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

2

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

26 **Summary**

27

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.

39

40

41 **Introduction**

42

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

51 borne by organisms (Jax, 2005). Previous work has described and categorized ecosystem
52 services, identifies methods for economic valuation, maps the supply and demand for
53 services, assesses threats and estimates economic values (Daily, 1997; Millennium
54 Ecosystem Assessment, 2005), but does not quantify the underlying role of biodiversity in
55 providing services (Kremen & Ostfeld, 2005). In contrast, published studies of the functional
56 role of biodiversity often examine communities whose structures differ markedly from those
57 providing services in real landscapes (Diaz *et al.*, 2003; Symstad *et al.*, 2003), and have been
58 restricted to a small set of ecosystem processes (Schwartz *et al.*, 2000). What is lacking is an
59 approach that will provide fundamental, ecological understanding of ecosystem services to
60 assist in devising the best management and policy tools for their conservation and sustainable
61 use (Kremen & Ostfeld, 2005). For this purpose, we need to identify the relationships that
62 exist between ecological entities and ecosystem functions or services, and to propose
63 different technical approaches to manipulate ecological entities with the aim of reaching
64 management objectives.

65 For ecosystem managers, a fundamental question is to determine whether all species
66 are equally important providers of ecosystem services or if some are more important than
67 others. In the latter case, it would clearly be most relevant to focus especially on the
68 management of specific providers. Literature reviews (Schwartz *et al.*, 2000; Thompson &
69 Starzomski, 2007) corroborate the ‘Drivers and Passengers’ hypothesis (Walker, 1992),
70 which stresses that only some species (the drivers) are important. These species are generally
71 known as keystone species (Power & Mills, 1995) or ecosystem engineers (Jones *et al.*,
72 1994). The drivers of ecosystem functions can be unique in an ecosystem; thus all the
73 bioturbation of sediments may be caused by only one species, such as the brittle star,
74 *Amphiura filiformis*, Müller (1776) in benthic habitats (Solan *et al.*, 2004). In the majority of
75 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.

97

98

99 **Scope of review**

100

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.

134

135

136 **Soil formation**

137

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).

225

226

227 **Soil structure**

228

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.

272

273

274 **Water regulation**

275

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

283 Ehlert (1975) showed that after ten years of earthworm inoculation, the infiltration
284 rate of water through soil increased from 15 to 27 mm hour⁻¹. In Mediterranean soil, water
285 infiltration was correlated with earthworm biomass ($r = 0.60$) and burrow length (0.66), and
286 strongly correlated with burrow surface ($r = 0.77$) (Bouché & Al-Addan, 1997). Across a
287 range of soil types, infiltration rate was measured as 150 mm h⁻¹ per 100 g m⁻² of
288 earthworms or 282 mm h⁻¹ per 100 g m⁻² of anecic earthworms (Bouché & Al-Addan, 1997).
289 In the tropics, inoculation of endogeic compacting species has a negative effect on infiltration
290 rate: changes in aggregate size proportions and bulk density (see above) resulted in a decrease
291 in infiltration rates and sorptivity (the capacity of the medium to absorb or desorb liquid by
292 capillarity), the latter decreased from 0.34 cm s⁻¹ in non-inoculated soils to 0.15 cm s⁻¹ in
293 treatments inoculated with 36 g m⁻² fresh biomass of earthworms (Alegre *et al.*, 1996). In
294 another experiment in the Côte d'Ivoire, the removal of macrofauna in the soil (control
295 treatment) was responsible for a slow infiltration rate (about 2.8 cm minute⁻¹). This
296 infiltration rate improved weakly (+22 to 27%) in the presence of two endogeic compacting
297 species, namely *R. omodeoi* and *Dichogaster terraenigrae* Omodeo & Vailland., 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 *Amyntas 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.

364

365

366 **Nutrient cycling**

367

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

372 digestion, some organic compounds are released into the environment as small organic
373 compounds or mineral nutrients. These mineral nutrients, especially nitrogen (N), are re-used
374 by plants. Nitrogen mineralization is thus increased in the presence of earthworms, either
375 directly through the release of N by their metabolic products (casts, urine, mucus which
376 contain NH_4^+ , urea, allantoin and uric acid) and dead tissues, or indirectly through changes in
377 soil physical properties, fragmentation of organic material, and through interactions with
378 other soil organisms (Lee, 1985; Bityutskii *et al.*, 2002).

379 Earthworms accelerate N mineralization from organic matter, but the effect depends
380 on the species and their interactions with other soil biota, soil characteristics and the location
381 of the organic matter (Butenschoen *et al.*, 2009). For instance in mesocosm experiments,
382 *Lumbricus rubellus* Hoffmeister (epigeic) and *L. terrestris* (anecic) earthworms increased the
383 mineralization of applied crop residues, but *Aporrectodea caliginosa* (endogeic) did not.
384 However, mineralization of soil organic matter was enhanced by *L. rubellus* and *A.*
385 *caliginosa*, but *L. terrestris* had no effect (Postma-Blaauw *et al.*, 2006). In the Lamto savana
386 (Côte d'Ivoire) the earthworm *R. omodeoi* provided 60% of the total population biomass and
387 was estimated to release 21.1 to 38.6 kg ha⁻¹ year⁻¹ of the total assimilable N in the form of
388 ammonium in faeces or labile organic N in dead earthworms and mucus. Total production of
389 mineral N by the entire earthworm community was estimated to be between 30 and 50 kg ha⁻¹
390 y⁻¹ (Lavelle *et al.*, 2004). Whalen & Parmelee (2000) reported that earthworms process 2–15
391 Mg ha⁻¹ year⁻¹ of organic matter from soil and litter, and that the annual flux of N through
392 earthworm biomass in temperate, cultivated agro-ecosystems ranges from 10 to 74 kg N ha⁻¹
393 year⁻¹. The annual N flux through earthworm populations was greater in plots with added
394 manure than in those with inorganic fertilizer, and ranged from 2.95 to 5.47 g N m⁻² year⁻¹ in
395 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⁻¹
401 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 NH₄⁺ 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 NO_x 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 CO₂ 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 (N₂O) emissions, for example by switching residue decomposition from an aerobic
519 process with a slow denitrification rate to situations with greater denitrification and N₂O

520 production (Rizhiya *et al.*, 2007). It has been estimated that bacteria within earthworms
521 account for up to 16 % of N₂O 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 N₂O emissions of up to 21.3 ± 2.8 mg m⁻²
524 hour⁻¹ in heated beds during the summer compared to a control of 3.9 ± 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 N₂O emissions (Lubbers *et al.*,
527 2013). Too few studies have discussed the earthworm effect on CH₄ 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 (CO₂, N₂O and CH₄) 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 m²) (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 m²), which was 49% greater than in the control, and not in the high
641 density treatment (424 per m²) (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

644 capacity. Moreover, it has been observed that earthworm activity is not correlated with plant
645 production (Callaham *et al.*, 2001). Undoubtedly, the complex effect of earthworms on
646 primary production is through the relationship between earthworms and plants, as plant
647 diversity and production involve a feedback on earthworm diversity and abundance and *vice*
648 *versa* (Brussaard, 1999; Kukkonen *et al.*, 2004).

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

668 A less direct impact of earthworms on primary productivity is through the use of
669 compost made by earthworms (vermicompost: 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 *Amyntas 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 earthworm 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

916 possibilities for understanding the role of earthworms in microbial community structure and
917 function. Indeed, PLFA-SIP (stable isotope probing) has been used to identify which
918 microorganisms and soil microfauna present in earthworm galleries were responsible from
919 organic matter degradation (Stromberger *et al.*, 2012). The coupling between DNA-SIP and
920 pyrosequencing showed that stimulation of both the mineralization of wheat residues and the
921 priming effect can be linked to the stimulation of several groups especially belonging to the
922 *Bacteroidetes* phylum (Bernard *et al.*, 2012). The RNA-SIP coupled with the sequencing of
923 the 16S ribosomal RNA has been used to study the diversity of active atrazine-degrading
924 bacteria in relation to atrazine degradation and to explore the impact of earthworm-soil
925 engineering with respect to this relationship (Monard *et al.*, 2011).

926 X-ray tomography is being used increasingly to understand earthworm burrows and
927 water movement although its application is still restricted to a few research groups (Joschko
928 *et al.*, 1991; Capowiez *et al.*, 1998; Jegou *et al.*, 1999; Jegou *et al.*, 2001; Bastardie *et al.*,
929 2003b) (Figure 4). In addition, researchers have begun to use radio-labelling of earthworms
930 to determine their movement in soil, *in situ* (Capowiez *et al.*, 2001; Bastardie *et al.*, 2003a)
931 (Figure 6).

932 Earthworm tagging is a technique that holds great potential to follow earthworm
933 movements inside the soil. Visual implant elastomer (VIE) (Northwest Marine Technology,
934 Accessed October 2012) is injected into the muscle tissue of the earthworms enabling
935 identification of individual earthworms and raised the possibility of tracking migration rates
936 of individual earthworms either in the field or laboratory experiments and of assessing
937 survival rates (Figure 7). Studies to date have shown that the coloured tag can last in
938 earthworms without any impact on earthworm mortality or reproduction for over two years,
939 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

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948

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952

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1591 CAPTIONS TO FIGURES

1592

1593 **Figure 1** The scope of the review encompasses different approaches that allow the effect of
1594 earthworms on ecosystem services to be studied. We classify these approaches according to a
1595 gradient from self-organized processes to the human application of products engineered by
1596 earthworms. Passive versus active bio-stimulation (Brun *et al.*, 1987) can be reported on this
1597 gradient, as well as several management techniques.

1598

1599 **Figure 2** (a) Two litre earthworm inoculation units (EIUs) ready for inoculation into an
1600 organically-enriched landfill cap in the south of England (from Butt *et al.*, 1995) and (b) Soil
1601 inoculation of a 4 litre Earthworm Inoculation Unit (EIU) at a landfill cap in the south of
1602 England by Kevin Butt.

1603

1604 **Figure 3** *Lumbricus terrestris* burrow ending on tile surface. At its end the burrow bends
1605 towards the tile. The plough layer has been removed and the cast starts from a depth of
1606 approximately 0.25 m. The tile is at a depth of 1.0 m. (from Nuutinen & Butt, 2003)

1607

1608 **Figure 4** (a) Burrow network created by earthworms, anecic species and endogeic species.
1609 Observations in 3-D obtained by X-Ray tomography and (b) Reconstruction of the interior of
1610 an earthworm burrow using medical software and X-Ray tomography (photographs by G.
1611 Pérès).

1612

1613 **Figure 5** Average abundance of exotic (open bars) and native (closed bars) earthworms in
1614 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).

1617

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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