

Using plant, microbe and soil fauna traits to improve the predictive power of biogeochemical models

Ellen L. Fry^{1*}, Jonathan R. De Long^{1,2*}, Lucía ÁlvarezGarrido^{3,7}, Nil Alvarez⁴, Yolima Carrillo³, Laura Castañeda-Gómez³, Mathilde Chomel¹, Marta Dondini⁵, John E. Drake^{3,6}, Shun Hasegawa⁷, Sara Hortal³, Benjamin G. Jackson⁸, Mingkai Jiang³, Jocelyn M. Lavalley¹, Belinda E. Medlyn³, Jennifer Rhymes^{1,9}, Brajesh K. Singh³, Pete Smith⁵, Ian C. Anderson³, Richard D. Bardgett¹, Elizabeth M. Baggs⁸ and David Johnson¹

¹ School of Earth and Environmental Sciences, Michael Smith Building, The University of Manchester, Manchester M13 9PT, UK

² Department of Terrestrial Ecology, Netherlands Institute of Ecology, P.O. Box 50, 6700 AB, Wageningen, The Netherlands

³ Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW 2751, Australia

⁴ IRTA Aquatic Ecosystems, Ctra. de Poble Nou km 5.5, 43540 Sant Carles de la Ràpita, Catalonia, Spain

⁵ Institute of Biological & Environmental Sciences, University of Aberdeen, 23 St Machar Drive, Aberdeen, AB24 3UU, UK

⁶ Department of Forest and Natural Resources Management, SUNY College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA

⁷ Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå SE-901 83, Sweden

⁷ Department of Animal Biology, Plant Biology and Ecology, University of Jaén, Jaén, Spain

⁸Royal (Dick) School of Veterinary Studies, University of Edinburgh, Midlothian, EH25 9RG,
UK

⁹School of Geography, Earth and Environmental Sciences, University of Plymouth, Drake
Circus, Plymouth, PL4 8AA, UK

*Shared first authorship

Corresponding author: Jonathan R. De Long

Phone: 00-31-64-595-9869

Email: j.delong@nioo.knaw.nl

Running head: Organismal traits inform process-based models

1 Abstract

- 2 1. Process-based models describing biogeochemical cycling are crucial tools to [understanding](#)
3 long-term nutrient [dynamics, especially](#) in the context of perturbations, such as climate and
4 land-use change. [Such models must effectively](#) synthesise ecological processes and
5 properties. For example, in terrestrial ecosystems, plants are the primary source of
6 bioavailable carbon, but turnover rates of essential nutrients are contingent on interactions
7 between plants and soil biota. Yet, biogeochemical models have traditionally considered
8 plant and soil communities [in broad terms. The next generation of models must consider](#) how
9 shifts in their diversity and composition affect ecosystem processes.
- 10 2. One promising approach to synthesise plant and soil biodiversity and their interactions into
11 models is to consider their diversity from a functional trait perspective. Plant traits, which
12 include heritable chemical, physical, morphological and phenological characteristics, are
13 increasingly being used to predict ecosystem processes at a range of scales, and to interpret
14 biodiversity-ecosystem function relationships. There is also emerging evidence that the traits
15 of soil microbial and faunal communities can be correlated with ecosystem functions such as
16 decomposition, nutrient cycling and greenhouse gas production.
- 17 3. Here, we draw on recent advances in measuring and using traits of [different](#) biota to predict
18 ecosystem processes, and provide a new perspective as to how biotic traits can be integrated
19 into biogeochemical models. We first describe an explicit trait-based model framework that
20 operates at small scales and uses direct measurements of ecosystem properties; second, an
21 integrated approach that [operates at medium scales and](#) includes interactions between
22 biogeochemical cycling and soil food webs; and third, an implicit trait-based model
23 framework that associates soil microbial and faunal functional groups with plant functional
24 groups, and operates at the Earth-system level. In each of these models we identify

25 opportunities for inclusion of traits from all three groups to reduce model uncertainty and
26 improve understanding of biogeochemical cycles.

27 4. These model frameworks will generate **improved** predictive capacity of how changes in
28 biodiversity regulate biogeochemical cycles in terrestrial ecosystems. Further, they will assist
29 in developing a new generation of process-based models that include plant, microbial and
30 faunal traits and facilitate dialogue between empirical researchers and modellers.

31

32 **1. Introduction**

33 Recent improvements in computational power and co-ordinated research efforts into modelling
34 ecosystem processes have advanced our understanding of biogeochemical cycles. However, a better
35 understanding of the interactions between plants, microbes and animals is crucial to reduce
36 uncertainty in carbon (C) cycling and the modelling of biogeochemical processes. Important aspects
37 of these cycles include C turnover times (He *et al.* 2016), soil organic matter dynamics (Cotrufo *et*
38 *al.* 2015), and soil carbon sink strength under a range of climate scenarios (Sofi *et al.* 2016). This
39 will help address pressing challenges such as soil C loss and food security (Lehmann & Kleber
40 2015). However, there is a gap between the requirements of modellers and the empirical data
41 produced through experimental research. Empirical data related to the functional role of organisms is
42 needed to parameterise models under a range of spatial and temporal scales, ecosystem types and
43 abiotic conditions. The consideration of functional traits promises to generate data that can help
44 inform biogeochemical models (Violle *et al.* 2007; Moretti *et al.* 2017). Functional traits are
45 heritable, morphological, physiological or phenological attributes of organisms that affect their
46 growth, survival or reproduction, and thus, indirectly, fitness (Reich 2014). Many traits are
47 commonly categorised as ‘effect traits’ and/or ‘response traits’. Effect traits determine the effect of
48 the organism on ecosystem processes, while response traits are characteristics that change in
49 response to an external driver such as climate (Lavorel & Garnier 2002). Many traits may be both
50 effect and response traits. Using functional effect traits instead of traditional diversity measures can
51 generate more meaningful model predictions, because traits can offer mechanistic insight into the
52 link between organisms and ecosystem function (Díaz *et al.* 2004; De Deyn, Cornelissen & Bardgett
53 2008; Faucon, Houben & Lambers 2017).

54 Traits have been widely used to predict how organisms influence ecosystem functioning, with a
55 large focus on plant traits (Lavorel & Garnier 2002; Faucon, Houben & Lambers 2017). For

56 example, in tropical forests, stoichiometric traits of the tree canopy are strongly linked with nutrient
57 cycling rates (Asner *et al.* 2015), while at local scales, physical and chemical traits of leaves and
58 roots can affect soil C storage (De Deyn, Cornelissen & Bardgett 2008) and decomposition (Carrillo
59 *et al.* 2017; Martin, Newton & Bullock 2017). One key advantage is that traits do not use taxonomy
60 or numbers of species to infer function, which has previously been criticised (see the diversity-
61 stability debate; McCann 2000). The intense focus on plant traits has resulted in the discovery of
62 resource-use and performance related strategies. For example, the ‘leaf economics spectrum’ uses
63 three plant traits (leaf nitrogen content, specific leaf area and leaf lifespan) to describe a continuum
64 ranging from ‘fast’ to ‘slow’ growing species that affects ecosystem functioning (Wright *et al.* 2004).
65 The principles employed in this approach may also apply to microbes and fauna, and literature is
66 beginning to emerge on this theme (Allison 2012; Krause *et al.* 2014; Aguilar-Trigueros *et al.* 2015).

67 Soil microbes and fauna are key drivers of ecosystem processes, and contribute to ecosystem
68 stability. However, frameworks to capture trait syndromes for soil organisms are in their infancy.
69 Given the importance of soil microbes and fauna for biogeochemical cycles (Carrillo, Ball, Bradford,
70 Jordan & Molina 2011; de Vries *et al.* 2013; Kardol, Throop, Adkins & de Graaff 2016), this
71 represents a major hurdle when incorporating soil microbial and faunal traits into C and
72 biogeochemical models. Furthermore, modelling ecosystem processes requires that traits must be
73 constrained into the most parsimonious set of descriptors, [so as not to overfit the model](#). Taking
74 lessons learned from plant trait literature, it may be possible to identify microbial and faunal
75 characteristics that are quantitatively linked to ecosystem processes to improve model
76 parameterisation without exhaustive screening (Díaz *et al.* 2016; Kardol, Throop, Adkins & de
77 Graaff 2016).

78 Soil biogeochemical models have long been used to describe the processes of C and elemental
79 cycling in soil, but plants and microbes, two of the key drivers of these processes, are typically

80 included only in reductionistic terms because of the difficulty of accurately characterising these
81 groups of organisms (Wieder, Grandy, Kallenbach, Taylor & Bonan 2015). The increasing rate of
82 collection of new data on plants, as well as soil microbes and fauna, offers an opportunity to build on
83 the advances made by previous models (e.g., CENTURY: Parton, Schimel, Ojima & Cole 1994;
84 DAYCENT: (Parton, Hartman, Ojima & Schimel 1998); TEM: (Zhuang *et al.* 2011); CLM4: (Koven
85 *et al.* 2013). Soil fauna have been included in biogeochemical models in broad terms, such as
86 nematode and microarthropod biomass C (Grandy, Wieder, Wickings & Kyker-Snowman 2016;
87 George *et al.* 2017). Increasingly, more nuanced models are possible due to better understanding of
88 the role of faunal groups and availability of more comprehensive data on traits of these groups at
89 different spatial and temporal scales. Evidence from soil food web models indicates that inclusion of
90 plant, microbial and soil faunal traits and their interactions is imperative to improve the predictive
91 power of biogeochemical models (Allison 2012; Wieder, Bonan & Allison 2013; Filser *et al.* 2016;
92 Faucon, Houben & Lambers 2017; Funk *et al.* 2017). To move forward, we propose that gaps in
93 knowledge of measuring and understanding functional traits must be addressed and general
94 principles must be identified.

95 Here we propose frameworks to incorporate plant, microbial and soil faunal traits in predictive
96 models to better simulate the dynamics of biogeochemical cycles in terrestrial ecosystems. We use
97 the decomposition of soil organic matter (SOM) as an example because it is a key driver of the
98 terrestrial C cycle, and will likely be affected by global climate change (Davidson & Janssens 2006).
99 Moreover, there are well-established mechanisms to suggest that plants, microbes and soil fauna
100 interact in context-specific ways to influence decomposition (Swift, Heal & Anderson 1979; Allison
101 2012; Filser *et al.* 2016), making them ideal candidates for inclusion in such models. First, we
102 highlight knowledge gaps in the traits framework and the potential for sets of traits (e.g.,
103 stoichiometry, resource capture strategy) between plants, microbes and soil fauna to correlate.

104 Second, we seek to bridge the gap between modellers and experimental ecologists by outlining what
105 types of data are feasible to collect and useful as inputs to models (Table 1). Finally, we discuss the
106 uses and limitations of three types of commonly used models (explicit, integrated and implicit) and
107 describe why incorporating traits from plants, microbes and fauna will help improve the predictive
108 power of these models.

109

110 **2. The potential for using traits to describe biogeochemical processes**

111 Plant traits have been used extensively to understand the links between plant communities,
112 ecosystem processes and environmental change (Funk *et al.* 2017). This approach has several
113 advantages, including cost and time effectiveness, and the ability to scale trait distributions from the
114 individual to the landscape level. For example, plant traits change predictably across climatic
115 envelopes (Díaz *et al.* 2004), elevational gradients (Read, Moorhead, Swenson, Bailey & Sanders
116 2014) and management regimes (de Vries *et al.* 2012). [In fact, exploring plant traits across
117 chronosequences \(i.e., space-for-time substitution, as seen across successional gradients; Walker,
118 Wardle, Bardgett & Clarkson 2010\) has allowed for a better understanding of how traits can predict
119 ecosystem processes at both temporal and spatial scales \(Wardle, Walker & Bardgett 2004;
120 Kumordzi *et al.* 2015\). Arguably the most important aspect of functional traits is the strong links
121 identified with biogeochemical processes. Soil C storage across biomes can be influenced by traits
122 including leaf nitrogen \(N\) content and relative growth rate \(De Deyn, Cornelissen & Bardgett
123 2008\), while similar traits drive decomposition \(Carrillo *et al.* 2017\). As such, aboveground plant
124 traits have typically been considered to fall on a spectrum between those promoting fast and slow
125 cycling of nutrients \(analogous to r- and k-strategists in microbial communities\), with plants with
126 ‘slow’ traits promoting the formation of more stable SOM than plants with ‘fast’ traits \(De Deyn,
127 Cornelissen & Bardgett 2008\). Extending this paradigm to microbial and faunal groups may be](#)

128 possible. For example, increasing leaf N is likely to increase palatability for soil fauna and microbes,
129 and so N-rich leaves are likely to be preferentially decomposed by highly exploitative r-selected
130 microbial and faunal groups. This suggests that plant, microbe and soil fauna traits might align in
131 predictable ways (Box 1). However, the fast-slow decomposition paradigm has recently been
132 challenged, with greater emphasis on the accessibility of SOM as opposed to the chemical
133 composition (Lehmann & Kleber 2015). Therefore, relative resource use rates of the three groups
134 may have important connotations for whether decomposable SOM is incorporated into microbial or
135 faunal biomass.

136 Recent literature has identified the most important microbial traits that can predict or be
137 predicted by ecological processes (Aguilar-Trigueros *et al.* 2015; Treseder & Lennon 2015); (Table
138 1). A key distinction has been drawn between free-living microbes and those dependent on host
139 species. It is assumed that responses of the free-living species are more environmentally mediated,
140 while microbes dependent on host species (e.g., mycorrhizal fungi, rhizobia) may respond primarily
141 to cues from the host plant (Friesen *et al.* 2011; Crowther *et al.* 2014). Fungi can have mutualistic,
142 pathogenic and saprotrophic life cycles, with accompanying variation in morphology, chemistry and
143 resource use efficiency (Aguilar-Trigueros *et al.* 2015). This variation creates a major hurdle for
144 those trying to find unifying principles across microbial groups. Additionally, the assembly of a free-
145 living fungal community is largely based on environmental gradients, with resource availability
146 being a key determinant. [This could mean a decoupling of plant and microbial community assembly
147 processes under environmental stress \(Box 1\)](#). Accordingly, Crowther *et al.* (2014) presented a
148 continuum based on resource use, with highly competitive fungal taxa occurring in resource-rich,
149 low-stress conditions, and stress-tolerant taxa occurring when resources are scarce or conditions are
150 harsh. However, the problem herein is that many of these spectra account for ‘response traits’ not
151 ‘effect traits’, and are therefore potentially too variable or context-specific for models that aim to

152 predict ecosystem function. Further, resource availability for plants may not match resource
153 availability for fungi, partly because of more conservative resource use, partly because of differing
154 stoichiometric requirements (de Vries *et al.* 2012). A similar problem is likely to apply to bacterial
155 distributions (Martiny, Jones, Lennon & Martiny 2015). Knowledge of abundances, or
156 presence/absence of certain important bacterial groups with specific functional traits, such as
157 methane oxidising bacteria and phosphate solubilising bacteria, is likely to be the most effective way
158 of including bacteria in models, given the problems with dormancy (Fierer 2017) and defining
159 bacterial species (Caro-Quintero & Konstantinidis 2012).

160 Trait classifications for soil fauna are beginning to emerge. For example, Pey *et al.* (2014)
161 suggest 20 trait measurements in five broad categories (morphology, physiology, feeding, life
162 history, and behaviour) that can be utilised across invertebrates. Moretti *et al.* (2017) proposed
163 standardized measurements for 29 traits known to be sensitive to global stressors and to affect
164 ecosystem processes (Table 1). As fauna tend to be mobile, community weighted mean (CWM) traits
165 may be useful to predict ecosystem processes. Traits such as feeding habit or body size are
166 particularly responsive to environmental changes (Farská, Prejzková & Rusek 2014), and functional
167 diversity metrics based on these traits are effective in describing decomposition (Milcu & Manning
168 2011). We need to identify traits that can encompass the structure of the food web to be able to
169 include several trophic groups and their interactions. Taken together, plant, microbial and soil faunal
170 traits offer a way to improve the accuracy of biogeochemical models, but for the latter two groups, a
171 crucial first step is to disentangle the role of response and effect traits.

172 There are some issues concerning the integration of plant, microbe and soil fauna traits into
173 biogeochemical models. One major consideration is the turnover rate of microbial and faunal
174 communities. In contrast to plants, microbes and soil fauna often have a high turnover rate, and they
175 can adapt their metabolism or feeding strategies quickly to new conditions. Additionally, faunal

176 composition may rapidly change. Resource use and turnover are likely useful traits to describe these
177 groups, because they correlate directly with biogeochemical processes, with relative biomass of each
178 group dictating the importance of that group in the system (Crowther *et al.* 2014; Fierer 2017).
179 Further, we need to find a set of easily measurable descriptors for traits across all three groups that
180 will describe key soil functions, such as decomposition, robustly across a range of conditions and
181 biomes. There are potential shortcuts using prior knowledge obtained from the plant trait literature.
182 The biomass ratio hypothesis states that the influence of an individual or species on a function is
183 proportionate to its biomass in the ecosystem (Grime 1998). Therefore, it is possible that rather than
184 measuring complex, continuous traits, categorical data such as feeding group could be constrained to
185 an ordinal scale and weighted by abundance (i.e., CWM) (Fierer *et al.* 2014). Assessing activity of
186 the whole community could offer a solution, and there are numerous methods, including the
187 measurement of enzyme activities involved in decomposition and respiration rates, to achieve this.

188 We also need to include interactions between plants, microbes and soil fauna into models
189 because these interactions can have large effects on C fluxes (Johnson *et al.* 2005; Kanters, Anderson
190 & Johnson 2015). Of primary consideration is the level of organization within soil food web
191 communities. There are extensive data regarding the assembly of soil food webs associated with
192 particular plant species that can inform explicit models (Yen *et al.* 2016), but such data needs to
193 demonstrate quantitative correlations with biogeochemical cycling. However, it remains uncertain as
194 to when, how and why these associations form and deteriorate across larger scales (Nilsson &
195 McCann 2016). Furthermore, transfers of C and N between plants, microbes and soil fauna are
196 relatively well characterized and have been used in models examining food web energy flows
197 (Pausch *et al.* 2016). The next step is to apply this knowledge to test broader hypotheses (Table 2).
198 Ideally, we need to know whether plant, microbial and faunal groups respond in the same direction
199 under a given scenario. For example, under a drought event, plants may temporarily stop

200 photosynthesizing, thereby reducing root exudation, which leads to a reduction in bacterial biomass
201 and thereby soil fauna (Box 1). There are likely to be other scenarios where one group can capitalize
202 on the decline of the others, and these scenarios are likely to be unpredictable and thus difficult to
203 include in models. Therefore, in order to create unifying principles across plants, microbes and soil
204 fauna, it is imperative to identify traits that have robust relationships with function (e.g., nutrient
205 requirements) and avoid highly plastic traits in order to be able to use them across large spatial scales
206 and contrasting environmental conditions.

207

208 **3. Incorporating a trait-based approach into biogeochemical models**

209 Models require several data formats, depending on their scope. For example, an explicit
210 decomposition model can use raw data from field experiments, such as CWM leaf traits or
211 abundance of soil fauna. Integrated and implicit models, however, may need data in the form of
212 correlation coefficients between the drivers of decomposition, as well as reasonable *a priori*
213 parameter values. These requirements make it difficult to acquire appropriate data for such models.
214 For the microbial and faunal traits, an ideal starting point would be to assemble databases of traits
215 across ecosystems, climates and land use types (Burkhardt *et al.* 2014) that resemble the TRY
216 database for plants (Kattge *et al.* 2011). However, as such databases are assembled for microbes and
217 soil fauna, caution must be taken to account for variability in the data that might be due to inherent
218 factors such as intraspecific variability, and the use of different methods to measure microbial and
219 faunal traits.

220 Recently, there has been considerable effort to develop working trait-based models, although
221 at the time of writing, models are yet to include all three taxonomic groups (i.e., plants, microbes
222 and fauna). For example, there are models based on plant community assembly (Xu, Medvigy,
223 Powers, Becknell & Guan 2016), microbial processes (Allison 2012; Wieder, Bonan & Allison

224 2013; Wieder, Grandy, Kallenbach & Bonan 2014; Hararuk, Smith & Luo 2015), and certain faunal
225 groups (van Bodegom, Douma & Verheijen 2014; Yen *et al.* 2016). However, model generalisation
226 remains challenging due to their complexity, limited data availability and scalability. [Uncertainty](#)
227 [in modelling biogeochemical processes has two components, namely that arising from detail and](#)
228 [precision in the data, and from the model itself \(Keenan, Carbone, Reichstein & Richardson 2011\).](#)
229 [Quantification of data and model uncertainties is therefore imperative to determine the accuracy](#)
230 [and interpretability of model predictions. Regardless of the type of model, it is important that they](#)
231 [are continually tested using appropriate data, and that they are used in ecosystems where they have](#)
232 [been developed and validated. The evaluation of a process-based model depends strictly on the](#)
233 [quality, type and frequency of the measured values used to test the model.](#)

234 In order to construct an effective model for linking biological communities with decomposition
235 rates across multiple trophic levels, there is a need for robust trait data that incorporates spatial and
236 temporal elements. Although there have been numerous case studies exploring individual response or
237 effect traits, little is known about interactions between traits (e.g., trade-off), association between
238 response and effect traits across and within trophic levels, and variation of traits within and between
239 species across space and time (i.e., trait plasticity) (Ackerly & Cornwell 2007; Krause *et al.* 2014).
240 Belowground biotic traits, such as specific root length or microbial growth efficiency, have not been
241 properly quantified in terms of their optima, intra- and interspecific variation, trade-offs, and
242 functionality (Bardgett 2017; Laliberté 2017). Quantifying which traits affect which processes and
243 how such relationships vary across space and time is vital for process-based models. As a first step,
244 well-coordinated data collection efforts are needed on trait correlations along trophic and
245 environmental gradients (Wieder *et al.* 2015). To achieve this, there is an urgent need to identify
246 traits that are relatively easy to measure yet informative so that they strongly interact with
247 environmental gradients and/or are crucial for fitness (McGill, Enquist, Weiher & Westoby 2006)

248 (Table 1). Once links between traits and ecosystem function have been established across contrasting
249 spatial and temporal scales, it will be important to evaluate if their inclusion improves the predictive
250 power of models.

251

252 **Types of models that will benefit from incorporating plant, microbial and soil faunal traits**

253 Depending on the complexity and the predictive power needed, microbes and soil fauna can be either
254 explicitly or implicitly represented in an ecosystem model (Figure 1). Below we outline three
255 possible frameworks to incorporate belowground organism traits and processes in biogeochemical
256 models: 1) an explicit trait-based model framework that operates at the small scale (space or time, or
257 both) and uses direct measurements of ecosystem properties 2) an integrated approach that operates
258 at a medium scale and includes interactions between a model component on biogeochemical cycling
259 and that on the soil food web, either of which could be populated with measured data; and 3) an
260 implicit trait-based model framework that operates at a large scale (i.e., Earth system) and associates
261 microbial and soil faunal functional groups with plant functional groups. To fit with the focus of this
262 manuscript, we separated the models based on how microbes and soil fauna are represented in the
263 models, as well as the spatial or temporal scale at which each model is best equipped to operate
264 (Figure 1). The scope of this separation is to discuss possible frameworks to incorporate
265 belowground traits into soil process based models. It should be noted that the classification system
266 proposed here is not the only way such models can be grouped or defined.

267

268 *Explicit models*

269 Explicit models seek to parameterise relationships between variables, typically known as the
270 dependent and independent variables. Such models in the context of biogeochemical cycling
271 explicitly include microbial biomass. The goal of these models is to predict the dependent variable

272 (e.g., decomposition) (Parton, Schimel, Cole & Ojima 1987). Explicit trait-based models, such as
273 those developed for the simulation of microbial communities (e.g., Allison 2012) and faunal
274 communities (Filser *et al.* 2016), require extensive knowledge of the intra- and interspecific trait
275 variation along environmental gradients and their effects on ecosystem pools and fluxes. Two major
276 advantages of this approach are: (1) the explicit parameterization of traits allows for measured values
277 as direct model input; and (2) complex interactions between organisms are allowed and may lead to
278 emergent properties, such as top-down or bottom-up regulation of food web structure. For example,
279 in Figure 1a, microbial communities could be represented by r-selected (R_{mic}) and K-selected (K_{mic})
280 groups, with R_{mic} defined by traits that exhibit fast-growing attributes that compete with plants for
281 easily available nutrients, and K_{mic} as slow-growing, but able to utilize recalcitrant materials (e.g.,
282 Wieder *et al.* 2015). To simulate these processes, we need to determine the growth and nutrient
283 uptake efficiencies of R_{mic} and K_{mic} , and the trait-function and trait-abiotic relationships. Further, the
284 relationship between R_{mic} and K_{mic} and soil fauna (i.e., grazers, predators) will need to be better
285 understood. This framework explicitly simulates trait trade-offs of different belowground biotic
286 groups, which is useful for understanding fine-scale, non-linear system dynamics. Understanding of
287 how belowground traits should be incorporated into the mathematical equations of such models has
288 shown promising development (McCormack *et al.* 2017) (e.g., specific root length, Table 1). In
289 addition, models incorporating this level of complexity may exhibit unrealistic simulation behaviours
290 (e.g., Hararuk, Smith & Luo 2015). Explicit trait-based models will benefit from efforts that quantify
291 how the traits of different biotic groups affect ecosystem processes across different ecosystems,
292 which may be achieved through meta-analysis and enhancement of trait databases (Table 2; Funk *et*
293 *al.* 2017).

294

295 *Integrated models*

296 Integrated models are a mix of measured and inferred variables. These process-based models have
297 been developed from an understanding of how soil is affected by its abiotic and biotic properties,
298 land management and climate (McGill 1981; Smith *et al.* 1998). This approach integrates
299 biogeochemical and soil food web (i.e., microbial and soil faunal interactions driven by inputs from
300 plants) models (see Table 2 for examples of potential research questions). Here, mass and C are
301 recycled in the former model, and plant, microbial and soil faunal functional traits affect the rate of
302 mass transfer as a consequence of simulation in the latter (Figure 1b). These two models operate at
303 different timescales and spatial resolutions, as the biogeochemical model does not directly simulate
304 population demography and community assembly. The level of complexity of the soil food web
305 model varies depending on the research question and data availability, with soil food webs either
306 condensed into a metric of biodiversity or explicitly represented by their respective plant, microbial
307 and soil faunal groups. A metric of community diversity could be calculated for the soil food web
308 model and used to modify the rate of decomposition in the biogeochemical model (dashed arrows in
309 Figure 1b). For this integrated model to work, however, connections on how soil food webs affect
310 elemental transfers, and how plant ecophysiology affects competition and demography must be
311 quantified. Additionally, the ability to track changes in vegetation functional trait composition
312 through time and space without tracking species composition along different trophic levels is
313 necessary.

314

315 *Implicit models*

316 Finally, implicit models are often used to attempt to predict functions or processes at the global scale.
317 Well-known examples of implicit models include the CENTURY model, which predicts soil C, N
318 and nutrient turnover based on SOM turnover and plant functional type (Parton, Schimel, Ojima &
319 Cole 1994). Implicit trait-based models (Figure 1c) incorporate belowground biotic traits by making

320 the assumptions that microbial and soil faunal functional traits have clear associations with plant
321 functional traits, and their responses to environmental perturbations are similarly predictive (see Box
322 1; Table 2). Such an approach would allow Earth system models to maintain the basic structure of
323 their simulation of decomposition. Implicit models assume that plant attributes exhibit top-down
324 control on processes such as decomposition. Therefore, microbial and soil faunal groups are
325 expected to be adapted to such controls. This means that relationships between diversity, disturbance
326 and productivity are well established in a given location. Most of the existing land surface models
327 operating at large spatiotemporal scales have adopted this approach (e.g., CLM: Yang et al., 2014;
328 CABLE: Wang et al., 2010; O-CN: Zaehle & Friend, 2010).

329 While this approach enables Earth system simulations at coarse spatial resolutions, [at the time of](#)
330 [writing, such simulations cannot incorporate](#) intraspecific trait variation of microbes and soil fauna
331 and their potential consequences for ecosystem processes. The possibility that plant, microbial and
332 faunal traits do not respond similarly to stress, and are not subject to the same spatial or temporal
333 patterns, [are also beyond the scope of the current models because of limitations in data \(Box 1\)](#). One
334 solution could be the integration of statistical tools such as Bayesian hierarchical modelling to
335 estimate intraspecific trait variation and species interactions (Funk *et al.* 2017). However, this only
336 provides a probabilistic estimate of the consequence of multiple ecosystem processes. Nevertheless,
337 this approach represents a compromise among factors such as data availability, scalability and
338 predictive power, and is practical based on existing Earth system models.

339

340 **The way forward**

341 Ultimately, without improved communication between those who collect empirical data and those
342 who model biogeochemical cycles, efforts to close the knowledge gaps are doomed to fail. Here we
343 suggest five important steps to unite research efforts:

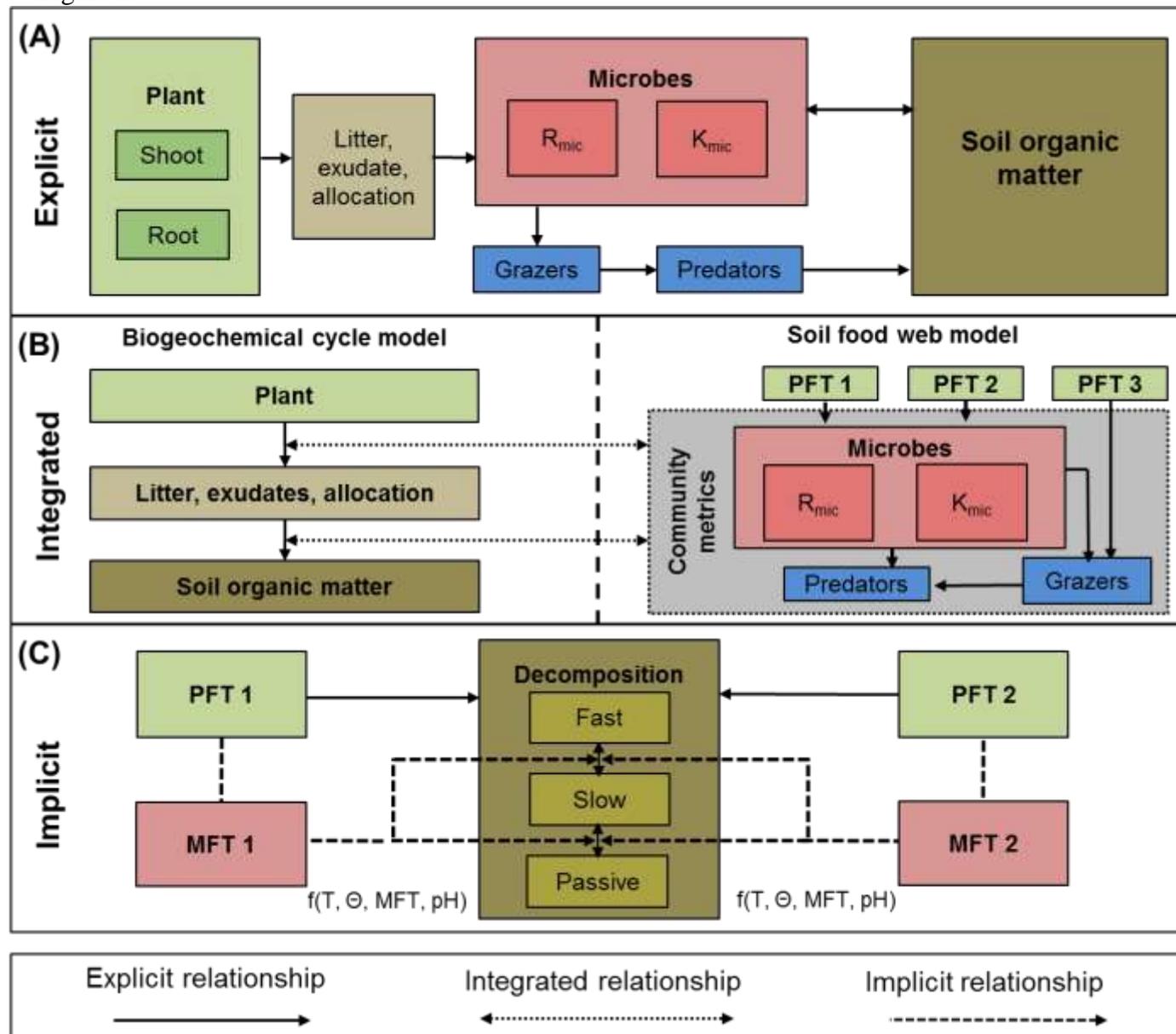
- 344 1. **Determine standardised approaches to measure microbial and soil faunal traits.** Plant
345 traits are typically easier to measure than microbe and soil fauna traits (Table 1), but this
346 hurdle must be overcome in order to successfully populate models with traits from all three
347 groups.
- 348 2. **Determine which plant, microbial and soil faunal traits are the best predictors.** Traits
349 that are associated with resource economy and stoichiometry are strong contenders, but traits
350 linked to morphology and longevity cannot be overlooked, as they potentially infer links with
351 amount of resources added to the system and turnover rate (Table 1). This stage will require
352 that models are run and their validity checked by comparing predicted outputs to real data.
- 353 3. **Acquire knowledge about the interactions between traits, between individuals (within
354 and between taxonomic groups), and trade-offs that might affect the model's predictive
355 ability.** For example, increasingly, alignment between mycorrhizal fungi and plant hosts are
356 known and can be included in models. Including data on habitat filtering of various
357 taxonomic groups from a trait based perspective would be extremely useful.
- 358 4. **Determine whether plant, microbe and fauna traits align in a predictable way,
359 particularly in response to stress and trophic and environmental gradients.** Assessing
360 the plasticity and inherent intraspecific variation of traits and also including “extended
361 phenotypes” (e.g., pathogen susceptibility, rhizosphere community composition), as traits
362 themselves would help achieve this goal.
- 363 5. **Determine how to generate the best data for the different model types (i.e., explicit,
364 integrated, explicit).** This aim requires close dialogue between modellers and field
365 ecologists to determine which questions can be answered using different models (Table 2).
- 366

367 More generally, when designing large scale or long-term empirical studies, we recommend including
368 the expertise of a modeller, in order to ensure the data is appropriate for use in models. Only through
369 integration of plant, microbial and soil faunal traits, as well as a more robust dialogue between
370 modellers and empiricists, will the next generation of biogeochemical models more accurately
371 represent Earth system processes.

372

373 **Acknowledgements**

374 ELF is supported by the NERC Soil Security Programme (NE/P013708/1); JRD and BGJ by the UK
375 Biotechnology and Biological Sciences Research Council (BBSRC) (Grants BB/I009000/2 and
376 BB/I009183/1). DJ receives partial support from the N8 AgriFood programme. This work was
377 supported by a BBSRC International Partnering award (BB/L026759/1) to EB, DJ, RB and PS.



379

380

381 Figure 1. Three biodiversity-biogeochemical model types that could be developed to incorporate
 382 biotic traits of plants, microbes and soil fauna. A) An explicit small-scale trait model that simulates
 383 plant traits (e.g., root and shoot stoichiometry, quality) and microbial traits (e.g., r- versus K-
 384 selected, carbon use efficiency) and trade-offs, with the transfer of carbon between the soil food web
 385 (including trophic cascades) and soil biogeochemical cycling (e.g., decomposition) explicitly
 386 simulated. B) An integrated small-scale model through the connection of a biogeochemical model

387 and a soil food web model. Carbon moves through the biogeochemical model, whereas the soil food
388 web model simulates functional trait attributes or community metrics of different plant functional
389 types (PFT), r- and K-selected microbes and soil fauna such as grazers and predators. Such models
390 only provide output to influence the rate of carbon movement in the biogeochemical model, here
391 decomposition. C) An implicit large-scale model, with microbial functional types (MFT) coupled
392 with PFT. Traits are used to parameterise the association and trade-offs among MFT and PFT.
393 Therefore, the traditional decay rate constant for soil organic matter is replaced by MFT-specific
394 functions that account for the size and type of the target MFT and abiotic factors (e.g., temperature,
395 energy transfer, soil pH). Soil organic matter that is decomposed is partitioned into fast, slow and
396 passively cycling pools to better account for variability in soil residency time. Scalability is enabled
397 through this approach, making such models more useful for Earth system modelling. Boxes represent
398 different physical and biological pools, and lines represent different coupling relationships (i.e.,
399 explicit, integrated, implicit).

400 **Table 1.** Hypothetical *a priori* usefulness and measurability of plant, microbial and faunal traits to our proposed explicit, integrated and implicit
401 biogeochemical models. Note that the measurability designations of easy, medium and hard in this table are approximations and may vary across
402 ecosystems and focal species.

Taxa	Trait	Measurability of trait			Usefulness for model			References
		Easy	Medium	Hard	Explicit model	Integrated model	Implicit model	
Plant	Morphology	Growth form		Root diameter				(Cornelissen <i>et al.</i> 2003)
	Longevity	Height		Root area	✓			
		Leaf area						
		Rooting architecture						
Stoichiometry	Relative growth rate				✓	✓	✓	
	Life span							
	Seed mass				✓	✓	✓	
Resource economy	Seed number							
	Seed bank longevity							
	Dispersal							
	Leaf/root C, N, P content/ratios				✓	✓	✓	
Microbe	Morphology	Leaf dry matter	Specific leaf area	Specific root length				(Aguilar-Trigueros <i>et al.</i> 2015; Buchkowski, Bradford, Grandy, Schmitz & Wieder 2017)
	Longevity	Leaf toughness	Photosynthetic/respiration capacity		✓	✓	✓	
		Regulation of stomatal conductance (g_1)						
Microbe	Morphology	Fungi: Hyphal exploration type	Fungi: Mycelial architecture		✓			(Aguilar-Trigueros <i>et al.</i> 2015; Buchkowski, Bradford, Grandy, Schmitz & Wieder 2017)
	Longevity	Bacteria: Gram negative or Gram positive	Hyphal length					
		All: Growth rate	Maximal hyphal growth rate	All: Death rate		✓	✓	
Microbe	Stoichiometry		Predation		✓			(Aguilar-Trigueros <i>et al.</i> 2015; Buchkowski, Bradford, Grandy, Schmitz & Wieder 2017)
			Competition					
Microbe	Stoichiometry		All: C:N:P ratios		✓		✓	(Aguilar-Trigueros <i>et al.</i> 2015; Buchkowski, Bradford, Grandy, Schmitz & Wieder 2017)

	Resource economy	Fungi: Hyphal diameter Chitin wall thickness Free-living to symbiotic Bacteria: Feeding substrate Substrate affinity Free-living to symbiotic	Fungi: Production of non-enzymatic substances (antibiotics) Enzyme activity Bacteria: C use efficiency Community dynamics	✓	
Fauna	Morphology	Mode of movement Aggregation /gregariousness		✓	(Pey <i>et al.</i> 2014)
	Longevity	Egg size Clutch size Age at maturity Population density	Growth rate Life span	✓	
	Stoichiometry	C:N:P ratios		✓	
	Resource economy	Feeding substrate	Activity time	✓	

404 **Table 2.** Questions that can be addressed by different trait-based ecosystem models. [Explicit,](#)
 405 [integrated and implicit models are best equipped to answer ecological questions across fine, medium](#)
 406 [and large spatial and/or temporal scales, respectively, and therefore the questions are organised to](#)
 407 [reflect this hierarchy.](#)

Type of model	Potential questions
Explicit model	<p>How can a particular trait be incorporated into an ecosystem model?</p> <p>How do different ecological strategies that are represented by different combinations of traits affect ecosystem fluxes and pools?</p> <p>What emergent processes arise from introducing complexity into soil C cycling?</p>
Integrated model	<p>How do alterations to the soil food web influence soil C storage?</p> <p>Is soil C storage differentially affected by ‘top-down’ vs. ‘bottom-up’ control of soil food webs?</p> <p>How does drought influence soil C storage?</p> <p>How does an increase in productivity change food webs?</p> <p>How does land management influence CO₂ emissions?</p> <p>How does earthworm invasion influence soil organic matter dynamics?</p> <p>How do changes in diversity affect soil organic matter composition?</p>
Implicit model	<p>What is the effect of land use or management change on soil C stock?</p> <p>How does spatial variation in the projected changes of climate drivers influence soil C storage?</p> <p>How does global warming affect soil C stocks?</p>

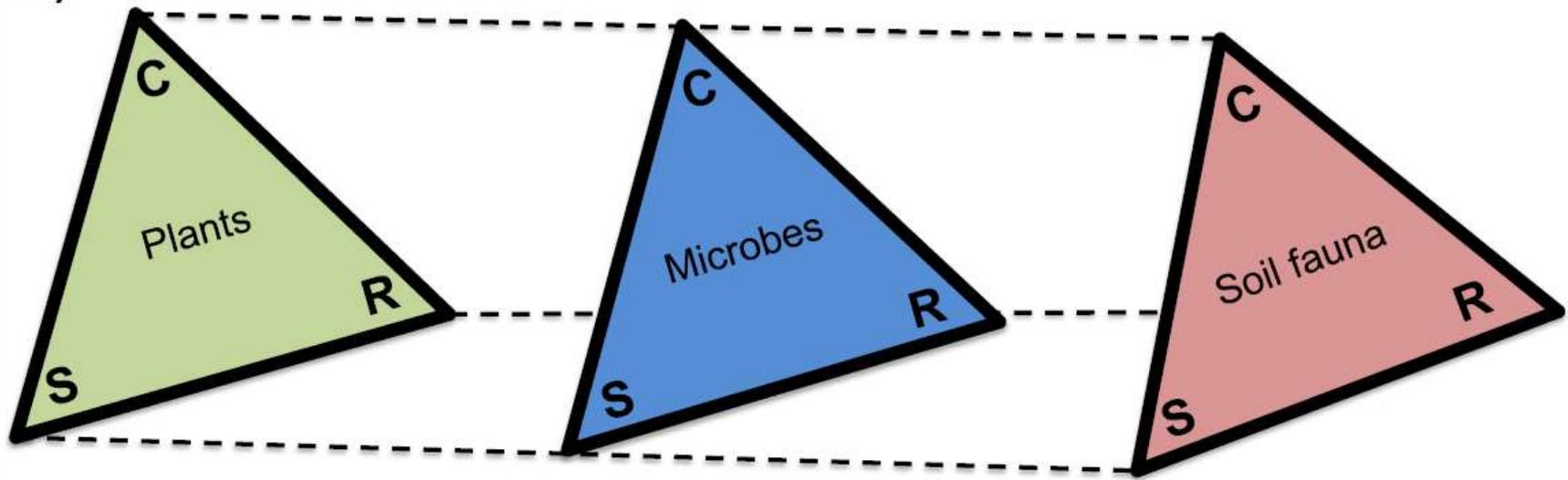
408

409 **Box 1. Connecting traits across groups: plants, microorganisms and animals**

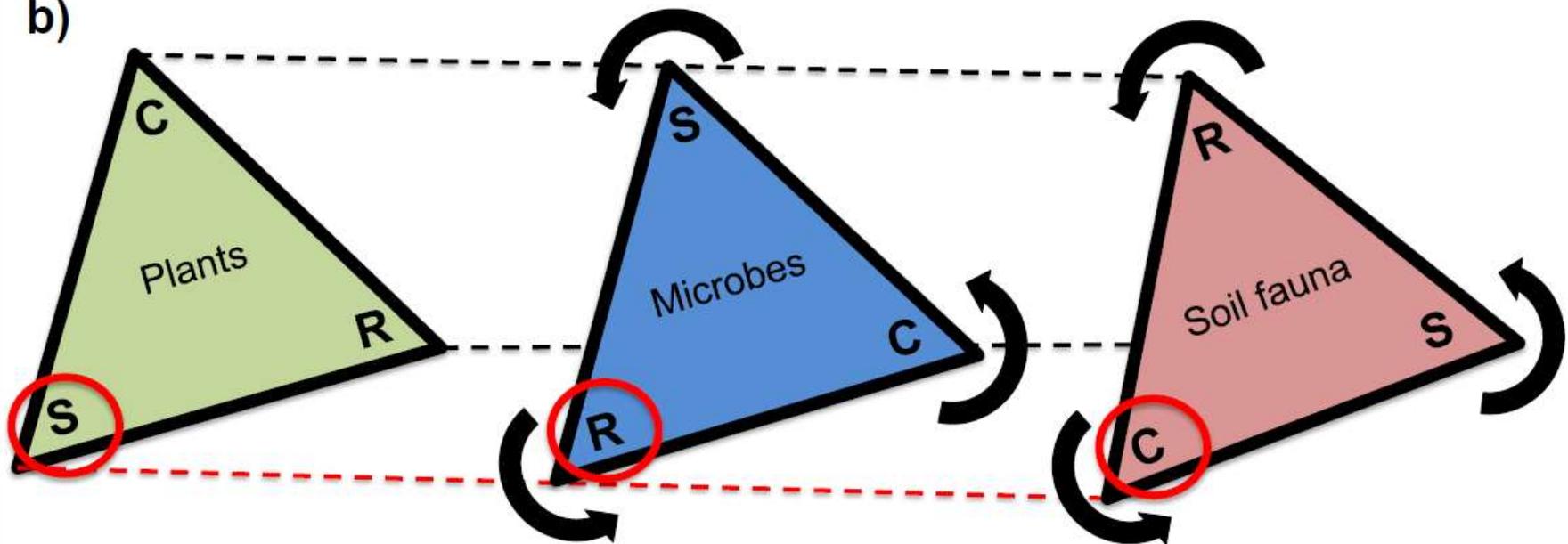
410 A number of paradigms have been proposed to classify organisms within groups according to their functional traits. For example,
411 Grime (1977) proposed the competitor/stress tolerator/ruderal (C-S-R) framework to explain how plants with different traits adapt under
412 different environments. Wright *et al.* (2004) built upon this concept, suggesting that plants can be globally classified along a spectrum
413 from those that are fast growing and promote fast nutrient cycling, to those that grow more slowly and promote slower nutrient cycling,
414 known as the ‘leaf economics spectrum’. It would be desirable from a modelling perspective to align functional effect traits across plants,
415 microbes and soil animals using one of these existing paradigms, but this presents challenges. Microbes have generally been classified
416 along an r-selected to K-selected continuum, which has been the main framework for including microbes in models (Figure 1; Wieder *et*
417 *al.* 2015). Further, soil animals exhibit ‘behavioural traits’ (Pey *et al.* 2014), adding additional complexity, and allowing them to readily
418 move between resource patches. Attempting to create such frameworks for soil animals is still in its infancy, though recently there has
419 been growing interest in attempting to describe the patterns (Grandy, Wieder, Wickings & Kyker-Snowman 2016). Certain links among
420 groups of organisms are relatively well established, particularly between plants and microbes. For example, out of 30 commonly measured
421 plant functional traits (Cornelissen *et al.* 2003), 14 have been identified as microbial mediated (Friesen *et al.* 2011). One way to further
422 develop these known links is to consider a ‘bottom up’ scenario, where plants influence microbes, which influence fauna in a simple
423 hierarchy. This is likely to select for different characteristics (i.e., different sectors of the C-S-R framework) for each group. For example,
424 a stressed plant (S) is likely to offer an increased resource pool due to root sloughing and exudation, which would favour the ruderal-
425 selected microbial community (R), which could offer opportunities for competitive groups of soil fauna (C). This is depicted in a
426 conceptual diagram showing C-S-R triangles rotated accordingly across taxonomic groups (see inset a). Krause *et al.* (2014) adapted the

427 C-S-R framework to explain microbial community functional traits, arguing that microbial communities employ similar strategies to those
428 used by plants. We suggest that on small or local scales, they often do not. This is because plants, microbes and animals operate at
429 different spatial, temporal scales and resource requirements, and a catastrophic event for one group could lead to an opportunity for
430 another (e.g., Birch 1958). Conversely, overall patterns of resource economy have been identified across larger landscape scales that
431 indicate that there are general patterns that may align with management intensity or climate. Intensive management often increases
432 nutrient availability, which selects for ‘competitive’ plant species (C) and bacterial-dominated food webs. Nutrient poor ecosystems select
433 for stress-tolerant (S) species, which leads to fungal-dominance (de Vries *et al.* 2012; de Vries *et al.* 2013, see inset b). This may therefore
434 be an appropriate assumption for larger scale implicit models, and thus plant functional type may be sufficient to infer the activity of the
435 rest of the soil food web (but see van Bodegom *et al.* (2012)). Please note that the C-S-R framework highlighted here is only one possible
436 scenario under which plant, microbial and soil faunal trait spectra may align. Alternative alignments of trait spectra between plants,
437 microbes and soil fauna that could help inform the creation of models are certainly possible.

a)



b)



439 **References**

440

- 441 Ackerly, D.D. & Cornwell, W.K. (2007) A trait-based approach to community assembly:
 442 partitioning of species trait values into within- and among-community components.
 443 *Ecology Letters*, **10**, 135-145.
- 444 Aguilar-Trigueros, C.A., Hempel, S., Powell, J.R., Anderson, I.C., Antonovics, J., Bergmann, J., . . .
 445 Rillig, M.C. (2015) Branching out: Towards a trait-based understanding of fungal
 446 ecology. *Fungal Biology Reviews*, **29**, 34-41.
- 447 Allison, S.D. (2012) A trait-based approach for modelling microbial litter decomposition.
 448 *Ecology Letters*, **15**, 1058-1070.
- 449 Asner, G.P., Anderson, C.B., Martin, R.E., Tupayachi, R., Knapp, D.E. & Sinca, F. (2015) Landscape
 450 biogeochemistry reflected in shifting distributions of chemical traits in the Amazon
 451 forest canopy. *Nature Geoscience*, **8**, 567-U114.
- 452 Bardgett, R.D. (2017) Plant trait-based approaches for interrogating belowground function.
 453 *Biology and Environment: Proceedings of the Royal Irish Academy*, **117B**, 1-13.
- 454 Birch, H.F. (1958) The effect of soil drying on humus decomposition and nitrogen availability.
 455 *Plant and Soil*, **10**, 9-31.
- 456 Buchkowski, R.W., Bradford, M.A., Grandy, A.S., Schmitz, O.J. & Wieder, W.R. (2017) Applying
 457 population and community ecology theory to advance understanding of belowground
 458 biogeochemistry. *Ecology Letters*, **20**, 231-245.
- 459 Burkhardt, U., Russell, D.J., Decker, P., Döhler, M., Höfer, H., Lesch, S., . . . Xylander, W.E.R. (2014)
 460 The Edaphobase project of GBIF-Germany—A new online soil-zoological data
 461 warehouse. *Applied Soil Ecology*, **83**, 3-12.
- 462 Caro-Quintero, A. & Konstantinidis, K.T. (2012) Bacterial species may exist, metagenomics
 463 reveal. *Environmental Microbiology*, **14**, 347-355.
- 464 Carrillo, Y., Ball, B.A., Bradford, M.A., Jordan, C.F. & Molina, M. (2011) Soil fauna alter the effects
 465 of litter composition on nitrogen cycling in a mineral soil. *Soil Biology & Biochemistry*,
 466 **43**, 1440-1449.
- 467 Carrillo, Y., Bell, C., Koyama, A., Canarini, A., Boot, C.M., Wallenstein, M. & Pendall, E. (2017)
 468 Plant traits, stoichiometry and microbes as drivers of decomposition in the rhizosphere
 469 in a temperate grassland. *Journal of Ecology*, **105**, 1750-1765.
- 470 Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., . . . Poorter, H.
 471 (2003) A handbook of protocols for standardised and easy measurement of plant
 472 functional traits worldwide. *Australian Journal of Botany*, **51**, 335-380.
- 473 Crowther, T.W., Maynard, D.S., Crowther, T.R., Peccia, J., Smith, J.R. & Bradford, M.A. (2014)
 474 Untangling the fungal niche: the trait-based approach. *Frontiers in Microbiology*, **5**.
- 475 Davidson, E.A. & Janssens, I.A. (2006) Temperature sensitivity of soil carbon decomposition
 476 and feedbacks to climate change. *Nature*, **440**, 165-173.
- 477 De Deyn, G.B., Cornelissen, J.H.C. & Bardgett, R.D. (2008) Plant functional traits and soil carbon
 478 sequestration in contrasting biomes. *Ecology Letters*, **11**, 516-531.
- 479 de Vries, F.T., Bloem, J., Quirk, H., Stevens, C.J., Bol, R. & Bardgett, R.D. (2012) Extensive
 480 management promotes plant and microbial nitrogen retention in temperate grassland.
 481 *Plos One*, **7**, e51201.
- 482 de Vries, F.T., Thebault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjornlund, L., . . . Bardgett, R.D.
 483 (2013) Soil food web properties explain ecosystem services across European land use

484 systems. *Proceedings of the National Academy of Sciences of the United States of America*,
485 **110**, 14296-14301.

486 Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., . . . Zak, M.R. (2004)
487 The plant traits that drive ecosystems: Evidence from three continents. *Journal of*
488 *Vegetation Science*, **15**, 295-304.

489 Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., . . . Gorne, L.D. (2016) The
490 global spectrum of plant form and function. *Nature*, **529**, 167-173.

491 Farská, J., Prejzková, K. & Rusek, J. (2014) Management intensity affects traits of soil
492 microarthropod community in montane spruce forest. *Applied Soil Ecology*, **75**, 71-79.

493 Faucon, M.-P., Houben, D. & Lambers, H. (2017) Plant functional traits: soil and ecosystem
494 services. *Trends in Plant Science*, **22**, 385-394.

495 Fierer, N. (2017) Embracing the unknown: disentangling the complexities of the soil
496 microbiome. *Nature Reviews Microbiology*, **15**, 579.

497 Fierer, N. & Barberán, A (2014) Seeing the forest for the genes: using metagenomics to infer the
498 aggregated traits of microbial communities. *Frontiers in Microbiology*, **5**.

499 Filser, J., Faber, J.H., Tiunov, A.V., Brussaard, L., Frouz, J., De Deyn, G., . . . Jiménez, J.J. (2016) Soil
500 fauna: key to new carbon models. *SOIL*, **2**, 565-582.

501 Friesen, M.L., Porter, S.S., Stark, S.C., von Wettberg, E.J., Sachs, J.L. & Martinez-Romero, E. (2011)
502 Microbially mediated plant functional traits. *Annual Review of Ecology, Evolution, and*
503 *Systematics*, Vol 42 (eds D.J. Futuyma, H.B. Shaffer & D. Simberloff), pp. 23-46. Annual
504 Reviews, Palo Alto.

505 Funk, J.L., Larson, J.E., Ames, G.M., Butterfield, B.J., Cavender-Bares, J., Firn, J., . . . Wright, J.
506 (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological
507 processes. *Biological Reviews*, **92**, 1156-1173.

508 George, P.B.L., Keith, A.M., Creer, S., Barrett, G.L., Lebron, I., Emmett, B.A., . . . Jones, D.L. (2017)
509 Evaluation of mesofauna communities as soil quality indicators in a national-level
510 monitoring programme. *Soil Biology & Biochemistry*, **115**, 537-546.

511 Grandy, A.S., Wieder, W.R., Wickings, K. & Kyker-Snowman, E. (2016) Beyond microbes: Are
512 fauna the next frontier in soil biogeochemical models? *Soil Biology and Biochemistry*,
513 **102**, 40-44.

514 Grime, J.P. (1977) Evidence for existence of three primary strategies in plants and its relevance
515 to ecological and evolutionary theory. *American Naturalist*, **111**, 1169-1194.

516 Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder
517 effects. *Journal of Ecology*, **86**, 902-910.

518 Hararuk, O., Smith, M.J. & Luo, Y. (2015) Microbial models with data-driven parameters predict
519 stronger soil carbon responses to climate change. *Global Change Biology*, **21**, 2439-
520 2453.

521 Johnson, D., Krsek, M., Wellington, E.M.H., Stott, A.W., Cole, L., Bardgett, R.D., . . . Leake, J.R.
522 (2005) Soil invertebrates disrupt carbon flow through fungal networks. *Science*, **309**,
523 1047-1047.

524 Kanters, C., Anderson, I. & Johnson, D. (2015) Chewing up the wood-wide web: selective
525 grazing on ectomycorrhizal fungi by collembola. *Forests*, **6**, 2560.

526 Kardol, P., Throop, H.L., Adkins, J. & de Graaff, M.A. (2016) A hierarchical framework for
527 studying the role of biodiversity in soil food web processes and ecosystem services. *Soil*
528 *Biology & Biochemistry*, **102**, 33-36.

529 Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., . . . Wirth, C. (2011) TRY - a
530 global database of plant traits. *Global Change Biology*, **17**, 2905-2935.

- 531 Krause, S., Le Roux, X., Niklaus, P.A., Van Bodegom, P.M., Lennon, J.T., Bertilsson, S., . . . Bodelier,
532 P.L.E. (2014) Trait-based approaches for understanding microbial biodiversity and
533 ecosystem functioning. *Frontiers in Microbiology*, **5**, 10.
- 534 Laliberté, E. (2017) Below-ground frontiers in trait-based plant ecology. *New Phytologist*, **213**,
535 1597-1603.
- 536 Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem
537 functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545-556.
- 538 Lehmann, J. & Kleber, M. (2015) The contentious nature of soil organic matter. *Nature*, **528**, 60-
539 68.
- 540 Martin, P.A., Newton, A.C. & Bullock, J.M. (2017) Impacts of invasive plants on carbon pools
541 depend on both species' traits and local climate. *Ecology*, **98**, 1026-1035.
- 542 Martiny, J.B.H., Jones, S.E., Lennon, J.T. & Martiny, A.C. (2015) Microbiomes in light of traits: A
543 phylogenetic perspective. *Science*, **350**, 9.
- 544 McCann, K.S. (2000) The diversity-stability debate. *Nature*, **405**, 228-233.
- 545 McCormack, M.L., Guo, D.L., Iversen, C.M., Chen, W.L., Eissenstat, D.M., Fernandez, C.W., . . .
546 Zanne, A. (2017) Building a better foundation: improving root-trait measurements to
547 understand and model plant and ecosystem processes. *New Phytologist*, **215**, 27-37.
- 548 McGill, B., Enquist, B., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from
549 functional traits. *Trends in Ecology & Evolution*, **21**, 178-185.
- 550 Milcu, A. & Manning, P. (2011) All size classes of soil fauna and litter quality control the
551 acceleration of litter decay in its home environment. *Oikos*, **120**, 1366-1370.
- 552 Moretti, M., Dias, A.T.C., de Bello, F., Altermatt, F., Chown, S.L., Azcárate, F.M., . . . Berg, M.P.
553 (2017) Handbook of protocols for standardized measurement of terrestrial invertebrate
554 functional traits. *Functional Ecology*, **31**, 558-567.
- 555 Nilsson, K.A. & McCann, K.S. (2016) Interaction strength revisited—clarifying the role of energy
556 flux for food web stability. *Theoretical Ecology*, **9**, 59-71.
- 557 Parton, W.J., Schimel, D.S., Cole, C.V. & Ojima, D.S. (1987) Analysis of factors controlling soil
558 organic matter levels in great plains grasslands. *Soil Science Society of America Journal*,
559 **51**, 1173.
- 560 Pausch, J., Kramer, S., Scharroba, A., Scheunemann, N., Butenschoen, O., Kandeler, E., . . . Ruess, L.
561 (2016) Small but active - pool size does not matter for carbon incorporation in below-
562 ground food webs. *Functional Ecology*, **30**, 479-489.
- 563 Pey, B., Nahmani, J., Auclerc, A., Capowicz, Y., Cluzeau, D., Cortet, J., . . . Hedde, M. (2014) Current
564 use of and future needs for soil invertebrate functional traits in community ecology.
565 *Basic and Applied Ecology*, **15**, 194-206.
- 566 Read, Q.D., Moorhead, L.C., Swenson, N.G., Bailey, J.K. & Sanders, N.J. (2014) Convergent effects
567 of elevation on functional leaf traits within and among species. *Functional Ecology*, **28**,
568 37-45.
- 569 Reich, P.B. (2014) The world-wide 'fast-slow' plant economics spectrum: a traits manifesto.
570 *Journal of Ecology*, **102**, 275-301.
- 571 Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in terrestrial ecosystems*.
572 Blackwell Scientific Publications., Oxford, UK.
- 573 Treseder, K.K. & Lennon, J.T. (2015) Fungal traits that drive ecosystem dynamics on land.
574 *Microbiology and Molecular Biology Reviews*, **79**, 243-262.
- 575 van Bodegom, P.M., Douma, J.C. & Verheijen, L.M. (2014) A fully traits-based approach to
576 modeling global vegetation distribution. *Proceedings of the National Academy of Sciences
577 of the United States of America*, **111**, 13733-13738.

- 578 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the
 579 concept of trait be functional! *Oikos*, **116**, 882-892.
- 580 Wang, Y.P., Law, R.M. & Pak, B. (2010) A global model of carbon, nitrogen and phosphorus
 581 cycles for the terrestrial biosphere. *Biogeosciences*, **7**, 2261-2282.
- 582 Wieder, W.R., Allison, S.D., Davidson, E.A., Georgiou, K., Hararuk, O., He, Y., . . . Xu, X. (2015)
 583 Explicitly representing soil microbial processes in Earth system models. *Global*
 584 *Biogeochemical Cycles*, **29**, 1782-1800.
- 585 Wieder, W.R., Bonan, G.B. & Allison, S.D. (2013) Global soil carbon projections are improved by
 586 modelling microbial processes. *Nature Climate Change*, **3**, 909-912.
- 587 Wieder, W.R., Grandy, A.S., Kallenbach, C.M. & Bonan, G.B. (2014) Integrating microbial
 588 physiology and physio-chemical principles in soils with the Microbial-Mineral Carbon
 589 Stabilization (MIMICS) model. *Biogeosciences*, **11**, 3899-3917.
- 590 Wieder, W.R., Grandy, A.S., Kallenbach, C.M., Taylor, P.G. & Bonan, G.B. (2015) Representing life
 591 in the Earth system with soil microbial functional traits in the MIMICS model.
 592 *Geoscientific Model Development*, **8**, 1789-1808.
- 593 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., . . . Villar, R. (2004)
 594 The worldwide leaf economics spectrum. *Nature*, **428**, 821-827.
- 595 Xu, X.T., Medvigy, D., Powers, J.S., Becknell, J.M. & Guan, K.Y. (2016) Diversity in plant hydraulic
 596 traits explains seasonal and inter-annual variations of vegetation dynamics in
 597 seasonally dry tropical forests. *New Phytologist*, **212**, 80-95.
- 598 Yang, X., Thornton, P.E., Ricciuto, D.M. & Post, W.M. (2014) The role of phosphorus dynamics in
 599 tropical forests – a modeling study using CLM-CNP. *Biogeosciences*, **11**, 1667-1681.
- 600 Yen, J.D.L., Cabral, R.B., Cantor, M., Hatton, I., Kortsch, S., Patrício, J. & Yamamichi, M. (2016)
 601 Linking structure and function in food webs: maximization of different ecological
 602 functions generates distinct food web structures. *Journal of Animal Ecology*, **85**, 537-
 603 547.
- 604 Zaehle, S. & Friend, A.D. (2010) Carbon and nitrogen cycle dynamics in the O-CN land surface
 605 model: 1. Model description, site-scale evaluation, and sensitivity to parameter
 606 estimates. *Global Biogeochemical Cycles*, **24**, 1-13.

607
 608
 609 **NEW REFERENCES TO BE INTEGRATED BEFORE SUBMISSION:**

- 610
 611 Cotrufo, M.F., Soong, J.L., Horton, A.J., Campbell, E.E., Haddix, M.L., Wall, D.H. & Parton, A.J.
 612 (2015) Formation of soil organic matter via biochemical and physical pathways of litter
 613 mass loss. *Nature Geoscience*, **8**, 776-+.
- 614 He, Y., Trumbore, S.E., Torn, M.S., Harden, J.W., Vaughn, L.J.S., Allison, S.D. & Randerson, J.T.
 615 (2016) Radiocarbon constraints imply reduced carbon uptake by soils during the 21st
 616 century. *Science*, **353**, 1419-1424.
- 617 Keenan, T.F., Carbone, M.S., Reichstein, M. & Richardson, A.D. (2011) The model-data fusion
 618 pitfall: assuming certainty in an uncertain world. *Oecologia*, **167**, 587.
- 619 Koven, C.D., Riley, W.J., Subin, Z.M., Tang, J.Y., Torn, M.S., Collins, W.D., . . . Swenson, S.C. (2013)
 620 The effect of vertically resolved soil biogeochemistry and alternate soil C and N models
 621 on C dynamics of CLM4. *Biogeosciences*, **10**, 7109-7131.
- 622 Kumordzi, B.B., de Bello, F., Freschet, G.T., Le Bagousse-Pinguet, Y., Leps, J. & Wardle, D.A.
 623 (2015) Linkage of plant trait space to successional age and species richness in boreal
 624 forest understorey vegetation. *Journal of Ecology*, **103**, 1610-1620.

625 McGill, W.B., Hunt, H.W., Woodmansee, R.G. & Reuss, J.O. (1981) *PHOENIX, a model of the*
626 *dynamics of carbon and nitrogen in grassland soil. In "Terrestrial Nitrogen Cycles,*
627 *Processes, Ecosystem, Strategies and Management Impacts".* Swedish Natural Science
628 Research Council, Stockholm, Sweden.

629 Parton, W.J., Hartman, M., Ojima, D. & Schimel, D. (1998) DAYCENT and its land surface
630 submodel: description and testing. *Global and Planetary Change*, **19**, 35-48.

631 Parton, W.J., Schimel, D., Ojima, D.S. & Cole, C.V. (1994) *Quantitative Modelling of Soil Forming*
632 *Processes.* Soil Science Society of America, Madison, Wisconsin, USA.

633 Smith, P., Andrén, O., Brussaard, L., Dangerfield, M., Ekschmitt, K., Lavelle, P. & Tate, K. (1998)
634 Soil biota and global change at the ecosystem level: describing soil biota in
635 mathematical models. *Global Change Biology*, **4**, 773-784.

636 Sofi, J.A., Lone, A.H., Ganie, M.A., Dar, N.A., Bhat, S.A., Mukhtar, M., . . . Ramzan, S. (2016) Soil
637 microbiological activity and carbon dynamics in the current climate change scenarios: a
638 review. *Pedosphere*, **26**, 577-591.

639 van Bodegom, P.M., Douma, J.C., Witte, J.P.M., Ordoñez, J.C., Bartholomeus, R.P. & Aerts, R.
640 (2012) Going beyond limitations of plant functional types when predicting global
641 ecosystem-atmosphere fluxes: exploring the merits of traits-based approaches. *Global*
642 *Ecology and Biogeography*, **21**, 625-636.

643 Walker, L.R., Wardle, D.A., Bardgett, R.D. & Clarkson, B.D. (2010) The use of chronosequences in
644 studies of ecological succession and soil development. *Journal of Ecology*, **98**, 725-736.

645 Wardle, D.A., Walker, L.R. & Bardgett, R.D. (2004) Ecosystem properties and forest decline in
646 contrasting long-term chronosequences. *Science*, **305**, 509-513.

647 Zhuang, Q., McGuire, A.D., Melillo, J.M., Clein, J.S., Dargaville, R.J., Kicklighter, D.W., . . . Hobbie,
648 J.E. (2011) Carbon cycling in extratropical terrestrial ecosystems of the Northern
649 Hemisphere during the 20th century: a modeling analysis of the influences of soil
650 thermal dynamics. *Tellus B: Chemical and Physical Meteorology*, **55**, 751-776.

651