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

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

26   **Summary**

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28   Biodiversity is responsible for the provision of many ecosystem services; human well-being

29   is based on these services, and consequently on biodiversity. In soil, earthworms represent the

30   largest component of the animal biomass and are commonly termed 'ecosystem engineers'.

31   This review considers the contribution of earthworms to ecosystem services through

32   pedogenesis, development of soil structure, water regulation, nutrient cycling, primary

33   production, climate regulation, pollution remediation and cultural services. Although there

34   has been much research into the role of earthworms in soil ecology, this review demonstrates

35   significant gaps in our knowledge related in particular to difficulties in identifying the effects

36   of species, land-use and climate. The review aims to assist people involved in all aspects of

37   land management including conservation, agriculture, mining or other industries to obtain a

38   broad knowledge of earthworms and ecosystem services.

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41   **Introduction**

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43   Biodiversity, the diversity of genes, organisms and ecosystems, has been clearly recognized

44   in the political agenda since the Convention on Biological Diversity in 1992. The cost of

45   inaction with regard to the loss of biodiversity is now equivalent to 50 billion € per year (1%

46   of world gross domestic product) and could reach 14 000 billion € in 2050 (7% of world

47   gross domestic product) (Braat & ten Brink, 2008). In parallel, ecosystem services have also

48   become a central political issue. Ecosystem services are the benefits provided by ecosystems

49   to humankind as well as other species (Millennium Ecosystem Assessment, 2005). A strong

50   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,

76 2001). Earthworms are typical ecosystem engineers as they have a large impact on soil

77 structure, which is not necessarily associated with trophic relationships. For example, the

78 tropical earthworm *Reginaldia omodeoi*, Sims formerly known as *Millsonia anomala*, can

79 ingest up to 30 times its own biomass of soil per day, but very little of the ingested organic

80 matter is then assimilated (8%). Furthermore, little of the assimilated carbon is used in

81 biomass production (6%); the remainder is respired (94%) during activity and physical

82 modifications of the soil (Lamotte & Bourlière, 1978; Lavelle, 1978). In temperate

83 ecosystems, earthworms also ingest large amounts of material (2 to 15% of organic matter

84 inputs) (Whalen & Parmelee, 2000) and expend much energy in their modification of the soil

85 (74 to 91% of assimilated carbon is respired) (Petersen & Luxton, 1982). Earthworms have

86 thus been recognized as typical ecosystem engineers (Jones *et al.*, 1994; Lavelle *et al.*, 1997),

87 and represent an excellent potential partner for humans in managing ecosystem services

88 (Byers *et al.*, 2006). Earthworms have been divided into three primary ecological categories

89 that may contribute differently to ecosystem processes and thus ecosystem services. Epigeic

90 species live in the litter and produce casts at the soil surface that affects its roughness and the

91 distribution of macro-pores. Anecic species live in vertical burrows, used as shelters, and

92 connected with the soil surface. Endogeic species make horizontal or randomly oriented

93 burrows in the mineral soil, considered as temporary structures because they are rarely re-

94 used (Bouché, 1977; Lee, 1985).

95   Here we present a synthesis of the impact of earthworms on ecosystem services,

96 initiated in a workshop held in Grenoble (France) in 2010.

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99 **Scope of review**

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101 Previous studies have emphasized the importance of soil (Dominati *et al.*, 2010), soil biota

102 (Barrios, 2007; Brussaard, 2012) or more specifically soil invertebrates (Lavelle *et al.*, 2006)

103 in the provision of ecosystem services. However, these studies have not focused on

104 earthworms. Our review considers specifically how earthworms modify ecosystem functions

105 and services. An exhaustive review of all the relevant research would require an entire book;

106 therefore, we summarize the different soil functions and ecosystem services that earthworms

107 contribute to, and methods of exploiting these in soil management. Within the terms of the

108 Millenium Ecosystem Assessment (2005), earthworms play the role of catalyst for two major

109 'supporting services', namely soil formation (Darwin, 1881) and nutrient cycling (Edwards,

110 2004), which are prerequisites to other services. Through their interactions with plants,

111 earthworms are involved in the provision of food, wood and fibre. They also influence major

112 services directly such as climate and flood regulation, water purification and can play a role

113 in remediation and restoration. Earthworms also provide cultural services, for example as

114 fishing bait and in burying archaeological artifacts. The services are reviewed in turn and

115 where relevant divided into different ecosystem processes (Dominati *et al.*, 2010). Where

116 possible, for each service we summarize how earthworms are involved in the service with

117 both a qualitative assessment such as positive, null or negative effects of earthworms and a

118 quantitative estimate of the impact of earthworms on a service. Of necessity these estimates

119 draw on a wide range of data from different ecological categories, land-use, management

120 practices and so on.

121 We identify two extremes in approach to consider the impacts of earthworms on

122 ecosystem services and soil function (Figure 1). At one extreme, the approach is based

123 completely on ecosystem self-organization. In 'conservation', the consequences of preserving

124 native earthworm species, compared with situations where they have disappeared, can

125 indicate the role of earthworms in ecosystem functioning. At the other extreme, the approach

126 can be based completely on the use of products engineered by earthworms in semi-industrial

127 production systems. The 'spreading of earthworm-created products' such as vermicompost,

128 belongs to this category. Intermediate to these extremes are studies that deal with earthworm

129 inoculation in the field, for example using the Stockdill method (Stockdill, 1959; 1966;

130 Martin & Stockdill, 1976) and earthworm inoculation units (EIUs, see Figure 2) (Butt *et al.*,

131 1997), and changes in ecosystems where 'recolonization' by earthworms becomes possible,

132 as with changes in agricultural practice such as moving to no-till systems and changes in

133 pesticide use.

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136 **Soil formation**

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138 Soil formation is a long-term process determined partly by climatic conditions and the nature

139 of the parent material (Chesworth, 1992). It involves the breakdown of primary minerals and

140 the incorporation of organic matter. Darwin (1881) was among the first to include biota,

141 especially earthworms, in the list of factors responsible for soil formation through the

142 accumulation of earthworm casts and mixing processes. The potential role of earthworms in

143 soil development is recognized in the term 'vermiform soils' for soil that has at least 50% or

144 more of the A horizon and >25% of the B horizon volume consisting of earthworm- or

145 animal-derived structures (burrows and castings, faecal material). Initially, the term was

146 applied only to Mollisols, but has recently been extended to other soil classes; the relevance

147 of this concept is still being discussed, since faunal activity is observed in the profile of most

148 soil types (Pop, 1998).

149 The importance of earthworms in chemical weathering was first studied by Darwin

150 (1881) in an experiment where the red colour of a red-oxide sand disappeared after passing

151   through earthworm intestines, probably because of dissolution of the oxide by acidic enzymes

152   in the earthworm's digestive tract. However, since the work of Darwin relatively little

153   research has considered the role of earthworms in mineral weathering. Pop (1998) showed

154   that *Octodrilus* earthworm species in the Romanian Carpathians affect the clay mineralogy

155   and formation of illite in the soil, a process that takes hundreds of thousands of years in the

156   absence of biota. In laboratory experiments, Carpenter *et al*., (2007) showed that the epigeic

157   earthworm *Eisenia veneta*, accelerated the weathering of anorthite, biotite, smectite and

158   kaolinite; smectite was transformed to illite and kaolinite reacted to produce a new mineral

159   phase (Carpenter *et al.*, 2007). Whether it is the earthworms, microorganisms stimulated in

160   their gut (Brown, 1995) or a collective action of both organisms that are responsible for the

161   mineral weathering effect is still open to debate.

162   Compared with mineral weathering, the role of earthworms in humus formation has

163   been investigated more thoroughly. The darkening of soil mould is a slow process, which

164   involves primarily chemical reactions and microbial activity. This process, nevertheless, may

165   be accelerated by earthworms that prepare the soil and litter mixtures composed of

166   fragmented and macerated leaves and fine soil particles for microbial attack. It is well known

167   by vermicompost producers that humus can be obtained from organic matter within a few

168   months (Edwards *et al.*, 2011). One of the most important roles of earthworms in soil may be

169   their control of humification rates through feeding, burrowing and casting activities and

170   interactions with microorganisms (Dell'Agnola & Nardi, 1987; Ponge, 1991; Bernier, 1998).

171   This appears to be mainly by controlling C inputs into the soil through burial of litter and by

172   enhancing its decomposition rate, in regulating microbial activities in the drilosphere (the soil

173   immediately surrounding earthworm burrows) and casts, and protecting C in stable

174   aggregates such as their castings (Brown *et al.*, 2000).

175   The data in Feller *et al*. (2003) from various land-use types under temperate climate

176   conditions in Europe suggest that the amounts of soil brought to the surface by earthworms

177   annually as castings is about 40 t ha^{-1} year^{-1} (based on 19 studies) contributing about 0.4 cm

178   (based on 13 studies) of top-soil per year. Under a temperate climate, earthworms can thus

179   potentially move about 40 cm of soil to the surface each century, or four metres per

180   millennium! However, this is probably an over-estimate because some soil is likely to be

181   moved more than once.

182   In addition to contributing towards mineral weathering and the formation of humus,

183   earthworms bury organic matter from the surface, and equally bring soil particles from deep

184   soil horizons to the surface. The contribution of earthworms to the burial of surface litter

185   (leaves, twigs and so on) at some locations may reach 90–100% of the litter deposited

186   annually on the soil surface by the above-ground vegetation from either 'natural' vegetation

187   or crops (Raw, 1962; Knollenberg *et al.*, 1985), representing up to several tonnes per hectare

188   per year of organic material. Recent organic matter is buried into the soil, whereas soil from

189   depth is brought to the soil surface by the deposition of casts above-ground, particularly by

190   the anecic species. These surface casts are then responsible for an apparent downward

191   migration of stones in the soil profile. The rate of surface cast deposition depends on the

192   number of earthworms present and their burrowing depth, the climate, vegetation and soil

193   type, and the depth of the previously deposited soil. The combined effects of leaf burial into

194   the soil and production of surface casts (which also buries surface-deposited materials) place

195   earthworms as key factors in the formation of mull soil (Langmaid, 1964; Brethes *et al.*,

196   1995). However, in spite of the huge deposition of casts at the soil surface, most anecic and

197   endogeic earthworm species probably deposit their casts primarily below ground, which will

198   markedly affect bulk density and aggregation (see below).

199   Erosion is also important in the formation of soil and again earthworms have a

200   significant role in this process, in particular through the production of casts on soil surfaces.

201   For a slope of 9°26', Darwin (1881) estimated that about 1140 kg ha^{-1} year^{-1} of earthworm

202   cast material was removed. A similar estimate of 1120 kg ha^{-1} year^{-1} has since been observed

203   for a grazed pasture in New Zealand (Sharpley *et al.*, 1979). These values are similar in order

204   of magnitude to mass displacements in major river basins such as the Mississippi. The

205   contribution of casts to erosion appears to occur following their breakdown by the impact of

206   rain, rather than the transport of intact cast material (Le Bayon & Binet, 1999; 2001).

207   However, there is debate as to whether more or less erosion would occur in the absence of

208   casts. Some authors suggest that surface-deposited casts of anecic species may give resistance

209   to run-off, thereby reducing erosion, whereas others suggest that the erosion of cast material

210   leads to a net increase in erosion (Shipitalo & Protz, 1987). Over longer time-scales

211   (thousands of years or more), this phenomenon could lead to vast amounts of sediment

212   accumulation in alluvial soil or floodplains (Feller *et al.*, 2003). We should be able to

213   distinguish between a planet with life versus one without based on an assessment of mountain

214   height, steepness or curvature, the sinuosity of rivers, the extent of the landscape with a soil

215   mantle and slope-area characteristics (Dietrich & Perron, 2006), with earthworms and plants

216   as the major causes of these differences.

217   Studies over the lengthy time scales necessary to observe soil formation are very rare.

218   However, it is important to study the effect of earthworms on soil formation because it could

219   be of great interest for restoring degraded soils, disused stone or sand quarries, burnt areas or

220   strongly polluted sites. In addition, suggestions have increased that bioturbation and soil

221   formation may have had a major impact on evolution since the appearance of the metazoans

222   more than 500 M years ago. Therefore, considering the role of earthworms in soil formation

223   may provide insight into the evolution and functioning of marine and terrestrial ecosystems

224   (Dietrich & Perron, 2006; Kennedy *et al.*, 2006; Meysman *et al.*, 2006).

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227   **Soil structure**

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229   The arrangement of soil particles and associated pore spaces gives rise to soil structure across

230   a range of scales and is a function of interacting physical forces on water status, the actions of

231   larger soil biota such as plant roots or earthworms, and the presence of organic matter and

232   soil tillage in some agricultural systems (Oades, 1993; Milleret *et al.*, 2009a; 2009b).

233   Earthworms both compact and loosen soil. For example, *Reginaldia omodeoi*

234   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

235   studies (Lavelle *et al.*, 2004). Alegre *et al.* (1996) also observed a significant increase in bulk

236   density from 1.12 to 1.23 g cm^{-3} and a decrease in porosity from 58 to 53% in the presence of

237   *Pontoscolex corethrurus* Muller. In another study, Blanchart *et al.* (1997) demonstrated that

238   *R. omodeoi*, a compacting endogeic earthworm, decreased total soil porosity by 3%, whereas

239   Eudrilidae (species unidentified), small de-compacting endogeic earthworms, increased it by

240   21%. De-compacting earthworms destroyed macro-aggregates formed by compacting ones,

241   whereas compacting earthworms did the same with the casts of de-compacting ones. Such

242   variability regulates soil structure in a dynamic way (Blanchart *et al.*, 1997).

243   Studies such as the above suggest that compacting earthworms can increase soil bulk

244   density by 15%. In a 20-year study, the experimentally induced absence of earthworms in a

245   grass sward also increased soil bulk density (Clements *et al.*, 1991), which suggested that

246   earthworms can also decrease bulk density. The absence of earthworms also decreased total

247   soil porosity; in a treatment with no earthworms, fine (< 0.4mm) aggregates increased

248 compared with treatments where earthworms were present (Blanchart *et al.*, 1997). Finally,

249 in some tropical situations, long-term field experimentation (Blanchart *et al.*, 1999) has

250 revealed interacting processes between compacting (*R. omodeoi*) and de-compacting (small

251 eudrilid) species resulting in the maintenance of soil structure.

252   Earthworms also affect aggregate size distribution. For example, some compacting

253 earthworms, such as *R. omodeoi*, inoculated under yam or maize culture can increase the

254 proportion of aggregates >2 mm in diameter from 29.8 to 53.5% or from 24.6 to 42.2%,

255 respectively (Gilot-Villenave *et al.*, 1996; Gilot, 1997). Similar effects have been observed

256 after the inoculation of the peregrine, pantropical, endogeic species *P. corethrurus* under a

257 traditional cropping system in Peruvian Amazonia. After six successive crops, earthworms

258 had increased the proportion of aggregates (> 2 mm) from 25.4 to 31.2 %, at the expense of

259 smaller (< 0.5mm) aggregates, which decreased from 35.4 to 27.4% (Lavelle *et al.*, 2004). In

260 another experiment (Alegre *et al.*, 1996), the proportion of macro-aggregates (>10 mm)

261 increased from 25.1 to 32.7% in inoculated treatments, whereas the proportion of small

262 aggregates (< 2 mm) decreased from 33.2 to 26.1%, and no change was observed in the

263 intermediate (2–10 mm) category.

264   In general, positive effects of earthworms on soil structure have been widely

265 demonstrated. However, if earthworm use is proposed as part of a soil management scheme,

266 there is a need for sufficient and appropriate preliminary soil measurements, and then

267 monitoring at appropriate time-scales. The combination of compacting and de-compacting

268 species could also be vital for inoculation to achieve the required objectives in soil structural

269 improvement, given their different behaviours. Recent modelling to simulate the effects of

270 earthworms on soil structure (Barot *et al.*, 2007a; Blanchart *et al.*, 2009) has great merit and

271 is worthy of further development as these activities are a major ecosystem service.

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Water regulation

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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

298   improved strongly (+77%) when *Hyperiodrilus africanus*, Beddard, the peregrine African de-

299   compacting species was the only one present (Guéi *et al.*, 2012). In another study, however,

300   infiltration did not vary in response to earthworm inoculation, despite an increase in the area

301   of macro-pores observed at 10-cm depth (Lachnicht *et al.*, 1997).

302   The increase in infiltration rate related to earthworm burrows can decrease soil

303   erosion by 50% (Sharpley *et al.*, 1979; Shuster *et al.*, 2002). In the tropics, endogeic de-

304   compacting species increase soil porosity and water infiltration thereby reducing runoff.

305   However, the same species also produce small-sized and labile casts that favour surface

306   sealing and contribute to soil losses (Blanchart *et al.*, 1999). Compacting species can create

307   water stable macro-aggregates that decrease the effects of splash and runoff. Unfortunately,

308   these species also decrease water infiltration by increasing bulk density (Blanchart *et al.*,

309   1999). The rainfall regime is probably an important determinant of the overall outcome of

310   these opposing factors.

311   In a temperate climate, anecic casts can create surface roughness, which is reinforced

312   by organic matter residues that form 'middens' and decrease surface runoff (Le Bayon *et al.*,

313   2002). This result is mainly explained by the greater stability of the casts compared to those

314   in the soil. However, some results from the tropics have been contradictory to this, related to

315   the coalescence of casts (Chauvel *et al.*, 1999) or the creation of a surface crust (Shuster *et*

316   *al.*, 2000). These results seem to be influenced by the number of earthworm species and the

317   presence of organic matter (Blanchart *et al.*, 1997; Hallaire *et al.*, 2000).

318   The experimentally-induced absence of earthworms in a grass sward greatly reduced

319   soil moisture and infiltration rate (Clements *et al.*, 1991). Surface runoff during rain was

320   negatively correlated with *Lumbricus terrestris* L. dry weight (Spearman's *r* coefficient = −

321   0.68) in observations made in the field in Finland (Pitkanen & Nuutinen, 1998). In

322   experimental conditions with a 40% slope in Vietnam, the surface covered by a given amount

323 of run-off water was about 600 mm² with physicogenic aggregates covering 60% of the soil

324 surface, whereas it was about 150 mm² with biogenic aggregates of *Amynthas khami* (Jouquet

325 *et al.*, 2008), leading to a reduced runoff by 75%. In three different soil tillage treatments

326 where earthworm populations were either reduced, increased or remained un-manipulated,

327 anecic earthworm biomass was identified as an important independent variable in runoff and

328 erosion models, after plot slope, soil moisture content and rainfall intensity (Valckx *et al.*,

329 2010). Erosion rates decreased exponentially as a function of anecic earthworm biomass. Path

330 analysis by structural equation modelling revealed that anecic earthworm biomass in itself

331 contributed to a reduction in soil erosion. This study underlines the need to promote

332 appropriate soil ecosystem management by farmers to support populations of anecic

333 earthworm species (non-inversion tillage, direct drilling) (Valckx *et al.*, 2010).

334 Water storage can differ according to the earthworm species and climate conditions.

335 The increase in bulk density by endogeic compacting species was associated with a 7%

336 decrease in water storage capacity of the soil, which could be detrimental to plant growth in

337 water-deficit conditions (Blouin *et al.*, 2007). Conversely, in a temperate climate, ten years

338 after the introduction of earthworms, the water storage was 25% greater (Ehlers, 1975).

339 Water movement through burrows is complex because it depends on the

340 morphological characteristics of the burrows, which are strongly related to the ecological

341 group of earthworms that made them. Increases in burrow diameter or inter-connectivity and

342 tortuosity can enhance water infiltration and conductivity (Shipitalo & Butt, 1999; Bastardie

343 *et al.*, 2002), whereas increases in branching rate decrease water conductivity (Pérès, 2003).

344 Anecic earthworms can produce semi-permanent vertical burrows up to 1-m deep; efficiency

345 in drainage is likely to be increased, especially when these galleries are in contact with

346 drainage tiles (Figure 3) in agro-ecosystems (Nuutinen & Butt, 2003).

347   Water cannot drain effectively into earthworm burrows unless they are open at the soil

348   surface (Allaire-Leung *et al.*, 2000). This requires regular maintenance of the burrow opening

349   and suggests, by default, that burrows do not regulate water movement effectively all year

350   round. This is especially so during periods of earthworm inactivity, when soil is either not

351   moist or warm enough (Eggleton *et al.*, 2009; Nuutinen & Butt, 2009). Consequently, the

352   efficiency of burrows with respect to water drainage is likely to vary greatly according to the

353   date of the study; for example, earthworm effect on infiltration rate was null in a study

354   performed in July (Lachnicht *et al.*, 1997). Moreover, burrow efficiency depends on

355   earthworm species: thus *Lumbricus terrestris*, which does not create branched burrows

356   (Jegou *et al.*, 1999) should be more effective in promoting water infiltration than

357   *Aporrectodea giardi* Ribaucourt which creates a more branched burrow network.

358   To explain the effect of earthworms on water regulation better, progress is needed to

359   link physical structure with soil hydraulic properties. The behaviour of earthworms in soil

360   (Figure 4) needs to be specifically characterized if we want to model the resulting effect on

361   water fluxes and storage. The rainfall distribution through the year is also an important

362   variable in determining the effects of earthworms on hydraulic properties, which has not been

363   fully investigated to date.

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366   **Nutrient cycling**

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368   Earthworms are heterotrophic organisms that are involved in the degradation of organic

369   matter and molecules, mainly produced by plants but also by other heterotrophic organisms.

370   Earthworms accelerate organic matter degradation by increasing the available surface area of

371   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).

396   Mineral nitrogen released from earthworms can be important in relation to crop N

397   requirements. In a prairie grassland system, James (1991) calculated that over a year the

398   amount of mineral N present in casts was equivalent to approximately 10–12% of annual

399   plant N uptake compared to half of the input from precipitation. The amount of P in the casts,

400   however, was equivalent to 50% of annual uptake (James, 1991). A flux of 63 kg N ha^{-1} year^{-}

401   ^{1} through earthworms in a no-till agro-ecosystem was equivalent to 38% of the total N uptake

402   by the sorghum crop (Parmelee & Crossley, 1988). In another experiment, the N flux through

403   earthworms was equivalent to 16–30% of crop N uptake during 1994–1995 and 11–18% of

404   crop N uptake during 1995–1996, with the difference attributed to unfavourable climatic

405   conditions during the latter half of 1995 (Whalen & Parmelee, 2000). In a study in which

406   carbaryl pesticide was used to remove earthworms prior to re-inoculation of the soil with

407   *Aporrectodea caliginosa* and *Lumbricus terrestris*, soil mineral N was positively correlated

408   with earthworm density, and N-microbial biomass and N-concentration in total grain-N per

409   soybean plant also increased (Eriksen-Hamel & Whalen, 2007).

410   Earthworms also modify the N cycle in other ways. Their casts have the potential for

411   microbial nitrification and denitrification (Palmer *et al.*, 2005; Costello & Lamberti, 2008). In

412   Mediterranean soil, *Nicodrilus nocturnus* Evans (anecic) accelerated nitrification,

413   denitrification and other biological activities (Cecillon *et al.*, 2008). In addition, earthworms

414   create soil conditions that favour autotrophic nitrifiers as aeration improves (Zhu & Carreiro,

415   1999), whereas NH_4^+ oxidizing bacteria have been associated with earthworm burrow walls

416   (Parkin & Berry, 1999). Elevated nitrate concentrations of the drilosphere soil are consistent

417   with elevated nitrifying bacterial populations indicating autotrophic nitrification in the

418   presence of earthworms (Araujo *et al.*, 2004). Earthworms increase mineral N in soil, and

419   also readily exchangeable phosphorous (P) (Suarez *et al.*, 2004), potassium, calcium and

420   magnesium (Adejuyigbe *et al.*, 2006). They can also increase leaching of mineral N and P

421 (Dominguez *et al.*, 2004; Suarez *et al.*, 2004; Costello & Lamberti, 2008) because of their

422 effects on soil structure (see Soil structure and Water regulation sections).

423   The above experiments deal with the short-term dynamics of nutrients in casts, but the

424 longer-term dynamics have been less well studied. However, it has been shown with models

425 that the effects of earthworms on primary production through increased mineralization of

426 organic matter and thus nutrient release occur only if there is a concomitant reduction in

427 system outputs (by leaching for example), or an increase in system inputs (through nitrogen

428 fixation for example) (Barot *et al.*, 2007b). If there are no increases in inputs or decrease in

429 outputs, the positive effect of earthworms would only be transient: earthworms would

430 consume organic matter and decrease this resource, which would lead to a reduction in

431 earthworm populations, an abatement in organic matter mineralization and consequently a

432 decrease in the effect of earthworms on primary production (Barot *et al.*, 2007b). Thus

433 manipulation of earthworm populations to modify soil functions cannot be carried out in

434 isolation. Due attention must be given to the soil system as a whole.

435   The degradation of organic matter by earthworms is a process which can be used to deal

436 with the huge amount of organic matter waste derived from urban environments. Waste

437 disposal through the sewage system requires large amounts of water. For example, as much

438 as 36 litres of water is required to dispose of 500 grams of food (Appelhof *et al.*, 1993). This

439 water has then to be cleaned using both additional energy and chemicals. The burial of

440 organic wastes in landfills also presents problems. In addition, there may be societal issues

441 related to acceptance of landfill as a disposal route. Similarly, incineration as a waste disposal

442 method is often viewed with suspicion due to health scares that often involve dioxin

443 emissions, which result from poorly operated incinerators. Most importantly, waste disposal

444 methods may fail to recover the energy present in organic waste at a time when fossil energy

445 is becoming increasingly expensive. Organic wastes can be processed locally by

446 vermicomposting, which decreases the cost of transport to water treatment plants,

447 incinerators or landfills. However, the benefits of vermicomposting may be offset by the

448 large NOx emissions associated with vermicompost production (see later).

449   Short-term experiments have shown that earthworms have a stimulating effect on

450 nutrient turn-over. However, long-term experiments to evaluate the need for regular additions

451 of organic matter to maintain earthworm populations would be valuable. In agro-ecosystems,

452 the return of plant organic matter to the soil (Riley *et al.*, 2008) or mulch application to the

453 soil surface (Pelosi *et al.*, 2009) is beneficial to earthworms but long-term experiments to

454 compare multiple natural systems would help to provide a better understanding of their effect

455 on nutrient cycling.

456

457

458 **Climate regulation**

459

460 Earthworms enhance the incorporation of organic matter into soil and the formation of

461 macro-aggregates through their burrowing, consumption and egestion activities

462 (Guggenberger *et al.*, 1996; Blanchart *et al.*, 1997) (see earlier). This suggests a role in

463 carbon sequestration because storage of carbon in compact stable aggregates is an important

464 process by which soil accumulates carbon and prevents its rapid release in the form of

465 greenhouse gases (Lavelle *et al.*, 2006). However, the extrapolation of carbon sequestration

466 from the level of the soil aggregate to sequestration at the field level is not straightforward.

467   Earthworm invasions can be considered as poorly constrained experiments in which

468 areas without earthworms act as control plots. In mixed hardwood forests in New York state,

469 USA, organic matter per gram of soil was 36% less in plots where the organic horizon was

470 mixed by earthworms compared with plots kept free from earthworm invasion, and where no

471 marked change in the mineral horizon was noted (Burtelow *et al.*, 1998). Similarly,

472 earthworm invasion of mixed deciduous forest in Minnesota, USA, decreased soil organic

473 matter to a depth of 50 cm by an estimated 600 kg ha^{-1} year^{-1} (Alban & Berry, 1994).

474 Many more controlled studies suggest earthworm-induced C stabilization in soil

475 organic matter. Don *et al*. (2008), using mesocosms in extensively managed grassland in

476 Germany showed that anecic earthworms increased C stocks in the linings of their vertical

477 burrows by 310 g cm^{-2} at the Mehrstedt site and 270 g cm^{-2} at the Jena site as compared with

478 the background soil profile. The estimated sequestration rate at the Jena site was 22 g C m^{-2}

479 year^{-1}. By studying abandoned burrows, they showed a rapid mineralization of this C within

480 3–5 years, suggesting that anecic earthworm activity does not substantially increase soil C

481 stocks (Don *et al.*, 2008). When earthworms are inoculated into a field without an increase in

482 organic carbon inputs, they tend to decrease the percentage C as they use part of the C

483 resources for their activity. Losses of C contained in *P. corethrurus* casts resulting from

484 mineralization were observed in direct-seeding, mulch-based cropping systems in

485 Madagascar (Coq *et al.*, 2007). Similar results were obtained at Lamto (Côte d'Ivoire): after

486 four years of maize cultivation, percentage C decreased from 13.37 to 9.75 mg g^{-1} in the

487 control and to 9.64 mg g^{-1} in the inoculated treatment (Lavelle *et al.*, 2004). However, in the

488 presence of *R. omodeoi*, soil C mineralization decreased by 5% after three years under yam

489 production (Gilot, 1997). In temperate agro-ecosystems, endogeic species are considered to

490 contribute to the sequestration of C in soil by initiating the formation of micro-aggregates,

491 which in turn affects the physical protection of SOM against microbial decay (Pulleman *et*

492 *al.*, 2005). Addition of *L terrestris* to a chisel-tilled soil cultivated with maize-soya bean

493 rotations in Ohio (USA) increased average soil organic carbon content from 16.1 to 17.9 g C

494 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).

495 To conclude, a recent meta-analysis (36 studies, 136 data points) showed that earthworms are

496 increasing CO_2 emissions by 33% through aerobic respiration (Lubbers *et al.*, 2013).

497 In agro-ecosystems, when management practices are modified with a resulting

498 reduction in the amount of organic matter returned to the soil, a decrease in carbon

499 sequestration is generally observed. Several studies in Scandinavia have confirmed that soil

500 organic matter levels decline after the transition from cropping systems with a large

501 proportion of leys to arable systems with annual ploughing (Uhlen, 1991; Cuvardic *et al.*,

502 2004). Riley *et al*. (2008) also observed that organic matter declined markedly over 15 years

503 in a conventional arable system with ploughing, and remained at a large concentration in

504 most other systems with leys where earthworm density, biomass and activity (number of

505 channels) remained large. Recently, it has been shown that earthworms enhance the

506 stabilization of soil organic matter only when organic residues are applied (Fonte & Six,

507 2010). Changes in management systems (Figure 1) are probably a better way of manipulating

508 carbon sequestration in agricultural contexts than the inoculation of earthworms when the soil

509 is not too degraded.

510 As far as long term effects are concerned, the CENTURY model (Parton &

511 Rasmussen, 1994) developed to predict long term C dynamics and the impact of management

512 practices, predicted that the elimination of earthworms would result in a 10% decrease in C

513 over a 30-year period (Lavelle *et al.*, 2004). Earthworms generally increase primary

514 production and thus carbon fixation by plants (see Primary production section). This could

515 have an impact on carbon sequestration in the ecosystem, depending on the balance of other

516 nutrients such as N and P (see Nutrient cycling section).

517 A growing body of literature indicates that earthworm activity can increase nitrous

518 oxide (N_2O) emissions, for example by switching residue decomposition from an aerobic

519 process with a slow denitrification rate to situations with greater denitrification and N_2O

520   production (Rizhiya *et al.*, 2007). It has been estimated that bacteria within earthworms

521   account for up to 16 % of N_2O emissions (0.6 μg m^{-2} hour^{-1}) from beech forest soil (Karsten

522   & Drake, 1997) and 33% of those (1.1 μg m^{-2} hour^{-1}) from garden soil (Matthies *et al.*, 1999).

523   Similarly, vermicomposting can result in substantial N_2O emissions of up to 21.3 $\pm$ 2.8 mg m^{-}

524   ^{2} hour^{-1} in heated beds during the summer compared to a control of 3.9 $\pm$1.7 mg m^{-2} hour^{-1}

525   (Frederickson & Howell, 2003). A meta-analysis (12 studies, 41 data points) concluded that

526   the presence of earthworms resulted in a 37% increase in N_2O emissions (Lubbers *et al.*,

527   2013). Too few studies have discussed the earthworm effect on CH_4 emission, making a full

528   meta-analysis impossible.

529   Available data on the effect of earthworms on the greenhouse gas balance of soil are

530   fragmentary, and the impact of earthworms on organic matter stocks has not been proved one

531   way or another. Effects arising from changes in earthworm populations observed in many

532   short-term experiments may not be applicable to long-term trends. Therefore, investigations

533   at the field scale are necessary to assess the long-term effects of earthworms. In these

534   experiments all the important greenhouse gases (CO_2, N_2O and CH_4) should be considered.

535

536

537   **Pollution remediation**

538

539   The use of earthworms for the restoration or remediation of contaminated soil can be based

540   on several different strategies depending on the nature of the contamination. Earthworms

541   could be introduced into soil to stimulate the microbial population, which in turn would

542   accelerate the degradation of organic contaminants. Metabolism of ingested soil may also

543   lead to direct mineralization of organic contaminants. For both organic and inorganic

544   contaminants earthworm activity may reduce the amount of sorption onto soil particles

545 through digestion of organic matter, modifications of soil chemistry, or both, leading to an

546 increase in the availability of contaminants and so reduce the time scales required for

547 phytoremediation. Studies that have explicitly examined the relationship between earthworms

548 and the remediation of organic and inorganic contaminants are next reviewed briefly. Also

549 pertinent to the use of earthworms in remediation is their effect on plant growth and nutrient

550 recycling (see Primary production and Nutrient cycling sections) and their impact on

551 microbial populations, which is beyond the scope of this review but is discussed in many

552 other papers (Edwards & Fletcher, 1988; Brown, 1995; Nechitaylo *et al.*, 2010; Wurst, 2010).

553 Much research has been done on the use of earthworms as bio-indicators of the extent of

554 contamination and toxicity of contaminated soil (Spurgeon *et al.*, 2005; Römbke *et al.*, 2006;

555 Nahmani *et al.*, 2007; Brulle *et al.*, 2010). Although this is related to their potential use for

556 remediation, it is not strictly an ecosystem service; as such it is not reviewed here.

557 A limited number of laboratory experiments have been performed on soil amended

558 with organic chemicals and a range of earthworms. These studies have generally used soil

559 amended with polychlorinated biphenols (Singer *et al.*, 2001; Kelsey *et al.*, 2011), petroleum

560 hydrocarbons (Schaefer *et al.*, 2005; Schaefer & Filser, 2007) or polyaromatic hydrocarbons

561 (PAHs) (Ma *et al.*, 1995; 1998; Eijsackers *et al.*, 2001; Contreras-Ramos *et al.*, 2008; 2009).

562 Soil samples are amended with the contaminant and then incubated with earthworms. After a

563 fixed period of time the concentrations of contaminant remaining in earthworm-present and

564 earthworm-absent treatments are compared. Studies usually use either epigeic or anecic

565 earthworms with only two authors using an endogeic earthworm (Schaefer *et al.*, 2005;

566 Schaefer & Filser, 2007; Kelsey *et al.*, 2011). In general, earthworms accelerate the

567 degradation of organic compounds, although the mechanism by which this is achieved is not

568 entirely clear. However, it seems likely that this is a combination of increased aeration of the

569 soil, stimulation of the microbial population, which in turn degrades the contaminants, and

570   metabolism of the contaminants by the earthworms themselves. The use of different organic

571   compounds and concentrations, earthworm species and soil types makes generalizations

572   difficult, but in the above studies the presence of earthworms resulted in mean increases in

573   organic compound degradation by about 30%.

574   The impact of earthworms on metal availability and mobility in soil, and following

575   from this the potential use of earthworms to remediate metal contaminated sites was

576   extensively reviewed recently (Sizmur & Hodson, 2009). The majority of studies showed that

577   plant biomass, extractable metals, pore-water concentrations and metal uptake by plants are

578   increased by earthworm activity. This holds for both amended and contaminated soil and

579   studies that use epigeic, anecic and endogeic earthworm species (Abdul Rida, 1996; Ma *et

580   al.*, 2003, 2006; Wen *et al.*, 2004; Cheng *et al.*, 2005; Liu *et al.*, 2005; Yu *et al.*, 2005; Wang

581   *et al.*, 2006; Dandan *et al.*, 2007; Ruiz *et al.*, 2011; Sizmur *et al.*, 2011a, 2011b; Jusselme *et

582   al.*, 2012). These studies have been done in the laboratory or in outdoor mesocosms, and

583   involve incubating earthworms in either metal-amended or contaminated soil and with

584   growing plants. The above studies indicate increases in metal concentration in plant tissues of

585   up to 410%; the mean maximum increase was 87% but with a standard deviation of 127%

586   indicating the large variability in the results. Earthworm activity almost always increases

587   plant uptake of metals. Use of different species of both earthworms and plants, different

588   metals and different types of soil makes it difficult to quantify the increase in metal uptake

589   caused by earthworms in a meaningful way. Sizmur & Hodson (2009) concluded that, of the

590   possible explanations for enhanced metal mobility and uptake, there were insufficient data to

591   determine whether this is results from stimulation of bacterial populations, change in soil pH,

592   alteration of the dissolved organic carbon content of soil or changes in metal speciation. The

593   studies suggest a modification of the organic matter in soil and soil pH are the most likely

594   cause (Sizmur *et al.*, 2011c).

595   For both inorganic and organic contaminants, studies with endogeic earthworms are in

596   the minority. This probably reflects the difficulties in the laboratory-based culture of

597   earthworms that fill this ecological niche (nevertheless see Lowe & Butt, 2005). Given that

598   any commercial remedial technique would require large numbers of earthworms, it is

599   probably advisable for studies to continue to concentrate on those epigeic and anecic

600   earthworms that are easier to cultivate and preserve. The most obvious need is to move from

601   small-scale laboratory experiments to large mesocosm-scale and then field-scale experiments.

602

603

604   **Primary production**

605

606   As earthworms are the most abundant biomass in most terrestrial ecosystems (Lavelle &

607   Spain, 2001), it is likely that plants have co-evolved with them, with adaptations to the

608   modifications induced by earthworms in soil. A beneficial effect of earthworms on plant

609   growth was recognized more than a century ago (Darwin, 1881). Consequently, the effect of

610   earthworms on primary production has been studied extensively in various kinds of

611   laboratory, greenhouse and field studies (Brown et al, 1999), and some experiments have

612   been monitored for several years (Giri, 1995; Blanchart *et al.*, 1997). However, knowledge of

613   the effects of earthworms on plant growth is biased; most studies investigate crop plants,

614   particularly cereals and pastures. Little is known about plant species in more natural

615   communities and most studies have investigated European earthworms (Lumbricidae)

616   (Scheu, 2003). We can but give a brief overview here of some of the vast literature currently

617   available on this topic (Lee, 1985; Edwards & Bohlen, 1996; Lavelle & Spain, 2001;

618   Edwards, 2004).

619   Brown *et al*. (1999) reviewed 246 experiments performed in tropical countries. Total

620   primary production was improved on average by 63% with positive results obtained in 75%

621   of cases. Above- and below-ground biomass and grain production showed different degrees

622   of improvement. Above-ground production was increased in 75% of the experiments with a

623   mean increase of 56%. Below-ground biomass showed a smaller mean increase of 66%;

624   increases were observed in 59% of the experiments. Grain biomass increased in 72% of the

625   experiments with a mean increase of 36%. In a second review of over 67 experiments in

626   temperate countries, Scheu (2003) showed that above-ground production was increased by

627   the presence of earthworms in 79% of cases, whereas it was reduced in 9%. Some 30 of the

628   studies included data only on below-ground biomass, but of these earthworms resulted in a

629   significant increase in biomass in 50% of the experiments and a decrease in 38% of them.

630   Therefore, it appears that above-ground biomass production generally increases in the

631   presence of earthworms, whereas below-ground shows contrasting responses. Up to a

632   maximum extent, plant production appears to increase with earthworm density, however, the

633   precise relationship between productivity and earthworm density is not clear. In some studies

634   the two appear to be linearly correlated, thus pasture production increased linearly with

635   increasing earthworm density (*Allolobophora caliginosa,* Savigny., *A. longa* Ude and *A.*

636   *trapezoid* Dugés); each was introduced at 114, 214, 429 and 643 earthworms per m^2) (Baker

637   *et al.*, 1999). Other studies, however, show that the positive effect of earthworms can

638   decrease above a given threshold. For example, in a study by Chan *et al*. (2004) the largest

639   dry matter production in pasture enriched with lime was detected in the low density *A. longa*

640   treatment (212 per m^2), which was 49% greater than in the control, and not in the high

641   density treatment (424 per m^2) (Chan *et al.*, 2004). Brown et *al.* (1999) report that the

642   relationship between earthworm density and the increase in plant production is curvilinear,

643   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).

668   A less direct impact of earthworms on primary productivity is through the use of

669   compost made by earthworms (vermicompos: Figure 1). Many studies report that

670   vermicompost has a greater positive effect on plant growth than other compost (Phuong *et al.*,

671   2011). Much literature is dedicated to the impact of vermicompost on plant growth. Results

672   suggest that a 20 to 40% volume of vermicompost in pots results in maximal increases in

673   plant production (Atiyeh *et al.*, 2000; Arancon & Edwards, 2011). However, the reasons for

674   the reported improved performance of vermicompost over other composts remain unclear.

675   Brown *et al*. (2004) identified several factors involved in the impact of earthworms on

676   primary production. The major factor responsible for 43% of the variation in plant response

677   was the type of soil, especially its texture and carbon content. Earthworms produced the

678   largest increase in plant production in sandy soil, with a slightly acid pH (Brown *et al.*, 2004;

679   Laossi *et al.*, 2010). Plant functional group was also an important driver: earthworms induced

680   a larger gain in production in perennial species (especially trees) than in annual species,

681   whereas legumes were sometimes negatively affected by earthworm presence (Brown *et al.*,

682   1999; 2004). Earthworm species, their survival and weight loss or gain, the presence of

683   organic matter input, duration of experiment and experimental set up (laboratory or field)

684   were responsible for smaller variations in the size of effect.

685   As far as ecological processes are concerned, five mechanisms are potentially

686   responsible for the positive effect of earthworms observed on plant production (Scheu, 2003;

687   Brown *et al.*, 2004): (i) increased mineralization of soil organic matter, which increases

688   nutrient availability (Barois *et al.*, 1987; Knight *et al.*, 1989; Subler *et al.*, 1998; see also

689   Nutrient cycling section); (ii) modification of soil porosity and aggregation, which induces

690   changes in water and oxygen availability to plants (Doube *et al.*, 1997; Blanchart *et al.*, 1999;

691   Shipitalo & Le Bayon, 2004; see also Soil structural maintenance and Water regulation

692   sections); (iii) bio-control of pests and parasites (Yeates, 1981; Senapati, 1992; Stephens *et*

693 *al.*, 1994; Clapperton *et al.*, 2001); (iv) production of plant growth regulators through the

694 stimulation of microbial activity (Muscolo *et al.*, 1998; Canellas *et al.*, 2002; Quaggiotti *et*

695 *al.*, 2004) and (v) stimulation of symbionts (Reddell & Spain, 1991; Gange, 1993; Pedersen

696 & Hendriksen, 1993). Recent papers that attempt to evaluate the relative importance of these

697 five mechanisms in controlled environmental conditions showed that earthworms can (i)

698 induce an increase in plant production even in a soil supplied with an excess of mineral

699 nitrogen (Blouin *et al.*, 2006; Laossi *et al.*, 2009a; Arancon & Edwards, 2011), (ii) produce a

700 positive effect on plant production in a well-watered treatment and induce a negative effect

701 with a water deficit because of modifications in soil structure that reduce the amount of water

702 (Blouin *et al.*, 2007) and (iii) induce a positive effect by increasing plant tolerance to parasitic

703 nematodes (Blouin *et al.*, 2005). Recently, several studies have supported hypotheses (iv) and

704 (v). Signal molecules can be responsible for positive or negative effects on plant growth,

705 depending on plant species; an *Arabidopsis thaliana* L. mutant for auxin transport had an

706 altered phenotype which was reverted in the presence of earthworms, suggesting that

707 earthworms were producing auxin-like compounds; a transcriptome analysis showed that

708 hormone signalling pathways were modified in the presence of earthworms (Puga-Freitas *et*

709 *al.*, in press). It is likely that such plant growth regulators produced in the presence of

710 earthworms were made by microorganisms, as suggested by a 46% increase in indole acetic

711 acid production by cultivable bacteria in the presence of earthworms (Puga-Freitas *et al.*,

712 2012). At the community level, earthworms have an impact on competition between plant

713 species (Laossi *et al.*, 2009b; 2011). The success of newcomers in plant communities is also

714 influenced by earthworms (Wurst *et al.*, 2011). This effect of earthworms on plant

715 communities should be taken into account better in restoration ecology (Butt, 2008).

716   Given that the positive effect of earthworms on primary production has been

717 established empirically, research could focus on three distinct directions. Firstly, it could

718 determine the reasons why some field inoculations lead to stable earthworm populations and

719 others do not (Martin & Stockdill, 1976; Brun *et al.*, 1991; Butt *et al.*, 1995). This could then

720 ensure a better probability of success in practical applications. Secondly, a deeper

721 understanding of the mechanisms involved in the effect of earthworms on primary production

722 is required in order to predict situations where earthworms will have positive, null or negative

723 effects. Earthworms affect different plant species differently (Eisenhauer *et al.*, 2009; Laossi

724 *et al.*, 2009b; Wurst *et al.*, 2011) because of the different sensitivity of each species to the

725 combination of mechanisms described above. Thus if earthworms are to be used to boost

726 primary productivity or, for example, in restoration ecology, the mechanisms involved in

727 boosting productivity must be fully understood or plant diversity or differential productivity

728 might be affected in ways other than those desired. Finally, research could assess the

729 economic viability of earthworm introduction technologies at the broad scale by agronomists

730 and economists. Some research in this direction has been attempted (Stockdill, 1982), but

731 such attempts are rare.

732

733

734 **Cultural services**

735

736 Earthworms provide a series of cultural services. Darwin (1881) observed that earthworms

737 "protect and preserve for an indefinitely long period every object, not liable to decay, which

738 is dropped on the surface of the land, by burying it beneath their castings". Some authors

739 (Wood & Johnson, 1978; Stein, 1983; Armour-Chelu & Andrews, 1994; Texier, 2000) have

740 brought attention to the importance of earthworm activities in protecting archaeological

741 remains. Most artifact burial estimates have been comparable to those of Darwin's of 0.35 cm

742 per year (Wood & Johnson, 1978), or slightly more (0.9–1.0 cm per year; Yeates &

743 Vandermeulen, 1995).

744   Earthworms are good tools for environmental education. Appelhof *et al.* (1993)

745 argued that earthworms have been converting organic residues to a re-usable form for 300

746 million years. Earthworms are thus a good pedagogic tool for teaching people about the

747 recycling of organic matter (see Nutrient cycling section). A worm bin in a classroom or in a

748 house demonstrates to children and adults that recycling organic waste furnishes a rich and

749 free material that can support plant growth in a few months. In addition, earthworms provide

750 bait for fishing (a recreational service).

751

752

753 **Use of earthworms to manage ecosystem services**

754

755 *General considerations*

756 Before using earthworms in ecosystem management, managers have to consider the

757 following constraints: external ones imposed by the socio-economic system, internal ones

758 imposed by the physical and biological properties of the ecosystem, and those linked with the

759 multi-functional character of ecosystems. When deciding to manage ecosystem services with

760 earthworms, the socio-economic context and landscape potential have to be taken into

761 account before choosing one of the diverse technical options described in Figure 1. For

762 example, the abundance of earthworms in nearby areas needs to be known before planning

763 the re-colonization of an area devoid of earthworms. When a strategy to add organic matter is

764 planned, socio-economic analyses should be undertaken to determine whether it has to be

765 imported from other areas, to confirm that the financial and carbon costs for transport are not

766 too great, and to determine whether there will be competition with another sector of activity

767 such as agriculture, forestry or industry. Tools such as life-cycle analysis (Asiedu & Gu,

768 1998) or the analysis of territorial metabolism (Wolman, 1965; Kennedy *et al.*, 2007),

769 developed in industrial ecology, could help to answer these questions.

770   Even when sociological and economic contexts are favourable to earthworm

771 management, constraints that are internal to ecosystem functioning have to be considered,

772 and may be the reason for the choice between the different technical approaches described in

773 Figure 1. In anthropogenic ecosystems, where human intervention is important, the

774 management system is often strongly constrained, the financial budget is important and the

775 risk taken has to be minimized. In these situations, 'high-cost' approaches with engineered

776 products (Figure 1) are probably the most relevant. As far as earthworms are concerned, the

777 spreading of vermicompost may be advised. Conversely, some ecological systems have been

778 strongly degraded by human activity (such as mining or gravel extraction). In these cases,

779 where the risk taken can be relatively large, 'middle-cost' approaches may be recommended,

780 for example through micro-ecosystem transplantation. When ecosystems are essentially

781 unmanaged and are close to 'natural' functioning, invasions of exogenous species may need

782 to be monitored or stopped early; 'low-cost' approaches based on ecosystem self-

783 organization can be recommended.

784   When the intention is to manage a specific ecosystem service, it is important to

785 consider the consequences of the planned management practices on other ecosystem services.

786 First, some ecosystem services listed above are strongly interdependent. For example,

787 earthworm inoculation to improve soil structure with the aim to reduce soil erosion will have

788 consequences on water retention, and thus on primary production. The resulting effect on

789 water infiltration and primary production will depend on the ecological context. For example,

790 in flooded areas, stronger aggregation with compacting earthworms can reduce water storage

791 capacity of the soil and increase drainage, which could be beneficial for plant growth and

792   primary production. Conversely, in dry areas a reduction in water storage capacity will be

793   negative for primary production. Second, ecosystems are multi-functional by nature. If one

794   ecosystem service is optimized at the expense of others, it places the provision of the other

795   services at risk. To integrate the constraints imposed better by the multi-functionality of

796   ecosystems, further research is required to understand the interaction between land-use,

797   different earthworm species and ecological processes more precisely.

798

799   *Two case studies*

800   The use of earthworm inoculations in Australia illustrates some of the considerations that

801   need to be given to the management of ecosystem services through the addition of

802   earthworms. Agricultural soils in southern Australia support a mixture of native species

803   (especially Megascolecidae) and exotic species (mostly European Lumbricidae) (Baker,

804   2004) (Figure 5). The balance between these two groups varies greatly, probably driven by

805   several factors such as dispersal by exotic species, level of habitat disturbance by man,

806   distance from native vegetation, physico-chemical traits of the site, competition between

807   species and so on. The agricultural and environmental benefits that common exotic species

808   (such as *A. caliginosa*, *A. trapezoides*, *A. rosea*) can produce, such as improved soil

809   structure, fertility, plant production and quality, root penetration, water infiltration, burial of

810   lime to offset soil acidity, burial of organic matter, root disease suppression for example have

811   been demonstrated (see references in Baker, 2004). Much less is known in this respect about

812   native species (Friend & Chan, 1995; Baker *et al.*, 1996; Baker *et al.*, 2003), but thus far they

813   have not proved to be as beneficial as the exotic species. There would seem to be much merit

814   in managing the exotic species to optimize the benefits they can provide to agriculture, and

815   even in further spreading them to locations they have yet to reach. However, what are the

816   down-sides, or environmental risks such as invasion of pristine habitats, or competition with

817   native biota including other soil fauna besides earthworms, in doing so? These are topics we

818   know little about; in fact we have little knowledge of the ecology and functional roles of the

819   native Australian megacolecids in general, although they seem to be numerous and diverse in

820   some native systems. We will need to strike a balance in these matters. Exotic species are

821   already present in the landscape, widespread (but patchy in abundance and very probably still

822   expanding) and of course impossible to eradicate should we need to: do we regard the exotic

823   species now as a true resource?

824   These considerations become more forceful when considering introductions of the

825   European *Aporrectodea longa* from Tasmania (where it is often very abundant) to mainland

826   Australia (where anecic species, such as *A. longa*, are very rare in agricultural soil). In the

827   heavy rainfall regions of mainland Australia, where *A. longa* is most likely to establish if

828   given the chance, it could bring major benefits to agricultural land through its deep burrowing

829   and thus improving water infiltration and root penetration to depth. These effects would be

830   likely to enhance, for example, the retention of nutrients on sloping land rather than their loss

831   into water-ways. Thus, there could be both production and conservation benefits. However,

832   the benefits would only be accrued over many years, given the basic ecology of this species

833   (relatively poor reproductive rate and dispersal ability). There is thus far no evidence that *A.*

834   *longa* will invade native ecosystems (Dalby *et al.*, 1998), but the evidence for this is still

835   quite weak. We need to be aware of the impacts that exotic earthworms, such as *Lumbricus*

836   *terrestris*, *L. rubellus* and *Amynthas hilgendorfi*, Michaelsen, are currently having on plant

837   and animal communities, leaf litter layers and soil biogeochemical processes in North

838   America (Bohlen *et al.*, 2004; Hale *et al.*, 2005; 2006; 2008; Greiner *et al.*, 2012; Holdsworth

839   *et al.*, 2012; Loss *et al.*, 2012). We should also note the probable result of the careless

840   disposal of fish bait (a recreational ecosystem service in itself provided by earthworms) has

841 made to the spread of invasive species such as *L. terrestris* into native ecosystems in North

842 America (Callaham *et al.*, 2006; Keller *et al.*, 2007; Hendrix *et al.*, 2008; Kilian *et al.*, 2012).

843   A good example of how the management of soil function and ecosystem processes by

844 earthworm introduction is a long-term process, dependent on not just inoculation but also on

845 land management, comes from an introduction of *L. terrestris* to a clay-rich, sub-drained field

846 in SW Finland. The introduction was done mainly to increase soil water permeability, which

847 in the prevailing conditions is enhanced by *L. terrestris* burrows particularly those in contact

848 with sub-drains (Figure 3) (Nuutinen & Butt, 2003; Shipitalo *et al.*, 2004). The *L. terrestris*

849 were entirely absent from the study site previously, but present in many nearby fields. In

850 1996 *L. terrestris* were inoculated into the field and its margins using the EIU-technique

851 (Nuutinen *et al.*, 2006) (Figure 2). Monitoring of the experiment in 1998 and 2003 showed

852 that the inoculated *L. terrestris* became established at the field margins, but not within the

853 field to any significant degree (Nuutinen *et al.*, 2006). In 2008, however, following a seven

854 year period as set-aside grass middens were observed inside the field indicating locally strong

855 *L. terrestris* activity. Field sampling in 2009 indicated that although populations were still

856 greatest around field margins, *L. terrestris* had begun to colonize the now cultivated field area

857 at an approximate rate of 4.6 m per year (Nuutinen *et al.*, 2011). The results demonstrated the

858 importance of tillage and drainage management for colonization: it was particularly marked

859 above the sub-drain lines and clearly greater in no-till areas compared with the ploughed parts

860 of the field. It is evident from the experiment that the field margins were decisive bridgeheads

861 for population establishment and that they later acted as source areas for colonization of the

862 field.

863

864

865 **Gaps in knowledge and opportunities for future research**

866

867 We identify avenues of further research that would help to advance our understanding of the

868 use of earthworms to modify soil function and provide ecosystem services in the sections

869 above. Some more general comments can also be made on this subject. Although earthworms

870 have been studied for many years there are still major gaps in our understanding of

871 earthworm biology and behaviour that hinder their use in the management of soil functions

872 and ecosystem services. However, new tools and techniques are being developed to overcome

873 the difficulties associated with the study of organisms in the solid and opaque environment

874 that is soil (Butt & Grigoropoulou, 2010). Taxonomic studies continue to reveal that what

875 were considered species are in fact assemblages of several taxa (Iglesias Briones *et al.*, 2009;

876 Dupont *et al.*, 2011), or that supra-family taxa are para- or poly-phyletic (James & Davidson,

877 2012). These continued discoveries mean that, despite studies on earthworm biological traits

878 (Bouché, 1972; 1977) and life cycle characteristics such as birth and survival rates, and

879 reproduction rates (Lowe & Butt, 2002), we still do not have sufficient knowledge to choose

880 the best earthworm species adapted to specific management contexts. A lack of knowledge on

881 how earthworms disperse across the environment is also a major impediment to the

882 development of earthworm management for ecosystem services provision. Understanding

883 passive dispersal for example through human activities such as fishing, is vital to understand

884 invasions of North-European earthworms in North-American soil (Hale, 2008). However,

885 understanding active dispersal (Mathieu *et al.*, 2010) is necessary to optimize inoculation

886 methods, for example to define an inoculation patch size large enough to favour rapid

887 colonization of a field and to determine the time frame necessary for ecosystem changes to be

888 brought about. Databases of earhworm traits, similar to the ones developed for plants (Kuhn

889 *et al.*, 2004; Kleyer *et al.*, 2008) or benthic macrofauna (Renaud *et al.*, 2009), will help to

890 overcome these obstacles.

891   Since ecosystems are by definition systems where many positive and negative

892   feedbacks can occur, it is difficult to make simple predictions about the consequences of

893   changing the size of the population of one organism. The preferential feeding of earthworms

894   and the fact that earthworm gut conditions favour some microfauna over others means that

895   variations in earthworm abundance can modify the structure of other soil organism

896   communities (Loranger *et al.*, 1998; Bernard *et al.*, 2012). In addition, earthworm abundance

897   affects plant pests such as aphids possibly because of effects on food quality (Scheu *et al.*,

898   1999; Wurst & Jones, 2003) as well as plant communities (Eisenhauer & Scheu, 2008;

899   Eisenhauer *et al.*, 2009; Laossi *et al.*, 2009b; 2011; Wurst *et al.*, 2011). As such, more

900   research is required into the trade-offs between the merits and risks of earthworm

901   introduction into fields (Baker *et al.*, 2006) and the interactions between earthworms, other

902   soil organisms and plants.

903   We need more robust data from earthworm studies regarding soil characteristics,

904   vegetation types, climate data, earthworm identification to species level and the presence of

905   other soil microfauna that should be recorded as a routine matter. This would provide

906   opportunities for meta-analyses so that where enough data have been collected for diverse

907   environments, they could become a useful tool for taking into account better context

908   specificity and management objectives when manipulating earthworms (Gurevitch *et al.*,

909   2001; Stewart, 2010).

910   Well-designed laboratory experiments and field experiments, preferably carried out

911   over several years, coupling basic biological and soil science measurements still have much

912   to offer in terms of filling our gaps in knowledge. In addition, molecular and isotopic

913   techniques are increasingly being used to elucidate how earthworms affect the environment.

914   The coupling of isotope labelling with molecular techniques is beginning to be used to

915   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).

940   Earthworms undoubtedly contribute significantly to many of the ecosystem services

941   provided by the soil, and whilst much is known about these processes, further research along

942   the lines discussed above will lead to a greater understanding of the role of earthworms in

943   ecosystem services provision and, ultimately, an increased ability to manage such services

944   through, amongst other things, manipulation of their abundances and diversity.

945

946

947   **Acknowledgements**

948

952

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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)

1615   and (b) the Southern Tablelands of New South Wales (104 sites). Sites are arranged in order

1616   from those with the least earthworms to those with the most (graphs from Baker, 2004).

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1618   **Figure 6** Photograph (a) and diagram (b) of X-ray tomography unit used for determining

1619   burrow topography and earthworm movement, and (c) tracking of earthworm movement

1620   using radio-labelled earthworms. I is for *L terrestris*. and II for *Nicodrilus giardia*. The two

1621   circles represent the top and bottom of the core. Each letter labels the beginning of a digging

1622   event in alphabetical order. The type of line indicates the number of crossings per segment

1623   (solid line: > 80; dashed line: $40 - 70$; dotted line: $0 - 40$) (from Bastardie et al., 2003b).

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1625   **Figure 7** *Allolobophora chlorotica* tagged with blue coloured Visual Implant Elastomer.

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