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# A review of earthworm impact on soil function and ecosystem services.

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*Short running head: Earthworm impact on ecosystem services.*

## Summary

Biodiversity is responsible for the provision of many ecosystem services; human well-being is based on these services, and consequently on biodiversity. In soil, earthworms represent the largest component of the animal biomass and are commonly termed 'ecosystem engineers'. This review considers the contribution of earthworms to ecosystem services through pedogenesis, development of soil structure, water regulation, nutrient cycling, primary production, climate regulation, pollution remediation and cultural services. Although there has been much research into the role of earthworms in soil ecology, this review demonstrates significant gaps in our knowledge related in particular to difficulties in identifying the effects of species, land-use and climate. The review aims to assist people involved in all aspects of land management including conservation, agriculture, mining or other industries to obtain a broad knowledge of earthworms and ecosystem services.

## Introduction

Biodiversity, the diversity of genes, organisms and ecosystems, has been clearly recognized in the political agenda since the Convention on Biological Diversity in 1992. The cost of inaction with regard to the loss of biodiversity is now equivalent to 50 billion € per year (1% of world gross domestic product) and could reach 14 000 billion € in 2050 (7% of world gross domestic product) (Braat & ten Brink, 2008). In parallel, ecosystem services have also become a central political issue. Ecosystem services are the benefits provided by ecosystems to humankind as well as other species (Millennium Ecosystem Assessment, 2005). A strong link exists between biodiversity and ecosystem services because many ecosystem services are borne by organisms (Jax, 2005). Previous work has described and categorized ecosystem services, identifies methods for economic valuation, maps the supply and demand for services, assesses threats and estimates economic values (Daily, 1997; Millennium Ecosystem Assessment, 2005), but does not quantify the underlying role of biodiversity in providing services (Kremen & Ostfeld, 2005). In contrast, published studies of the functional role of biodiversity often examine communities whose structures differ markedly from those providing services in real landscapes (Diaz *et al.*, 2003; Symstad *et al.*, 2003), and have been restricted to a small set of ecosystem processes (Schwartz *et al.*, 2000). What is lacking is an approach that will provide fundamental, ecological understanding of ecosystem services to assist in devising the best management and policy tools for their conservation and sustainable use (Kremen & Ostfeld, 2005). For this purpose, we need to identify the relationships that exist between ecological entities and ecosystem functions or services, and to propose different technical approaches to manipulate ecological entities with the aim of reaching management objectives.

For ecosystem managers, a fundamental question is to determine whether all species are equally important providers of ecosystem services or if some are more important than others. In the latter case, it would clearly be most relevant to focus especially on the management of specific providers. Literature reviews (Schwartz *et al.*, 2000; Thompson & Starzomski, 2007) corroborate the 'Drivers and Passengers' hypothesis (Walker, 1992), which stresses that only some species (the drivers) are important. These species are generally known as keystone species (Power & Mills, 1995) or ecosystem engineers (Jones *et al.*, 1994). The drivers of ecosystem functions can be unique in an ecosystem; thus all the bioturbation of sediments may be caused by only one species, such as the brittle star, *Amphiura filiformis*, Müller (1776) in benthic habitats (Solan *et al.*, 2004). In the majority of terrestrial ecosystems, earthworms are the most abundant animal biomass (Lavelle & Spain, 2001). Earthworms are typical ecosystem engineers as they have a large impact on soil structure, which is not necessarily associated with trophic relationships. For example, the tropical earthworm *Reginaldia omodeoi*, Sims formerly known as *Millsonia anomala*, can ingest up to 30 times its own biomass of soil per day, but very little of the ingested organic matter is then assimilated (8%). Furthermore, little of the assimilated carbon is used in biomass production (6%); the remainder is respired (94%) during activity and physical modifications of the soil (Lamotte & Bourlière, 1978; Lavelle, 1978). In temperate ecosystems, earthworms also ingest large amounts of material (2 to 15% of organic matter inputs) (Whalen & Parmelee, 2000) and expend much energy in their modification of the soil (74 to 91% of assimilated carbon is respired) (Petersen & Luxton, 1982). Earthworms have thus been recognized as typical ecosystem engineers (Jones *et al.*, 1994; Lavelle *et al.*, 1997), and represent an excellent potential partner for humans in managing ecosystem services (Byers *et al.*, 2006). Earthworms have been divided into three primary ecological categories that may contribute differently to ecosystem processes and thus ecosystem services. Epigeic species live in the litter and produce casts at the soil surface that affects its roughness and the distribution of macro-pores. Anecic species live in vertical burrows, used as shelters, and connected with the soil surface. Endogeic species make horizontal or randomly oriented burrows in the mineral soil, considered as temporary structures because they are rarely re-used (Bouché, 1977; Lee, 1985).

Here we present a synthesis of the impact of earthworms on ecosystem services, initiated in a workshop held in Grenoble (France) in 2010.

## Scope of review

Previous studies have emphasized the importance of soil (Dominati *et al.*, 2010), soil biota (Barrios, 2007; Brussaard, 2012) or more specifically soil invertebrates (Lavelle *et al.*, 2006) in the provision of ecosystem services. However, these studies have not focused on earthworms. Our review considers specifically how earthworms modify ecosystem functions and services. An exhaustive review of all the relevant research would require an entire book; therefore, we summarize the different soil functions and ecosystem services that earthworms contribute to, and methods of exploiting these in soil management. Within the terms of the Millenium Ecosystem Assessment (2005), earthworms play the role of catalyst for two major 'supporting services', namely soil formation (Darwin, 1881) and nutrient cycling (Edwards, 2004), which are prerequisites to other services. Through their interactions with plants, earthworms are involved in the provision of food, wood and fibre. They also influence major services directly such as climate and flood regulation, water purification and can play a role in remediation and restoration. Earthworms also provide cultural services, for example as fishing bait and in burying archaeological artifacts. The services are reviewed in turn and where relevant divided into different ecosystem processes (Dominati *et al.*, 2010). Where possible, for each service we summarize how earthworms are involved in the service with both a qualitative assessment such as positive, null or negative effects of earthworms and a quantitative estimate of the impact of earthworms on a service. Of necessity these estimates draw on a wide range of data from different ecological categories, land-use, management practices and so on.

We identify two extremes in approach to consider the impacts of earthworms on ecosystem services and soil function (Figure 1). At one extreme, the approach is based completely on ecosystem self-organization. In 'conservation', the consequences of preserving native earthworm species, compared with situations where they have disappeared, can indicate the role of earthworms in ecosystem functioning. At the other extreme, the approach can be based completely on the use of products engineered by earthworms in semi-industrial production systems. The 'spreading of earthworm-created products' such as vermicompost, belongs to this category. Intermediate to these extremes are studies that deal with earthworm inoculation in the field, for example using the Stockdill method (Stockdill, 1959; 1966; Martin & Stockdill, 1976) and earthworm inoculation units (EIUs, see Figure 2) (Butt *et al.*, 1997), and changes in ecosystems where 'recolonization' by earthworms becomes possible, as with changes in agricultural practice such as moving to no-till systems and changes in pesticide use.

## Soil formation

Soil formation is a long-term process determined partly by climatic conditions and the nature of the parent material (Chesworth, 1992). It involves the breakdown of primary minerals and the incorporation of organic matter. Darwin (1881) was among the first to include biota, especially earthworms, in the list of factors responsible for soil formation through the accumulation of earthworm casts and mixing processes. The potential role of earthworms in soil development is recognized in the term 'vermiform soils' for soil that has at least 50% or more of the A horizon and >25% of the B horizon volume consisting of earthworm- or animal-derived structures (burrows and castings, faecal material). Initially, the term was applied only to Mollisols, but has recently been extended to other soil classes; the relevance of this concept is still being discussed, since faunal activity is observed in the profile of most soil types (Pop, 1998).

The importance of earthworms in chemical weathering was first studied by Darwin (1881) in an experiment where the red colour of a red-oxide sand disappeared after passing through earthworm intestines, probably because of dissolution of the oxide by acidic enzymes in the earthworm's digestive tract. However, since the work of Darwin relatively little research has considered the role of earthworms in mineral weathering. Pop (1998) showed that *Octodrilus* earthworm species in the Romanian Carpathians affect the clay mineralogy and formation of illite in the soil, a process that takes hundreds of thousands of years in the absence of biota. In laboratory experiments, Carpenter *et al*., (2007) showed that the epigeic earthworm *Eisenia veneta*, accelerated the weathering of anorthite, biotite, smectite and kaolinite; smectite was transformed to illite and kaolinite reacted to produce a new mineral phase (Carpenter *et al.*, 2007). Whether it is the earthworms, microorganisms stimulated in their gut (Brown, 1995) or a collective action of both organisms that are responsible for the mineral weathering effect is still open to debate.

Compared with mineral weathering, the role of earthworms in humus formation has been investigated more thoroughly. The darkening of soil mould is a slow process, which involves primarily chemical reactions and microbial activity. This process, nevertheless, may be accelerated by earthworms that prepare the soil and litter mixtures composed of fragmented and macerated leaves and fine soil particles for microbial attack. It is well known by vermicompost producers that humus can be obtained from organic matter within a few months (Edwards *et al.*, 2011). One of the most important roles of earthworms in soil may be their control of humification rates through feeding, burrowing and casting activities and interactions with microorganisms (Dell'Agnola & Nardi, 1987; Ponge, 1991; Bernier, 1998). This appears to be mainly by controlling C inputs into the soil through burial of litter and by enhancing its decomposition rate, in regulating microbial activities in the drilosphere (the soil immediately surrounding earthworm burrows) and casts, and protecting C in stable aggregates such as their castings (Brown *et al.*, 2000).

The data in Feller *et al*. (2003) from various land-use types under temperate climate conditions in Europe suggest that the amounts of soil brought to the surface by earthworms annually as castings is about 40 t $ha^{-1}$ $year^{-1}$ (based on 19 studies) contributing about 0.4 cm (based on 13 studies) of top-soil per year. Under a temperate climate, earthworms can thus potentially move about 40 cm of soil to the surface each century, or four metres per millennium! However, this is probably an over-estimate because some soil is likely to be moved more than once.

In addition to contributing towards mineral weathering and the formation of humus, earthworms bury organic matter from the surface, and equally bring soil particles from deep soil horizons to the surface. The contribution of earthworms to the burial of surface litter (leaves, twigs and so on) at some locations may reach 90–100% of the litter deposited annually on the soil surface by the above-ground vegetation from either 'natural' vegetation or crops (Raw, 1962; Knollenberg *et al.*, 1985), representing up to several tonnes per hectare per year of organic material. Recent organic matter is buried into the soil, whereas soil from depth is brought to the soil surface by the deposition of casts above-ground, particularly by the anecic species. These surface casts are then responsible for an apparent downward migration of stones in the soil profile. The rate of surface cast deposition depends on the number of earthworms present and their burrowing depth, the climate, vegetation and soil type, and the depth of the previously deposited soil. The combined effects of leaf burial into the soil and production of surface casts (which also buries surface-deposited materials) place earthworms as key factors in the formation of mull soil (Langmaid, 1964; Brethes *et al.*, 1995). However, in spite of the huge deposition of casts at the soil surface, most anecic and endogeic earthworm species probably deposit their casts primarily below ground, which will markedly affect bulk density and aggregation (see below).

Erosion is also important in the formation of soil and again earthworms have a significant role in this process, in particular through the production of casts on soil surfaces. For a slope of 9°26', Darwin (1881) estimated that about 1140 kg $ha^{-1}$ $year^{-1}$ of earthworm cast material was removed. A similar estimate of 1120 kg $ha^{-1}$ $year^{-1}$ has since been observed for a grazed pasture in New Zealand (Sharpley *et al.*, 1979). These values are similar in order of magnitude to mass displacements in major river basins such as the Mississippi. The contribution of casts to erosion appears to occur following their breakdown by the impact of rain, rather than the transport of intact cast material (Le Bayon & Binet, 1999; 2001). However, there is debate as to whether more or less erosion would occur in the absence of casts. Some authors suggest that surface-deposited casts of anecic species may give resistance to run-off, thereby reducing erosion, whereas others suggest that the erosion of cast material leads to a net increase in erosion (Shipitalo & Protz, 1987). Over longer time-scales (thousands of years or more), this phenomenon could lead to vast amounts of sediment accumulation in alluvial soil or floodplains (Feller *et al.*, 2003). We should be able to distinguish between a planet with life versus one without based on an assessment of mountain height, steepness or curvature, the sinuosity of rivers, the extent of the landscape with a soil mantle and slope-area characteristics (Dietrich & Perron, 2006), with earthworms and plants as the major causes of these differences.

Studies over the lengthy time scales necessary to observe soil formation are very rare. However, it is important to study the effect of earthworms on soil formation because it could be of great interest for restoring degraded soils, disused stone or sand quarries, burnt areas or strongly polluted sites. In addition, suggestions have increased that bioturbation and soil formation may have had a major impact on evolution since the appearance of the metazoans more than 500 M years ago. Therefore, considering the role of earthworms in soil formation may provide insight into the evolution and functioning of marine and terrestrial ecosystems (Dietrich & Perron, 2006; Kennedy *et al.*, 2006; Meysman *et al.*, 2006).

## Soil structure

The arrangement of soil particles and associated pore spaces gives rise to soil structure across a range of scales and is a function of interacting physical forces on water status, the actions of larger soil biota such as plant roots or earthworms, and the presence of organic matter and soil tillage in some agricultural systems (Oades, 1993; Milleret *et al.*, 2009a; 2009b).

Earthworms both compact and loosen soil. For example, *Reginaldia omodeoi* increased bulk density from 1.24 to 1.31 g $cm^{-3}$, and from 1.37 to 1.48 g $cm^{-3}$ in two different studies (Lavelle *et al.*, 2004). Alegre *et al*. (1996) also observed a significant increase in bulk density from 1.12 to 1.23 g $cm^{-3}$ and a decrease in porosity from 58 to 53% in the presence of *Pontoscolex corethrurus* Muller. In another study, Blanchart *et al.* (1997) demonstrated that *R. omodeoi*, a compacting endogeic earthworm, decreased total soil porosity by 3%, whereas Eudrilidae (species unidentified), small de-compacting endogeic earthworms, increased it by 21%. De-compacting earthworms destroyed macro-aggregates formed by compacting ones, whereas compacting earthworms did the same with the casts of de-compacting ones. Such variability regulates soil structure in a dynamic way (Blanchart *et al.*, 1997).

Studies such as the above suggest that compacting earthworms can increase soil bulk density by 15%. In a 20-year study, the experimentally induced absence of earthworms in a grass sward also increased soil bulk density (Clements *et al.*, 1991), which suggested that earthworms can also decrease bulk density. The absence of earthworms also decreased total soil porosity; in a treatment with no earthworms, fine (< 0.4mm) aggregates increased compared with treatments where earthworms were present (Blanchart *et al.*, 1997). Finally, in some tropical situations, long-term field experimentation (Blanchart *et al.*, 1999) has revealed interacting processes between compacting (*R. omodeoi*) and de-compacting (small eudrilid) species resulting in the maintenance of soil structure.

Earthworms also affect aggregate size distribution. For example, some compacting earthworms, such as *R. omodeoi*, inoculated under yam or maize culture can increase the proportion of aggregates >2 mm in diameter from 29.8 to 53.5% or from 24.6 to 42.2%, respectively (Gilot-Villenave *et al.*, 1996; Gilot, 1997). Similar effects have been observed after the inoculation of the peregrine, pantropical, endogeic species *P. corethrurus* under a traditional cropping system in Peruvian Amazonia. After six successive crops, earthworms had increased the proportion of aggregates (> 2 mm) from 25.4 to 31.2 %, at the expense of smaller (< 0.5mm) aggregates, which decreased from 35.4 to 27.4% (Lavelle *et al.*, 2004). In another experiment (Alegre *et al.*, 1996), the proportion of macro-aggregates (>10 mm) increased from 25.1 to 32.7% in inoculated treatments, whereas the proportion of small aggregates (< 2 mm) decreased from 33.2 to 26.1%, and no change was observed in the intermediate (2–10 mm) category.

In general, positive effects of earthworms on soil structure have been widely demonstrated. However, if earthworm use is proposed as part of a soil management scheme, there is a need for sufficient and appropriate preliminary soil measurements, and then monitoring at appropriate time-scales. The combination of compacting and de-compacting species could also be vital for inoculation to achieve the required objectives in soil structural improvement, given their different behaviours. Recent modelling to simulate the effects of earthworms on soil structure (Barot *et al.*, 2007a; Blanchart *et al.*, 2009) has great merit and is worthy of further development as these activities are a major ecosystem service.

## Water regulation

The link between soil physical structure and hydraulic properties is difficult to establish because of the complex structure of soil. Despite this lack of understanding, it is well-known that earthworms affect soil water regulation because of their modification of soil porosity through the production of macro-posity (burrows or aestivation chambers), meso-porosity and micro-porosity (casts) (Pérès *et al.*, 1998). The diversity of pore shapes and sizes derived from the various behaviours and sizes of separate species and developmental stages within them, may allow soil to transfer, and also to store, water at a wide range of potentials.

Ehlers (1975) showed that after ten years of earthworm inoculation, the infiltration rate of water through soil increased from 15 to 27 mm hour$^{-1}$. In Mediterranean soil, water infiltration was correlated with earthworm biomass ($r$ = 0.60) and burrow length (0.66), and strongly correlated with burrow surface ($r$ = 0.77) (Bouché & Al-Addan, 1997). Across a range of soil types, infiltration rate was measured as 150 mm h$^{-1}$ per 100 g m$^{-2}$ of earthworms or 282 mm h$^{-1}$ per 100 g m$^{-2}$ of anecic earthworms (Bouché & Al-Addan, 1997). In the tropics, inoculation of endogeic compacting species has a negative effect on infiltration rate: changes in aggregate size proportions and bulk density (see above) resulted in a decrease in infiltration rates and sorptivity (the capacity of the medium to absorb or desorb liquid by capillarity), the latter decreased from 0.34 cm s$^{-1}$ in non-inoculated soils to 0.15 cm s$^{-1}$ in treatments inoculated with 36 g m$^{-2}$ fresh biomass of earthworms (Alegre *et al.*, 1996). In another experiment in the Côte d'Ivoire, the removal of macrofauna in the soil (control treatment) was responsible for a slow infiltration rate (about 2.8 cm minute$^{-1}$). This infiltration rate improved weakly (+22 to 27%) in the presence of two endogeic compacting species, namely *R. omodeoi* and *Dichogaster terraenigrae* Omodeo & Vaillaud., but improved strongly (+77%) when *Hyperiodrilus africanus*, Beddard, the peregrine African de-compacting species was the only one present (Guéi *et al.*, 2012). In another study, however, infiltration did not vary in response to earthworm inoculation, despite an increase in the area of macro-pores observed at 10-cm depth (Lachnicht *et al.*, 1997).

The increase in infiltration rate related to earthworm burrows can decrease soil erosion by 50% (Sharpley *et al.*, 1979; Shuster *et al.*, 2002). In the tropics, endogeic de-compacting species increase soil porosity and water infiltration thereby reducing runoff. However, the same species also produce small-sized and labile casts that favour surface sealing and contribute to soil losses (Blanchart *et al.*, 1999). Compacting species can create water stable macro-aggregates that decrease the effects of splash and runoff. Unfortunately, these species also decrease water infiltration by increasing bulk density (Blanchart *et al.*, 1999). The rainfall regime is probably an important determinant of the overall outcome of these opposing factors.

In a temperate climate, anecic casts can create surface roughness, which is reinforced by organic matter residues that form 'middens' and decrease surface runoff (Le Bayon *et al.*, 2002). This result is mainly explained by the greater stability of the casts compared to those in the soil. However, some results from the tropics have been contradictory to this, related to the coalescence of casts (Chauvel *et al.*, 1999) or the creation of a surface crust (Shuster *et al.*, 2000). These results seem to be influenced by the number of earthworm species and the presence of organic matter (Blanchart *et al.*, 1997; Hallaire *et al.*, 2000).

The experimentally-induced absence of earthworms in a grass sward greatly reduced soil moisture and infiltration rate (Clements *et al.*, 1991). Surface runoff during rain was negatively correlated with *Lumbricus terrestris* L. dry weight (Spearman's $r$ coefficient = –0.68) in observations made in the field in Finland (Pitkanen & Nuutinen, 1998). In experimental conditions with a 40% slope in Vietnam, the surface covered by a given amount of run-off water was about 600 mm² with physicogenic aggregates covering 60% of the soil surface, whereas it was about 150 mm² with biogenic aggregates of *Amynthas khami* (Jouquet *et al.*, 2008), leading to a reduced runoff by 75%. In three different soil tillage treatments where earthworm populations were either reduced, increased or remained un-manipulated, anecic earthworm biomass was identified as an important independent variable in runoff and erosion models, after plot slope, soil moisture content and rainfall intensity (Valckx *et al.*, 2010). Erosion rates decreased exponentially as a function of anecic earthworm biomass. Path analysis by structural equation modelling revealed that anecic earthworm biomass in itself contributed to a reduction in soil erosion. This study underlines the need to promote appropriate soil ecosystem management by farmers to support populations of anecic earthworm species (non-inversion tillage, direct drilling) (Valckx *et al.*, 2010).

Water storage can differ according to the earthworm species and climate conditions. The increase in bulk density by endogeic compacting species was associated with a 7% decrease in water storage capacity of the soil, which could be detrimental to plant growth in water-deficit conditions (Blouin *et al.*, 2007). Conversely, in a temperate climate, ten years after the introduction of earthworms, the water storage was 25% greater (Ehlers, 1975).

Water movement through burrows is complex because it depends on the morphological characteristics of the burrows, which are strongly related to the ecological group of earthworms that made them. Increases in burrow diameter or inter-connectivity and tortuosity can enhance water infiltration and conductivity (Shipitalo & Butt, 1999; Bastardie *et al.*, 2002), whereas increases in branching rate decrease water conductivity (Pérès, 2003). Anecic earthworms can produce semi-permanent vertical burrows up to 1-m deep; efficiency in drainage is likely to be increased, especially when these galleries are in contact with drainage tiles (Figure 3) in agro-ecosystems (Nuutinen & Butt, 2003).

Water cannot drain effectively into earthworm burrows unless they are open at the soil surface (Allaire-Leung *et al.*, 2000). This requires regular maintenance of the burrow opening and suggests, by default, that burrows do not regulate water movement effectively all year round. This is especially so during periods of earthworm inactivity, when soil is either not moist or warm enough (Eggleton *et al.*, 2009; Nuutinen & Butt, 2009). Consequently, the efficiency of burrows with respect to water drainage is likely to vary greatly according to the date of the study; for example, earthworm effect on infiltration rate was null in a study performed in July (Lachnicht *et al.*, 1997). Moreover, burrow efficiency depends on earthworm species: thus *Lumbricus terrestris*, which does not create branched burrows (Jegou *et al.*, 1999) should be more effective in promoting water infiltration than *Aporrectodea giardi* Ribaucourt which creates a more branched burrow network.

To explain the effect of earthworms on water regulation better, progress is needed to link physical structure with soil hydraulic properties. The behaviour of earthworms in soil (Figure 4) needs to be specifically characterized if we want to model the resulting effect on water fluxes and storage. The rainfall distribution through the year is also an important variable in determining the effects of earthworms on hydraulic properties, which has not been fully investigated to date.

## Nutrient cycling

Earthworms are heterotrophic organisms that are involved in the degradation of organic matter and molecules, mainly produced by plants but also by other heterotrophic organisms. Earthworms accelerate organic matter degradation by increasing the available surface area of organic matter through comminution (Ingham *et al.*, 1985; Seeber *et al.*, 2008). After digestion, some organic compounds are released into the environment as small organic compounds or mineral nutrients. These mineral nutrients, especially nitrogen (N), are re-used by plants. Nitrogen mineralization is thus increased in the presence of earthworms, either directly through the release of N by their metabolic products (casts, urine, mucus which contain $NH_4^+$, urea, allantoin and uric acid) and dead tissues, or indirectly through changes in soil physical properties, fragmentation of organic material, and through interactions with other soil organisms (Lee, 1985; Bityutskii *et al.*, 2002).

Earthworms accelerate N mineralization from organic matter, but the effect depends on the species and their interactions with other soil biota, soil characteristics and the location of the organic matter (Butenschoen *et al.*, 2009). For instance in mesocosm experiments, *Lumbricus rubellus* Hoffmeister (epigeic) and *L. terrestris* (anecic) earthworms increased the mineralization of applied crop residues, but *Aporrectodea caliginosa* (endogeic) did not. However, mineralization of soil organic matter was enhanced by *L. rubellus* and *A. caliginosa*, but *L. terrestris* had no effect (Postma-Blaauw *et al.*, 2006). In the Lamto savana (Côte d'Ivoire) the earthworm *R. omodeoi* provided 60% of the total population biomass and was estimated to release 21.1 to 38.6 kg $ha^{-1}$ $year^{-1}$ of the total assimilable N in the form of ammonium in faeces or labile organic N in dead earthworms and mucus. Total production of mineral N by the entire earthworm community was estimated to be between 30 and 50 kg $ha^{-1}$ $y^{-1}$ (Lavelle *et al.*, 2004). Whalen & Parmelee (2000) reported that earthworms process 2–15 Mg $ha^{-1}$ $year^{-1}$ of organic matter from soil and litter, and that the annual flux of N through earthworm biomass in temperate, cultivated agro-ecosystems ranges from 10 to 74 kg N $ha^{-1}$ $year^{-1}$. The annual N flux through earthworm populations was greater in plots with added manure than in those with inorganic fertilizer, and ranged from 2.95 to 5.47 g N $m^{-2}$ $year^{-1}$ in 1994–1995 and 1.76 to 2.92 g N $m^{-2}$ $year^{-1}$ in 1995–1996 (Whalen & Parmelee, 2000).

Mineral nitrogen released from earthworms can be important in relation to crop N requirements. In a prairie grassland system, James (1991) calculated that over a year the amount of mineral N present in casts was equivalent to approximately 10–12% of annual plant N uptake compared to half of the input from precipitation. The amount of P in the casts, however, was equivalent to 50% of annual uptake (James, 1991). A flux of 63 kg N $ha^{-1}$ $year^{-1}$ through earthworms in a no-till agro-ecosystem was equivalent to 38% of the total N uptake by the sorghum crop (Parmelee & Crossley, 1988). In another experiment, the N flux through earthworms was  equivalent to 16–30% of crop N uptake during 1994–1995 and 11–18% of crop N uptake during 1995–1996, with the difference attributed to unfavourable climatic conditions during the latter half of 1995 (Whalen & Parmelee, 2000). In a study in which carbaryl pesticide was used to remove earthworms prior to re-inoculation of the soil with *Aporrectodea caliginosa* and *Lumbricus terrestris*, soil mineral N was positively correlated with earthworm density, and N-microbial biomass and N-concentration in total grain-N per soybean plant also increased (Eriksen-Hamel & Whalen, 2007).

Earthworms also modify the N cycle in other ways. Their casts have the potential for microbial nitrification and denitrification (Palmer *et al.*, 2005; Costello & Lamberti, 2008). In Mediterranean soil, *Nicodrilus nocturnus* Evans (anecic) accelerated nitrification, denitrification and other biological activities (Cecillon *et al.*, 2008). In addition, earthworms create soil conditions that favour autotrophic nitrifiers as aeration improves (Zhu & Carreiro, 1999), whereas $NH_4^+$ oxidizing bacteria have been associated with earthworm burrow walls (Parkin & Berry, 1999). Elevated nitrate concentrations of the drilosphere soil are consistent with elevated nitrifying bacterial populations indicating autotrophic nitrification in the presence of earthworms (Araujo *et al.*, 2004). Earthworms increase mineral N in soil, and also readily exchangeable phosphorous (P) (Suarez *et al.*, 2004), potassium, calcium and magnesium (Adejuyigbe *et al.*, 2006). They can also increase leaching of mineral N and P

(Dominguez *et al.*, 2004; Suarez *et al.*, 2004; Costello & Lamberti, 2008) because of their effects on soil structure (see Soil structure and Water regulation sections).

The above experiments deal with the short-term dynamics of nutrients in casts, but the longer-term dynamics have been less well studied. However, it has been shown with models that the effects of earthworms on primary production through increased mineralization of organic matter and thus nutrient release occur only if there is a concomitant reduction in system outputs (by leaching for example), or an increase in system inputs (through nitrogen fixation for example) (Barot *et al.*, 2007b). If there are no increases in inputs or decrease in outputs, the positive effect of earthworms would only be transient: earthworms would consume organic matter and decrease this resource, which would lead to a reduction in earthworm populations, an abatement in organic matter mineralization and consequently a decrease in the effect of earthworms on primary production (Barot *et al.*, 2007b). Thus manipulation of earthworm populations to modify soil functions cannot be carried out in isolation. Due attention must be given to the soil system as a whole.

The degradation of organic matter by earthworms is a process which can be used to deal with the huge amount of organic matter waste derived from urban environments. Waste disposal through the sewage system requires large amounts of water. For example, as much as 36 litres of water is required to dispose of 500 grams of food (Appelhof *et al.*, 1993). This water has then to be cleaned using both additional energy and chemicals. The burial of organic wastes in landfills also presents problems. In addition, there may be societal issues related to acceptance of landfill as a disposal route. Similarly, incineration as a waste disposal method is often viewed with suspicion due to health scares that often involve dioxin emissions, which result from poorly operated incinerators. Most importantly, waste disposal methods may fail to recover the energy present in organic waste at a time when fossil energy is becoming increasingly expensive. Organic wastes can be processed locally by vermicomposting, which decreases the cost of transport to water treatment plants, incinerators or landfills. However, the benefits of vermicomposting may be offset by the large NOx emissions associated with vermicompost production (see later).

Short-term experiments have shown that earthworms have a stimulating effect on nutrient turn-over. However, long-term experiments to evaluate the need for regular additions of organic matter to maintain earthworm populations would be valuable. In agro-ecosystems, the return of plant organic matter to the soil (Riley *et al.*, 2008) or mulch application to the soil surface (Pelosi *et al.*, 2009) is beneficial to earthworms but long-term experiments to compare multiple natural systems would help to provide a better understanding of their effect on nutrient cycling.

**Climate regulation**

Earthworms enhance the incorporation of organic matter into soil and the formation of macro-aggregates through their burrowing, consumption and egestion activities (Guggenberger *et al.*, 1996; Blanchart *et al.*, 1997) (see earlier). This suggests a role in carbon sequestration because storage of carbon in compact stable aggregates is an important process by which soil accumulates carbon and prevents its rapid release in the form of greenhouse gases (Lavelle *et al.*, 2006). However, the extrapolation of carbon sequestration from the level of the soil aggregate to sequestration at the field level is not straightforward.

Earthworm invasions can be considered as poorly constrained experiments in which areas without earthworms act as control plots. In mixed hardwood forests in New York state, USA, organic matter per gram of soil was 36% less in plots where the organic horizon was mixed by earthworms compared with plots kept free from earthworm invasion, and where no marked change in the mineral horizon was noted (Burtelow *et al.*, 1998). Similarly, earthworm invasion of mixed deciduous forest in Minnesota, USA, decreased soil organic matter to a depth of 50 cm by an estimated 600 kg $ha^{-1}$ $year^{-1}$ (Alban & Berry, 1994).

Many more controlled studies suggest earthworm-induced C stabilization in soil organic matter. Don *et al*. (2008), using mesocosms in extensively managed grassland in Germany showed that anecic earthworms increased C stocks in the linings of their vertical burrows by 310 g $cm^{-2}$ at the Mehrstedt site and 270 g $cm^{-2}$ at the Jena site as compared with the background soil profile. The estimated sequestration rate at the Jena site was 22 g C $m^{-2}$ $year^{-1}$. By studying abandoned burrows, they showed a rapid mineralization of this C within 3–5 years, suggesting that anecic earthworm activity does not substantially increase soil C stocks (Don *et al.*, 2008). When earthworms are inoculated into a field without an increase in organic carbon inputs, they tend to decrease the percentage C as they use part of the C resources for their activity. Losses of C contained in *P. corethrurus* casts resulting from mineralization were observed in direct-seeding, mulch-based cropping systems in Madagascar (Coq *et al.*, 2007). Similar results were obtained at Lamto (Côte d'Ivoire): after four years of maize cultivation, percentage C decreased from 13.37 to 9.75 mg $g^{-1}$ in the control and to 9.64 mg $g^{-1}$ in the inoculated treatment (Lavelle *et al.*, 2004). However, in the presence of *R. omodeoi*, soil C mineralization decreased by 5% after three years under yam production (Gilot, 1997). In temperate agro-ecosystems, endogeic species are considered to contribute to the sequestration of C in soil by initiating the formation of micro-aggregates, which in turn affects the physical protection of SOM against microbial decay (Pulleman *et al.*, 2005). Addition of *L terrestris* to a chisel-tilled soil cultivated with maize-soya bean rotations in Ohio (USA) increased average soil organic carbon content from 16.1 to 17.9 g C $kg^{-1}$ for the 0–10-cm depth, and from 12.4 to 14.7 g $kg^{-1}$ at 10–20 cm (Shuster *et al.*, 2001).

To conclude, a recent meta-analysis (36 studies, 136 data points) showed that earthworms are increasing $CO_2$ emissions by 33% through aerobic respiration (Lubbers *et al.*, 2013).

In agro-ecosystems, when management practices are modified with a resulting reduction in the amount of organic matter returned to the soil, a decrease in carbon sequestration is generally observed. Several studies in Scandinavia have confirmed that soil organic matter levels decline after the transition from cropping systems with a large proportion of leys to arable systems with annual ploughing (Uhlen, 1991; Cuvardic *et al.*, 2004). Riley *et al*. (2008) also observed that organic matter declined markedly over 15 years in a conventional arable system with ploughing, and remained at a large concentration in most other systems with leys where earthworm density, biomass and activity (number of channels) remained large. Recently, it has been shown that earthworms enhance the stabilization of soil organic matter only when organic residues are applied (Fonte & Six, 2010). Changes in management systems (Figure 1) are probably a better way of manipulating carbon sequestration in agricultural contexts than the inoculation of earthworms when the soil is not too degraded.

As far as long term effects are concerned, the CENTURY model (Parton & Rasmussen, 1994) developed to predict long term C dynamics and the impact of management practices, predicted that the elimination of earthworms would result in a 10% decrease in C over a 30-year period (Lavelle *et al.*, 2004). Earthworms generally increase primary production and thus carbon fixation by plants (see Primary production section). This could have an impact on carbon sequestration in the ecosystem, depending on the balance of other nutrients such as N and P (see Nutrient cycling section).

A growing body of literature indicates that earthworm activity can increase nitrous oxide ($N_2O$) emissions, for example by switching residue decomposition from an aerobic process with a slow denitrification rate to situations with greater denitrification and $N_2O$

production (Rizhiya *et al.*, 2007). It has been estimated that bacteria within earthworms account for up to 16 % of $N_2O$ emissions (0.6 μg $m^{-2}$ $hour^{-1}$) from beech forest soil (Karsten & Drake, 1997) and 33% of those (1.1 μg $m^{-2}$ $hour^{-1}$) from garden soil (Matthies *et al.*, 1999). Similarly, vermicomposting can result in substantial $N_2O$ emissions of up to 21.3 ± 2.8 mg $m^{-2}$ $hour^{-1}$ in heated beds during the summer compared to a control of 3.9 ±1.7 mg $m^{-2}$ $hour^{-1}$ (Frederickson & Howell, 2003). A meta-analysis (12 studies, 41 data points) concluded that the presence of earthworms resulted in a 37% increase in $N_2O$ emissions (Lubbers *et al.*, 2013). Too few studies have discussed the earthworm effect on $CH_4$ emission, making a full meta-analysis impossible.

Available data on the effect of earthworms on the greenhouse gas balance of soil are fragmentary, and the impact of earthworms on organic matter stocks has not been proved one way or another. Effects arising from changes in earthworm populations observed in many short-term experiments may not be applicable to long-term trends. Therefore, investigations at the field scale are necessary to assess the long-term effects of earthworms. In these experiments all the important greenhouse gases ($CO_2$, $N_2O$ and $CH_4$) should be considered.

## Pollution remediation

The use of earthworms for the restoration or remediation of contaminated soil can be based on several different strategies depending on the nature of the contamination. Earthworms could be introduced into soil to stimulate the microbial population, which in turn would accelerate the degradation of organic contaminants. Metabolism of ingested soil may also lead to direct mineralization of organic contaminants. For both organic and inorganic contaminants earthworm activity may reduce the amount of sorption onto soil particles through digestion of organic matter, modifications of soil chemistry, or both, leading to an increase in the availability of contaminants and so reduce the time scales required for phytoremediation. Studies that have explicitly examined the relationship between earthworms and the remediation of organic and inorganic contaminants are next reviewed briefly. Also pertinent to the use of earthworms in remediation is their effect on plant growth and nutrient recycling (see Primary production and Nutrient cycling sections) and their impact on microbial populations, which is beyond the scope of this review but is discussed in many other papers (Edwards & Fletcher, 1988; Brown, 1995; Nechitaylo *et al.*, 2010; Wurst, 2010). Much research has been done on the use of earthworms as bio-indicators of the extent of contamination and toxicity of contaminated soil (Spurgeon *et al.*, 2005; Römbke *et al.*, 2006; Nahmani *et al.*, 2007; Brulle *et al.*, 2010). Although this is related to their potential use for remediation, it is not strictly an ecosystem service; as such it is not reviewed here.

A limited number of laboratory experiments have been performed on soil amended with organic chemicals and a range of earthworms. These studies have generally used soil amended with polychlorinated biphenols (Singer *et al.*, 2001; Kelsey *et al.*, 2011), petroleum hydrocarbons (Schaefer *et al.*, 2005; Schaefer & Filser, 2007) or polyaromatic hydrocarbons (PAHs) (Ma *et al.*, 1995; 1998; Eijsackers *et al.*, 2001; Contreras-Ramos *et al.*, 2008; 2009). Soil samples are amended with the contaminant and then incubated with earthworms. After a fixed period of time the concentrations of contaminant remaining in earthworm-present and earthworm-absent treatments are compared. Studies usually use either epigeic or anecic earthworms with only two authors using an endogeic earthworm (Schaefer *et al.*, 2005; Schaefer & Filser, 2007; Kelsey *et al.*, 2011). In general, earthworms accelerate the degradation of organic compounds, although the mechanism by which this is achieved is not entirely clear. However, it seems likely that this is a combination of increased aeration of the soil, stimulation of the microbial population, which in turn degrades the contaminants, and metabolism of the contaminants by the earthworms themselves. The use of different organic compounds and concentrations, earthworm species and soil types makes generalizations difficult, but in the above studies the presence of earthworms resulted in mean increases in organic compound degradation by about 30%.

The impact of earthworms on metal availability and mobility in soil, and following from this the potential use of earthworms to remediate metal contaminated sites was extensively reviewed recently (Sizmur & Hodson, 2009). The majority of studies showed that plant biomass, extractable metals, pore-water concentrations and metal uptake by plants are increased by earthworm activity. This holds for both amended and contaminated soil and studies that use epigeic, anecic and endogeic earthworm species (Abdul Rida, 1996; Ma *et al.*, 2003, 2006; Wen *et al.*, 2004; Cheng *et al.*, 2005; Liu *et al.*, 2005; Yu *et al.*, 2005; Wang *et al.*, 2006; Dandan *et al.*, 2007; Ruiz *et al.*, 2011; Sizmur *et al.*, 2011a, 2011b; Jusselme *et al.*, 2012). These studies have been done in the laboratory or in outdoor mesocosms, and involve incubating earthworms in either metal-amended or contaminated soil and with growing plants. The above studies indicate increases in metal concentration in plant tissues of up to 410%; the mean maximum increase was 87% but with a standard deviation of 127% indicating the large variability in the results. Earthworm activity almost always increases plant uptake of metals. Use of different species of both earthworms and plants, different metals and different types of soil makes it difficult to quantify the increase in metal uptake caused by earthworms in a meaningful way. Sizmur & Hodson (2009) concluded that, of the possible explanations for enhanced metal mobility and uptake, there were insufficient data to determine whether this is results from stimulation of bacterial populations, change in soil pH, alteration of the dissolved organic carbon content of soil or changes in metal speciation. The studies suggest a modification of the organic matter in soil and soil pH are the most likely cause (Sizmur *et al.*, 2011c).

For both inorganic and organic contaminants, studies with endogeic earthworms are in the minority. This probably reflects the difficulties in the laboratory-based culture of earthworms that fill this ecological niche (nevertheless see Lowe & Butt, 2005). Given that any commercial remedial technique would require large numbers of earthworms, it is probably advisable for studies to continue to concentrate on those epigeic and anecic earthworms that are easier to cultivate and preserve. The most obvious need is to move from small-scale laboratory experiments to large mesocosm-scale and then field-scale experiments.

## Primary production

As earthworms are the most abundant biomass in most terrestrial ecosystems (Lavelle & Spain, 2001), it is likely that plants have co-evolved with them, with adaptations to the modifications induced by earthworms in soil. A beneficial effect of earthworms on plant growth was recognized more than a century ago (Darwin, 1881). Consequently, the effect of earthworms on primary production has been studied extensively in various kinds of laboratory, greenhouse and field studies (Brown et al, 1999), and some experiments have been monitored for several years (Giri, 1995; Blanchart *et al.*, 1997). However, knowledge of the effects of earthworms on plant growth is biased; most studies investigate crop plants, particularly cereals and pastures. Little is known about plant species in more natural communities and most studies have investigated European earthworms (Lumbricidae) (Scheu, 2003). We can but give a brief overview here of some of the vast literature currently available on this topic (Lee, 1985; Edwards & Bohlen, 1996; Lavelle & Spain, 2001; Edwards, 2004).

Brown *et al*. (1999) reviewed 246 experiments performed in tropical countries. Total primary production was improved on average by 63% with positive results obtained in 75% of cases. Above- and below-ground biomass and grain production showed different degrees of improvement. Above-ground production was increased in 75% of the experiments with a mean increase of 56%. Below-ground biomass showed a smaller mean increase of 66%; increases were observed in 59% of the experiments. Grain biomass increased in 72% of the experiments with a mean increase of 36%. In a second review of over 67 experiments in temperate countries, Scheu (2003) showed that above-ground production was increased by the presence of earthworms in 79% of cases, whereas it was reduced in 9%. Some 30 of the studies included data only on below-ground biomass, but of these earthworms resulted in a significant increase in biomass in 50% of the experiments and a decrease in 38% of them. Therefore, it appears that above-ground biomass production generally increases in the presence of earthworms, whereas below-ground shows contrasting responses. Up to a maximum extent, plant production appears to increase with earthworm density, however, the precise relationship between productivity and earthworm density is not clear. In some studies the two appear to be linearly correlated, thus pasture production increased linearly with increasing earthworm density (*Allolobophora caliginosa,* Savigny., *A. longa* Ude and *A. trapezoid* Dugés); each was introduced at 114, 214, 429 and 643 earthworms per $m^2$) (Baker *et al.*, 1999). Other studies, however, show that the positive effect of earthworms can decrease above a given threshold. For example, in a study by Chan *et al*. (2004) the largest dry matter production in pasture enriched with lime was detected in the low density *A. longa* treatment (212 per $m^2$), which was 49% greater than in the control, and not in the high density treatment (424 per $m^2$) (Chan *et al.*, 2004). Brown et *al.* (1999) report that the relationship between earthworm density and the increase in plant production is curvilinear, possibly possibly because of too large an earthworm density relative to the soil's carrying capacity. Moreover, it has been observed that earthworm activity is not correlated with plant production (Callaham *et al.*, 2001). Undoubtedly, the complex effect of earthworms on primary production is through the relationship between earthworms and plants, as plant diversity and production involve a feedback on earthworm diversity and abundance and *vice versa* (Brussaard, 1999; Kukkonen *et al.*, 2004).

In addition to their impact on biomass production several studies have investigated the impact of earthworms on the composition of that biomass, but this is relatively neglected in the literature. Baker *et al*. (1997) showed that *A. trapezoides* increased the N content of wheat grain whereas *A. rosea* Savigny did not; neither species influenced clover N content (Baker *et al.*, 1997). However, in a follow-up study although *A. trapezoides* and *A. rosea* increased the yield of oats (*Avena fatua* L.) and lupins (*Lupinus angustifolius* L.) the concentration of N in the straw and grain was not affected. The presence of *L. terrestris*.can increase the N concentration in the tissues of both grasses (*Phleum pretense* L. *Dactylis glomerata* L. and *Lolium* perenne L.) and legumes (*Trifolium pretense* L., *T. repens* L. and *Medicago varia* L. Martyn). When plant biomass was taken into account, however, earthworms affected N uptake in the grasses only (Eisenhauer & Scheu, 2008). Whilst the reasons for these results are not clear, they could realte to differences in the feeding activity of the earthworms and consequent release of nutrients. Another mechanism could involve the low molecular size fraction of humic substances produced by earthworms, which are responsible for an over-expression of specific genes in plant roots. These genes encode two putative maize nitrate transporters (ZmNrt2.1 and ZmNrt1.1) and two maize H+-ATPase isoforms (Mha1 and Mha2); as a consequence, the uptake of nitrate by roots is higher and its accumulation in leaves greater than in a control plant grown without humic substances (Quaggiotti *et al.,* 2004).

A less direct impact of earthworms on primary productivity is through the use of compost made by earthworms (vermicompos: Figure 1). Many studies report that vermicompost has a greater positive effect on plant growth than other compost (Phuong *et al.*, 2011). Much literature is dedicated to the impact of vermicompost on plant growth. Results suggest that a 20 to 40% volume of vermicompost in pots results in maximal increases in plant production (Atiyeh *et al.*, 2000; Arancon & Edwards, 2011). However, the reasons for the reported improved performance of vermicompost over other composts remain unclear.

Brown *et al*. (2004) identified several factors involved in the impact of earthworms on primary production. The major factor responsible for 43% of the variation in plant response was the type of soil, especially its texture and carbon content. Earthworms produced the largest increase in plant production in sandy soil, with a slightly acid pH (Brown *et al.*, 2004; Laossi *et al.*, 2010). Plant functional group was also an important driver: earthworms induced a larger gain in production in perennial species (especially trees) than in annual species, whereas legumes were sometimes negatively affected by earthworm presence (Brown *et al.*, 1999; 2004). Earthworm species, their survival and weight loss or gain, the presence of organic matter input, duration of experiment and experimental set up (laboratory or field) were responsible for smaller variations in the size of effect.

As far as ecological processes are concerned, five mechanisms are potentially responsible for the positive effect of earthworms observed on plant production (Scheu, 2003; Brown *et al.*, 2004): (i) increased mineralization of soil organic matter, which increases nutrient availability (Barois *et al.*, 1987; Knight *et al.*, 1989; Subler *et al.*, 1998; see also Nutrient cycling section); (ii) modification of soil porosity and aggregation, which induces changes in water and oxygen availability to plants (Doube *et al.*, 1997; Blanchart *et al.*, 1999; Shipitalo & Le Bayon, 2004; see also Soil structural maintenance and Water regulation sections); (iii) bio-control of pests and parasites (Yeates, 1981; Senapati, 1992; Stephens *et* *al.*, 1994; Clapperton *et al.*, 2001); (iv) production of plant growth regulators through the stimulation of microbial activity (Muscolo *et al.*, 1998; Canellas *et al.*, 2002; Quaggiotti *et al.*, 2004) and (v) stimulation of symbionts (Reddell & Spain, 1991; Gange, 1993; Pedersen & Hendriksen, 1993). Recent papers that attempt to evaluate the relative importance of these five mechanisms in controlled environmental conditions showed that earthworms can (i) induce an increase in plant production even in a soil supplied with an excess of mineral nitrogen (Blouin *et al.*, 2006; Laossi *et al.*, 2009a; Arancon & Edwards, 2011), (ii) produce a positive effect on plant production in a well-watered treatment and induce a negative effect with a water deficit because of modifications in soil structure that reduce the amount of water (Blouin *et al.*, 2007) and (iii) induce a positive effect by increasing plant tolerance to parasitic nematodes (Blouin *et al.*, 2005). Recently, several studies have supported hypotheses (iv) and (v). Signal molecules can be responsible for positive or negative effects on plant growth, depending on plant species; an *Arabidopsis thaliana* L. mutant for auxin transport had an altered phenotype which was reverted in the presence of earthworms, suggesting that earthworms were producing auxin-like compounds; a transcriptome analysis showed that hormone signalling pathways were modified in the presence of earthworms (Puga-Freitas *et al.*, in press). It is likely that such plant growth regulators produced in the presence of earthworms were made by microorganisms, as suggested by a 46% increase in indole acetic acid production by cultivable bacteria in the presence of earthworms (Puga-Freitas *et al.*, 2012). At the community level, earthworms have an impact on competition between plant species (Laossi *et al.*, 2009b; 2011). The success of newcomers in plant communities is also influenced by earthworms (Wurst *et al.*, 2011). This effect of earthworms on plant communities should be taken into account better in restoration ecology (Butt, 2008).

Given that the positive effect of earthworms on primary production has been established empirically, research could focus on three distinct directions. Firstly, it could determine the reasons why some field inoculations lead to stable earthworm populations and others do not (Martin & Stockdill, 1976; Brun *et al.*, 1991; Butt *et al.*, 1995). This could then ensure a better probability of success in practical applications. Secondly, a deeper understanding of the mechanisms involved in the effect of earthworms on primary production is required in order to predict situations where earthworms will have positive, null or negative effects. Earthworms affect different plant species differently (Eisenhauer *et al.*, 2009; Laossi *et al.*, 2009b; Wurst *et al.*, 2011) because of the different sensitivity of each species to the combination of mechanisms described above. Thus if earthworms are to be used to boost primary productivity or, for example, in restoration ecology, the mechanisms involved in boosting productivity must be fully understood or plant diversity or differential productivity might be affected in ways other than those desired. Finally, research could assess the economic viability of earthworm introduction technologies at the broad scale by agronomists and economists. Some research in this direction has been attempted (Stockdill, 1982), but such attempts are rare.

## Cultural services

Earthworms provide a series of cultural services. Darwin (1881) observed that earthworms "protect and preserve for an indefinitely long period every object, not liable to decay, which is dropped on the surface of the land, by burying it beneath their castings". Some authors (Wood & Johnson, 1978; Stein, 1983; Armour-Chelu & Andrews, 1994; Texier, 2000) have brought attention to the importance of earthworm activities in protecting archaeological remains. Most artifact burial estimates have been comparable to those of Darwin's of 0.35 cm per year (Wood & Johnson, 1978), or slightly more (0.9–1.0 cm per year; Yeates & Vandermeulen, 1995).

Earthworms are good tools for environmental education. Appelhof *et al*. (1993) argued that earthworms have been converting organic residues to a re-usable form for 300 million years. Earthworms are thus a good pedagogic tool for teaching people about the recycling of organic matter (see Nutrient cycling section). A worm bin in a classroom or in a house demonstrates to children and adults that recycling organic waste furnishes a rich and free material that can support plant growth in a few months. In addition, earthworms provide bait for fishing (a recreational service).

## Use of earthworms to manage ecosystem services

### *General considerations*

Before using earthworms in ecosystem management, managers have to consider the following constraints: external ones imposed by the socio-economic system, internal ones imposed by the physical and biological properties of the ecosystem, and those linked with the multi-functional character of ecosystems. When deciding to manage ecosystem services with earthworms, the socio-economic context and landscape potential have to be taken into account before choosing one of the diverse technical options described in Figure 1. For example, the abundance of earthworms in nearby areas needs to be known before planning the re-colonization of an area devoid of earthworms. When a strategy to add organic matter is planned, socio-economic analyses should be undertaken to determine whether it has to be imported from other areas, to confirm that the financial and carbon costs for transport are not too great, and to determine whether there will be competition with another sector of activity such as agriculture, forestry or industry. Tools such as life-cycle analysis (Asiedu & Gu, 1998) or the analysis of territorial metabolism (Wolman, 1965; Kennedy *et al.*, 2007), developed in industrial ecology, could help to answer these questions.

Even when sociological and economic contexts are favourable to earthworm management, constraints that are internal to ecosystem functioning have to be considered, and may be the reason for the choice between the different technical approaches described in Figure 1. In anthropogenic ecosystems, where human intervention is important, the management system is often strongly constrained, the financial budget is important and the risk taken has to be minimized. In these situations, 'high-cost' approaches with engineered products (Figure 1) are probably the most relevant. As far as earthworms are concerned, the spreading of vermicompost may be advised. Conversely, some ecological systems have been strongly degraded by human activity (such as mining or gravel extraction). In these cases, where the risk taken can be relatively large, 'middle-cost' approaches may be recommended, for example through micro-ecosystem transplantation. When ecosystems are essentially unmanaged and are close to 'natural' functioning, invasions of exogenous species may need to be monitored or stopped early; 'low-cost' approaches based on ecosystem self-organization can be recommended.

When the intention is to manage a specific ecosystem service, it is important to consider the consequences of the planned management practices on other ecosystem services. First, some ecosystem services listed above are strongly interdependent. For example, earthworm inoculation to improve soil structure with the aim to reduce soil erosion will have consequences on water retention, and thus on primary production. The resulting effect on water infiltration and primary production will depend on the ecological context. For example, in flooded areas, stronger aggregation with compacting earthworms can reduce water storage capacity of the soil and increase drainage, which could be beneficial for plant growth and primary production. Conversely, in dry areas a reduction in water storage capacity will be negative for primary production. Second, ecosystems are multi-functional by nature. If one ecosystem service is optimized at the expense of others, it places the provision of the other services at risk. To integrate the constraints imposed better by the multi-functionality of ecosystems, further research is required to understand the interaction between land-use, different earthworm species and ecological processes more precisely.

*Two case studies*

The use of earthworm inoculations in Australia illustrates some of the considerations that need to be given to the management of ecosystem services through the addition of earthworms. Agricultural soils in southern Australia support a mixture of native species (especially Megascolecidae) and exotic species (mostly European Lumbricidae) (Baker, 2004) (Figure 5). The balance between these two groups varies greatly, probably driven by several factors such as dispersal by exotic species, level of habitat disturbance by man, distance from native vegetation, physico-chemical traits of the site, competition between species and so on. The agricultural and environmental benefits that common exotic species (such as *A. caliginosa*, *A. trapezoides*, *A. rosea*) can produce, such as improved soil structure, fertility, plant production and quality, root penetration, water infiltration, burial of lime to offset soil acidity, burial of organic matter, root disease suppression for example have been demonstrated (see references in Baker, 2004). Much less is known in this respect about native species (Friend & Chan, 1995; Baker *et al.*, 1996; Baker *et al.*, 2003), but thus far they have not proved to be as beneficial as the exotic species. There would seem to be much merit in managing the exotic species to optimize the benefits they can provide to agriculture, and even in further spreading them to locations they have yet to reach. However, what are the down-sides, or environmental risks such as invasion of pristine habitats, or competition with native biota including other soil fauna besides earthworms, in doing so? These are topics we know little about; in fact we have little knowledge of the ecology and functional roles of the native Australian megacolecids in general, although they seem to be numerous and diverse in some native systems. We will need to strike a balance in these matters. Exotic species are already present in the landscape, widespread (but patchy in abundance and very probably still expanding) and of course impossible to eradicate should we need to: do we regard the exotic species now as a true resource?

These considerations become more forceful when considering introductions of the European *Aporrectodea longa* from Tasmania (where it is often very abundant) to mainland Australia (where anecic species, such as *A. longa*, are very rare in agricultural soil). In the heavy rainfall regions of mainland Australia, where *A. longa* is most likely to establish if given the chance, it could bring major benefits to agricultural land through its deep burrowing and thus improving water infiltration and root penetration to depth. These effects would be likely to enhance, for example, the retention of nutrients on sloping land rather than their loss into water-ways. Thus, there could be both production and conservation benefits. However, the benefits would only be accrued over many years, given the basic ecology of this species (relatively poor reproductive rate and dispersal ability). There is thus far no evidence that *A. longa* will invade native ecosystems (Dalby *et al.*, 1998), but the evidence for this is still quite weak. We need to be aware of the impacts that exotic earthworms, such as *Lumbricus terrestris*, *L. rubellus* and *Amynthas hilgendorfi*, Michaelsen, are currently having on plant and animal communities, leaf litter layers and soil biogeochemical processes in North America (Bohlen *et al.*, 2004; Hale *et al.*, 2005; 2006; 2008; Greiner *et al.*, 2012; Holdsworth *et al.*, 2012; Loss *et al.*, 2012). We should also note the probable result of the careless disposal of fish bait (a recreational ecosystem service in itself provided by earthworms) has made to the spread of invasive species such as *L. terrestris* into native ecosystems in North America (Callaham *et al.*, 2006; Keller *et al.*, 2007; Hendrix *et al.*, 2008; Kilian *et al.*, 2012).

A good example of how the management of soil function and ecosystem processes by earthworm introduction is a long-term process, dependent on not just inoculation but also on land management, comes from an introduction of *L. terrestris* to a clay-rich, sub-drained field in SW Finland. The introduction was done mainly to increase soil water permeability, which in the prevailing conditions is enhanced by *L. terrestris* burrows particularly those in contact with sub-drains (Figure 3) (Nuutinen & Butt, 2003; Shipitalo *et al.*, 2004). The *L. terrestris* were entirely absent from the study site previously, but present in many nearby fields. In 1996 *L. terrestris* were inoculated into the field and its margins using the EIU-technique (Nuutinen *et al.*, 2006) (Figure 2). Monitoring of the experiment in 1998 and 2003 showed that the inoculated *L. terrestris* became established at the field margins, but not within the field to any significant degree (Nuutinen *et al.*, 2006). In 2008, however, following a seven year period as set-aside grass middens were observed inside the field indicating locally strong *L. terrestris* activity. Field sampling in 2009 indicated that although populations were still greatest around field margins, *L. terrestris* had begun to colonize the now cultivated field area at an approximate rate of 4.6 m per year (Nuutinen *et al.*, 2011). The results demonstrated the importance of tillage and drainage management for colonization: it was particularly marked above the sub-drain lines and clearly greater in no-till areas compared with the ploughed parts of the field. It is evident from the experiment that the field margins were decisive bridgeheads for population establishment and that they later acted as source areas for colonization of the field.

## Gaps in knowledge and opportunities for future research

We identify avenues of further research that would help to advance our understanding of the use of earthworms to modify soil function and provide ecosystem services in the sections above. Some more general comments can also be made on this subject. Although earthworms have been studied for many years there are still major gaps in our understanding of earthworm biology and behaviour that hinder their use in the management of soil functions and ecosystem services. However, new tools and techniques are being developed to overcome the difficulties associated with the study of organisms in the solid and opaque environment that is soil (Butt & Grigoropoulou, 2010). Taxonomic studies continue to reveal that what were considered species are in fact assemblages of several taxa (Iglesias Briones *et al.*, 2009; Dupont *et al.*, 2011), or that supra-family taxa are para- or poly-phyletic (James & Davidson, 2012). These continued discoveries mean that, despite studies on earthworm biological traits (Bouché, 1972; 1977) and life cycle characteristics such as birth and survival rates, and reproduction rates (Lowe & Butt, 2002), we still do not have sufficient knowledge to choose the best earthworm species adapted to specific management contexts. A lack of knowledge on how earthworms disperse across the environment is also a major impediment to the development of earthworm management for ecosystem services provision. Understanding passive dispersal for example through human activities such as fishing, is vital to understand invasions of North-European earthworms in North-American soil (Hale, 2008). However, understanding active dispersal (Mathieu *et al.*, 2010) is necessary to optimize inoculation methods, for example to define an inoculation patch size large enough to favour rapid colonization of a field and to determine the time frame necessary for ecosystem changes to be brought about. Databases of earhworm traits, similar to the ones developed for plants (Kuhn *et al.*, 2004; Kleyer *et al.*, 2008) or benthic macrofauna (Renaud *et al.*, 2009), will help to overcome these obstacles.

Since ecosystems are by definition systems where many positive and negative feedbacks can occur, it is difficult to make simple predictions about the consequences of changing the size of the population of one organism. The preferential feeding of earthworms and the fact that earthworm gut conditions favour some microfauna over others means that variations in earthworm abundance can modify the structure of other soil organism communities (Loranger *et al.*, 1998; Bernard *et al.*, 2012). In addition, earthworm abundance affects plant pests such as aphids possibly because of effects on food quality (Scheu *et al.*, 1999; Wurst & Jones, 2003) as well as plant communities (Eisenhauer & Scheu, 2008; Eisenhauer *et al.*, 2009; Laossi *et al.*, 2009b; 2011; Wurst *et al.*, 2011). As such, more research is required into the trade-offs between the merits and risks of earthworm introduction into  fields (Baker *et al.*, 2006) and the interactions between earthworms, other soil organisms and plants.

We need more robust data from earthworm studies regarding soil characteristics, vegetation types, climate data, earthworm identification to species level and the presence of other soil microfauna that should be recorded as a routine matter. This would provide opportunities for meta-analyses so that where enough data have been collected for diverse environments, they could become a useful tool for taking into account better context specificity and management objectives when manipulating earthworms (Gurevitch *et al.*, 2001; Stewart, 2010).

Well-designed laboratory experiments and field experiments, preferably carried out over several years, coupling basic biological and soil science measurements still have much to offer in terms of filling our gaps in knowledge. In addition, molecular and isotopic techniques are increasingly being used to elucidate how earthworms affect the environment. The coupling of isotope labelling with molecular techniques is beginning to be used to identify microbial communities involved in labelled-source degradation. It opens new possibilities for understanding the role of earthworms in microbial community structure and function. Indeed, PLFA-SIP (stable isotope probing) has been used to identify which microorganisms and soil microfauna present in earthworm galleries were responsible from organic matter degradation (Stromberger *et al.*, 2012). The coupling between DNA-SIP and pyrosequencing showed that stimulation of both the mineralization of wheat residues and the priming effect can be linked to the stimulation of several groups especially belonging to the *Bacteroidetes* phylum (Bernard *et al.*, 2012). The RNA-SIP coupled with the sequencing of the 16S ribosomal RNA has been used to study the diversity of active atrazine-degrading bacteria in relation to atrazine degradation and to explore the impact of earthworm-soil engineering with respect to this relationship (Monard *et al.*, 2011).

X-ray tomography is being used increasingly to understand earthworm burrows and water movement although its application is still restricted to a few research groups (Joschko *et al.*, 1991; Capowiez *et al.*, 1998; Jegou *et al.*, 1999; Jegou *et al.*, 2001; Bastardie *et al.*, 2003b) (Figure 4). In addition, researchers have begun to use radio-labelling of earthworms to determine their movement in soil, *in situ* (Capowiez *et al.*, 2001; Bastardie *et al.*, 2003a) (Figure 6).

Earthworm tagging is a technique that holds great potential to follow earthworm movements inside the soil. Visual implant elastomer (VIE) (Northwest Marine Technology, Accessed October 2012) is injected into the muscle tissue of the earthworms enabling identification of individual earthworms and raised the possibility of tracking migration rates of individual earthworms either in the field or laboratory experiments and of assessing survival rates (Figure 7). Studies to date have shown that the coloured tag can last in earthworms without any impact on earthworm mortality or reproduction for over two years, although after this time it becomes harder to identify the tag (Butt *et al.*, 2009).

Earthworms undoubtedly contribute significantly to many of the ecosystem services provided by the soil, and whilst much is known about these processes, further research along the lines discussed above will lead to a greater understanding of the role of earthworms in ecosystem services provision and, ultimately, an increased ability to manage such services through, amongst other things, manipulation of their abundances and diversity.

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CAPTIONS TO FIGURES

**Figure 1** The scope of the review encompasses different approaches that allow the effect of earthworms on ecosystem services to be studied. We classify these approaches according to a gradient from self-organized processes to the human application of products engineered by earthworms. Passive versus active bio-stimulation (Brun *et al.*, 1987) can be reported on this gradient, as well as several management techniques.

**Figure 2** (a) Two litre earthworm inoculation units (EIUs) ready for inoculation into an organically-enriched landfill cap in the south of England (from Butt *et al.*, 1995) and (b) Soil inoculation of a 4 litre Earthworm Inoculation Unit (EIU) at a landfill cap in the south of England by Kevin Butt.

**Figure 3** *Lumbricus terrestris* burrow ending on tile surface. At its end the burrow bends towards the tile. The plough layer has been removed and the cast starts from a depth of approximately 0.25 m. The tile is at a depth of 1.0 m. (from Nuutinen & Butt, 2003)

**Figure 4** (a) Burrow network created by earthworms, anecic species and endogeic species. Observations in 3-D obtained by X-Ray tomography and (b) Reconstruction of the interior of an earthworm burrow using medical software and X-Ray tomography (photographs by G. Pérès).

**Figure 5** Average abundance of exotic (open bars) and native (closed bars) earthworms in pastures in two regions of Australia: (a) the Mount Lofty Ranges, South Australia (113 sites) and (b) the Southern Tablelands of New South Wales (104 sites).  Sites are arranged in order from those with the least earthworms to those with the most (graphs from Baker, 2004).

**Figure 6** Photograph (a) and diagram (b) of X-ray tomography unit used for determining burrow topography and earthworm movement, and (c) tracking of earthworm movement using radio-labelled earthworms. I is for *L terrestris*. and II for *Nicodrilus giardia*. The two circles represent the top and bottom of the core. Each letter labels the beginning of a digging event in alphabetical order. The type of line indicates the number of crossings per segment (solid line: > 80; dashed line: 40 – 70; dotted line: 0 – 40) (from Bastardie et al., 2003b).

**Figure 7** *Allolobophora chlorotica* tagged with blue coloured Visual Implant Elastomer.

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7