

1 **Title page**

2 **Soil fauna: key to new carbon models**

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49 **Abstract**

50 Soil organic matter (SOM) is key to maintaining soil fertility, mitigating climate change,
51 combatting land degradation, and conserving above- and below-ground biodiversity and
52 associated soil processes and ecosystem services. In order to derive management options for
53 maintaining these essential services provided by soils, policy makers depend on robust, predictive
54 models identifying key drivers of SOM dynamics. Existing SOM models and suggested
55 guidelines for future SOM modelling are defined mostly in terms of plant residue quality and
56 input and microbial decomposition, overlooking the significant regulation provided by soil fauna.
57 The fauna control almost any aspect of organic matter turnover, foremost by regulating the
58 activity and functional composition of soil microorganisms and their physical-chemical
59 connectivity with soil organic matter. We demonstrate a very strong impact of soil animals on
60 carbon turnover, increasing or decreasing it by several dozen percent, sometimes even turning C
61 sinks into C sources or vice versa. This is demonstrated not only for earthworms and other larger
62 invertebrates but also for smaller fauna such as Collembola. We suggest that inclusion of soil
63 animal activities (plant residue consumption and bioturbation altering the formation, depth,
64 hydraulic properties and physical heterogeneity of soils) can fundamentally affect the predictive
65 outcome of SOM models. Understanding direct and indirect impacts of soil fauna on nutrient
66 availability, carbon sequestration, greenhouse gas emissions and plant growth is key to the
67 understanding of SOM dynamics in the context of global carbon cycling models. We argue that
68 explicit consideration of soil fauna is essential to make realistic modelling predictions on SOM
69 dynamics and to detect expected non-linear responses of SOM dynamics to global change. We
70 present a decision framework, to be further developed through the activities of KEYSOM, a
71 European COST action, for when mechanistic SOM models include soil fauna. The research
72 activities of KEYSOM, such as field experiments and literature reviews, together with dialogue
73 between empiricists and modellers, will inform how this is to be done.
74

75 **Keywords**

76 Carbon turnover, soil organic matter modelling, soil invertebrates, aggregate formation, spatial
77 heterogeneity, regional differences, ecosystem engineers, COST Action KEYSOM
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79 **1. Introduction**

80 Despite continuous refinement over the past decades, estimates of the global carbon cycle still
81 show large discrepancies between potential and observed carbon fluxes (Ballantyne et al., 2012;
82 Schmitz et al., 2014). Soils contain more carbon than the atmosphere and aboveground vegetation
83 together (Brevik et al., 2015) and play an important role for many of the recently adopted UN
84 Sustainable Development Goals (Keestra et al., 2016). Therefore soil organic matter (SOM)
85 modelling is key to understanding and predicting changes in global carbon cycling and soil
86 fertility in a changing environment. SOM models can facilitate a better understanding of the
87 factors that underlie the regulation of carbon cycling and the persistence of SOM. The predictive
88 power of current global SOM models is, however, limited, as the majority relies on a relatively
89 restricted set of input parameters such as climate, land use, vegetation, pedological characteristics
90 and microbial biomass (Davidson and Janssens, 2006). Other parameters, such as the leaching of
91 organic matter or soil erosion of organic matter have been suggested for improving model
92 predictions, and recent research has demonstrated what drastic effects e.g. living roots (Lindén et
93 al., 2014) and soil fungi (Clemmensen et al., 2013) exert on SOM persistence. In an overview on
94 the performance of SOM models, none of 11 tested models could predict global soil carbon

95 accurately, nor were 26 regional models able to assess gross primary productivity across the US
96 and Canada (Luo et al., 2015).
97 Some years ago Schmidt et al. (2011) proposed eight “key insights” to enrich model predictions
98 on the persistence of SOM. However, they ignored a major component of SOM dynamics, soil
99 fauna, which play a fundamental role in most of the insights they propose (e.g. Fox et al., 2006;
100 Jimenez et al., 2006; Osler and Sommerkorn, 2007; De Deyn et al., 2008; Wilkinson et al., 2009).
101 By moving through and reworking soil, feeding on living plant roots, detritus and all types of
102 microorganisms growing on these, soil animals are intimately involved in every step of SOM
103 turnover. Omission of soil fauna from SOM models will, therefore, hamper the potential
104 predictive power of these models.
105 In a review focusing mostly on large mammals, terrestrial herbivores and aquatic ecosystems,
106 Schmitz et al. (2014) recently called for “animating the carbon cycle”. Bardgett et al. (2013)
107 argued that differential responses of various trophic groups of aboveground and belowground
108 organisms to global change can result in a decoupling of plant-soil interactions, with potentially
109 irreversible consequences for carbon cycling. A correlative large scale field study has suggested
110 that including soil animal activities could help clarify discrepancies in existing carbon models (de
111 Vries et al., 2013). Similar attempts to connect animal activity to carbon cycling occurred in the
112 past (e.g. Lavelle and Martin, 1992; Lavelle et al., 1998; Lavelle and Spain, 2006; Osler and
113 Sommerkorn, 2007; Brussaard et al., 2007; Sanders et al., 2014), without any further change in
114 the structure of carbon models. This was partly due to a lack of communication between
115 modellers and experimenters, but also because the magnitude of animal effects on SOM
116 dynamics remains poorly quantified (Schmitz et al., 2014).
117 Here we use the ‘key insights’ proposed by Schmidt et al. (2011) as a basis to review current
118 evidence and to identify research needs on the relationship of soil fauna to SOM dynamics. Our
119 review justifies the relevance of incorporating the soil fauna into SOM models. How important
120 animal activities are for manifold geological and pedological processes has been reviewed
121 repeatedly (e.g. Swift et al., 1979; Wilkinson et al., 2009), but carbon turnover – which is highly
122 dynamic and both directly and indirectly affected by animals – never had been the focus. Due to
123 their prime role in most processes in soil (Briones, 2014) we mostly focus on earthworms, but
124 also give examples for other groups of soil fauna whose role in C turnover appears to be much
125 more relevant than thought thus far (e.g. David, 2014). We point out regional differences in
126 climate, soils and land use with respect to soil fauna composition, abundance and activity and
127 derive implications for SOM modelling. Finally, we introduce a new COST Action (ES 1406)
128 that is working on the implementation of soil fauna into SOM models, also exploring the pros and
129 caveats in such a process.
130

131 **2. Key insights**

132 The eight ‘key insights’ compiled by Schmidt et al. (2011) are shown in Fig. 1, together with the
133 most important activities of soil animals affecting them. As many animal-mediated processes are
134 tightly interconnected, they also matter for most of these insights. For instance, aggregate
135 formation in faeces simultaneously affects molecular structure, humic substances, physical
136 heterogeneity and soil microorganisms. In the following text we briefly summarize the role of
137 animal activities for each of the ‘key insights’. As a more detailed example of animal impacts on
138 SOM turnover, we consider their role on soil aggregate formation in a separate section.

139 **2.1. Molecular structure**

140 The molecular structure of root exudates and dead organic matter is modified during
141 metabolisation, decomposition and associated food web transfer, both by microorganisms and
142 soil fauna. Prominent examples are the release of ammonium by bacterivorous protozoans and

143 nematodes, due to their higher C:N ratio compared to their bacterial prey (Osler and
144 Sommerkorn, 2007), or the strong mediation of the direction and rate of humus formation by soil
145 animals (see 2.2). Recently, the significant impact of eight different species of ants over 25 years
146 on mineral dissolution and accumulation of calcium carbonate has even been discussed in the
147 context of geoengineering and carbon sequestration (Dorn, 2014).

148 Many soil animals ingest and process SOM (and accompanying microorganisms) in their gut
149 system, where it is partly assimilated with the help of mutualistic gut microflora and partly
150 egested. Metabolisation alters the chemical structure of ingested SOM (Jiménez and Lal, 2006;
151 Hedde et al., 2005; Coulis et al., 2009; Frouz, 2015b; Schmitz et al., 2014) and, consequently, the
152 decomposition dynamics of animal faeces, which can be a substantial component of SOM
153 (humus). Humification as such renders SOM less decomposable (Blume et al., 2009; Dickinson,
154 2012) whereas the alkaline milieu in invertebrate midguts accelerates mineralisation (e.g. Li and
155 Brune, 2007).

156 For instance, earthworm casts have species-specific NIR spectral signatures, indicating presence
157 of specific organic compounds (Hedde et al., 2005). Under grass/legume pasture they are
158 characterized by significant enrichment of slightly-altered plant residues in the sand particle size
159 (> 53 µm). CPMAS ¹³C NMR (Cross-Polarization Magic Angle Spinning Carbon-13 Nuclear
160 Magnetic Resonance) spectra showed that earthworm casts and surrounding soil were dominated
161 by carbohydrates, with a decrease of O-alkyl C and an increase of alkyl C with decreasing
162 particle size (Guggenberger et al., 1996). Moreover, earthworms likely possess a unique
163 capability of neutralizing plant polyphenols that otherwise strongly decrease decomposition rates
164 of fresh plant litter (Liebeke et al., 2015). Micro- and mesofauna excrete ammonium or dissolved
165 organic carbon (Filser, 2002; Fox et al., 2006; Osler and Sommerkorn, 2007), and affect the
166 quantity of microbial metabolites (Bonkowski et al., 2009). Gut passage, defecation, excretion
167 together with bioturbation by macro- and mesofauna facilitate humification and decomposition,
168 altering also nutrient stoichiometry (Bohlen et al., 2004). These modifications in the molecular
169 structure of SOM due to soil fauna activity have significant effects on its dynamics (Swift et al,
170 1979; Guggenberger et al., 1995; Blume et al., 2009; Dickinson, 2012 and other references
171 related to points 1 and 2 in Table 1).

172 **2.2. Humic substances**

173 As stated above, humification increases SOM stability. The term “humic substances” (here
174 defined as very large and highly complex, poorly degradable organic molecules with manifold
175 aromatic rings; Lehmann and Kleber, 2015) may be considered problematic by part of the
176 scientific community: neither is the concept itself clear, nor is there any evidence that the often
177 mentioned highly complex large organic molecules play any relevant role in organic matter
178 stabilisation under natural conditions (Schmidt et al., 2011; Lehmann and Kleber, 2015).
179 However, here we stick to it when referring to the “insights”, simply for reasons of consistency
180 with the article our argumentation is based on Schmidt et al. (2011). We acknowledge that
181 “humus” or “humic substances” represent a continuum of more or less decomposed dead organic
182 matter of which energy content and molecule size mostly should decrease over time, and that
183 water solubility, sorption to the mineral matrix and accessibility for microorganisms are highly
184 relevant for OM turnover (Lehmann and Kleber, 2015).

185 Humic substances are formed during the gut passage: organic matter in young soils and humic
186 horizons almost completely consists of soil animal faeces (Lavelle, 1988; Martin and Marinissen,
187 1993; Brussaard and Juma, 1996). Humus forms mainly comprise animal casts, e.g. casts of ants,
188 isopods, millipedes, beetle larvae or termites in deadwood, of insect larvae and spiders in leaf
189 litter, or casts of collembolans, mites and enchytraeids in raw humus. In his review, David (2014)
190 considered macroarthropod casts being a factor of partial SOM stabilisation, rather than hotspots
191 of microbial activity. The dark colour of casts (compared to the ingested organic material)
192 visually demonstrates the strong chemical OM modification in animal guts, which is

193 accompanied by a substantial physical modification. Clay-humus complexes, physically
194 protecting organic matter (Jiménez and Lal, 2006), are mainly faeces of earthworms and
195 diplopods (see also Sect. 2.5 on physical heterogeneity). Due to differences in feeding
196 preferences, gut microflora, SOM quantities consumed etc. of soil animals, their faeces vary in
197 size, shape and quality not only between fauna groups, but also between species within one group
198 (see Sect. 3 on aggregate formation). Discovering the important role of animal faeces in
199 humification is essential to improve our understanding of carbon dynamics in soil.

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202 **2.3. Fire-derived carbon**

203 Fire-derived carbon is chemically highly condensed and thus often hardly degradable. However,
204 its stability in soil is variable and still poorly understood (Schmidt et al., 2011; Wang et al.,
205 2016). Two of the factors identified by a meta-analysis on the stability of biochar in soil were
206 association with aggregates and translocation in the soil profile (Wang et al., 2016), which are
207 both strongly affected by soil fauna (see Sect. 2.5, 2.6 and 3). Microbial recolonisation of burned
208 sites is mediated by wind and soil animals that survived in soil or emigrated from neighbouring
209 areas, e.g. by macro- and mesofauna, birds and mice (Malmström, 2012; Zaitsev et al., 2014).
210 Besides, soil fauna also ingest the charcoal particles (Eckmeier et al., 2007; see Table 1). Due to
211 animal activity, charcoal is sorted by size and translocated down the soil profile. Mice and
212 earthworms (Eckmeier et al., 2007) and the tropical earthworm *Pontoscolex corethurus*
213 (Topoliantz and Ponge 2003; Topoliantz et al., 2006) had been suggested as responsible for rapid
214 incorporation of charcoal into the soil. Quantitative data are however scarce (Table 1). In spite of
215 potentially great importance, the effect of soil animals on the fate of the “black carbon” in soil
216 remains practically unknown (Ameloot et al., 2013).

217 **2.4. Roots**

218 Roots not only represent a major input pathway of carbon into soil, but together with associated
219 microflora they also have a large influence on the turnover dynamics of existing soil carbon
220 (Finzi et al., 2015). Roots preferably grow in existing soil cavities (Jiménez and Lal, 2006),
221 mostly formed by soil fauna (Wilkinson et al., 2009). Both burrowing and non-burrowing soil
222 animals have a strong impact on root growth, allocation, length and density (Brown et al., 1994;
223 Bonkowski et al., 2009; Arnone and Zaller, 2014). Animal grazing of root bacteria and
224 mycorrhiza affects their activity and community composition, and animal excreta are enriched in
225 micronutrients and selectively affect plant nutrition (Brown, 1995; Filser, 2002; Brussaard et al.,
226 2007). Root herbivores and rhizosphere grazers affect C allocation of roots (Wardle et al., 2004)
227 and largely regulate nutrient acquisition and plant productivity (Bonkowski et al., 2009). Not
228 only root herbivores, but also saprotrophic/microbivorous soil animals may obtain a significant
229 proportion of energy from plant roots (Pollierer et al., 2007). This suggests an animal-mediated
230 regulatory loop that connects plant roots and SOM.

231 **2.5. Physical heterogeneity**

232 Schmidt et. al. (2011) considered the physical disconnection between decomposers and organic
233 matter to be one reason for SOM persistence in deep soil. Yet, physical heterogeneity in soils
234 occurs at all spatial scales, and animals play a fundamental role in the distribution of organic
235 matter and associated microorganisms. According to body size, decomposers act at various
236 spatial scales, from micro-aggregates to landscapes (Ettema & Wardle, 2002; Jouquet et al.,
237 2006). They fragment organic residues, perform bioturbation, distribute dead organic matter and
238 generate smaller and larger organic matter hot spots (e.g. faecal pellets, ant and termite mounds).

239 Mounds and burrows made by soil fauna are obvious signs of physical heterogeneity created by
240 ecosystem engineers (Meysmann et al., 2006; Wilkinson et al., 2009; Sanders et al., 2014), which
241 significantly affect microorganisms, plants (Chauvel et al., 1999; Frelich et al., 2006), aggregate
242 stability (Bossuyt et al., 2005; 2006), hydraulic properties (Bottinelli et al., 2015; Andriuzzi et al.,
243 2016), sorption and degradation of sparingly soluble organic compounds (Edwards et al., 1992;
244 Bolduan and Zehe, 2006) and C emissions (Wu et al., 2013; Lopes de Gerenyu et al., 2015).
245 Earthworms in particular feed on organic and mineral parts of the soil and mix them (Eckmeier et
246 al., 2007; Wilkinson et al., 2009). The resulting clay-organic matter complexes considerably
247 increase SOM retention of soils (Jiménez and Lal, 2006; Fox et al., 2006; Brussaard et al., 2007),
248 although C loss from fresh casts is much higher than from surrounding soil (Zangerlé et al.,
249 2014). The impact on soil processes and physical heterogeneity varies considerably between
250 different groups of ecosystem engineers (Jouquet et al., 2006; Bottinelli et al., 2015). For
251 instance, some earthworm species strongly affect their physical environment while others are
252 more linked to the soil organic matter content (Jiménez et al. 2012).

253 **2.6. Soil depth**

254 In most soil types, pore volume, carbon content, associated biotic processes and temperature
255 variability strongly decrease with depth whereas other parameters such as bulk density and water
256 content increase – all of which significantly affect SOM turnover rates. The depth of organic
257 horizons varies with soil type, from almost zero to several metres. Thus, Schmidt et al. (2011)
258 identified soil depth as another “key insight”. Yet, digging animals play a key role in the
259 development of soil depth. A considerable part of physical heterogeneity are animal burrows that
260 can reach several meters deep. Bioturbation (e.g. by earthworms, termites, ants, beetle and
261 Diptera larvae, spiders, solitary bees and wasps, snails, isopods and amphipods, puffins, lizards,
262 porcupines, pigs, moles, voles, rabbits, foxes, or badgers) is a key process to the formation of soil
263 depth, soil structure and associated C translocation, as shown by several examples in Table 1 and
264 reviewed e.g. by Wilkinson et al. (2009).

265 **2.7. Permafrost**

266 In permafrost soil up to $1,672 * 10^{15}$ g carbon is stored (Tarnocai et al. 2009). Organism activity
267 is mostly restricted to the short periods of time when the upper cm of the soil isare thawed. Due
268 to unfavourable environmental conditions (resulting in low animal biomass, activity and
269 diversity), there is only little impact of fauna in permafrost soils (De Deyn et al., 2008). However,
270 fauna invasions, especially of the above-mentioned soil engineers, due to soil melting in tundra
271 and boreal forests are likely to have drastic effects (Frelich et al., 2006; Van Geffen et al., 2011).
272 Data on earthworm invasions in North American forests (Bohlen et al., 2004; Frelich et al., 2006;
273 Eisenhauer et al., 2007) show that they must be taken into consideration in carbon-rich soils,
274 particularly in melting permafrost soils (Frelich et al., 2006; Schmidt et al., 2011) where they
275 may affect many soil functions.
276

277 **2.8. Soil microorganisms**

278 After roots, microorganisms constitute by far the largest share of biomass in soil biota.
279 Accordingly, they have a crucial role in SOM turnover. They consume root exudates, dead
280 organic matter, attack plants and animals as pathogens or support them as mutualists. Finally,
281 microorganisms are the most important food source for the majority of soil animals, and to a
282 considerable part also for aboveground insects and vertebrates. Soil fauna comprise ecosystem
283 engineers as well as an armada of mobile actors connecting elements of the soil system,
284 mediating microbial processes (Briones, 2014). Countless isopods, ants, termites, enchytraeids,

285 microarthropods, nematodes or protozoans make large contributions to SOM turnover
286 underground (Persson, 1989; Filser, 2002; Wardle et al., 2004; Fox et al., 2006; Osler and
287 Sommerkorn, 2007; Wilkinson et al., 2009; Wu et al., 2013). They affect the activity and
288 community composition of soil microorganisms in multiple ways such as feeding, burrowing,
289 facilitating the coexistence of different fungal species (Crowther et al., 2011) or by modifying
290 micro-habitat conditions. Litter comminution by detritivores increases SOM accessibility for
291 microorganisms, and propagules are dispersed with body surface and casts. The gut environment
292 provides protected microsites with modified biotic and abiotic conditions, which increase
293 bacterial abundance substantially – e.g. by three orders of magnitude in earthworm guts (Edwards
294 and Fletcher, 1988). Grazing affects microbial biomass, activity and community composition, and
295 animal excreta modify nutrient availability for microorganisms (Brown, 1995; Filser, 2002).

296
297 Table 1 contains quantitative examples of animal activity taken from different biomes and land-
298 use types, showing that earthworms alone strongly affect each of the ‘key insights’. However,
299 much smaller soil animals can also have substantial effects (Table 1). It has to be kept in mind
300 that the separation of animals’ effects according to the insights is somewhat arbitrary as the
301 associated soil processes are often interconnected. This is particularly obvious for molecular
302 structure, humic substances, roots, physical heterogeneity, soil depth and microorganisms:
303 metabolisation implies by definition an alteration of the molecular structure, often associated with
304 the formation of humic substances. The stability of the latter has a very strong association with
305 physical protection, and whether metabolisation of dead organic matter occurs at all depends on
306 its horizontal and vertical distribution. For instance, earthworms will (a) translocate dead organic
307 matter both vertically and horizontally, (b) transform part of it via metabolisation, (c) mix
308 ingested OM with minerals, thus affecting its physical protection, (d) increase and alter the
309 microbial community and (e) affect hydraulic properties and aeration of the soil through digging
310 and tunnelling, which has an immediate impact on the activity of microorganisms and on root
311 growth.

312 As this example illustrated only the most important aspects of interacting processes,, the next
313 section provides a more elaborate overview on aggregate formation.

314 3. Aggregate formation

315 The modern view on the stability of organic matter in soils requires a thorough understanding of
316 aggregate structure and formation including the role of soil biota (Lehmann and Kleber, 2015).
317 Soil aggregation is the process by which aggregates of different sizes are joined and held together
318 by different organic and inorganic materials. Thus, it includes the processes of formation and
319 stabilisation that occur more or less continuously, and can act at the same time. With clay
320 flocculation being a pre-requisite for soil aggregation, the formation of aggregates mainly occurs
321 as a result of physical forces, while their stabilisation results from a number of factors, depending
322 in particular on the quantity and quality of inorganic and organic stabilising agents (Amézketa,
323 1999).

324 By bioturbation, feeding and dispersal of microbial propagules soil animals regulate all of the
325 above forces and agents, and are therefore a crucial factor in the formation and stabilisation of
326 soil aggregates. Earthworms, many insect larvae and other larger fauna may stabilise aggregate
327 structure by ingesting soil and mixing it intimately with humified organic materials in their guts,
328 and egesting it as casts or pellets (Tisdall and Oades, 1982; Oades, 1993).

329 Earthworms have a direct and fast impact on microaggregate formation and the stabilisation of
330 new C within these microaggregates (Bossuyt et al., 2005) (Table 1). There are several
331 mechanisms to explain the increase of micro- and macroaggregate stability by earthworms, but no
332 mechanism has been quantified in relation to population size yet. Effects are related to ecological
333 groups of earthworms, associated with feeding habit, microhabitat in the soil profile, and burrow
334 morphology. However, irrespective of this classification, species may enhance or mitigate soil

335 compaction (Blanchart et al., 1997; Guéi et al., 2012). The tensile strength of casts (roughly
336 defined as the force required to crush dried aggregates, i.e. an indirect measure of physical SOM
337 protection) appears to be species dependent: for example, the casts of *Dendrobaena octaedra*
338 have a lower tensile strength compared to those of *L. terrestris* (Flegel et al., 1998). Similarly,
339 organic carbon and water-stable aggregation was significantly higher in casts of *L. terrestris* than
340 in casts of *A. caliginosa* (Schrader and Zhang, 1997).

341 Some research, however, suggests that earthworm activity can also evoke soil degradation.
342 Shipitalo and Protz (1988) proposed that ingestion of soil by earthworms results in disruption of
343 some existing bonds within micro-aggregates and realignment of clay domains. Therefore, fresh
344 casts are more dispersible than uningested soil, contributing to soil erosion and crusting.
345 Significant improvement in the water stability of fresh, moist casts only occurs when
346 incorporated organic debris from the food sources is present and when moist casts are aged or
347 dried. Nevertheless, in the long term, casting activity enhances soil aggregate stability.

348 However, our understanding of the contribution of soil fauna to aggregate formation and
349 stabilisation is limited, and mostly qualitative in nature. Different methodologies complicate the
350 comparison among aggregate stability data (Amézketa, 1999). Data in terms of functional
351 response to density are limited as many studies have been conducted in arable systems, where the
352 diversity and abundance of soil animals are reduced as a consequence of tillage, mineral
353 fertilizers and pesticide use. Recently, some studies have emerged. A negative correlation
354 between earthworm abundance and total macroaggregates and microaggregates within
355 macroaggregates in arable treatments without organic amendments could be linked to the
356 presence of high numbers of *Nematogena lacuum*, an endogeic species that feeds on excrements
357 of other larger epigeic worms and produces small excrements (Ayuke et al., 2011). Under the
358 conditions studied, differences in earthworm abundance, biomass and diversity were more
359 important drivers of management-induced changes in aggregate stability and soil C and N pools
360 than differences in termite populations. Another study highlighted that in fields converted to no-
361 tillage earthworms incorporated C recently fixed by plants and moved C from soil fragments and
362 plant residues to soil aggregates of >1 mm (Arai et al., 2013). Thus, soil management practices
363 altering fauna activities may have a significant effect on the re-distribution of soil organic matter
364 in water-stable aggregates, impacting agronomically favourable size fractions of water-stable
365 macro-aggregates, and water-stable micro-aggregates which are the most important source of
366 carbon sequestration (Šimanský and Kováčik, 2014).

367

368 **4. Regional differences in climate, soils and land use**

369 In a global meta-analysis spanning several continents, García-Palacios et al. (2013) show that
370 across biomes and scales the presence of soil fauna contributes on average 27% to litter
371 decomposition. Depending on the situation this contribution can be substantially lower or higher.
372 For instance, the authors report an average increase in decomposition rates of 47% in humid
373 grasslands whereas in coniferous forests this figure amounts to only 13%. The high impact of soil
374 fauna in humid grasslands is all the more important as such grasslands are among those
375 ecosystems that are most severely affected by global environmental change (Chmura et al., 2003;
376 Davidson and Janssen, 2006).

377 Many of our examples refer to earthworms and temperate regions as they have been studied most
378 intensively. However, we suggest that any dominant group of soil fauna, irrespective of body size
379 or the ability to create larger soil structures, may substantially affect carbon dynamics. Table 1
380 gives a number of respective case studies. The key players and specific effects of soil animals
381 vary across space (Fig. 2), with increasing importance for SOM dynamics in humid-warm and
382 nutrient-limited conditions (Persson, 1989; Filser, 2002; Wardle et al., 2004; Fox et al., 2006;
383 Osler and Sommerkorn, 2007; De Deyn et al., 2008; Briones, 2014). Once key players in a given
384 ecosystem have been identified as relevant for being included in SOM models (see Sect. 6 and

385 Fig. 3), more detailed information on their biology is required, in particular on their activity, their
386 ecological niche and corresponding tolerance limits. All this varies with species, and often
387 extremely within one systematic group. Variation in drought or soil temperature towards limiting
388 conditions will first increase (stress response, e.g. downward migration) and then strongly
389 decrease activity (mortality or transition to inactive resting stage). Some key players will exhibit
390 high abundance and be extremely active throughout the year (Wilkinson et al., 2009), others
391 might only be moderately relevant during a short period of time; the contribution of a third group
392 might be considered insignificant.

393 Also ecosystem engineers differ between soil types, biomes and land-use types, from rodents and
394 ants in dry areas to termites, earthworms and millipedes in tropical rainforests. They consume
395 different types of organic matter, make deep or shallow, narrow or wide burrows, and differ in
396 aggregation behaviour (e.g. more or less regularly distributed earthworms versus distinct ant nests
397 and termite mounds). Accordingly, their role in SOM re-distribution and turnover differs as well.
398 In cold ecosystems – where, together with wetlands and peatlands, the majority of terrestrial
399 carbon is stored (Davidson and Janssens, 2006) – the response of detritivores to climatic change
400 is expected to be most pronounced (Blankinship et al., 2011). Melting of permafrost soil might
401 lead to northward expansion of soil macro-invertebrates, associated with accelerated
402 decomposition rates (van Geffen et al., 2011). Further examples are shown in Table 1.

403 More information is needed on how existing abiotic and biotic constraints to SOM decomposition
404 will vary with changing climate and in different regions (Davidson and Janssens, 2006). Finally,
405 human activity comes into play: any significant land use change, particularly soil sealing and
406 conversion of native forest to agricultural land, has dramatic consequences for abundances and
407 species composition of soil communities. The same holds true for management intensity and
408 pollution (Filser et al., 1995; Filser et al., 2002; Filser et al., 2008; De Vries et al., 2012). Yet,
409 even seemingly harmless activities can be significant, as we will show for the case of fishing in
410 the end of Sect. 5 – pointing out the relevance of human activities for soil fauna beyond impact
411 on global warming and land use change. How we address all this biogeographical and ecological
412 variation is shown in Sect. 5 and 6.

413 **5. Implications for modelling**

414 As there is no unambiguous scientific support for the widespread belief in “humic substances”,
415 the question how long organic carbon remains in soil is largely related to a) physical protection
416 and b) how often the once photosynthesized dead organic matter is recycled in the soil food web.
417 For both processes soil animals are of great importance, as we have shown above. Biomass and
418 abundance of soil animals are generally constrained by temperature, humidity and food (living or
419 dead organic matter). However, the effects of these constraints on their activity are not simply
420 additive, nor is there any simple relation between biomass and activity. For example, despite
421 overall unfavourable conditions for the majority of soil organisms, burrowing activity in deserts
422 can be extremely high (Filser and Prasse, 2008). Moreover there is increasing evidence that fauna
423 effects on energy and nutrient flow can be at least partly decoupled from other abiotic and biotic
424 factors (Frouz et al., 2013). De Vries et al. (2013) even concluded that “Soil food web properties
425 strongly and consistently predicted processes of C and N cycling across land use systems and
426 geographic locations, and they were a better predictor of these processes than land use”. This
427 implies that knowledge of fauna may increase our prediction power. The thermodynamic
428 viewpoint makes the issue even more relevant: reaction speed increases with temperature, but
429 most soil organisms are rather adapted to relatively cool conditions and might thus be pushed
430 beyond their niche limits – with eventually negative consequences on their activity, see Sect. 4.
431 Changes in climate (Blankinship et al., 2011), land use (Filser et al. 2002; Tsiafouli et al., 2014),
432 resource availability and biotic interactions (De Vries et al., 2012; see Table 2) alter the
433 distribution, community composition, activity and associated impact of soil animals on
434 distribution and turnover rate of SOM (Wall et al., 2008) to the extent that underlying

435 assumptions of SOM models may no longer be valid (Swift et al., 1998; Bardgett et al., 2013;
436 Schmitz et al., 2014). Therefore it is opportune to include approaches that have been developed
437 during the past decades (Filser, 2002; Jiménez and Lal, 2006; Osler and Sommerkorn, 2007;
438 Brussaard et al., 2007; Meysmann et al., 2006; Wall et al., 2008; Sanders et al., 2014). For
439 instance, Lavelle et al. (2004) implemented earthworm activity in the CENTURY model. For this
440 purpose, observations on long-term incubated earthworm casts and sieved control had been used
441 as a reference. Afterwards earthworm activity was simulated with CENTURY by replacing the
442 active and slow soil C decomposition rates of the model with those obtained by calibration with
443 the control soil. The simulations revealed a 10% loss of the slow C pool within 35 years
444 compared to the original model without earthworms.

445 Without considering the role of animals, models are less accurate: in a field study spanning four
446 countries from Sweden to Greece, soil food web properties were equally important as abiotic
447 factors and predicted C and N cycling processes better than patterns of land use (De Vries et al.,
448 2013). In their study, earthworms enhanced CO₂ production whereas Collembola and
449 bacterivorous nematodes increased leaching of dissolved organic carbon. Mechanistic
450 experiments confirm that earthworms have a detrimental effect on the greenhouse gas balance
451 under nitrogen-rich conditions (Lubbers et al., 2013) and under no-till (Lubbers et al., 2015).
452 Inclusion of group-specific diversity of mesofauna in models of global-scale decomposition rates
453 increased explained variance from 70 to 77% over abiotic factors alone (Wall et al., 2008). Also
454 García-Palacios et al (2013) provide additional evidence on the argument that soil fauna activity
455 is not merely a product of climate, soil properties and land use but an independent parameter.
456 These examples indicate that the actors that play an important role in SOM dynamics should be
457 considered in SOM models.

458 Model parameters are often measured *in situ* at relatively large spatial scales – at least compared
459 with the size or activity range of most soil animals. As a result, the fauna effect is *de facto*
460 included, although not appreciated (Swift et al., 1998). However, in many cases parameters are
461 measured or extrapolated by combining *in situ* methods (e.g. monitoring of gas flux or litterbag
462 experiments) and *ex situ* techniques such as laboratory experiments at controlled, highly
463 simplified conditions. Especially the results of the latter may be sensitive to neglecting soil fauna.
464 A relationship between animal activity and C turnover may vary with scale, for instance when
465 soil properties or animal abundance differ at larger distance. However, as data are often
466 insufficient, it will be context-dependent if the inclusion of fauna is sensible or not (see Sect. 6).
467 On the other hand, not taking explicitly into account the spatial heterogeneity created by soil
468 fauna in field measurements might lead to substantial errors in calculating carbon budgets (Wu et
469 al., 2013; Lopes de Gerenyu et al, 2015). It is thus crucial to develop sound (and biome-specific)
470 strategies for combining *in-* and *ex-situ* measurements as parameters in more realistic SOM
471 models.

472 Next to space, scale effects also apply to temporal patterns – which poses a great challenge for
473 SOM modelling as most studies refer to rather short periods of time. We illustrate this by the
474 comparatively well studied impact of invasive earthworms. The meta-analysis of Lubbers et al.
475 (2013) suggests that the effect of earthworms on total SOC contents is on average relatively
476 small. In contrast, in certain situations earthworms can strongly affect greenhouse gas emission.
477 These data were however mainly obtained in relatively short-term experiments. Over a period of
478 months to years and even decades, earthworms can reduce C decomposition by physical
479 protection of C in ageing casts (Six et al., 2004, see Table 1).

480 Thus, long-lasting effects of invasive earthworms on the total SOC storage cannot be determined
481 with certainty in short-term experiments, whereas field observations are rather controversial. For
482 instance, Wironen and Moore (2006) reported ca. 30% increase in the total soil C storage in the
483 earthworms-invaded sites of an old-growth beech-maple forest in Quebec. Other studies (e.g.
484 (Sackett et al., 2013; Resner et al., 2014) suggest a decrease in C storage. Zhang et al. (2013)
485 introduced the sequestration quotient concept to predict the overall effect of earthworms on the C
486 balance in soils differing in fertility, but the question remains strongly understudied.

487 These well documented examples of the impact of earthworms on soil C storage are related to
488 invasive species. The presence of these species cannot be inferred directly from the climatic, soil
489 and vegetation properties. The distributions of European invasive earthworms in North America,
490 North European forests or South Africa are largely driven by human activity. Often fishing (due
491 to lost baits), imported plants or potting material of colonizing farmers (Reinecke, 1983) are more
492 important for these than habitat transformation – without human’s help earthworms are not active
493 invaders (Stoscheck et al., 2012; Tiunov et al., 2006; Wironen and Moore, 2006). Thus the
494 presence of earthworms can be an environment-independent parameter of SOM dynamics.
495 Another fundamental issue in the large-scale approach is often neglected: When including the
496 effects of the soil fauna implicitly, this assumes that the soil fauna will always have the same
497 effects under the same conditions, and hence that the soil fauna are essentially static. This
498 assumption is increasingly unrealistic in a fast-changing world where both biodiversity and the
499 climate are changing at accelerated paces, and where we are likely to witness major
500 reorganisations of plant, animal and microbial communities. Therefore explicit representation of
501 the soil fauna, where possible, should increase the predictive ability of SOM models.
502 Given the fact that this issue had been raised decades back (see above) it appears somewhat
503 astonishing that attempts to pursue it have not yet made any significant progress. We believe
504 there are mainly three reasons for this: a) missing information, b) too much detail, irrespective of
505 spatial scale, and c) too little communication between empiricists and modellers. This is why we
506 decided to bring into life a COST Action as an appropriate instrument to bridge these gaps. The
507 next section gives an overview on it.

508 **6. Ways to proceed: COST Action ES 1406**

509 Based on the arguments compiled here, a COST Action entitled “Soil fauna - Key to Soil Organic
510 Matter Dynamics and Modelling (KEYSOM)” was launched in March 2015
511 (http://www.cost.eu/COST_Actions/essem/ES1406). An interdisciplinary consortium of soil
512 biologists and biogeochemists, experimenters and modellers from 23 European countries plus the
513 Russian Federation and the USA cooperates to implement soil fauna in improved SOM models as
514 a basis for sustainable soil management. The main aim of KEYSOM is to test the hypothesis that
515 the inclusion of soil fauna activities into SOM models will result in a better mechanistic
516 understanding of SOM turnover and in more precise process descriptions and output predictions
517 of soil processes, at least locally. A number of workshops address key challenges in
518 experimentation and modelling of SOM and soil fauna and support research exchange and access
519 to experimental data. Special attention is given to education of young scientists. The Action
520 comprises four Working Groups (WG) with the following topics:

- 521 1. Knowledge gap analysis of SOM – soil fauna interactions;
- 522 2. Potentials and limitations for inclusion of soil fauna effects in SOM modelling;
- 523 3. Data assemblage and data sharing;
- 524 4. Knowledge management and advocacy training.

525 After an intensive and enthusiastic workshop held in Osijek, Croatia in October 2015, first
526 activities included compilation of literature, the setup and permanent update of a website
527 (<http://keysom.eu/>). Meanwhile short-term scientific missions for early-career scientists have
528 been launched (<http://keysom.eu/stsm/KEYSOM-STSMs-are-open-for-application>), aiming for
529 complementing the Action’s activities. The second workshop was held in Prague in April 2016.

530 Next to a first compilation of knowledge gaps in this article, present activities of KEYSOM
531 involve

- 532 - a literature review on biome-specific effects of soil fauna impact on SOM turnover

- 533 - a literature review on the impact of soil fauna other than earthworms on SOM turnover
- 534 - a compilation of the potentials and limitations of existing SOM models
- 535 - the development of a simple SOM model that also explicitly incorporates soil animals and
- 536 associated processes in it, based on the current state of knowledge exchange between
- 537 empiricists and modellers within KEYSOM
- 538 - the preparation of a common European-wide field study into the impact of soil fauna
- 539 composition and abundance on SOM breakdown, distribution and aggregate formation,
- 540 which will start in autumn 2016
- 541 - the preparation of a summer school, to be held in early October 2016 in Coimbra,
- 542 Portugal

543 Fig. 3 illustrates the present state of our interdisciplinary discussions, providing a roadmap how
544 SOM models could be supplemented with the effects of soil fauna. In the first phase, empiricists
545 (Fig. 3A) and modellers (Fig. 3B) work in parallel. Mutual exchange between these groups is
546 guaranteed by the regular workshop meetings such as in Osijek and Prague.

547 The stepwise approach functions like a decision tree, with various feedback loops and options at
548 every step if and how known effects of soil fauna could be implemented into SOM. It also
549 identifies under which circumstances additional research (literature review or experimental
550 studies) needs to be initiated before proceeding further. As many existing models, also the new
551 model should have a modular structure so that different modules can be used and combined
552 according to the respective biome- and scale-specific scenario (Fig. 3C). It can also be seen that
553 we do not aim to include every detail everywhere: in some situations (Fig. 3A) the impact of soil
554 fauna on SOM dynamics might be too small (or existing information too scanty) to be included,
555 and not all input parameters will be feasible or relevant at each scale (miniature in Fig. 3C). This
556 keeps the model manageable, and also flexible enough to allow for more precise predictions in
557 critical scenarios, like in the case of earthworm invasions sketched in Sect. 5. We generally think
558 that focusing on such critical scenarios (analogous to e.g. global biodiversity hotspots) is a crucial
559 precondition for well-informed management decisions, one of the final aims of KEYSOM.

560 As an example, box no. 1 in Fig. 3A stands for the first literature review in the above list.
561 Depending on the outcome, for each biome a decision will be made if the impact of fauna on
562 SOM turnover is unknown, relevant or low. In the first case, more research is needed, in the last
563 case the faunal effect can be ignored. Depending on the outcome of additional research, the
564 knowledge base will be improved and the decision between ignoring and proceeding further can
565 be made anew. If a strong effect is expected, the next question (box no. 2 in Fig. 3A) will be
566 addressed and so forth.

567 Once the procedure in Fig. 3A has reached box no. 4, intensive exchange with modellers (Fig.
568 3B) is mandatory to identify the relevant model parameters and the type of functional relationship
569 (box 5). Mechanistic aspects (such as chemical transformation in the gut, physical protection
570 within aggregates or impact on hydraulic soil properties via digging) are of prime importance
571 here as each of these examples may have different effects on C turnover. Effects of fauna
572 abundance or biomass (in comparison to presence-absence) on the shape of the function will be
573 addressed as well. Note, however, that to date necessary data for such an approach appear to be
574 limited (García-Palacios et al., 2013). – In the meantime, the modellers will have developed a
575 basic model structure and compare it with the structures of existing SOM models concerning
576 potentials and limitations for including fauna effects (Fig. 3B).

577 The second phase (Fig. 3C) starts with the practical tests of the collected model parameters
578 (boxes 6 and 7), using data that have been compiled by then by WG 3, allowing for selecting the
579 best model (box 8). At this point, spatial scale comes into play, which is likely to be the most

580 critical issue: As we have seen also while preparing this article, existing data on the impact of soil
581 fauna on SOM turnover are highly diverse, from short-term and often highly artificial
582 experiments at controlled conditions to large-scale correlative field studies in all kinds of
583 different environments (and with a strong bias what comes to certain biomes). The type of
584 relationship between faunal abundance and SOM turnover will in most cases vary with scale. If
585 data for different scales are not available (box 9), further research is needed. In the second case,
586 one can proceed with boxes 10 and 11.

587 Importantly, the idea is not to include the fauna in every situation everywhere. Rather we aim at
588 identifying critical hotspots and scenarios (see above) where faunal activities play a crucial role
589 in SOM turnover, as demonstrated in Sect. 5. Due to the abovementioned differences between
590 biomes and scale effects, these scenarios will be biome- and scale-specific. An example is shown
591 in the lower left corner of Fig. 3C. For Biome A, hydraulic properties have been identified to be
592 crucial for SOM dynamics. Thus, data are needed on animals that affect these, such as digging
593 earthworms or rodents. Instead, the analyses for Biome B have revealed aggregate structure and
594 microorganisms being most relevant – claiming for respective data at the small scale. On a larger
595 scale such data for microorganisms might not be available, which implies proceeding with
596 aggregate structure alone.

597 Overall, the whole approach requires a modular model structure, allowing for using different
598 models according to the respective situation and data availability. This is what WG 2 is currently
599 developing. – Certainly all the research outlined here cannot be done within one single COST
600 Action. Based on the outcome of our work, we hope to come up with a more detailed roadmap
601 how to further proceed to improve SOM modelling. This roadmap, together with what could be
602 achieved with the limited resources of KEYSOM, will provide information material, decision
603 tools and management options for decision makers and politicians (WG 4).

604

605 **7. Conclusions and outlook**

606 Understanding and modelling SOM is essential for managing the greenhouse gas balance of the
607 soil, for land restoration from desertification, for sustaining food production and for the
608 conservation of above- and belowground biodiversity and associated ecosystem services (Nielsen
609 et al., 2015). Soil animal abundance, biodiversity, species traits and interactions are crucial for
610 SOM turnover (Chauvel et al., 1999; Bohlen et al., 2004; Wardle et al., 2004; Wall et al., 2008;
611 Uvarov, 2009). In Table 2 we give recommendations how the known impact of soil fauna on
612 SOM turnover could be used for improving carbon models. Due to the pronounced differences
613 with respect to climate, soil and land use outlined above, it is important that these
614 recommendations are considered region- and scale-specific, taking into account the key players
615 and their specific activities in the respective area.

616

617 **Author contribution**

618 J. Filser wrote the article, prepared Fig. 1 and 3 and the tables and compiled the contributions
619 from all co-authors. These are listed according to their quantitative and qualitative impact on the
620 manuscript, except for J.J. Jiménez who was placed last as he is the chair of COST Action ES
621 1406 (KEYSOM). L. Brussaard suggested including Fig. 2.

622

623

624 **Acknowledgements**

625 Three anonymous referees are acknowledged for their critical comments which significantly
626 contributed to the revision of the original manuscript. We thank Antje Mathews for compiling the
627 references and editing the manuscript. Many thanks to Karin Nitsch for linguistic proof-reading.
628 Oxford University Press and Wiley and Sons are acknowledged for the permission to include Fig.
629 2. This paper is a contribution to the COST Action ES1406 (KEYSOM) lead by the first and last
630 author. A lot of the writing was inspired by the lively discussions within the workshop meetings
631 of KEYSOM – thanks to all contributors! We thank COST Association for financially supporting
632 collaboration and networking activities across Europe.

633

634

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- 903

904 **Tables**

905 **Table 1.** Quantitative examples of the impact of earthworms and selected groups of other soil fauna on
 906 soil properties and processes involved in soil organic matter (SOM) turnover. If not mentioned otherwise,
 907 any numbers or percentages refer to the control without fauna. Selected particularly striking examples are
 908 printed in bold.

Insight*	Examples	Source
	Earthworms	
1. Molecular structure	An indicator of lignin degradation in earthworm casts was twice that of the surrounding soil	Guggenberger et al., 1995
2. Humic substances	Introduced earthworms can double microaggregate formation and the stabilisation of new C in the topsoil C protection is promoted by microaggregates within large macroaggregates, and earthworms can add 22% anew to this C pool Exclusion of earthworms reduced SOC accumulation by 0 (at 0-10 cm depth) to 75% (at 30-40 cm depth), associated with a decrease in percentage of water-stable aggregates In organic layers of a Canadian aspen forest, in locations with earthworms, N (1.5–0.8%) and especially C concentrations (25.3–9.8%) were strongly reduced, together with C/N ratio (16.7–13.2) and soil pH (6.5–6.1); in brackets: control values vs. values with earthworms. This suggests a shift towards a faster cycling system, resulting in a net loss of C from the soil and turning Northern temperate forests from C sinks into C sources	Marashi and Scullion, 2003; Six et al., 2004 Bossuyt et al., 2005 Albrecht et al., 2004, cited in Schmidt et al., 2011 Eisenhauer et al., 2007
3. Fire-derived carbon	Small charcoal particles from burned plots after one year increased by 21% in 0-1 cm depth. One year later they were concentrated in earthworm casts at the soil surface, after 6.5 years such casts were found at 8 cm depth	Eckmeier et al., 2007
4. Roots	Presence of earthworms in a continuous maize plot in Peruvian Amazonia increased the organic C input from roots by 50%	Jiménez et al., 2006
5. Physical heterogeneity (see also insights no. 2, 3, 6 and 7)	Up to 50% of soil aggregates in the surface layer of temperate pastures are earthworm casts Mull-type forest soil top layers and wooded savanna soils consist almost entirely of earthworm casts Earthworm inoculation in pastures on young polder soils completely removed within 8-10 years the organic surface layer, incorporated it into deeper layers, creating an A horizon. This affected manifold measures, increasing e.g. grass yield by 10%, root content in 0-15% from 0.38 to 1.31 g dm⁻³, C content in 0-20 cm from 1.78 to 16.9 kg C * 10³ ha⁻¹, and water infiltration capacity from 0.039 to 4.6 m 24 h⁻¹. In turn, penetration resistance at 15 cm depth decreased from 35 to 22 kg cm⁻². In average temperature pasture and grasslands, earthworms cast 40-50 t ha ⁻¹ year ⁻¹ on the surface and even more below surface Passage of a tropical soil through the gut of the invading earthworm <i>Pontoscolex corethrurus</i> reduced macroporosity from 21.7 to 1.6 cm³ g⁻¹, which exceeded the effect of mechanically compacting the same soil at 10³ kPa (resulting macroporosity: 3 cm³g⁻¹) After invasion of European earthworms into a Canadian aspen forest a thick layer of their cast material (thickness up to 4 cm) on top of organic layers was developed	Van de Westeringh, 1972 Kubienna, 1953; Lavelle, 1978 Hoogerkamp et al., 1983 Lee, 1985 Wilkinson et al., 2009 Eisenhauer et al., 2007
6. Soil depth	Burrows of anecic earthworms are up to several meters deep and last for many years	Edwards and Bohlen, 1996

* According to Schmidt et al. (2011)

909 **Table 1.** (continued)

Insight*	Examples	Source
Earthworms		
7. Permafrost and boreal areas	Earthworm invasions in boreal forests completely transformed mor to mull soils and significantly altered the entire plant community	Frelich et al., 2006
8. Soil microorganisms	Earthworms may lower actual microbial activity (by 11-23%) but markedly (by 13-19%) optimize microbial resource utilization.	Scheu et al., 2002
Ants and termites		
2. Humic substances	In a degraded marsh in NE China, ant mounds were CH₄ sinks, contrary to the control soils which were CH₄ sources (-0.39 – -0.19 mg vs. 0.13 – 0.76 m² h⁻¹)	Wu et al., 2013
5. Physical heterogeneity	Ant and termite mounds can occupy up to 25% of the land surface	Bottinelli et al., 2015
5. Physical heterogeneity and	Underground nests of leafcutter ants (e.g. <i>Atta</i> spp.) can cover up to 250 m² and extend down to 8 m., which is associated with a massive impact on forest vegetation	Correa et al., 2010
6. soil depth		
Collembola		
8. Soil microorganisms	Grazing by Collembola affected community composition of ectomycorrhizal fungi and on average reduced ¹⁴ CO ₂ efflux from their mycelia by 14%	Kanters et al., 2015
	Grazing by <i>Protaphorura armata</i> at natural densities on AM fungi disrupted carbon flow from plants to mycorrhiza and its surrounding soil by 32%	Johnson et al., 2005
	The presence of a single Collembola species may enhance microbial biomass by 56%	Filser, 2002
	At elevated temperature, litter decay rates were up to 30% higher due to Collembola grazing	A'Bear et al., 2012
Various or mixed groups		
1. Molecular structure	Microbial grazing by Collembola or enchytraeids alone enhanced leaching of NH ₄ ⁺ or DOC by up to 20% ⁵	Filser, 2002
	Feeding by millipedes and snails reduced the content of condensed tannins in three Mediterranean litter species from 9–188 mg g⁻¹ dry matter to almost zero	Coulis et al., 2009
	Long-term mineralisation of fauna faeces may be slower than the mineralisation of litter from which the faeces were produced. This decrease in decomposition rate corresponds to a decrease in the C:N ratio and in the content of soluble phenols.	Frouz et al., 2015a,b
	Due to stoichiometric constraints, soil animals tend to reduce the C concentration of SOM, but increase N and P availability. About 1.5% of the total N and P in the ingested soil was mineralized during gut passage in humivorous larvae of the scarabaeid beetle <i>Pachnoda ephippiata</i> . In <i>Cubitermes ugandensis</i> termites, the ammonia content of the nest material was about 300-fold higher than that of the parent soil.	Li et al., 2006; Li and Brune, 2007; Ji and Brune, 2006
2. Humic substances	In a laboratory experiment, activity of earthworms, Collembola, enchytraeids and nematodes in coarse sand liberated >40% from the insoluble C pool as compared to the control	Fox et al., 2006
	Radiolabelled proteins and phenolic compounds in litter are faster transformed to humic acids (as revealed by alkaline extraction and acid precipitation) via feces of Bibionidae (Diptera) than from litter not eaten by fauna	Frouz et al., 2011
	The quantitative contribution of invertebrates (mainly beetles and termites) to wood decomposition ranges between 10-20%	Ulyshen, 2014
	Depending on fungal and animal species (Collembola, isopods and nematodes), grazing on fungi colonising wood blocks altered (mostly decreased) their decay rates by more than 100%. Isopods and nematodes had opposite effects in this study.	Crowther et al., 2011

* According to Schmidt et al. (2011)

Table 1. (continued)

Insight*	Examples	Source
	Various or mixed groups	
2. Humic substances (continued)	Carbon and nitrogen losses from soil followed by drought and rewetting were substantially affected by microarthropod richness, which explained 42% of the residual variance.	De Vries et al., 2012
5. Physical heterogeneity	Bioturbation rates of soil animal groups typically range between 1 and 5 Mg ha⁻¹ y⁻¹ but may reach up to 10 (crayfish, termites), 20 (vertebrates), 50 (earthworms) and > 100 Mg ha⁻¹ y⁻¹ (earthworms in some tropical sites), which is equivalent to maximum rates of tectonic uplift	Wilkinson et al., 2009
8. Soil microorganisms	In the course of a 2.5-yr succession, fauna activities (especially of nematodes and mesofauna during the first year, and later of earthworms) accelerated microbial decomposition of clover remains in an arable soil by 43%	Uvarov, 1987
	Depending on vegetation, animal group and climate, soil animals directly or indirectly increased C mineralisation between 1% and 32%. However, intensive grazing by fungal feeders may even reduce C mineralisation	Persson, 1989

* According to Schmidt et al. (2011)

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912 **Table 2.** “Insights” (compiled after Schmidt et al., 2011) for future soil organic matter models and
 913 recommendations for further improvements by implementing effects of soil fauna

SOM modelling element (“Insight”)	Recommendations*
1. Molecular structure	Incorporate the knowledge on the structure of organic substances and element concentrations in faunal casts and excreta in SOM decay rate models. Consider linkage between C and N cycling mediated by fauna. See 8.
2. Humic substances	Add physical and chemical stability of casts, patterns of their microbial colonisation and degradation dynamics. See 1, 3, 5, 6, 7, 8.
3. Fire-derived carbon	Include recolonisation and inoculation potential of surviving soil fauna and adjacent fauna. Initiate studies on the impact of fauna on the fate of black carbon (fragmentation, gut, casts, decomposition, and recolonisation).
4. Roots	Add activity of bioturbators, rhizosphere microbial grazers and root herbivores. See 1, 5, 6, 8.
5. Physical heterogeneity	Consider spatial and physicochemical heterogeneity created by soil fauna, including consequences of soil aggregation and dis-aggregation (e.g. bulk density, infiltration rate, preferential flow, casts). See 1, 2, 6, 8.
6. Soil depth	Incorporate burrowing depth and annual transport rates of bioturbators and animal-induced spatial heterogeneity of old and young carbon in the deep soil. See 5.
7. Permafrost	For warming scenarios, take into account short- and long-term invasion effects, particularly of earthworms and enchytraeids.
8. Soil microorganisms	Add microbial grazer effects, effects on microorganisms during gut passage and faunal impact on C and N coupling. See 1-7.

914 * Recommendations refer to site-specific keystone groups of animals (dominating in terms of biomass or impact; see
 915 Fig. 2). Their prevalence is determined by climate, bedrock and land use (e.g. rodents or ants in deserts, earthworms in
 916 temperate grasslands or microarthropods and enchytraeids in acidic Northern forests).

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919 **Figure Captions**

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921 **Figure 1.** Main animal-mediated processes (boxes) affecting the eight insights (symbols)
922 identified by Schmidt et al. (2011) that should be considered for improving SOM models

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924 **Figure 2.** Dominant soil types and characteristic soil forming invertebrates across biomes (major
925 global change threats are shown in italics). MAT = mean annual temperature, MAP = mean
926 annual precipitation. Sources for data and biomes see Brussaard et al. (2012).

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930 **Figure 3.** Flow scheme for an improved understanding of the role of soil fauna for soil organic
931 matter (SOM) turnover. This scheme is basically followed within the COST Action ES 1406
932 (KEYSOM). Activities in A) and B) run parallel, followed by C) which ends with an improved
933 SOM model. Exemplarily shown are scenarios for two biomes. Further explanations see text.

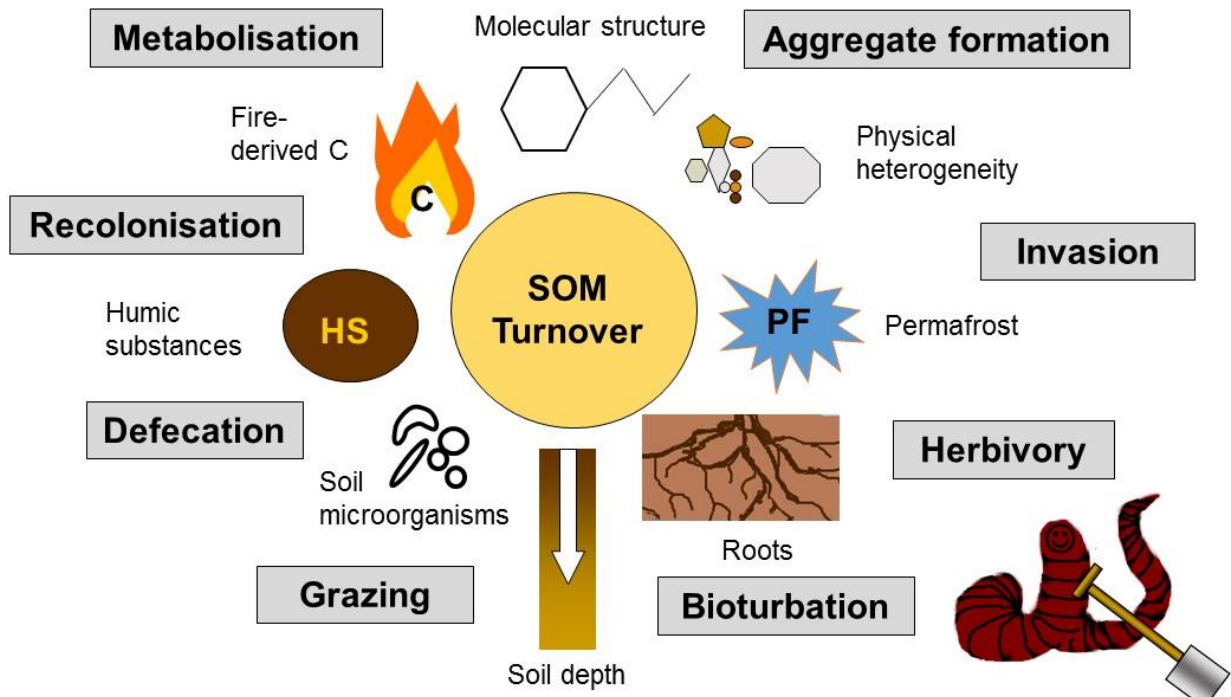
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937 **Figures**

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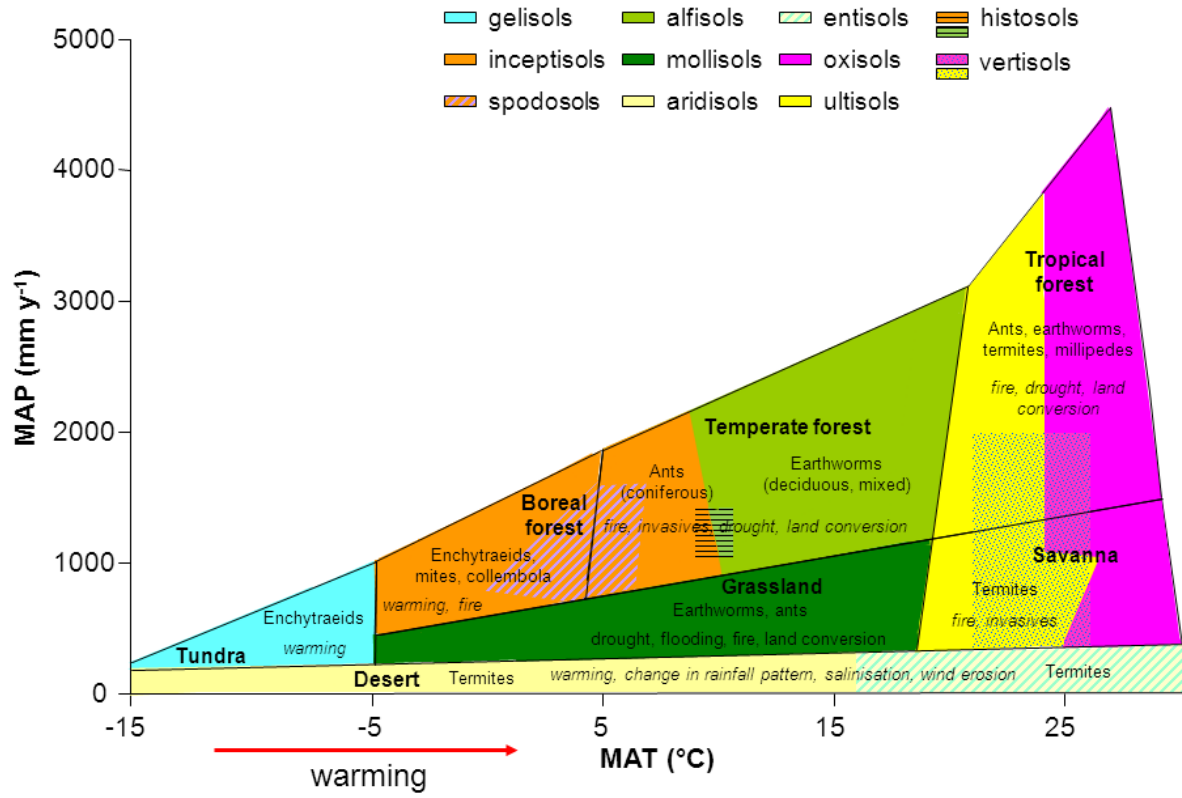
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944 **Figure 1**

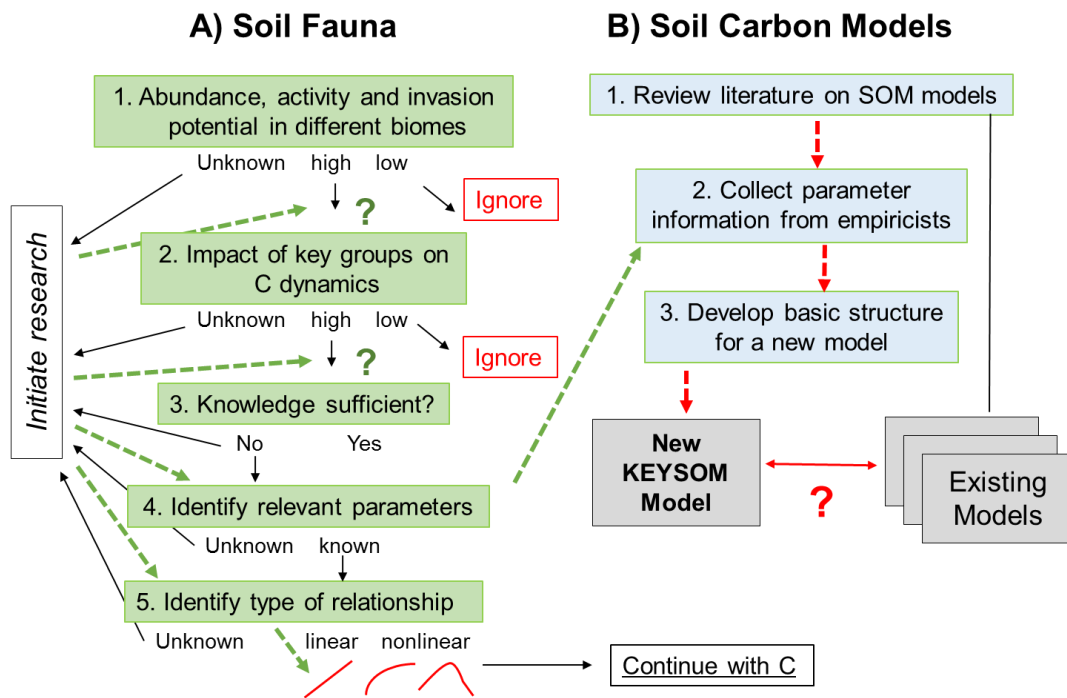
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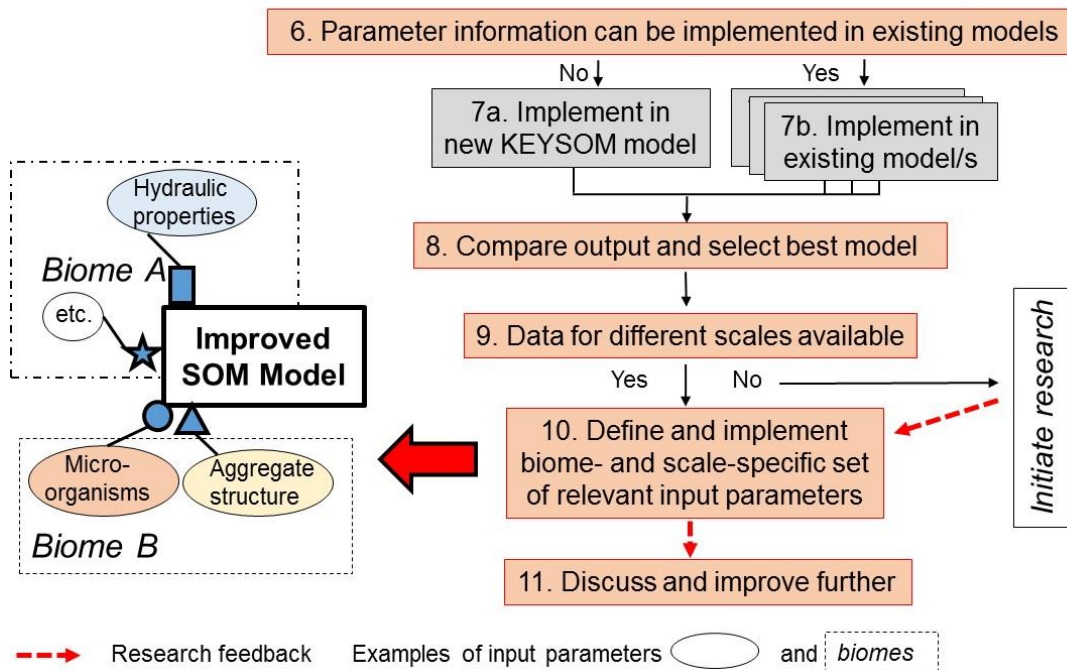
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951 **Figure 2**
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C) Model Synthesis



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Figure 3