1   **Breaking ground: pedological, geological, and ecological implications of soil bioturbation**

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9

10   **Abstract**

11   Soil and its biota are a fundamental component of the "Critical Zone": Earth's living skin that most

12   directly sustains life. Within that zone, geologically rapid soil and saprolite displacement by biota,

13   particularly invertebrate meso- and macrofauna, affects a large proportion of Earth's soils. Primary effects

14   include soil production from saprolite, the formation of surface mounds and soil burial, which we quantify

15   herein. In concert with surface geomorphic processes, fundamental and far-reaching properties of soil are

16   altered including particle size distribution, porosity, the content of carbon and other nutrients, and creep

17   flux rate. The precise influence of bioturbation is regulated by its potency and depth function, both of

18   which we quantify, herein. Biotic soil displacement can be as rapid as sustained maximum rates of tectonic

19   uplift, and it declines with increasing soil depth.

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21   Many aspects of bioturbation are not appreciated because, although late 19th century observers on both

22   sides of the Atlantic Ocean regarded bioturbation as fundamental to soil formation, both an agronomical

23   focus of soil scientists and the dominant paradigm of landscape evolution relegated bioturbation from

24   further consideration. Only in the last few decades has a re-evaluation of bioturbation commenced,

25   whence, in a range of disciplines, it appears that soil biota are not only incredibly diverse but they perform

26   a number of functions at a range of spatial and temporal scales that extend beyond soil to landscape

27   denudation, ecosystem engineering, niche construction, and carbon cycling. Understanding these

28   linkages—which have operated since the evolution of particular terrestrial invertebrates in the mid-Tertiary

29   or earlier—is of growing importance as we seek a fuller picture of Earth's history to predict and manage its

30   future.

31

32   Keywords: bioturbation; soil production; soil creep; soil carbon

33

1. Introduction

Soil science is challenged with understanding complex interactions between physical, chemical and biotic processes (Paton, 1978; Young and Crawford, 2004; Amundson et al., 2007). Soil biota comprise a large proportion of Earth's biodiversity (Giller, 1996) and these organisms perform fundamental ecosystem functions (Bardgett et al., 2005; Lavelle et al., 2006). Soil bioturbation (physical mixing by organisms) is a key process that influences ecosystem functioning via soil development (Lavelle et al., 1997). Ecologists recognise the importance of soil as a complex habitat for biota ranging in size from that of microbes to vertebrates (Lavelle et al., 1997; Young and Crawford, 2004)—that both influence and are influenced by aboveground biota (Wardle et al., 2004)—and as a temporary store of soil organic matter (SOM) (Lal, 2004; Johnson et al., 2005a). Furthermore, biota affect the geochemistry of soil and bedrock to great depths (Richter and Markewitz, 1995). However, the pedogenic and geomorphic affects of biotic soil displacement—first noticed by Darwin (1881)—had received limited attention until the last quarter of a century (Humphreys and Mitchell, 1983; Johnson, 1990; Paton et al., 1995) when bioturbation was advanced as a primary process in soil formation and soil creep.

Recent research recognises that biotic disturbance of soils and underlying bedrock is a key driver of the liberation of soil particles from bedrock (soil production) and downslope soil transport (creep) (Heimsath et al., 1999; Gabet et al., 2003). In concert with surface processes, bioturbation engineers the medium through which ecosystems draw their nutrients, while storing organic detritus from those ecosystems. Bioturbation has also been considered from an ecological and evolutionary perspective via feedbacks between abiotic and biotic ecosystem components in both the present day and geologic past (Jouquet et al., 2006; Meysman et al., 2006; Corenblit et al., 2008). Thus, not only have bioturbators been raised to the status of *ecological engineers* that modify resource availability within ecosystems (Jones et al., 1994; Wright and Jones, 2006), but bioturbators are also considered to have created conditions of evolutionary significance, a process known as *niche construction* (Odling-Smee et al., 2003). Soils store twice as much carbon as the

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58 atmosphere and biosphere combined, and soil biota are thought to play a large role in soil carbon

59 dynamics, and thus climate regulation (Lavelle et al., 2006; McCarl, 2007). Combined with the evolutionary

60 status afforded to bioturbation, it appears we are witnessing the emergent understanding of a key

61 mechanism that both transcends biological and geological systems and unites them and other Earth system

62 sciences.

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64 The purpose of this paper is to complement existing reviews in the fields of geomorphology (Gabet et al.,

65 2003), evolutionary biology (Meysman et al., 2006) and ecology (Huhta, 2007) by highlighting neglected

66 themes in the literature. We do so by presenting a history of the concept of bioturbation with a focus on

67 pedogenesis, and by making connections with this and other Earth system sciences, as outlined in Figure 1.

68 We focus mainly on earthworms, ants, and termites (invertebrate meso- or macrofauna, depending on

69 species and classification scheme e.g. Swift et al., 1979; Dindal, 1990), vertebrates and higher plants that

70 interact directly with soil, and note in passing the wealth of literature on smaller organisms that live as

71 independent organisms or as symbionts within those of our focus. While soil biota may be considered from

72 a geochemical perspective (e.g. Richter and Markewitz, 1995), our primary aim is to examine the

73 mechanical effects of biota on soil and those reactions, which appear to be driven by physical

74 displacement.

75

76 **2. Darwin, Shaler and nascent pedology**

77 Notions that soil biota affect gross soil morphology by alteration of particle size, organic material content

78 and fabric were first recorded by Charles Darwin. Darwin (1881) made observations on the prodigious

79 mixing of plant and mineral matter in soil by earthworms, and drew several conclusions about their casting

80 activity. Foremost was that the organic-rich topsoil (termed *vegetable mould* by him and others at this time) in

81 many situations was made up of casts and the remnants of casts, with disturbance by earthworms notable

82 in the subsoil, at depths of up to 2.5 m below the surface. He also considered the longer-term impact of

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83   casts on the soil and other objects, noting for example that objects too large to be transported by

84   earthworms are increasingly buried over time. His observations on the gradual but progressive burial of

85   paving stones at his residence over a 30-year period were instrumental in this conclusion. Importantly, he

86   calculated mounding rates for earthworms, and burial rates over various time scales by examining

87   agricultural material, bones, artefacts, Roman ruins and Druid Stones that were originally deposited on the

88   surface years to thousands of years earlier (Table 1). Darwin's estimates of burial rates (calculated over

89   years to decades) are generally greater than his estimates of mounding rates (calculated over months to

90   years). He suggested that soil loss from mounds between casting and sampling occurred, and that ants,

91   moles, and aeolian dust, which he did not sample, also contribute to topsoil thickness.

92

93   Darwin speculated on the role of mineral dissolution by earthworm intestinal acids and mechanical

94   breakdown by their gizzards, and the reduced rate of bedrock weathering beneath thick layers of vegetable

95   mould due to reduced thermal variation and frost shattering. The latter, we failed to note in an earlier paper

96   on the history of the soil production function (Humphreys and Wilkinson, 2007)—Darwin's observation

97   appears to be the second earliest reference to such an idea, following those of Gilbert (1877), and imply an

98   inverse relationship between soil production rate and soil thickness. Observing the fate of casts deposited

99   on the surface, Darwin realised that downslope soil transport occurred during rainfall and the resulting

100   casts were deficient in fine particles. Thus he postulated a mechanism of soil creep, before the seminal

101   works of both Davis (1892) and Gilbert (1909). Additionally, he estimated the mass flux due to

102   redistribution of earthworm casts (Table 2). Therefore, Darwin introduced many important themes, and

103   was the first to describe and quantify fundamental processes in soils-geomorphology (e.g. Feller *et al.* 2003;

104   Johnson 2002; Meysman *et al.* 2006).

105

106   A short time later, on the other side of the Atlantic, these notions were developed by Shaler (1891), who

107   recognized the role of many other bioturbators, especially ants and tree uprooting. Shaler attributed gross

108   soil morphology to bioturbation and he recognised the primacy of burial, resulting from mounding and

109   burrow infilling, in the maintenance of organic matter within soil. Additionally, he recognised that particle

110   distributions reflect the sorting effect of bioturbators on soils, most notably stone-free mantles resulting

111   from the redistribution of invertebrate mounds by surface wash. Several line drawings clearly attest to this,

112   such as the re-organization of till, and the distinction between bioturbated soil and unaffected subsoil

113   (saprolite, where the subsoil is formed in bedrock), including the burial of stones to a depth no greater than

114   the topsoil-saprolite interface and the incorporation of SOM by mounding and subsequent mixing. Some

115   of these are illustrated in Figure 2. He, like Darwin, estimated rates of biogenic mounding.

116

117   These observations of Darwin and Shaler disseminated widely for nearly 50 years, but the dominance of

118   nascent pedology by the U.S. Department of Agriculture and its focus on crop production meant that

119   bioturbation, and pedogenesis generally, were surpassed by agronomical matters (Johnson et al. 2005b). It

120   was also a reflection of the dominance of Davisian geomorphology in Earth sciences, in which

121   biomechanical processes were absent (see Johnson, 2002). For example, Merrill (1897) preferred to view

122   soils as primarily a product of weathering and, whilst acknowledging the role of soil biota as illustrated by

123   Shaler, he treated them as a disruptive force on the pervasive organizational control exerted by weathering.

124   In effect, Merrill overturned the status afforded to biota by Shaler and Darwin.

125

126   Until the 1980s, bioturbation remained a peripheral issue in pedogenesis and a synthesised understanding

127   was absent, although the effects of tree uprooting on soil morphology had continued to be examined (e.g.

128   Lutz and Griswold, 1939). A century passed before the important lead shown by Darwin and Shaler was

129   applied in a central way to soil formation (Johnson, 1990; Paton et al., 1995), following at least one prior

130   lead (Williams, 1968). This was aided by the emergence of a genetic language (Johnson 2002). The term

131   *bioturbation* appears in the title of a paper by Schäfer (1952) to help describe and understand the effects of

132   faunal mixing in marine sediments. It was first used to describe pedogenesis by Blum and Ganseen (1972,

133 cited in Johnson, 2002) and first used in the title of a soils-geomorphic paper by Humphreys and Mitchell

134 (1983), subsequently becoming commonplace in these disciplines. Other related terms have emerged in

135 pedological, ecological and geomorphological contexts (Table 3). For instance, bioturbators are recognised

136 as an *ecosystem engineer* in ecological literature that influences entire ecosystems, both within and above the

137 soil via pedospheric connections to the biosphere (Jones et al., 1994; Wright and Jones, 2006).

138

139 **3. Soil displacement: mounding, mixing and burial**

140 Biota that interact with soil and saprolite (chemically altered but physically intact bedrock) displace

141 individual particles and small aggregates over spatial scales of millimetres to decimetres, depending on the

142 organism involved (Figure 1). Soil displacement below the surface, within or between soil horizons and in

143 any direction, is known as *mixing* (*Mx*). Displacement may or may not then lead to the formation of

144 millimetre to decimetre scale mounds when soil is deposited on the surface, again depending on the

145 organism involved (e.g. Evans and Guild, 1947; Paton et al., 1995), which leads to indirect burial of

146 undisturbed soil. Such *mounding* (*Md*) is easy to observe and quantify in comparison with mixing, although

147 mounded soil may arrive on the surface by multiple displacements from a variety of biota. Additionally,

148 rates of mounding and mixing at a site generally appear to differ substantially (Table 1).

149

150 A great variety of fauna, at various life-cycle stages, are known to penetrate soil and saprolite to feed,

151 gestate and/or shelter, and it is such animal activity that is behind the vast majority of bioturbation globally

152 (Paton et al. 1995). Mounded soil may be incorporated or reworked into nests or fashioned into masonry

153 structures. For example, turrets built by cicada nymphs extend a burrow, and termites use soil to make

154 protective covers (sheaths) of subaerial passages and to pack the eaten parts of wood. More familiar

155 examples of mounding by soil animals are ant mounds, termitaria, earthworm casts, molehills and gopher

156 mounds. Mounds also include surface scrapes made by a variety of small mammals and birds.

157

158   Soil in mounds is generally vulnerable to surface processes and associated reworking (Darwin, 1881; Shaler,

159   1891; Paton et al., 1995), however not equally so. Ephemeral mounds that are highly susceptible to erosion,

160   e.g. earthworm casts, some ant mounds, have been classified by Humphreys and Mitchell (1983) as type-I

161   mounds, while type-II mounds are longer-lived, larger structures that are often cemented and repaired

162   when necessary, e.g. some ant mounds, termitaria. Rates of soil mounding associated with type-I mounds

163   are higher despite the larger soil mass usually associated with type-II mounds. Surface processes that act on

164   mounds may be biotic, because termitaria and ant mounds attract predators such as echidnas, porcupines,

165   aardvarks and armadillos that erode mounded soil as they prey.

166

167   The role of flora is also substantial. Following Shaler's (1891) lead, tree uprooting has been shown to cause

168   substantial soil displacement in a variety of environments, including temperate (Lutz and Griswold, 1939;

169   Stephens, 1956), tropical (Putz, 1983), subalpine (Burns and Tonkin, 1987; Osterkamp et al., 2005) and

170   spruce forests (Bormann et al., 1995; Ulanova, 2000). These disturbances also produce mounds, the

171   mechanisms of which have been well-illustrated (see Shaler, 1891; Gabet et al., 2003; Norman et al., 1995;

172   Schaetzl and Follmer, 1990), as well as mixing or inverting the soil profile (Shaler, 1891; Schaetzl, 1986;

173   Bormann et al., 1995). Other mechanisms of 'floralturbation' are generally more subtle, such as the

174   displacement of soil with root growth and subsequent infilling of macropores when roots and stumps

175   decay. These can nonetheless be significant in soil transport too and facilitate mixing (Gabet et al. 2003a;

176   Phillips et al., 2005; Phillips and Marion 2006; Roering et al. 2002).

177

178   Biota will displace weak bedrock in search of food or shelter. Thus, bioturbation affects the subsoil or

179   saprolite, especially in residual soils, in a process known as *soil production* (review in Humphreys and

180   Wilkinson, 2007). The resulting soil generally overlies saprolitic subsoil and is known as topsoil or the

181   *biomantle* (e.g. Johnson, 1990 and references therein; Paton et al., 1995; Johnson et al., 2005b). When roots

182   grow through saprolite, biotic soil production occurs both directly by mass displacement and indirectly by

183 weathering processes that physical penetration facilitate. Tree uprooting may simultaneously result in soil

184 production and mounding (Lutz and Griswold, 1939; Heimsath et al., 2001). Although soil production

185 research has invoked the role of biota in physically converting saprolitic subsoil into overlying soil, analysis

186 has highlighted the dependence of soil production rates on saprolitic lithology and its degree of weathering

187 (Dietrich et al., 2003) rather than the role of local bioturbators. The small range of studies conducted thus

188 far, in diverse geologic settings, has revealed that soil production rates generally occupy a range of $10 - 100$

189 m My^{-1} (Wilkinson and Humphreys, 2005).

190

191 Soil *burial* is an indirect consequence of various mixing processes. It is exemplified by the high density of

192 cicada emergence burrows that follow each cicada brood (e.g. Humphreys, 2005): that soil does not

193 resemble Swiss cheese, riddled with evermore burrows, emphasises that unmaintained burrows are infilled

194 by surface material and that considerable soil burial is a result. Burial of large clasts, by both invertebrate

195 mounding and undermining, has been noted by many authors (e.g. Shaler, 1891; Johnson, 1989; Paton et

196 al., 1995). Darwin (1881) used buried historic objects to estimate burial rates, from which he also inferred

197 mounding rates, but mounding may exceed burial if mounded soil is sourced from recently buried soil at

198 shallow depths. In the last decade, burial rates have been determined using optically stimulated

199 luminescence (OSL) dating which extends the estimation timescale to the limits imposed by both the

200 ionising radiation rate of the soil and the capacity of the target mineral to absorb that radiation: this is

201 generally $10^1 - 10^6$ years (Wilkinson and Humphreys, 2005). OSL techniques focus on quartz and feldspar

202 minerals and have progressed from measuring the optical signal of large aliquots that contain $10^2 - 10^3$ soil

203 grains to single-grain aliquots. This represents a considerable advance for bioturbation studies because

204 adjacent soil particles with similar physical and chemical traits are likely to have arrived in their current

205 position via very different paths.

206

207 Soil displacement is of interest to ecologists in terms of energy expenditure. Observations by one of us

208 (GSH) indicate that the invertebrates that dominate bioturbation at a well-studied site in southeastern

209 Australia (Humphreys, 1994; Humphreys and Field, 1998) show no preferred direction of subsurface

210 transport, so flux is not relevant here. However, biotic soil displacement may lead to downslope transport

211 by mounding alone (Gabet, 2000), or when soil is subsequently transported by surface processes (Fig. 1). In

212 a geomorphic context, direction is relevant and considerable importance is attached to the amount of

213 material displaced downslope, which is recorded as a flux.

214

215 **4. Downslope flux and creeping biomantles**

216 Hillslopes transport sediment and nutrients to fluvial networks. To constrain such processes and the long-

217 term development of landscapes, geomorphic research over the last two decades has sought to qualify the

218 agents and processes of hillslope soil flux and to quantify flux to parameterise conservation of mass

219 equations for input into numeric landscape models (e.g. Dietrich et al., 1995; Gabet, 2000; Anderson,

220 2002). The *biotic soil flux* (Q_{sb}) records the amount of soil displaced downslope resulting from biotic

221 interactions with soil (Table 2).

222

223 **4.1. Direct and indirect flux**

224 Biotic flux may be divided into two components. *Direct* flux is soil that is displaced by the sum of

225 mounding, mixing, burial and soil production. The *indirect flux* includes soil displaced by both biotic and

226 abiotic processes that act on mounded soil (Shaler, 1891; Paton et al., 1995). The latter also includes the

227 collapse of biogenic macropores—biovoids or *biopores* (Gabet et al., 2003), and subsurface soil transport

228 through biovoids. The indirect biotic flux is of great geomorphic and pedologic importance because the

229 surface component has been identified as a strong driver of biomantle mobility which was previously

230 explained as *en masse*, abiotic soil creep (see below). When mounded soil is not afforded protection by

231 vegetation it is both sorted and transported by surface processes (Fig. 1). While this includes biotic

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232 reworking and aeolian processes, *rainwash*—a combination of rainsplash, slopewash, and the rafting of

233 leaves, charcoal and materials of similar density—is thought to dominate in humid settings (Paton et al.,

234 1995). Although overland flow on ridge crests is generally no more than several millimetres in depth, these

235 flows display similar but smaller scale features to their valley-floor, channelised cousins (Mitchell and

236 Humphreys, 1987). That is, overland flow transports a floating-, suspended- and bed-load. This results in

237 the rapid transport of fines down the hillslope while bedload is trapped in *microterraces* behind *litter dams*

238 (Mitchell and Humphreys, 1987; Eddy et al., 1999). The depth limit of soil affected by these processes, the

239 net effect of which is downslope transport, is directly related to the depth limit of biotic soil mining and

240 biovoid creation (Paton et al., 1995). Thus, the entire biomantle "creeps" downslope.

241

242 While a moderate but growing number of estimates of total aggregate soil flux exist, we are aware of only

243 three estimates that have isolated the biotic component (Table 2). Darwin's (1881) focus on earthworms

244 included an estimate of downslope soil flux resulting from the displacement of their casts by rain. The

245 Pocket Gopher (*Thomomys bottae*), which constructs large mounds and extensive burrows, has been

246 highlighted for its role in biomantle production (Johnson, 1989) and estimates of its soil flux have also

247 been made (Black and Montgomery, 1991; Gabet, 2000; Yoo et al., 2005). Research has begun to focus on

248 the functional dependence of biotic flux processes and hillslope gradient (Gabet, 2000; 2003). From these

249 works, it appears that biotic soil flux is important and may dominate local hillslope soil transport. At this

250 stage, there is not enough data to say which functional group is most potent.

251

252 **4.2. Modes of creep**

253 Creep has been attributed to soil rheid flow and abiotic heave (e.g. Davis, 1892; Carey, 1954). The latter is a

254 two-stage process in the mobile layer, involving expansion normal to the surface and subsequent vertical

255 contraction. Agents of expansion included water—liquid or solid—and heat. In recent years, soil creep has

256 been attributed to the net effects on soil flux by biota, such as tree uprooting, and heave due to vertebrate

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257   burrowing. However, Paton et al. (1995) proposed another two-stage model—involving essentially the

258   same processes observed by Darwin (1881)—whereby soil flux is dominated by overland flow which

259   transports single grains and aggregates of surface soil previously deposited in biogenic mounds.

260

261   Similar processes to those invoked by Paton et al. (1995) have been modelled with moderate success on the

262   Great Escarpment of SE Australia, with assessment provided by Optically Stimulated Luminescence

263   (OSL—see Wilkinson and Humphreys (2005) for applications of OSL to pedogenesis) profiles of the

264   biomantle (Heimsath et al., 2002). Soil displacement by trees has been demonstrated to dominate soil flux

265   at a site on the South Island of New Zealand over the Holocene using the concentration of tephra of

266   known age (Roering et al., 2002). Field measurements of the direct flux from burrow excavation by

267   gophers illustrates that these vertebrates are important agents of soil transport in the Californian ranges

268   (Black and Montgomery, 1991). Dry ravel resulting from biotic disturbance is likely important on arid

269   slopes when soil cohesion is minimised (Gabet, 2003), and is conspicuous following fire on the Oregon

270   Coast Range where it may comprise large proportions of the long-term total soil flux on steep slopes

271   (Roering and Gerber, 2005). In the Rocky Mountains, where freeze-thaw is dominant creep process,

272   Anderson (2002) used terrestrial cosmogenic nuclides (TCN) sampled from profiles within the creeping

273   mantle that constrain soil flux rates (Small et al., 1999) to successfully model the deglaciated slopes.

274

275   Thus both biotic and abiotic processes contribute to soil creep. Those that have been quantified by field

276   methods are summarised in Table 2. Biotic creep, where attributed to a specific functional group, appears

277   to range from an order of magnitude less potent to on-par with soil flux attributed to abiotic processes.

278   Variation is likely to be explained by biome and soil type.

279

280   **5. Rates of bioturbation by fauna**

281

5.1. Mounding rates

Of mounding, mixing, burial, soil production and downslope flux, there is only a moderate amount of data on mounding by various organisms. Darwin (1881) first recorded the rapid soil mounding of earthworms and now several compilations of mounding rate data exist (Paton et al., 1995; Butler, 1995; Schaetzl and Anderson, 2005). Any evaluation of these mounding rate estimates must consider the following caveat: low rates will occur under sub-optimal conditions and may preclude that taxon from further study.

In moist soils that do not freeze, earthworms are tremendous bioturbators with over half of the studies recording casting rates of 10 – 50 t/ha/y or more. In some tropical locations, rates exceed 100 t/ha/y (e.g. Madge, 1965, 1969; Watanabe and Ruaysoongnern, 1984; Krishnamoorthy, 1985). Ants are active mounders in moist and dry settings but their activity is generally considered to be much lower than that of earthworms. Most studies record 1 – 5 t/ha/y with a few studies recording 5 – 10 t/ha/y (Madge, 1969; Humphreys, 1981). Two studies report higher estimates exceeding >50 t/ha/y (Shaler, 1891; Humphreys, 1985). Some ants spread excavated soil over the surface rather than constructing piles, and estimates of their activity are difficult to produce. Termites, often conspicuous via their large termitaria in drier and warmer settings, mostly exhibit maximum mounding rates of 1 – 5 t/ha/y (i.e. similar to those of ants). Rarely have higher rates been recorded; an exception is a tropical study by Lepage (1984) who records a rate of up to 11.2 t/ha/y for *Macrotermes bellicosus* in Côte d'Ivoire. Termites also transport soil up into standing vegetation, often metres above the ground, but rates have yet to be established. Some termite species also use soil to form a protective sheath over surface passageways. Over a period of 121 days, Gupta et al. (1981) recorded soil sheathing equivalent to 64.8 t/ha/y. Clearly the combined effect of all termite mounding activity could be much higher than indicated in studies to date. A diverse array of other soil invertebrates transports considerable amounts of soil, including beetles (Kalisz and Stone, 1984), cicada nymphs (Humphreys, 1989), woodlice (Yair and Rutin, 1981) and burrowing arachnids (Polis et al., 1986; Formanowicz and Ducey, 1991). Most rates are <1 t/ha/y but estimates of crayfish mounding indicate

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307   rates of 5 – 10 t/ha/y in favoured habitats (Thorp, 1949). Rates of mounding by vertebrates are commonly

308   1 – 5 t/ha/y (i.e. similar to those of ants and termites), though the most prodigious fossorial mammals

309   such as pocket gophers and moles may mound at rates of 10 – 20 t/ha/y (e.g. Abaturov, 1972; Ellison,

310   1946). The amount of quantitative data decreases as body size increases and the mammals become less

311   closely associated with the soil (Paton *et al.*, 1995), although many vertebrates are evidently effective

312   bioturbators (Table 4).

313

314   In many situations more than one type of bioturbator exists at a site, including more than one species of a

315   bioturbating taxonomic group. However, very few studies have explored this theme and the existing data

316   only relates to mounding. In southeastern Australia, for example, individual sites often contain several

317   species of mounding ants as well as termites, earthworms, cicadas, trapdoor spiders, and various

318   vertebrates (Humphreys and Mitchell, 1983).

319

320   **5.2. Burial and mixing rates**

321   Local mounding rates can outweigh burial rates by an order of magnitude (Table 1) but the two generally

322   record rates over different timescales (Table 6). When comparing components of bioturbation at a single

323   site, it appears a large proportion of the soil within mounds was mined recently from shallow burial depths

324   (Figure 3) and burial rate estimates that sample below such depths are likely to reflect slower turnover.

325   Burial is also likely to be slower for larger particles that require more undermining. For instance, Darwin's

326   (1881) estimates on the burial of ruins are generally an order of magnitude slower than those of smaller

327   particles. This effect is also noticeable for sand fractions. Figure 4 reports data from an optical dating study

328   of bioturbated soil, which indicates that smaller particles are buried more rapidly than larger particles

329   (Wilkinson, 2005). Burial rates of each size fraction decreases with increasing burial depth because biotic

330   activity decreases with increasing depth (we discuss bioturbation-depth functions, below).

331

332 However, Darwin (1881) noted that his estimates of burial, calculated over years to decades, generally

333 outweigh his estimates of mounding (calculated over months to years). His explanation was that soil loss

334 occurred from mounds between casting and sampling. Additionally, he noted that ants and moles that he

335 did not sample in his mounding estimates also produce vegetable mould, and that dust deposition might

336 contribute to burial.

337

338 Whilst burial rates of bioturbated particles can be readily used to infer mixing rates, there are few direct

339 estimates of mixing because of the difficulty in procuring this information. The most significant of these

340 estimates come from rates of soil ingestion by earthworms (e.g. Evans, 1948; Satchell, 1967; Lavelle, 1978)

341 and a unique 17-year assessment of subsurface processes using a column of dyed soil (Humphreys and

342 Field, 1998). Results from the latter demonstrate that all soil particles in the 15-cm thick A horizon have an

343 average displacement period of 22 years. Such mixing rates are on par with mounding rates reported by

344 Evan (1948) and Satchell (1967) (Table 1).

345

346 **6. Biofabrics and bioturbation-depth functions**

347 Earthworms, termites, ants, arthropods and tree roots produce a number of secondary soil fabric features

348 (Oades 1993). They create voids in the form of burrows, nests, chambers, galleries and root channels

349 (Paton et al., 1995; Lavelle et al., 1997). Additionally, earthworms and ants aggregate soil and deposit them

350 on and below the soil surface. The variation in bioturbation with depth below the soil surface has been

351 determined indirectly by fabric analysis using resin-impregnated soil in a few studies. Biofabric analysis

352 presents both a snapshot of current biotic activity within soil and a record of former activity. Biotic soil

353 macropores, such as open tunnels and chambers, are the most recent alteration of soil fabric resulting from

354 bioturbation. When these are infilled, by fallen surface material or the excretion of casts from earthworms,

355 the resulting structure is known as a *pedotubule*. Thus, pedotubules may represent older, abandoned *biovoids*

356 or they may indicate the recent passage of a worm. *Maculae* (Humphreys, 1994) are the result of repeated

15

357   burrowing that intersects old, infilled pedotubules (i.e. re-bioturbation) and as such occupy the historical

358   end of the spectrum of observable biofabrics. Maculae are patches, spots and/or blotches of the same

359   dimensions as pedotubules but of a different colour to the surrounding soil, from which they are separated

360   by a sharp boundary at least in part of the perimeter (Figure 5). Both pedotubules and maculae are indirect

361   metrics, best observed in impregnated soil sections (>1 mm thick) rather than in thin sections or in the

362   field where they are often overlooked. Soil bulk density may also be used to infer biotic activity because it

363   captures both void creation and organic matter content, both of which are likely to be greater with higher

364   levels of bioturbation. Bulk density is generally lower in soils with higher levels of invertebrate and

365   vertebrate activity (e.g. Lobry de Bruyn and Conacher, 1990; Gabet et al. 2003).

366

367   These studies conclude that biotic activity declines non-linearly with depth, with notable differences

368   between horizons, both within the biomantle and at the biomantle-(stonelayer)-saprolite interface

369   (Humphreys, 1994; Humphreys and Field, 1998; Wilkinson, 2005). Figure 6 presents data from Wilkinson

370   (2005) to illustrate these trends. Any stepwise decrease in bioturbation may reflect depth limits of dominant

371   bioturbators that occupy ranges based on habitat requirements. The defining characteristic of the biofabric

372   study by Humphreys and Field (1998) is that the age of the fabrics is known. Thus rates of mixing have

373   been calculated and indicate the 15-cm thick A horizon is mixed about three times faster than the E

374   horizon (depth: 15-37 cm).

375

376   **6.1. Implications for soil production**

377   There are several important implications of the general decrease in bioturbation with depth below the soil

378   surface. Firstly, the form of the soil production function at a site will be heavily dependent on the

379   bioturbation-depth function where soil production is largely biogenic. Only in a small number of studies

380   has the soil production function sought to be quantified (Humphreys and Wilkinson, 2007) and two basic

381   models appear to be most applicable: one where the soil production rate decreases exponentially with

16

382 increasing soil thickness with a maximum on bare saprolite, and a similar one with a peak in soil

383 production on thinly mantled saprolite. Quantifying the functional dependence of soil production on soil

384 thickness involves the measurement of *in situ* (TCN) from saprolite immediately underlying the topsoil

385 (Wilkinson and Humphreys, 2005). While a peak in soil production under a thin mantle has been

386 hypothesised, its existence may be difficult to prove directly, although surface process models that employ

387 such a "humped function" successfully reproduce spatial patterns of soil thickness (Wilkinson and

388 Humphreys, 2005). Additionally, it should be noted that theoretical support for a humped function appears

389 to be based on the production of soil from bedrock rather than saprolite; because bioturbators can mine

390 saprolite (e.g. Humphreys and Groth, 2001), soil production from saprolite is likely to be maximised where

391 a topsoil is absent. Where both soil and saprolite have been eroded to expose fresh bedrock and

392 subsequently soil thickening occurs, the soil production function appears to follow a humped function

393 (Wilkinson et al*., 2005). The general coincidence of bioturbation-depth functions and soil production-

394 depth functions implies that bioturbators are likely to be fundamental to soil production at all depth values

395 where freeze-thaw is absent.

396

397 Distinct decreases in biotic activity across the soil-saprolite interface have been inferred from quantification

398 of variables such as bulk density, pedotubule density, gravel content and optical age of slope sediments

399 (Humphreys, 1994; Wilkinson, 2005). Because biotic activity is also present in saprolite, although at much

400 lower levels than overlying soil, the saprolite represents a depth where biotic regolith alteration is severely

401 curtailed but not eliminated. This view is supported by the presence of stonelayers that overlie saprolite

402 and underlie a relatively stone-free biomantle, indicating that the undermining of large particles by

403 invertebrate soil mining slows markedly at such depths. However, small tree roots can penetrate saprolite

404 and fractured bedrock without destroying overlying stonelayers if root breakage during tree uprooting

405 occurs above the stonelayer.

406

6.2. Implications for horizonisation

Rapid soil mixing does not preclude horizonisation. In fact, the opposite may be true, as indicated by the estimates of mixing in the A and E horizons of Humphreys and Field (1998). Bioturbation leads to pedogenic soil layers, the number and type of which depends on the assemblage of bioturbators on-site and the suite of abiotic pedogenic processes (Johnson, 1990). Certainly, some bioturbators are capable of reducing the number of horizons by relatively indiscriminant exhumation of all calibres of solid soil components, particularly where their activity is rapid and/or to significant depth (Johnson et al., 1987). Trees and large vertebrates are examples (Roering et al., 2002). However not all bioturbators are so competent. Soils in which bioturbation is dominated by invertebrates will likely exhibit pedogenic horizons (Figure 2), especially when surface processes can sort mounded soil: this is the central thesis of texture-contrast soil formation advocated by Paton et al. (1995). Additionally, where clasts are present within the profile that are too large to be moved directly, these sink through the profile as a result of undermining and burial and form a stonelayer or stoneline at the base of the biomantle (Darwin, 1881; Johnson, 1989, 1993; Paton et al., 1995; Phillips 2004; 2008).

Where vegetation is particularly dense and earthworm casts and other mounds cannot be reworked, particle-size sorting is curtailed and the formation of a coarse residuum is impaired. Similarly, parent materials that weather to unimodal size fractions will not illustrate the effects of either biogenic or slopewash sorting. Despite this, the effect of bioturbation on soil is noticeable.

As described above, soil biomantles may display aggregates and voids related to biotic activity, despite reworking by both biotic and abiotic surface processes. Thus, at the very least, a fabric-contrast soil is produced by bioturbation (Paton et al., 1995). Weathering is also enhanced by soil biota. The faecal material of "litter transformers" (Lavelle et al., 1997) includes organic acids that enhance mineral weathering (e.g. Lavelle et al., 1996; Suzuki et al., 2003) and complements the exudates of higher plants,

432   lichen, bacteria and fungi. By increasing both the porosity and organic content of the zone in which they

433   operate, bioturbators increase the water holding capacity of soils and reduce runoff. Thus there are a range

434   of pedogenic variables that may be detected in soil columns that reflect the presence of soil biota.

435

436   In the absence of bioturbation, physical and chemical soil traits would be vastly different, such that texture

437   and nutrient profiles would largely reflect in situ weathering and aerosol input, while fabric would be

438   dominated by the influence of that of the parent material and abiotic heave. Thus, the fundamental

439   pedogenic role of soil biota has lead to their recognition as ecosystem engineers (Folgarait, 1998; Lavelle et

440   al., 1997, 2006) and keystone species (Huhta, 2007) (Fig. 1). The vertical distribution of SOM is addressed

441   below.

442

443   **6.3. Implications for creep**

444   Bearing in mind that biotically disturbed soil decreases with depth, it appears highly likely that horizons

445   with higher biotic activity move faster downslope for several reasons, and thus display a downslope

446   velocity profile that is greatest at the surface and decreases non-linearly with depth. Soil that is mounded

447   more often is exposed to rainwash and concomitant downslope movement. Surface soil is generally buried

448   only shallowly and the apparent tight cycling of mounded and near-surface soil suggests the uppermost soil

449   horizons are undergoing the greatest flux. Deeper soil, by contrast, is not only mounded less but also

450   underlain by progressively less bioturbated soil that experiences less void creation and subsequent collapse.

451   This reduces its ability to creep via expansion and contraction. Velocity profiles similar to that described

452   here have been reported from field and laboratory data measuring freeze-thaw and wet-dry cycles, and

453   subsequently modelled generically and reproduced in laboratory experiments by Roering (2004).

454

455   **7. Soils of the past and future**

456

7. Soils of the past and future

7.1. Evolution of biota and soils

The disturbance of marine sediments by foraging biota has been noted by sedimentologists and

ichnologists for many decades and the evolution of marine sediment bioturbators is rather obvious in the

fossil record. Such bioturbation is thought to have begun immediately prior to the Cambrian Period

(Jensen 2003). Although ties between the biosphere and pedosphere are more cryptic, they do imply a

terrestrial analogue with marine sediments, such that biologic evolution is likely to have driven soil

evolution. Both marine and terrestrial bioturbators are recognised as ecological engineers because they

organise fundamental habitat requirements for many elements of ecosystems. Thus, there is likely a degree

of co-evolution between soils and biota that has taken place.

The development of trees in the Devonian Period marks the first occurrence of fundamental characteristics

of Earth's pedosphere. Algeo and Scheckler (1998) suggest that both soil weathering processes and areal

extent of soils were significantly enhanced due to deeper root networks and seed evolution associated with

trees, which permitted plants to move away from moist surfaces that were previously required for sperm

dispersal. Thus, bioturbation by tree root penetration and uprooting would have facilitated mineral

weathering and burial of soil organic matter, thereby contributing to soil carbon pumping over a much

larger soils volume than the pre-Devonian.

Establishing the precise chronology of mesofauna evolution is not easy because ideal fossils that connect

ancestral taxa to modern bioturbators are rare, due to their low preservation potential. Traditionally, body

fossils have been used to determine evolutionary sequences, however a consideration of trace fossils

(ichnofossils) in palaesols provides interesting insights for the development of soil bioturbation.

482   The evolution of earthworms (Oligochaeta) from their marine ancestors (Polychaeta) is difficult to locate

483   precisely. In his review, Buatois (1998) notes that there are worm traces in Devonian rocks from Antartica

484   that may be non-marine, but more definitive evidence comes from traces of earthworm burrows and

485   termite nests in Jurassic rocks from Colorado, and Triassic palaeosols in New South Wales (Retallack,

486   1997).

487

488   Ichnofossil nests of ants (Hymenoptera) and termites (Isoptera) palaeosols remain preserved because

489   chamber and gallery walls are often reinforced with bodily secretions or by compaction. Thus, Hasiotis

490   (2003) details extant and fossil nest structures by these and other burrowing soil organisms and notes that

491   such nests have changed very little in 225 My. By considering the biogeography of fossil and modern

492   organisms within their palaeogeographic context, Hasiotis (2003) suggests these organisms had evolved by

493   the early Triassic Period, prior to rifting of Pangea.

494

495   Thus, bioturbation of terrestrial soils, involving similar agents and processes that operate today, is likely to

496   have begun operating in the Devonian Period, associated with trees, and become amplified during the early

497   Triassic Period when ants, termites, and earthworms left traces now preserved in palaeosols. Because

498   mammals are dominant bioturbators in arid and semi-arid environments, soils in these climatic regions

499   were probably bioturbated by invertebrates until the Cretaceous-Tertiary boundary, excepting polar soils

500   (Paton et al. 1995).

501

502   However, the formation of texture-contrast soils from mixed-clast saprolite by slopewash sorting relies on

503   a balance between surface processes that transport fines rapidly, and sands and gravels slowly (Paton et al.,

504   1995). These processes depend not only on the bioturbators, but on subsidiary organisms. The impediment

505   to coarse hillslope sediment transport by vegetation has only been in existence since the evolution of

506   terrestrial vegetation in the Devonian, and would have become much more effective with the expansion of

507   grasses during the Tertiary (Jacobs et al. 1999).

508

509   **7.2. Soil organic carbon (SOC)**

510   Observations of biomechanical mixing of organic and mineral soil components have their roots in

511   Darwin's (1881) observations on the feeding habits of anecic earthworms that use permanent burrows to

512   commute from depth to gather litter. Burial of "forest mould" by pit infill associated with tree uprooting,

513   or the reworking of biogenic mounds, was noted by Shaler (1891) who saw the phenomenon as beneficial

514   to soil fertility—a contention that is still upheld (Tiessen et al., 1994). Recent decades have witnessed a

515   focus on soil carbon sequestration as part of an effort to understand both the function of the grand

516   biodiversity of soils (Giller, 1996; Bardgett et al., 2005) and Earth's carbon cycle (Falkowski, 2000;

517   Amundson, 2001; Van Oost et al., 2007; 2008).

518

519   The soil carbon pool is a large reservoir of actively cycling carbon that holds 2344 Pg C in the top 3 m

520   from the surface (Jobbagy and Jackson, 2000) and an estimated 1500 Pg C in the top 1 m alone

521   (Amundson, 2001)—more than the atmosphere (720 Pg C as CO_2) and biosphere (600 Pg C) combined

522   (Janzen, 2004; Powlson, 2005). While the total SOC of the world's naturally vegetated soils is primarily

523   controlled by climate and soil textures that control microbial SOC breakdown, the vertical distribution of

524   SOC is thought to reflect inputs such as shoot-to-root ratios and vertical patterns of root distribution, and

525   is thus related to plant functional type (Jobbagy and Jackson, 2000).

526

527   Additionally, the mechanisms controlling soil organic carbon (SOC) turnover remain poorly understood

528   (Fontaine et al., 2007) and the influence of physical mixing is yet to be fully explored. Bioturbators drive

529   both inputs and outputs of this reservoir (Table 8). For instance, meso- and macrofauna are known to

530   affect the activity, composition and distribution of fungi and bacteria communities in a complex fashion

531 (Anderson, 1988; Johnson et al., 2005). This is supported by Humphreys et al. (in prep) who have

532 demonstrated a correlation between bioturbation of quartz grains in A and E horizons and the SOC

533 residence time at similar depths at other sites. Large soil aggregates in which carbon may be cached for

534 long durations are disintegrated by bioturbation (Ewing et al., 2006). Furthermore, at the global scale, those

535 environments with higher soil carbon turnover rates (such as the tropics) also have higher bioturbation

536 rates; this correspondence might warrant further investigation.

537

538 A component of the atmospheric CO_2 flux between glacial and interglacial cycles is related to soil area and

539 soil stability. Glacial climates involve reduced global soil area due to large ice sheets, while aridity leads to a

540 contraction of forests and larger deserts. Such conditions reduce the ability of Earth's soils to sequester

541 carbon (Adams and Faure, 1998.)

542

543 **7.3. Pedogenesis, soil function and humans**

544 Pedogenesis is an on-going and multidirectional suite of processes, and soils, like the landscapes in which

545 they reside, can be considered a palimpsest. Humans use approximately half of Earth's land surface for

546 agriculture (Kareiva et al., 2007), and physical, chemical and biotic soil processes are influenced by human

547 activities (Yaalon, 2007). Such human-induced pedogenesis—termed "anthropopedogenesis" by Richter

548 (2007)—is thought to have contributed to the failure of past civilisations (Diamond, 2005; Montgomery,

549 2007). Such concerns are more relevant now than ever as humans face the challenge of feeding a world

550 population that has the potential to double within half a century.

551

552 Modern agricultural practices affect the biotic mediation of soil formation and nutrient cycling, which are

553 replaced by artificial tillage and fertilisation that have varying but mostly negative effects. Upon agricultural

554 conversion, species and soil functional diversity generally decrease and imbalance the ecosystem; while this

555 may lead to an increase in soil biomass it may also involve biotic soil pests that reduce crop production

23

556   (Matson et al., 1997). Habitat changes include a reduction in food quantity and diversity, altered thermal

557   and moisture regimes, and the introduction of fertilisers and pesticides (e.g. Lobry de Bruyn, 1999).

558   Minimum tillage practices combined with the retention of crop residue appear to be sustainable approaches

559   to agricultural production that facilitate biotic soil formation.

560

561   Managing soils and their functionality most effectively ideally requires knowledge of soil from its pre-

562   agricultural state to its current state, a transition that has likely involved several distinct phases of soil

563   characteristics some of which result from an altered assemblage of soil biota, and feedbacks between biota

564   and both hydrologic and geochemical regimes. If remediation to a pre-agricultural state is the desired

565   outcome, for those soils in which bioturbation was an important pedogenic element, it will likely require

566   creating habitat to re-establish a suite of soil fauna that closely resembles—taxonomically or functionally—

567   the pre-agricultural soil ecosystem or an earlier productive phase. While this may be possible in the new

568   world, it appears near impossible where intense soil utilisation has a longer history.

569

570   One of the most concerning management issues for soil management is maximising its potential as a

571   carbon reservoir. Soil cultivation has been estimated to cause up to 60% reduction in natural SOC in

572   temperate climates, and 75% loss in the tropics (Lal, 2004), with the transition from native forest to crop

573   averaging a 42% decrease, and pasture to crop a 59% decrease (Guo and Gifford, 2002). Loss of SOC

574   results from erosion, oxidation by continued ploughing, and a reduction in above-ground organic matter

575   input. However, there is debate about whether agricultural erosion constitutes a net sink of atmospheric

576   carbon or not (Lal and Pimentel, 2008; Van Oost et al., 2008). The reduction in SOC by agriculture may

577   also result from soil ecosystem modification whereby biogenic SOC input is curtailed and output is

578   accelerated.

579

580   As vegetation responds to future atmospheric CO_2 fertilisation and changes in precipitation, the response

581   of total SOC and its vertical distribution are unknown. Humification may keep pace with changing litter

582   inputs or react non-linearly, as Fontaine et al. (2007) demonstrated. Climate-induced biogeographic

583   changes are likely to lead to changes in pedogenesis and soil function.

584

585   **8. Conclusions**

586   The cumulative effects of biotic soil displacement, which individually are somewhat cryptic because they

587   generally measure small length-scales, have a tremendous impact on Earth systems by their profound

588   influence on pedosphere function. Bioturbation by organisms such as earthworms, ants and tree roots

589   featured as a primary pedogenic force in the models of Darwin (1881) and Shaler (1891) at a time that may

590   be regarded as pedology's birth. Observations and quantification by Darwin (1881) lay separate and nearly

591   forgotten during pedology's youth when crop production was a primary focus. However, recent syntheses,

592   mature hindsight and new field observations have revived the biotic component of pedogenesis. Similarly,

593   geomorphology considered landscape evolution by measuring and modelling soil transport without

594   considering biotic input, which is now recognised as a powerful assemblage of transport agents in many

595   climates.

596

597   Soil biota, especially earthworms, ants, termites, and particular vertebrates displace great volumes of soil, at

598   a comparable rate to tectonic uplift where uplift is most vigorous. Bioturbation rates have been estimated

599   for a range of species in many climatic settings for over a century. Simple methods, first employed by

600   Darwin (1881) and Shaler (1891), are now complemented by optical dating which extends the timescale

601   over which rate estimates are made. Mounds are the most obvious form of biotic soil displacement but

602   subsoil mixing can outweigh mounding by an order of magnitude. Both are likely to be underestimated in

603   field surveys. Biotic creep may form a large component of local hillslope soil flux.

604

25

605 Soils and their diverse biota are increasingly being appreciated for the functions they perform. Soil

606 management has generally focused on physical and chemical soil properties, such as loss by erosion,

607 salinisation and nutrient leaching; however, the realization that biota interacting with soil are fundamentally

608 responsible for soil profile development, especially supra-saprolite horizons, adds to an increasing body of

609 knowledge that creates an impetus for soil to be managed as a dynamic biologic system. This poses a

610 particular challenge for re-establishing and maintaining soil productivity as the human population grows

611 and regional biota respond to global climate change. Additionally, a consideration of SOC storage

612 dynamics appears warranted if soil management is to reverse historic SOC oxidation and maximise soil

613 carbon sequestration. Furthermore, the quantity of information on soil bioturbation and the primacy of its

614 effects make it worthy of inclusion not only in pedology and geomorphology textbooks but also in those

615 whose focus is Earth systems science.

616

622

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Captions

Figure 1: The effects of bioturbation (biotic mixing or displacement) are primarily pedologic, but link to other Earth system sciences. Some effects are omitted for clarity—see the text for details. Primary biotic processes are in bold, while secondary processes are normal; primary products are in italics and the net products are in caps.

[a]Indirect burial includes undermining.

[b]Surface processes include abiotic surface wash and wind, and biotic redistribution.

[c]A variety of soil characteristics appear to be influenced by the depth function of bioturbation, including fabric, porosity, texture, degree of weathering, SOM content,

[d]Soils with these characteristics are an end-member, and form when such processes operate for sufficient time and other processes do not tend otherwise.

Figure 2: Figures in Shaler (1891) that depict horizonisation and/or the incorporation of organic matter into soil, resulting from biotic activity. (a) Redistribution of mounded soil creates a new horizon and buries the organic and mineral soil component (Fig. 11, p. 279). (b) Organisation of glacial till by ants and earthworms that have mounded finer soil fractions and increased soil permeability (Fig. 2, p. 238). (c) Tree uprooting, resulting in a depression that is filled with organic material and subsequently by mineral soil from the root ball (Fig. 8, p. 273; see also Fig. 9, p.274 for resulting horizons follow tree decay). Public domain.

Figure 3: Biotically-mediated soil displacement rates on a schematic residual soil profile referenced with tectonic uplift, expressed as a logarithm with units in m/My. Unbracketed ranges are global maxima and minima while bracketed numbers are from Cattai (authors' data), on the SE Australian passive margin. Sources: uplift at convergent plate setting (various sources); burial (Heimsath et al. 2002; Humphreys et al.

42

1011 in prep.); mixing (Paton et al. 1995); soil production, rainwash, and mounding (Wilkinson and Humphreys

1012 2005). Soil flux is treated in Table 3. Some estimates apply over different timescales (Table 6). Vegetation is

1013 omitted from this cartoon for clarity, however plants are typically associated with litter dams that trap

1014 rainwashed soil resulting in microterraces (Eddy et al. 1999). Total biotic activity is likely to be greater than

1015 these estimates for two reasons: these estimates are minima as a result of quantification issues, and they

1016 record displacment rather than distance.

1017

1018 Figure 4: Median and standard error of large aliquot OSL ages, plotted against sample depth for Pit 3 at

1019 Marrangaroo (Wilkinson 2005; Wilkinson et al. 2005); see Table 5 for a profile description. Sand fraction

1020 sizes are in μm.

1021

1022 Figure 5: [To be printed in colour, on the web and in print].

1023 Impregnated soil from 18–27 cm (B_w–C_{ox} transition) in Pit 3 at Marrangaroo (Wilkinson 2005; Wilkinson et

1024 al. 2005). Dashed line marks the boundary between macular and non-macular soil. Above this boundary,

1025 pedotubules have a variety of colours and degrees of preservation, whereas below this boundary

1026 pedotubules are less common and less spatially interrupted. This boundary strikingly coincides with the

1027 terminus of an infilled burrow, the dimensions of which are consistent with a cicada or trapdoor spider

1028 burrow. The pedotubule contains material that appears to have fallen from the surface, because of the high

1029 proportion of charcoal and comparatively dark matrix. OB indicates open biovoids. Curved marks in the

1030 top left of the block were made by a circular saw. Scale bar measures 1 cm.

1031

1032 Figure 6: Biotic activity variation with depth from Pit 3 at Marrangaroo (Wilkinson 2005; Wilkinson et al.

1033 2005), a residual soil (Dystric regosol) on the SE Australian passive margin. A profile description is in

1034 Table 5. Bioturbation is dominated by ants and worms, and supplemented by termites, cicadas, tree

1035 uprooting, wombats and spiders. (a) Burrows (crosses), infilled burrows (pedotubules – diamonds) and

1036 total burrows, i.e. open + infilled (stars); dashed line is a best fit to the total burrows data, excluding the

1037 data point at 1.0 cm; *depth* = -19 * ln(*proportion*) + 64, and r^2 = 0.86. (b) Maculae (reworked biofabrics—see

1038 text for details); dashed line is a best fit to the data, excluding the data point at 1.0 cm; *depth* = -7.7 *

1039 ln(*proportion*) + 46, and r^2 = 0.88. (c) Bulk density; dashed line is a best fit; *depth* = exp(4.5 * *density*) * 0.031,

1040 r^2 = 0.90. Dashed horizontal lines represent soil horizons, with nomenclature following Table 5. Panels

1041 record median soil depth of impregnated soil blocks against average proportion of variables in mapped

1042 block faces at each depth (*n* = 2, average surface area = 150 cm^2).

1043

1044 Table 4: Most burrows here are multi-purpose, being used to reach food and for shelter and nesting. Like

1045 those of invertebrates, these burrows have associated surface mounds (e.g. molehills) of geomorphic

1046 significance, which has been particularly well noted for the rodents. Many other vertebrates, such as

1047 crocodilians and muskrats, can become important in coastal, fluvial and wetland settings (see Butler, 1995).

Figure 1
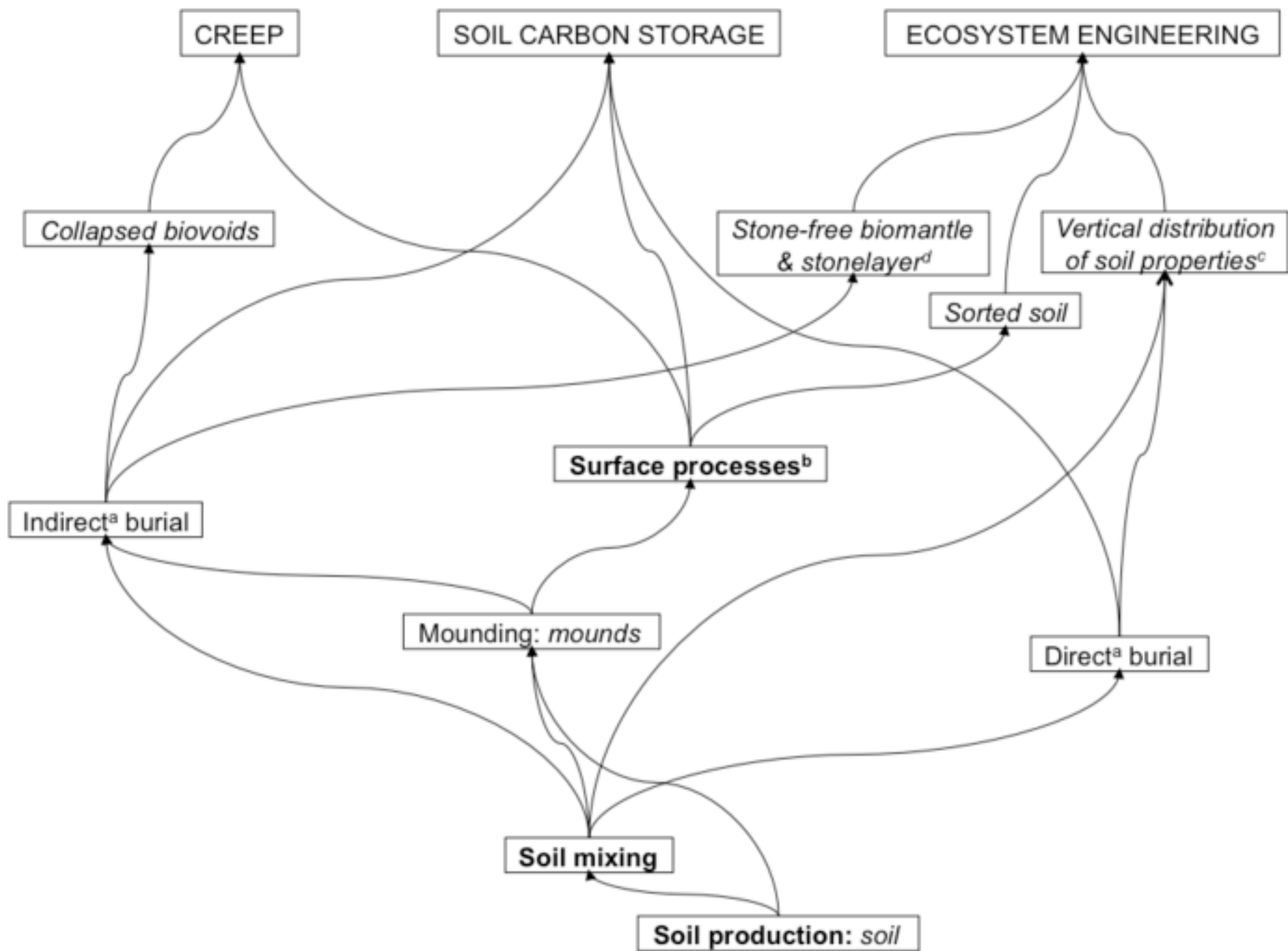[Click here to download high resolution image](#)

Figure showing relationships between soil processes and outcomes.

Boxes: CREEP, SOIL CARBON STORAGE, ECOSYSTEM ENGINEERING, Collapsed biovoids, Stone-free biomantle & stonelayer[d], Vertical distribution of soil properties[c], Sorted soil, Surface processes[b], Indirect[a] burial, Mounding: mounds, Direct[a] burial, Soil mixing, Soil production: soil
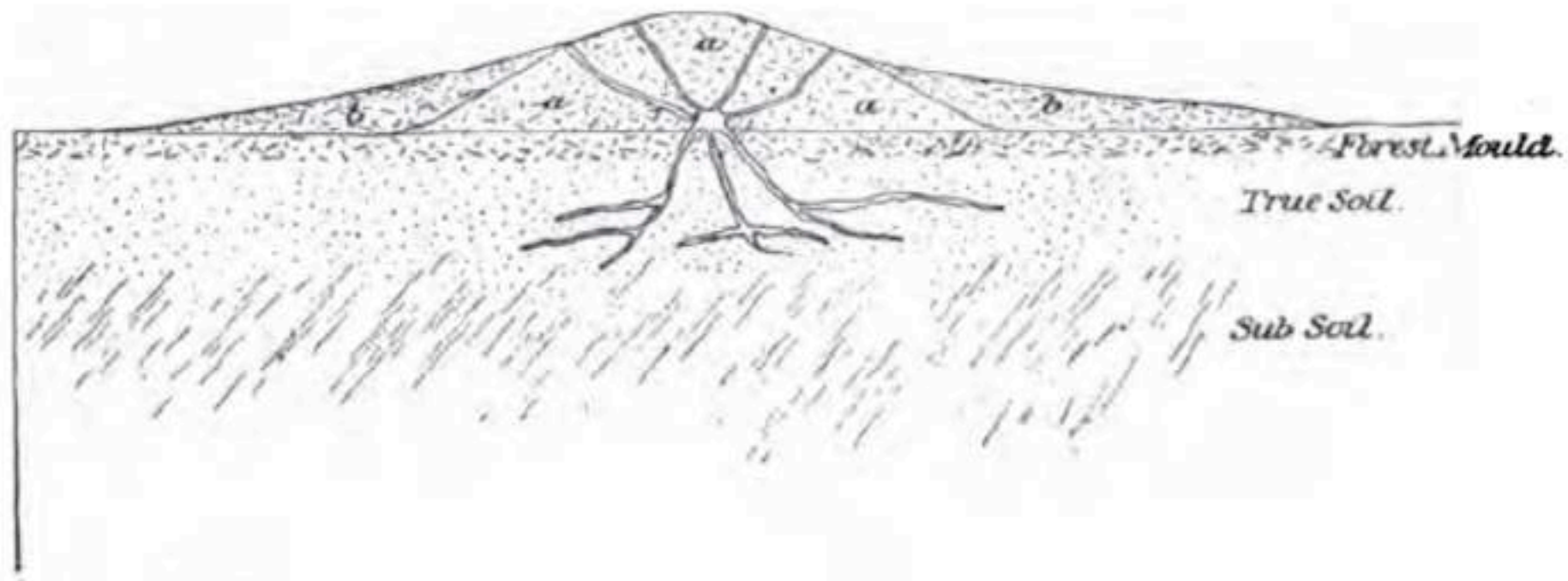
FIG. 11.—Effect of ant-hills on soil. *a a*, sand accumulated in hill; *b b*, material washed from hill, mingled with vegetable mold.
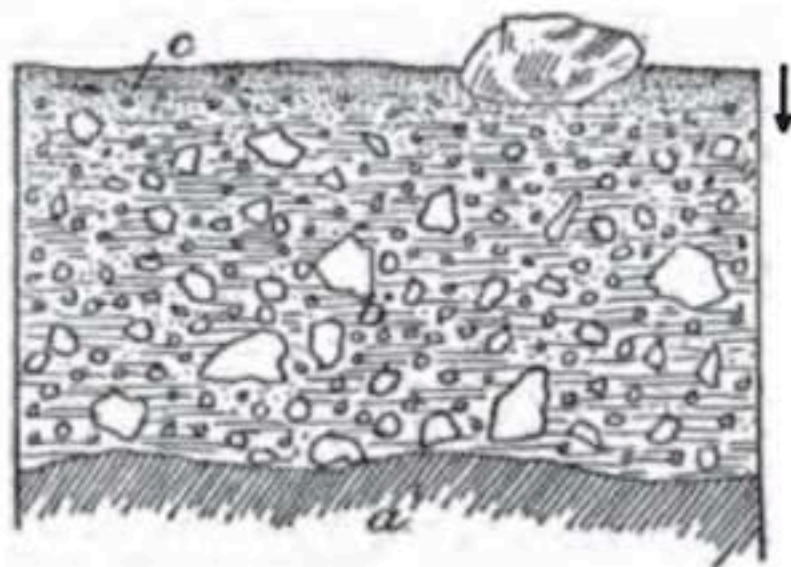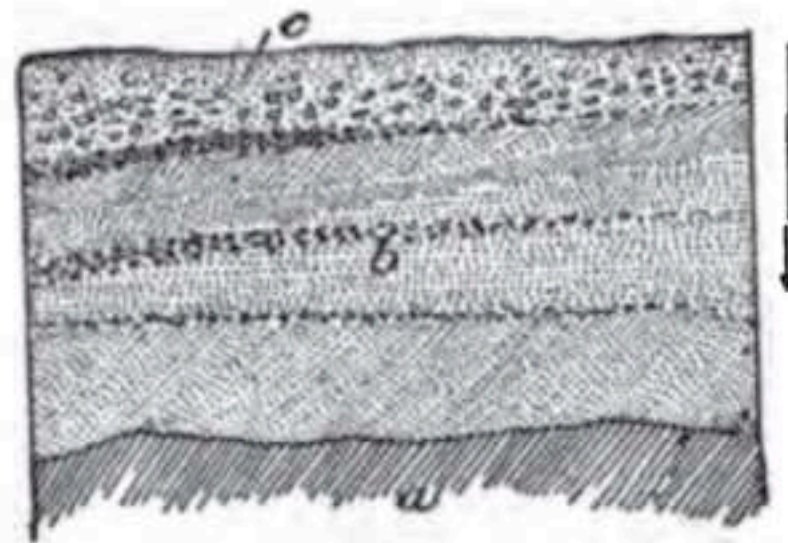
Till or bowlder clay.   *Stratifed drift.*

FIG. 2.—Sections showing the two common varieties of glacial detritus; a, bed rock; b, glacial detritus; c c, fine sand and clay brought up by ants and earthworms. The arrows show the relative permeability of the materials to water.
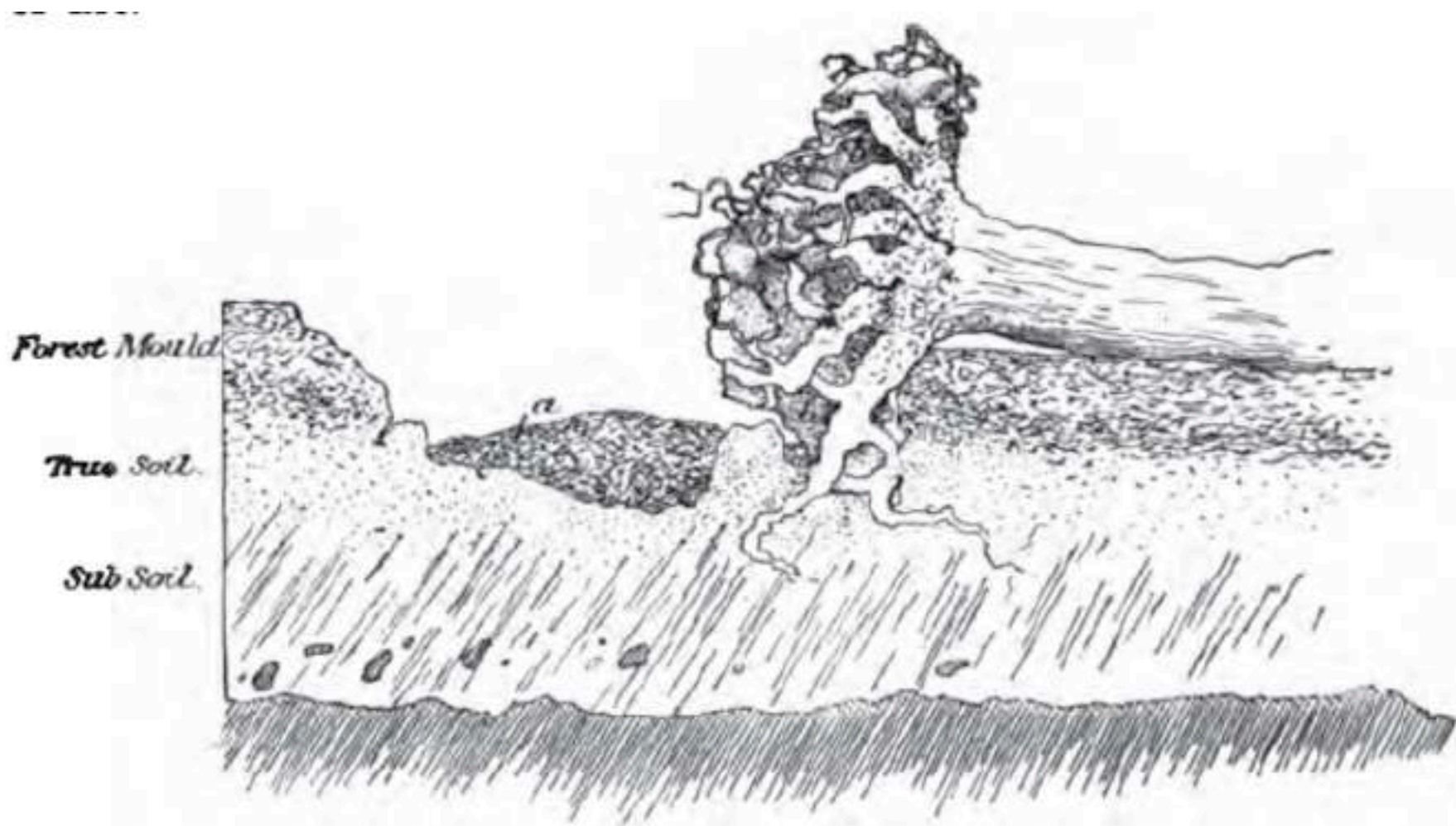
Forest Mould

True Soil.

Sub Soil.

FIG. 8.—First effect of overturned trees in introducing vegetable matter in soils. *a*, leaf mold accumulated in pit. (See also Fig. 3.)
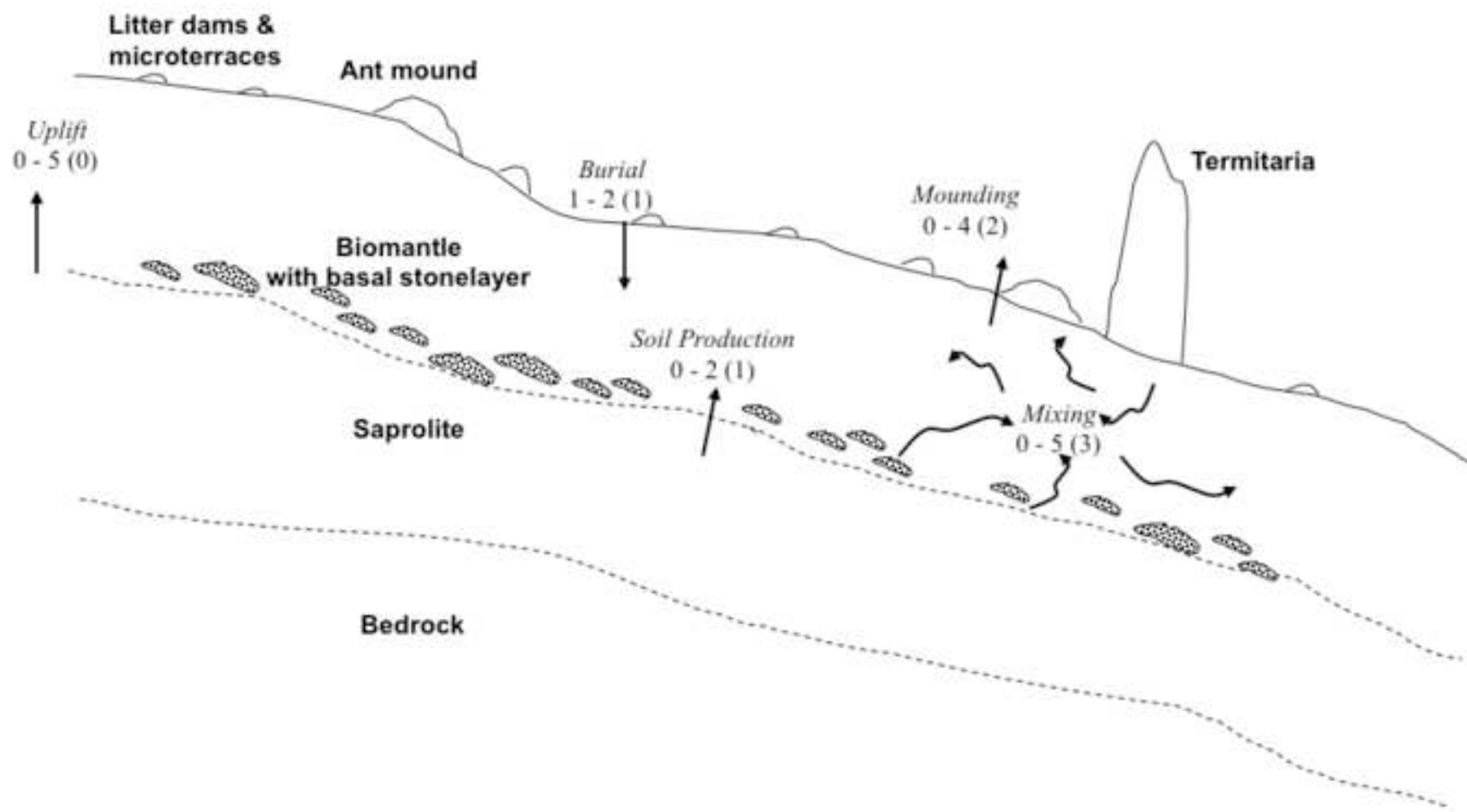
Figure 3
[Click here to download high resolution image](#)

Litter dams & microterraces

Ant mound

Uplift
0 - 5 (0)

Termitaria

Burial
1 - 2 (1)

Mounding
0 - 4 (2)

Biomantle with basal stonelayer

Soil Production
0 - 2 (1)

Saprolite

Mixing
0 - 5 (3)

Bedrock

Marangaroo Forest, large aliquot SAR protocol, age (ka)

Figure 5
[Click here to download high resolution image](#)
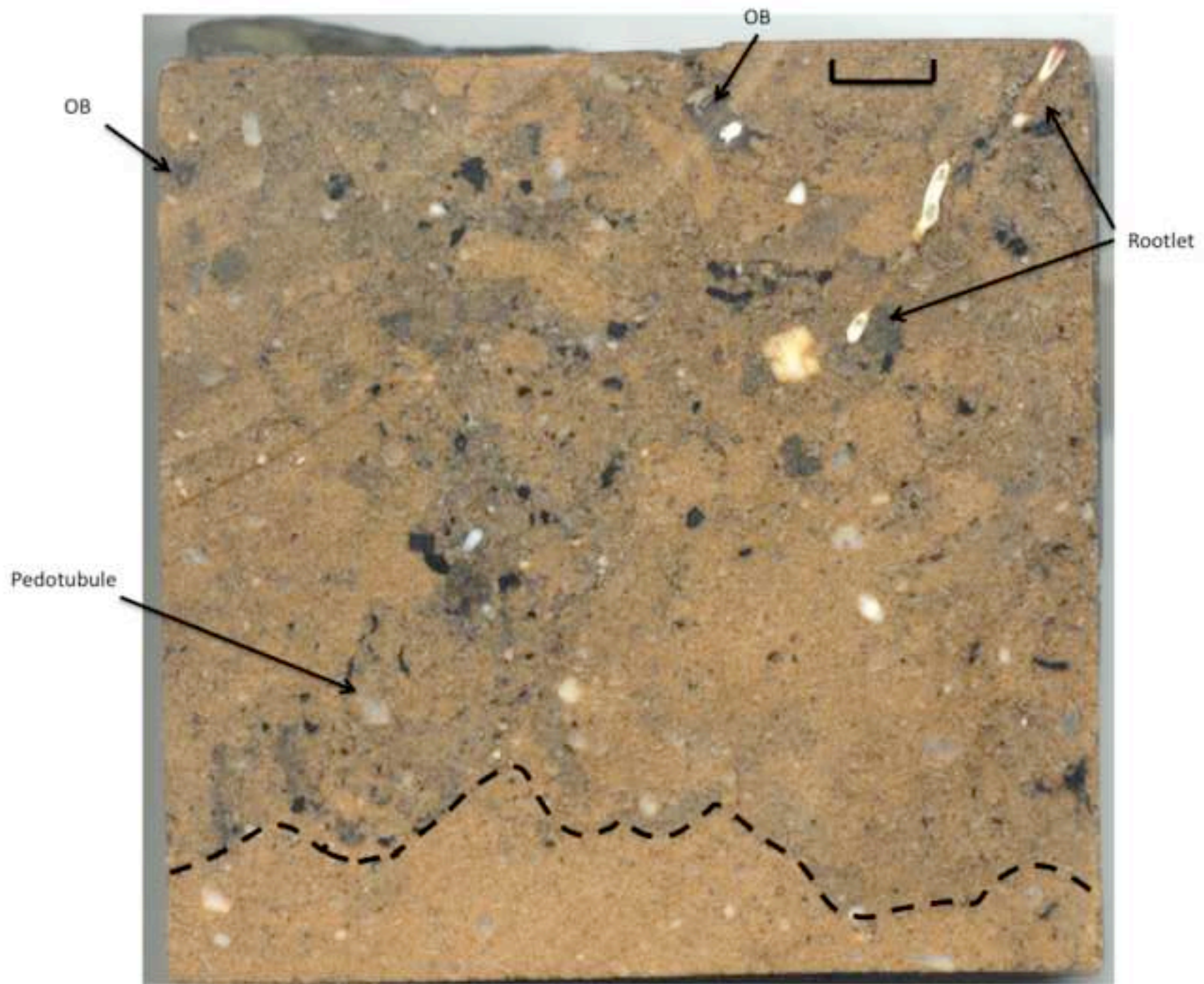
Table 1: A comparison of soil mounding, mixing and burial rates.

Fauna	Location	Climate[a]	M_d (t ha^{-1} y^{-1})[b]	M_x (t ha^{-1} y^{-1})	Burial rate (t ha^{-1} y^{-1})	Mixing factor[c]	Burial factor[d]	Reference
E'worms	Various locations, UK	Temperate maritime	19 – 40	26[f]	2 – 152[g]	0.65 – 1.4	0.05 – 8.0	Multiple[e]
"	East Lothian, UK	Temperate maritime	3 – 63	5 – 53	nr	0.08 – 18		Evans (1948)
"	France	Temperate maritime	20	20	nr	1.0		Bouché 1981 in Müller-Lemans & van Dorp (1996)
Ants & e'worms	Côte d'Ivoire	Tropical wet & dry	22 – 28	730 – 1100	nr	26 – 50		Lavelle (1978)
E'worms	NSW, Australia	Humid subtropics	5 – 6	127	nr	21 – 26		Humphreys and Field (1998)

nr = not recorded

[a]After Young and Saunders (1986)

[b]Units t/ha/y can be converted to m/My, using soil density (nominally 1.4 g cm^{-3})

[c]Mixing factor = mixing rate / mounding rate

[d]Burial factor = burial rate / mounding rate

[e]Surrey, Darwin (1881) which is similar to Evans and Guild (1947), East Lothian.

[f]Rate of ingestion in Cumbria, Satchell (1967)

[g]Various sites, Darwin (1881)

Table 2: Maximum estimates of biotic and aggregate soil flux for various field sites.

Flux type	Location	Climate	Flux ($cm^2\,a^{-1}$)	Methods	Reference
Earthworms	Greater London, UK	Temperate maritime	0.244	Field survey	Darwin (1881)
Thomomys bottae (Pocket Gopher)	California, USA	Mediterranean	0.48 – 6.31	Field survey	Black and Montgomery (1991)
Thomomys bottae (Pocket Gopher)	California, USA	Mediterranean	30.8	Field survey	Gabet (2000)
Tree uprooting[a]	Canterbury, New Zealand	Temperate maritime	12 ± 8	22.6 ka tephra	Roering et al. (2002)
Biotic[b]	NSW, Australia	Temperate maritime	37.5 ± 12.2	TCN	Heimsath et al. (2000; 2002)
Frost-creep	Wyoming, USA	Polar/montane	182 ± 20; 169 ± 14	TCN	Small et al. (1999)
Aggregate	Pacific North West, USA	Temperate maritime	49 ± 37		Reneau (1988) cited in McKean et al. (1993)
Aggregate	Oregon, USA	Temperate maritime	36 ± 16		Roering et al. (1999)
Aggregate	Oregon, USA	Temperate maritime	32 ± 23	[14]C	Reneau and Dietrich 1991
Post-fire dry ravel	Oregon, USA	Temperate maritime	110 ± 35	Field survey	Roering and Gerber (2005)
Aggregate	California, USA	Mediterranean	360 ± 15	MCN	McKean et al. (1993)

TCN = in situ terrestrial cosmogenic nuclides

MCN = meteoric cosmogenic nuclides

[a]Presumably other functional groups too

[b]Several functional groups

Table 3: Synonyms and variants of the term bioturbation in soil science.

Synonym/variant	Reference	Comments
Pedoturbation, with a prefix such as 'biological', 'biotic', 'faunal', or 'ant'	Hole (1961), Baxter & Hole (1967)	Pedoturbation is used in older soil science literature to refer to any form of soil mixing, therefore requiring a prefix to refer to forms of bioturbation.
Faunalturbation	Johnson (1990)	Bioturbation by animals only.
Floralturbation	Johnson (1990)	Bioturbation by plants only.
Biopedoturbation	Whitford & Kay (1999)	A combination of the older and newer terms. Rarely used.
Biomixing (or 'mixing' with a prefix such as 'biotic')	Johnson et al. (2005)	Used in the context of general mixing where a distinction from 'abiotic mixing' is required. Refers to subsurface activity only. Rarely used in soil science, more common in marine sciences.

Table 4: Twenty examples of terrestrial vertebrate bioturbators.

Group	Common name	Activity/Formation	Key reference(s)
Rodents	Pocket gopher	Burrows	Thorn, 1978; Johnson, 1989; Gabet, 2000; Reichman and Seabloom, 2002
	Ground squirrel	Burrows	Khodashova and Dinesman, 1961; Price, 1971
	Prairie dog	Burrows (towns)	Thorp, 1949; Sheets et al., 1971
	Mole rat	Burrows	Reichman and Jarvis, 1989
	Marmot	Burrows	Tadzhiyev and Odinoshoyev, 1987
	Mole	Burrows	Imeson, 1976
	Rabbit	Burrows (warrens)	Eldridge et al., 2006
	Armadillo	Burrows	Zimmerman, 1990
	Wombat	Burrows (warrens)	Löffler and Margules, 1980; McIlroy et al., 1981
Other mammals	Badger	Burrows (setts) and predatory digging	Voslamber and Veen, 1985; Johnson and Johnson, 2004
	Aardvark	Burrows, excavates ant/termite mounds	Dean and Siegfried, 1991
	Arctic fox	Burrows (dens)	Smits et al., 1988
	Grizzly bear	Foraging/predatory digging and burrows (dens and daybeds)	Butler, 1992
Birds	Lyrebird	Display mounds and foraging	Adamson et al., 1983; Mitchell, 1988
	Brush Turkey	Incubation mounds and foraging	Troy and Elgar, 1991

Reptiles	European bee-eater	Burrows	Casas-Criville and Valera, 2005
	Bull Snake	Burrows	Carpenter, 1982
	Iguana	Burrows	Mora, 1989; Burger and Gochfeld, 1991
	Gopher tortoise	Burrows	Butler, 1995
Amphibians	Manitoba toad	Hibernation mounds	Ross et al., 1968

Table 5: Description of Dystral Regosoil from Pit 3 at Marrangaroo (Wilkinson 2005; Wilkinson et al. 2005).

Horizon	Depth (cm)	Description
O_i	Surface	
A	0-5	Light olive brown, 2.5Y5/3d to olive brown, 2.5Y4/3 m; loamy (coarse) sand; few, small, quartz pebbles; single grain fabric; soft; non-sticky; field pH 4.5-5; sharp, wavy to:
E	5-8	Light olive brown, 2.5Y5/4d and 2.5Y5/3m; sandy loam; few, small, quartz pebbles; earthy fabric; slightly hard; very slightly sticky; field pH 5; clear planar to:
B_w	8-28	Brownish yellow, 10YR6/8d to yellowish brown, 10YR5/8m; sandy loam; few to common, small to medium, quartz pebbles; earthy fabric; friable; very slightly sticky; field pH 5-5.5; gradual, planar to:
C_{ox}	28-55	Brownish yellow, 10YR6/8d and m; clayey (coarse) sand; common, medium, quartz pebbles; earthy fabric; friable; non-sticky; field pH 5.5-6; clear wavy to:
C_r	55-86	Weathered sandstone. Yellow, 2.5Y7-8/4d and 2.5Y7/6m; sand with patches of clayey sand; few, medium, quartz pebbles; single grain fabric; slightly hard; non-sticky; field pH 6;

Table 6: Comparison of bioturbation metrics

Symbol	Description	Estimation methods & timescales	Units
M_d	*Mounding*: soil deposited at the surface by soil animals. Three types of ecological and geomorphic significance are recognised (Humphreys and Mitchell, 1983). *Type-1 mounds*. Soil is deposited at the surface as if it was waste and consists of loose particles or aggregates. There is no attempt to rework the material and it does not form part of the nest system. Examples include earthworm casts, many ant species such as the funnel ant, gopher mounds etc. *Type-2 mounds*. Soil is used to construct an above surface mound and becomes part of the nest system. Examples include termitaria and many mound building ant species. *Scrapes*. Shallow surface excavations, diggings etc mostly performed in the pursuit of food or in gathering litter and soil to construct a nest. Examples of the former include bandicoots, and many birds, and of the later megapodes and lyrebirds	Mounds are collected from quadrats, dried and weighed. Alternatively, mound dimensions are measured for volume. Estimates apply over sample period (typically 10^0 y)	$L^3 L^{-2} T^{-1}$ or $M L^{-2} T^{-1}$
M_x	*Mixing*: soil redistributed below the surface within the soil profile. In many situations the same species involved in mounding also undertake mixing. But there are many species that only or are mostly involved in mixing including many earthworm species. Of potential interest is the mixing that takes place within a pedologic horizon compared to mixing between horizons.	Mixing has been determined by earthworm ingestion rates and, for other fauna, soil fabric studies. Optically Stimulated Luminescence (OSL) estimates burial, one component of mixing, over $10^1 – 10^6$ y (Wilkinson and Humphreys, 2005). Soil production has been measured using cosmogenic radionuclides (Wilkinson and Humphreys, 2005)	$L^3 L^{-2} T^{-1}$ or $M L^{-2} T^{-1}$
Q_{sb}	*Biotic soil flux*: bioturbated soil displaced downslope as a result of biotic activity within soil. This can involve mounds, specifically the portion of the mound in the downslope position following excavation, which is a surface flux, Q_{smb}, or within	When involving mounds, measurements can be made of dry weight or volume of transported soil and its displacement distance in both an	$L^3 L^{-1} T^{-1}$ or $M L^{-1} T^{-1}$

the soil, Q_{smx}. Both of these are of geomorphic interest as they are tied to soil creep and hence diffusive explanations of soil transport and hillslope evolution. The units of measure differ from M_d and M_x because it is the amount of soil that passes a point (expressed as a unit length) on the slope rather than an area that is of interest.

upslope and downslope direction from point of origin

Table 7: Relative importance of different biota that mound and mix soil (Paton et al., 1995)

Climate[a]	Ranking
Polar/montane	vertebrates > ?
Temperate continental	earthworms > vertebrates ≥ ants > other invertebrates
Temperate maritime	earthworms > ants > vertebrates
Mediterranean	earthworms > vertebrates > termites ≥ ants
Semi arid	vertebrates > termites ≥ ants
Humid subtropics	ants = earthworms = vertebrates > termites
Tropical wet & dry	earthworms > termites = ants
Humid tropics	earthworms > termites
Arid	vertebrates > invertebrates

[a]After Young and Saunders (1986)

Table 8: The possible role of bioturbation in soil organic carbon (SOC) turnover, via direct and indirect links.

Links	Inputs	Outputs
Direct	Litter sequestration into nests, termitaria, burrows, etc. (Darwin, 1881, Jegou et al., 1998; Lobry de Bruyn, 1999; Mariani et al., 2007; Yoo *et al.* 2005) Bioturbator wastes e.g. casts, root exudates, dead tissues (Bossuyt et al., 2004; Pulleman et al., 2005; Zhang and Hendrix, 1995) Bioturbator respiration	Bioturbator respiration (Millikin and Bowden, 1996; Tripathi and Sharma, 2006) Iterations of comminution & subsequent respiration Erosion via direct creep processes
Indirect	Infilling of biogenic pits with litter (Shaler, 1891) Redistribution of biogenic mounds & associated litter burial (Shaler, 1891) Subsurface mixing & burial: transport to microbe-poor sites	Mixing & mounding: transport to microbe-rich sites & subsequent heterotrophic respiration Erosion via indirect creep processes