

Anonymous Referee #3	Comment no.	Line
<p>Although the main text justifies the incorporation of the COST action, it is not so clearly demonstrated in the Abstract, and the way it is currently incorporated in the Abstract still reads like an 'advert' to me, while the last sentence re: field experiment, experimental data and so forth are too vague (in my opinion) for an Abstract. I believe the abstract would be stronger, if KEYSOM is still to be included, with a conclusion such as: "We argue that explicit consideration of the soil fauna is essential to make realistic modelling predictions on SOM dynamics and to detect expected non-linear responses to global change. We present a decision framework, to be further developed through the activities of KEYSOM, a European COST action, for when mechanistic SOM models should include soil fauna. The research activities of KEYSOM, such as field experiments and literature reviews, together with dialogue between empiricists and modellers, will inform how this is to be done."</p>	1. Thank you - we adopted this suggestion.	68ff
<p>You could also include KEYSOM in the keywords if you want it to be searchable.</p>	2. Done	77
<p>Key insights: Although some sections within this part now clearly demonstrate the link between the key insight and SOM dynamics (and then the importance of soil fauna in modifying the key insight) e.g. 2.6 on soil depth, other parts go straight into how animals affect the key insight, without stating how the key insight affects SOM. I realise the latter is included in Schmidt, but I think it might be clearer for readers to show how each insight affects SOM (briefly as with soil depth, not exhaustively), and then introduce the substantial body of the review regarding soil faunal effects on the key insight.</p>	3. Done	137ff
<p>Table 1: I found the examples in Table 1 very interesting. However, I did not follow how many of the earthworm examples in 2. Humic substances, were to do with this insight, as they appeared most related to aggregate stability. It is also not immediately clear how e.g. casting 40-50 t/ha/yr influences 'physical heterogeneity' and so on and so forth.</p>	4. We added a few sentences to better explain this.	296ff
<p>As another example, for 'Various or mixed groups' what does microbial grazing leading to leaching of DOC and NH₄⁺ have to do with 'molecular structure'? Don't some of these substances already exist in the absence of animals, whereas your points, at least as I understood the main text, are to do with animals modifying the molecular structure of SOM and thus influencing its</p>	5. Please note that this always relates to the control without animals. Whenever leaching of DOC etc. is increased this means a transition of solid OM into the aquatic phase, subject to potential leaching, plant uptake or microbial metabolism. NH ₄ ⁺ is clearly an effect	139ff

decomposition dynamics?	on molecular structure. Admittedly, the leaching of such an unspecific item like DOC cannot directly be related to an analogous process – yet on the other hand the assumption that increased leaching is merely an effect of desorption seems quite unlikely. Thus, we left this unchanged.	
In other words, for all of the examples, make it really clear how they relate to the key insights and the explanations in the main text.	6. See answers no. 4 and 5	
I am surprised there isn't at least some discussion as to whether other processes could be important in improving SOM models (e.g. dissolved and particulate organic matter leaching, soil erosion, better parameterisation of litter inputs), and not just the requirement to include animals. I think it would be good to briefly mention alternative explanations for current model discrepancies; I am not suggesting these are reviewed.	7. We added this to the introduction	88 ff
I like the insertion of Figure 3. However, please explain what 'Etc' means. I would consider taking out the shaded miniature on the figure as I think it unnecessarily confuses and modify the main text accordingly. However, retain an explanation about what happens when data are not available at different scales. I think I found this somewhat confusing as to my geographical mind, 'biome' is a given scale e.g. boreal forest, tropical forest etc. Also, the flow from 6 to 7 to 8 is not clear, given the additional white box with 'compare output with previous models/versions'. I would consider redrawing this to a linear flow, similar to A) and B).	8. Figure and text were modified accordingly, and the significance of "etc." in now correct spelling should be clear.	581ff 947
MINOR COMMENTS / GRAMMATICAL CORRECTIONS		
I was surprised by the standard of the English in parts of the ms; I would suggest giving it a careful proof read before any final submission and, if accepted, publication.	9. A native speaker has proof-read the manuscript.	523
Line 57: Suggest "Fauna control..." [fauna are plural, as are data later in the ms (line 423)], rather than "The fauna controls"	10. Done (well, another referee once had corrected data to singular...)	57
Line 59: "We show lots of quantitative examples" sounds very colloquial; I would suggest deleting and just stating "We demonstrate a very strong impact of soil animals on carbon turnover"	11. Done	59
Lines 88-89: key to understandING and predictING changes in global carbon cycling	12. Done	82-83
Suggest "Some years ago" on line 96 be the start of a new paragraph.	13. Done	94
Line 108: Suggest "A correlative large scale field study has shown that including soil animal activities could help clarify discrepancies in existing carbon models"	14. Done (slightly modified)	106f

Line 116: Suggest split this sentence to: "Here we use the 'key insights' proposed by ...on the relationship of soil fauna to SOM dynamics. Our review justifies the relevance of incorporating soil fauna into SOM models"	15. Done	115f
When you state, on line 118, that there have been repeated reviews it begs the question why therefore you have done this review. Are SOM dynamics different to 'geological and pedological processes' - if so, I would state it explicitly, or just remove this sentence.	16. Done	118f
Line 123 - the Dorn reference to ants seems far too detailed for an Introduction - I would place it within an appropriate part of the review of key insights.	17. We moved it to Sect. 2.1	142ff
Line 147/148 - I presume 'humification' means, in this context, 'decomposition dynamics of animal faeces'. If so, I would put the parentheses after animal faeces, not where it is presently.	18. We corrected this to "humus"	150
It may also be worth clarifying what the relationship is (if there is one) between 'humification', 'humic substances' and 'humus' (both of which are introduced in the next section). Also, you define humic substances on line 371 in a more explicit way than in section 2.2 - I would insert the definition on line 371 into section 2.2.	19. Done	170ff
Line 218: Suggest delete 'any'.	20. Done	234
Line 294 - still unsure of what the relationship of tensile strength is to SOM dynamics - please elucidate.	21. We added an explanation	331ff
Line 331-333: Reference(s) required for suggestion that humid grasslands are "among those ecosystems that are most severely affected by global environmental change"	22. Two references were added.	371f
Line 341: "more detailed information on their biology is required". State why this is required for the modelling. As pointed out by review 1 (for the initial submission), it is very difficult for the modelling community to include lots and lots of details as it makes model interpretation and validation problematic. Your calls for more detailed biological information therefore needs to be justified from a modelling perspective.	23. Supplemented accordingly	380f
Line 397: I still find the CENTURY example oddly phrased. You discuss 'implementing earthworm activity' and then state what happens 'without earthworms', all in the same sentence. Please rephrase.	24. Done	434ff
Line 444: Unclear what 'richness' refers to. Could mean species richness, although could also mean e.g. soil fertility. I assume you mean fertility but not sure...	25. Reworded	482
Line 472: THE main aim of KEYSOM...of soil fauna activity into SOM models...	26. Done	510
Line 493 - provide a bit more detail about 'the development of a simple SOM model' - I presume you mean a model that explicitly incorporates faunal processes in it, but you don't actually state this.	27. Done	531

1 **Title page**

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

3

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5

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52 Abstract

53 Soil organic matter (SOM) is key to maintaining soil fertility, mitigating climate change,
 54 combatting land degradation, and conserving above- and below-ground biodiversity and
 55 associated soil processes and ecosystem services. In order to derive management options for
 56 maintaining these essential services provided by soils, policy makers depend on robust, predictive
 57 models identifying key drivers of SOM dynamics. Existing SOM models and suggested
 58 guidelines for future SOM modelling are defined mostly in terms of plant residue quality and
 59 input and microbial decomposition, overlooking the significant regulation provided by soil fauna.
 60 The fauna control almost any aspect of organic matter turnover, foremost by regulating the
 61 activity and functional composition of soil microorganisms and their physical-chemical
 62 connectivity with soil organic matter. We demonstrate a very strong impact of soil animals on
 63 carbon turnover, increasing or decreasing it by several dozen percent, sometimes even turning C
 64 sinks into C sources or vice versa. This is demonstrated not only for earthworms and other larger
 65 invertebrates but also for smaller fauna such as Collembola. We suggest that inclusion of soil
 66 animal activities (plant residue consumption and bioturbation altering the formation, depth,
 67 hydraulic properties and physical heterogeneity of soils) can fundamentally affect the predictive
 68 outcome of SOM models. Understanding direct and indirect impacts of soil fauna on nutrient
 69 availability, carbon sequestration, greenhouse gas emissions and plant growth is key to the
 70 understanding of SOM dynamics in the context of global carbon cycling models. We argue that
 71 explicit consideration of soil fauna is essential to make realistic modelling predictions on SOM
 72 dynamics and to detect expected non-linear responses of SOM dynamics to global change. We
 73 present a decision framework, to be further developed through the activities of KEYSOM, a
 74 European COST action, for when mechanistic SOM models include soil fauna. The research
 75 activities of KEYSOM, such as field experiments and literature reviews, together with dialogue
 76 between empiricists and modellers, will inform how this is to be done.
 77

78 Keywords

79 Carbon turnover, soil organic matter modelling, soil invertebrates, aggregate formation, spatial
 80 heterogeneity, regional differences, ecosystem engineers, COST Action KEYSOM
 81

82 1. Introduction

83 Despite continuous refinement over the past decades, estimates of the global carbon cycle still
 84 show large discrepancies between potential and observed carbon fluxes (Ballantyne et al., 2012;
 85 Schmitz et al., 2014). Soil organic matter (SOM) modelling is key to understanding and
 86 predicting changes in global carbon cycling and soil fertility in a changing environment. SOM
 87 models can facilitate a better understanding of the factors that underlie the regulation of carbon
 88 cycling and the persistence of SOM. The predictive power of current global SOM models is,
 89 however, limited, as the majority relies on a relatively restricted set of input parameters such as
 90 climate, land use, vegetation, pedological characteristics and microbial biomass (Davidson and
 91 Janssens, 2006). Other parameters, such as the leaching of organic matter or soil erosion of
 92 organic matter have been suggested for improving model predictions, and recent research has
 93 demonstrated what drastic effects e.g. living roots (Lindén et al., 2014) and soil fungi
 94 (Clemmensen et al., 2013) exert on SOM persistence. In an overview on the performance of SOM
 95 models, none of 11 tested models could predict global soil carbon accurately, nor were 26
 96 regional models able to assess gross primary productivity across the US and Canada (Luo et al.,
 97 2015).

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Gelöscht: show lots of quantitative examples that

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Gelöscht: We argue that explicit consideration of the soil fauna is essential to make realistic modelling predictions on SOM dynamics and to detect expected non-linear responses to global change, and we suggest that guidelines for future SOM modelling should implement the role of soil fauna. This had been the reason for bringing into being the COST (European Cooperation in Science and Technology) Action ES 1406 (KEYSOM – Soil fauna: key to new carbon models), which we briefly introduce. KEYSOM brings together biogeochemists and soil ecologists from 23 EU countries and provides a research network for improving SOM models by implementing the role of the soil fauna as a basis for sustainable soil management. An interdisciplinary platform of experimentalists and modellers is presently identifying the most burning research gaps and working on a new modelling approach. The current state of discussion is presented here. In the next years KEYSOM will also perform a large-scale field experiment, assure better access to experimental data, and inform decision makers.

19 Some years ago Schmidt et al. (2011) proposed eight “key insights” to enrich model predictions
 20 on the persistence of SOM. However, they ignored a major component of SOM dynamics, soil
 21 fauna, which play a fundamental role in most of the insights they propose (e.g. Fox et al., 2006;
 22 Jimenez et al., 2006; Osler and Sommerkorn, 2007; De Deyn et al., 2008; Wilkinson et al., 2009).
 23 By moving through and reworking soil, feeding on living plant roots, detritus and all types of
 24 microorganisms growing on these, soil animals are intimately involved in every step of SOM
 25 turnover. Omission of soil fauna from SOM models will, therefore, hamper the potential
 26 predictive power of these models.

27 In a review focusing mostly on large mammals, terrestrial herbivores and aquatic ecosystems,
 28 Schmitz et al. (2014) recently called for “animating the carbon cycle”. Bardgett et al. (2013)
 29 argued that differential responses of various trophic groups of aboveground and belowground
 30 organisms to global change can result in a decoupling of plant-soil interactions, with potentially
 31 irreversible consequences for carbon cycling. A correlative large scale field study has
 32 shown suggested that including soil animal activities could help clarify discrepancies in existing
 33 carbon models, (de Vries et al., 2013). Similar attempts to connect animal activity to carbon
 34 cycling occurred in the past (e.g. Lavelle and Martin, 1992; Lavelle et al., 1998; Lavelle and
 35 Spain, 2006; Osler and Sommerkorn, 2007; Brussaard et al., 2007; Sanders et al., 2014), without
 36 any further change in the structure of carbon models. This was partly due to a lack of
 37 communication between modellers and experimenters, but also because the magnitude of animal
 38 effects on SOM dynamics remains poorly quantified (Schmitz et al., 2014).

39 Here we use the ‘key insights’ proposed by Schmidt et al. (2011) as a basis to review current
 40 evidence and to identify research needs on the relationship of soil fauna to SOM dynamics. Our
 41 review justifies the relevance of incorporating the soil fauna into SOM models. How important
 42 animal activities are for manifold geological and pedological processes has been reviewed
 43 repeatedly (e.g. Swift et al., 1979; Wilkinson et al., 2009), but carbon turnover – which is highly
 44 dynamic and both directly and indirectly affected by animals – never had been the focus. Due to
 45 their prime role in most processes in soil (Briones, 2014) we mostly focus on earthworms, but
 46 also give examples for other groups of soil fauna whose role in C turnover appears to be much
 47 more relevant than thought thus far (e.g. David, 2014). We point out regional differences in
 48 climate, soils and land use with respect to soil fauna composition, abundance and activity and
 49 derive implications for SOM modelling. Finally, we introduce a new COST Action (ES 1406)
 50 that is working on the implementation of soil fauna into SOM models, also exploring the pros and
 51 caveats in such a process.
 52

153 2. Key insights

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

161 2.1. Molecular structure

62 The molecular structure of root exudates and dead organic matter is modified during
 63 metabolisation, decomposition and associated food web transfer, both by microorganisms and
 64 soil fauna. Prominent examples are the release of ammonium by bacterivorous protozoans and
 65 nematodes, due to their higher C:N ratio compared to their bacterial prey (Osler and
 66 Sommerkorn, 2007), or the large contribution strong mediation of soil animals to the direction and

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Gelöscht: Other research has shown that including soil animal activities could help clarifying the discrepancies in existing carbon models, based on a large-scale correlative field study

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[3] nach unten: Recently, the significant impact of eight different species of ants over 25 years on mineral dissolution and accumulation of calcium carbonate has even been discussed in the context of geoengineering and carbon sequestration (Dorn, 2014).

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[1] nach unten: Table 1 contains quantitative examples of animal activity taken from different biomes and land use types, showing that earthworms alone strongly affect each of the ‘key insights’. However, much smaller soil animals can also have substantial effects on them (Table 1).

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84 rate of humus formation by soil animals (see 2.2). Recently, the significant impact of eight
 85 different species of ants over 25 years on mineral dissolution and accumulation of calcium
 86 carbonate has even been discussed in the context of geoengineering and carbon sequestration
 87 (Dorn, 2014).

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188 Many soil animals ingest and process SOM (and accompanying microorganisms) in their gut
 189 system, where it is partly assimilated with the help of mutualistic gut microflora and partly
 190 egested. Metabolisation alters the chemical structure of ingested SOM (Jiménez and Lal, 2006;
 191 Hedde et al., 2005; Coulis et al., 2009; Frouz, 2015b; Schmitz et al., 2014) and, consequently, the
 192 decomposition dynamics of animal faeces, which can be a substantial component of SOM
 193 (humus). Humification as such renders SOM less decomposable (Blume et al., 2009; Dickinson,
 194 2012) whereas the alkaline milieu in invertebrate midguts accelerates mineralisation (e.g. Li and
 195 Brune, 2007).

Gelöscht: humification

196 For instance, earthworm casts have species-specific NIR spectral signatures, indicating presence
 197 of specific organic compounds (Hedde et al., 2005). Under grass/legume pasture they are
 198 characterized by significant enrichment of slightly-altered plant residues in the sand particle size
 199 (> 53 µm). CPMAS 13C NMR (Cross-Polarization Magic Angle Spinning Carbon-13 Nuclear
 200 Magnetic Resonance) spectra showed that earthworm casts and surrounding soil were dominated
 201 by carbohydrates, with a decrease of O-alkyl C and an increase of alkyl C with decreasing
 202 particle size (Guggenberger et al., 1996). Moreover, earthworms likely possess a unique
 203 capability of neutralizing plant polyphenols that otherwise strongly decrease decomposition rates
 204 of fresh plant litter (Liebeke et al., 2015). Micro- and mesofauna excrete ammonium or dissolved
 205 organic carbon (Filser, 2002; Fox et al., 2006; Osler and Sommerkorn, 2007), and affect the
 206 quantity of microbial metabolites (Bonkowski et al., 2009). Gut passage, defecation, excretion
 207 together with bioturbation by macro- and mesofauna facilitate humification and decomposition,
 208 altering also nutrient stoichiometry (Bohlen et al., 2004). These modifications in the molecular
 209 structure of SOM due to soil fauna activity have significant effects on its dynamics (Swift et al,
 210 1979; Guggenberger et al., 1995; Blume et al., 2009; Dickinson, 2012 and other references
 211 related to points 1 and 2 in Table 1).

212 2.2. Humic substances

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

Kommentiert [JF2]: 19

225 Humic substances are formed during the gut passage: organic matter in young soils and humic
 226 horizons almost completely consists of soil animal faeces (Lavelle, 1988; Martin and Marinissen,
 227 1993; Brussaard and Juma, 1996). Humus forms mainly comprise animal casts, e.g. casts of ants,
 228 isopods, millipedes, beetle larvae or termites in deadwood, of insect larvae and spiders in leaf
 229 litter, or casts of collembolans, mites and enchytraeids in raw humus. In his review, David (2014)
 230 considered macroarthropod casts being a factor of partial SOM stabilisation, rather than hotspots
 231 of microbial activity. The dark colour of casts (compared to the ingested organic material)
 232 visually demonstrates the strong chemical OM modification in animal guts, which is
 233 accompanied by a substantial physical modification. Clay-humus complexes, physically

236 protecting organic matter (Jiménez and Lal, 2006), are mainly faeces of earthworms and
 237 diplopods (see also Sect. 2.5 on physical heterogeneity). Due to differences in feeding
 238 preferences, gut microflora, SOM quantities consumed etc. of soil animals, their faeces vary in
 239 size, shape and quality not only between fauna groups, but also between species within one group
 240 (see Sect. 3 on aggregate formation). Discovering the important role of animal faeces in
 241 humification is essential to improve our understanding of carbon dynamics in soil.
 242
 243

244 2.3. Fire-derived carbon

245 Fire-derived carbon is chemically highly condensed and thus often hardly degradable. However,
 246 its stability in soil is variable and still poorly understood (Schmidt et al., 2011; Wang et al.,
 247 2016). Two of the factors identified by a meta-analysis on the stability of biochar in soil were
 248 association with aggregates and translocation in the soil profile (Wang et al., 2016), which are
 249 both strongly affected by soil fauna (see Sect. 2.5, 2.6 and 3). Microbial recolonisation of burned
 250 sites is mediated by wind and soil animals that survived in soil or emigrated from neighbouring
 251 areas, e.g. by macro- and mesofauna, birds and mice (Malmström, 2012; Zaitsev et al., 2014).
 252 Besides, soil fauna also ingest the charcoal particles (Eckmeier et al., 2007; see Table 1). Due to
 253 animal activity, charcoal is sorted by size and translocated down the soil profile. Mice and
 254 earthworms (Eckmeier et al., 2007) and the tropical earthworm *Pontoscolex corethurus*
 255 (Topoliantz and Ponge 2003; Topoliantz et al., 2006) had been suggested as responsible for rapid
 256 incorporation of charcoal into the soil. Quantitative data are however scarce (Table 1). In spite of
 257 potentially great importance, the effect of soil animals on the fate of the “black carbon” in soil
 258 remains practically unknown (Ameloot et al., 2013).

Gelöscht: highly

259 2.4. Roots

260 Roots not only represent a major input pathway of carbon into soil, but together with associated
 261 microflora they also have a large influence on the turnover dynamics of existing soil carbon
 262 (Finzi et al., 2015). Roots preferably grow in existing soil cavities (Jiménez and Lal, 2006),
 263 mostly formed by soil fauna (Wilkinson et al, 2009). Both burrowing and non-burrowing soil
 264 animals have a strong impact on root growth, allocation, length and density (Brown et al., 1994;
 265 Bonkowski et al., 2009; Arnone and Zaller, 2014). Animal grazing of root bacteria and
 266 mycorrhiza affects their activity and community composition, and animal excreta are enriched in
 267 micronutrients and selectively affect plant nutrition (Brown, 1995; Filser, 2002; Brussaard et al.,
 268 2007). Root herbivores and rhizosphere grazers affect C allocation of roots (Wardle et al., 2004)
 269 and largely regulate nutrient acquisition and plant productivity (Bonkowski et al., 2009). Not
 270 only root herbivores, but also saprotrophic/microbivorous soil animals may obtain a significant
 271 proportion of energy from plant roots (Pollierer et al., 2007). This suggests an animal-mediated
 272 regulatory loop that connects plant roots and SOM.

Gelöscht: Plant r

Gelöscht: Plant roots

273 2.5. Physical heterogeneity

274 Schmidt et. al. (2011) considered the physical disconnection between decomposers and organic
 275 matter to be one reason for SOM persistence in deep soil. Yet, physical heterogeneity in soils
 276 occurs at all spatial scales, and animals play a fundamental role in the distribution of organic
 277 matter and associated microorganisms. According to body size, decomposers act at various
 278 spatial scales, from micro-aggregates to landscapes (Ettema & Wardle, 2002; Jouquet et al.,
 279 2006). They fragment organic residues, perform bioturbation, distribute dead organic matter and
 280 generate smaller and larger organic matter hot spots (e.g. faecal pellets, ant and termite mounds).
 281 Mounds and burrows made by soil fauna are obvious signs of physical heterogeneity created by

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[2] nach oben: According to body size, they act at various spatial scales, from micro-aggregates to landscapes (Ettema & Wardle, 2002; Jouquet et al., 2006).

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

304 2.6. Soil depth

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

316 2.7. Permafrost

In permafrost soil up to $1.672 \cdot 10^{15}$ g carbon is stored (Tarnocai et al. 2009). Organism activity is mostly restricted to the short periods of time when the upper cm of the soil is thawed. Due to unfavourable environmental conditions (resulting in low animal biomass, activity and diversity), there is only little impact of fauna in permafrost soils (De Deyn et al., 2008). However, fauna invasions, especially of the above-mentioned soil engineers, due to soil melting in tundra and boreal forests are likely to have drastic effects (Frelich et al., 2006; Van Geffen et al., 2011). Data on earthworm invasions in North American forests (Bohlen et al., 2004; Frelich et al., 2006; Eisenhauer et al., 2007) show that they must be taken into consideration in carbon-rich soils, particularly in melting permafrost soils (Frelich et al., 2006; Schmidt et al., 2011) where they may affect many soil functions.

328 2.8. Soil microorganisms

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

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342 underground (Persson, 1989; Filser, 2002; Wardle et al., 2004; Fox et al., 2006; Osler and
 343 Sommerkorn, 2007; Wilkinson et al., 2009; Wu et al., 2013). They affect the activity and
 344 community composition of soil microorganisms in multiple ways such as feeding, burrowing,
 345 facilitating the coexistence of different fungal species (Crowther et al., 2011) or by modifying
 346 micro-habitat conditions. Litter comminution by detritivores increases SOM accessibility for
 347 microorganisms, and propagules are dispersed with body surface and casts. The gut environment
 348 provides protected microsites with modified biotic and abiotic conditions, which increase
 349 bacterial abundance substantially – e.g. by three orders of magnitude in earthworm guts (Edwards
 350 and Fletcher, 1988). Grazing affects microbial biomass, activity and community composition, and
 351 animal excreta modify nutrient availability for microorganisms (Brown, 1995; Filser, 2002).

352
 353 Table 1 contains quantitative examples of animal activity taken from different biomes and land-
 354 use types, showing that earthworms alone strongly affect each of the ‘key insights’. However,
 355 much smaller soil animals can also have substantial effects (Table 1). It has to be kept in mind
 356 that the separation of animals’ effects according to the insights is somewhat arbitrary as the
 357 associated soil processes are often interconnected. This is particularly obvious for molecular
 358 structure, humic substances, roots, physical heterogeneity, soil depth and
 359 microorganisms: metabolisation implies by definition an alteration of the molecular structure,
 360 often associated with the formation of humic substances. The stability of the latter has a very
 361 strong association with physical protection, and whether metabolisation of dead organic matter
 362 occurs at all depends on its horizontal and vertical distribution. For instance, earthworms will (a)
 363 translocate dead organic matter both vertically and horizontally, (b) transform part of it via
 364 metabolisation, (c) mix ingested OM with minerals, thus affecting its physical protection, (d)
 365 increase and alter the microbial community and (e) affect hydraulic properties and aeration of the
 366 soil through digging and tunnelling, which has an immediate impact on the activity of
 367 microorganisms and on root growth.
 368 As this example illustrated only the most important aspects of interacting processes, the next
 369 section provides a more elaborate overview on aggregate formation.

370 3. Aggregate formation

371 The modern view on the stability of organic matter in soils requires a thorough understanding of
 372 aggregate structure and formation including the role of soil biota (Lehmann and Kleber, 2015).
 373 Soil aggregation is the process by which aggregates of different sizes are joined and held together
 374 by different organic and inorganic materials. Thus, it includes the processes of formation and
 375 stabilisation, that occur more or less continuously, and can act at the same time. With clay
 376 flocculation being a pre-requisite for soil aggregation, the formation of aggregates mainly occurs
 377 as a result of physical forces, while their stabilisation results from a number of factors, depending
 378 in particular on the quantity and quality of inorganic and organic stabilising agents (Amézketa,
 379 1999).

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

385 Earthworms have a direct and fast impact on microaggregate formation and the stabilisation of
 386 new C within these microaggregates (Bossuyt et al., 2005) (Table 1). There are several
 387 mechanisms to explain the increase of micro- and macroaggregate stability by earthworms, but no
 388 mechanism has been quantified in relation to population size yet. Effects are related to ecological
 389 groups of earthworms, associated with feeding habit, microhabitat in the soil profile, and burrow
 390 morphology. However, irrespective of this classification, species may enhance or mitigate soil
 391 compaction (Blanchart et al., 1997; Guéi et al., 2012). The tensile strength of casts roughly

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408 defined as the force required to crush dried aggregates, i.e. an indirect measure of physical SOM
409 protection) appears to be species dependent: for example, the casts of *Dendrobaena octaedra*
410 have a lower tensile strength compared to those of *L. terrestris* (Flegel et al., 1998). Similarly,
411 organic carbon and water-stable aggregation was significantly higher in casts of *L. terrestris* than
412 in casts of *A. caliginosa* (Schrader and Zhang, 1997).
413 Some research, however, suggests that earthworm activity can also evoke soil degradation.
414 Shipitalo and Protz (1988) proposed that ingestion of soil by earthworms results in disruption of
415 some existing bonds within micro-aggregates and realignment of clay domains. Therefore, fresh
416 casts are more dispersible than uningested soil, contributing to soil erosion and crusting.
417 Significant improvement in the water stability of fresh, moist casts only occurs when
418 incorporated organic debris from the food sources is present and when moist casts are aged or
419 dried. Nevertheless, in the long term, casting activity enhances soil aggregate stability.
420 However, our understanding of the contribution of soil fauna to aggregate formation and
421 stabilisation, is limited, and mostly qualitative in nature. Different methodologies complicate the
422 comparison among aggregate stability data (Amézketa, 1999). Data in terms of functional
423 response to density are limited as many studies have been conducted in arable systems, where the
424 diversity and abundance of soil animals are reduced as a consequence of tillage, mineral
425 fertilizers and pesticide use. Recently, some studies have emerged. A negative correlation
426 between earthworm abundance and total macroaggregates and microaggregates within
427 macroaggregates in arable treatments without organic amendments could be linked to the
428 presence of high numbers of *Nematogena lacuum*, an endogeic species that feeds on excrements
429 of other larger epigeic worms and produces small excrements (Ayuke et al., 2011). Under the
430 conditions studied, differences in earthworm abundance, biomass and diversity were more
431 important drivers of management-induced changes in aggregate stability and soil C and N pools
432 than differences in termite populations. Another study highlighted that in fields converted to no-
433 tillage earthworms incorporated C recently fixed by plants and moved C from soil fragments and
434 plant residues to soil aggregates of >1 mm (Arai et al., 2013). Thus, soil management practices
435 altering fauna activities may have a significant effect on the re-distribution of soil organic matter
436 in water-stable aggregates, impacting agronomically favourable size fractions of water-stable
437 macro-aggregates, and water-stable micro-aggregates which are the most important source of
438 carbon sequestration (Šimanský and Kováčik, 2014).
439

440 4. Regional differences in climate, soils and land use

441 In a global meta-analysis spanning several continents, García-Palacios et al. (2013) show that
442 across biomes and scales the presence of soil fauna contributes on average 27% to litter
443 decomposition. Depending on the situation this contribution can be substantially lower or higher.
444 For instance, the authors report an average increase in decomposition rates of 47% in humid
445 grasslands whereas in coniferous forests this figure amounts to only 13%. The high impact of soil
446 fauna in humid grasslands is all the more important as such grasslands are among those
447 ecosystems that are most severely affected by global environmental change (Chmura et al., 2003;
448 Davidson and Janssen, 2006).
449 Many of our examples refer to earthworms and temperate regions as they have been studied most
450 intensively. However, we suggest that any dominant group of soil fauna, irrespective of body size
451 or the ability to create larger soil structures, may substantially affect carbon dynamics. Table 1
452 gives a number of respective case studies. The key players and specific effects of soil animals
453 vary across space (Fig. 2), with increasing importance for SOM dynamics in humid-warm and
454 nutrient-limited conditions (Persson, 1989; Filser, 2002; Wardle et al., 2004; Fox et al., 2006;
455 Osler and Sommerkorn, 2007; De Deyn et al., 2008; Briones, 2014). Once key players in a given
456 ecosystem have been identified as relevant for being included in SOM models (see Sect. 6 and
457 Fig. 3), more detailed information on their biology is required, in particular on their activity, their

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460 ecological niche and corresponding tolerance limits. All this varies with species, and often
461 extremely within one systematic group. Variation in drought or soil temperature towards limiting
462 conditions will first increase (stress response, e.g. downward migration) and then strongly
463 decrease activity (mortality or transition to inactive resting stage). Some key players will exhibit
464 high abundance and be extremely active throughout the year (Wilkinson et al., 2009), others
465 might only be moderately relevant during a short period of time; the contribution of a third group
466 might be considered insignificant.

467 Also ecosystem engineers differ between soil types, biomes and land-use types, from rodents and
468 ants in dry areas to termites, earthworms and millipedes in tropical rainforests. They consume
469 different types of organic matter, make deep or shallow, narrow or wide burrows, and differ in
470 aggregation behaviour (e.g. more or less regularly distributed earthworms versus distinct ant nests
471 and termite mounds). Accordingly, their role in SOM re-distribution and turnover differs as well.

472 In cold ecosystems – where, together with wetlands and peatlands, the majority of terrestrial
473 carbon is stored (Davidson and Janssens, 2006) – the response of detritivores to climatic change
474 is expected to be most pronounced (Blankinship et al., 2011). Melting of permafrost soil might
475 lead to northward expansion of soil macro-invertebrates, associated with accelerated
476 decomposition rates (van Geffen et al., 2011). Further examples are shown in Table 1.

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

487 5. Implications for modelling

488 As there is no unambiguous scientific support for the widespread belief in “humic substances”,
489 the question how long organic carbon remains in soil is largely related to a) physical protection
490 and b) how often the once photosynthesized dead organic matter is recycled in the soil food web.
491 For both processes soil animals are of great importance, as we have shown above. Biomass and
492 abundance of soil animals are generally constrained by temperature, humidity and food (living or
493 dead organic matter). However, the effects of these constraints on their activity are not simply
494 additive, nor is there any simple relation between biomass and activity. For example, despite
495 overall unfavourable conditions for the majority of soil organisms, burrowing activity in deserts
496 can be extremely high (Filser and Prasse, 2008). Moreover there is increasing evidence that fauna
497 effects on energy and nutrient flow can be at least partly decoupled from other abiotic and biotic
498 factors (Frouz et al., 2013). De Vries et al. (2013) even concluded that “Soil food web properties
499 strongly and consistently predicted processes of C and N cycling across land use systems and
500 geographic locations, and they were a better predictor of these processes than land use”. This
501 implies that knowledge of fauna may increase our prediction power. The thermodynamic
502 viewpoint makes the issue even more relevant: reaction speed increases with temperature, but
503 most soil organisms are rather adapted to relatively cool conditions and might thus be pushed
504 beyond their niche limits – with eventually negative consequences on their activity, see Sect. 4.
505 Changes in climate (Blankinship et al., 2011), land use (Filser et al. 2002; Tsiafouli et al., 2014),
506 resource availability and biotic interactions (De Vries et al., 2012; see Table 2) alter the
507 distribution, community composition, activity and associated impact of soil animals on
508 distribution and turnover rate of SOM (Wall et al., 2008) to the extent that underlying
509 assumptions of SOM models may no longer be valid (Swift et al., 1998; Bardgett et al., 2013;

Geföscht: (here defined as very large and highly complex, poorly degradable organic molecules with manifold aromatic rings; Lehmann and Kleber, 2015)

513 Schmitz et al., 2014). Therefore it is opportune to include approaches that have been developed
 514 during the past decades (Filser, 2002; Jiménez and Lal, 2006; Osler and Sommerkorn, 2007;
 515 Brussaard et al., 2007; Meysmann et al., 2006; Wall et al., 2008; Sanders et al., 2014). **For**
 516 **instance, Lavelle et al. (2004) implemented** earthworm activity in the CENTURY model. For this
 517 purpose, observations on long-term incubated earthworm casts and sieved control had been used
 518 as a reference. Afterwards earthworm activity was simulated with CENTURY by replacing the
 519 active and slow soil C decomposition rates of the model with those obtained by calibration with
 520 the control soil. **The simulations revealed a 10% loss of the slow C pool within 35 years**
 521 **compared to the original model without earthworms.**

522 Without considering the role of animals, models are less accurate: in a field study spanning four
 523 countries from Sweden to Greece, soil food web properties were equally important as abiotic
 524 factors and predicted C and N cycling processes better than patterns of land use (De Vries et al.,
 525 2013). In their study, earthworms enhanced CO₂ production whereas Collembola and
 526 bacterivorous nematodes increased leaching of dissolved organic carbon. Mechanistic
 527 experiments confirm that earthworms have a detrimental effect on the greenhouse gas balance
 528 under nitrogen-rich conditions (Lubbers et al., 2013) and under no-till (Lubbers et al., 2015).
 529 Inclusion of group-specific diversity of mesofauna in models of global-scale decomposition rates
 530 increased explained variance from 70 to 77% over abiotic factors alone (Wall et al., 2008). Also
 531 García-Palacios et al (2013) provide additional evidence on the argument that soil fauna activity
 532 is not merely a product of climate, soil properties and land use but an independent parameter.
 533 These examples indicate that the actors that play an important role in SOM dynamics should be
 534 considered in SOM models.

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

549 Next to space, scale effects also apply to temporal patterns – which poses a great challenge for
 550 SOM modelling as most studies refer to rather short periods of time. We illustrate this by the
 551 comparatively well studied impact of invasive earthworms. The meta-analysis of Lubbers et al.
 552 (2013) suggests that the effect of earthworms on total SOC contents is on average relatively
 553 small. In contrast, in certain situations earthworms can strongly affect greenhouse gas emission.
 554 These data were however mainly obtained in relatively short-term experiments. Over a period of
 555 months to years and even decades, earthworms can reduce C decomposition by physical
 556 protection of C in ageing casts (Six et al., 2004, see Table 1).

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

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571 These well documented examples of the impact of earthworms on soil C storage are related to
 572 invasive species. The presence of these species cannot be inferred directly from the climatic, soil
 573 and vegetation properties. The distributions of European invasive earthworms in North America,
 574 North European forests or South Africa are largely driven by human activity. Often fishing (due
 575 to lost baits), imported plants or potting material of colonizing farmers (Reinecke, 1983) are more
 576 important for these than habitat transformation – without human’s help earthworms are not active
 577 invaders (Stoscheck et al., 2012; Tiunov et al., 2006; Wironen and Moore, 2006). Thus the
 578 presence of earthworms can be an environment-independent parameter of SOM dynamics.

579 Another fundamental issue in the large-scale approach is often neglected: When including the
 580 effects of the soil fauna implicitly, this assumes that the soil fauna will always have the same
 581 effects under the same conditions, and hence that the soil fauna are essentially static. This
 582 assumption is increasingly unrealistic in a fast-changing world where both biodiversity and the
 583 climate are changing at accelerated paces, and where we are likely to witness major
 584 reorganisations of plant, animal and microbial communities. Therefore explicit representation of
 585 the soil fauna, where possible, should increase the predictive ability of SOM models.

586 Given the fact that this issue had been raised decades back (see above) it appears somewhat
 587 astonishing that attempts to pursue it have not yet made any significant progress. We believe
 588 there are mainly three reasons for this: a) missing information, b) too much detail, irrespective of
 589 spatial scale, and c) too little communication between empiricists and modellers. This is why we
 590 decided to bring into life a COST Action as an appropriate instrument to bridge these gaps. The
 591 next section gives an overview on it.

592 6. Ways to proceed: COST Action ES 1406

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

- 605 1. Knowledge gap analysis of SOM – soil fauna interactions;
- 606 2. Potentials and limitations for inclusion of soil fauna effects in SOM modelling;
- 607 3. Data assemblage and data sharing;
- 608 4. Knowledge management and advocacy training.

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

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

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

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- 620 - a literature review on the impact of soil fauna other than earthworms on SOM turnover
- 621 - a compilation of the potentials and limitations of existing SOM models
- 622 - the development of a simple SOM model that also explicitly incorporates soil animals and
- 623 associated processes in it, based on the current state of knowledge exchange between
- 624 empiricists and modellers within KEYSOM
- 625 - the preparation of a common European-wide field study into the impact of soil fauna
- 626 composition and abundance on SOM breakdown, distribution and aggregate formation,
- 627 which will start in autumn 2016
- 628 - the preparation of a summer school, to be held in early October 2016 in Coimbra,
- 629 Portugal

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

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

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

654 Once the procedure in Fig. 3A has reached box no. 4, intensive exchange with modellers (Fig.
655 3B) is mandatory to identify the relevant model parameters and the type of functional relationship
656 (box 5). Mechanistic aspects (such as chemical transformation in the gut, physical protection
657 within aggregates or impact on hydraulic soil properties via digging) are of prime importance
658 here as each of these examples may have different effects on C turnover. Effects of fauna
659 abundance or biomass (in comparison to presence-absence) on the shape of the function will be
660 addressed as well. Note, however, that to date necessary data for such an approach appear to be
661 limited (García-Palacios et al., 2013). – In the meantime, the modellers will have developed a
662 basic model structure and compare it with the structures of existing SOM models concerning
663 potentials and limitations for including fauna effects (Fig. 3B).

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

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

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

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685 Overall, the whole approach requires a modular model structure, allowing for using different
686 models according to the respective situation and data availability. This is what WG 2 is currently
687 developing. – Certainly all the research outlined here cannot be done within one single COST
688 Action. Based on the outcome of our work, we hope to come up with a more detailed roadmap
689 how to further proceed to improve SOM modelling. This roadmap, together with what could be
690 achieved with the limited resources of KEYSOM, will provide information material, decision
691 tools and management options for decision makers and politicians (WG 4).
692

693 7. Conclusions and outlook

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

704

705 Author contribution

706 J. Filser wrote the article, prepared Fig. 1 and 3 and the tables and compiled the contributions
707 from all co-authors. These are listed according to their quantitative and qualitative impact on the
708 manuscript, except for J.J. Jiménez who was placed last as he is the chair of COST Action ES
709 1406 (KEYSOM). L. Brussaard suggested including Fig. 2.

710

714

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994 **Tables**

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

Kommentiert [JF3]: 5

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	Marashi and Scullion, 2003; Six et al., 2004
	C protection is promoted by microaggregates within large macroaggregates, and earthworms can add 22% anew to this C pool	Bossuyt et al., 2005
	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	Albrecht et al., 2004, cited in Schmidt et al., 2011
	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	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	Van de Westeringh, 1972
	Mull-type forest soil top layers and wooded savanna soils consist almost entirely of earthworm casts	Kubiens, 1953; Lavelle, 1978
	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.	Hoogerkamp et al., 1983
	In average temperate pasture and grasslands, earthworms cast 40-50 t ha ⁻¹ year ⁻¹ on the surface and even more below surface	Lee, 1985
	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)	Wilkinson et al., 2009
	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	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

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* According to Schmidt et al. (2011)

1001 **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	Freligh 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 6. soil depth	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
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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1004 **Table 2.** “Insights” (compiled after Schmidt et al., 2011) for future soil organic matter models and
 1005 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.

1006 * Recommendations refer to site-specific keystone groups of animals (dominating in terms of biomass or impact; see
 1007 Fig. 2). Their prevalence is determined by climate, bedrock and land use (e.g. rodents or ants in deserts, earthworms in
 1008 temperate grasslands or microarthropods and enchytraeids in acidic Northern forests).

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1011 **Figure Captions**

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1013 **Figure 1.** Main animal-mediated processes (boxes) affecting the eight insights (symbols)
1014 identified by Schmidt et al. (2011) that should be considered for improving SOM models

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1016 **Figure 2.** Dominant soil types and characteristic soil forming invertebrates across biomes (major
1017 global change threats are shown in italics). MAT = mean annual temperature, MAP = mean
1018 annual precipitation. Sources for data and biomes see Brussaard et al. (2012).

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1022 **Figure 3.** Flow scheme for an improved understanding of the role of soil fauna for soil organic
1023 matter (SOM) turnover. This scheme is basically followed within the COST Action ES 1406
1024 (KEYSOM). Activities in A) and B) run parallel, followed by C) which ends with an improved
1025 SOM model. Exemplarily shown are scenarios for two biomes. Further explanations see text.

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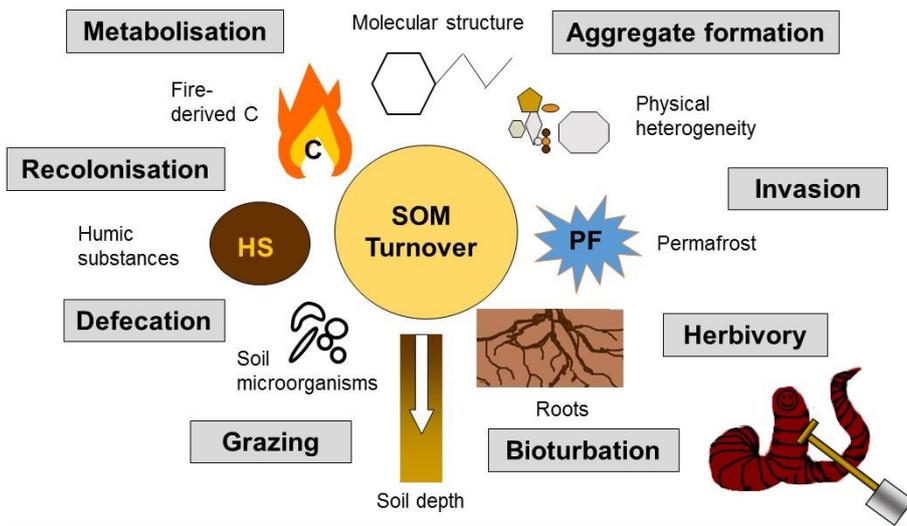
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1031 **Figures**

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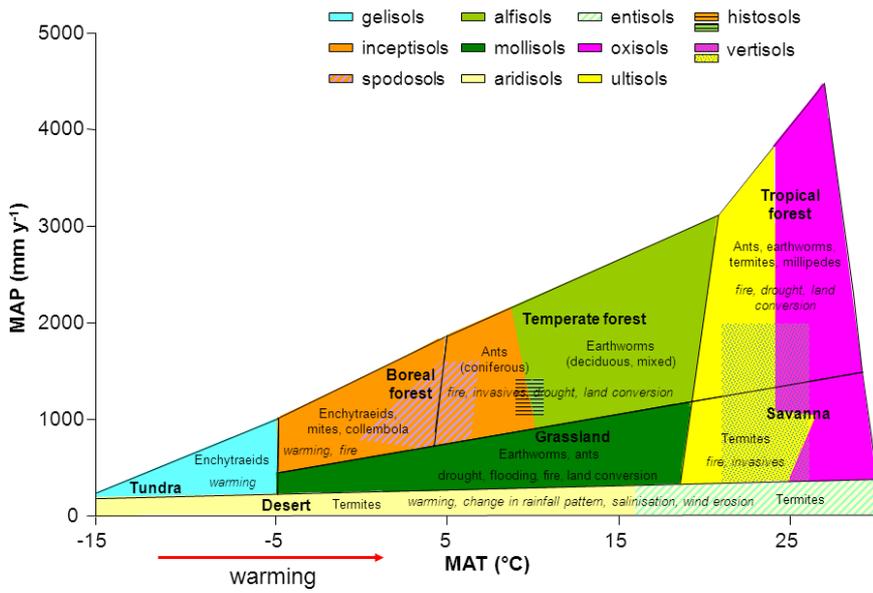
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1038 **Figure 1**

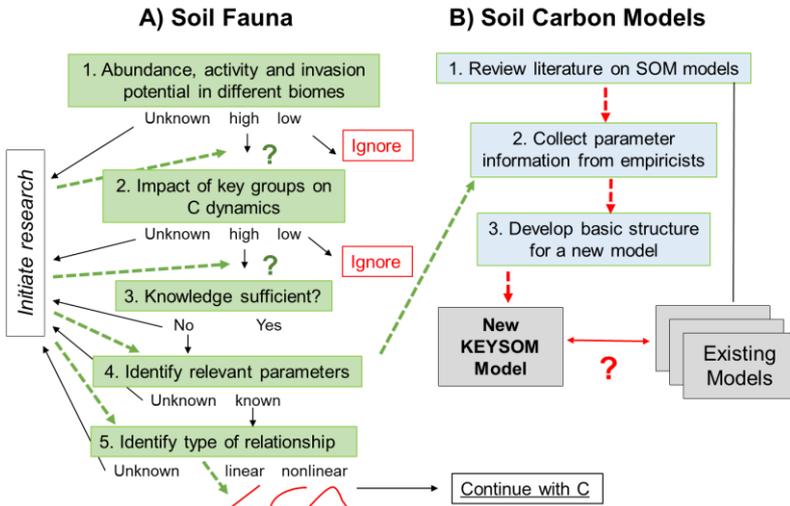
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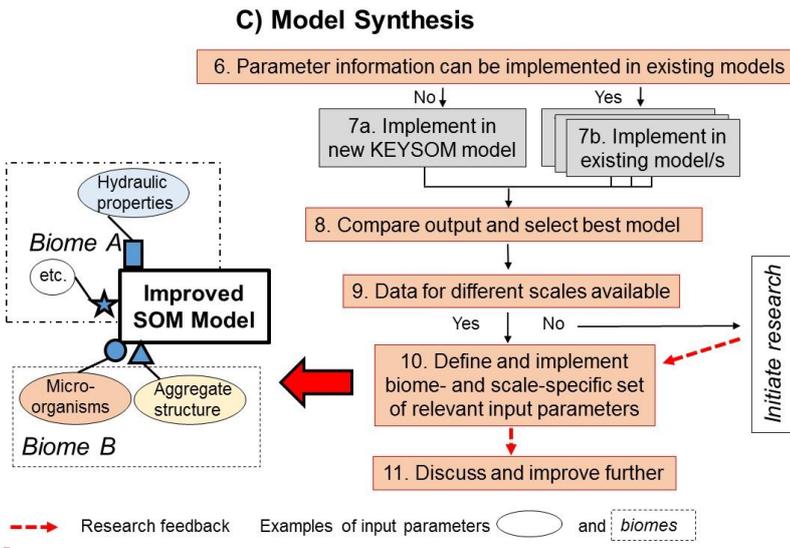


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1045 **Figure 2**
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Figure 3

