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1 **Food web uncertainties influence predictions of climate change**
2 **effects on soil carbon sequestration in heathlands.**
3

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36 **Abstract**

37 Carbon cycling models consider soil carbon sequestration a key process for climate change
38 mitigation. However, these models mostly focus on abiotic soil processes and, despite its
39 recognized critical mechanistic role, do not explicitly include interacting soil organisms. Here, we
40 use a literature study to show that even a relatively simple soil community (heathland soils)
41 contains large uncertainties in temporal and spatial food web structure. Next, we used a Lotka-
42 Volterra-based food web model to demonstrate that, due to these uncertainties, climate change
43 can either increase or decrease soil carbon sequestration to varying extents. Both the strength and
44 direction of changes strongly depend on: (1) the main consumer's (enchytraeid worms) feeding
45 preferences; and (2) whether decomposers (fungi) or enchytraeid worms are more sensitive to
46 stress. Hence, even for a soil community with a few dominant functional groups and a simulation
47 model with a few parameters, filling these knowledge gaps is a critical first step towards the
48 explicit integration of soil food web dynamics into carbon cycling models in order to better assess
49 the role soils play in climate change mitigation.

50 **Keywords**

51 Climate change; soil carbon sequestration; food web; modelling; heathlands; stress.

52 **Introduction**

53 Human-induced climate change affects global carbon cycles and threatens important ecosystem
54 services. Sequestration of carbon into soils as organic matter is considered as an important
55 process of the global carbon cycle because it mitigates climate change by reducing excessive
56 atmospheric CO₂ concentrations [1]. However, a key question is whether climate change
57 increases or decreases the capacity of soils to sequester carbon, and hence whether ecosystems
58 will buffer or accelerate climate change.

59 Numerous studies, some of which based on predictive simulation models, have projected changes
60 in the soil carbon balance of ecosystems due to various climate change-induced stressors [2]–[4].
61 However, most of these models do not explicitly consider the key role of soil decomposer biota in
62 nutrient and carbon cycling but simulate decomposition through, for example, first-order kinetics
63 that are only affected by abiotic conditions, such as temperature and moisture [3], [4]. In these
64 models, the soil community is thus considered a “black box”, implicitly assuming that its
65 composition and functioning does not matter for biogeochemical cycling.

66 This strongly contrasts with findings that soil organisms drive the process of organic matter
67 decomposition. The importance of their composition in regulating the effects of climate change
68 on ecosystem processes such as carbon cycling has been discussed extensively [5], [6]. Hence, in
69 contrast to what is implicitly assumed in conventional soil carbon models, shifts in soil
70 community composition due to environmental stressors can have significant consequences for
71 carbon cycling because of associated shifts in ecosystem functioning. Several studies have
72 acknowledged the link between soil food web composition and carbon sequestration, and the

73 need to incorporate this relationship into predictive carbon cycling models [7]–[12]. However, it
74 remains unclear to what extent climate change will affect soil carbon budgets of ecosystems.

75 In this study, we performed a literature search to identify uncertainties regarding soil food web
76 structure and its consequence for carbon cycling, and the sensitivity of soil biota to environmental
77 stressors. Next, we use a generalized Lotka-Volterra model to investigate how these uncertainties
78 translate to projections of climate change-induced shifts of soil carbon sequestration. We focus
79 on heathlands because: (1) they are among the most carbon rich containing soils compared to most
80 other terrestrial systems (Panel 1); and (2) they are relatively simple, which makes modelling
81 them more tractable.

Panel 1: Heathlands as a study system

Dry heathlands are semi-natural habitats dominated by ericaceous dwarf-shrubs, primarily the heather species *Calluna vulgaris*, and are a globally relevant study system because they share many similarities with other ericoid dominated shrubland systems, such as tundra [40]. Heathland currently covers an estimated 350 000 ha in Europe, which represents approximately 1% of total land area. Moreover, soil carbon content in heathland is among the highest of all biomes, after wetlands and boreal forests, and can therefore be considered as potentially significant carbon sinks. This ecosystem is under threat from land-use and climate change, which lead to a 10- to 20-fold decline in its occurrence since the middle of the 19th century. Available carbon cycling simulation models are less accurate for carbon rich soils, such as heathland, than for others, such as grasslands [41]. Field experiments further suggest that the effect of climate change-related stressors such as drought on heathland soil carbon balances vary considerably among sites, with a tendency of increased sequestration (sink) at drier sites and decreased sequestration (source) at wetter sites [26], [42]. However, the underlying mechanisms of these changes are very poorly understood.

82

83 **Uncertainty regarding food web structure and function**

84 Sources of soil organic matter (SOM) input consist of plant litter, root exudates and microbial
85 and soil faunal necromass (Fig. 1). The organic compounds entering the soil have different
86 turnover rates. Solubles are generally less recalcitrant than polysaccharides, which are in turn less
87 recalcitrant than polyphenols. However, their degradability is heavily influenced by abiotic (e.g.
88 accessibility, temperature, moisture) and biotic (e.g. decomposer catabolic ‘toolbox’) factors [13],
89 [14]. Within heathland soils, microbes are the main decomposers and the microbial decomposition
90 of SOM is mainly driven by fungi, as bacterial abundance is low due to high soil acidity [15].
91 Two important fungal functional groups are ericoid mycorrhizal fungi and saprotrophic fungi.

92 The net effect of fungi on soil carbon sequestration depends on the balance between their effects
93 on carbon loss via decomposition and stabilization of soil organic carbon (SOC) via conversion
94 of assimilated solubles and polysaccharides into more recalcitrant polyphenolic compounds in
95 their fungal tissues, which enter the SOM pool upon mortality. Although microbial necromass
96 varies considerably across ecosystems and is affected by environmental stressors such as drought,
97 it can account for up to 80% of the organic carbon in soil [16]. The contribution of microbial
98 necromass to the soil carbon pool is likely to be high in heathlands soils because of the high
99 abundance of recalcitrant melanin-rich fungi [17].

100 Some groups of soil fauna can contribute to the decomposition of the microbial necromass, such
101 as Collembola (springtails), Acari (mites) and enchytraeid worms. Enchytraeid worms are in
102 terms of biomass the most abundant consumers in nutrient poor acidic organic soils [18],
103 including dry heathlands, where *Cognettia sphagnetorum* (actually a complex of several cryptic
104 species [19]) is the keystone species with an estimated dominance of up to 80% [20]. The

105 necromass of enchytraeids and other soil animals is considered to be easily degradable [21], but
106 excrement of soil fauna can actually be even more recalcitrant than ingested compounds, thereby
107 fostering carbon sequestration. Despite these insights, the acknowledgement that excrement and
108 necromass of soil organisms potentially contribute significantly to carbon sequestration remains
109 largely unexplored. Therefore, we consider it to be a major knowledge gap regarding the
110 functioning of heathland soil food webs (Table 1).

111 Despite extensive research illustrating the importance of soil fauna for processes such as SOM
112 degradation, we currently still lack a fundamental mechanistic knowledge on their functional role
113 for carbon cycling [12]. Although knowledge on food preferences of enchytraeid worms has been
114 extensively synthesized [22], it still remains uncertain whether enchytraeids, and *C.*
115 *sphagnetorum* in particular, *in situ* actively forage for fungal mycelium or bulk feed on SOM, as
116 earthworms do in forests. Moreover, the extent to which they are able to assimilate various
117 recalcitrant fungal-derived compounds (e.g. melanin) and carbon substrates and, hence, the
118 differential contribution of various sources to their diet is unknown. Consequently, their
119 functional role regarding carbon cycling within the heathland soil food web remains uncertain
120 (Table 1).

121 **Uncertainty regarding the effects of climate change on soil food webs**

122 Extreme climatic events such as prolonged drought and warming comprises one of the most
123 important environmental change drivers affecting terrestrial ecosystems, especially in western
124 Europe [23]. As most soil organism are sensitive to changes in soil water potential, soil moisture
125 content is a key abiotic factor that determines their activity and community composition. Drought
126 lowers heathland soil carbon influx in the short-term, as both root exudation [24] and litter
127 production [25] are reduced. The long term *in situ* experimental effects of drought on soil carbon
128 stocks are highly variable in heathlands [26]. As such, the mechanisms governing context
129 dependent responses to drought are very poorly understood, which adds to the uncertainties how
130 strong extreme climatic events affect carbon sequestration.

131 Regarding impacts on soil organisms, drought induces osmotic stress which impedes
132 reproduction and decreases activity and survival of enchytraeids [18]. Furthermore, drought
133 might indirectly affect enchytraeids through altered availability of food resources [20]. However,
134 reported global change manipulations effects on the diversity of heathland soil fauna are
135 generally low [27]. Drought also affects soil microbial community structure by selecting for
136 drought tolerant species [28] and decreasing enzymatic activities involved in the decomposition
137 process [29]. Further, while drought causes osmotic stress and lowers growth rates of fungi, they
138 are generally more resistant to drought than bacteria because of their thick cell walls and more
139 conservative growth strategies [28].

140 In general, differences in stress tolerance are relatively well studied within functional or
141 taxonomic groups [30] but less so between functional groups and across trophic levels [31].
142 However, Franken and colleagues [31] for example found high interspecific variation in

143 temperature tolerance among trophic levels in a soil arthropod community, which potentially
144 causes trophic mismatches during extreme events. We expect a similar difference in sensitivity of
145 functional groups for drought and this adds to our limited understanding of the fundamental
146 mechanistic link between stress-induced changes in food web composition, and net changes in
147 soil carbon budgets. Therefore, we consider the stress sensitivities of soil organisms, especially
148 fungi and enchytraeids that dominate the soil food web of heathlands, as an important knowledge
149 gap (Table 1). For example, drought might indirectly foster sequestration of carbon by selecting
150 stress tolerant fungal species that are often highly melanized [17], since melanized fungal
151 biomass decomposes slower than hyaline fungal biomass [32]. This critical dual role of melanin
152 in both drought stress sensitivity as well as decomposability illustrates that functional traits of
153 fungi driving susceptibility to environmental stressors are not necessarily independent from traits
154 driving ecosystem processes.

155 **Modelling drought stress effects on carbon sequestration**

156 Given the multitude of uncertain factors identified above and summarized in Table 1, it is a
157 challenge is to quantify how these factors modify the impact of climate change on soil carbon
158 sequestration. Disentangling these factors and quantifying their potential impact on carbon
159 cycling is an important task because: (1) it enhances mechanistic understanding of the role of
160 food web ecology for carbon sequestration; and (2) it pinpoints those factors for which reducing
161 uncertainty is most critical to enhance predictive capacity. Here, we implement drought stress
162 effects in a well-known food web simulation model and inspect the implications of current
163 uncertainties regarding soil food web structure and dynamics for predicting the effect of climate
164 change on carbon sequestration in heathlands.

165

166 **Parameters and simulations**

167 To assess how uncertainty in some of the assumptions behind soil food web models impact carbon
168 cycling, we constructed a food web model based on the presence of dominant functional groups in
169 heathlands. A Lotka-Volterra-based simulation model was structured and parameterized based on
170 the model from Eklöf and Ebenman [33], but where necessary adapted to the heathland soil food
171 web (Panel 2; ESM Table 1 and Panel 1). Growth of basal functional groups is determined by
172 their intrinsic growth rate, competition with other basal groups, and losses due to grazing.
173 Consumers and predators grow when gains through grazing are larger than losses through
174 mortality. The food web structure is encoded through a food-web matrix, listing who eats whom.
175 The model uses plant litter as an input into three carbon pools and predicts community dynamics
176 (i.e. the abundance of all groups through time).

177 To assess the impact of drought on soil carbon sequestration, no, low, medium and high drought
178 stress was modelled using a 0%, 10-30%, 40-60%, and 70-90% reduction of fungal
179 decomposition and soil fauna grazing rates. We simulated the effects of the four drought stress
180 levels on soil carbon contents for a total of nine scenarios (three x three), whereby each scenario
181 represents a unique combination of uncertainties related to food web structure (three levels) and
182 functional group stress sensitivity (three levels). Based on our review of the literature, we
183 identified one 'default' food web structure and two variant structures that both illustrate a specific
184 important uncertainty (Fig. 2). In the default food web structure, enchytraeids consume only
185 fungi, and fungi have a large contribution to the polyphenolic carbon pool. In the second food
186 web, enchytraeids bulk feed on SOM, but not on fungi, while fungi have a strong effect on SOM
187 degradation. In the third structure, fungi contribute little to the polyphenolic carbon pool, and
188 enchytraeids consume only fungi. Within each of these three food web structures, three
189 different scenarios of stress sensitivities were simulated, giving a total of nine scenarios: i) fungi
190 and enchytraeids were equally sensitive to drought stress; ii) fungi were more sensitive than
191 enchytraeids (with no reduction of enchytraeid grazing rates); and iii) enchytraeids were more
192 sensitive than fungi (with no reduction of fungi decomposition rates). For each scenario, 1000
193 simulations were run until equilibrium was reached.

Panel 2: Food web model characteristics

We described food web dynamics by a generalized Lotka-Volterra model as in Eklöf and Ebenman [33]. The change in population density through time (dx_i/dt) of each functional group (i) of the food web is described by its density (x_i), multiplied by the sum of its intrinsic per capita growth rate (b_i) and the interactions with all other components (S) of the food web. These interactions are described as the per-capita effect (α_{ij}) of the other functional group (j) on the focal functional group (i) multiplied by the density of the other functional group (x_j). We have added a density-independent addition (A_i) to the focal functional group to represent plant derived carbon input.

$$\frac{dx_i}{dt} = x_i \left(b_i + \sum_{j=1}^S \alpha_{ij} x_j \right) + A_i \quad \text{for } i = 1, \dots, S.$$

The interaction effect of functional group j on functional group i (α_{ij}) is negative when j consumes i and positive when j is consumed by i . Multiple negative consumption effects of a consumer on different prey (or resources) are weighed based on the relative strength of the interactions with a total effect of -0.5. Opposite interaction strengths, the positive effects of prey on consumers (α_{ji}), are derived from the α_{ij} interaction value by: $\alpha_{ji} = -e \cdot \alpha_{ij}$, with 'e' representing the assimilation efficiency with which prey biomass is converted into consumer biomass. Soil carbon contents are expressed as the sum of the three SOM components (solubles, polysaccharides and polyphenols).

194

195

196 Results

197 Our results show that a difference in the sensitivity of fungi and enchytraeids to drought stress

198 was more important than food web structure for predicting drought stress effects on carbon

199 sequestration. Drought increased carbon sequestration when fungi were more sensitive than

200 enchytraeids (F) or when both were equally sensitive (S) (Fig. 3 panels a-f). Drought stress

201 decreased carbon sequestration when enchytraeids were more sensitive than fungi (E) (Fig. 3
202 panels g-i). Moreover, our food web simulations show that the feeding behavior of enchytraeids
203 affected the extent of these sensitivity dependent stress-induced changes. When enchytraeids only
204 fed on fungi and were less sensitive for drought than fungi (Fig. 3 panel d), their abundance
205 reduced along with the stress-induced decrease in fungal abundance (as they had no alternative
206 food source), resulting in the same outcome as for equal sensitivity (Fig. 3 panel a). However, if
207 enchytraeids fed solely on SOM when being less sensitive for drought than fungi (Fig. 3 panel e),
208 access to readily available carbon substrates allowed them to increase in abundance despite the
209 decrease in fungal biomass. This resulted in a higher stress-induced carbon sequestration increase
210 by enchytraeids compared to them being solely fungivorous (Fig. 3 panel d) or having the same
211 drought sensitivity as fungi (Fig. 3 panel b). The rate of carbon flow from fungi to the
212 polyphenolic carbon pool shows only a minor impact on stress-induced carbon sequestration
213 changes (Fig. 3: panels a, d and g are very similar to panels c, f and i).

214

215 **Food web complexity**

216 Our results illustrated that even a very simple food web already has so many uncertainties in
217 some of its assumptions that, based on the currently available data, it is very difficult to make
218 accurate predictions on the responses of soil carbon sequestration to future environmental
219 changes. However, soil food webs can even be much more complex for other ecosystems than for
220 heathland soils [34], [35], and there are parts of heathland soil food webs (e.g predators) that we
221 did not consider so far. For this reason, we repeated the simulations using a more comprehensive
222 representation of heathland soil food web, by including less dominant functional groups of

223 consumers (springtails and saprophagous mites) and arthropod predators; such as predaceous
224 mites, spiders and predatory beetles (ESI Fig 1).

225 This more complex food web was structured and parameterized in the same way as previously for
226 the food web based on the dominant functional groups only (ESI panel 2). Moreover, for optimal
227 comparison, the same three variations of food web structures are considered, comprising the same
228 two major uncertainties: i) degree of direct SOM consumption of consumers and ii) degree of
229 feedback to the SOM pool of fungi and fauna. Within these three different structures, sensitivity
230 uncertainty is again captured by modelling different sensitivity scenarios: i) all groups having the
231 same drought sensitivity (S), ii) fungi (F), iii) all consumers (C) or iv) predators (P) are more
232 drought sensitive than the other trophic levels, leading to a total of twelve different scenarios.

233 For this more complex food web (Fig. 4), drought-induced changes in soil carbon content showed
234 a similar trend among all different scenarios but were even more variable than for the food web
235 based on the dominant functional groups only (Fig. 3). For example, the high increase in carbon
236 sequestration when fungi were more drought-sensitive and, together with the fauna, feed back to
237 the SOM pool, was augmented from 240 to 300% (Fig. 3 panel f compared to Fig. 4 panel f).
238 This quantitatively illustrates that the predictability of the effect of climate change on soil carbon
239 sequestration decreases when food web complexity increases, as it implies making even more
240 assumptions based on uncertain parameters. Thus, while even our simulations including
241 additional consumers and predators are a simplistic representation of reality (as any model is by
242 definition), this only strengthens our point that limited knowledge about soil food webs strongly
243 limits our understanding of how soil carbon stocks will respond to climate change.

244

245 **Model complexity**

246 The role of food web structure within carbon cycling can be mathematically modeled using
247 approaches of varying ecological scales and physiological mechanisms and consequently varying
248 complexities. Hence, several potential model additions or different approaches should lead to a
249 more comprehensive representation of (heathland) soil food web functioning. These include:
250 legacy effects of drought, nitrogen (N) mineralization, changes in plant carbon input quantity and
251 quality, evolutionary adaptations and interactions within functional groups. However, small-scale
252 models capturing fundamental ecological mechanisms without excessive (mathematical)
253 complexity are crucial before up-scaling towards global predictive models [3].

254 In line with an increased food web complexity, an increased model complexity entails more
255 assumptions based on unknown parameters, thereby reducing tractability, robustness and
256 potentially predictive capacity. For example, using a model with more parameters than ours, Berg
257 *et al.* [34] found up to two-fold differences between measured and simulated carbon
258 mineralization rates in a pine forest soil. Thus, for both food web complexity as well as model
259 complexity, a balance needs to be found between tractability and realism, because even relatively
260 simple models, such as in this study, require more understanding of soil food webs to accurately
261 predict quantitative and even qualitative responses of soil carbon sequestration to increased
262 droughts.

263 **Conclusions**

264 The importance of soil food web structure and community diversity for ecosystem processes has
265 been extensively illustrated both by theoretical and empirical studies [5], [6]. Therefore, adding
266 of soil organisms in carbon simulation models may improve our assessment of the climate change
267 mitigation potential of soils [7]–[12]. However, we demonstrate that stressed food webs of
268 varying structural complexity can both increase and decrease soil carbon sequestration in
269 heathlands, depending on differential stress sensitivities of and trophic links between consumers
270 and decomposers. In addition, our results show that when food web structures differ among
271 heathland sites, for example because of spatiotemporal variability [36], we can expect highly
272 contrasting local or regional effects of climate change on carbon sequestration.

273 Thus, our results highlight that, even for a a relatively uncomplicated system with a few dominant
274 functional groups and a simulation model with a few but essential parameters, quantification of
275 the relative stress-sensitivities of functional groups and how and to which extend these interact is
276 needed in order to improve the forecast of carbon cycling models by adding the biotic drivers. As
277 these uncertainties are potential important aspects among a variety of soils worldwide [37], we
278 argue that more empirical research on these properties, in combination with simple mechanistic
279 models such as ours, could potentially enhance understanding in other ecosystems as well.

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380

381 **Tables**

382 **Table 1: Heathland soil food web uncertainties**

Uncertainty	Description	Explanation
Decomposer's input to SOM.	The proportion of SOM that is derived from fungi and soil animals is unknown due to the uncertainty regarding the rate of recalcitrant carbon flow of dead fungi and animal faeces to the SOM pool.	Fungi and soil animals exert both a degradation and a stabilization effect via conversion of assimilated solubles and polysaccharides into more recalcitrant polyphenolic compounds in their fungal tissues, which enter the SOM pool upon mortality (fungi) or as faeces (soil fauna).
Consumer's feeding behavior.	The ratio of fungi vs. organism-derived carbon substrates in the diet of enchytraeid worms is unknown.	It remains uncertain whether enchytraeids <i>in situ</i> actively forage for fungal mycelium or bulk feed on SOM. Given the difference in C/N ratio of fungi vs SOM this uncertainly largely contributes to the net effect of Enchytraeidae on carbon sequestration
Stress sensitivities of decomposers and consumers.	The stress sensitivities of heathland soil fungi and enchytraeids to common abiotic stresses such as an increase in the frequency, duration and amplitude of heat waves and dry spells are unknown.	Knowledge on stress sensitivities of different functional groups of soil organisms remains scarce, limiting our understanding of the fundamental mechanistic link between stress-induced changes in food web composition and net changes in soil carbon budgets.

383

384 **Figure captions**

385 **Fig. 1** Overview of carbon flow in the heathland soil food web whereby the considered uncertain links
386 between groups are dashed. Circular illustrations (not to scale) from left to right: an ericoid mycorrhizal
387 fungus (ERM) in symbiosis with its host plant, saprotrophic fungal (SF) mycelium and an enchytraeid
388 worm. For the depiction of ERM and SF, figures were re-used with permission from respectively Starrett
389 *et al.*[38] and Crowther *et al.*[39].

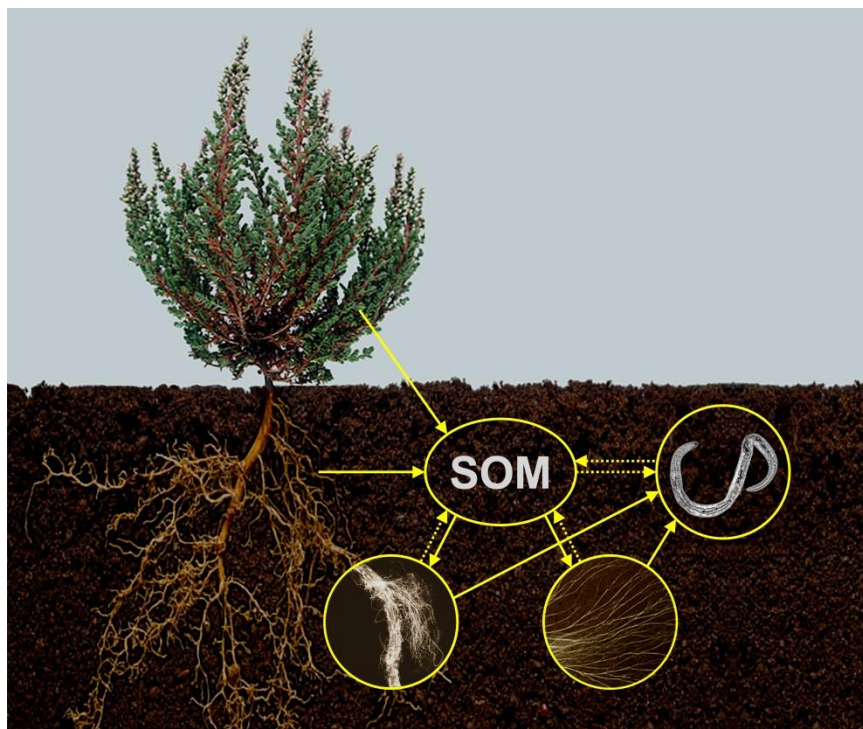
390
391 **Fig. 2** Overview of the three different food web structures considered. First structure: enchytraeids are
392 fungivorous, and fungal input to polyphenolic carbon pool is large. Second structure: enchytraeids are
393 bulk SOM feeders, and fungal input to polyphenolic carbon pool is large. Third structure: enchytraeids are
394 fungivorous and fungal input to polyphenolic carbon pool is low. Arrow thickness depicts rate of carbon
395 flow. Default structure in black, uncertainty related differences in yellow.

396
397 **Fig. 3** Model simulation results showing the effect of different degrees of drought stress (low, medium
398 and high) on soil carbon contents, expressed as the ratio of the carbon content in the drought stress
399 simulation over the carbon content in the control simulation (no reduction of grazing rates). Nine different
400 cases (a-i) are shown in separate panels: structures 1, 2 and 3 with the three different scenarios of stress
401 sensitivities (same sensitivity (S); fungi more sensitive (F) and enchytraeids more sensitive (E))

402
403 **Fig. 4** Model simulation results of the more complex food web. Twelve different cases (a-l) are shown in
404 separate panels: structures 1, 2 and 3 with the four different scenarios of stress sensitivities (same
405 sensitivity (S); fungi more sensitive (F); consumers (enchytraeids, springtails and saprophagous mites)
406 more sensitive (C) and arthropod predators (P) more sensitive). Drought induced soil carbon content
407 changes are similar but more variable then for the standard food web complexity (Fig. 3).

408 **Figures**

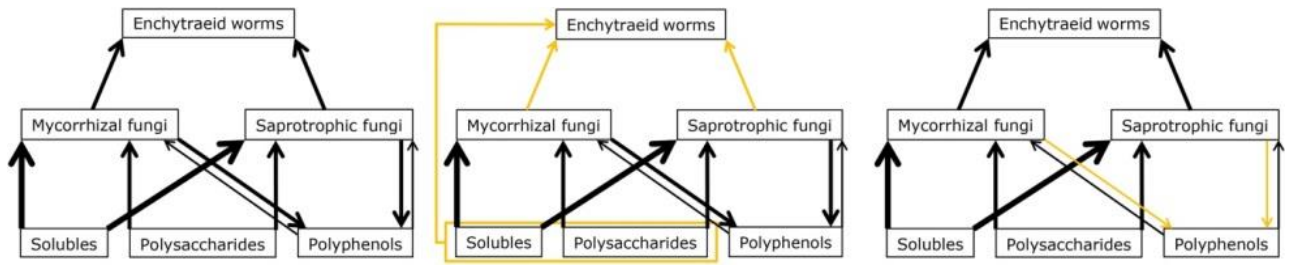
409 **Fig. 1**



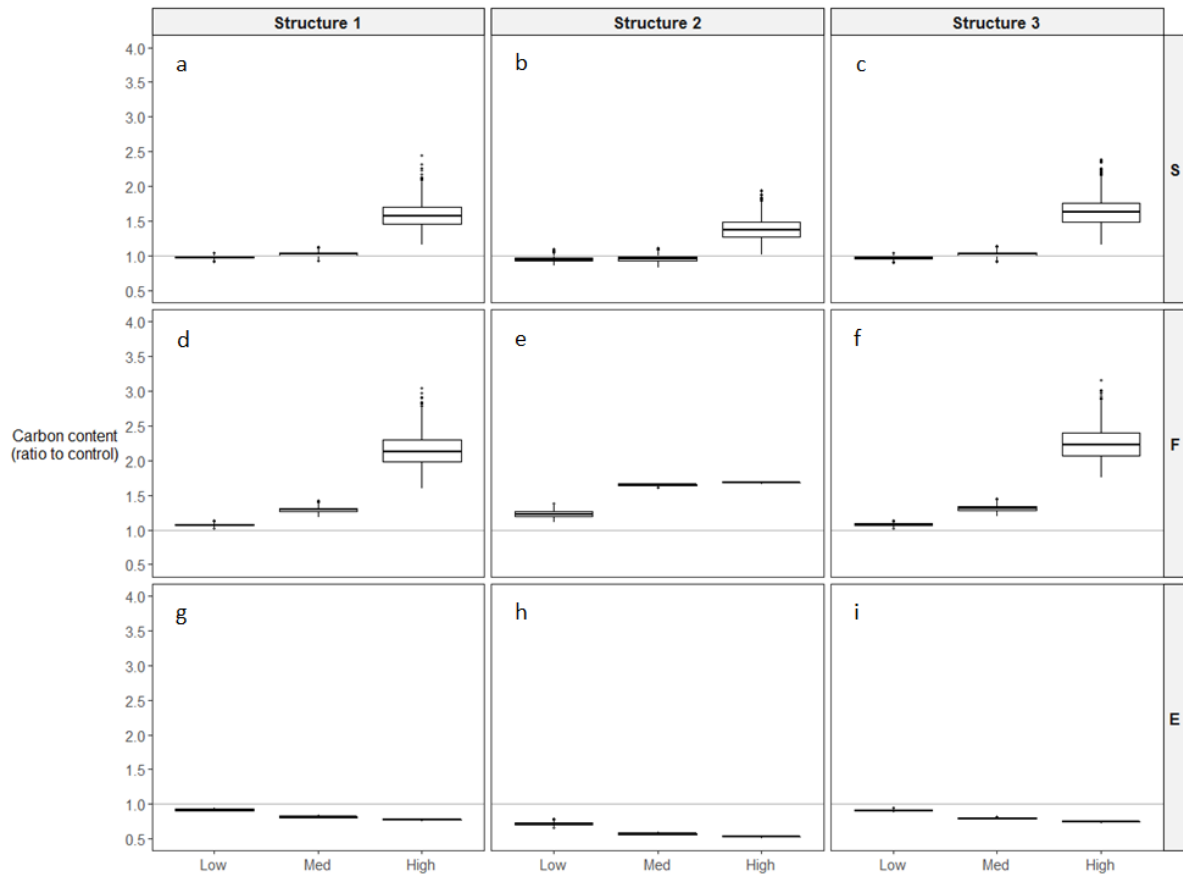
410

411 **Fig. 2**

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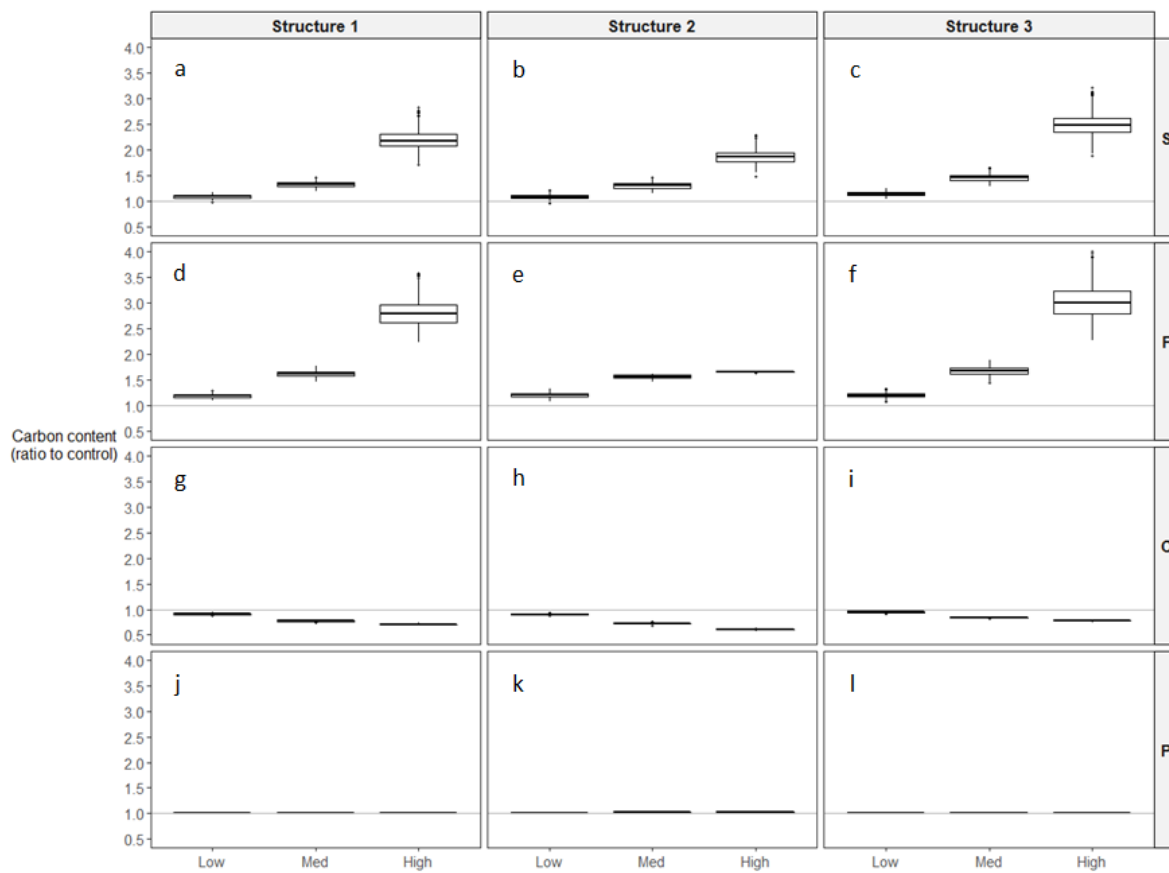


413 **Fig. 3**



414

415 **Fig. 4**



416