evidence for the significantly different responses to tillage by ecological groups and also individual species of earthworms (Figs. 10a,c). For a full understanding of tillage effects on earthworms and their functions, it is therefore imperative that species (or ecological groups) are reported and considered separately, taking account of their biology, habitat requirements, survival strategies and so on.

One common survival strategy exhibited by earthworms during adverse environmental conditions is to move down to deeper layers and enter into a resting stage (by emptying their gut and coiling up into a tight ball inside an aestivation chamber which has been made previously by mixing casts and mucus; Lee, 1985). By disturbing the soil (e.g. by inversion tillage) during inactive periods of the year (late autumn, early spring) and exposing the earthworms that have entered into this inactive stage to the surface, where they can be easily predated, can cause severe reductions in their populations (Curry *et al.*, 2002). The most likely species to be affected by these disturbances are surface dwellers (i.e. belonging to the epigeic ecological group) and the anecic worms that build vertical burrows open to the surface where they feed and cast, whereas the small endogeics living in the mineral horizons exhibit fewer alterations in their populations.

Furthermore, in the case of well-studied anecic species, such as *L. terrestris*, there is evidence suggesting that their burrows are permanent or semi-permanent structures that can be inherited by their offspring (Butt *et al.*, 2003; Grigoropoulou *et al.*, 2008). This low mobility might also explain why this species showed the greatest positive effect from reducing tillage operations. Indeed, our meta-analyses showed very clearly that *L. terrestris* exhibited the strongest positive response to reduced tillage, by increasing the average number of their populations by about 124% compared to the overall mean.

In the case of other anecic species reported in the literature and included in our meta-analyses, such as *A. longa* and *A. trapezoides,* although they also benefited from reducing tillage intensity, the magnitude of their responses was less marked. Therefore, species identity plays a determining role in the overall response of earthworm populations to tillage and can explain a good number of inconsistent results observed in the literature, where the communities in these cultivated soils were mainly dominated by these species (Hubbard *et al.*, 1999; Johnson-Maynard *et al.*, 2007). However, as is also shown in our meta-analyses, the earthworm responses to reduced forms of tillage were modulated by their specific sensitivity to tillage techniques (with deep soil loosening having the most detrimental effects on the recovery of all investigated species) and to the presence/absence of harvest residues on the soil surface.

Long-term recover of earthworm populations after tillage is also influenced by survival of their offspring (cocoons and juveniles). Unfortunately, the majority of results reported in the literature were based on total or adult individuals, in most cases because adults are easier to identify. However, it is well known that earthworm populations mainly consist of immature worms, with some reports indicating they can make up to 76-90% of the population (Marwitz *et al.*, 2012; Domínguez & Bedano, 2016), and that they are extremely sensitive to tillage (Ulrich *et al.*, 2010). Therefore, future research efforts should incorporate the effects of tillage operations on young worms. Juvenile earthworms can occupy a different niche than adults by feeding on the surface layers irrespective of the ecological grouping (Gerard, 1967; Rundgren, 1975) and it has been observed that performing tillage operations during those periods when their numbers are high results in more severe reductions of this age group than in the adult numbers (De St. Remy & Day-Nard, 1982).

As seen before, adding supplementary food material can counteract some of the negative effects of tillage (Curry, 2004). Farmyard manures derived from livestock are very rich in nitrogen and release organic material rapidly (Leroy *et al.*, 2008) and that is why they represent preferential sites for the earthworms to lay their cocoons and for the juveniles to grow (Binet *et al.*, 1997). Plant roots also provide good environments for earthworm reproduction (Gerard, 1967; Satchell, 1977); however, when the crop is harvested and soil turned over, the supply of fresh plant material is ploughed under which might then benefit the deep burrower adult worms but seriously compromise the survival of the newly born worms.

Taken together, these findings suggest that feeding habits, body size and burrowing activities determine the survival of earthworm species to tillage. Future research could expand the present analysis even further by analysing traits rather than species of life forms (e.g. Bokhorst *et al.*, 2012). Importantly, the fact that our results confirmed that epigeic and, more importantly, anecic worms, are the functional groups first to disappear from tilled soils has far-reaching implications for the functioning of these agricultural systems. For instance, the absence of deep burrowers will mean that the maintenance of soil structure and drainage, the incorporation of organic matter down the soil profile together with the mixing of the soil will not be carried out to the same extent by the natural plough of the Earth. The lack of surface dwellers will also have negative effects on the degradation of fresh inputs of organic matter. In turn, the disappearance of the surface casting activities of these two important ecological groupings will profoundly affect microbial activities and overall, the recycling of nutrients and the long-term functioning of the soil. Therefore, as seen here, various forms of reduced tillage can be adopted to achieve soils with larger and functionally diverse earthworm communities.

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References

Aslam T, Choudhary M.A, Saggar S (1999) Tillage impacts on soil microbial biomass C, N and P, earthworms and agronomy after two years of cropping following permanent pasture in New Zealand. *Soil and Tillage Research*, **51**, 103–111.

Auclerc A, Nahmani JY, Huguier P, Capowiez Y, Aran D, Guérold F (2011) Adapting ecotoxicological tests based on earthworm behavior to assess the potential effectiveness of forest soil liming. *Pedobiologia*, **54S (Suppl.)**, S63–S68.

Ayuke FO, Pulleman MM, Vanlauwe B., de Goede R.G.M., Six J, Csuzdi C, Brussaard L (2011) Agricultural management affects earthworm and termite diversity across humid to semi-arid tropical zones. *Agriculture, Ecosystems and Environment*, **140**, 148–154.

Baker GH, Carter PJ, Curry JP, Cultren O, Beck A (1988) Clay content of soil and its influence on the abundance of *Aporrectodea trapezoides* Dugès (Lumbricidae). *Applied Soil Ecology*, **9**, 333–337.

Bakken AK, Brandsæter LO, Eltun R, Hansen S, Mangerud K, Pommeresche R, Riley H (2009) Effect of tractor weight, depth of ploughing and wheel placement during ploughing in an organic cereal rotation on contrasting soils. *Soil and Tillage Research*, **103**, 433–441.

Bamminger C, Zaiser N, Zinsser P, Lamers M, Kammann C, Marhan S (2014) Effects of biochar, earthworms, and litter addition on soil microbial activity and abundance in a temperate agricultural soil. *Biology and Fertility of Soils*, **50**, 1189–1200.

Barley KP (1959) The influence of earthworms on soil fertility. I. Earthworm populations found in agricultural land near Adelaide. *Australian Journal of Agricultural Research*, **10**, 171–178.

Barnes BT, Ellis FB (1979) Effects of different methods of cultivation and direct drilling, and disposal of straw residues, on populations of earthworms. *Journal of Soil Science*, **30**, 669–679.

Berner A, Hildermann I, Fliessbach A, Pfiffner L, Niggli U, Mäder P (2008) Crop yield and soil fertility response to reduced tillage under organic management. *Soil and Tillage Research*, **101**, 89–96.

Betrand M, Barot S, Blouin M, Whalen J, de Oliveira T, Roger-Estrade J (2015) Earthworm services for cropping systems. A review. *Agronomy for Sustainable Development*, **35**, 553–567.

Binet F, Hallaire V, Curmi P (1997) Agricultural practices and the spatial distribution of earthworms in maize fields. Relationships between earthworm abundance, maize plants and soil compaction. *Soil Biology and Biochemistry*, **29**, 577–583.

Birkas M, Jolánkai M, Gyuricza C, Percze A (2004) Tillage effects on compaction, earthworms and other soil quality indicators in Hungary. *Soil and Tillage Research*, **78**, 185–196.

Birkas M, Bottlik L Stingli A, Gyuricza C, Jolánkai M (2010) Effect of soil physical state on the earthworms in Hungary. *Applied and Environmental Soil Science*, Vol. 2010, Article ID 830853. doi:10.1155/2010/830853.

Bittman S, Kowalenko CG (2004). *Advanced Silage Corn Management*. Pacific Field Corn Association, Agassiz.

Blanchet G, Gavazov K, Bragazza L, Sokrat S (2016) Responses of soil properties and crop yields to different inorganic and organic amendments in a Swiss conventional farming system. *Agriculture, Ecosystems and Environment*, **230**, 116–126.

Blevins RL, Smith MS, Thomas GW, Frye WW (1983) Influence of conservation tillage on soil properties. *Journal of Soil and Water Conservation*, **38**, 301–305.

Bogužas V, Kairytė A, Jodaugienė D (2010) Soil physical properties and earthworms as affected by soil tillage systems, straw and green manure management. *Žemdirbystė – Agriculture*, **97**, 3–14.

Bokhorst S, Phoenix GK, Bjerke JW, Callaghan TV, Huyer-Brugman F, Berg MP (2012) Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. *Global Change Biology*, **18**, 1152–1162.

Borenstein M, Hedges LV, Higgins JPT, Rothstein HR (2009) *Introduction to Meta-Analysis (Chapter 20 Meta-Regression)*. John Wiley & Sons, Ltd, Chichester, UK. doi: 10.1002/9780470743386.ch20

Boström U (1988) *Ecology of Earthworms in Arable Land. Population Dynamics and Activity in Four Cropping Systems*. Report 34. Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, Uppsala.

Boström U (1995) Earthworm populations (Lumbricidae) in ploughed and undisturbed leys. *Soil and Tillage Research*, **35**, 125–133.

Bot A, Benites J (2005) *The Importance of Soil Organic Matter: key to drought-resistant soil and sustained food production* (FAO Soils Bulletins **80**). FAO, Rome, 94 pp.

Bouché MB (1972) *Lombriciens de France. Ecologie et systematique*. Institut National de la Recherche Agronomique, Paris, 671 pp.

Bouché MB (1977) Stratégies lombriciennes. In: *Soil Organisms as Components of Ecosystems* (eds Lohm U, Persson T), pp. 122–132. Ecological Bulletin, **25**, Stockholm, Sweden.

Boudiaf NKM, Metheri MS, Mouas BS, Derridj A (2015) Climate impact on the abundance of soil macroinvertebrates in Algerian olive orchards. *Agriculture and Food*, **3**, 320–324.

Briones MJI (2014) Soil fauna and soil functions: a jigsaw puzzle. *Frontiers in Environmental Science*, **2**, 7. doi: 10.3389/fenvs.2014.00007

Briones MJI, Bol R (2003) Natural abundance of ^{13}C and ^{15}N in earthworms from different cropping treatments. *Pedobiologia*, **47**, 560–567. doi:10.1016/S0031-4056(04)70238-3.

Brito-Vega H, Espinosa-Victoria D, Fragoso C, Mendoza D, De la Cruz Landero N, Alderete-Chavez A (2009) Soil organic matter particle and presence of earthworm under different tillage systems. *Journal of Biological Sciences*, **9**, 180–183.

Brussaard L, Aanen DK, Briones MJI, Decaëns T, De Deyn GB, Fayle TM, James SW, Nobre T (2012) Biogeography and phylogenetic community structure of soil invertebrate ecosystem engineers. In: *Soil Ecology and Ecosystem Services* (eds Wall DH, Bardgett RD, Behan-Pelletier V, Herrick JE, Jones TH, Ritz K, Six J, Strong DR, van der Putten WH), pp. 201–232. Oxford University Press, Oxford.

Buckerfield JC, Wiseman D (1997) Earthworm populations recover after potato cropping. *Soil Biology and Biochemistry*, **29**, 609–612.

Butt KR, Nuutinen V, Siren T (2003) Resource distribution and surface activity of adult *Lumbricus terrestris* L. in an experimental system. *Pedobiologia*, **47**, 548–553.

Capowiez Y, Cadoux S, Bouchant P, Ruy S, Roger-Estrade J, Richard G, Boizard H (2009a) The effect of tillage type and cropping system on earthworm communities, macroporosity and water infiltration. *Soil Tillage and Research*, **105**, 209–216. doi:10.1016/j.still.2009.09.002.

Capowiez Y, Cadoux S, Bouchand P, Roger-Estrade J, Richard G, Boizard H (2009b) Experimental evidence for the role of earthworms in compacted soil regeneration based on field observations and results from a semi-field experiment. *Soil Biology and Biochemistry*, **41**, 711–717.

Carter MR, Sanderson JB, Ivany JA, White RP (2002) Influence of rotation and tillage on forage maize productivity, weed species, and soil quality of a fine sandy loam in the cool-humid climate of Atlantic Canada. *Soil and Tillage Research*, **67**, 85–98.

Chan KY (2001) An overview of some tillage impacts on earthworm population abundance and diversity – implications for functioning in soils. *Soil and Tillage Research*, **57**, 179–191. doi:10.1016/S0167-1987(00)00173-2.

Clapperton MJ (1999) Tillage practices, and temperature and moisture interactions affect earthworm populations and species composition. *Pedobiologia*, **43**, 658–665.

Clapperton MJ, Miller JJ, Larney FJ, Lindwall CW (1997) Earthworm populations as affected by long-term tillage practices in southern, Alberta, Canada. *Soil Biology and Biochemistry*, **29**, 631–633.

Conyers M, Liu DL, Kirkegaard J, Orgill S, Oates A, Li G, Poile G, Kirkby C (2015) A review of organic carbon accumulation in soils within the agricultural context of southern New South Wales, Australia. *Field Crops Research*, **184**, 177–182.

Crittenden SJ, Eswaramurthy T, de Goede RGM Brussaard L, Pulleman MM (2014) Effect of tillage on earthworms over short- and medium-term in conventional and organic farming. *Applied Soil Ecology*, **83**, 140–148.

Cuendet C. (1983) Predation on earthworms by the black-headed gull (*Larus ribibundus* L.). In: *Earthworm Ecology. From Darwin to Vermiculture* (ed Satchell JE), pp. 415–424. Chapman and Hall, London.

Curry JP (2004). Factors affecting the abundance of earthworms in soils. In: *Earthworm Ecology* (ed Edwards CA), pp. 91–113. CRC Press, Boca Raton.

Curry JP, Byrne D, Schmidt O (2002) Intensive cultivation can drastically reduce earthworm populations in arable land. *European Journal of Soil Biology*, **38**, 127–130.

Curtis PS, Mengersen K, Lajeunesse MJ, Rothstein HR, Stewart G (2013). Extraction and critical appraisal of data. In: *Handbook of Meta-analysis in Ecology and Evolution* (eds Koricheva J, Gurevitch J). Princeton University Press, Princeton.

Darwin CR (1881) *The Formation of Vegetable Mould, Through the Action of Worms*. John Murray, London.

Datta S, Singh J, Singh S, Singh J (2016). Earthworms, pesticides and sustainable agriculture: a review. *Environmental Science and Pollution Research*, **23**, 8227–8243. DOI 10.1007/s11356-016-6375-0.

De St. Remy EA, Day-Nard TB (1982) Effects of tillage methods on earthworm populations in monoculture corn. *Canadian Journal of Soil Science*, **62**, 699–703.

Derpsch R, Friedrich T, Kassam A, Hongwen L (2010) Current status of adoption of no–till farming in the world and some of its main benefits. *International Journal of Agricultural and Biological Engineering*, **3**, 1–25.

D'Hose T, Ruysschaert G, Viaene N *et al.* (2016) Farm compost amendment and non-inversion tillage improve soil quality without increasing the risk for N and P leaching. *Agriculture, Ecosystems and Environment*, **225**, 126–139.

Domínguez A, Bedano JC (2016) Earthworm and Enchytraeid co-occurrence pattern in organic and conventional farming: Consequences for ecosystem engineering. *Soil Science*, **181**, 148–156.

Doube BM, Schmidt O (1997) Can the abundance or activity of soil macrofauna be used to indicate the biological health of soils? In: *Biological Indicators of Soil Health* (eds Pankhurst CE, Doube BM, Gupta VVSR), pp. 265–295. CAB International, Wallingford, UK.

Edwards CA (1983) Earthworm ecology in cultivated soils. In: *Earthworm Ecology: from Darwin to Vermiculture* (ed Satchell JE), pp. 123–137, Chapman & Hall, London.

Edwards CA, Bohlen PJ (1996) *Biology and Ecology of Earthworms*. Chapman & Hall, London.

Edwards CA, Lofty JR (1982) The effects of direct drilling and minimal cultivation on earthworm populations. *Journal of Applied Ecology*, **19**, 723–734.

Eichhorn von H, Tebrügge F (1990) Die Art der Bodenbearbeitung und ihre Folgen. *Spiegel der Forschung*, **1/90**, 27–34. [In German]

El Titi A (2003) *Soil Tillage in Agroecosystems*. CRC Press, Boca Raton.

Ellis FB, Elliott JG, Barnes BT, Howse KR (1977) Comparison of direct drilling, reduced cultivation and ploughing on the growth of cereals. 2. Spring barley on a sandy loam soil; soil physical conditions and root growth. *Journal of Agricultural Science*, **89**, 631–642.

Emmerling C (2001) Response of earthworm communities to different types of soil tillage. *Applied Soil Ecology*, **17**, 91–96.

Errouissi F, Moussa-Machraoui SB, Ben-Hammouda M, Nouira S (2011) Soil invertebrates in durum wheat (*Triticum durum* L.) cropping system under Mediterranean semi arid conditions: a comparison between conventional and no-tillage management. *Soil and Tillage Research*, **112**, 122–132.

Fortune T, Kennedy T, Mitchell B, Dunne B (2003) Reduced cultivations – agronomic and environmental aspects. Teagasc National Tillage Conference Proceedings, Carlow, Ireland, January 2003, 70–82.

Fortune T, Kennedy T, Mitchell B, Dunne B, Murphy K, Connery J, Grace J (2005) Reduced Cultivations – Update from Oak Park Experiments. In: *Proceedings of the National Tillage Conference 2005*. Teagasc, Oak Park, Carlow, Ireland, pp. 18–34.

Fragoso C, Lavelle, P (1992) Earthworm communities of tropical rain forests. *Soil Biology and Biochemistry*, **24**, 1397–1408.

Fusilero MA, Mangubat J, Ragas RE, Baguinon N, Taya H, Rasco E (2013) Weed management systems and other factors affecting the earthworm population in a banana plantation. *European Journal of Soil Biology*, **56**, 89–94.

Gajri PR, Arora VK, Prihar SS (2002) *Tillage for Sustainable Cropping*. Food Products Press, New York.

García-Pérez JA, Alarcón-Gutiérrez E, Perroni Y, Barois I (2014) Earthworm communities and soil properties in shaded coffee plantations with and without application of glyphosate. *Applied Soil Ecology*, **83**, 230–237. doi:10.1016/j.apsoil.2013.09.006.

García-Pérez JA, Alarcón E, Hernández Y, Hernández C (2016) Impact of litter contaminated with glyphosate-based herbicide on the performance of *Pontoscolex corethrurus*, soil phosphatase activities and soil pH. *Applied Soil Ecology*, **104**, 31–41.

García-Torres T, Giuffré L, Romaniuk R, Ríos RP, Pagano EA (2014) Exposure assessment to glyphosate of two species of annelids. *Bulletin of Environmental Contamination and Toxicology*, **93**, 209–214.

Gaupp-Berghausen M, Hofer M, Rewald B, Zaller JG (2015) Glyphosate-based herbicides reduce the activity and reproduction of earthworms and lead to increased soil nutrient concentrations. *Scientific Reports*, **5**, 12886. doi:10.1038/srep12886

Gerard BM (1967) Factors affecting earthworms in pastures. *Journal of Animal Ecology*, **36**, 235–252.

Gerard BM, Hay RKM (1979) The effect on earthworms of ploughing, tined cultivation, direct drilling and nitrogen in a barley monoculture system. *Journal of Agricultural Science*, **93**, 147–155.

Gillman GP (1985) Influence of organic matter and phosphate content on the point of zero charge of variable charge components in oxidic soils. *Australian Journal of Soil Research*, **23**, 643–646.

Givaudan N, Binet F, Le Bot B, Wiegand C (2014) Earthworm tolerance to residual agricultural pesticide contamination: field and experimental assessment of detoxification capabilities. *Environmental Pollution*, **192**, 9–18.

Grigoropoulou N, Butt KR, Lowe CN (2008) Effects of adult *Lumbricus terrestris* on cocoons and hatchlings in Evans' boxes. *Pedobiologia*, **51**, 343–349.

Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: a meta-analysis. *Global Change Biology*, **8**, 345–360.

Hackenberger DK, Hackenberger BK (2014) Earthworm community structure in grassland habitats differentiated by climate type during two consecutive seasons. *European Journal of Soil Biology*, **61**, 27–34.

Haukka J (1988). Effect of various cultivation methods on earthworm biomasses and communities on different soil types. *Annales Agriculturae Fenniae*, **27**, 263–269

Haynes RJ, Mokolobate MS (2001) Amelioration of Al toxicity and P deficiency in acid soils by additions of organic residues: a critical review of the phenomenon and the mechanisms involved. *Nutrient Cycling in Agroecosystems*, **59**, 47–63.

Hedges LV, Gurevitch J, Curtis PS (1999) The Meta-Analysis of Response Ratios in Experimental Ecology. *Ecology*, **80**, 1150–1156.

Hendrix PF, Muller BR, Bruce RR, Langdale GW, Parmelee RW (1992) Abundance and distribution of earthworms in relation to landscape factors on the Georgia piedmont, U.S.A. *Soil Biology and Biochemistry*, **24**, 1357–1361.

Henke W (1994) Einfluß der Bodenbearbeitung aur die Lumbricidenpopulation und deren Aktivität in verschiedenen Ackerböden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, **89**, 89–100. [In German with English summary]

Herrmann KM, Weaver LM (1999) The shikimate pathway. *Annual Review of Plant Physiology and Plant Molecular Biology*, **50**, 473–503.

Hubbard VC, Jordan D, Stecker JA (1999) Earthworm response to rotation and tillage in a Missouri claypan soil. *Biology and Fertility of Soils*, **29**, 343-347.

Hutcheon JA, Iles DR, Kendall DA (2001) Earthworm populations in conventional and integrated farming systems in the LIFE Project (SW England) in 1990–2000. *Annals of Applied Biology*, **139**, 361-372.

Ivask M, Kuu A, Sizov E (2007) Abundance of earthworm species in Estonian arable soils. *European Journal of Soil Biology*, **43**, S39–S42. doi:10.1016/j.ejsobi.2007.08.006.

Jeffery S, Verheijen FGA, van der Velde M, Bastos AC (2011) A quantitative review of the effects of biochar application to soils on crop productivity using meta-analysis. *Agriculture, Ecosystems and Environment*, **144**, 175–187.

Jodaugienė D, Raudonius S, Špokienė N, Trečiokas K (2005) The influence of ploughing and ploughless soil tillage on soil properties in winter wheat crop. *Agronomijas Vestis – Latvian Journal of Agronomy*, **8**, 200–205.

Johnson-Maynard JL, Umiker KJ, Guy SO (2007) Earthworm dynamics and soil physical properties in the first three years of no-till management. *Soil and Tillage Research*, **94**, 338–345.

Jordan D, Gantzer CJ, Brown JR, Stecker JA, Hubbard VC, Zhu J (1997a) *Earthworms in a Missouri Claypan Soil*. Final Report (Project 94-2). Department of Natural Resources, Jefferson City, Missouri, 41 pp.

Jordan D, Stecker JA, Cacnio-Hubbard VN, Li F, Gantzer CJ, Brown JR (1997b) Earthworm activity in no-tillage and conventional tillage systems in Missouri soils: A preliminary study. *Soil Biology and Biochemistry*, **29**, 489–491. doi: 10.1016/S0038-0717(96)00038-7.

Joschko M, Gebbers R, Barkusky D, Rogasik J, Höhn W, Hierold W, Fox CA, Timmer J (2009) Location-dependency of earthworm response to reduced tillage on sandy soil. *Soil and Tillage Research*, **102**, 55–66.

Joschko M, Barkusky D, Rogasik J *et al.* (2012) On–farm study of reduced tillage on sandy soil: effects on soil organic carbon dynamic and earthworm abundance. *Archives of Agronomy and Soil Science*, **58**, S252–S260.

Kanianska R, Jaďuďová J, Makovniková J, Kizeková M (2016) Assessment of relationships between earthworms and soil abiotic and biotic factors as a tool in sustainable agricultural. *Sustainability*, **8**, 906. doi:10.3390/su8090906.

Karlen DL, Wollenhaupt NC, Erbach DC, Berry EC, Swan JB, Eash NS, Jordahl JL (1994) Long-term tillage effects on soil quality. *Soil and Tillage Research*, **32**, 313–327.

Kassam A, Friedrich T, Shaxson F, Pretty J (2009) The spread of Conservation Agriculture: justification, sustainability and uptake. *International Journal of Agricultural Sustainability*, **7**, 292–320.

Kennedy TF, Connery J, Fortune T, Forristal D, Grant J (2013) A comparison of the effects of minimum-till and conventional-till methods, with and without straw incorporation, on slugs, slug damage, earthworms and carabid beetles in autumn-sown cereals. *Journal of Agricultural Science*, **151**, 605–629.

Kibet LC, Blanco-Canqui H, Jasa P (2016) Long-term tillage impacts on soil organic matter components and related properties on a Typic Argiudoll. *Soil and Tillage Research*, **155**, 78–84.

Kladivko EJ, Akhouri NM, Weesies G (1997) Earthworm populations and species distributions under no-till and conventional tillage in Indiana and Illinois. *Soil Biology and Biochemistry*, **29**, 613–615.

Köppen W (1923) *Die Klimate der Erde*. Walter de Gruyter, Berlin.

Köppen W (1931) *Die Klimate der Erde. Grundriss der Klimakunde*, 2nd edn. Walter de Gruyter, Berlin.

Kouwenhoven JK, Perdok UD, Boer J, Oomen GJM (2002) Soil management by shallow mouldboard ploughing in The Netherlands. *Soil and Tillage Research*, **65**, 125–139.

Krabbe EL, Driemeyer DJ, Antoniolli ZI, Giracca EMN (1993) Avaliação populacional de oligoquetas e características físicas do solo em diferentes sistemas de cultivo. *Ciência Rural*, **23**, 21–28. [In Portuguese with English summary]

Krabbe EL, Driemeyer DJ, Antoniolli ZI, Giracca EMN (1994) Efeitos de diferentes sistemas de cultivos sobre a populacão de oligoquetas e caracteríticas físicas do solo. *Ciência Rural*, **24**, 49–53. [In Portuguese with English summary]

Lal R (2013) Enhancing ecosystem services with no-till. *Renewable* Agriculture and Food Systems, **28**, 102–114.

László P (2007) *Adirektvetéses és a Bakhátas Vetési és Mũvelési Rendszer Hatása a Talaj Fizikai és Biológiai Állapotára*. PhD Thesis, Doktori értekezés, Gödöllő, Hungary. [In Hungarian]

Lavelle P, Spain AV (2001) *Soil Ecology*. Kluwer Scientific, Amsterdam, 678 pp.

Lee KE (1985) *Earthworms: Their Ecology and Relationships with soils and Land Use*. Academic Press, Sydney.

Leroy BLM, Schmidt O, Van den Bossche A, Reheul D, Moens M (2008) Earthworm population dynamics as influenced by the quality of exogenous organic matter. *Pedobiologia*, **52**, 139–150. doi:10.1016/j.pedobi.2008.07.001.

Low AJ (1972) The effect of cultivation on the structure and other physical characteristics of grassland and arable soils (1945–1970). *Journal of Soil Science*, **23**, 363–380. doi:10.1111/j.1365-2389.1972.tb01668.x.

Lugato E, Bampa F, Panagos P, Montanarella L, Jones A (2014) Potential carbon sequestration of European arable soils estimated by modelling a comprehensive set of management practices. *Global Change Biology*, **20**, 3557–3567.

Mallet JB, Lang PM, Arathoon AJ (1987) Changes in a Doveton clay loam after 12 years of direct drill maize production. *South African Journal of Plant and Soil*, **4**, 188–192.

Marchão RL, Lavelle P, Celini L, Balbino LC, Vilela L, Becquer T (2009) Soil macrofauna under integrated crop-livestock systems in a Brazilian Cerrado Ferralsol. *Pesquisa Agropecuária Brasileira*, **44**, 1011–1020.

Marinissen JCY (1992) Population dynamics of earthworms in a silt loam soil under conventional and “integrated" arable farming during two years with different weather patterns. *Soil Biology and Biochemistry*, **24**, 1647–1654.

Marwitz A, Ladewig E, Märländer B (2012) Impact of herbicide application intensity in relation to environment and tillage on earthworm population in sugar beet in Germany. *European Journal of Agronomy*, **39**, 25–34.

McAuley L, Pham B, Tugwell P, Moher D (2000) Does the inclusion of grey literature influence estimates of intervention effectiveness reported in meta-analyses? *Lancet*, **356**, 1228–1231.

Meteorological Office (1982) *Tables of Temperature, Relative Humidity, Precipitation and Sunshine for the World. Part III. Europe and the Azores*. Meteorological Office, London.

Miura F, Nakamoto T, Kaneda S, Okano S, Nakajima M, Murakami T (2008) Dynamics of soil biota at different depths under two contrasting tillage practices. *Soil Biology and Biochemistry*, **40**, 406–414

Moron-Rios A, Rodriguez MA, Perez-Camacho L, Rebollo S (2010) Effects of seasonal grazing and precipitation regime on the soil macroinvertebrates of a Mediterranean old-field. *European Journal of Soil Biology*, **46**, 91–96.

Morris N, Miller P, Froud-Williams R (2010) The adoption of non-inversion tillage systems in the United Kingdom and the agronomic impact on soil, crops and the environment: a review. *Soil and Tillage Research*, **108**, 1–15.

Mubarak AR, Elshami OME, Azhari AA (2005) Long- and short-term effects of cultivation on properties of a Vertisol under sugarcane plantation. *Soil and Tillage Research*, **84**, 1–6.

Müller MJ (1982) *Selected Climatic Data for a Global Set of Standard Stations for Vegetation Science*. Dr W Junk Publishers, The Hague.

Nachtergaele F, van Velthuizen H, Verelst L *et al.* (2008) *Harmonized World Soil Database (version 1.0)*. FAO, Rome, Italy and IIASA, Laxenburg, Austria.

Najar IA, Khan AB (2011) Earthworm communities of Kashmir Valley, India. *Tropical Ecology*, **52**, 151–162.

Nieminen M, Ketoja E, Mikola E, Terhivuo J, Sirén T, Nuutinen V (2011) Local land use effects and regional environmental limits on earthworm communities in Finnish arable landscapes. *Ecological Applications*, **21**, 3162–3177.

Parmelee RW, Beare MH, Cheng W, Hendrix PF, Rider SJ, Crossley DA, Coleman DC (1990) Earthworms and enchytraeids in conventional and no-tillage agroecosystems: a biocide approach to assess their role in organic matter breakdown. *Biology and Fertility of Soils*, **10**, 1–10.

Parvin N, Parvage MM, Etana A (2014) Effect of mouldboard ploughing and shallow tillage on sub-soil physical properties and crop performance. *Soil Science and Plant Nutrition*, **60**, 38–44.

Pekrun C, Schneider N, Wüst C, Jauss F, Claupein, W (2003) Einfluss reduzierter Bodenbearbeitung auf Ertragsbildung, Unkrautdynamik und Regenwurmpopulationen im Ökologischen Landbau. In: *Ökologischer Land-bau der Zukunft. Beiträge zur 7. Wissenschafts-tagung zum Ökologischen Landbau* (ed Freyer B), pp. 21–24. Universität für Bodenkultur, Vienna. [In German]

Petersen H, Luxton M (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, **39**, 288–388.

Piccoli I, Chiarini F, Carletti P *et al.* (2016) Disentangling the effects of conservation agriculture practices on the vertical distribution of soil organic carbon. Evidence of poor carbon sequestration in North-Eastern Italy. *Agriculture, Ecosystems and Environment*, **230**, 68–78.

Pommeresche R, Loes A-K (2009) Soil quality indicator response to tillage and residue management on semi-arid Mediterranean cropland. *Dynamic Soil, Dynamic Plant*, **3**, 129–142.

Potthoff M (1999) *Synchronisation des Stoffkreislaufs durch Förderung bodenbiologischer Prozesse im Ackerbau*. PhD Thesis, Göttingen University, Cuvillier Verlag Göttingen, Germany, ISBN 3-89712-666-4.

Potthoff M, Beese F (1998) Regenwurmgesellschaften in Ackerböden des integriert extensivierten Landbaus – Aspekte von Bodenschutz- und Wasserschutzmaβnahmen. *Venhandlungen der Gesellschaft für Ökologie*, **28**, 545–550.

Radford BJ, Key AJ, Robertson LN, Thomas GA (1995) Conservation tillage increases soil water storage, soil animal populations, grain yield, and response to fertiliser in the semi-arid subtropics. *Australian Journal of Experimental Agriculture*, **35**, 223-232.

Radford BJ, Wilson-Rummenie AC, Simpson GB, Bell KL, Fergusson MA (2001) Compacted soil affects soil macrofauna populations in a semi-arid environment in central Queensland. *Soil Biology and Biochemistry*, **33**, 1869–1872.

Ramos M, Nacci S, Pla I (2003) Effect of raindrop impact and its relationship with aggregate stability to different disaggregation forces. *Catena*, **53**, 365–376.

Räty M (2004) Growth of *Lumbricus terrestris* and *Aporrectodea caliginosa* in an acid forest soil, and their effects on enchytraeid populations and soil properties. *Pedobiologia*, **48**, 321–328.

Reddy MV, Reddy VR, Balashouri P, Kumar VPK, Cogle AL, Yule DF, Babu M (1997). Responses of earthworm abundance and production of surface casts and their physico-chemical properties to soil management in relation to those of an undisturbed area ona semi-arid tropical alfisol. *Soil Biology and Biochemistry*, **29**, 617–620.

Redmond CT, Kesheimer A, Potter DA (2014) Earthworm community composition, seasonal population structure, and casting activity on Kentucky golf courses. *Applied Soil Ecology*, **75**, 116–123.

Reeleder RD, Miller JJ, Ball Coelho BR, Roy RC (2006) Impacts of tillage, cover crop, and nit-rogen on populations of earthworms, microarthropods, and soil fungi in a cultivated fragile soil. *Applied Soil Ecology*, **33**, 243–257.

Reich PB, Oleksyn, Modrzynski J *et al.* (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecology Letters*, **8**, 811–818.

Rice CW (2002) Organic matter and nutrient dynamics. In: *Encyclopedia of Soil Science* (ed Lal R), pp. 925–928. Marcel Dekker Inc., New York.

Riley H, Ekeberg E (1998) Effects of depth and time of ploughing on yields of spring cereals and potatoes and on soil properties of a morainic loam soil. *Acta Agriculturae Scandinavica, Section B — Soil and Plant Science*, **48**, 193–200.

Riley H, Pommeresche R, Eltun R, Hansen S, Korsaeth A (2008) Soil structure, organic matter and earthworm activity in a comparison of cropping systems with contrasting tillage, rotations, fertilizer levels and manure use. *Agriculture, Ecosystems and Environment*, **124**, 275–284.

Roarty S, Schmidt O (2013) Permanent and new arable field margins support large earthworm communities but do not increase in-field populations. *Agriculture, Ecosystems and Environment*, **170**, 45–55

Rosas-Medina MA, de Leon-Gonzalez F, Flores-Macias A, Payan-Zelaya F, Borderas-Tordesillas F, Gutierrez-Rodriguez F, Fragoso-Gonzalez C (2010) Effect of tillage, sampling date and soil depth on earthworm population on maize monoculture with continuous stover restitutions. *Soil and Tillage Research*, **108**, 37–42.

Rosenberg MS, Adams DC, Gurevitch J (1997) *Meta Win: Statistical Software for Meta-Analysis with Resampling Tests. Ver. 1.0*. Sinauer Associates, Sunderland, Massachusetts.

Rosenberg MS, Adams DC, Gurevitch J (2000) *MetaWin Statistical Software for Meta-Analysis, Version 2*. Department of Ecology and Evolution, State University of New York at Stony Brook. Sinauer Associates, Inc., Sunderland, Massachusetts.

Rosenthal R, Rosnow R (1991) *Essentials of Behavioral Research: Methods and Data Analysis*. McGraw Hill, New York.

Rothstein H, Sutton A, Borenstein M (2005) *Publication Bias in MA: Prevention, Assessment and Adjustments*. Wiley, Hoboken, NJ.

Rovira AD, Smettem KRJ, Lee KE (1987) Effect of rotation and conservation tillage on earthworms in a red-brown earth under wheat. *Australian Journal of Agricultural Research*, **38**, 829–834.

Rundgren S (1975) Vertical distribution of lumbricids in southern Sweden. *Oikos*, **26**, 299–306.

Rutgers M, Orgiazzi A, Gardi C *et al.* (2016). Mapping earthworm communities in Europe. *Applied Soil Ecology*, **97**, 98–111.

Satchell JE (1977) Lumbricidae. In: *Soil Biology*. 3rd edn (eds Burges A, Raw F), pp. 259–322. Academic Press, London.

Schirrmann M, Joschko M, Gebbers R, Kramer E, Zörner M, Barkusky D, Timmer J (2016) Proximal soil sensing – A contribution for species habitat distribution modelling of earthworms in agricultural soils? *PLoS One*, **11**, e0158271. doi:10.1371/journal.pone.0158271.

Schmidt O, Clements RO, Donaldson G (2003) Why do cereal-legume intercrops support large earthworm populations. *Applied Soil Ecology*, **22**, 181–190.

Severon T, Joschko M, Barkusky D, Graefe U (2012) The impact of conventional and reduced tillage on the Enchytraeidae population in sandy soil and their correlation with plant residue and earthworms. *Landbauforschung*, **357**, 45–52. (Newsletter on Enchytraeidae no. **12**)

Singh P, Heikkinen J, Ketoja E *et al*. (2015) Tillage and crop residue management methods had minor effects on the stock and stabilization of topsoil carbon in a 30-year field experiment. *Science of the Total Environment*, **518**, 337–344.

Six J, Ogle SM, Breidt FJ, Conant RT, Mosier AR, Paustian K (2004) The potential to mitigate global warming with no-tillage management is only realized when practised in the long term. *Global Change Biology*, **10**, 155–160.

Smith P, House JI, Bustamante M *et al.* (2016) Global change pressures on soils from land use and management. *Global Change Biology*, **22**, 1008–1028.

Soane BD, Ball BC, Arvidsson J, Basch G, Moreno F, Roger-Estrade J (2012) No-till in northern, western and south-western Europe: A review of problems and opportunities for crop production and the environment. *Soil and Tillage Research*, **118**, 66–87.

Söchtig W (1992) *Wechselwirkungen zwischen der Lumbricidenfauna und unterschiedlicher mechanischer Bodenverdichtung einer Löß-Parabraunerde in Freiland und Laboruntersuchungen*. PhD Thesis, Technical University Brunswick. [In German]

Söchtig W, Larink O (1992) Effect of soil compaction on activity and biomass of endogeic lumbricids in arable soils. *Soil Biology and Biochemistry*, **24**, 1595–1599.

Spagnollo E (2004) *Dinâmica da Matérica Orgânica em Agroecosistemas Submetidos a Queima e Manejo dos Resíduos Culturais*. PhD thesis, UFSM, Santa Maria, RS, Brazil.

Srimurali S, Govindaraj S, Kumar SK, Rajendran RB (2015) Distribution of organochlorine pesticides in atmospheric air of Tamilnadu, southern India. *International Journal of Environmental Science and Technology*, **12**, 1957–1964.

Stancevičius A, Jodaugienė D, Špokienė N, Raudonius S, Trečiokas K (2003) Ilgamečio arimo ir beplügio žemės dirbimo įtaka dirvožemiui ir vasarinių miežių pasėliui. *Žemdirbystė – Agriculture*, **3**, 40–51. [In Lithuanian]

Stroud JL, Irons D, Watts CW, Whitmore AP (2016) *Lumbricus terrestris* abundance is not enhanced after three years of compost amendments on a reduced tillage wheat cultivation conversion. *Applied Soil Ecology*, **98**, 282–28.

Tan CS, Drury CF, Soultani M, van Wesenbeeck IJ, Ng HY, Gaynor JD, Welacky TW (1998) Effect of controlled drainage and tillage on soil structure and tile drainage nitrate loss at the field scale. *Water Science and Technology*, **38**, 103–110.

Tan CS, Drury CF, Reynolds WD, Gaynor JD, Zhang TQ, Ng HY (2002). Effect of long-term conventional tillage and no-tillage systems on soil and water quality at the field scale. *Water Science and Technology*, **46**, 183–90.

Tanck BCB, Santos HR, Dionísio JA (2000) Influência de diferentes sistemas de uso e manejo do solo sobre a flutuação populacional do oligo-queta edáfico *Amynthas* spp. *Revista Brasileira de Ciência do Solo*, **24**, 409–415. [In Portuguese with English summary]

Tsiafouli MA, Thébault E, Sgardelis SP *et al.* (2015) Intensive agriculture reduces soil biodiversity across Europe. *Global Change Biology*, **21**, 973–985. doi: 10.1111/gcb.12752.

Tummers B (2006) *DataThief III*. 2006 http://datathief.org/.

Ulrich S, Tischer S, Hofmann B, Christen O (2010) Biological soil properties in a long-term tillage trial in Germany. *Journal of Plant Nutrition and Soil Science*, **173**, 483–489.

van Capelle C, Schrader S, Brunotte J (2012) Tillage-induced changes in the functional diversity of soil biota—a review with a focus on German data. *European Journal of Soil Biology*, **50**, 165–181.

Velki M, Ecimovic S (2015) Changes in exposure temperature lead to changes in pesticide toxicity to earthworms: A preliminary study. *Environmental Toxicology and Pharmacology*, **40**, 774–784.

Vršič S (2011) Soil erosion and earthworm population responses to soil management systems in steep-slope vineyards. *Plant, Soil and Environment*, **57**, 258–263.

Weber M, Emmerling C (2005) Long-term effects of reduced and conservation tillage in organic farming on soil organic matter and nutrient content, and soil biological properties. In: 8. *Wissenschaftstagung Ökologischer Landbau: Ende der Nische* (eds Heß, J, Rahmann G), pp. 5-–8. Kassel, Germany. [In German with English summary]

Wilson-Rummenie AC, Radford BJ, Robertson LN, Simpson GB, Bell KL (1999) Reduced tillage increases population density of soil macrofauna in a semi-arid environment in central Queensland. *Environmental Entomology*, **28**, 163–172.

Wyss E, Glasstetter M, Kretzschmar A (1992) Tillage treatments and earthworm distribution in a Swiss experimental corn field. *Soil Biology and Biochemistry*, **24**, 1635–1639.

Zaller JG, Heigl F, Ruess L, Grabmaier A (2014) Glyphosate herbicide affects belowground interactions between earthworms and symbiotic mycorrhizal fungi in a model ecosystem. *Scientific Reports*, **4**, 5634. doi: 10.1038/srep05634.

Zhang GS, Chan KY, Oates A, Heenan DP, Huang GB (2007) Relationship between soil structure and runoff/soil loss after 24 years of conservation tillage. *Soil and Tillage Research*, **92**, 122–128.

Zhao X, Liu SL, Pu C *et al.* (2016) Methane and nitrous oxide emissions under no-till farming in China: a meta-analysis. *Global Change Biology*, **22**, 1372–1384

Zida Z, Ouédraogob E, Mandoc A, Stroosnijder L (2011) Termite and earthworm abundance and taxonomic richness under long-term conservation soil management in Saria, Burkina Faso, West Africa. *Applied Soil Ecology*, **51**, 122–129.

Figure legends

Fig. 1 Number of included studies on the effect of tillage practices on earthworm abundances by continent of origin.

Fig. 2 The effect of sampling method on earthworm abundance (a) and biomass (b) as a percentage change of the control. Mean effect and 95% confidence intervals are shown. Sample sizes are shown on the right of each confidence interval, first the number of control–treatment pairs followed (after the slash) by the number of studies from which the comparisons were derived.

Fig. 3 The effect of the different forms of reduced tillage treatments on earthworm abundance (a) and biomass (b) as a percentage of the control. For treatment codes see Table 1. Mean effect and 95% confidence intervals are shown. Sample sizes are shown on the right of each confidence interval, first the number of control–treatment pairs followed (after the slash) by the number of studies from which the comparisons were derived.

Fig. 4 The effect of ploughing depth in the Conventional control (a and b), organic matter (OM) additions (c and d), agrochemicals use (e and f; P = pesticides, HG = glyphosate was used as herbicide; HnoG = any other type of herbicides was used for crop protection but no glyphosate) and the number of years of cultivation (g and h) on earthworm abundance (left) and biomass (right) as a percentage of the control. Mean effect and 95% confidence intervals are shown. Sample sizes are shown on the right of each confidence interval, first the number of control–treatment pairs followed (after the slash) by the number of studies from which the comparisons were derived.

Fig. 5 Random-effects model – regression of the log response ratio of earthworm abundance (a) and biomass (b) versus reported ploughing depth in the Conventional control.

Fig. 6 Random-effects model – regression of the log response ratio of earthworm abundance (a) and biomass (b) versus years of cultivation.

Fig. 7 The effect of annual rainfall (a and b; in mm) and the Köppen climate classification (c and d; the first letter refers to the main climates: A=tropical rain climate without cool season, B=dry climates, C=warm temperate climates and D=snow climates, and the second letter to the further sub-divisions according to the seasonal distribution and amount of rainfall and to the winter and summer temperature regimes: f=sufficient moisture in all months; s=dry season in the summer of the respective hemisphere; w=dry season in the winter of the respective hemisphere) on earthworm abundance and biomass as a percentage of the control. Mean effect and 95% confidence intervals are shown. Sample sizes are shown on the right of each confidence interval, first the number of control–treatment pairs followed (after the slash) by the number of studies from which the comparisons were derived.

Fig. 8. The effect of soil texture (a and b), soil clay content (c and d; in %), soil organic carbon content (e and f; in %) and soil pH (g and h) on earthworm abundance and biomass as a percentage of the control. Mean effect and 95% confidence intervals are shown. Sample sizes are shown on the right of each confidence interval, first the number of control–treatment pairs followed (after the slash) by the number of studies from which the comparisons were derived.

Fig. 9. Random-effects model – regression of the log response ratio of earthworm abundance (a) and biomass (b) versus soil clay content (%).

Fig. 10 (a) Mean changes in the abundance of individually reported earthworm species as a percentage of the control in response to reduced forms of tillage (AH = *Allolobophora chlorotica*, AC = *Aporrectodea caliginosa*, AG = *A. georgii*, AI = *A. icterica*, AL = *A. longa*, AT = *A. trapezoides*, ATUB = *A. tuberculata*, ATUG = *A. turgida*, AR = *A. rosea*, LT= *Lumbricus terrestris*, LR = *L. rubellus*, LC = *L. castaneus*, OCTO = *Octolasion* spp.). (b) Mean changes in earthworm abundance of different age groups as a percentage of the control in response to reduced forms of tillage. (c) Mean changes in earthworm ecological groups' abundance as a percentage of the control in response to reduced forms of tillage. Mean effect and 95% confidence intervals are shown. Sample sizes are shown on the right of each confidence interval, first the number of control–treatment pairs followed (after the slash) by the number of studies from which the comparisons were derived.

Table 1 Tillage grouping categories used in the meta-analyses

Tillage categories (codes in brackets)	**Common terminology for reduced tillage treatments used in the literature**
No-Tillage (NT)	No tillage, no-till No tillage+chemicals Zero Tillage Direct Seeding Direct Sowing Direct Drilling Cutting 3-4 cm wide slots by hand tool Unploughed Narrow-point openers (5-10 cm)
Shallow Soil Loosening (SLL) (Superficial Tillage or Soil Loosening <15 cm, non-inversion tillage)	Minimum tillage Minimum tillage with soil loosening Minimal cultivation by Dutzi non-inversion cultivator and drilling Superficial tillage Coulter disk for planting Disking Tined cultivation Chisel Rotatory harrow Rotary hoe Sub-till or subsurface tillage Cultivators Shallow Loosening
Deep Soil Loosening (DSL) (Deep loosening >15 cm, Vertical tillage, non-inversion tillage)	Minimum Tillage Erosion plough Chisel plough Chisel disking Deep tine cultivation Harrowing Rotary hoe Disk harrow Cultivators Deep Loosening Paraplow Ripping
Reduced Tillage (RT)	Shallow ploughing Reduced ploughing

(Shallow Ploughing, inversion tillage)	Ridge Ecomat (shallow inversive ploughing 10 cm) Two-layer ploughing (the double-layer plough turned the soil in the upper 15 cm and loosened it 10 cm below)
Conservation Agriculture (CA)	Conservation Agriculture Conservation Tillage Layer cultivations No tillage (with crop residues retained and standing stubble or with cover crops as living mulch) Zero loading Shred-bedding (shredding stalks after harvest, followed by bedding on the old rows) Dibble stick to create a planting hole where seeds are placed plus crop residues retained as surface mulch ECO-Tillage Volunteer ryegrass production Ridge till

Fig. 1

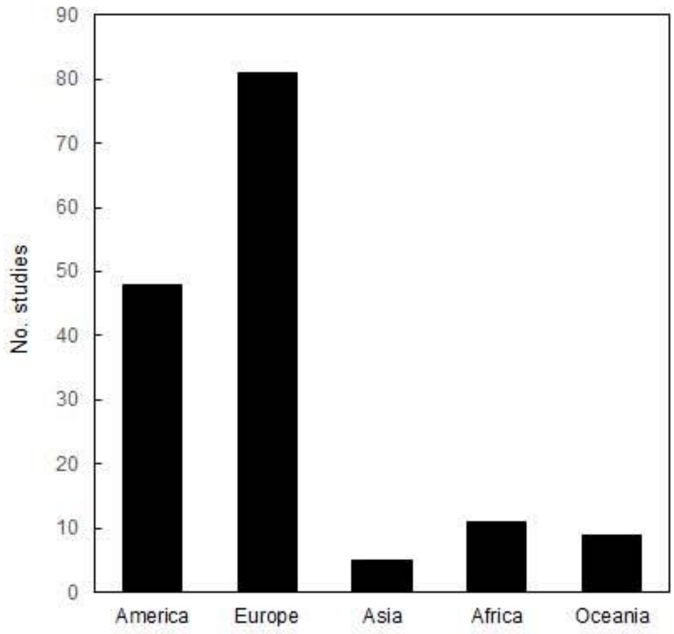

No. studies
0
10
20
30
40
50
60
70
80
90
America
Europe
Asia
Africa
Oceania

Fig. 2

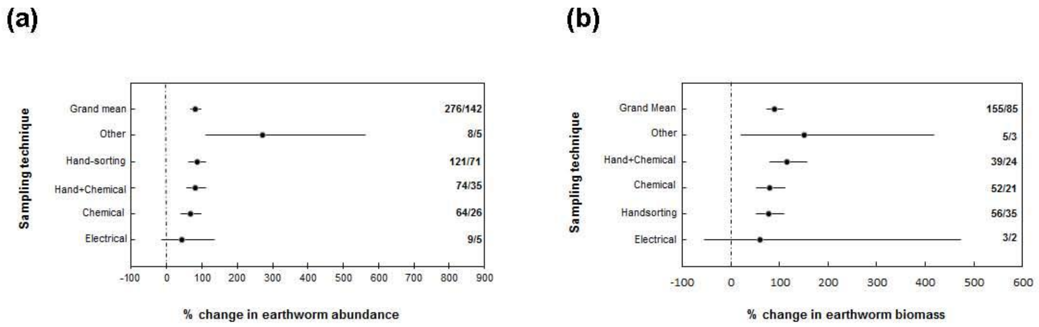

(a)
Sampling technique
Grand mean
Other
Hand-sorting
Hand+Chemical
Chemical
Electrical
276/142
8/5
121/71
74/35
64/26
9/5
% change in earthworm abundance
(b)
Sampling technique
Grand Mean
Other
Hand+Chemical
Chemical
Handsorting
Electrical
155/85
5/3
39/24
52/21
56/35
3/2
% change in earthworm biomass

Fig. 3

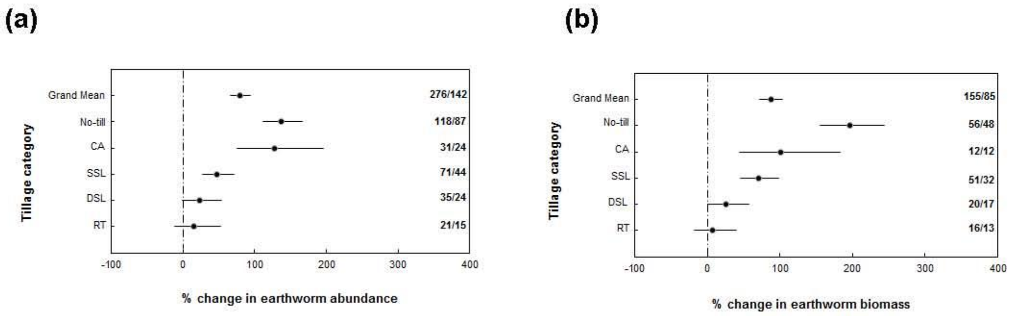

(a)
Grand Mean
No-till
CA
SSL
DSL
RT
Tillage category
276/142
118/87
31/24
71/44
35/24
21/15
-100
0
100
200
300
400
% change in earthworm abundance
(b)
Grand Mean
No-till
CA
SSL
DSL
RT
Tillage category
155/85
56/48
12/12
51/32
20/17
16/13
-100
0
100
200
300
400
% change in earthworm biomass

Fig. 4

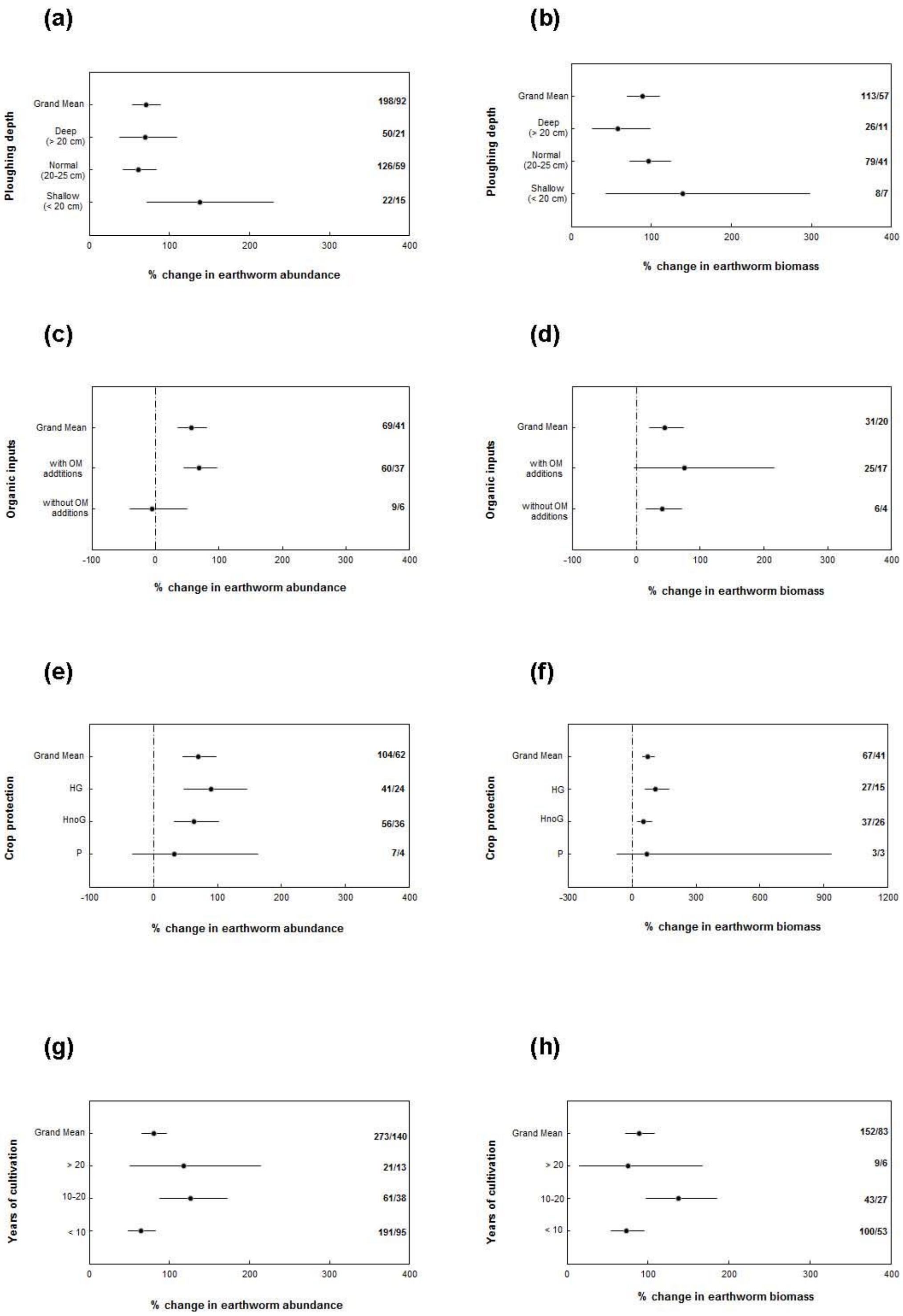

(a)
Ploughing depth
Grand Mean
Deep (> 20 cm)
Normal (20-25 cm)
Shallow (< 20 cm)
198/92
50/21
126/59
22/15
0 100 200 300 400
% change in earthworm abundance
(b)
Ploughing depth
Grand Mean
Deep (> 20 cm)
Normal (20-25 cm)
Shallow (< 20 cm)
113/57
26/11
79/41
8/7
0 100 200 300 400
% change in earthworm biomass
(c)
Organic inputs
Grand Mean
with OM addtitions
without OM additions
69/41
60/37
9/6
-100 0 100 200 300 400
% change in earthworm abundance
(d)
Organic inputs
Grand Mean
with OM additions
without OM additions
31/20
25/17
6/4
-100 0 100 200 300 400
% change in earthworm biomass
(e)
Crop protection
Grand Mean
HG
HnoG
P
104/62
41/24
56/36
7/4
-100 0 100 200 300 400
% change in earthworm abundance
(f)
Crop protection
Grand Mean
HG
HnoG
P
67/41
27/15
37/26
3/3
-300 0 300 600 900 1200
% change in earthworm biomass
(g)
Years of cultivation
Grand Mean
> 20
10-20
< 10
273/140
21/13
61/38
191/95
0 100 200 300 400
% change in earthworm abundance
(h)
Years of cultivation
Grand Mean
> 20
10-20
< 10
152/83
9/6
43/27
100/53
0 100 200 300 400
% change in earthworm biomass

Fig. 5

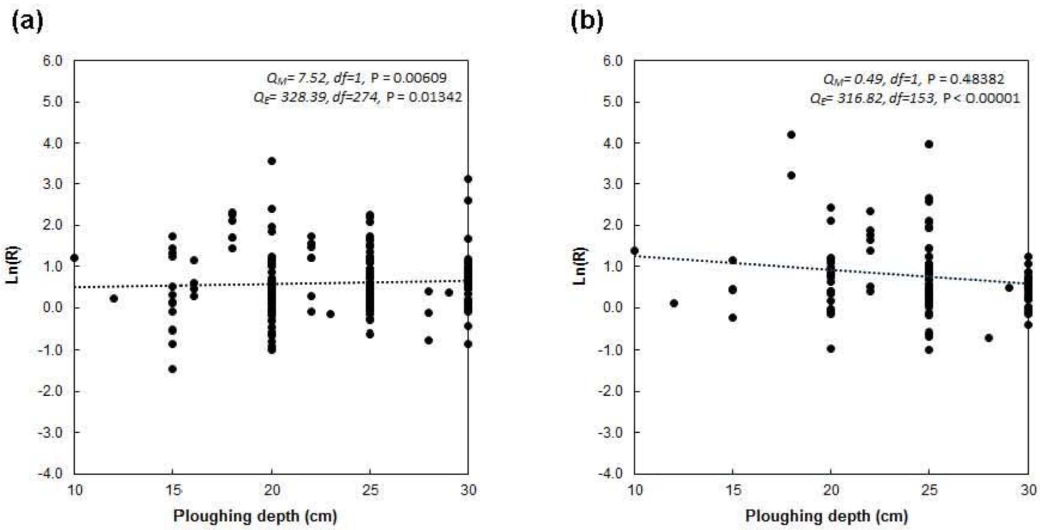

(a)
Q_M= 7.52, df=1, P = 0.00609
Q_E= 328.39, df=274, P = 0.01342
Ln(R)
Ploughing depth (cm)
(b)
Q_M= 0.49, df=1, P = 0.48382
Q_E= 316.82, df=153, P< 0.00001
Ln(R)
Ploughing depth (cm)

Fig. 6

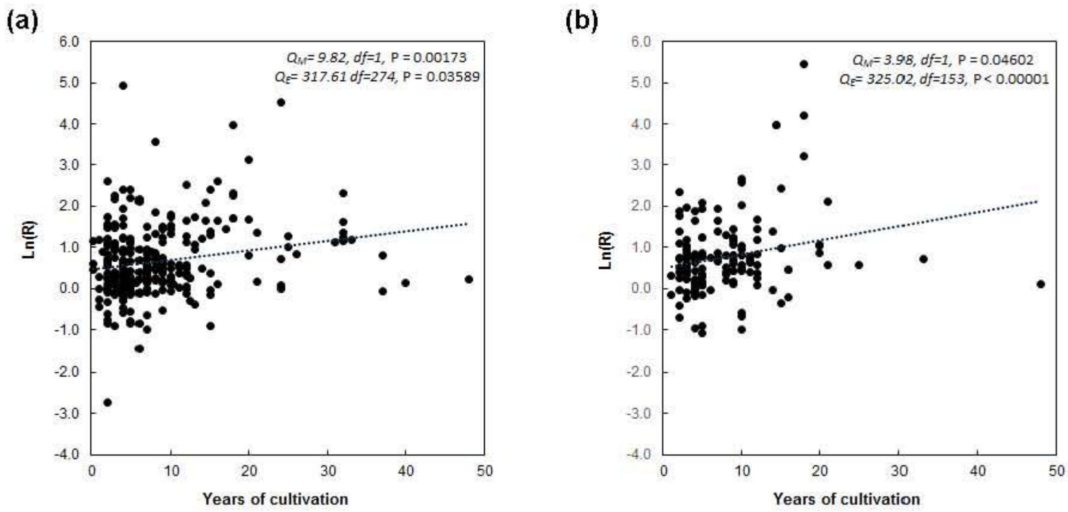

(a)
Q_M= 9.82, df=1, P = 0.00173
Q_E= 317.61 df=274, P = 0.03589
Ln(R)
Years of cultivation
6.0
5.0
4.0
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
-4.0
0
10
20
30
40
50
(b)
Q_M= 3.98, df=1, P = 0.04602
Q_E= 325.02, df=153, P < 0.00001
Ln(R)
Years of cultivation

Fig. 7

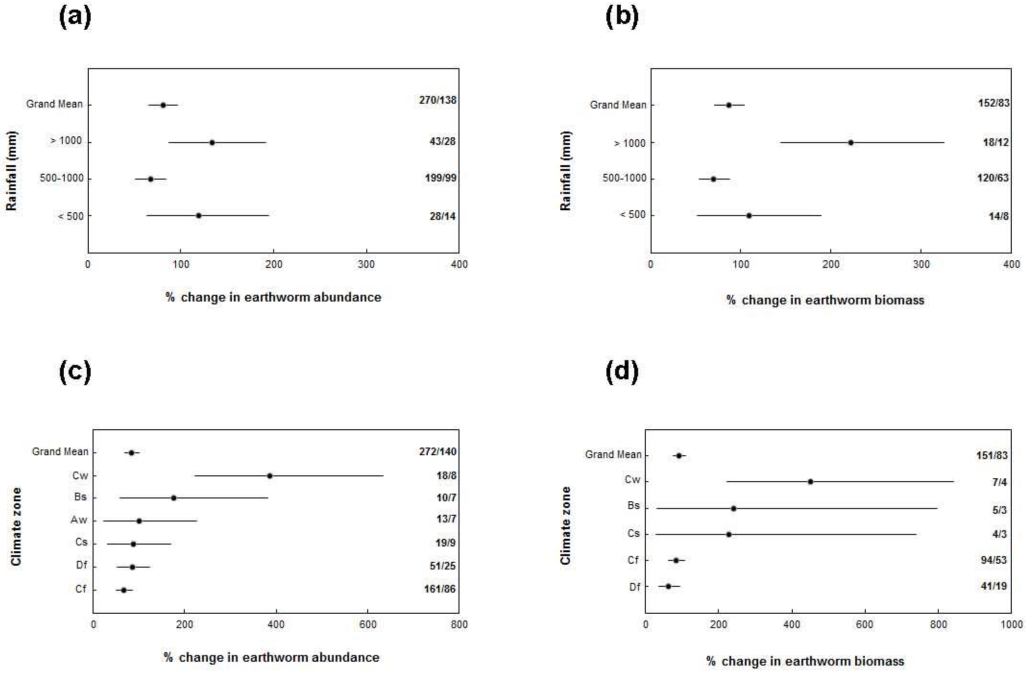
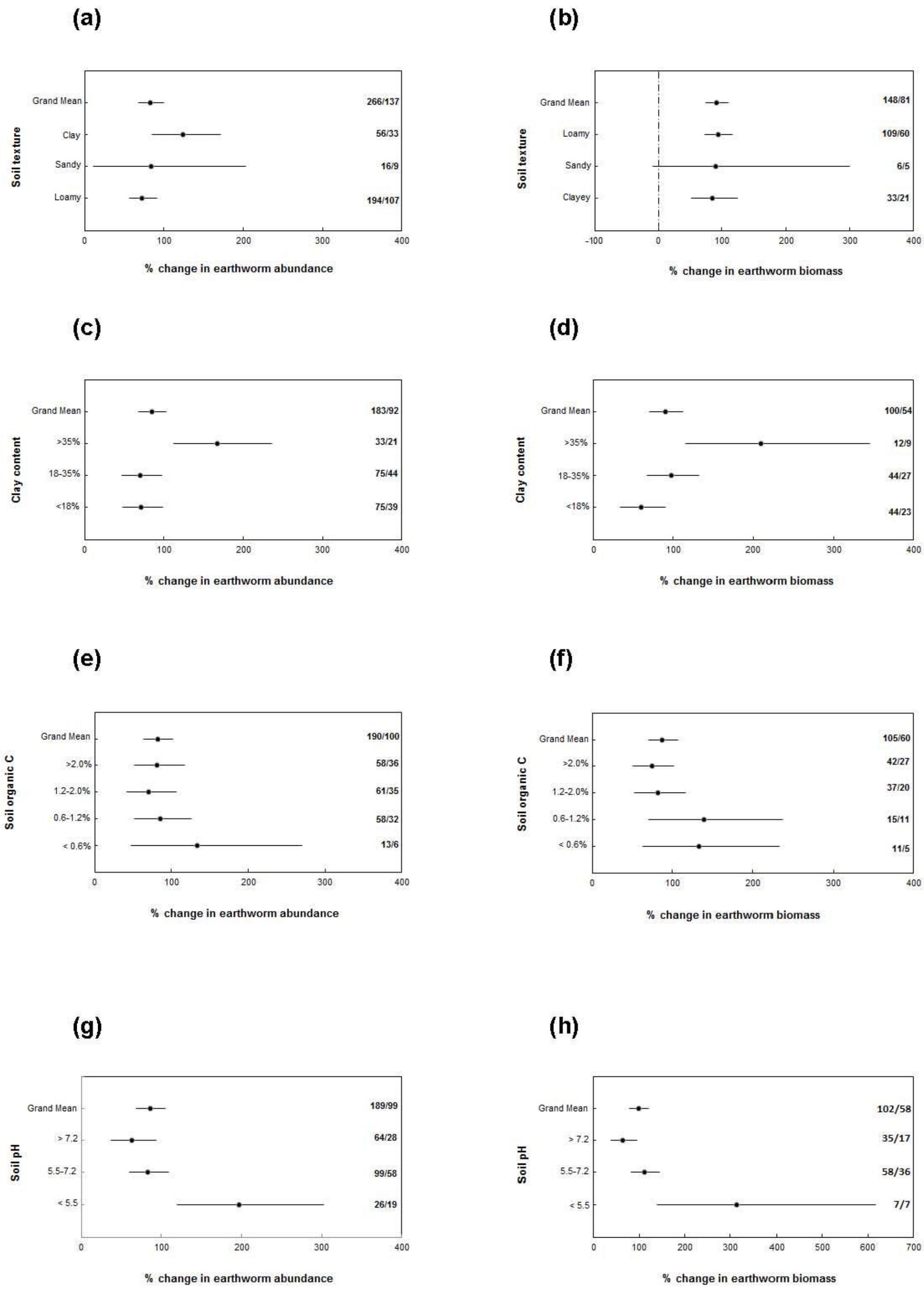

(a)
Rainfall (mm)
Grand Mean
> 1000
500-1000
< 500
270/138
43/28
199/99
28/14
0
100
200
300
400
% change in earthworm abundance
(b)
Rainfall (mm)
Grand Mean
> 1000
500-1000
< 500
152/83
18/12
120/63
14/8
0
100
200
300
400
% change in earthworm biomass
(c)
Climate zone
Grand Mean
Cw
Bs
Aw
Cs
Df
Cf
272/140
18/8
10/7
13/7
19/9
51/25
161/86
0
200
400
600
800
% change in earthworm abundance
(d)
Climate zone
Grand Mean
Cw
Bs
Cs
Cf
Df
151/83
7/4
5/3
4/3
94/53
41/19
0
200
400
600
800
1000
% change in earthworm biomass

Fig. 8



(a)
Soil texture
Grand Mean
Clay
Sandy
Loamy
266/137
56/33
16/9
194/107
0
100
200
300
400
% change in earthworm abundance
(b)
Soil texture
Grand Mean
Loamy
Sandy
Clayey
148/81
109/60
6/5
33/21
-100
0
100
200
300
400
% change in earthworm biomass
(c)
Clay content
Grand Mean
>35%
18-35%
<18%
183/92
33/21
75/44
75/39
% change in earthworm abundance
(d)
Clay content
Grand Mean
>35%
18-35%
<18%
100/54
12/9
44/27
44/23
% change in earthworm biomass
(e)
Soil organic C
Grand Mean
>2.0%
1.2-2.0%
0.6-1.2%
< 0.6%
190/100
58/36
61/35
58/32
13/6
% change in earthworm abundance
(f)
Soil organic C
Grand Mean
>2.0%
1.2-2.0%
0.6-1.2%
< 0.6%
105/60
42/27
37/20
15/11
11/5
% change in earthworm biomass
(g)
Soil pH
Grand Mean
> 7.2
5.5-7.2
< 5.5
189/99
64/28
99/58
26/19
% change in earthworm abundance
(h)
Soil pH
Grand Mean
> 7.2
5.5-7.2
< 5.5
102/58
35/17
58/36
7/7
0
100
200
300
400
500
600
700
% change in earthworm biomass

Fig. 9

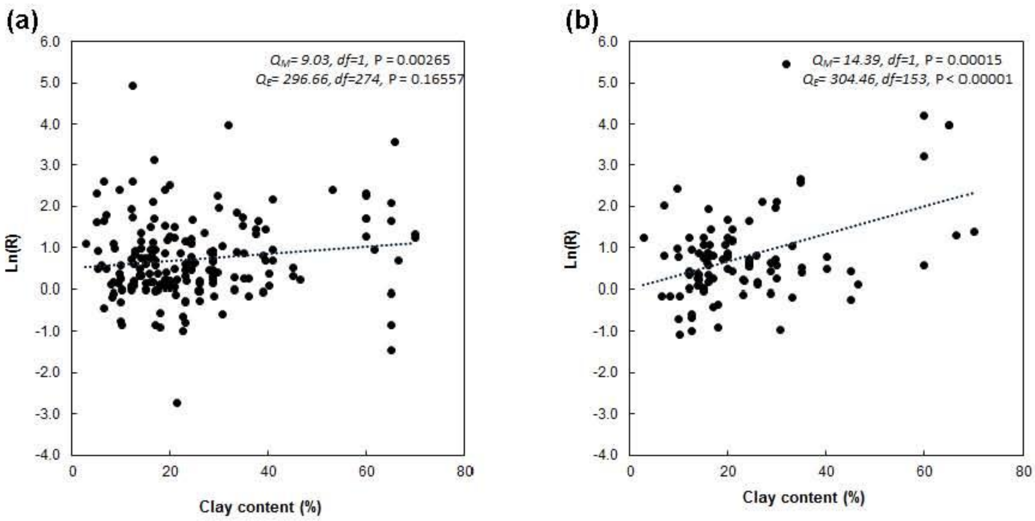
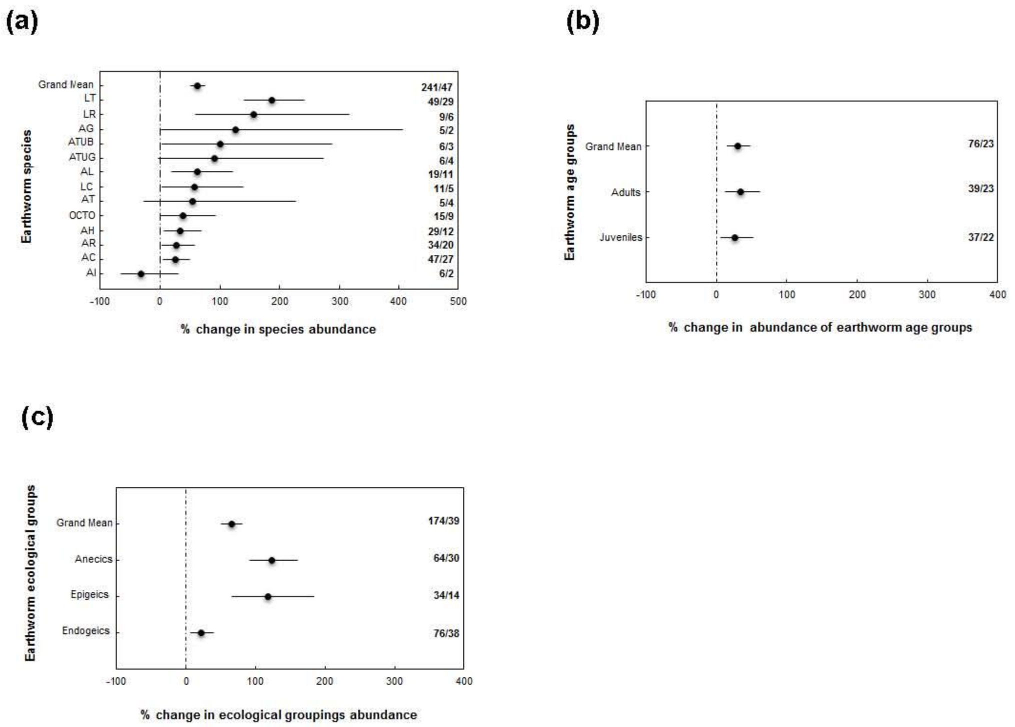

(a)
Q_M= 9.03, df=1, P = 0.00265
Q_E= 296.66, df=274, P = 0.16557
Ln(R)
Clay content (%)
(b)
Q_M= 14.39, df=1, P = 0.00015
Q_E= 304.46, df=153, P < 0.00001
Ln(R)
Clay content (%)

Fig. 10


(a)
Earthworm species
Grand Mean
LT
LR
AG
ATUB
ATUG
AL
LC
AT
OCTO
AH
AR
AC
AI
241/47
49/29
9/6
5/2
6/3
6/4
19/11
11/5
5/4
15/9
29/12
34/20
47/27
6/2
-100
0
100
200
300
400
500
% change in species abundance
(b)
Earthworm age groups
Grand Mean
Adults
Juveniles
76/23
39/23
37/22
-100
0
100
200
300
400
% change in abundance of earthworm age groups
(c)
Earthworm ecological groups
Grand Mean
Anecics
Epigeics
Endogeics
174/39
64/30
34/14
76/38
-100
0
100
200
300
400
% change in ecological groupings abundance