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

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Abstract

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

Keywords

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

Introduction

Human-induced climate change affects global carbon cycles and threatens important ecosystem services. Sequestration of carbon into soils as organic matter is considered as an important process of the global carbon cycle because it mitigates climate change by reducing excessive atmospheric CO_2 concentrations [1]. However, a key question is whether climate change increases or decreases the capacity of soils to sequester carbon, and hence whether ecosystems will buffer or accelerate climate change.

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

This strongly contrasts with findings that soil organisms drive the process of organic matter decomposition. The importance of their composition in regulating the effects of climate change on ecosystem processes such as carbon cycling has been discussed extensively [5], [6]. Hence, in contrast to what is implicitly assumed in conventional soil carbon models, shifts in soil community composition due to environmental stressors can have significant consequences for carbon cycling because of associated shifts in ecosystem functioning. Several studies have acknowledged the link between soil food web composition and carbon sequestration, and the need to incorporate this relationship into predictive carbon cycling models [7]–[12]. However, it remains unclear to what extent climate change will affect soil carbon budgets of ecosystems.

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

Uncertainty regarding food web structure and function

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

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

Some groups of soil fauna can contribute to the decomposition of the microbial necromass, such as Collembola (springtails), Acari (mites) and enchytraeid worms. Enchytraeid worms are in terms of biomass the most abundant consumers in nutrient poor acidic organic soils [18], including dry heathlands, where *Cognettia sphagnetorum* (actually a complex of several cryptic species [19]) is the keystone species with an estimated dominance of up to 80% [20]. The necromass of enchytraeids and other soil animals is considered to be easily degradable [21], but excrement of soil fauna can actually be even more recalcitrant than ingested compounds, thereby fostering carbon sequestration. Despite these insights, the acknowledgement that excrement and necromass of soil organisms potentially contribute significantly to carbon sequestration remains largely unexplored. Therefore, we consider it to be a major knowledge gap regarding the functioning of heathland soil food webs (Table 1).

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

Uncertainty regarding the effects of climate change on soil food webs

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

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

In general, differences in stress tolerance are relatively well studied within functional or taxonomic groups [30] but less so between functional groups and across throphic levels [31]. However, Franken and collegues [31] for example found high interspecifc variation in temperature tolerance among trophic levels in a soil arthropod community, which potentially causes trophic mismatches during extreme events. We expect a similar difference in sensitivity of functional groups for drought and this adds to our limited understanding of the fundamental mechanistic link between stress-induced changes in food web composition, and net changes in soil carbon budgets. Therefore, we consider the stress sensitivities of soil organisms, especially fungi and enchytraeids that dominate the soil food web of heathlands, as an important knowledge gap (Table 1). For example, drought might indirectly foster sequestration of carbon by selecting stress tolerant fungal species that are often highly melanized [17], since melanized fungal biomass decomposes slower than hyaline fungal biomass [32]. This critical dual role of melanin in both drought stress sensitivity as well as decomposability illustrates that functional traits of fungi driving susceptibility to environmental stressors are not necessarily independent from traits driving ecosystem processes.

Modelling drought stress effects on carbon sequestration

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

Parameters and simulations

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

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

Results

Our results show that a difference in the sensitivity of fungi and enchytraeids to drought stress was more important than food web structure for predicting drought stress effects on carbon sequestration. Drought increased carbon sequestration when fungi were more sensitive than enchytraeids (F) or when both were equally sensitive (S) (Fig. 3 panels a-f). Drought stress decreased carbon sequestration when enchytraeids were more sensitive than fungi (E) (Fig. 3 panels g-i). Moreover, our food web simulations show that the feeding behavior of enchytraeids affected the extent of these sensitivity dependent stress-induced changes. When enchytraeids only fed on fungi and were less sensitive for drought than fungi (Fig. 3 panel d), their abundance reduced along with the stress-induced decrease in fungal abundance (as they had no alternative food source), resulting in the same outcome as for equal sensitivity (Fig. 3 panel a). However, if enchytraeids fed soley on SOM when being less sensitive for drought than fungi (Fig. 3 panel e), access to readily available carbon substrates allowed them to increase in abundance despite the decrease in fungal biomass. This resulted in a higher stress-induced carbon sequestration increase by enchytraeids compared to them being solely fungivorous (Fig. 3 panel d) or having the same drought sensitivity as fungi (Fig. 3 panel b). The rate of carbon flow from fungi to the polyphenolic carbon pool shows only a minor impact on stress-induced carbon sequestration changes (Fig. 3: panels a, d and g are very similar to panels c, f and i).

Food web complexity

Our results illustrated that even a very simple food web already has so many uncertainties in some of its assumptions that, based on the currently available data, it is very difficult to make accurate predictions on the responses of soil carbon sequestration to future environmental changes. However, soil food webs can even be much more complex for other ecosystems than for heathland soils [34], [35], and there are parts of heathland soil food webs (e.g predators) that we did not consider so far. For this reason, we repeated the simulations using a more comprehensive representation of heathland soil food web, by including less dominant functional groups of consumers (springtails and saprophagous mites) and arthropod predators; such as predaceous mites, spiders and predatory beetles (ESI Fig 1).

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

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

Model complexity

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

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

Conclusions

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

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

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Tables

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 *in situ* 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, duaration 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.

Figure captions

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

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

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

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

Figures

Fig. 1

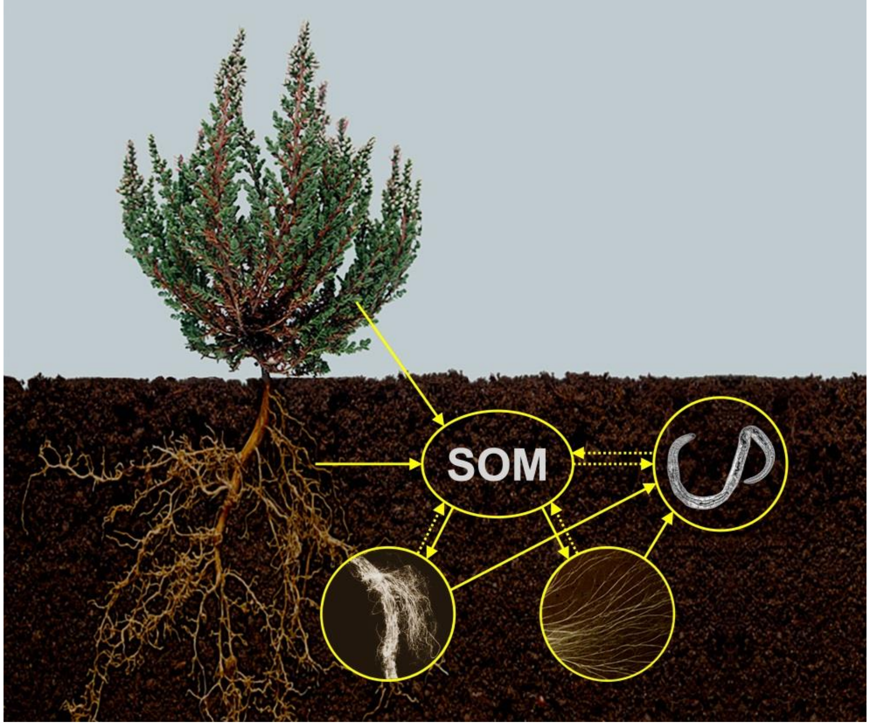


Fig. 2

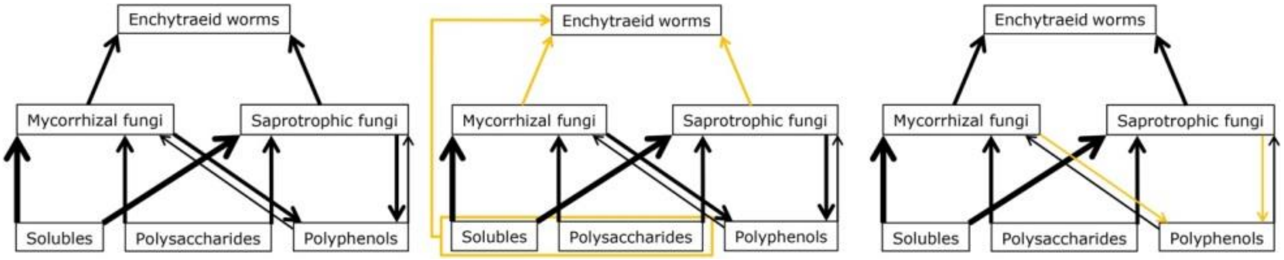
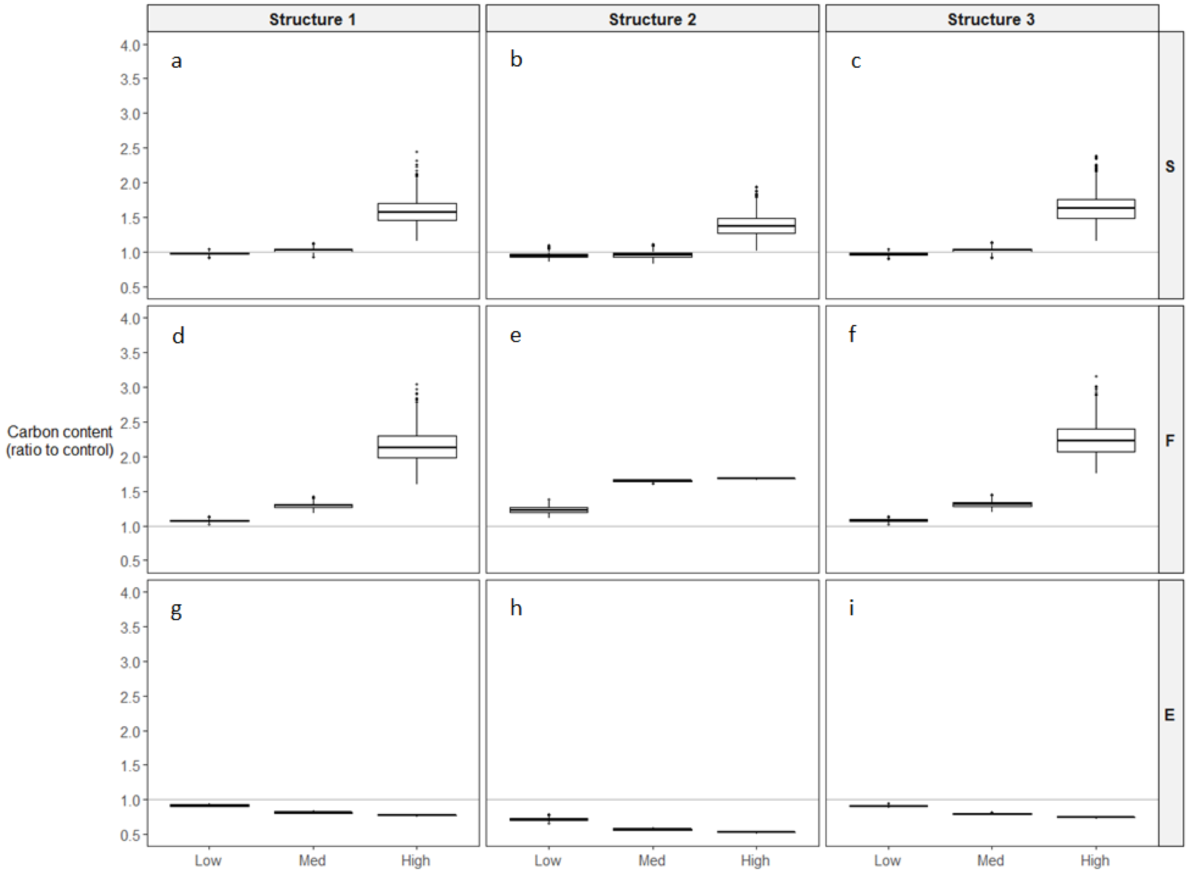
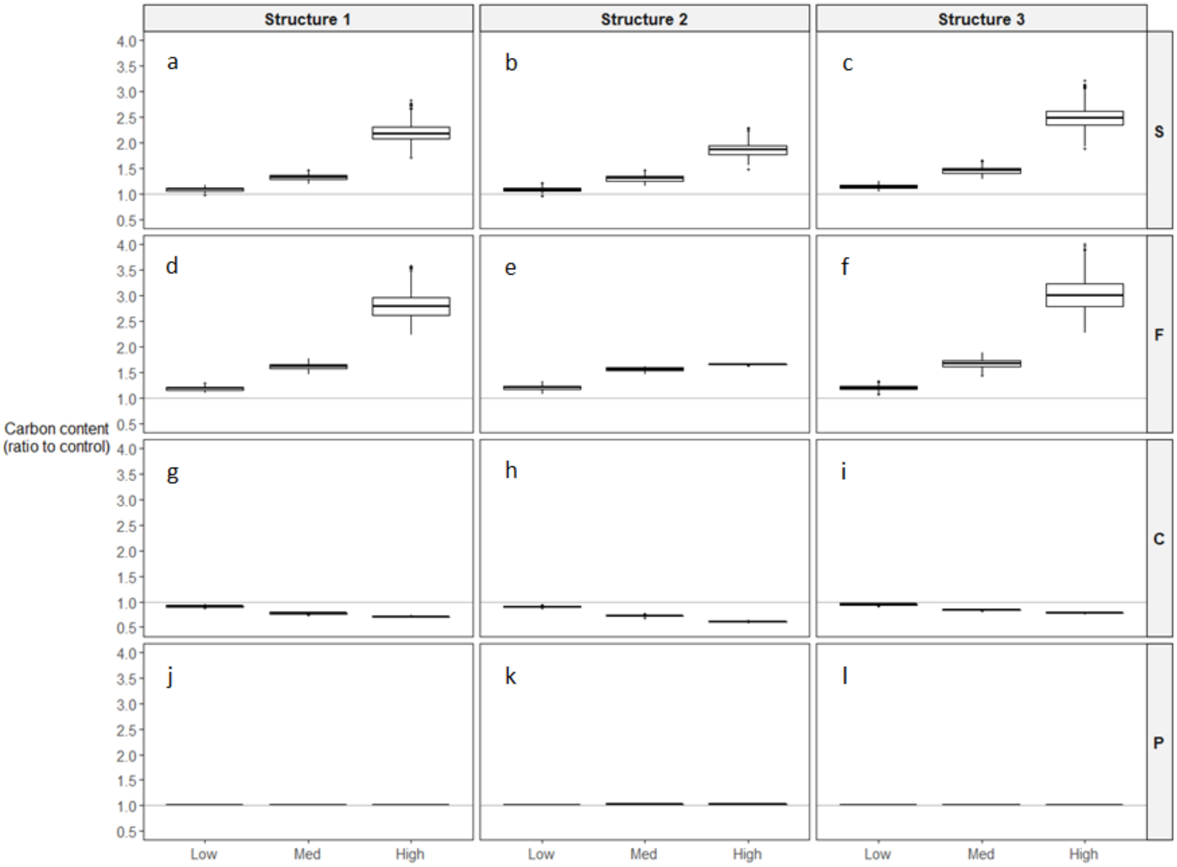

Enchytraeid worms
Mycorrhizal fungi
Saprotrophic fungi
Solubles
Polysaccharides
Polyphenols
Enchytraeid worms
Mycorrhizal fungi
Saprotrophic fungi
Solubles
Polysaccharides
Polyphenols
Enchytraeid worms
Mycorrhizal fungi
Saprotrophic fungi
Solubles
Polysaccharides
Polyphenols

Fig. 3



Structure 1
Structure 2
Structure 3
a
b
c
d
e
f
g
h
i
S
F
E
Carbon content (ratio to control)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
Low
Med
High

415 **Fig. 4**


Structure 1
Structure 2
Structure 3
a
b
c
d
e
f
g
h
i
j
k
l
S
F
C
P
Carbon content (ratio to control)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
Low
Med
High

416