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Global change effects on a mechanistic decomposer food web model

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Abstract

Global change may affect the structure and functioning of decomposer food webs through qualitative changes in freshly fallen litter. We analyzed the predicted effects of a changing environment on a dynamic model of a donor-controlled natural decomposer ecosystem near Wekerom, the Netherlands. This system consists of fungi, bacteria, fungivores, bacterivores and omnivores feeding on microbiota and litter as well. The model concentrates on carbon and nitrogen flows through the trophic niches that define this decomposer system, and is designed to predict litter masses and abundances of soil biota. For modeling purposes, the quality of freshly fallen leaf litter is defined in terms of nitrogenous and non-nitrogenous components, of which refractory and labile forms are present. The environmental impacts of elevated CO_2, enhanced UV-B and eutrophication, each with their own influence on leaf litter quality, are studied. The model predicts steady-state dynamics exclusively, for all three scenarios. Environmental changes impact most demonstratively on the highest trophic niches, and affect microbiotic abundances and litter decomposition rates to a lesser extent. We conclude that the absence of trophic cascade effects may be attributed to weak trophic links, and that non-equilibrium dynamics occurring in the system are generally because of encounter rates based on fractional substrate densities in the litter. We set out a number of experimentally testable hypotheses that may improve understanding of ecosystem dynamics.

Keywords: decomposer food web, ecosystem function, global change scenarios, mathematical model, stability, stoichiometry

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Introduction

Although the earth has continuously changed since its origin, we have become aware that alterations in the earth system are now occurring at an accelerated pace (Stouffer *et al*., 1994; Cox *et al*., 2000; Gillet *et al*., 2003). Ozone depletion leading to enhanced UV-B levels, increases in atmospheric greenhouse gases, elevated temperature, and changes in the use of natural resources have been experimentally shown to affect biological systems in many ways (Walther *et al*., 2002). However, from a theoretical point of view, their effect on the structure of communities and long-term functioning of ecosystems is only moderately understood.

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Element cycling, and the role of global change therein, is a central theme in ecology. Different aspects of global change impact on the quality of litter, and litter decomposition plays a key role in the cycling of resources in terrestrial donor-controlled ecosystems. The decomposition rate of detritus depends on its nutritional quality to decomposer organisms (Cotrufo & Ineson, 1993; Gallardo & Merino, 1993; Moore *et al*., 1999). In turn, the dynamics of soil food webs depend on interactions between decomposers and higher trophic levels (Berg *et al*., 1993; Fox, 2003; Smith & Bradford, 2003; Bakker *et al*., 2004). Therefore, it is to be expected that the functioning of such donor-controlled ecosystems depends on the composition of the litter provided.

Temperature and soil humidity directly influence the activity of soil decomposers and play a key role in litter decomposition (Berg *et al*., 1993). Other environmental

factors influence this process indirectly. Enhanced levels of UV-B have been shown to alter the chemical composition of fresh plant litter into more recalcitrant forms (Rozema, 1999; Laakso *et al.*, 2000; Rozema, 2000; Kinnunen *et al.*, 2001; Lavola *et al.*, 2003). Furthermore, increased levels of atmospheric CO_2 potentially increase the carbon content of leaf litters, and their lignin : N ratios (Cotrufo *et al.*, 1994, 1998; Norby & Cotrufo, 1998; King *et al.*, 2001; Norby *et al.*, 2001). In contrast, although eutrophication with nitrogen has toxic effects on soil microflora (Wollecke *et al.*, 1999), it enhances the nitrogen content of leaf litters (Heinsdorf, 1993; Prietzel *et al.*, 1997), and so potentially augments soil species with nutrients that were originally limiting their activity and this may increase decomposition rates (Hogervorst *et al.*, 2003). Antagonistic effects on the quality of litters make it hard to predict the effects of global change on the functioning of donor-controlled ecosystems.

In the past decades, our understanding of the physiology and function of soil micro-organisms has increased rapidly (Nannipieri *et al.*, 2003). Moreover, there has been an increased knowledge of trophic channels along which energy and nutrients are transferred in natural ecosystems (Cox *et al.*, 2000; Moore *et al.*, 2003). Therefore, currently, many natural ecosystems have been successfully charted. At this stage, it may have become possible to make the step from empirically based descriptive models, which have successfully outlined the basic structure and functioning of food webs, but are limited in their use for understanding long-term ecosystem dynamics, to mechanistic models of natural food webs, which may be used to discover general patterns in ecosystem dynamics and functioning. In this paper, we develop such a mechanistically based food web model, and we will use it to predict how different scenarios of global change might affect soil ecosystems both quantitatively (changes in net litter composition and masses of litter and soil functional groups) and qualitatively (changes in community structure, stability, top-down vs. bottom-up regulation). Our goal is to put forward experimentally testable predictions on long-term effects of global change on soil communities, and to point out gaps in knowledge required to advance in the understanding of dynamics of soil ecosystems.

In this study we employ a dynamic model of a Scots pine forest soil ecosystem in Wekerom, the Netherlands, which has been described in detail in Berg & Verhoef (1997), Berg *et al.* (2001). Because of the large number of functional groups, sensu (Moore *et al.*, 1988), involved, this web is essentially beyond the complexity at which a complete analysis is still feasible. Therefore, we have reduced the total number of groups by lumping species that belong to the same trophic group.

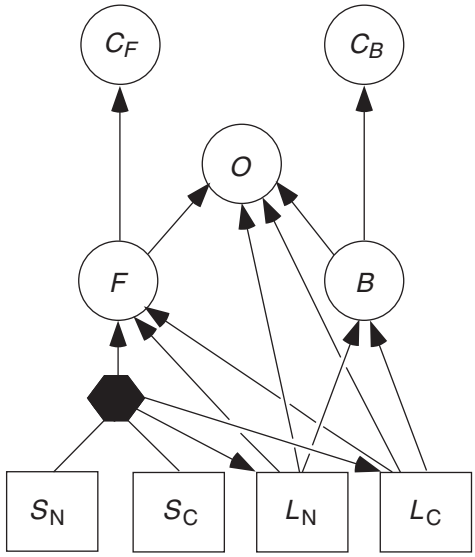

Fig. 1 Conceptual model of trophic flows in the Wekerom Scots pine forest ecosystem. Arrows refer to flows of resources, rectangles are litter components, large circles are trophic guilds and the small hexagon represents the function of exogenous fungal enzymes that excavate labile components from stable components, which may be used by fungi. Table 1 summarizes the notation.

This leaves groups of bacteria, fungi, bacterivores, fungivores and omnivores feeding on both detritus and microflora. Figure 1 shows the simplified trophic structure of the forest soil. Fresh litter supplied to the system is divided into nitrogenous and carbonous components, which are, in turn, split up in refractory and labile parts. The abundance of the four resulting components in the regular litter fall is affected by several aspects of global change. In this study, we will analyze the effect of alterations in litter composition on the dynamics of the Wekerom food web. We will concentrate on eutrophication, UV-B enhancement and elevated CO_2 levels in this study, as these aspects of global change have been shown to affect the composition of leaf material. Litter is generally biochemically degraded by fungi and bacteria, although enchytraeids are also known to decompose litter (Didden & Rombke, 2001). Bacterivores and fungivores graze on the soil microflora, in which they find competitors in the enchytraeids, which can use both detritus and microbial biomass for growth (Didden & Rombke, 2001). Litter degradation comprises both chemical decomposition and fragmentation. In this study, we will model the upper litter layer, as this is the layer in which the majority of decomposition takes place (Berg *et al.*, 1997). We assume that fragmented materials, as well as the biota that live on them, are physically transported to the fragmentation layer, which is out of the scope of this study.

Litter quality is usually defined in terms of nitrogen and energy availability, and litter C : N ratios have traditionally been used as a measure for litter quality. Here, lower C : N ratios usually refer to a higher nutritional quality of litter. However, some nitrogenous compounds are recalcitrant (e.g. nitrogenous materials stored in a persistent lignin matrix) while soluble nitrogen-deficient hydrocarbons can generally be easily degraded, which obscures the concept of litter quality (Bosatta & Ågren, 1999; Berg, 2000). We pay due attention to the characteristics of the particular chemical substances in the litter, by using a compound-based, rather than an element-based stoichiometric model. We model the biota's acquisition and utilization of potentially limiting resources using a model module, called the synthesizing unit (SU) (Kooijman, 1998). Mathematically, this method connects closely to enzyme kinetics where concentrations of substrates transform into products. In this study, SUs model the flows of carbon and nitrogen, in their different forms, through the food web. This theoretical approach was earlier used in Kooi *et al*. (2004), Kooijman (1998), Kuijper *et al*. (2004a, b), Muller *et al*. (2001). Using this approach, we augment classic food chain theory with aspects of nutritional physiology of soil biota, based on field biology data (Berg, 1997).

The paper's organization is as follows. In the next section, we set out the model philosophy and assumptions in some detail. In the results section, we show model predictions as to how changes in litter quality, caused by nutrient enrichment and enhanced UV-B and CO_2, affect the dynamics of the litter layer. Here, we discuss these model predictions in detail. Our focus will be on three aspects of food web functionality. These are (1) competitive changes between bacteria and fungi, (2) changes in food web productivity, and (3) cascading effects of these changes within the web. Furthermore, we put forward a number of experimentally testable ecological hypotheses, instilled by the results of the dynamic model. In doing so, we emphasize the need for collaborations between experimentalists and theoreticians. Furthermore, we concentrate on the dynamic behavior of the model, and compare it with theoretical predictions from theoretical ecology. We conclude by pointing out implications of using a mechanistic modeling approach in the analysis and understanding of soil ecosystems.

Model setup and assumptions

The model is about energy and nutrient flows across the soil ecosystem. This requires the characterization of transformations of litter components into biota and transformations of prey into predators. We assume homeostasis for all components (i.e. the stoichiometry of all biota and particular litter components is constant). This approach is somewhat questionable from a nutritional point of view, as the elemental composition of organisms generally depends on their nutrition (Kooijman, 2000; Boersma & Kreutzer, 2002; Cross *et al*., 2003). However, it prevents the model from becoming very complex. Using variable elemental composition implies the use of several state variables for the mathematical description of each trophic group (Droop, 1983; Kooijman, 2000) and this is beyond the scope of this study.

We use C-moles per square meter as unit of mass. Table 1 contains the assumed biochemical composition of the food web components in terms of their N : C ratios. The N : C ratio of the labile nitrogenous litter is based on average C : N of proteins (≈ 3, Vollenweider, 1985), although it must be conceived of as a blend of all available nitrogen for micro-organisms (amino acids, minerals bound to organic matrices and other water soluble nitrogen sources). Stable nitrogenous litter is comprised of a non-nitrogenous lignin matrix (Adler, 1977), in which labile nitrogenous organics are stored. For modeling purposes, it has been given an N : C ratio of 0.05. Biota are given a biologically realistic N : C (0.1–0.2, cf. Schröter *et al*., 2003), where fungi have a somewhat lower C : N than other biota. Biochemical transformations are listed in Table 2. The stoichiometry of these transformations follows from literature assimilation and production efficiencies (Berg *et al*., 2001) and the N : C ratios of the forest ecosystem's participants. We assume that external nitrogen sources dominate, so that nitrogenous minerals, formed in the production of mesobiotic biomass are lost from the system. The model parameters are listed in Table 3. Maximum production rates, which can be regarded as the intrinsic growth rates of the associated populations, have been given a biologically plausible value. Degradation rates of stable litter are conjectured from Minderman (1968). The litter

Table 1 Actors in the upper litter layer and their biochemical representations as C : N ratios

Soil component	Notation	N : C
Stable nitrogen	S_N	0.05
Stable carbon	S_C	0
Labile nitrogen	L_N	0.35
Labile carbon	L_C	0
Fungi	F	0.1
Bacteria	B	0.2
Fungivores	C_F	0.2
Bacterivores	C_B	0.2
Omnivores	O	0.2

input rate and composition are based on local observations (Berg, 1997). For simplicity, the natural residence time of litter components is taken 1 year, hence the value of $D = 1/365$ per day. Unfortunately, there is no data available for estimating the parameters of interactions between soil organisms and substrates. Therefore, we used a standardized biologically plausible value for all searching rates and substrate affinities. Appendix A contains the mathematical expressions for the dynamic interactions in the top litter layer. Note that plants are not included in the model, as our focus is on the top litter layer, in which plant roots are virtually absent in the Wekerom system (Berg, 1997). However, different aspects of global change affect plant production, which consequently impacts on litterfall quantitatively. We did not explicitly model such effects. However, we modeled all interactions according to the law of mass action. This law holds that reaction rates depend fully on density-based encounter rates. These encounter rates are independent on litterfall rates, as long as the composition of the freshly fallen litters does not change. Therefore, the qualitative model outcomes are independent on litter input rates, and the quantitative model outcomes scale proportionally with the litter input rate. This model property corresponds well to the finding that in the Wekerom system, densities of biota are not related significantly to the mass of the top litter layer (Berg *et al.*, 2001).

Table 2 Biochemical transformations occurring in the top litter layer

No.	Transformation	Biochemical reaction
1	Stable litter breakdown by fungi	$S_N \rightarrow \frac{1}{7}L_N + \frac{6}{7}CO_2$
		$S_C \rightarrow \frac{1}{5}L_N + \frac{4}{5}CO_2$
2	Fungal growth	$\frac{2}{7}L_N + 3\frac{5}{7}L_C \rightarrow F + 3CO_2$
3	Bacterial growth	$\frac{4}{7}L_N + 2\frac{3}{7}L_C \rightarrow B + 2CO_2$
4	Fungivore growth	$F \rightarrow \frac{3}{20}C_F + \frac{7}{100}NH_3 + \frac{17}{20}CO_2$
5	Bacterivore growth	$B \rightarrow \frac{1}{4}C_B + \frac{3}{20}NH_3 + \frac{3}{4}CO_2$
6	Onivore assimilation	$L_C \rightarrow \frac{9}{50}H + \frac{4}{5}L_C + \frac{1}{50}CO_2$
		$L_N \rightarrow \frac{7}{20}P + \frac{1}{2}L_N + \frac{21}{400}NH_3 + \frac{3}{20}CO_2$
		$B \rightarrow \frac{12}{35}P + \frac{9}{35}H + \frac{2}{25}NH_3 + \frac{14}{35}CO_2$
		$F \rightarrow \frac{6}{35}P + \frac{3}{7}H + \frac{2}{50}NH_3 + \frac{14}{35}CO_2$
7	Omnivore growth	$\frac{4}{7}P + \frac{16}{21}H \rightarrow O + \frac{1}{3}CO_2$

Fungi

In the Wekerom soil ecosystem, fungi dominate the degradation of recalcitrant litter components. In this

Table 3 Environmental constants and parameters of interactions between soil biota and their recources

Parameter	Interpretation	Dimension	Value
$j_{L_N,Dm}$	Maximum degradation rate of S_N	day^{-1}	$7.14 \times 10{-}3$
$j_{L_C,Dm}$	Maximum degradation rate of S_C	day^{-1}	$4.0 \times 10{-}3$
$j_{F,Gm}$	Maximum fungal specific growth rate	day^{-1}	5.0
$j_{B,Gm}$	Maximum bacterial specific growth rate	day^{-1}	10.0
$j_{C_F,Gm}$	Maximum fungivore specific growth rate	day^{-1}	$3.0 \times 10{-}1$
$j_{C_B,Gm}$	Maximum bacterivore specific growth rate	day^{-1}	$5.0 \times 10{-}1$
$j^O_{L_C,I}$	Maximum omnivore ingestion rate of L_C	day^{-1}	1.0
$a^F_{S_N}$	Fungal enzymatic affinity for S_N	day^{-1}	5.0
$a^F_{S_C}$	Fungal enzymatic affinity for S_C	day^{-1}	5.0
$a^F_{L_N}$	Fungal affinity for L_N	day^{-1}	5.0
$a^F_{L_C}$	Fungal affinity for L_C	day^{-1}	5.0
$a^B_{L_N}$	Bacterial affinity for L_N	day^{-1}	5.0
$a^B_{L_C}$	Bacterial affinity for L_C	day^{-1}	5.0
$a^{C_F}_F$	Fungivorous searching rate coefficient	day^{-1}	5.0
$a^{C_B}_B$	Bacterivorous searching rate coefficient	day^{-1}	5.0
$a^O_{L_C}$	Omnivorous searching rate coefficient	day^{-1}	5.0
$J_{C_{in}}$	Litter input rate	$C\,mol\,day^{-1}$	$5.0 \times 10{-}2$
$j_{L_N,Dm}$	Loss rate	day^{-1}	1/365
Varied parameter	**Interpretation**	**Dimension**	**Default value**
θ_{S_N}	Fraction of S_N in supplied litter	day^{-1}	0.20
θ_{S_C}	Fraction of S_C in supplied litter	day^{-1}	0.45
θ_{L_N}	Fraction of L_N in supplied litter	day^{-1}	0.05
θ_{L_C}	Fraction of L_C in supplied litter	day^{-1}	0.30

process, using exogenous enzymes, brown-rot fungi release and utilize energy rich resources from the matrix of stable components (Kirk & Farell, 1987). White-rot fungi may metabolize refractory materials directly (Kirk & Fenn, 1982). We use Michaelis–Menten kinetics to model this process of excision. We assume that the production of labile organic nitrogen is efficient, so that no nitrogen is lost in mineral form. The process rate of persistent litter degradation is slow, as compared with other transformation processes. Fungi have prior access to the labile components released from the persistent matrix and they can use them in addition to other labile components in the litter to form biomass. This process of merging soil substrates for growth is modeled with a complementary SU (Kooijman, 1998), which describes the process rate of a biochemical transformation in which two or more resources are required (see Appendix A). A graphic representation of how a complementary SU works is given in Fig. 2. The availability of nitrogen and energy determines the growth rate of fungi, which models the influence of resource quality. We assume that the maximum carbon growth efficiency of fungi is approximately 25% (using 45% production efficiency; Berg *et al*., 2001) and a biologically plausible 75% uptake efficiency, rounded off downward in contrast to bacteria which need less complex structures and may therefore be more efficient). Furthermore, as nitrogen is generally considered to be the limiting nutrient in the initial phase of litter degradation, we assume that nitrogen can be used at a potential 100% efficiency.

Bacteria

Although many species of bacteria are capable of lignin and holo-cellulose degradation under anaerobic circumstances, these species are deemed to comprise only a small fraction of the total soil bacterial biomass, especially in the rarely waterlogged top litter layer. Therefore, in the model bacteria can only use labile components in the litter, including labile organic matter released from persistent litter, but left unused by fungi. Bacteria effectively compete with fungi for labile components of litter. As bacterial structural components are less complex than eukaryote fungal structures, we assume 33% maximum carbon growth efficiency for bacteria (approximately 45% production efficiency; Berg *et al*., 2001 and 75% uptake efficiency), which is slightly higher than the fungal efficiency with respect to carbon, and gives bacteria a slight competitive advantage. Hence, we model a slow degradation route dominated by fungi and a fast route dominated by bacteria, sensu (Moore *et al*., 2003). We assume that bacteria can use nitrogen 100% efficiently. Analogous to fungal production, a complementary SU conducts the merging process of nitrogenous and carbonous substrates for bacterial growth. For simplicity, we assume that bacteria and fungi can access labile litters equally efficient. This translates into identical values for uptake affinities in Table 3.

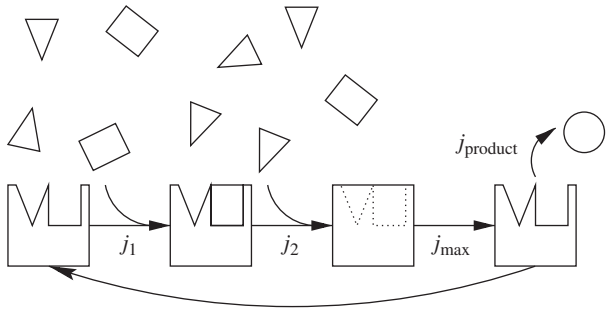

Fig. 2 Graphic representation of the complementary Synthesizing unit, using two substrates. The synthesizing unit accepts fluxes of substrates 1 and 2 while the binding sites are vacant. When both binding sites are filled, it enters the production phase, after which products are formed.

Fungivores

In the model, fungivores comprise the group of animals that feed on fungi. These are collemboles, oribatids, prostigmatids and fungivorous nematodes. Although many species are known to consume detritus as well (Filser, 2002), they are generally selective grazers for fungi. Therefore, in the model they feed on fungi exclusively. We assume that the grazing rate on fungi depend on the density of fungi in the litter, and use a Holling type-II functional response to model the interaction between fungi and fungivores. The net production efficiency of fungivores is approximately 15% (calculated from Berg *et al*., 2001, based on assimilation and gross production efficiencies). To keep the number of model parameters low, a constant loss term models predation, physical transport and natural death of all mesofauna. This holds a simplification of the biological decay processes, but an unpublished preanalysis in which we used an additional death loss rate for each trophic group resulted in qualitatively similar results compared with the model presented here.

Bacterivores

Flagellates, ciliates, amoeba and bacterivorous nematodes comprise the bacterivorous trophic group in the Wekerom soil ecosystem. We use a type-II response for bacterivorous consumption also. Moreover, we employ the same grazing rate and digestion time for

bacterivores and fungivores for convenience. However, we assume that chitin sheaths of fungi are harder to metabolize than bacterial structures, and therefore, bacterivores have a higher assimilation efficiency (25%, calculated from Berg *et al.*, 2001) than fungivores in the model.

Omnivores

The soil omnivores comprise omnivorous nematodes and enchytraeids, of which the latter are dominant in the Wekerom system. Therefore, we base the omnivores dynamics on the food acquisition method of enchytraeids, as described by Didden (1993), Didden & Rombke (2001). Enchytraeids feed by grazing the organic constituents of litter, and with the ingestion of litter, they automatically take up fungi and bacteria. Labile organic matter, as well as the bacteria and fungi, contain amino acids and hydrocarbons, which can be used in combination for growth. In this case, again a complementary SU rules the merging process, where carbon is used at a potential 75% gross growth efficiency, which is the predicted theoretical maximum efficiency for heterotrophs (Calow, 1977), and nitrogen can be used at a maximum 100% gross growth efficiency. The labile carbon part is an important source for hydrocarbon assimilates; labile nitrogenous litter components contribute to the amino-acid pool. Fungi and bacteria donate both hydrocarbons and amino acids. Therefore, litter composition, as well as the abundance of soil microbiota, is important for the dynamics of the enchytraeid population.

Results

Modeling global change scenarios

We simulate three scenarios where aspects of global change affect litter quality, namely elevated CO_2 levels, enhanced UV-B irradiation and eutrophication with nitrogen. This section deals with the quantitative effects of these changes on litter quality, and the indirect effects on the accumulation of litter and the persistence of functional groups. We focus on changes in competition between bacteria and fungi, changes in effective productivity because of alterations in the relative amount of stable and refractory litter parts, and cascading effects of changes in the external forces on the higher trophic groups.

Environmental changes are modeled by imposing changes in the composition of incoming litter. We aim to observe trends in the dynamic properties of the system, following upon changes in environmental conditions. Therefore, we employ modest perturbations from the default situation. Here, the relative difference in the composition of freshly fallen litter from the ambient conditions is called 'impact factor', and will never exceed 20%.

Elevated CO_2

Elevated levels of CO_2 increase the carbon and lignin content in plant materials (Cotrufo *et al.*, 1994, 1998; Norby & Cotrufo, 1998; King *et al.*, 2001; Norby *et al.*, 2001). This implies that the stable nitrogen content (θ_{S_N}), and the stable and labile carbon content $(\theta_{S_C}, \theta_{L_C})$ increase with increasing CO_2 levels, and consequently, the labile nitrogen content (θ_{L_N}) decreases simultaneously. We model the effect of elevated CO_2 by lowering $\theta_{L_N}$and increasing fractions θ_{S_N}, $\theta_{S_C}$and θ_{L_C}, while preserving the default relative proportions (Berg, 1997) of these three litter components for simplicity.

The CO_2 impact factor, which is on the horizontal axis of the diagrams (Figs 3 and 4), increases with increasing atmospheric CO_2 concentrations. The factor refers to the percentual reduction of labile nitrogenous organic matter in the litter. The ambient percentage of this litter component is 5%, which corresponds to an impact factor of 1. An increment to 1.2 corresponds with a reduction of this percentage from 5% to $5/12 \approx 4.17\%$.

None of the litter components are affected by CO_2 enhancement, although the quality of the litterfall is lower because of an inherent smaller fraction of labile nitrogenous compounds (Fig. 3, upper panel). Although fungal and bacterial densities in the litter seem unaffected, enhanced CO_2 impacts on the omnivore and fungivore populations (Fig. 3, lower panel). Omnivores suffer from reduced quality of the litter input, while the fungivore population becomes larger. The net effect is a slightly reduced food web productivity (total biomass decreases, Fig. 4). Although their resource densities remain more or less constant, the model predicts pronounced effects of elevated CO_2 on the higher trophic groups. As there is no direct effect of litter quality on soil fauna, these changes in population size must be attributed to bottom-up effects. The model predicts that the change in fresh litter composition imposes an indirect shift in the competition ability of the omnivore enchytraeids. They suffer from a lower access to labile nitrogenous organics in the litter provided, which results in a lower population size and lower grazing pressure on fungi. Specialist fungivores benefit from this reduced competition with omnivores. Whether this model prediction holds when applied to natural systems, remains to be tested.

The C : N ratio increases as a consequence of CO_2 enhancement (Fig. 4), which is an indirect effect of the reduced population density of omnivores, which

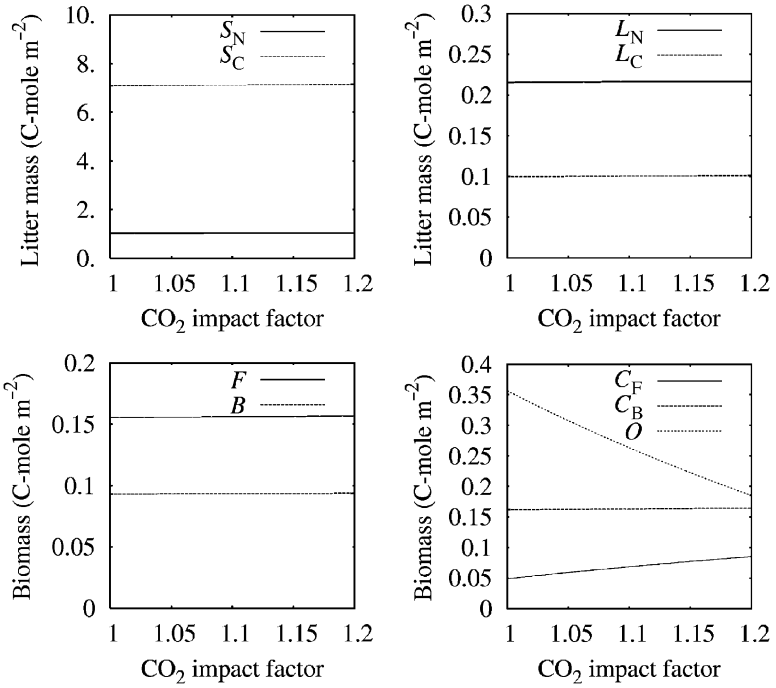

Fig. 3 Masses of organic materials and biota in the top litter layer. The impact factor of CO_2 is on the horizontal axis. Here, a factor 1 refers to ambient conditions, while a factor 1.2 corresponds to a 1.2-fold less contribution of labile nitrogen to the fresh litter, caused by elevated CO_2 levels.

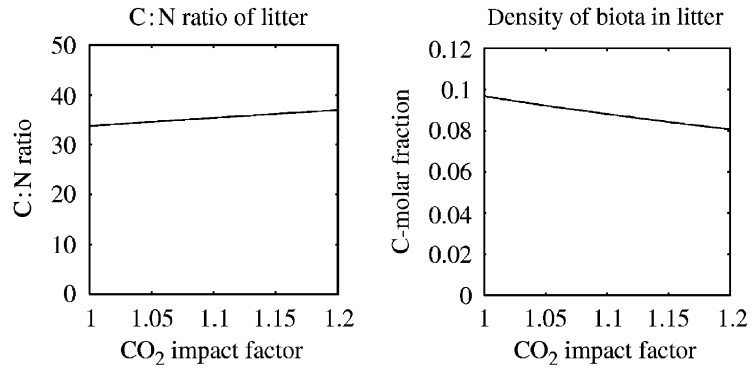

Fig. 4 Characteristics of the top litter layer as a function of elevated CO_2. The determination of the molar C:N ratio considers both abiotic litter constituents and soil biota. The density of biota in the litter is defined as the lumped biotic biomasses in C-moles, divided by the lumped litter masses.

generally have a high nitrogen content. As can be observed from Fig. 3 (upper panel) the mass and C:N of the abiotic litter pack itself are hardly affected by CO_2 elevation. In conclusion, the effects of CO_2 elevation-induced changes in fresh litter composition only become apparent in the highest trophic levels.

UV-B enhancement

Higher plants grown under elevated UV-B generally have higher phenolic content (Rozema, 1999, 2000; Lavola *et al.*, 2003) and thicker cuticles (Manetas *et al.*, 1977; Solovchenko & Merzlyak, 2003). In modeling terms, this implies that UV-B enhancement results in higher fractions of recalcitrant litters (θ_{S_N}, θ_{S_C}) and lower fractions of labile litters (θ_{L_N}, θ_{L_C}). We implemented UV-B enhancement by taking a proportional increase in the fractions θ_{S_N} and θ_{S_C} and a simultaneous proportional decrease in fractions θ_{L_N} and θ_{L_C}.

On the horizontal axis of the diagrams (Figs 5 and 6) is the UV-B impact factor. Here, a value of 1 corresponds to the ambient fresh litter composition as

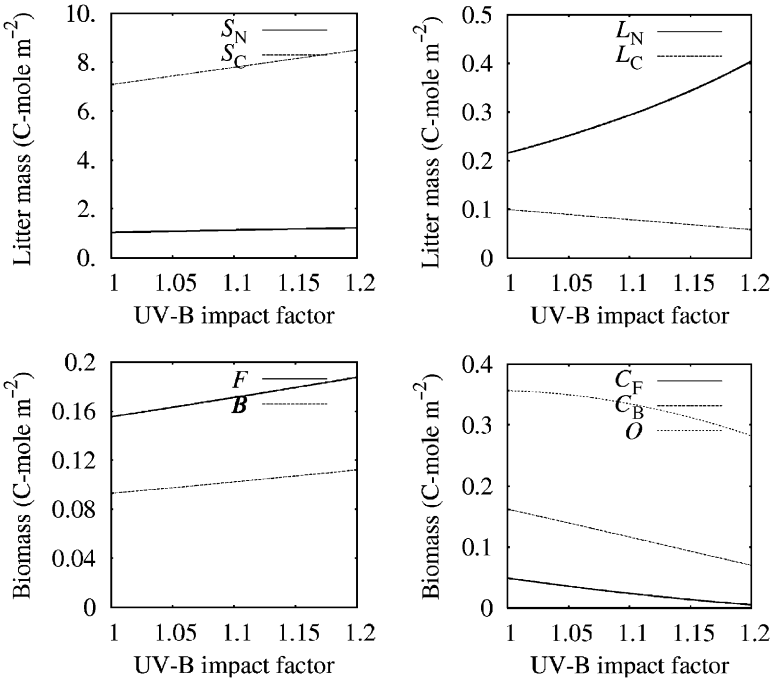

Fig. 5 Masses of organic materials and biota in the top litter layer. The impact factor of UV-B is on the horizontal axis. Here, a factor 1 refers to ambient conditions, while a factor 1.2 corresponds to a 1.2-fold contribution of refractory constituents in the fresh litter, caused by UV-B enhancement.

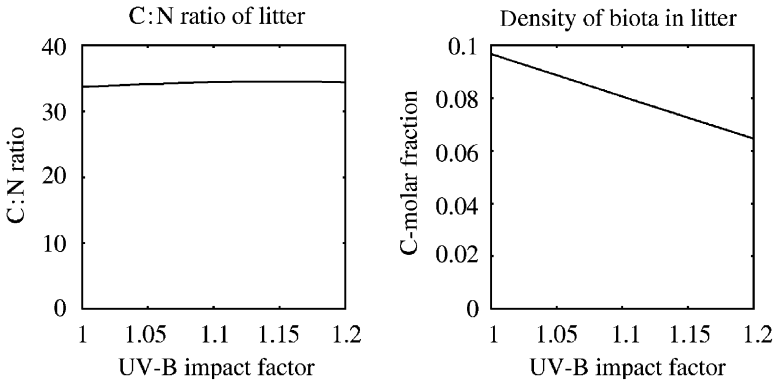

Fig. 6 Characteristics of the top litter layer as a function of enhanced UV-B. The determination of the molar C : N ratio considers both abiotic litter constituents and soil biota. The density of biota in the litter is defined as the lumped biotic biomasses in C-moles, divided by the lumped litter masses.

given in Table 3. An increment in this factor corresponds to a proportional increment in the stable litter fractions (θ_{S_N}, θ_{S_C}) as compared with ambient conditions, so that an UV-B impact factor of 1.2 corresponds to a 120% increase in stable components in the fresh litter.

Contrary to the consequences of elevated CO_2, UV-B enhancement has pronounced effects on the composition of the top litter layer (Fig. 5, upper panel). The model predicts that UV-B enhancement results in a thicker resident litter pack. This is mainly caused by the accumulation of refractory litter components, although labile nitrogenous litter also accumulates. The model predicts a decline in labile carbonous substances with increasing levels of UV-B.

The size of the microbial populations increases with increasing UV-B, however, their density in the litter remains approximately constant, as the litter mass increases in a proportional manner (Fig. 5). The graph to the right demonstrates that the mass and density of all soil mesofauna is suppressed under enhanced UV-B. Hence, the productivity of the decomposer food web is

lower under elevated UV-B. As both fungi and bacteria utilize labile organic substances, this substrate type may be regarded as the system's primary resource. UV-B enhancement causes a decrease in labile carbonous substrates, which corresponds to an effective decline in energy availability to both bacteria and fungi. This limits their growth capacity, and reduces the potential for transforming organic nitrogen, which therefore accumulates. This result demonstrates that UV-B enhancement may shift the decomposition activity from nitrogen to energy limitation. The exploitation ecosystem hypothesis (Oksanen *et al*., 1981; Oksanen & Oksanen, 2000) predicts a correlation between resource availability and herbivore density, and this might also be what happens in the model: a reduction in energy availability reduces the abundance of higher trophic niches in the litter, while leaving densities of the microflora intact.

Although UV-B imposes an evident shift in litter composition (cf. Fig. 5), the C : N ratio remains virtually constant over the range of UV-B impacts analyzed (Fig. 6). Here, the model shows that a summary statistic such as the litter C : N ratio may not always be sufficient for the assessment of its nutritional quality to microbiota. This reasoning is in agreement with the results of Berg *et al*. (2001), who calculated net N immobilization by enchytraeids, which is impossible for heterotrophs, when food quality was expressed in terms of C : N.

Eutrophication with nitrogen

Enhanced nitrogen deposition elevates the nitrogen content of plants. Concentrations of both labile (Baron *et al*., 2000) and stable nitrogen-rich leaf components (Penuelas & Filella, 2001) become higher with increased nitrogen provisions. We model the effect of eutrophication on litterfall composition by assuming a proportional increase of nitrogenous litter fractions (θ_{S_N}, θ_{L_N}). Simultaneously, the fractions of nitrogen-deficient litter fractions (θ_{S_C}, θ_{L_C})are lowered.

The eutrophication factor is on the horizontal axis of the associated diagrams (Figs 7 and 8), and a value of 1 corresponds to ambient conditions. A factor of 1.2 raises the litterfall content of labile and refractory nitrogenous material to 120% of the ambient content (i.e. $\theta_{S_N} = 0.24$, $\theta_{L_N} = 0.06$). Increasing the provision of nitrogen strongly affects litter quality for decomposers and it has been studied extensively in models by Ågren *et al*. (2001), Franklin *et al*. (2003).

The model predicts that eutrophication reduces the carbonous content of the litter, while both stable and labile forms of organic nitrogen increase. The model furthermore predicts that eutrophication has no pronounced effects on total litter accumulation. This results contrasts with the findings of Berg & Meentemeyer (2002). However, our model does not take into account potential toxicity (Hogervorst *et al*., 2003) and retardation

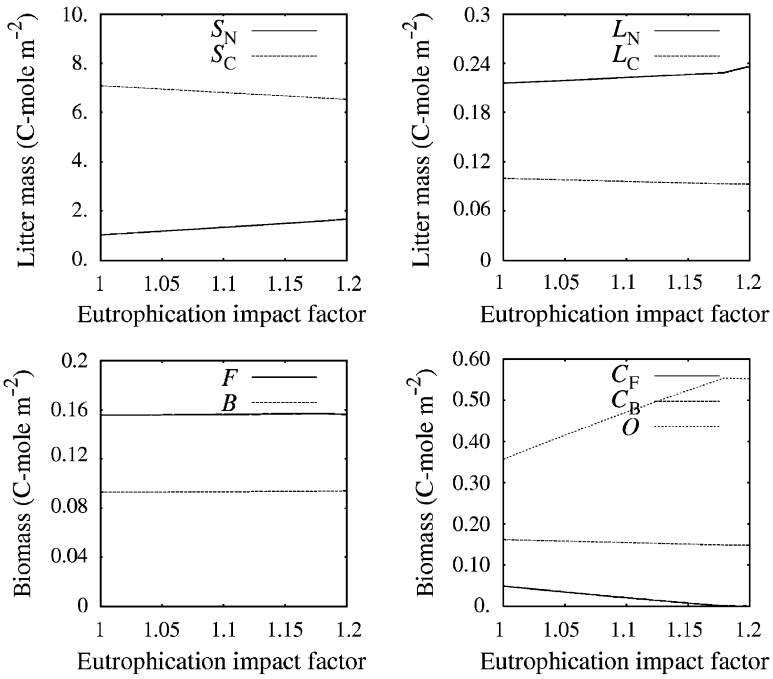

Fig. 7 Masses of organic materials and biota in the top litter layer. The eutrophication impact factor is on the horizontal axis. Here, a factor 1 refers to ambient conditions, while a factor 1.2 corresponds to a 1.2-fold contribution of nitrogenous constituents in the fresh litter, caused by eutrophication.

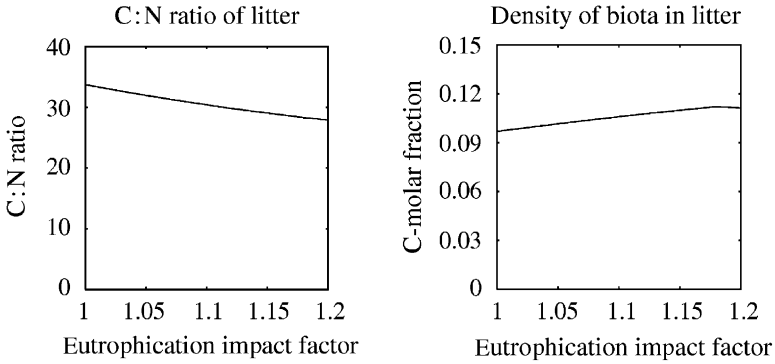

Fig. 8 Characteristics of the top litter layer as a function of nitrogen enrichment. The determination of the molar C : N ratio considers both abiotic litter constituents and soil biota. The density of biota in the litter is defined as the lumped biotic biomasses in C-moles, divided by the lumped litter masses.

of ligninolytic enzymes under high nitrogen levels (Leatham & Kirk, 1983; Reid, 1991; Lodge, 2001), both of which have been demonstrated in natural systems. Furthermore, we have not assumed net increased rates of litterfall, as is known to happen in natural systems (Franklin *et al*., 2003).

The microbial activity is not affected by the nitrogen enrichment (Fig. 7). Effects are most demonstrative at the highest trophic groups, which again suggest strong bottom-up relationships in the ecosystem. In the model, the fungivore population does not survive high nitrogen levels (factor ≥ 1.17). This finding contrasts with field observations. However, explanations may be found in that the model takes into account neither changes in species composition within the functional group, nor changes in trophic structure because of changes in environmental conditions (for instance, collemboles may change their behavior and become omnivorous when fungal nutrition does not suffice). Still, the model predicts that among mesofauna, fungivores should be especially sensitive to nitrogen enrichment, a modeling result that may be tested empirically. Bacterivores are slightly hampered under nitrogen enrichment, but the omnivore population will grow larger. Effectively, the biological productivity of the web increases as the omnivore's density increase exceeds the decrease in the other mesofaunal densities, and microbiota are hardly affected. The omnivore's success may be caused by an improved quality of ingested litter by the omnivores. As the omnivore population grows larger with the improving nutritional quality of litterfall, it exerts a higher competitive pressure on the bacterivore and fungivore populations. This may cause the extinction of fungivores at high levels of nitrogen enrichment. Furthermore, this may explain why the incline in population size (Fig. 7, bottom right graph) halts at the point where fungivores are ousted.

In the model, eutrophication reduces the C : N ratio of the top litter layer, which is known to happen in natural systems (Parker *et al*., 2001), and the biomass density becomes larger (Fig. 8). The latter can be attributed to the increased growth of the omnivore population. However, the fungivore population may vanish under severe eutrophication, so that eutrophication may cause the system to become structurally unstable, an effect that is not observed when effects of CO_2 enhancement and elevated UV-B irradiation are implemented.

Discussion and conclusions

Qualitative effects on food web characteristics

The model presented in this paper bases on field observations of litter mass and composition, biomass of functional groups, and food web architecture. It predicts biologically feasible steady-state quantities of litter and biomasses for the particular food web components. In all simulations, stable fractions dominate the mass of the top litter layer, while the availability of labile compounds is much lower. The masses of microbiota and mesobiota are of the same order of magnitude, but enchytraeids generally constitute the larger part of biomass in the litter, which largely corresponds to field situations (Persson & Lohm, 1977; Petersen & Luxton, 1982). However, a word of caution is required here. Model predictions of biomasses and densities are sensitive to changes in interaction parameters associated to the different trophic guilds. To our knowledge, there is no available data on these interactions parameters, so we conjectured them from existing ideas of soil dynamics (cf. model setup and assumptions).

The ecosystem modeled in this study is large as compared with most mechanistically oriented models (Vollenweider, 1985; McCann & Hastings, 1997; Kooi

et al., 2004). The studies of May (1972) and Pimm & Lawton (1978) showed that when food webs are modeled with Lotka–Volterra-type trophic interactions, they tend to become more unstable as they become larger. On the other hand, models of simple food chains where the trophic interaction is modeled by the Holling type-II functional response (for instance the Rosenzweig–MacArthur model; Rosenzweig, 1971; Kuznetsov & Rinaldi, 1996) for bi- or tritrophic food chains, also predict complex behavior, but only when nutrient input is large. Therefore, complex dynamic behavior predicted by our model cannot be excluded *a priori*.

Recent investigations have shown that large systems may be stable, provided that the food web contains a number of weak interactions among trophic niches (McCann *et al*., 1998; Polis, 1998; McCann, 2000). Our system qualifies as such a food web. Firstly, besides the competitive interactions between fungi and bacteria, there exists a weak link as fungi release labile compounds from refractory litters and this also indirectly supplies bacteria with resources. A second weak interaction involves the enchytraeids, which are omnivores spreading their control over other trophic niches. Omnivory has been theoretically shown to be a stabilizing factor in food webs (Mylius *et al*., 2001; Kooi *et al*., 2002; Kuijper *et al*., 2003).

The model yields equilibrium dynamics in all of the scenarios; there are no oscillatory or chaotic dynamics, nor does the model exert multiple stable states in any part of the tested parameter space. This result suggests that the model's weak trophic interactions may have contributed to the stability of the food web. However, complex dynamics may be expected in situations where limiting resources are abundant, exclusively (Rosenzweig, 1971). The status of nutritional value in our model cannot easily be compared with that in more traditional models (e.g. chemostat models). In our model, the organisms themselves determine the absolute volume of the medium. Hence, the uptake of nutrients depends on the relative contribution of utilizable resources in the litter matrix (i.e. m_X instead of X), whereas the size of the litter pack, or the absolute availability of resources, does not affect the system's dynamics. Changes in the composition of incoming litter may not be as drastic as changes in nutritional concentrations in, for instance, chemostat systems, and this may limit the potential for the 'paradox of enrichment' in the system under examination. An unpublished analysis suggests that this model property may contribute to the exclusive occurrence of steady states. We conclude that both the omnipresence of weak interactions and the modeling of nutrient supply, pertinent to the current model, may contribute to the model's stability.

The model consists of a large number of parameters, of which the interaction parameters have not been measured in the field. It is impractical, and beyond the scope of the study, to perform a full bifurcation analysis of the system, including the effects of changes in all parameter values on the dynamics of the system. Therefore, it is at this stage unknown whether complex dynamics can occur when interaction parameters, such as searching or maximum degradation rates, are varied simultaneously. Unpublished analyses, however, suggested that the trends, as shown in this work are robust with respect to changes in single interaction parameters.

We divided the food web into a limited number of functional groups. In the model, this number can easily be expanded by, for instance, making a distinction between fungivorous prostigmata, which feed exclusively on fungi, and fungivorous collembola, which may consume quantities of litter in addition to fungi. This expansion comes at the cost of extra model variables and parameters, and requires the mathematical implementation of differences in physiology between the splitted populations. The expansion also comes with the establishment of additional trophic links. If among them weak links are common, and if weak links are at least partially responsible for the stability as found in our model, the resulting extended model should, in theory, also behave stable. We hypothesize that if weak interactions indeed stabilize ecosystem dynamics, increasingly realistic models of natural ecosystems should tend to become more stable.

Effects of global change on trophic groups

The model predicts that elevated CO_2 and eutrophication do not result in thicker litter packs, although eutrophication alters the chemical quality of litter. In the model, UV-B enhancement causes litter to become more persistent, resulting in an increased accumulation of litter. None of the scenarios, however, affect the density of microbiota in the soil. In contrast, the model predicts pronounced effects on the higher trophic niches. Trophic cascade theory predicts reciprocal effects on the abundance of adjacent trophic niches (Pace *et al*., 1999). This suggests that decreasing grazer population densities should coincide with increasing microbial population sizes and lower litter masses. In correspondence to soil food web experiments of (Mikola & Setälä, 1998), our model does not predict such trophic cascade effects to occur. The absence of trophic cascades can be explained by the general structure of the model, where all trophic levels are occupied by more than one species (Abrams, 1993). Both the competitive interactions between the enchytraeids

on the one hand, and bacterivores and fungivores on the other, may reduce the potential for trophic cascades. Moreover, omnivorous activity has been empirically shown to reduce the potential for trophic cascades in soil food webs (Mikola & Setälä, 1999), which is in line with the results presented.

In the model omnivores and fungivores are most demonstratively affected by global change. Although the bacterivore population is predicted to decline with increasing UV-B irradiation, this trophic guild is hardly affected by other aspects of global change. Elevated CO_2 and UV-B enhancement affect omnivores and fungivores in an adverse manner. This suggests that the competition ability of higher trophic guilds is affected by the quality of litter. Omnivores tend to benefit when litters of higher nutritional quality (i.e. higher doses of labile litters), are provided to the system, while fungivores profit from larger contributions of refractory material. Whether this theoretical finding is valid in natural systems could serve as a hypothesis for an experimental test.

Formulating testable hypotheses using mechanistic models

Many traditional dynamic food web models focus on effects of trophic structures on stability properties of food webs. Although these models have been subject to debate because of their, sometimes extreme, simplifications of biological interactions, they have revealed some valuable patterns in ecosystem dynamics. Among these patterns are the 'paradox of enrichment', where it can be shown that food chains may become unstable because of nutrient enrichment (Rosenzweig, 1971; Fussman *et al*., 2000), and the potential for multiple stable states, where small perturbations in environmental circumstances can have dramatic irreversible effects on the structure and functioning of an ecosystem (Kuznetsov, 1998; Scheffer *et al*., 2001; Scheffer & Carpenter, 2003). Unfortunately, traditional models usually lack the required detail to answer situation specific questions that experimental ecologists are faced with. Historically, this has made cooperations between empiricists and theoreticians rare. However, improved insight in the nature of ecological interactions, in combination with faster methods of solving the mathematical problems involved opens new ground for such collaborations.

The model presented in this study bases mainly on qualitative knowledge of decomposition in litter strata. It has to be noted that the model is simplistic in many respects. For instance, we used a number of parameters of which realistic values have, to our knowledge, hardly been established in laboratory experiments (e.g. searching rates and substrate affinities). In addition, we simplified aspects of biotic physiology. Metabolic maintenance or death were merely modeled implicitly in the litter loss rate D. Moreover, we have assumed structural homeostasis for all trophic levels, allowing us to use a model with a limited number of differential equations. We used a simple model as a starting point, while physiologically based models allowing for more biological detail and consistency are available (i.e. DEB theory; Kooijman, 2000, 2001). We need to make long-term predictions based on short-term experiments. Descriptive models cannot be used for that purpose, and we need to ultimately involve more physiology in the models used. Our goal is to bring forward a modeling methodology that may be used for such long-term predictions step by step.

The model yields a series of experimentally testable hypotheses. Examples are: fungivores are more sensitive to changes in environmental conditions than bacterivores, omnivores limit the potential for trophic cascades, and, natural ecosystems tend to equilibria because of the presence of weak trophic links. Furthermore, the model effectively uncloaks a number of largely unknown parameters in the study of decomposer food webs. We conclude that mechanistic models are helpful in directing experimental research, and this emphasizes that collaborations between empiricists and theoreticians are essential for understanding the structure and long-term functioning of ecosystems.

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References

Abrams PA (1993) Effect of increased productivity on the abundances of trophic levels. *American Naturalist*, **141**, 351–371.

Adler E (1977) Lignin chemistry – past, present and future. *Wood Science and Technology*, **11**, 169–218.

Ågren GI, Bosatta E, Magill AH (2001) Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. *Oecologia*, **128**, 94–98.

Bakker ES, Olff H, Boekhoff M *et al*. (2004) Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia*, **138**, 91–101.

Baron JA, Rueth HM, Wolfe AM *et al*. (2000) Ecosystems responses to nitrogen deposition in the Colorado Front Range. *Ecosystems*, **3**, 352–368.

Berg B (2000) Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management*, **133**, 13–22.

Berg B, Berg MP, Bottner P *et al*. (1993) Litter mass loss rates in pine forest of Europe and Eastern United States: some relationships with climate and litter quality. *Biogeochemistry*, **20**, 127–159.

Berg B, Meentemeyer V (2002) Litter quality in a north European transect versus carbon storage potential. *Plant and Soil*, **242**, 83–92.

Berg MP (1997) *Decomposition, nutrient flow and food web dynamics in a stratified pine forest soil*. PhD thesis, Vrije Universiteit, Amsterdam.

Berg MP, De Ruiter P, Didden WAM *et al*. (2001) Community food web, decomposition and nitrogen mineralisation in a stratified Scots pine forest soil. *Oikos*, **94**, 130–142.

Berg MP, Kniese JP, Zoomer HR *et al*. (1997) Long-term decomposition of a nitrogen-saturated Scots pine forest soil. *Forest Ecology and Management*, **107**, 159–172.

Berg MP, Verhoef HA (1997) Ecological characteristics of a nitrogen-saturated coniferous forest in The Netherlands. *Biology and Fertility of Soils*, **26**, 258–267.

Boersma M, Kreutzer C (2002) Life at the edge: is food quality really of minor importance at low quantities. *Ecology*, **83**, 2552–2561.

Bosatta A, Ågren GI (1999) Soil organic matter quality interpreted thermodynamically. *Soil Biology and Biochemistry*, **31**, 1889–1891.

Calow P (1977) Conversion efficiencies in heterotrophic organisms. *Biological Reviews*, **52**, 385–409.

Cotrufo MF, Ineson P (1993) Effects of enhanced atmospheric CO_2 and nutrient supply on the quality and subsequent decomposition of fine roots of *Betula pendula* Roth and *Picea sitchensis* (Bong) Carr. *Plant and Soil*, **170**, 267–277.

Cotrufo MF, Ineson P, Rowland AP (1994) Decomposition of tree leaf litters grown under elevated CO_2-effect of litter quality. *Plant and Soil*, **163**, 121–130.

Cotrufo MF, Ineson P, Scott A (1998) Elevated CO_2 reduces the nitrogen concentration of plant tissues. *Global Change Biology*, **4**, 43–54.

Cox PM, Betts RA, Jones CD *et al*. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–187.

Cross WF, Benstead JP, Rosemond AD *et al*. (2003) Consumer resource stoichiometry in detritus-based streams. *Ecology Letters*, **6**, 721–732.

Didden WAM (1993) Ecology of terrestrial enchytraeidae. *Pedobiologia*, **37**, 2–29.

Didden WAM, Rombke J (2001) Enchytraeids as indicator organisms for chemical stress in terrestrial ecosystems. *Ecotoxicology and Environmental Safety*, **50**, 25–43.

Droop MR (1983) 25 years of algal growth kinetics. *Botanica Marina*, **26**, 99–112.

Filser J (2002) The role of collembola in carbon and nitrogen cycling soil. *Pedobiologia*, **46**, 234–245.

Fox CA (2003) Characterizing soil biota in Canadian agroecosystems: state of knowledge in relation to soil organic matter. *Canadian Journal of Soil Science*, **83**, 245–257.

Franklin O, Hogberg P, Ekblad A *et al*. (2003) Pine forest floor carbon accumulation in response to N and PK additions: Bomb ^{14}C modelling and respiration studies. *Ecosystems*, **6**, 644–658.

Fussman GF, Ellner SP, Shertzer KW *et al*. (2000) Crossing the Hopf bifurcation in a live predator–prey system. *Science*, **290**, 1358–1360.

Gallardo A, Merino J (1993) Leaf decomposition in 2 Mediterranean ecosystems of Southwest Spain – influence of substrate quality. *Ecology*, **74**, 152–161.

Gillet NP, Zwiers FW, Weaver AJ *et al*. (2003) Detection of human influence on sea-level pressure. *Nature*, **422**, 292–294.

Heinsdorf D (1993) The role of nitrogen in declining Scots pine forest (*Pinus sylvestris*) in the lowland of East-Germany. *Water Air and Soil Pollution*, **69**, 21–35.

Hogervorst RF, Dijkhuis MAJ, Van Der Schaar MA *et al*. (2003) Indications for the tracking of elevated nitrogen levels through the fungal route in a soil food web. *Environmental pollution*, **126**, 257–266.

King JA, Pregitzer KS, Zak DR *et al*. (2001) Correlation and litter chemistry of sugar maple, *Acer saccharum*, as effected by elevated CO_2 and varying N availability, and effects on decomposition. *Oikos*, **94**, 403–416.

Kinnunen H, Huttunen S, Laakso K (2001) UV-B absorbing compounds and waxes in Scots pine needles during a third growing season of supplemental UV-B. *Environmental Pollution*, **112**, 215–220.

Kirk TK, Farell RL (1987) Enzymatic 'combustion': the microbial degradation of lignin. *Annual Review of Microbiology*, **4**, 465–505.

Kirk TK, Fenn P (1982) Formation and action of the ligninolytic system in basidiomycetes. In: *Decomposer Basidiomycetes: Their Biology and Ecology* (eds Frankland JC, Hedger JN, Swift MJ), pp. 67–90. Cambridge University Press, Cambridge.

Kooi BW, Kuijper LDJ, Boer MP *et al*. (2002) Numerical bifurcation analysis of a tri-trophic food web with omnivory. *Mathematical Biosciences*, **177**, 201–228.

Kooi BW, Kuijper LDJ, Kooijman SALM (2004) Consequences of symbiosis for food web dynamics, **49**, 227–271.

Kooijman SALM (1998) The synthesizing unit as a model for the stoichiometric fusion and branching of metabolic fluxes. *Biophysical Chemistry*, **73**, 179–188.

Kooijman SALM (2000) *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press, Cambridge.

Kooijman SALM (2001) Quantitative aspects of metabolic organization; a discussion of concepts. *Philosophical Transactions of the Royal Society B*, **356**, 331–349.

Kuijper LDJ, Anderson TR, Kooijman SALM (2004a) C and N gross growth efficiencies of copepod egg production studied using a dynamic energy budget model. *Journal of Plankton Research*, **26**, 213–226.

Kuijper LDJ, Kooi BW, Anderson TR *et al*. (2004b) Stoichiometry and food chain dynamics. *Theoretical Population Biology*, **66**, 323–339.

Kuijper LDJ, Kooi BW, Zonneveld C *et al*. (2003) Omnivory and food web dynamics. *Ecological Modelling*, **163**, 19–32.

Kuznetsov YA (1998) *Elements of Applied Bifurcation Theory*. Springer Verlag, Berlin.

Kuznetsov YA, Rinaldi S (1996) Remarks on food chain dynamics. *Mathematical Biosciences*, **124**, 1–33.

Laakso K, Sullivan JH, Huttunen S (2000) The effects of UV-B radiation on epidermal anatomy in loblolly pine (*Pinus taeda* L.) and Scots pine (*Pinus sylvestris* L.). *Plant Cell and Environment*, **23**, 461–472.

Lavola A, Aphalo PJ, Lahti M *et al*. (2003) Nutrient availability and the effect of increasing UV-B radiation on secondary plant compounds in Scots pine. *Environmental and Experimental Botany*, **49**, 49–60.

Leatham GF, Kirk TK (1983) Regulation of lignolytic activity by nutrient nitrogen in white-rot Basidiomycetes. *FEMS Microbiology Letters*, **16**, 65–67.

Lodge DJ (2001) Implications for nitrogen additions from air pollutants on litter decay and ecosystem processes. *Mycological Research*, **105**, 898–899.

Manetas Y, Petropoulou Y, Stamatakis K *et al*. (1977) Benificial effects of enhanced UV-B radiation under field conditions: improvement of needle water relations and survival capacity of *Pinus pinea* L. seedlings during the dry Mediterranean summer. *Plant Ecology*, **128**, 100–108.

May RM (1972) Will a large complex system be stable? *Nature*, **238**, 413–414.

McCann KS (2000) The diversity-stability debate. *Nature*, **405**, 228–233.

McCann KS, Hastings A (1997) Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society of London series B–Biological Sciences*, **264**, 1249–1254.

McCann KS, Hastings A, Huxel GR (1998) Weak trophic interactions and the balance of nature. *Nature*, **395**, 794–798.

Mikola J, Setälä H (1998) No evidence of trophic cascades in an experimental microbial-based soil food web. *Ecology*, **79**, 153–164.

Mikola J, Setälä H (1999) Interplay of omnivory, energy channels and C availability in a microbial based soil food web. *Biology and Fertility of Soils*, **28**, 212–218.

Minderman G (1968) Addition, decomposition and accumulation of organic matter in forests. *Journal of Ecology*, **56**, 355–362.

Moore JC, McCann KS, Setälä H *et al*. (2003) Top down is bottom-up: does predation in the rhizosphere regulate aboveground dynamics? *Ecology*, **84**, 846–857.

Moore JC, Trofimow JA, Taylor B *et al*. (1999) Litter decomposition rates in Canadian forests. *Global Change Biology*, **5**, 75–82.

Moore JC, Walter DE, Hunt H (1988) Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. *Annual Review of Entomology*, **33**, 419–439.

Muller EB, Nisbet RM, Kooijman SALM *et al*. (2001) Stoichiometric food quality and herbivore dynamics. *Ecology Letters*, **4**, 519–529.

Mylius SD, Klumpers K, De Roos AM, Persson L (2001) Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *American Naturalist*, **158**, 259–276.

Nannipieri P, Ascher J, Ceccherini MT *et al*. (2003) Microbial diversity and soil functions. *European Journal of Soil Science*, **54**, 655–670.

Norby RJ, Cotrufo MF (1998) Global change – a question of litter quality. *Nature*, **396**, 17–18.

Norby RJ, Cotrufo MF, Ineson P *et al*. (2001) Elevated CO_2, litter chemistry and decomposition: a synthesis. *Oecologie*, **127**, 153–165.

Oksanen L, Fretwell SD, Arruda A *et al*. (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240–261.

Oksanen L, Oksanen T (2000) The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist*, **155**, 703–723.

Pace ML, Cole JJ, Carpenter SR *et al*. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14**, 483–488.

Parker JL, Fernandez IJ, Rustad LE *et al*. (2001) Effects of nitrogen enrichment, wildfire and harvesting on forest-soil carbon and nitrogen. *Soil Science Society of America Journal*, **65**, 1248–1255.

Penuelas J, Filella I (2001) Herbaria century record of increasing eutrophication in Spanish terrestrial ecosystems. *Global Change Biology*, **7**, 427–433.

Persson T, Lohm U (1977) Energetical significance of the annalids and arthropods in a Swedish grassland soil. *Ecological Bulletin*, **23**, 1–211.

Petersen H, Luxton M (1982) A comparative analysis of soil fauna population and their role in decomposition processes. *Oikos*, **39**, 287–388.

Pimm SL, Lawton JH (1978) On feeding on more than one trophic level. *Nature*, **275**, 542–544.

Polis GA (1998) Stability is woven by complex webs. *Nature*, **395**, 744–745.

Prietzel J, Kolb E, Rehfuss KE (1997) Long-term study of formerly litter-rakes Scots pine ecosystems in NE Bavaria: recent changes in soil chemical properties and stand nutrition. *Forstwissenschaftliches Centralblatt*, **116**, 269–290.

Reid ID (1991) Nutritional regulation of synthetic lignin (DHP) degradation by Phlebia (Merulius) tremellosa: effects of nitrogen. *Canadian Journal of Botany*, **69**, 156–160.

Rosenzweig ML (1971) Paradox of enrichment: the destabilization of exploitation ecosystems in ecological time. *Science*, **171**, 385–287.

Rozema J (1999) UV-B radiation and terrestrial ecosystems: processes, structure and feedback loops. In: *Stratospheric Ozone Depletion, the Effects of Enhanced UV-B Radiation on Terrestrial Ecosystems* (ed. Rozema J), pp. chapter 6. Backhuys Publishers, Leiden, the Netherlands.

Rozema J (2000) Effects of solar UV-B radiation on terrestrial biota. In: *Issues in Environmental Science and Technology* No. 14 (eds Hester RE, Harrison RM), pp. 85–105. Royal Society of Chemistry, Cambridge, UK.

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*, **18**, 648–655.

Scheffer M, Carpenter SR, Foley JA *et al*. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.

Schröter D, Wolters V, De Ruiter P (2003) C and N mineralisation in the decomposer food webs of a European forest transect. *Oikos*, **192**, 294–308.

Smith VC, Bradford MA (2003) Litter quality impacts on grassland litter decomposition are dependent on soil fauna across time. *Applied Soil Ecology*, **24**, 197–203.

Solovchenko A, Merzlyak M (2003) Optical properties and contribution of cuticle to UV protection in plants: experiments with apple fruit. *Photochemical and Photobiological Sciences*, **2**, 861–866.

Stouffer RJ, Manabe S, Vinnikov KY (1994) Model assessment of the role of natural variability in recent global warming. *Nature*, **367**, 6334–6336.

Vollenweider RA (1985) Elemental and biochemical composition of plankton biomass; some comments and explorations. *Archives of Hydrobiology*, **105**, 11–29.

Walther GR, Post E, Convey P *et al*. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wollecke J, Munzenberger B, Huttl RF (1999) Some effects of N on ectomycorrhizal diversity of Scots pine (*Pinus sylvestris* L.) in northeastern Germany. *Water Air and Soil Pollution*, **116**, 135–140.

Appendix A

The complementary SU

We model production fluxes involved in biochemical transformations using a complementary SU, as described by Kooijman (1998). An SU is a mathematical model which translates substrate fluxes into to production rates. The method is very similar to enzyme kinetics. The complementary SU has binding sites for all required substrates. Once the SU is saturated with the right portion of all substrates, it enters the production phase. Figure 2 gives a graphic representation of this process. For a transformation involving two essential substrates, the general mathematical formulation is

$$j_{\text{product}} = \left(\frac{1}{j_{\max}} + \frac{y_{j_1,\text{product}}}{j_1} + \frac{y_{j_2,\text{product}}}{j_2} - \frac{1}{y_{j_1,\text{product}}/j_1 + y_{j_2,\text{product}}/j_2} \right)^{-1}. \quad \text{(A1)}$$

Here, j_{product} is a biomass specific product flux, j_1 and j_2 are the substrate arrival fluxes and $y_{j_1,\text{product}}$and $y_{j_2,\text{product}}$are the relative amount of substrate units required for the synthesis of one unit of product (i.e. the stoichiometric couplers). Parameter $j_{\max}$ is the maximum attainable production flux (i.e. the production rate when the substrate fluxes are infinitely large). In the model fluxes may be metabolites used for growth, or substrates which can be taken up from the litter pack. Biomass specific fluxes, as used in the model, are fluxes, consistently scaled to units of biomass carbon of the species involved.

Degradation of refractory litter

Fungal exogenic enzymes excavate labile materials from persistent litters. Their activity is described with the Michaelis–Menten equation (type-II functional response, which works similar to an SU requiring only one substrate), so that biomass specific production of labile materials from recalcitrant litters amounts to

$$j_{L_N,D} = \left(\frac{1}{j_{L_N,Dm}} + \frac{7}{a^F_{S_N} m_{S_N}} \right)^{-1}, \qquad j_{L_C,D} = \left(\frac{1}{j_{L_C,Dm}} + \frac{5}{a^F_{S_C} m_{S_C}} \right)^{-1}, \quad \text{(A2)}$$

in which $j_{L_N,D}$and $j_{L_C,D}$are the biomass specific fluxes of released labile nitrogen and carbon, respectively, $j_{L_N,Dm}$and $j_{L_C,Dm}$are the associated maximum production rates and parameters $a^F_{S_N}$and $a^F_{S_C}$map the fractional density of the respective refractory litters in the soil to a biomass specific flux that can essentially be used by the fungal enzymes. The numbers 7 and 5 are the stoichiometric coupling coefficients, corresponding to transformation 1 in Table 2. The variables $m_{S_N}$and $m_{S_C}$are the fractional contributions of refractory nitrogen and carbon to the bulk litter mass. Densities m_X are defined as

$$m_X = \frac{X}{S_N + S_C + L_N + L_C}, \quad \text{(A3)}$$

so that $m_{S_N}, m_{S_C}, m_{L_N}, m_{L_C}$have a value between 0 and 1. Densities of biota, m_B, m_F, referring to fractional densities of bacteria and fungi, are also scaled to the mass of the litter pack. Expressing substrates and biomasses in terms of fractional contributions to the mass of a habitat is unconventional. However, this step is required to formulate a model according to the law of mass action, as organisms experience densities of substrates and other organisms in the litter matrix, and in the dynamic model the size of this matrix is variable. The parameters a comprise aspects of organismal affinities for particular resources present in the top litter layer, and map the dimensionless fractions between 0 and 1 to biomass specific fluxes, as experienced by the soil organisms. In turn, biomass specific fluxes can be multiplied by the biomass of the species involved to obtain net mass fluxes, occurring in the top litter layer.

Fungal growth

In addition to direct uptake of available labile components, fungi may utilize labile material released from the persistent matrix. We employ the complementary SU from Eqn (A1), and rewrite them to describe the fungal uptake process. The biomass specific fungal

production is

$$j_{F,G} = \left(\frac{1}{j_{F,Gm}} + \frac{26}{7j^F_{L_C,I}} + \frac{2}{7j^F_{L_N,I}} - \frac{1}{(7/26)j^F_{L_C,I} + (7/2)j^F_{L_N,I}} \right)^{-1}, \tag{A4}$$

in which the arrival fluxes $j^F_{L_C,I}$ and $j^F_{L_N,I}$ are the combined direct and indirect uptake fluxes

$$j^F_{L_C,I} = a^F_{L_C} m_{L_C} + j_{L_C,D}, \tag{A5a}$$

$$j^F_{L_N,I} = a^F_{L_N} m_{L_N} + j_{L_N,D}, \tag{A5b}$$

where the first term of the right-hand side is the part of labile components originally present in the top litter layer, whereas the second term is the part excavated from the refractory litter material, as calculated in Eqn (A2). The numbers 2, 7 and 26 in Eqn (A4) are the stoichiometric couplers for the conversion of labile material into fungal biomass according to transformation 2 in Table 2.

Bacterial growth

Bacteria can only use the labile litter constituents L_N and L_C. These are merged by the bacterial complementary SU. The biomass specific growth rate of bacteria is

$$j_{B,G} = \left(\frac{1}{j_{B,Gm}} + \frac{17}{7a^B_{L_C} m_{L_C}} + \frac{4}{7a^B_{L_N} m_{L_N}} - \frac{1}{(7/17)a^B_{L_C} m_{L_C} + (7/4)a^B_{L_N} m_{L_N}} \right)^{-1}. \tag{A6}$$

The stoichiometric coefficients are according to transformations 3 in Table 2.

Fungivores and bacterivores

Type-II functional responses model the specific growth rates of the fungivore and bacterivore populations. The specific growth rates are

$$j_{C_F,G} = \left(\frac{1}{j_{C_F,Gm}} + \frac{20}{3a^{C_F}_F m_F} \right)^{-1}, \tag{A7a}$$

$$j_{C_B,G} = \left(\frac{1}{j_{C_B,Gm}} + \frac{20}{3a^{C_B}_B m_B} \right)^{-1}, \tag{A7b}$$

in which the stoichiometric numbers correct for the yield of the grazers on their particular resources. We recall that m_B and m_F are defined in Eqn (A3). The fungivores and bacterivores have to search for food and, therefore, the parameters a can be intuitively linked to searching rates as occurring in the classical functional response. However, their physical interpretation is different as they are multiplied by fractional densities, rather than absolute densities of microbiota living in the litter.

Omnivores

Omnivores graze on litter and we use a type-II response for the modeling of litter ingestion, based on the fractional density of labile carbon in the litter. Uptake of bacteria and fungi is taken proportional to their densities in the litter. Ingestion of material quantifies as

$$j^O_{L_C,I} = \left(\frac{1}{j_{L_C,Im}} + \frac{1}{a^O_{L_C} m_{L_C}} \right)^{-1}, \tag{A8a}$$

$$j^O_{L_N,I} = \frac{L_N}{L_C} j^O_{L_C,I}, \tag{A8b}$$

$$j^O_{F,I} = \frac{F}{L_C} j^O_{L_C,I}, \tag{A8c}$$

$$j^O_{B,I} = \frac{B}{L_C} j^O_{L_C,I}. \tag{A8d}$$

Ingested materials are processed and partly transformed in nitrogenous (P) and non-nitrogenous (H) precursor materials that can be used for growth (Table 2 transformations 6). Unassimilable materials are returned to their original litter pools. The quantities of H and P available for omnivore growth are

$$j^O_{H,A} = \tfrac{9}{50} j^O_{L_C,I} + \tfrac{3}{7} j^O_{F,I} + \tfrac{9}{35} j^O_{B,I}, \tag{A9a}$$

$$j^O_{P,A} = \tfrac{7}{20} j^O_{L_N,I} + \tfrac{6}{35} j^O_{F,I} + \tfrac{12}{35} j^O_{B,I}. \tag{A9b}$$

Another complementary SU transforms the available precursors into omnivore biomass according to scheme 7 in Table 2. The biomass specific growth of omnivores amount to

$$j_{O,G} = \left(\frac{16}{21j^O_{H,A}} + \frac{4}{7j^O_{P,A}} - \frac{1}{(21/16)j^O_{H,A} + (7/4)j^O_{P,A}} \right)^{-1}. \tag{A10}$$

Here, production is not a saturating function of precursor arrival (i.e. there is no maximum production flux $j_{O,Gm}$ in this equation). However, ingestion is a saturating function of labile litter density and this effectively bounds the omnivore population growth. Thus, assimilation is modeled using a SU complex consisting of two coupled simple SUs, the first of which selects assimilable precursors from resources and the second of which transforms the precursors into biomass.

Model summary

The complete model can be constructed from the synthesis above. It resumes to

$$\frac{\mathrm{d}}{\mathrm{d}t}S_{\mathrm{N}} = \theta_{S_{\mathrm{N}}}J_{\mathrm{C_{in}}} - 7j_{L_{\mathrm{N}},D}F - DS_{\mathrm{N}}, \tag{A11a}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}S_{\mathrm{C}} = \theta_{S_{\mathrm{C}}}J_{\mathrm{C_{in}}} - 5j_{L_{\mathrm{C}},D}F - DS_{\mathrm{C}}, \tag{A11b}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}L_{\mathrm{N}} = \theta_{L_{\mathrm{N}}}J_{\mathrm{C_{in}}} + \left(j_{L_{\mathrm{N}},D} - \frac{2}{7}j_{F,G}\right)F - \frac{4}{7}j_{B,G}B - \frac{1}{2}j^{O}_{L_{\mathrm{N}},I}O - DL_{\mathrm{N}}, \tag{A11c}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}L_{\mathrm{C}} = \theta_{L_{\mathrm{C}}}J_{\mathrm{C_{in}}} + \left(j_{L_{\mathrm{C}},D} - 3\frac{5}{7}j_{F,G}\right)F - 2\frac{3}{7}j_{B,G}B - \frac{1}{5}j^{O}_{L_{\mathrm{C}},I}O - DL_{\mathrm{C}}, \tag{A11d}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}F = j_{F,G}F - \frac{20}{3}j_{C_F,G}C_F - j^{O}_{F,I}O - DF, \tag{A11e}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}B = j_{B,G}B - 4j_{C_B,G}C_B - j^{O}_{B,I}O - DB, \tag{A11f}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}C_F = j_{C_F,G}C_F - DC_F, \tag{A11g}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}C_B = j_{C_B,G}C_B - DC_B, \tag{A11h}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}O = j_{O,G}O - DO, \tag{A11i}$$

in which $J_{\mathrm{C_{in}}}$ is the absolute daily litter input per square meter in C-moles, and $\theta_{S_{\mathrm{N}}}$, $\theta_{S_{\mathrm{C}}}$, $\theta_{L_{\mathrm{N}}}$, $\theta_{L_{\mathrm{C}}}$ are the respective fractions of stable, and labile nitrogenous and carbonous components in the litter. Parameter D models the simplified physical transport and abiotic decay of litters and death and predation by higher trophic levels of biota.