Seventh Framework Programme
Theme 6
Environment (including Climate Change)

Collaborative project

Deliverable D 2.1
Land management effects on soil diversity and water (and soil organic matter) regulation.

Due date of deliverable: M11
Actual submission date: M16
Start date of the project: January 1st, 2011
Duration: 48 months

Organisation name of lead contractor: Alterra
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Revision: V 1
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OVERVIEW

Soil organisms contribute to the provision of ecosystem services in a number of ways. Even though they are recognized as functional important, there are to date relatively few systematic analyses of how land management and land-use affects key soil taxa. Even more uncertain are the links between soil community change and the provision of key ecosystem service. In this Deliverable, a meta-analysis approach has been used to investigate the effects of changes in land use and land management across a successional / intensification gradient (conventional arable < no or reduce tillage < pasture < wooded land) on communities of two taxa, earthworms and soil fungi. These taxa were selected for study because they are important regulators of soil structural properties and so potentially of soil hydrological properties. Analysis of diversity effects have the also been supported by re-analysis of data from national surveys to investigate if those trends seen for earthworms and fungi are mirrored for the soil mesofauna. Functional consequences of biodiversity change have then also been assessed by considering effects of earthworm community parameters on water infiltration rates. Based on separate review of 100 of published data-set, the meta-analysis approach used highlights a consistent trend for increase earthworm abundance and greater fungal community abundance and complexity across the gradient. Greatest changes are seen for early stage change, such as introduction of reduced tillage regime and pasture conversion from arable. National surveys results suggest that the trends seen in plot experiments are mirrored in natural communities across broad geographic areas. When coupled with the observed effects of earthworms on water infiltration rates, these changes point to the potential for difference in ecosystem service provision resulting from soil biodiversity change under different land-uses. This raises the potential to manage landscapes to increase ecosystem service provision from soil fauna.

1. INTEGRATION OF SOIL BIODIVERSITY INTO HYDROLOGICAL MODELS – CONCLUSIONS AND NEXT STEPS

Analysis of studies that have compared soil management and soil community (earthworm abundance and species composition) effects suggested a positive relationship between earthworm activity and infiltration rate, but encountered large variations in earthworm abundance and infiltration rates within the published data-sets. Constructions of models using data from literature studies indentified that the earthworm abundance, tillage system and habitat type each had a significant effect on water infiltration rate. From the review of the effects of individual earthworm functional groups, anecic and epigeic earthworms were shown to increase water infiltration significantly, but this effect was not seen for the endogeic worms. This result was expected for the deep dwelling anecic worms as a result of burrow formation. However, the result for the epigeic worms was novel and may be explainable by the surface dwelling habit of these species.
The clear effects of earthworm abundance and in particular of the specific of earthworm functional groups on water infiltration rates can provide essential information that can be included in soil hydrology models. Bardgett et al (2001) have published a conceptual view of the potential way that biodiversity can be conceptually linked to soil hydrological processes. The role of both the anecic and epigeic worm can be represented through the effects of water transport to the deeper soil layer and ultimately to groundwater. The epigeic worms can act both to prevent the formation of surface crusts and mats and also may contribute to the interflow of water through soil layers. Within simple hydrological model the scaling of these parameters in accordance with the changes in earthworm abundance and biodiversity that may feature under different land management and land use regimes may offer an approach to the incorporation of quantitative measures of biodiversity to soil hydrological process. Coupling these data to representations of the effects of earthworm abundance and ecological group representation on soil infiltration rates can provide an approach through which it may be feasible to parameterise the consequences of earthworm abundance change for water flow processes occurring both above and below the soil surface. Such models can provide a potential route to the the identification and valuation of the role of earthworms and wide soil biodiversity community status on water regulation in terrestrial ecosystems.

• 1.1. DEFINING THE CONTEXT, SCOPE AND AIMS OF THE STUDY

The activities of the soil biota, which in this context includes micro-organisms (e.g. soil bacteria, Achaea, fungi etc), mesofauna (e.g. protozoa, nematodes, mites, Collembola etc.) and macroinvertebrates (e.g. earthworm, molluscs, insects and their larvae etc.), are critical for the mediation of many important soil functions and resulting provision of ecosystem goods and services (Fitter et al., 2005). These include many essential commodities provided by terrestrial ecosystems such as biomass and food production; storing, filtering and transforming nutrients, contaminants and water; interaction with and habitat provision for aboveground biodiversity; and acting as a biodiversity pool from which future novel applications and products can be garnered (Power, 2010).

Because they are intimately involved in many important soil functions, the biological components of soils are naturally an important focus for biodiversity, ecosystem process and ecosystem services research (Lemanceau, 2011). This is particularly pertinent given that the structure and function of soil communities is known to be sensitive to anthropogenic influences. For example, it is widely recognised that trace metal and organic chemical pollution, soil erosion and soil sealing can each have profound influences on the compositional diversity of micro-, meso- and macro-faunal soil communities (Filser et al., 2008; Spurgeon and Hopkin, 1999; Wang et al., 2007). Agricultural intensification in support of enhanced food production has also been strongly linked both to changes in the diversity of the soil fauna and also to change in the status of a range of indicators of soil health (Culman et al., 2010).
National surveys that have characterised soil biodiversity have identified differences in the size and biodiversity of soil invertebrate and soil microorganism communities associated with a range of habitats and land use types. These include from the Great Britain wide Countryside Survey 2007 project (involving samples from approximately 1000 individual plots for microbial diversity, microbial function and microarthropod diversity) (Emmett et al., 2010), the CréBeo National Soil Biodiversity project in Ireland (60 sites covering five land uses and seven organism groups)(Schmidt et al., 2011; Keith et al., 2012) and Dutch Biological Indicator system for Soil Quality (BISQ) program (samples from 200 locations for microbial, meso- and macro-faunal diversity)(Rutgers et al., 2009). Results from these studies have all highlighted patterns in the distribution of soil taxa related to land use and land management practice (see later sections for results from the GB Countryside Survey project).

Due to their multiple complementary and competing beneficial effects on soil processes and resulting ecosystems services, a large number of smaller site and regional based studies have attempted to characterize land management and land-use influences on the composition of soil communities. These include studies of soil communities within field experiments that have compared

1. reduce tillage and conventional tillage regimes;
2. conversion of managed arable land to natural or managed pasture;
3. successional conversion or afforestation of pasture to wooded lands.

In this deliverable, the effects of these three specific land-use and land management changes on the composition of key components of the soil fauna are assessed in a series of initial systematic reviews for each land management change. These systematic reviews focus on the effects of land management changes on those taxa identified as being key to the regulation of soil properties, such as soil organic matter and aggregate status and water infiltration rate, which are known to regulate soil water flow. The work focuses on biota relevant to this service because the effects of soil biodiversity on the provision and valuation of ecosystem service related to the regulation of water flow are a particular focus for work in EcoFinder in WP 2 (e.g. D2.4 Modeling module for biological diversity and functions in land surface water balance due in Month 40) and also in WP 5 Valuation of Soil Ecosystem Services, where regulation of water flows will be a case study for economic valuation.

Any influences on soil community structure under different land management or land use regimes that are identified within meta-analysis are subsequently related to relevant soil properties relevant for the ecosystem service provision of water regulation in terrestrial habitats. In this case, with the focus on the regulation of water flows from surface soils to the deeper soil layers, this includes particularly quantitative measurements of infiltration rates. These relationships are established from a further set of initial systematic reviews. When combined with the data on land management and land use effects on key biodiversity, the assembled data-sets, meta-analyses and other statistical interpretations provide a series of parameters incorporation into hydrological models that describe water flow rates across and within soils. These can then feed ultimately into analysis of the valuation of ecosystem service and/or the patterns of their delivery at the landscape scale.
1.2. INTRODUCTION TO SOIL BIODIVERSITY

At present comparatively little is known about the biodiversity of soil when compared to, for example, above ground diversity or the fauna of freshwater river and lake (Anderson, 1975). For the various components of the soil microbial community, molecular approaches such as terminal restriction fragment length polymorphism (tRFLP), phylogenetic microarrays and metagenomic fingerprinting are just now beginning to reveal the true complexity and variety of patterns in the diversity and distribution of soil microbes (Griffiths et al., 2011). For the soil meio-, meso- and macro-fauna, molecular approaches to biodiversity assessment still remain in development (Porazinska et al., 2009), including work being conducted within the EcoFINDERS project. This means that for surveys of this component of the soil community, traditional morphological taxonomy remains the dominant approach. For some key groups, such as earthworms and springtails, good morphological keys do exist, although, even in these cases, traditional taxonomy can be hampered by cryptic speciation (i.e. occurrence of groups of closely related species which are reproductively isolated from each other, but which have high morphological similarity) (Andre et al., 2009; King et al., 2008) and other taxonomic uncertainties (Hopkin, 1997).

Beyond these better known groups, for even common and widely distributed taxa such as the protozoa, nematodes and mites, there are significant issues for morphological identification associated with the lack of keys, laborious nature of the work and declining expert base (Hopkin, 1997).

Although the full characterisation of biodiversity to high taxonomic resolution in many of the groups of widely distributed soil organisms has traditionally been, and remains, challenging, evidence is beginning to emerge that previous portrayals of soil biota as a black box of “decomposers”, that is a functionally redundant trophic level through which organic material generated above ground is recycled, is almost certainly too simplistic (Sugden et al., 2004). This change has come about because of the mounting evidence from laboratory and field studies. These have shown that soil communities can be not only equally as complex as those aboveground, but also that this diversity, whether expressed taxonomically or functionally, can influence the rates and states of soil processes (Heemsbergen et al., 2005; Wardle, 2006). This increased recognition has highlighted that our understanding of the extent to which the abundance and diversity of soil communities influence individual soil process and ultimately underpin the multi-functionality and natural capital of terrestrial ecosystems remains to be developed. It is also recognised that the extent to which anthropogenic influences of man can compromise the functions and services provided by soils is an important issue for research and survey.
• **1.3. KEY SOIL BIODIVERSITY FOR SOIL WATER (AND SOM) REGULATION**

As outlined, the focus of this deliverable is to determine how changes in the land management and land use affected the structure of soil communities. How these changes affect the regulation of water flow within and across soils is also considered. The regulation of soil water flow is associated with a number of soil features. Relevant parameters known to be important include texture, organic matter content, soil bulk density, fine and coarse aggregates densities, frequency of surface cracking (e.g. in clay soils) and the density and connectivity of plant roots and macroinvertebrates burrows.

*Burrowing soil fauna mediation of water flow*

The biotic components of the soil can influence the properties that regulate soil water flows in a number of ways. The most obvious is through the production of burrows in the soil profile that offer conduits through which the rapid passage of water from the soil surface to the deeper soil layers can be mediated (Bastardie et al., 2005; Jegou et al., 2001). The production of burrows in the soil is particularly associated with the activities of those soil invertebrate taxa that have been identified as “ecosystem engineers” (Lavelle et al., 1997; Lavelle et al., 2006). These taxa tend to include the larger bodied soil invertebrate species such as isopods, millipedes, molluscs and earthworms. While all these groups have been shown to make a notable contribution to soil structural characteristics including burrow formation, the sheer abundance and biomass of earthworms to be found in many terrestrial biomes (except the deserts and the arctic) and across many broad habitats (except the most acidic heathland and bogs) identify this group as the macroinvertebrate taxa most likely to contribute significantly to the engineering of soil to control water infiltration rates and flows.

The wider importance of earthworms in relation to soil health was initially recognized and explored by Darwin, in his treatise *The Formation of Vegetable Mould Through the Action of Worms With Observations on Their Habits* (Darwin, 1883). Since this first well known work, an extensive literature has been established for this key taxa and today, we know that earthworms are essential in many managed and natural soils because they enhance a large number of soil processes including drainage and soil aeration; the breakdown of organic matter and nutrient cycling (Edwards, 2004); the dispersal of microorganisms in soils (Clegg et al. 1995); the provision of an essential dietary item for a range of species (e.g. farmland birds) of conservation interest; the promotion of plant growth (Edwards and Arancon, 2004; Laossi et al., 2010); and the suppression of plant disease (Stephens et al., 1994). Although it is likely that many if not all earthworm species will influence those properties that control water balance, it is likely that the exact nature of such influences may vary between different earthworms species. In his seminal work, Bouché (1972) recognized that the diversity of earthworms known to exist in soils could be divided into three major functional groups. Each of which can be found in both temperate and tropical soils. These groups, and examples of common European species for each, are outline below.

- Epigeic species live in permanent burrow systems in the litter and upper mineral soils layers of the soil profile. These species often maintain horizontal burrow systems in the surface layers, living in and feeding on surface deposited organic
material including animal dung and leaf litter. Typical epigeic species include *Lumbricus rubellus*, *Dendrodrilus rubida* and *Dendrobaena octaedra*. Compost dwelling species such as *Eisenia fetida* and *Eisenia veneta* are also classified as epigeic.

- Endogeic worms produce lateral burrow systems in the surface and deeper layers of the upper mineral soil. These burrow systems may be permanent (i.e. they are maintained) or temporary (i.e. the worm passes through the soil in an ad-hoc manner). Endogeic species rarely come to the soil surface (except following severe rainfall), instead staying within these burrow systems where they feed on decayed organic matter embedded in the mineral soil. Common endogeic species include *Aporrectodea caliginosa*, *Aporrectodea rosea* and *Octolasion cyaneum*.

- Anecic worms build permanent, vertical burrows that extend from the deeper soil layers (up to 2 m) to the soil surface. The anecic species may come to the soil surface to feed, to egest cast materials (as in the case of *Allolobophora longa*) or to mate (as for *Lumbricus terrestris*). Because these species produce vertical burrows, they may be particularly important in controlling water infiltration rates.

Soil organisms mediating soil micro-aggregate formation

While direct burrowing through soil by macroinvertebrates may provide clear conduits for water flow, other characteristics of the soil can also be important. In particular the tendency of soil particles to form larger aggregates is important in determining soil bulk density and porosity. It has been demonstrated that differences in the management of land, and in particular the choice of tillage regime in agricultural areas can affect soil aggregate formation and conservation (Bhattacharyya et al., 2009; Munkholm, 2011). As well as management practice, it has also been shown that soil macroinvertebrates, such as earthworms (Fonte et al., 2010; Larink et al., 2001; Marashi and Scullion, 2003) and millipedes (Fujimaki et al., 2010) can contribute to the formation and maintenance of soil aggregates. These effects include direct influences, such as the production of mucous material that can bind soil particles and also the direct production of cast which have been shown to contribute an extensively to the soil aggregate complement (Davidson and Grieve, 2006). Additionally, influences on invertebrates on the soil microbial compliment, which are recognized as major facilitators of soil aggregation, can also be important determinants.

In addition to the macrofauna, it has long been recognized that components of the soil microbial community may play an important role in the formation of soil aggregates (Aspiras et al., 1971). Among microbial taxa, the fungi, which can produce dense net like structures of hyphae through the soil profile, are widely recognized as important for aggregate formation. While fungal hyphae themselves are almost certainly important, recent evidence has been found to suggest that some fungal species may have additional roles in aggregation. One important finding was the identification of glomalin. This is a fungal glycoprotein initially identified by Wright et al. (1998). Named after the Glomales order of fungi from which it has been identified, Glomalin is a sticky substance that has been shown to be secreted by fungal hyphae. On production it is able to permeate organic matter and to interact at the surfaces of silt, sand, and clay particles. The sticky nature of glomalin means
that once they are coated, soil particles tend to become stuck together, starting the processes of aggregate formation, as a major step to soil structural formation.

Because of the important role that is played by both the fungal hyphae themselves and also secreted products such as glomalin, this review also focus on assess the role that land management change will play in determining the nature of fungal communities under different land management and land use regimes. This is important because changes in fungal communities have the potential to feed through to effects on soil structure. This, thus, provides a combined approach to assessing land management effects on taxa relevant to soil structural properties.

Focus of review and analysis

In the present review, the main focus of the analysis will on systematic analysis of the effects of land use and land management of earthworm numbers and fungal community structure and the potential consequences of these changes for water infiltration rate. The review is based on a systematic review of the literature that allows the compilation of comparative data-sets which compare the abundances of earthworms and fungi under a range of paired land management and land-use scenarios. The review focuses on comparison of earthworm abundance and community metrics for soil fungi. The limitations of this approach are recognized, since different functional groups and taxonomic branches of earthworms and fungi are considered as equivalent with respect to their effects on soil processes. Based on the current state of knowledge there, however, remains continued uncertainty as to the extent of different land management practices and land use change influences on different taxonomic and functional groups. Further, apart from a small number of studies (Heemsbergen et al., 2005; Sheehan et al., 2008), the relative importance of inter and intra species functional diversity on ecosystem process, including those that regulate soil water flow, remain poorly known. Even despite these limitations, the comprehensive nature of the systematic review approach does allow characterization of the major effects on communities under different land-uses. This can then later be expanded to include species specific information as further insights emerge.

While earthworm (as ecosystem engineers that produce burrow conduits for water flow) and fungi (as a key taxa determining the nature of soil aggregation) are included as the primary focus of this review and the contained initial meta-analyses, the effects of land use on other component of the soil biodiversity are also likely to be relevant to soil structural parameters and so should be considered. To investigate the effects of land management and land-use on these other relevant soil taxa, the range of soil biodiversity information that is available through a national ecosystem monitoring program has been utilized. This program, the Great Britain Countryside Survey scheme, assess the status of above and below ground communities, as well as freshwater habitats at over 3000 separate locations across GB. As part of the program, an assessment of the soil communities present at almost 1000 of the visited sites has been conducted. The nature of the sampling, which is dependent on a small soil core, means that the measurement made are best suited for the analysis for the soil mesofauna community and in particular, the number and broad taxonomic grouping of the soil Collembola and mites (nb. the taxonomic richness of soil bacteria and archaea has also been measured). While not as extensive as the meta-analysis approach that is applied for the earthworm and fungi, an initial analysis of the effect of land use change on the communities of these mesofaunal taxa within this survey can be used to assess whether
effects on these group mirror those seen for the two main focus taxa included within the systematic review. The analysis for the GB Countryside Survey project is supported by data for earthworm communities taken for the Ireland CréBeo National Soil Biodiversity program.

1.4. LAND USE/MANAGEMENT AS A DRIVER OF SOIL BIODIVERSITY CHANGE

Studies in agronomy and later in soil ecology and conservation ecology have demonstrated that there are a number of stressors that can affect the abundance and diversity of soil communities. It is often perceived that the greatest pressure on soil communities occurs when the land is exposed to intensive management. Factors such as the regular tillage of soils and the loading of agrochemicals including fertilizer and pesticides clearly represent a threat to the long-term stability of soil communities. There has been a relative wealth of studies that have investigated how these potential stressors influence soil communities. This information is potentially important to consider when interpreting meta-analysis results.

In the case of tillage regime, effects on macroinvertebrate communities are most likely to be driven through direct mechanical damage and increases in predation rate that occur when soil are turned during ploughing. The subsequent effects on soil structure and properties, such as the disruption of burrow networks and the aeration of the soil which can lead to more rapid oxidation of some organic matter may also be important. Because of concerns over the effects of tillage on soil biodiversity, a number of experimental and working farms have trialed the use of no-till or reduced tillage regimes. One of the aims of this study is to assess, through meta-analysis, the extent to which these reduced tillage regimes benefit the key components of the soil fauna relevant to hydrological processes.

Fertilizers play an essential part in agricultural ecosystems. They are applied to farmland in either organic (e.g. slurry and sewage sludge) or inorganic form (e.g. synthetic NPK fertilizer). It is difficult to define how inorganic nitrogen in arable systems would directly impact either positively or negatively on earthworm or fungi themselves; although effects mediated through changes in soil pH or direct burning or negative osmotic effects associated with high fertilizer loadings could be possible. Many components of the soil fauna, including earthworms and fungi, do feed on fresh organic matter that is itself derived from the deposited leaf-litter generated from plant growth. Hence, it is most likely that if nitrogen increases crop production and that this in turn increases litter production and root exudation through rhizodeposition, this may then increase food resources for earthworms. This can sustain a higher total biomass. This highlights the potential role that productivity may play in determining community structure for soil species.

Pesticides can affect soil organisms at a number of scales. Sub-lethal effects (such as impairment of the immune system) are important because even though a well-dosed pesticide may not cause direct mortality, it can increase susceptibility to infection. While sub-lethal effects are important endpoints for consideration, it is only when these effects cause measurable effects on vitality rates (reduce survival, reproduction, growth etc.) that
impacts on populations and communities will emerge. Among pesticides used, generally the greatest non-target toxicity will occur amongst species closely related to the target taxa for which the pesticide is used, such as soil arthropods for the insecticides and soil fungi for the fungicides. However, cases are also known of toxicity to species not taxonomically related to the target group (e.g. carbamate fungicides for earthworms). Consequently, the precise effects of pesticides on the composition of the soil community can be difficult to estimate and certainly when applied at sufficient levels with regularity, the impacts on the soil community cannot be predicted with certainty.

2. APPROACH FOR ANALYSIS OF LAND USE EFFECTS ON BIODIVERSITY AND WATER REGULATION

With the stressors associated with agricultural production known to potential influence the belowground biota, it is understandable that there is a perception that biodiversity of soils is likely to be affected as land use and land management regimes move from low intensity activities (conservation management) towards high intensity practices (conventional arable farming). While this pattern of biodiversity change is often assumed, and indeed has been shown in individual studies, there are to date very few systematic studies that have sought to identify the magnitude of the negative effects of intensification on key soil taxa (Beare et al., 1997; Wardle, 1995). In our study, we have sought to specifically quantify the magnitude of biodiversity changes that occur when land management practices and land use transfer from more intensive to less intensive activities. To allow this comparison between land uses, we have conducted a series of initial systematic reviews to quantify how shifts in land management regimes and land use impact on earthworm abundance and fungal community parameters. The land use and management practices that are compared are listed below.

- Results from paired experiments in which plots within the same region are subjected to conventional tillage and reduced till or no-till management. These studies are hereafter referred to as the “Tillage comparison” meta-analyses.

- Results from studies in which separate fields within a region have been kept under conventional arable land use or converted to grassland (either natural systems or grazing pasture) or which have been under arable and pasture use for at least a know period. These studies are hereafter referred to as the “Arable to pasture conversion” meta-analyses.

- Results from studies in which separate areas within a region have been kept under either a grassland use (natural or grazing) or have been allowed to either undergo natural succession to woodland (either tropical, deciduous or coniferous) or planted with tree species for later cropping (agroforestry). These studies are hereafter referred to as the “Pasture to woodland conversion” meta-analyses.
For each of these comparisons, separate initial systematic reviews have been conducted to assess the effect of the difference in practice on the size (abundance) of the earthworm and fungal communities. These initial reviews have been conducted as an intermediate step towards a full systematic review. They are designed to provide provisional characterization of the evidence base and an indication of effects within the available data, without the need for the formation of stakeholder groups and extensive other outreach and consultation activities that are associated with completion of a full systematic review. This makes the execution of multiple initial systematic reviews a feasible proposition within the budget available for this activity within WP 2 of EcoFINDE RS.

- 2.1. STUDY IDENTIFICATION AND DATA COLLECTION

All assessments have been conducted following a systematic approach for the identification of scientific studies that could provide empirical data which can contribute towards the statistical comparison of community size metrics under different land management and land use regimes. The approach used was first to conduct a comprehensive search within the Web of Knowledge database to identify a set of potential references for detailed analysis. For the biodiversity studies, the search terms that were used for this initial reference search were:

**Fungal community tillage to reduced tillage** - fung* OR arbuscular* OR mycorrhiza* OR saprotroph* combined with tillage OR no-till OR reduced-till.

<table>
<thead>
<tr>
<th></th>
<th>A. Earthworms</th>
<th>B. Fungi</th>
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</table>

**Earthworm populations arable to pasture conversion** - earthworm* combined with arable OR conversion OR crop* OR farmland OR grass* OR grassland OR ley OR livestock OR pasture OR rotation.

**Fungal community arable to pasture conversion** - fung* OR arbuscular* OR mycorrhiza* OR saprotroph* combined with arable OR conversion OR crop* OR farmland OR grass* OR grassland OR ley OR livestock OR pasture OR rotation.
Earthworm populations pasture to woodland conversion - *earthworm* combined with OR abandonment OR afforestation OR agroforestry OR encroachment OR forest AND succession OR scrub OR shrub OR tree AND succession OR woodland OR woody.

Fungal community pasture to woodland conversion - *fung* OR *arbuscular* OR *mycorrhiza* OR *saprotroph* combined with OR abandonment OR afforestation OR agroforestry OR encroachment OR forest AND succession OR scrub OR shrub OR tree AND succession OR woodland OR woody.

Table 1. Total number of papers identified from Web of Science search for each set of search terms used for preliminary review

<table>
<thead>
<tr>
<th>Search Terms</th>
<th>Papers Identified</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tillage vs Reduced tillage</td>
<td>552</td>
</tr>
<tr>
<td>Arable to Pasture conversion</td>
<td>1466</td>
</tr>
<tr>
<td>Pasture to woodland conversion</td>
<td>212</td>
</tr>
</tbody>
</table>

Use of these terms within the different Web of Knowledge searches resulted in the identification of the number of references for each search shown in Table 1. Generally fungal community focused search terms produced a higher number of references than the searches for earthworms. For the arable to pasture conversion searches, the number of references identified for the fungal search was too high to be manageable for even an initial assessment (>10,000) and hence the searches for these terms were slightly modified so that the search terms for *crop* and *grass* were excluded from the search. This produced a more manageable sub-set of 3594 references for first pass assessment.

Once collated, the references identified that associated earthworm and fungal communities with the relevant land management and land-use terms, were reviewed separately by two scientists. This analysis was done independently by the two researchers without consultation as a step towards developing a short-list of papers for detailed appraisal. During the review each individual used the reference title and keywords to generate a list of papers that each thought would be likely to contain data relevant to the systematic review theme. The two lists generated by each researcher were then combined and a two stage strategy followed.

1. For those articles where both researchers identified the potential for the paper to contain relevant data, the full article was accessed and carefully reviewed. Any data in the paper was collated into a single data resource (separate Excel spreadsheet) for each meta-analysis.

2. For those articles where only one researcher identified the potential for the paper to contain relevant data, the abstract of the article was accessed and reviewed by one of the two researchers. Only if the abstract confirmed the potential for the paper to contain relevant data was the full article reviewed and any data incorporated.

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\(^1\) The combination of the search terms *crop*, *grass* and *conversion* with *fung* OR *arbuscular* OR *mycorrhiza* OR *saprotroph* produced an unmanageable number of references. These combinations were therefore omitted.
2.2. DATA HANDLING

Once the full data-sets were each assembled for each separate meta-analysis, the data was then subject to a range of analyses. This included the use of traditional quantitative techniques (t-test, analysis of variance, linear and no-linear regression); the application of method for quantitative meta-analysis including simple approaches such as vote counting (i.e. compare responses showing a positive and negative response) and meta-analysis statistics and also the use of narrative analysis for the most relevant articles. The analysis that was applied to each data-set was tailored to address a range of specific questions that emerged during the course of the process. Each assessment is reported separately.

3. EARTHWORMS POPULATION/COMMUNITY RESULTS

For earthworms the three separate Web of Knowledge searches identified 100s to 1000s of potentially relevant articles. This was expected because earthworms are widely recognized for their value to agronomy and ecosystem processes and so have been focal taxa for research in these areas. Such a large number of papers gave cause for some optimism that a suitable quantity of data was likely to be available for use within each of the separate meta-analyses.

3.1. EFFECTS OF TILLAGE REGIME

In total, 53 published articles, reports and unpublished theses were used, containing 101 independent studies (replicated, paired experiments with variance estimates, comparing conventional tillage with reduced tillage) on earthworm abundance and 57 datasets on earthworm biomass.

Four categories of tillage were defined: 1) “Conventional tillage” which is inversion tillage to a depth of +/- 30 cm mostly using a mouldboard plough; 2) “No-till” is the practice of strictly no soil disturbance other than a small incision for placing the seed and is sometimes called “direct drilling” or “direct seeding”; 3) “Non-inversion tillage” which we defined here as tillage where the soil is loosened, broken or lifted but not inverted, usually by the use of a chisel plough or other tined tools; 4) The category ‘other’ contains all studies of which the tillage method was either unclear (e.g. treatments only described as ‘conservation tillage’) or the treatments involves a different form of reduced tillage (e.g. shallow inversion tillage).

Compared to conventional tillage, earthworm abundance was 150% higher in no-tillage systems (Figure 1A), and biomass was about 270% times higher (Figure 1B), both statistically significant effect. Non-inversion tillage did not significantly increase earthworm population or biomass. The ‘other tillage’ group did not have a significant effect on
earthworm abundance, but a small significant positive effect on earthworm biomass of approximately 45% was found.

The effect size (ES) of earthworm abundance and biomass was higher for small populations and decreased as the overall population level (as measured in the tilled plots) increased (Figure 2A and 2B).

Figure 1. Percentage change in earthworm (A) abundance and (B) biomass in comparisons of three reduced tillage systems with conventional tillage. Squares are means, bars represent 95% confidence intervals (n, number of paired observations). An asterisk indicates a significant within-group heterogeneity.
Figure 2. Percentage change in earthworm (A) abundance and (B) biomass in comparisons of all reduced tillage systems with conventional tillage, grouped by initial population sizes. Squares are means, bars represent 95% confidence intervals (n, number of paired observations). An asterisk indicates a significant within-group heterogeneity.

The following other variables were included in the dataset to test whether they influence the ES: sampling method, sampling depth, soil texture class (categorical variables), clay content, organic carbon content and soil pH (continuous variables). No effects were found for sampling depth or sampling method (data not shown). Most studies were conducted on loam-textured soils, and there was no difference in effects size for earthworm abundance between loam, silt, and clay soils (Figure 3A). Non-inversion and ‘other’ reduced tillage systems were associated with significantly higher earthworm populations only on silt and clay soils, respectively, but the number of studies on these soil textural classes was low (Figure 3B and 3C).

Among the other environmental variables, soil clay content itself was not correlated with ES (data not shown). In the no-tillage treatment, earthworm abundance was weakly but significantly positively correlated with soil organic carbon content, and negatively correlated with soil pH (graphs not shown).
Figure 3. Percentage change in earthworm abundance, grouped by soil texture classes, for (A) no-tillage, (B) non-inversion tillage (these include studies with an artificial standard deviation) and (C) ‘other’ tillage. Squares are means, bars represent 95% confidence intervals (n, number of paired observations).

Too few studies reported earthworms species or at least ecological groups in a way (i.e. with individual estimate of variance) that would permit meta-analysis. This study can, therefore, not add quantitative analyses to the existing narrative reviews of earthworm ecological group responses to tillage (Chan, 2001).

3.2. ARABLE PASTURE CONVERSION

As outlined in Table 1, the search terms used for the Arable to pasture conversion review identified an initial set of 1466 potential papers for consideration. From the analysis by the two independent researchers, one expert identified 84 of these papers as potentially likely to contain relevant data; the other identified 321 papers. This highlights a clear discrepancy in
the stringency of the criteria applied for study identification by the two experts. Of the identified references, 56 of the short-listed papers were common between the two selected sets. Additionally there were 293 papers that were identified by only one expert as possibly useable. Of the non-shared references, an analysis of the abstracts of each paper conducted by a single expert identified a further 71 papers within which it was feasible that relevant data could be included. Together with the jointly identified papers, this gave a total of 127 articles for detailed review for data collection. When reviewed, 37 articles were found to contain a total of 105 separate data-set in which the population density of earthworms (No./m$^2$) was measured from separate plots located within a single site or region under pasture and arable land uses.

The average population density of earthworms (mean of stated population abundances ± standard deviation) across all studies under arable land was 62.3 ± 68.3. This compares to an average population density for pastures of 222 ± 206 (Fig. 4). Comparison by T-test indicated that the differences in abundance between arable and grassland plots was highly significant (t=7.55, p<0.001).

The simplest form of meta-analysis, beyond comparison of all mean abundance values for the two treatments across all studies (as above), is a simple vote counting approach. For vote count analysis, the number of studies within a comparison that show positive and negative effects on the measurement parameter (in this case earthworm abundance) are counted. In the arable to pasture conversion data-set, 89 data pairs showed high earthworm abundance in the pasture plots. This corresponds to 83% of all included studies. Of the remaining studies, 13 (13%) showed the higher earthworm abundance in the arable fields, while in 3 studies (3%), earthworm abundances were the same under both management conditions. This analysis confirms a frequent positive effect of pasture conversion on earthworm abundance.

A second approach that can be used for more quantitative meta-analysis utilizes regression based techniques to provide a quantitative (statistical) estimate of the net benefit aggregated over all included studies. Within this form of synthesis based meta-analysis, different types of models can be used. These include both fixed and random effects meta-regression methods. On the basis of these models, comparisons can be made that integrate studies with regard to the ES, variance (standard deviation) and sample size of each study to assess whether or not there is robust evidence of a treatment based difference.

The results of a synthesis based meta-analysis can be visualized in graphical format using a forest plot (Fig. 5). This illustrates the relative strength of treatment effects across the multiple quantitative studies. Within the forest plot individual studies are displayed showing
the measure of effect (e.g. standardized mean difference) for each studies represented by a square with confidence intervals represented by horizontal lines. The x-axis displays the ES as a natural logarithmic scale when using ratio-based effect measures, so that the confidence intervals are symmetrical about the study mean. Within the meta-analysis statistic studies are weighed according to the sample size within the study. This is represented in the forest plot by the size of the sample square. The overall integrated meta-analysis effect measure is represented by a vertical line in the plot which culminates in a diamond, the lateral extent of which indicate the confidence intervals for the overall effect.

A synthesis based regression analysis was conducted using a random effect model and the resulting analysis was integrated within a forest plot for the arable pasture conversion data-set. The substantive increases that are seen in many of the arable pasture conversion data-sets result in an effect in the overall meta-analysis that indicates the scale of increase following pasture conversion. This overall effect shows a significant increase following conversion with the confidence intervals for the synthesis effect not overlapping zero. This result, however, should be treated with some caution, because of the heterogeneity within the data-set.

Within any forest plot, the differences in the results for the individual studies represent the within study heterogeneity. This heterogeneity may be due to differences in the study protocols, such as differences in treatments, or study populations. Within the arable to pasture conversion meta-analysis, study heterogeneity was assessed the Cochran's Q test to give the I² value. This can range from 0%, indicating no heterogeneity to 100% indicating that all study variation is due to heterogeneity. An I² value less than 40%, indicates low heterogeneity (and a fixed effect model should be used). A moderate levels of heterogeneity, indicated by an I² value between 40% and 84%, is optimal for random effect model (as used in this study). If an I² value of 85% or more is seen, then the meta-analysis may not be valid, since the studies are too different to combine together. In the pasture arable conversion data-set, the heterogeneity analysis indicates an I² value of 96.7%. This suggests that a large proportion of the variation may be associated with heterogeneity. This may be associated with the particular differences between studies such as the sample method, regional climate, soil types and species compliments that are associated with each study. The extent of heterogeneity found, indicates that the results of the meta-analysis may not be robust. However, the relatively large ES seen in the studies does remain as an indication that an increase in earthworm abundance is the most likely conversion outcome.
To understand in greater detail the potential drivers of earthworm abundance change following arable to pasture conversion, a further set of stratified analyses of the assembled data-set was conducted. To assess whether the management regime applied to the converted pasture had an effect on earthworm abundance, statistical analysis of the data-set was conducted to assess how ultimate grassland use influences the magnitude of difference in abundance. For these assessments which were conducted using a range of regression and ANOVA based approaches, the magnitude of change in the size of the pasture population compared to arable was calculated as a percentage increase relative to the size of the arable population.

\[
\text{Pasture population (\% arable)} = \frac{\text{No. pasture} - \text{No. arable}}{\text{No. arable}} \times 100
\]

The magnitude of change for the pasture population (as a \% of arable numbers) was used as an input into an ANOVA to assess the effects of grazing on earthworm abundances as compared to ungrazed plots. Grazing was considered as an intensive grassland land use, since it is inevitably associated with the commercial rearing of livestock. The use of grassland for grazing could potentially have positive or negative effects on earthworm abundance when compared to ungrazed systems. On the one hand, livestock may have a detrimental effect on earthworms, due to stresses associated with the application of agrochemicals, trafficking of vehicle and poaching of soil through trampling. On the other hand the addition of fodder material and the increased deposition of manure to the pasture may provide a source of food for earthworms that could increase overall abundances.

The median \% population increase of the pasture populations compared to the site matched arable populations size was 211\% for ungrazed grassland and 269\% for the grazed systems (Fig. 6). Comparison by t-test indicated no significant effect of grazing status on the magnitude of earthworm abundance change in the grasslands (t=-0.46, p>0.05). Intensity of grassland management, thus, did not have any clear beneficial or detrimental effect on the magnitude of difference of earthworm numbers in grasslands when compared to paired arable fields.

A second important factor that may influence the magnitude of change in the abundance of earthworms in pastures converted from arable lands is the time that has elapsed since conversion. In comparison to many invertebrate taxa, earthworms are relatively slow growing and long lived. Under ideal conditions in the laboratory it can take up to six month for some species of earthworm to reach maturity (Spurgeon et al., 2003) and some individuals have been shown to live for up to 7 years (Kammenga et al., 2003). As a result it might be expected that population increase following any broadly beneficial land use
conversion may take years to occur. The fact that earthworms are also relatively sedentary in their habitat and only disperse over a distance of several meters yearly (Marinissen, 1992; Stockdill, 1982) further adds to this expectation. This is because the potential for populations in newly converted pasture to be augmented by colonization from adjacent high abundance areas may be limited.

To assess the influence of time since conversion, the % population increase in pastures compared to the site matched arable population was plotted against time since conversion as taken from the information provided in the individual research articles (n.b. papers in which the minimum time since conversion could not be estimated were left within an unassigned category). Results from this analysis indicated a considerable scatter across the data-set (Fig. 7). Lowest magnitude changes were generally associated with the shorter time since conversion periods, however, when fitted to a linear model, the trend for an increase in pasture population size with time elapsed from conversion approached significance, but ultimately did not meet the relevant statistical criteria (P=0.09).

Confirmation of the relatively limited influence of time since conversion on magnitude of increase in pasture population was further supported by an analysis of the influence of a range of conversion class categories on the magnitude of community size change. For this analysis, values for minimum time since conversion were used to assign individual data-sets to one of five time class categories (Fig. 8). These were studies where measures were conducted 1-3, 4-8, 9-20, 21-30, 31-50 and 51+ years after arable conversion. An ANOVA to assess whether the population size increase was significantly associated with classification to these time categories did not identify any significant effect (F=1.43, p=0.23).

The limited influence of time to conversion on the change in earthworm counts points to a rapid dynamic of earthworm population increase in the time immediately following land-use change. This takes abundances from those present in arable systems to multiple times this number in the establishing pastures in quick time. The rapid nature of this increase, when contrasted with the
relatively slow rates that earthworms are thought to colonize new sites, suggests that these population increases are driven primarily by the recruitment of new progeny to the population as produced by the existing adult worms of species originally living in the crop.

The very rapid nature of the increase in earthworm populations following pasture conversion is illustrated if an exponential model is fitted to the data for pasture site population increase and time since conversion (Fig. 9). A significant exponential model can be fitted to this data-set \((F=6.05, p<0.02)\). This model actually explains only a small portion of the observed variance \((r^2 = 0.07)\). However the nature shape of the curve, which shows a quick rise to a stable value, does highlight the very rapid nature of the time dependent increase in earthworm abundance that frequently follow conversion to pasture.

### 3.3. PASTURE AFFORESTATION

The search terms for the pasture to woodland conversion initial systematic review identified a set of 212 potential research papers to take forward for further analysis. This number is less that 1/6 that was identified for the arable pasture conversion review. It is likely that this difference reflects the greater interest in the population and community dynamics and the associated functional roles of earthworms in soils used for food production rather than those of a range of woodland types.

During the analysis by each of the two independent researchers, one of the experts identified 46 of the 212 papers as potentially likely to contain relevant data; the other identified 81 papers. Of the identified references, 29 were common to the two selected sets. Additionally there were also a further 69 papers that were identified by only one expert, of these a further 31 papers were identified as likely to contain relevant information following abstract review. Combined, this gave a total of 60 references for appraisal for inclusion within the meta-analysis database. Of the 60 papers that were considered for the detailed review, 21 articles were found to contain relevant data, producing a total of 49 separate data-sets containing quantitative information on earthworm density (No./m\(^2\)) in separate paired pasture and deciduous, coniferous, tropical or orchard/agroforestry woodland plots.

The average population density (mean of all stated population densities ± standard deviation) in the grassland fields was 320 ± 375. This is above the average values for all pasture sites in the arable to pasture conversion review (222 ± 206). In the sampled woodlands, average stated earthworm density was 249 ± 374. Comparison of the two sets
of values using T-test indicated that there was no significant difference in earthworm counts between pasture and woodland plots (t-value=0.91, df=91, p=0.367)(Fig. 10).

A preliminary vote count analysis of the effects of land use change from pasture to woodland on the size of the earthworm population identified that in 20 (41%) of the assembled data-sets, earthworm populations were greatest under the woodland plots. In the remaining 29 cases (59%) abundances were higher in the pasture systems. When coupled to the T-test results outlined above, this suggests that earthworm population density changes following woodland conversion are not as great as those that occur following arable to pasture conversion.

Synthesis based regression analysis conducted using a random effect model was used to evaluate the overall treatment effect within the pasture to woodland conversion data-set. Results were summarised within a forest plot. The results of the meta-analysis reveal a relative small overall ES identifying slightly greater earthworm abundance in pasture habitats. This is, however, only a marginal difference and indeed within the meta-analysis the magnitude of this change was not statistically significant as demonstrated by the overlap of the confidence interval with the zero ES line (Fig. 11). Further, the within the meta-analysis, an assessment of heterogeneity by calculation of the Cochran’s Q test value indicated an I² value of 96.7%. This again indicates that a large proportion of the variation may be associated with heterogeneity. This means that the results of the meta-analysis may not be robust. Hence due to the small ES and heterogeneity within the meta-analysis there is no basis for concluding a systematic effect of pasture to woodland conversion on earthworm numbers. Further mining of the data-set, may, however have the chance to reveal more subtle characteristics within the data.

The comparisons of populations under pasture and woodland using T-test statistics and the meta-analysis both highlight that earthworm community sizes remain relatively unaffected by the presence of wooded species. Such analyses that consider effects across the full data-set may, however, be too course to identify a number of more subtle
influences. To investigate the extent to which both the age and nature of woodland type may influence earthworm counts, a set of further analyses were conducted to assess the effect that both age since pasture transition (i.e. the age of tree stand in the developed woodlands) and also woodland type (temperate deciduous, temperate coniferous, tropical, agroforestry) have on the associated earthworm communities. These analyses for the pasture to woodland data-set were conducted using a range of regression and ANOVA based statistics. As for the arable to pasture conversion data-set, the analysis was based on assessment of the change in the size of the forest population compared to pasture field calculated as a percentage increase relative to initial pasture population size.

The effect of time conversion on the magnitude of change of the woodland earthworm community compared to pasture counts was assessed in relation to the time elapsed since conversion. As was the case when comparing the effects of time in the arable to pasture conversion meta-analysis, there was a considerable scatter of points (Fig. 12). Across this variation, there was an approximate equal distribution of positive and negative population shifts (as indicated by vote counting).

Fitting of a linear regression model to the data indicated no significant time associated trend within the data. The best fit model indicated only a small, non-significant reduction in abundance associated with time since woodland conversion. Evidently consideration of conversion time does not increase understanding of the effects of woodland conversion on earthworm numbers. An ANOVA using the same conversion age classes also used for the arable to pasture conversion study further confirmed this point (Fig. 1). Thus, while the ANOVA approached significance (F=2.38, P=0.08), no clear time related effect was seen across the treatment and indeed the two treatments that were closest to significance within a Tukey analysis (t=2.83, p=0.06) were actually the two oldest conversion age classes and not the short- and long-term studies. This, thus, further indicates the limited extent of the time dependent effect.

**Fig. 12.** Time elapsed since land use change and the magnitude of increase in abundance of earthworms under woodland compared to site matched pasture plots. The fitted line shows the best fit linear regression (non-significant).

**Fig. 13.** Box plots of earthworm population change as a percentage of numbers in matched pasture plots for a series of class categories for age since land use conversion from pasture to woodland land-use. Boxes indicate lower and upper quartile values, mid line the median value and whiskers the 95% confidence intervals.
Woodlands of different types could potentially differ in their suitability as habitats for earthworms, since the plant species present may offer, thorough leaf fall, food sources that differ in their palatability and nutrient quality (Piearce, 1978). The effects that different tree species may also have on the chemistry and physical structure of underlying soils may also affect soil habitat suitability for earthworms. To assess whether forest type had a significant effect on the magnitude of change of earthworm communities following conversion, the resulting woodland habitats were categorized into four forest types. These were temperate deciduous, temperate coniferous, tropical and orchard/agroforestry (Fig.14). An ANOVA to assess if forest type had a significant effect of the magnitude of change of earthworm populations indicated that a significant influence was present (F=3.72, p<0.02). Across forest types, there was an average reduction in earthworm population size under coniferous woodland, while in deciduous and especially soil under agroforestry there were increases. For the comparison of coniferous forests and agroforestry this difference was clearly significant (Tukey T=2.919, p<0.05) and was also close to significance (T=2.607, P=0.058) for the coniferous and deciduous woodland comparison.

Some earthworm species, and in particular those that do not possess active calciferous glands are known to be intolerant of acidic soils (Piearce, 1972), as well as other soil physiochemical stresses such as trace metals (Spurgeon and Hopkin, 1999). Further, under coniferous soils, it is recognized that the inputs of plant derived chemicals can result in a gradual reduction of the pH of surface soil layers. The acidification effect that is commonly associated with conifer growth could potentially be a contributing factor to the reduction in earthworm numbers in conifer plots, when compared to pasture and other forest types. To investigate this possibility, for those cases where soil pH was specified, these were used to calculate the magnitude of shift in the soil pH following pasture to woodland transition. A linear model was then used to assess whether this change in pH was linked to changes in earthworm abundance (Fig.15). Within this analysis, the effects of pH on population change after conversion was not statistically significant (y = 36.1 +55.2 x, F=3.77, p=0.07). Nonetheless, the greatest population increases were found in those cases in which pH increased, while the
largest reductions were generally found when pH was reduced. This suggest that future work to assess the extent to which changes in soil pH impact on earthworm communities following land use conversion could be warranted.

3.4. SYNTHESIS OF EFFECT OF LAND USE CHANGE ACROSS A SUCCESSION (cf LAND-USE INTENSITY) GRADIENT ON EARTHWORMS

In the context of land management and land use, the comparisons selected for the series of meta-analyses conducted represent a typical succession gradient for terrestrial ecosystems. Thus after the abandonment of the bare land that typifies tilled arable fields at certain times of year, areas will first be subject to colonization by small herbaceous species including grasses and forbs. This change is analogous to the conversion of land use from arable to pasture and indeed some of the papers used for data extraction describe results from exactly this kind of successional study (Pizl, 1992, 1999). Over time woody species will next begin to move into these grassland/herbaceous fields leading to a transition into scrub vegetation. This may be followed by colonization and establishment of deciduous or coniferous trees depending on the nature and location of the site. This later transition to wooded land is comparable to the woodland conversion scenario assessed in this study.

As well as representing a typical successional pattern, the conversion studies also accord to a gradient of land use intensities. The conventional arable system, with the associated deep or surface tillage and high input agrochemical use, represents a high intensity management condition. In these areas, soils are subjected to regular disturbance due to both physical and chemical perturbations. Introduction of no-till management practices reduces the intensity of physical disturbance and in this respect is clearly a reduction in intensity. Conversion to pasture represents a further reduction in the intensity of land use, since soils under pasture are left to establish a normal depth profile and also the use of pesticides and fertilizers on these soils is often greatly reduced when compared to arable systems. Woodland conversion provides, what for soils, can often be a low intensity management condition with regard to both the extent of physical soil disturbance. The frequency of pesticide and nutrient inputs may be low and there is a consistent input of leaf litter at periods throughout the year.

The initial meta-analysis conducted to compare shifts from conventional to a reduced tillage regime for arable sites and of land-use transitions from conventional arable to grazed and ungrazed pastures to woodlands each highlight some clear patterns of change in the

![Fig. 16. Box and whisker plot of earthworm population under a gradient of land-uses from conventional arable to woodland. Boxes indicate lower and upper quartile values, mid line the median value and whiskers the 95% confidence intervals.](image-url)
associated earthworm communities. When the results of the separate meta-analyses are brought together with an assessment of the full gradient of successional and/or land-use intensity change, a positive relationship of numbers with succession and/or declining land-use intensity is indicated (except for coniferous woodland) (Fig. 12). An ANOVA using earthworm abundance data for all habitats highlights a number of statistically significant differences in earthworm abundances. Thus the population count found under conventional arable, reduced tillage arable and pasture are all significantly different from each other, with numbers increasing in the order conventional arable < reduce till arable < pasture (Fig. 16). These increases in earthworm abundance occur even when the changes in the intensity of land-use are relatively modest. Thus a change to reduced tillage management provides almost half of the beneficial effect on earthworm populations that is associated with a full transition of conventional arable practice to grassland. Full succession to deciduous woodland is associated with the retention and even further augmentation of the benefits on earthworm population that is obtained from pasture conversion. Only in coniferous woodland are some of the benefits of reduced land use intensity lost. This is possibly associated with changes in the underlying soil such as pH modification – although this requires further conformational work.

A practical conclusion that can be taken from this analysis is that the beneficial effects of earthworm activity on soil ecosystem processes can be gained even by relative small changes in land-management practice. Earthworm mediated ecosystem processes can be enhanced by reduced tillage practice, or by production of grassland buffer strips in arable fields which can maintain greatly increased earthworm numbers and which can act as a reservoir of diversity in farming landscapes. This analysis, thus, highlights the potential to manage earthworm abundances through marginal modifications to land management practices. In the later part of this review, the consequences of these changes for soil hydrology will be discussed.

• 4. SOIL FUNGAL POPULATIONS/COMMUNITY RESULTS

For fungal community measures the three separate Web of Knowledge searches identified thousands of potentially relevant articles (Table 1). On completion of the expert screening it was clear that these searches returned a large proportion relating to crop and plant pathology. There were still, however, hundreds of articles assessed as being relevant for each land use transition (see below). The detailed screening of these selected papers resulted in data coming from 14 papers for the tillage comparison (Annex IV), 24 papers for the arable to pasture conversion (Annex V) and 18 papers for the pasture to woodland conversion (Annex VI). A number of additional papers examined suitable land use transitions, but the data presented were not adequate to calculate standardized effect size for meta-analysis. Authors were contacted in these cases to request the data which was included if received.

In contrast to the earthworm community, the data extraction for fungal populations raised the issue of the variety of methods and measures used to examine the fungal community in
soils. For example, screened papers reported land use effects on the fungal community using data as diverse as Colony-forming Units (CFU), spore density and diversity, plant root-length colonized by mycorrhiza, ectomycorrhizal root tips, Glomalin-related soil protein (Wright et al., 1998), ergosterol (see Ruzicka et al., 2000), phospholipid fatty acid (PLFA) and neutral lipid fatty acid (NLFA) biomarkers, and glucosamine sugars. We categorized measures into either ‘Biomass’, ‘Colonisation’ and ‘Diversity’ types for the purposes of analysis, and also between ‘Bioassay’ and ‘Field’ sources (Table 2). The meta-analyses in following sections concentrate on the ‘Field’ measures as they are expected to be most closely related to the land use changes. The number of comparisons made across land use transitions tended to differ between measure types. For example, measures of hyphae and Glomalin were the most common biomass measures for the tillage comparison, Glomalin and PLFA/NLFA in the arable to pasture conversion, and spores (or spore density) in the pasture to woody conversion (Table 2). These general patterns may contribute to observed differences in the magnitude and sign of the effect size and are discussed.

4.1. EFFECTS OF TILLAGE REGIME

The search terms for the Tillage comparison produced an initial set of 1710 papers to review (Table 1). Due to time constraints these were screened by only one expert and this resulted in the identification of 42 papers as likely to contain relevant data. As an additional measure these were supplemented by other potentially relevant papers identified in the screening of the Arable to pasture set, thus resulting in a total of 95 papers for more detailed screening. Eleven out of the 42 papers from the shared selection, and another three of the additional papers from the arable to pasture set, contained both suitable transitions and useable data. This resulted in 14 papers with a total of 94 ‘Field’ datasets comparing quantitative changes in fungal communities from conventional tillage to reduced or no-tillage. A further 10 papers contained suitable transitions but the data presented was insufficient to calculate effect size. Due to the variety of measure types we use Hedges’ G standardized ES to examine the influence of different land use transitions on fungal populations. Given the different systems from which data were extracted (e.g. experimental plots, managed fields and, in the case of other transitions, natural successions) and the diverse types of fungal measure a high level of heterogeneity may be expected.

The overall effect size of a change in fungal measures from conventional tillage to reduced tillage or no-till was significantly positive (ES = 0.699 ± 0.215 95%CI, P < 0.0001). Forest plots are not presented for the fungi transitions due to large number of comparisons but the studies demonstrated a moderate level of heterogeneity (Q = 205.3, I² = 52.7%). A number of random effects models were tested to examine the source of the heterogeneity. There was no influence on effect size of ‘comparison type’ (whether the transition was assessed under a known temporal change, e.g. chronosequence data, or simple comparison)(QM=0.114, P=0.736). There was also no difference between the effect size of Biomass, Colonisation and Diversity measure types (QM = 1.19, P-value = 0.552). In contrast, the significant heterogeneity of measure subtypes (QM = 12.45, P-value = 0.029) indicates that a proportion of study heterogeneity can be related to these different measures.
of fungal communities. There were significant positive effect size for land use change from conventional to reduced or no tillage for Biomass (P < 0.05), Glomalin (P < 0.001), Root length (P < 0.001) and Spore density (P < 0.05), but not for fungal hyphae or PLFA measures (Fig. 17). These generally positive effect sizes highlight that the increase in fungal biomass and fungal-derived substances through a reduction in tillage intensity has the potential to improve soil physical structure and, in turn, organic matter and hydrological properties. Though all measures are positive the differences also suggest that focusing on particular measures such as glomalin and root length colonized may provide the most reliable in assessing effects of reduced tillage on the fungal community.

Table 2: Numbers of comparisons extracted from data on land use transitions for fungal populations broken down by measure source and types.

<table>
<thead>
<tr>
<th>Measure details</th>
<th>Source</th>
<th>Type</th>
<th>Subtype</th>
<th>Tillage comparison</th>
<th>Arable to pasture conversion</th>
<th>Pasture to woody conversion</th>
<th>Total</th>
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<td>Field</td>
<td>Biomass</td>
<td>Biomass</td>
<td>1</td>
<td>-</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>DNA</td>
<td>-</td>
<td>-</td>
<td>6</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ergosterol</td>
<td>-</td>
<td>-</td>
<td>4</td>
<td>12</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Glomalin</td>
<td>20</td>
<td>47</td>
<td>5</td>
<td>72</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hyphae</td>
<td>28</td>
<td>7</td>
<td>4</td>
<td>39</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>PLFA/ NLFA</td>
<td>11</td>
<td>46</td>
<td>4</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Spores</td>
<td>11</td>
<td>24</td>
<td>36</td>
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<td></td>
<td></td>
<td>Colonization</td>
<td>Hyphae</td>
<td>-</td>
<td>4</td>
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<td></td>
<td></td>
<td></td>
<td>Root length</td>
<td>21</td>
<td>6</td>
<td>10</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Root tips</td>
<td>-</td>
<td>-</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Diversity</td>
<td>Molecular</td>
<td>-</td>
<td>24</td>
<td>-</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Spores</td>
<td>2</td>
<td>5</td>
<td>-</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(94)</td>
<td>(173)</td>
<td>(85)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>99</td>
<td>198</td>
<td>116</td>
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</tr>
</tbody>
</table>
Another random model was tested to determine whether the level of reduction in tillage intensity could explain heterogeneity in effect size. The difference in effect size between reduced tillage and no tillage was not significantly different (QM = 1.1901, P-value = 0.2753) but reduced tillage had a greater average effect size (Fig. 18). It is not clear why reduced tillage would show greater differences from conventional tillage than no tillage but it may be that specific measures respond more strongly to reduced tillage management practices. Borie et al. (2000) showed in a chronosequence of no-till cultivation, although no conventional comparison was presented, that glomalin doubled between 4 and 20 years after the no tillage treatment was initiated. However, there was little evidence of time since change from conventional tillage being strongly related to the effect size (Fig. 19).

![Fig. 17. Effect size of tillage comparison by different measure subtypes of ‘Field’ data. Bars represent 95% confidence intervals.](image1)

![Fig. 18. Effect size of Reduced-till and No-till comparisons of ‘Field’ data. Bars represent 95% confidence intervals.](image2)
Fig. 19. Time since land use change and effect size in the comparison of conventional tillage with reduced tillage or no tillage.

4.2. ARABLE PASTURE COVERSION

The search terms for Arable to pasture conversion (excluding 'crop*' and 'grass*') produced an initial set of 3594 potential papers for review (Table 1). Following a first screening, one expert identified 90 of these papers likely to contain relevant data; the other expert identified 196 papers. Again, this highlights a discrepancy in the stringency of the criteria applied for study identification but demonstrates the benefits of screening by more than one individual. From these identified papers 44 were shared in the experts’ selection of potentially useful data sources and 198 were identified by only one expert. 16 out of the 44 papers from the shared selection, and another eight of the additional papers from the set identified by only one expert, contained both suitable transitions and useable data. This resulted in 24 papers with a total of 173 ‘Field’ datasets comparing quantitative changes in fungal communities with arable conversion to pasture. A further six papers contained suitable transitions but the data presented was insufficient to calculate effect size and another 117 papers from unique screened but were not suitable.

Like the tillage comparison, the overall effect size of a change in fungal measures after conversion from arable to pasture was significantly positive (effect size = 1.65 ± 0.299 95%CI, P < 0.001) but demonstrated a greater level of heterogeneity amongst studies (Q = 676.2, I² = 79.5%). There was also, as above, no significant difference in effect size between comparison types (QM=0.383, P=0.536) or measure types (QM=0.1536, P=0.464). Heterogeneity in the effect size of measure subtypes was highly significant (QM = 28.615, P-value = 0.0004)(Fig. 20). Measures of ergosterol, hyphae or NLFA did not seemingly respond to conversion from arable to pasture whereas DNA (P < 0.001),
Glomalin ($P < 0.0001$), Molecular richness ($P < 0.0001$), PLFA ($P < 0.0001$), Root length colonized ($P < 0.0001$) and Spore density ($P < 0.0001$) did (Fig. 20).

![Figure 20. Effect size of arable to pasture conversion by different measure subtypes of ‘Field’ data. Bars represent 95% confidence intervals.](image)

Another random model was tested to determine whether the presence of grazers could explain heterogeneity in effect size of the arable to pasture conversion. The difference in effect size between grazed and ungrazed comparisons was not significantly different (QM = 0.4820, P-value = 0.488)(Fig. 21). The study by Franzluebbers et al. (2000), used in this meta-analysis, also indicated that grazing may have little influence on glomalin. However, the greater variability in effect size of grazed pasture was noted as it has been demonstrated that the history and intensity of grazing can alter the composition of microbial communities (Bardgett et al., 2001b).

![Graph showing effect size of grazed vs ungrazed](image)
4.3. PASTURE AFORESTATION

The search terms for pasture to woodland conversion identified an initial set of 2441 potential papers for review (Table 1). Following a first screening, one expert identified 182 of these papers likely to contain relevant data; the other expert identified 143 papers. A total of 51 of these identified papers were shared in the experts’ selection of potentially useful data sources and 223 were identified by only one expert. 12 out of the 51 papers from the shared selection, and another six papers from the set identified by only one expert, contained both suitable transitions and useable data. This resulted in 18 papers with a total of 85 ‘Field’ datasets comparing quantitative changes in fungal communities with pasture conversion to woodland. A further four papers contained suitable transitions but the data presented was insufficient to calculate effect size and another 163 papers from unique screened but were not suitable.

In contrast to the other two land use transitions, the overall effect size of a change in fungal measures with pasture conversion to woodland was significantly negative (effect size = -0.264 ± 0.485 95%CI, P < 0.0001) and the studies demonstrated the greatest level of heterogeneity (Q = 298.9, I² = 89.5%). There was also a significant difference in effect size between comparison types (QM=4.295, P=0.038) with ‘chronosequence’ comparisons having no significant effect size (effect size =0.334 ± 0.742 95%CI) and simple comparison
having a significant negative effect size (effect size = -0.698 ± 0.634 95% CI, P < 0.05). This may reflect the fact that older woodlands tend to be more common in simple comparisons. Heterogeneity between the effect size of measure types was also significant (QM = 5.283, P-value = 0.022) with Biomass measures having a negative and Colonisation measures a positive effect size (Fig. 23). This was also largely reflected in the heterogeneity of measure subtypes (QM = 92.1, P-value < 0.0001) with PLFA/NLFA measures significantly negative (P < 0.0001) and root tip measures significantly positive (P < 0.0001) (Fig. 23). It may not be expected that fungal PLFAs should decrease under woodland where fungi are known to be dominant but this may be related to the specific biomarkers examined. For example, the PLFA marker for arbuscular mycorrhizal (AM) fungi may be predicted to decrease from pasture to woodland due to changes in the composition of vegetation. The transition from pasture to woodland switches the fungal community from one dominated by AM fungi to one dominated by ectomycorrhizal fungi, i.e. those associated closely with tree species. This is supported by the positive effect size on the root tip measure, which would be ectomycorrhizal.

The analysis of Forest classes (Agroforestry, Tropical, Deciduous, Coniferous, Evergreen) highlighted significant differences in heterogeneity of effect size between them (QM = 23.622, P-value = 0.0003) with Deciduous having a significant negative effect size (P-value < 0.01) (Fig. 24). However, the effect size of all these forest classes except Deciduous should be treated with some caution as sample size is generally small and could be confounded to some extent by climatic and soil factor. It is possible that time since conversion from pasture to woodland, or aforestation, plays an important role in the development of the fungal community. Rao et al. (1997) found ectomycorrhizal mycorrhizal infection and diversity to increase in a chronosequence of pine stands from 2 to 17 years old. In contrast, our analysis suggests an overall negative relationship with fungal measures and time since conversion (Fig. 25). It is noted, however, that this relationship is highly influenced by the few datapoints 50 years since conversion (Fig. 25). This indicates our analyses may be most relevant to AM fungi.
Figure 23. Effect size of pasture to woodland conversion by different measure subtypes of ‘Field’ data. Bars represent 95% confidence intervals.

Figure 24. Effect size of Forest classes by different measure subtypes of ‘Field’ data. Bars represent 95% confidence intervals.
4.4. SYNTHESIS OF EFFECT OF LAND USE CHANGE ACROSS A SUCCESSION (cf LAND-USE INTENSITY) GRADIENT ON FUNGI

These findings are in agreement with a number of studies which have examined land use and fungal communities using independent sites over larger spatial scales (e.g. Carpenter-Bach et al., 2010; Boggs et al., 2003; Drenovsky et al., 2010; Halverson and Gonzalez, 2006; Oehl et al., 2003; Steenwerth et al., 2002; van der Wal et al., 2006). Reducing tillage has a generally positive impact on the fungal community, grasslands or pasture supports a greater quantity of fungal biomass and there is a generally positive response of fungal biomass across a chronosequence of time since conversion to grassland. In Nebraska, USA, Bach et al. (2010) demonstrated an asymptotic increase in the arbuscular mycorrhizal biomass between 0 and 18 years of restoration; sites with 18 years restoration had levels of AM biomass equivalent to native prairie. Similarly, van der Wal et al. (2006) showed increases in fungal biomass and ergosterol across a chronosequence of abandoned arable land in the Netherlands. When arable sites were excluded, however, regressions with time since abandonment were not significant. This indicates that fungal populations may respond within only a few years to establish levels comparable to that of older grassland. Indeed, tree species planted directly into arable land also increase fungal biomass and diversity (e.g. McLean and Huhta, 2002; Wojewoda and Russel, 2003; Rillig et al. 2003).

In all transitions a large proportion of the heterogeneity between studies was not accounted for by comparison and measure types. Further analyses will benefit by examining other environmental sources of variation e.g. regional climate and soil type. As was shown for
earthworm community, the effect size of reduced tillage was modified by soil type. It will also be useful to explore other methodological sources of variation, in particular sampling depth. For example, Halverson and Gonzalez (2006) demonstrated that the biomass of Glomalin-related soil protein was significantly different between cultivated, grassland and forest soils at 0 to 5 cm depth but not below this depth. Greater fungal biomass, as determined from estimates of fungal hyphae, has also been measured under No Till compared to Conventional Till at 0 to 5 cm depth but not 5 to 20 cm depth (Frey et al., 1999). This pattern may be further modified by specific land management practices, e.g. tillage method, and often in cultivated soils fungal biomass may be greater at the depth of the plough layer.

• 5. LAND USE EFFECTS ON SOIL INVERTEBRATES (ESPECIALLY MESOFAUNA) IN NATIONAL SURVEYS

The results of the initial meta-analyses for earthworm and fungi clearly demonstrate that communities of these two taxa are responsive to changes in land management and to land-use conversions. These changes, as indicated by the fold change levels of difference in average abundance across different habitats, can occur even when the time elapsed since conversion of management or land-use is relatively small. These community differences can be expected to impact on ecosystem functions dependent on the activities of these important taxa. This includes the structural characteristics of the soil and also the soil hydrological properties which form the focus of the functional component of this review (see below). As well as soil structural properties, soil processes related to the carbon and nutrient dynamics; the attenuation of contaminants; and food supply within terrestrial food webs can be altered.

Earthworms were sampled across 60 sites in the Republic of Ireland as part of the CréBeo national soil biodiversity project (Schmidt et al., 2011). The patterns of earthworm populations across land use types in this national survey closely mirror the findings of the meta-analysis. Total abundance of earthworms was two to three times greater in pasture sites as compared to arable or tilled sites (Fig. 26). Furthermore, deciduous or broadleaved forests contained greater populations of earthworms compared to coniferous forests (Fig. 26). Similar findings have been demonstrated the Biological Indicator of Soil Quality (BISQ) network in the Netherlands (Rutgers et al. 2009). This indicates that effects observed within the meta-analysis are relevant to natural populations and the regional and national scale.
While earthworms and fungi are known to influence the nature of soil hydrological properties, they are far from being the only taxa that may contribute. Other taxa that are also numerous in soils can also be important. One of the most important groups of organisms in soils are the meso-fauna. Taxa such as Collembola and Oribatid mites are frequently present in soils in numbers in the range of 100-1000s of individuals per square metre. To assess whether land use has similar effects on soil invertebrate taxa, and in particular on the Collembola and oribatid mites, as those indicated from the initial meta-analyses for earthworms, results from a national survey that included an analysis of changes in the abundance of soil taxa have been reanalysed.

To assess how soil meso-faunal communities vary in relation to current land use, data collected as part of the Countryside Survey monitoring program undertaken by NERC was analysed. The Countryside Survey is a national monitoring scheme in which broad habitats characteristics, vegetation diversity and the physical and biological status of surface water and soils are measured at a large number (>3000 – although not all sites are used for all analyses) of locations across Great Britain. Surveys have been conducted on five occasions (1978, 1984, 1990, 1998, 2007). Soil physicochemistry and soil invertebrate communities have been assessed at selected plots in both 1998 (~1100 plots) and in 2007 (~925 plots) survey. The analysis of soil biodiversity was conducted using tullgren funnel extractions of 4 cm diameter, 8 cm long soil cores. On the basis of an enumeration of the soil invertebrates extracted from these cores, assessment of the number of taxa represented (identified to low taxonomic resolution such as family or order) and also the number of individual in key taxa, such as the numbers of Collembola and mites present in each sample, can be assessed across a range of plots located within different land use types.

For soil sampling, the cores were knocked into the ground and then the intact soil sample removed. After capping and return to the laboratory, soil invertebrates were extracted using a dry Tullgren extraction method. This uses surface heating of the exposed surface of the core to drive the soil fauna downwards out of the open bottom end of the core and into the 70% ethanol preservative below. Once collected, soil invertebrates were identified to major taxa at Taxonomic level 1 and counted for each sample. The broad taxa categories used for enumeration was acari, araneae, chilopoda – geophilomorpha, chilopoda – lithobiomorpha, coleoptera, collembola – entomobryoida, collembola – neelidae, collembola – poduroidea, collembola – sminthuridae, copepoda, diptera, diplura, diplopoda, gastropoda, hemiptera, hymenoptera, isopoda, lepidoptera, oligochaeta, opiliones, pauropoda, protura, pseudoscorpions, pscoptera, pulmonata, symphylla, thysanura, thysanoptera. Identification at this taxonomic level allows the patterns in the data for a range of biodiversity parameters to be assessed, while keeping the taxonomic burden to a manageable level. Here we use this data of counts for each of the broad taxa in each core to assess land-use patterns in 1) the number of broad taxa represented by at least one individual in a core; and 2) the total catch of mites and springtails in the core. Community characteristics were assessed under different land uses including arable, improved, neutral
and acid grasslands and deciduous and coniferous woodland habitats across the two surveys. The analysis also indicated an assessment of the change in the measurement parameters between the two surveys. A summary of the full data-set available for the analysis is presented in Table 3.

Table 3: Overview of soil invertebrate samples different levels of taxonomic resolution for Countryside Survey conducted in 1998 and 2007

<table>
<thead>
<tr>
<th></th>
<th>1998</th>
<th>2007</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>X-plots</td>
<td>km-squares</td>
</tr>
<tr>
<td>Total sampled</td>
<td>1286</td>
<td>256</td>
</tr>
<tr>
<td>Broad invertebrate taxa</td>
<td>1076</td>
<td>237</td>
</tr>
<tr>
<td>Mites (Acari)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Separated to broad group</td>
<td>2</td>
<td>238</td>
</tr>
<tr>
<td>Checked for Oribatid presence</td>
<td>963</td>
<td>237</td>
</tr>
<tr>
<td>Oribatids present</td>
<td>504</td>
<td>182</td>
</tr>
<tr>
<td>Oribatids identified to species</td>
<td>504</td>
<td>182</td>
</tr>
<tr>
<td>Springtails (Collembola)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Checked for Collembola presence/ Separated to broad group</td>
<td>1076</td>
<td>237</td>
</tr>
<tr>
<td>Collembola present</td>
<td>837</td>
<td>233</td>
</tr>
<tr>
<td>Collembola identified to species</td>
<td>336</td>
<td>176</td>
</tr>
</tbody>
</table>

The mean number of invertebrate taxa represented by at least one individual in Countryside Survey soil cores was 4.34 in 1998 and 3.85 in 2007 (Table 4). This represented an overall decrease of 11% in average taxa representation in Countryside Survey 2007 compared to Countryside Survey 1998. When analysed by Broad Habitats, Arable and Horticultural systems had lowest taxa richness. Taxa numbers in the three grasslands represented in the survey were higher than in arable systems indicated a greater complexity of community structure in these less intensively managed systems. This is consistent with the indications of abundance change between arable and pasture plots indicated by meta-analyses.

Table 4. Frequency and change in number of sampled taxa represented by at least one individual in 0-8 cm depth soil samples under a range of Land-use types across Great Britain. Numbers denote taxa number from the Countryside Survey 1998 and 2007 and arrows denote a significant directional change in taxa numbers (p<0.05) between the surveys.

\[\text{2} \text{ Separated into Oribatids, Mesostigmatids and Prostigmatids}\]
\[\text{3} \text{ Presence/Absence data only}\]
\[\text{4} \text{ Separated into Entomobryoidea, Poduroidea, Neelidae and Sminthuridae}\]
Deciduous woodland showed highest taxonomic diversity among the individual habitats, with Coniferous woodlands showing taxonomic diversity that was comparable with the grassland systems across the two surveys, although slightly below that for the deciduous woodland. Overall the patterns of taxonomic diversity found from the survey for taxa numbers closely match those found for earthworms within the meta-analysis of literature data, thus as for earthworm abundance, taxonomic diversity is greater in grassland than in cultivated land and higher still in deciduous woodland but not in coniferous forests.

In 1998 Collembola and oribatid mites comprised 74.3% of all invertebrates captured and in 2007 this was higher at 93.6%. These two taxa, in numerical terms, represent the dominant portion of the soil invertebrate taxa collected and numerated in the cores collected in each survey. The average catch of mites and springtails per core in 1998 was 38.9 and in 2007 this number was 72.1 (Table 5). This indicates an approximate two fold increase in catches of these two meso-fauna groups between surveys. The precise cause of this increase is at present not fully clear, although the nationwide scale of the difference suggests that variables applicable to larger scales, such as variations in annual or seasonal climate may be important.

Between habitats the lowest catches per core of Collembola and mites were made in Arable and Horticultural plots. Improved grasslands also showed relatively low counts compared to the other habitats sampled, although even here numbers were almost twice those in Arable and Horticultural habitats in the 2007 survey. Neutral and Acid Grasslands, which are less intensively managed than Improved Grassland, showed catches that were 3-4 fold those in arable areas, while Woodland and especially Coniferous Woodlands produced the highest catches of any of the featured sampled habitats.

Table 5. Sum of Collembola and mites collected in 0-8 cm depth soil samples under a range of Land-use types across Great Britain. Numbers denote catches (average number of individuals present within core samples) for surveys in 1998 and 2007 and arrows denote significant directional change (p<0.05) between surveys.
With respect to these two common mesofaunal taxa, total catches of both Collembola and oribatid mites generally reflected a trend within which reduced land use intensity associated both with grassland and especially woodland habitats is related to increases in abundances. As previously indicated for earthworms and for fungi by the literature meta-analyses, there is greater abundance under pasture than for arable, although for the mesofauna, this increase is not to the same scale as that found for the earthworms. For less intensively managed pasture and woodlands, especially under conifers, further increases in soil mesofauna catches were found in both survey years. The community characteristic of the springtails and mites suggest a general trend in which abundances are higher as transitions occur along a successional and land-use intensity gradient. Between different taxa, the steps along the gradient at which population sizes are higher may vary between taxa. These potentially being following arable to pasture conversion for earthworm and (managed) pasture conversion to woodland for the mites and springtails. Nonetheless the general trend for abundance increase between land-use types is evident across multiple taxa.

### 6. SOIL BIODIVERSITY AND SOIL HYDROLOGY

Earthworms play an important role in agro ecosystems by influencing water infiltration and run off in soils (Chan, 2004; Lee, 1985). Studies on the effect of earthworms on infiltration rate however show mixed results. Most studies focused on burrows made by anecic species such as *Lumbricus terrestris* since these earthworms make large and vertical burrows often open to the surface. For example, Shipitalo et al. (2004) found that infiltration rates were positively correlated with *L. terrestris* numbers and biomass. It is though important to note that this ecological type of earthworm is rarely dominant in abundance in arable lands (Lee, 1985). In contrast for endogeic earthworms, which are frequently the most common ecological group of earthworms in arable soils, the influences of burrowing on water infiltration rates have only been rarely studied (Capowiez et al., 2009).

Of the studies of earthworm burrow effects on soil hydrology that have been conducted in arable fields, Capowiez et al (2009) observed a significant correlation in reduced tillage...
RT) plots between larger macropores (diameter > 6 mm) and water infiltration. This illustrates the potential positive effect of earthworms in these plots. Tillage had a clear negative effect on macroporosity both in terms of abundance and continuity. This did not, however, result in decreased water infiltration since the decrease in macroporosity was offset by the significant decrease in soil bulk density in conventional till (CT) plots as a result of the use of mouldboard ploughing in these areas. On the other hand, soil compaction significantly decreased water infiltration due to the combined effect of the decrease in number of larger macropores and the increase in soil bulk density. Ernst et al (2007) performed a laboratory experiment to assess the impact of ecologically different earthworm species on soil water characteristics, such as soil tension, water content, and water infiltration rate. The effect of three earthworm species from different ecological groups (Lumbricus rubellus, Aporrectodea caliginosa, L. terrestris) was determined. The results showed evidence, that ecologically different earthworms modify soil water characteristics in clear and distinct ways. This suggests that the addition of species information for earthworm could benefit current understanding of soil hydrology.

Tebrügge & Düring (1999) also studied the effect of tillage regimes during 18 years on earthworm and soil hydrology in different arable soils ranging from sand to a silt loam. The long-term application of RT and NT resulted in significantly higher earthworm populations and biopores numbers. This resulted in improved infiltration. Alhassoun (2009) observed the highest infiltration rate in forest (no earthworms present), followed by grassland and the lowest rate in arable land. The soil infiltration rate was considerably affected by agricultural management practices in the arable fields. Organic farming resulted in a better soil structure and supported higher earthworm populations resulting in high numbers of biopores and significantly increased water infiltration. Conservation tillage and RT systems resulted in a high soil aggregate stability and produced larger numbers of earthworms, in particular anecics, resulting in higher numbers of macropores with high continuity and connectivity. These have an important role for the enhancement of water infiltration rates into the soil profile. Bouché and Al-Addan (1997) also found a positive correlation between earthworm biomass and infiltration rate but not with earthworm numbers. There are, thus, a number of studies that has demonstrated a positive effect of earthworms on soil porosity.

In contrast to results above, a number of studies have in contrast found there to be no effect of earthworms on infiltration rates. Van Eekeren. (2010) found that the number of earthworm burrows at 10 and 20 cm depth was not significantly correlated with water infiltration. Also Shipitalo & Butt (1999) found no significant relationships between infiltration rates and burrow geometrical properties or earthworm biomass in their study. Ouellet et al. (2008) did not find a significant relationship between infiltration (i.e., field saturated hydraulic conductivity and air entry tensions) and earthworm biomass. The number of earthworms in a study by Radke & Berry (1993) also did not correlate positively with infiltration rate.

The actual impact of tillage on earthworm populations is a result of a number of factors including tillage depth, tillage intensity, tillage timing, soil type, soil conditions and subsequent weather (Chan, 2001). Agricultural intensification affects abundances of taxonomic groups with larger body size such as earthworms (Postma-Blaauw et al., 2010). This is highlighted by the conventional and no-till meta-analysis conducted. With the intensification of arable land use in past decades the deterioration of agroecosystem
functioning has emerged as a major issue. Sustainable tillage systems are intended to exploit the natural biotic mechanisms to maintain or restore soil structure, fertility and drainage (Pfiffner and Luka, 2007). The effects of tillage on earthworm communities thus have been studied numerous times. Within this Deliverable, the integration of over 100 of these comparisons within a meta-analysis identifies the trend for greater diversity and higher number of earthworms under reduced tillage regimes (Chan, 2001).

To assess how changes in earthworm abundance may relate to soil hydrological process that control water balance, infiltration and run off, we also investigated the relationship between the average number and biomass of earthworms, tillage system (CT= conventional tillage, NT= no tillage, RT= reduced tillage), habitat type (grassland, arable), soil texture class and measures of infiltration rate. The analysis adopted a partial systematic review approach focussed on the identification and combined analysis of available experimental data-sets.

### 6.1. SOIL HYDROLOGY META-ANALYSIS METHOD

We performed a limited search on infiltration rates and earthworm abundance using Google Scholar (keywords: “soil water infiltration” and earthworm* yielding 174 hits). Articles on (semi)arid and tropical systems were omitted in this study. Data on earthworm abundance, earthworm biomass and infiltration rate was limited. Data used in the analysis (Table 6) were taken from articles published by Allhassoun (2009), Johnson-Maynard et al (2007), Ouellet et al. (Ouellet et al., 2008), Wuest (2001) and Faber et al. (unpublished). Data on juvenile earthworm density (N/m2) from Faber et al. (unpublished) were omitted because this was the only study where sampling was done in autumn. Density during autumn was biased due to a large numbers of juveniles in one plot (>400/m2) in this study.

Infiltration rate was included as the measurement parameter. The infiltration rate is the velocity of water entering into soil (mm/h). There are two different terms: *initial infiltration rate*, indicating the fast entry of water into dry soil, and *equilibrium infiltration rate*, indicating the steady state infiltration rate which nearly equals the saturated hydraulic conductivity of soil ($K_s$). Data on the near equilibrium infiltration state were used in this study ($K_{s\_mm\_h}$).

For the statistical analysis of the compiled systematic review data, we performed a generalized linear model (GLMs) analysis using Genstat Version 14 with a normal link function (Lane, 1993). The best model was selected using all subsets regression using Akaike weights information criterion.
Table 6. Data used in the analysis on earthworm abundance.

<table>
<thead>
<tr>
<th>Ref.</th>
<th>Country</th>
<th>Plot Source</th>
<th>Sampling time</th>
<th>Sampling method</th>
<th>Avg Nworms</th>
<th># Samples</th>
<th>Earthworm ecological group</th>
<th>Ks (mm/h)</th>
<th>N Fluctuations</th>
<th>Soil texture</th>
<th>Clay (%)</th>
<th>C-org (%)</th>
<th>Soil pH</th>
<th>Land use</th>
<th>Tillage system</th>
<th>Use history (yrs)</th>
<th>Mean precipit. (mm/yr)</th>
</tr>
</thead>
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*References: 1= Alhassoun, 2009; 2=Johnson-Maynard et al., 2007; 3= Wuest, 2001; 4=Faber, unpublished*
6.2. SOIL HYDROLOGY META-ANALYSIS RESULTS

The best fitting GLM model was $\text{Constant+tillage\_system+land\_use+avg\_Nworms}$ with factor reference level tillage\_system CT, type arable (Table 7). Earthworm abundance, tillage system and habitat type had a significant effect on infiltration rate (Table 8; Fig 27). An alternative model was tested including interactions between the number of earthworms*tillage system and earthworms*type. Interactions were not significant and were therefore excluded from the model (avg Nworms.tillage system NT, avg Nworms.tillage system RT and avg Nworms.type grass resp. p=0.573, p=0.896, p=0.176).

Table 7. : Akaike information criterion and Akaike weights. Terms: (1) Soil\_texture\_class (3) type (2) tillage\_system (4) avg\_Nworms

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Table 8. Statistical output for relationships between infiltration rate and tillage\_system, habitat type, Soil\_texture\_class and avg N earthworms. Factor reference level: tillage\_system CT, type arable. Explained variance 61.3%, overall significance p<0.001.
To analyse the effect of ecological type of earthworms on infiltration rate we excluded data from the USA data since no data on ecological types was available on some of the species that were encountered in these studies. Limiting the dataset still showed a significant relationship between the number of earthworms and infiltration rate (Table 9). Among the ecological groups, the anecic and epigeic earthworms both increased infiltration (Table 10, 11), while endogeics worms did not have a significant effect.

Table 9. Statistical output for the relationship between infiltration rate and tillage_system, habitat type, Soil_texture_class and avg N earthworms. Factor reference level: tillage_system CT, type arable. Explained variance 56.2%, overall significance p<0.001.

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Table 10. Statistical output for the relationship between infiltration rate and tillage_system, habitat type, Soil_texture_class and avg N anecic earthworms. Factor reference level: tillage_system CT, type arable. Explained variance 52.9%, overall significance p=0.002

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Table 11. Statistical output for the relationship between infiltration rate and tillage_system, habitat type, Soil_texture and avg N epigeic earthworms. Factor reference level: tillage_system CT, type arable. Explained variance 54.3%, overall significance p=0.001

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</table>

To investigate the possible relationship between earthworm biomass and infiltration rate data summarized in Table 12 has been used. The best model (Table 13) found was Constant+tillage_system+land_use+soil_texture. The alternative model including all our terms yielded no significant impact of earthworm biomass on infiltration rate (p=0.323).

Table 12. Data used in the analysis for earthworm biomass.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Country</th>
<th>Plot</th>
<th>Biomass (g/m2)</th>
<th>Ks (mm/h)</th>
<th>Soil texture</th>
<th>Land use type</th>
<th>Tillage system</th>
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<tbody>
<tr>
<td>Alhassoun 2009</td>
<td>Germany</td>
<td>Braunschweig F36/4A</td>
<td>24.68</td>
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<td>loamy sand</td>
<td>arable</td>
<td>CT</td>
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<tr>
<td>Alhassoun 2009</td>
<td>Germany</td>
<td>Braunschweig F36/4B</td>
<td>28.8</td>
<td>107.64</td>
<td>loamy sand</td>
<td>arable</td>
<td>CT</td>
</tr>
<tr>
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<td>Braunschweig F36/4C</td>
<td>27.47</td>
<td>107.64</td>
<td>loamy sand</td>
<td>arable</td>
<td>CT</td>
</tr>
<tr>
<td>Alhassoun (2009)</td>
<td>Germany</td>
<td>avg F36</td>
<td>35.87</td>
<td>107.64</td>
<td>loamy sand</td>
<td>arable</td>
<td>CT</td>
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<td>Study</td>
<td>Country</td>
<td>Location</td>
<td>Soil Textural Class</td>
<td>Land Use</td>
<td>Depth</td>
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<tr>
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<td>Braunschweig 10-A</td>
<td>loamy sand</td>
<td>arable</td>
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<td>Braunschweig 10-B</td>
<td>loamy sand</td>
<td>arable</td>
<td>CT</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alhassoun</td>
<td>Germany</td>
<td>Braunschweig Succession</td>
<td>loamy sand</td>
<td>grass</td>
<td>NT</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alhassoun</td>
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<td>Trenthorst FV8</td>
<td>sandy loam</td>
<td>arable</td>
<td>RT</td>
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<td>Trenthorst FV11</td>
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<td>arable</td>
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<td>Trenthorst FV29</td>
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<td>Trenthorst FV51</td>
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<tr>
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<td>Mariensee Schlag1 shallow</td>
<td>sandy loam</td>
<td>arable</td>
<td>RT</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alhassoun</td>
<td>Germany</td>
<td>Mariensee Schlag1 deep</td>
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<td>Germany</td>
<td>Mariensee F/grass</td>
<td>sandy loam</td>
<td>grass</td>
<td>NT</td>
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<tr>
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<td>Mariensee F/succession</td>
<td>sandy loam</td>
<td>grass</td>
<td>NT</td>
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<tr>
<td>Faber</td>
<td>Netherlands</td>
<td>FAB - 1</td>
<td>silt loam</td>
<td>arable</td>
<td>RT</td>
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</tr>
<tr>
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<td>Netherlands</td>
<td>FAB - 2</td>
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</tr>
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<td>Faber</td>
<td>Netherlands</td>
<td>FAB - 3</td>
<td>silt loam</td>
<td>arable</td>
<td>RT</td>
<td></td>
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</tr>
<tr>
<td>Faber</td>
<td>Netherlands</td>
<td>FAB - 4</td>
<td>silt loam</td>
<td>arable</td>
<td>RT</td>
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<td></td>
</tr>
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<td>Faber</td>
<td>Netherlands</td>
<td>FAB - 5</td>
<td>silt loam</td>
<td>arable</td>
<td>RT</td>
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<tr>
<td>Faber</td>
<td>Netherlands</td>
<td>FAB - 6</td>
<td>silt loam</td>
<td>arable</td>
<td>RT</td>
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<tr>
<td>Faber</td>
<td>Netherlands</td>
<td>FAB - 7</td>
<td>silt loam</td>
<td>grass</td>
<td>CT</td>
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<td>Faber</td>
<td>Netherlands</td>
<td>FAB - 8</td>
<td>silt loam</td>
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<td>Netherlands</td>
<td>FAB - 9</td>
<td>silt loam</td>
<td>arable</td>
<td>CT</td>
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<td>Netherlands</td>
<td>FAB - 10</td>
<td>silt loam</td>
<td>arable</td>
<td>CT</td>
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</table>
Table 13. Akaike information criterion and Akaike weights. Terms: earthworm biomass (1), soil texture class (2), tillage_system (3), type (4)

<table>
<thead>
<tr>
<th>Terms</th>
<th>Aic</th>
<th>Exp(AICmin-AICi)/2</th>
<th>Akaike weight</th>
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<td>1</td>
<td>2</td>
<td>42.033</td>
<td>0.00</td>
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<tr>
<td>3</td>
<td>46.916</td>
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<td>1</td>
<td>67.854</td>
<td>0.00</td>
<td>0.00</td>
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<tr>
<td>4</td>
<td>74.045</td>
<td>0.00</td>
<td>0.00</td>
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<tr>
<td>2</td>
<td>2+3</td>
<td>36.698</td>
<td>0.06</td>
</tr>
<tr>
<td>3+4</td>
<td>37.935</td>
<td>0.03</td>
<td>0.02</td>
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<tr>
<td></td>
<td>2+4</td>
<td>43.440</td>
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<td>1+2</td>
<td>43.975</td>
<td>0.00</td>
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<td>0.00</td>
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<td>1.00</td>
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<td>1+3+4</td>
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<td>1+2+3</td>
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<td>1+2+4</td>
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<td>4</td>
<td>1+2+3+4</td>
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6.3. SOIL HYDROLOGY META-ANALYSIS DISCUSSION

The results of the meta-analysis studies conducted clearly indicate that earthworm can increase infiltration rates and do so increasingly with increasing community size. However, the study is based on a very limited amount of data, and a more extended survey of the literature might yield more information. Searching Google scholar with keywords “water infiltration” and earthworm* yielded more than 4000 hits. Time was too limited to perform a full literature scan on this number of references.

Data used in this study is based on a limited sample size and probably does not account for spatial and temporal variation within sampling sites (Brussaard et al., 2007). Spatial heterogeneity in soil organism distributions is shaped by environmental factors, intrinsic population processes (dispersal, competition, reproduction) and disturbance. Nuutinen et al. (1998) suggested a positive relationship between earthworm activity and infiltration rate, but these authors encountered large spatial variations in earthworm abundance and infiltration rates within sampling sites. Total numbers of earthworms and numbers of *L. terrestris* were positively correlated with water infiltration. However, comparison of the spatial distribution within the sampling site showed that this positive correlation was not at all obvious. While the percolation of water tended to be in association with *L. terrestris* densities, the infiltration rate showed notable variability not related to *L. terrestris* abundances.
Soil surface infiltration vary with time due to tilling regime, crop rotation, surface seal formation after heavy rain, and soil cracking under drying conditions. Temporal variation of infiltration rate therefore can be much greater than management-induced variation (Le Bayon et al., 2002; Logsdon et al., 1993). Earthworm density from Faber (unpublished data) in our study was biased due to a large numbers of juveniles in a single plot, illustrating large spatial and temporal variation. This data was omitted for reasons of comparability in terms of community age distribution. When included in the analysis no significant impact of earthworm numbers on infiltration rate was found.

Infiltration rate can be hampered due to soil compaction, a lack of biopores, and surface sealing due to poor aggregate stability. Usually the presence of earthworms is associated with an improvement in soil condition, rather than a degradation of the soil (Shuster et al. 2000). Soil structure porosity depends on the balance between the production and degradation of earthworm casts and the forming of stable micro aggregates (Bottinelli et al., 2010). When cast degradation exceeds production, infiltration rates will decrease. The overall effect of earthworm additions in the study by Shuster et al. (2002) was an increase in anecic earthworms, a decrease in surface residue cover, and more pronounced crusting, which decreased mesopore conductivity.

Tebrügge & Düring (1999) found an increased aggregate stability from conventional to reduced and no-till during the growing season. Reduced and no-till resulted in significantly higher earthworm populations and number of biopores, which improved infiltration rates, with NT systems showing a lower susceptibility for slaking. From our review anecic and epigeic earthworms were shown to increase water infiltration. This result is to be expected for deep dwelling anecics, as they maintain their vertical burrows for feeding and/or casting at the soil surface. However, the phenomenon cannot be explained as easily for epigeic species. Epigeics are surface dwellers that live above the surface in litter layers and do not make burrows (Lee, 1985; Lee and Foster, 1991), but epigeic L. rubellus shows an endo-epigeic feeding and burrowing behaviour (Ernst et al., 2009; Francis and Fraser, 1998). A positive effect of such epigeic species is potentially that because of their surface activity they are able to open up sealed soil surfaces. Endogeic worms which do not have either the burrow formatting or surface active habits do not have the effects of soil hydrology that are indicated for anecic and epigeic worms.

Other faunal activity not established in the studies used in our dataset may affect infiltration rates. Mesofauna such as Collembola and Enchytraeidae are known influence sealed soil surfaces, crust formation and infiltration rate (Langmaack et al., 2001). A review by Strudley et al. (2008) concludes that, given the current state of knowledge concerning no-till versus conventional till, it is impossible to generalize results from any given study without detailed information on all controlling factors. Experimental results from field and laboratory studies do not support consistent effects of management on soil hydraulic properties. There is however a tendency that macropore connectivity is increased under no-till compared to conventional practices, whilst differences in total porosity and soil bulk density are inconsistent. This corresponds to a general increase in ponded or near-zero tension infiltration rates and saturated hydraulic conductivity (Ks) for no-till. Our study indicated an
increase in water infiltration under reduced till, while infiltration rates under no-till are lower. This result is comparable to the Polish study by Lipiec et al. (2006) for no-till. Infiltration rate was highest under conventional management, and was reduced by 36-62% in reduced and 61% in no-till soil.

The effect of earthworm abundance and community diversity on soil hydraulic properties is still hardly studied and remains largely unclear. More data need to be gathered in order to assess the effect of earthworms on infiltration rates incorporating additional factors (C%, clay content, slaking%, mesofauna, crop cover, climate etc.) as well as spatial and temporal variation. Collection of such data is recognised as a research aim within the EcoFINDERS project.

- 7 SUMMARY

7.1. MAJOR TRENDS OF LAND USE CHANGE IMPACTS ON KEY SOIL TAXA BIODIVERSITY

The results of the studies conducted to assess the influence of different land management and land use transition on soil biodiversity highlight a consistent trend across the taxa investigated. Community parameters show lowest values in soil under intensive arable management. This is likely to be because these soils are subjected to regular disturbance due to both physical and chemical perturbations. Introduction of reduced or no-till management practices reduces the intensity of physical disturbance and this most frequently result in an increase in the composition and size of the studied components of the soil community. These include macroinvertebrates as demonstrated for earthworm and for the soil fungi. Conversion to pasture represents a further reduction in the intensity of land use, since soils under pasture are left to establish a normal depth profile and also the use of pesticides and fertilizers on these soils is often greatly reduced. Conversion to pasture benefits the abundance of earthworm communities as shown by meta-analysis. Reductions in tillage and conversion from arable to pasture land use have a generally positive effect on the fungal community. National surveys of the soil community also confirm that there is a greater meiofaunal abundance and high resolution taxonomic diversity in pasture soils when compared to arable systems. Woodland conversion further maintains or enhances increase in abundance of earthworm, fungi and the meiofauna.
7.2. INTEGRATION OF SOIL BIODIVERSITY INTO HYDROLOGICAL MODELS – CONCLUSIONS AND NEXT STEPS

Analysis of studies that have compared soil management and soil community (earthworm abundance and species composition) effects suggested a positive relationship between earthworm activity and infiltration rate, but encountered large variations in earthworm abundance and infiltration rates within the published data-sets. Constructions of models using data from literature studies identified that the earthworm abundance, tillage system and habitat type each had a significant effect on water infiltration rate. From the review of the effects of individual earthworm functional groups, anecic and epigeic earthworms were shown to increase water infiltration significantly, but this effect was not seen for the endogeic worms. This result was expected for the deep dwelling anecic worms as a result of burrow formation. However, the result for the epigeic worms was novel and may be explainable by the surface dwelling habit of these species.

The clear effects of earthworm abundance and in particular of the specific of earthworm functional groups on water infiltration rates can provide essential information that can be included in soil hydrology models. Bardgett et al (2001) have published a conceptual view of the potential way that biodiversity can be conceptually linked to soil hydrological processes. The role of both the anecic and epigeic worm can be represented through the effects of water transport to the deeper soil layer and ultimately to groundwater. The epigeic worms can act both to prevent the formation of surface crusts and mats and also may contribute to the interflow of water through soil layers. Within simple hydrological model the scaling of these parameters in accordance with the changes in earthworm abundance and biodiversity that may feature under different land management and land use regimes may offer an approach to the incorporation of quantitative measures of biodiversity to soil hydrological process. Coupling these data to representations of the effects of earthworm abundance and ecological group representation on soil infiltration rates can provide an approach through which it may be feasible to parameterise the consequences of earthworm abundance change for water flow processes occurring both above and below the soil surface. Such models can provide a potential route to the identification and valuation of the role of earthworms and wide soil biodiversity community status on water regulation in terrestrial ecosystems.
Fig. 13. A conceptual model of the role of soil biodiversity in hydrological processes in soil according to Bardgett et al. (2001).
REFERENCES


Jegou, D., Capowiez, Y., Cluzeau, D., 2001. Interactions between earthworm species in artificial soil cores assessed through the 3D reconstruction of the burrow systems. Geoderma 102, 123-137.


ANNEX I Papers used for data collection in the earthworms in conventional and reduced tillage analysis


ANNEX II Papers used for data collection in the earthworm arable to pasture conversion analysis


Fraser, P.M., Haynes, R.J., Williams, P.H., 1994. Effects of pasture improvement and intensive cultivation on microbial biomass, enzyme-activities, and composition and size of earthworm populations. Biology and Fertility of Soils 17, 185-190.


ANNEX III Papers used for data collection in the earthworm pasture to woodland conversion analysis


ANNEX IV Papers used for data collection in the fungi ‘Tillage comparison’ analysis


ANNEX V Papers used for data collection in the fungi ‘Arable to pasture conversion’ analysis


ANNEX VI Papers used for data collection in the fungi ‘Pasture to woodland conversion’ analysis


