Theoretical Ecology
https://doi.org/10.1007/s12080-020-00500-8

ORIGINAL PAPER

Seasonal effects on the stoichiometry of microbes, primary production, and nutrient cycling

Kristin Carfora[1] · **Eric Forgoston**[1] · **Lora Billings**[1] · **Jennifer Adams Krumins**[2]

Received: 16 January 2020 / Accepted: 21 December 2020

Abstract
We develop a compartment model inspired by producer–herbivore–microbe soil food webs and determine how the naturally occurring seasonal variation in producer and detrital quality affects microbial nutrient cycling and the feedback to primary production. We show that seasonal changes in the stoichiometric quality of the producer coupled with the efficiency of herbivore grazing could induce a switch in the stoichiometric signature and therefore the functioning of the microbial community. Microbial decomposers are responsible for the flux of essential nutrients through an ecosystem. Our model enables one to quantitatively understand the tipping points between bacterially or fungally dominated decomposer communities, and more generally, the complex relationships between microbial decomposers, primary production, and nutrient cycling.

Keywords Plant-herbivore-microbe interactions · Seasonal effects · Bacterial–fungal cycling · Stoichiometry

Introduction

The composition and function of ecological communities can fluctuate with changing environmental conditions and resource constraints. The microbial communities of the rhizosphere, at the interface of roots and soil, are responsible for the bulk of nutrients that are cycled and fed back to plants. In terrestrial ecosystems, rhizosphere microbial communities have famously been divided into two channels through which nutrients and energy flow to plants and their wider network. The 'slow channel' has fungal processes at its base, and the 'fast channel' has bacterial processes at its base (Moore 2005; Hedlund 2004). The temporal separation between fungal and bacterial processes has meaningful implications for the outcome of availability of nutrients in soils. Differences in community composition significantly affect carbon (C) and nutrient cycling (Schlesinger 2000; Schmidt 2007; Bardgett 2014). At the most fundamental level, the differential in stoichiometric quality (C/N/P ratio, or for our purposes, C/N ratio) between either fungi or bacteria and soil organic matter creates the mechanism that determines rates of decomposition and mineralization of nutrients like nitrogen (N) and phosphorous (P) (Rousk and Bååth 2007; Waring 2013). This interacts with the fact that, due to their basic physiology, fungi tend to decompose more recalcitrant organic matter (e.g., lignin), while bacteria tend to decompose more labile organic matter (e.g. amino acids and root exudates) (Bardgett 1999; Lopez-Sangil et al. 2011; Rousk and Bååth 2007; Rousk 2015). The ecological and abiotic factors that determine when fungal or bacterial processes dominate a system have been studied in soils (De Vries 2006) but face numerous experimental challenges (Strickland 2010).

Environmental constraints determine when fungi or bacteria dominate a soil community (Bardgett 1999; De Vries 2006). A pervasive driver of environmental variability in ecological systems is seasonal forcing, and it has been studied in diverse systems at both the population and community levels (Aron 1984; Roberts and Grenfell 1991; Cornell 2008; Taylor 2015; Wehr et al. 2016; Billings and Forgoston 2018). Most obviously,

✉ Eric Forgoston
eric.forgoston@montclair.edu

Kristin Carfora
kristin.carfora@gmail.com

Lora Billings
billingsl@montclair.edu

Jennifer Adams Krumins
kruminsj@montclair.edu

[1] Department of Applied Mathematics and Statistics, Montclair State University, 1 Normal Avenue, Montclair NJ 07043, USA

[2] Department of Biology, Montclair State University, 1 Normal Avenue, Montclair NJ 07043, USA

seasonality affects primary production (Wehr et al. 2016), but also, it logically affects the associated microbial communities of plants (Penuelas 2012). Variations in seasonality will alter these rhizosphere interactions and have a profound effect on primary production and its responses to a changing climate of the future (Hashimoto 2019).

We know that the microbial communities of the rhizosphere are taxonomically and functionally diverse (Wall 2010), and the relative dominance of fungal versus bacterial biomass can have a significant influence on functionality and feedbacks to plants (Buée et al. 2009). Seasonality will indirectly drive the transition between microbes mineralizing excess nitrogen and immobilizing supplementary nitrogen, which could indicate a shift in the relative balance of fungi to bacteria and therefore their feedbacks to primary producers. However, a mechanistic model-based understanding of the relationship between seasonality, primary producers, and microbial nutrient cyclers is not well developed. To fill this gap, we have formulated a model based on stoichiometric variation at the community level taking inspiration from other stoichiometric network models (Cherif and Loreau 2007; Cherif and Loreau 2013). The model serves as a valuable tool to understand rhizosphere interactions with respect to seasonal variation. In contrast to complicated numerical models such as the CENTURY model (Parton 2005), our model's relative simplicity allows one to analytically determine steady-state solutions and to better understand the dynamics of fundamental processes.

In this paper we consider a plant-herbivore-microbe compartmental model inspired by soil food webs where primary production is determined entirely by the availability of inorganic nitrogen (N). Inorganic N moves through the network via assimilation by microbial decomposers, herbivore excretion, and producer uptake. We implement seasonal forcing that causes plant quality (producer C/N ratio) to change throughout the calendar year (Agren 2008). This in turn induces a change in the herbivore efficiency, a sloppy feeding parameter where some plant biomass never makes it into the herbivore, but rather falls to the ground and enters the detritus compartment to be decomposed by the microbes. Our work demonstrates how seasonality affects the decomposer compartment, primary production, and nutrient cycling.

Methods

In traditional soil communities, microbial decomposers take in organic matter from the detritus, and either mineralize excess nitrogen to the inorganic nitrogen compartment, or immobilize nitrogen from the inorganic nitrogen compartment to supplement nutrient requirements (Frost 2006; Manzoni 2008; Manzoni 2017). The tipping point between assimilation and mineralization from the microbial decomposer compartment is determined by the decomposer threshold elemental ratio (TER), also known as the demand ratio. In order to assimilate nutrients into biomass, microbes need carbon and nitrogen in a ratio equal to their own; however, they also need excess carbon to support basal metabolic processes. When one considers the decomposer C/N ratio along with the amount of excess carbon that is needed, the result is the decomposer demand ratio (Cherif and Loreau 2007; Frost 2006; Anderson 2005). The decomposer compartment is considered carbon limited when decomposers either mineralize excess nitrogen from the detrital compartment, or when the inorganic nitrogen compartment is large enough to adequately supplement the decomposers' need for more nitrogen. Microbial decomposers are nitrogen limited when the inorganic nitrogen compartment does not have sufficient mass to supplement the nutrients from the detritus.

Model description

We have developed a plant-herbivore-microbe compartmental model where primary production is determined entirely by inorganic nutrient availability. Inorganic nutrients are made available through the network via mineralization by microbial decomposers and herbivore excretion. Our model analyzes the interaction of carbon (C) and a secondary limiting nutrient. While in this paper we take nitrogen (N) to be the secondary nutrient, it is important to recognize that our model is general, and can be applied to any secondary nutrient (e.g., phosphorus) depending on the model setting, ecosystem parameter values, and question of interest. The compartment model (Fig. 1) consists of nine interacting C and N pools from five compartments. Specifically, these are: producer C and N (C_P and N_P), herbivore C and N (C_H and N_H), detrital C and N (C_D and N_D), microbial decomposer C and N (C_M and N_M), and inorganic nitrogen (N_I). Carbon and nitrogen are in ratio, so there is only one independently varying pool from each compartment. All parameter values are inspired by and taken from prior models and research in grassland and forested ecosystems (Table 1).

The producer compartment includes plant roots and shoots. In our model, we assume unlimited carbon for primary production, but nitrogen is limited and taken from the mineral inorganic nutrient compartment. Mass lost from the producer compartment is limited to herbivory or death to the detrital compartment.

The herbivore compartment is modeled on plant parasitic nematodes. Herbivore growth is determined entirely by herbivory, and the herbivores respire excess carbon which leaves the system completely, with any excess nitrogen excreted to the inorganic nutrient compartment. The herbivore C/N ratio is held constant. This model accounts for herbivore efficiency, the percentage of plant biomass that is ingested by the herbivore rather than left behind to enter the detritus pool.

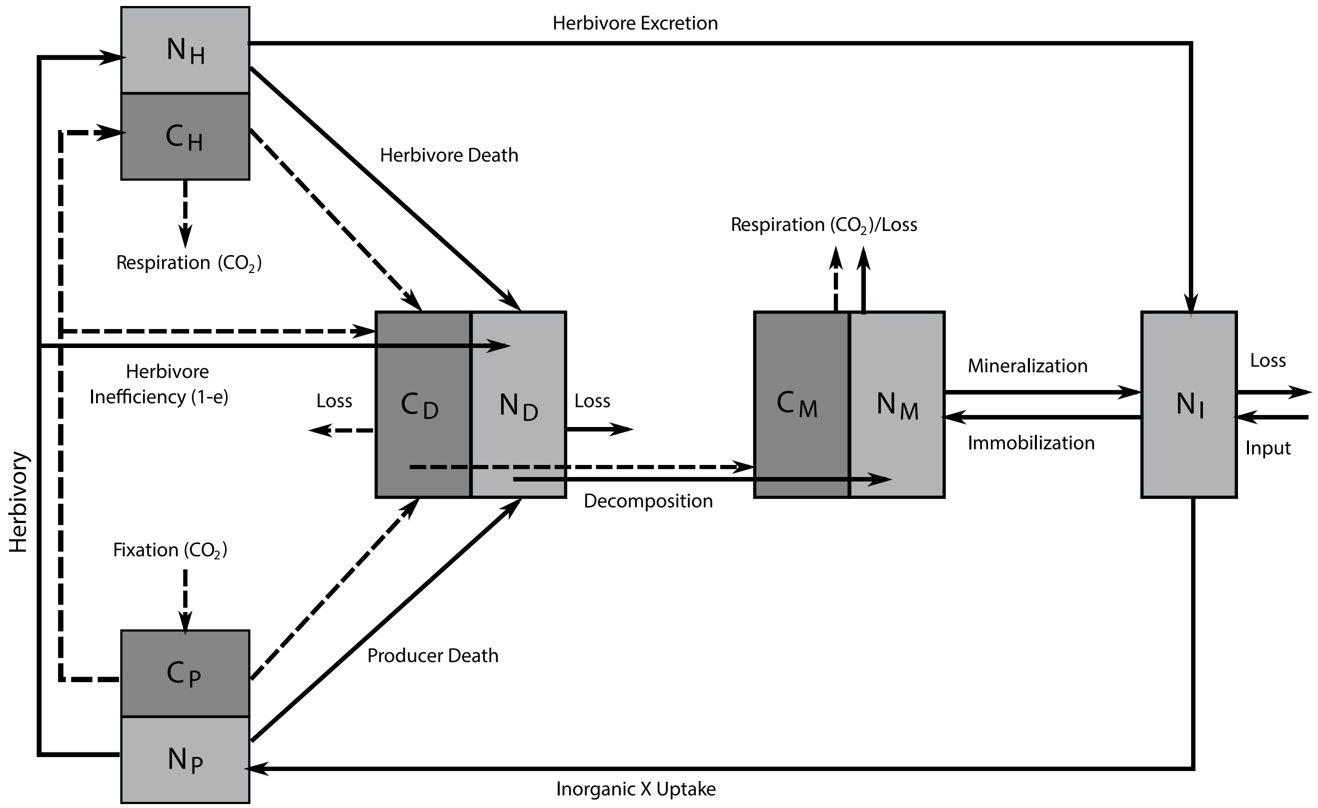

Fig. 1 Compartment model showing the flow of carbon (C) and nitrogen (N) through a producer–herbivore–decomposer soil system consisting of five compartments representing producers (C_P and N_P), herbivores (C_H and N_H), detritus (C_D and N_D), decomposers (C_M and N_M), and inorganic nitrogen (N_I)

(Krumins 2015). With respect to herbivore biomass loss, we assume no outside predation, although biomass is lost to the detrital compartment due to natural death.

The detritus compartment is supplied by both plant and herbivore biomass due to death and inefficient herbivory. It is assumed that once producer or herbivore biomass enters the detritus, it is well-mixed and not discriminated by microbes. Most loss from the detritus compartment is due to decomposition in the microbial decomposer compartment, though we account for a small amount of general loss from the detritus that exits the system completely (Cherif and Loreau 2013). We do not consider microbial death to detritus. However, there is a small general loss term from the decomposer compartment.

The inorganic nutrient compartment gains mass via herbivore excretion and from microbes mineralizing excess nitrogen when they are carbon limited. Decomposers consume dead plant and herbivore biomass, and either mineralize excess nitrogen to the inorganic compartment, or immobilize nitrogen from the inorganic compartment in order to supplement nutrient requirements (Cherif and Loreau 2007). In N limitation, an immobilization rate is established and determines the decomposition rate. In C limitation, a decomposition rate is first established, and determines the mineralization or immobilization rate. Note that it is the differential between the detritus C/N and microbial ratios that determines whether microbes are mineralizing or immobilizing N. We account for a general input from outside the system as deposition, as well as general loss that leaves the system as leaching, but most inorganic nutrient flux is due to producer uptake.

We assume the system is donor-controlled, with the exception of herbivory, following the rationale of Cherif and Loreau (2013).

Model equation derivations

The mass balance equation for nitrogen in the producer compartment is given by

$$\begin{aligned}\frac{dN_P}{dt} &= \text{inorganic N uptake - herbivory - death}\\ &= u_I N_I - hN_H N_P - d_P N_P,\end{aligned} \tag{1}$$

where u_I is the producer inorganic nitrogen uptake rate, h is the herbivory rate, and d_P is the producer death rate. Because C and N are in ratio, $\frac{dC_P}{dt} = \alpha \frac{dN_P}{dt}$, where α is the producer

Table 1 Variables and parameter values. Parameter values are associated with grassland and forested ecosystems. Units for the ecosystem parameters were derived using the fact that all variables must have units of g/m^2 and all stoichiometric parameters must have units of g/g

Type	Symbol	Value	Units	Definition	Citation
Variables	N_P		g/m^2	Plant N biomass	
	N_H		g/m^2	Herbivore N biomass	
	N_D		g/m^2	Detritus N	
	N_I		g/m^2	Inorganic N	
Stoichiometric Parameters	α	20 - 40	g/g	Plant C/N ratio	Krumins 2015
	β	varies	g/g	Microbial C/N ratio	
	γ	7	g/g	Herbivore C/N ratio	Krumins 2015
	δ	β/c	g/g	Microbial demand ratio	calculated
	μ	varies	g/g	Detritus C/N ratio	calculated
Ecosystem Parameters	u_I	0.34	day^{-1}	Plant N_I uptake rate	Cherif 2013
	d_P	$4.8 \cdot 10^{-6}$	day^{-1}	Plant death rate	Cherif 2013
	h	$3 \cdot 10^{-5}$	$m^2/(g \cdot day)$	Herbivory rate	Cherif 2013
	e	0.3 - 0.8	–	Herbivory efficiency	Krumins 2015
	d_H	0.003	day^{-1}	Herbivore death rate	Krumins 2015
	r_H	0.014	day^{-1}	Herbivore respiration rate	estimated
	l_D	$8.4 \cdot 10^{-4}$	day^{-1}	Detritus loss rate	Cherif 2013
	l_M	$3.3 \cdot 10^{-3}$	day^{-1}	Microbial loss rate	Cherif 2013
	m_N	$4.34 \cdot 10^{-3}$	day^{-1}	C-lim microbial uptake rate	Cherif 2013
	I_I	0.03	$g/(m^2 \cdot day)$	N_I input rate	Cherif 2013
	l_I	$3 \cdot 10^{-4}$	day^{-1}	N_I loss rate	Cherif 2013
	r_I	0.09	day^{-1}	N-lim microbial N_I uptake rate	Cherif 2013
	N_M	7.480	g/m^2	Microbial N mass	calculated
	c	varies	–	Microbial growth efficiency	

C/N ratio. The mass balance equations for carbon in the producer compartment are

$$\begin{aligned}\frac{dC_P}{dt} &= \text{fixation - herbivory - death} \\ &= \alpha\left(u_I N_I - hN_H N_P - d_P N_P\right).\end{aligned} \tag{2}$$

The mass balance equation for herbivore nitrogen is

$$\begin{aligned}\frac{dN_H}{dt} &= \text{herbivory - death - excretion} \\ &= ehN_H N_P - d_H N_H - \text{excretion},\end{aligned} \tag{3}$$

where e is the herbivore efficiency (percent of producer biomass removed from the plant during grazing that is actually ingested by the herbivore) and d_H is the herbivore death rate. We formulate the equation for herbivore carbon to derive the herbivore excretion term. First, because C and N are in ratio for the herbivores, we have $\frac{dC_H}{dt} = \gamma \frac{dN_H}{dt}$ where γ is the herbivore C/N ratio. Then

$$\begin{aligned}\frac{dC_H}{dt} &= \gamma\left(ehN_H N_P - d_H N_H - \text{excretion}\right) \\ &= \gamma ehN_H N_P - \gamma d_H N_H - \gamma(\text{excretion}).\end{aligned} \tag{4}$$

From the model, we also have

$$\frac{dC_H}{dt} = \text{herbivory - death - respiration.}$$

Herbivory is associated with the producer compartment and herbivore death is associated with the herbivore compartment. Using Eq. (3), we find

$$\frac{dC_H}{dt} = \alpha(ehN_H N_P) - \gamma(d_H N_H) - \gamma r_H N_H, \tag{5}$$

where r_H represents the herbivore respiration rate.

Setting Eqs. (4) and (5) equal and solving for excretion gives

$$\text{excretion} = \frac{\gamma - \alpha}{\gamma} ehN_H N_P + r_H N_H,$$

which leads to the following equation for herbivore nitrogen

$$\frac{dN_H}{dt} = ehN_H N_P - d_H N_H - \left[\frac{\gamma - \alpha}{\gamma} ehN_H N_P + r_H N_H\right]. \tag{6}$$

In order to derive the mass balance equations for the remaining pools, we first discuss microbial decomposer mineralization and immobilization (Cherif and Loreau 2007).

We denote the flux of C and N from detritus to microbes as ϕ_{MC} and ϕ_{MN} respectively, and the flux from the inorganic N compartment to the microbial compartment as ϕ_I. Note that ϕ_{MC} and ϕ_{MN} are always positive, but ϕ_I can be positive (indicating immobilization) or negative (indicating mineralization). The microbial decomposer C/N ratio is $\beta = C_M/N_M$, and the decomposer demand ratio is $\delta = \beta/c$, where c is the decomposer growth efficiency. We also note that $\phi_{MC} = \mu\phi_{MN}$, where μ is the detritus C/N ratio, as decomposition is associated with the detritus compartment (details regarding μ can be found in Appendix A).

The mass balance equation for microbial decomposer nitrogen is

$$\begin{aligned}\frac{dN_M}{dt} &= \text{decomposition + mineralization/immobilization - loss}\\ &= \phi_{MN} + \phi_I - l_M N_M,\end{aligned} \tag{7}$$

where l_M is the microbial loss rate. The mass balance equation for microbial carbon is

$$\begin{aligned}\frac{dC_M}{dt} &= \text{decomposition - respiration - loss}\\ &= \phi_{MC} - (1-c)\phi_{MC} - l_M C_M\\ &= c\phi_{MC} - l_M C_M.\end{aligned} \tag{8}$$

Because $\frac{dN_M}{dt}$ and $\frac{dC_M}{dt}$ must be in ratio, one has

$$c\phi_{MC} - l_M C_M = \beta\left[\phi_{MN} + \phi_I - l_M N_M\right]. \tag{9}$$

Noting that $\frac{\beta}{c} = \delta$, $C_M = \beta N_M$, and $\phi_{MC} = \mu\phi_{MN}$, and solving for ϕ_{MN},

$$\phi_{MN} = \frac{\delta}{\mu - \delta}\phi_I. \tag{10}$$

Solving for ϕ_I gives

$$\phi_I = \frac{\mu - \delta}{\delta}\phi_{MN}. \tag{11}$$

If microbial decomposers are carbon limited (C-limited), growth will be determined by their uptake from the detritus. We set $\phi_{MN} = m_N N_D$, where m_N is the uptake rate (details regarding m_N can be found in Appendix B). Substitution into Eq. (11) gives

$$\phi_I = \frac{\mu - \delta}{\delta} m_N N_D. \tag{12}$$

If microbial decomposers are nitrogen limited (N-limited), their uptake of inorganic nitrogen will determine their growth. We set $\phi_I = r_I N_I$, where r_I is the inorganic N uptake rate. Substitution into Eq. (10) gives

$$\phi_{MN} = \frac{\delta}{\mu - \delta} r_I N_I. \tag{13}$$

By Liebig's Law of the Minimum, decomposer growth depends only on the availability of detrital carbon when $m_N N_D < \frac{\delta}{\mu - \delta} r_I N_I$, and depends on the availability of inorganic N when $m_N N_D > \frac{\delta}{\mu - \delta} r_I N_I$. The decomposition term in the mass balance equations is then given by

$$\text{decomposition} = Min\left[m_N N_D, \frac{\delta}{\mu - \delta} r_I N_I\right], \tag{14}$$

and the mineralization/immobilization term is

$$\text{mineralization/immobilization} = Min\left[\frac{\mu - \delta}{\delta} m_N N_D, r_I N_I\right]. \tag{15}$$

The mass balance equation for microbial decomposer nitrogen is therefore

$$\begin{aligned}\frac{dN_M}{dt} &= Min\left[m_N N_D, \frac{\delta}{\mu - \delta} r_I N_I\right]\\ &\quad + Min\left[\frac{\mu - \delta}{\delta} m_N N_D, r_I N_I\right] - l_M N_M.\end{aligned} \tag{16}$$

Using Eq. (8)

$$\frac{dC_M}{dt} = cMin\left[\mu m_N N_D, \frac{\delta\mu}{\mu - \delta} r_I N_I\right] - \beta l_M N_M. \tag{17}$$

The mass balance equation for detritus is given by

$$\begin{aligned}\frac{dN_D}{dt} &= \text{producer death + herbivore death + herbivory inefficiency}\\ &\quad \text{- decomposition - loss}\\ &= d_P N_P + d_H N_H + (1-e)hN_P N_H\\ &\quad - Min\left[m_N N_D, \frac{\delta}{\mu - \delta} r_I N_I\right] - l_D N_D,\end{aligned} \tag{18}$$

where l_D is the detritus loss rate.

Because in all compartments C and N are in ratio (α for producers, γ for herbivores, and μ for detritus),

$$\begin{aligned}\frac{dC_D}{dt} &= \text{producer death + herbivore death + herbivory inefficiency}\\ &\quad \text{- decomposition - loss}\\ &= \alpha d_P N_P + \gamma d_H N_H + \alpha(1-e)hN_P N_H\\ &\quad - \mu Min\left[m_N N_D, \frac{\delta}{\mu - \delta} r_I N_I\right] - \mu l_D N_D.\end{aligned} \tag{19}$$

Finally, the mass balance equation for the inorganic nitrogen compartment is

$$\begin{aligned}\frac{dN_I}{dt} &= \text{input} + \text{excretion - loss - producer uptake}\\ &\quad \text{- mineralization/immobilization}\\ &= I_I + \left[\frac{\gamma-\alpha}{\gamma}ehN_HN_P + r_HN_H\right] - l_IN_I - u_IN_I\\ &\quad - Min\left[\frac{\mu-\delta}{\delta}m_NN_D, r_IN_I\right],\end{aligned} \tag{20}$$

where I_I is the inorganic N input rate and l_I is the inorganic N loss rate.

Our model can be represented by the following five ordinary differential equations (ODEs):

$$\frac{dN_P}{dt} = u_IN_I - hN_HN_P - d_PN_P \tag{21}$$

$$\begin{aligned}\frac{dN_H}{dt} &= ehN_HN_P - d_HN_H\\ &\quad - \left[\frac{\gamma-\alpha}{\gamma}ehN_HN_P + r_HN_H\right].\end{aligned} \tag{22}$$

$$\begin{aligned}\frac{dN_M}{dt} &= Min\left[m_NN_D, \frac{\delta}{\mu-\delta}r_IN_I\right]\\ &\quad + Min\left[\frac{\mu-\delta}{\delta}m_NN_D, r_IN_I\right] - l_MN_M.\end{aligned} \tag{23}$$

$$\begin{aligned}\frac{dN_D}{dt} &= d_PN_P + d_HN_H + (1-e)hN_PN_H\\ &\quad - Min\left[m_NN_D, \frac{\delta}{\mu-\delta}r_IN_I\right] - l_DN_D,\end{aligned} \tag{24}$$

$$\begin{aligned}\frac{dN_I}{dt} &= I_I + \left[\frac{\gamma-\alpha}{\gamma}ehN_HN_P + r_HN_H\right]\\ &\quad - l_IN_I - u_IN_I - Min\left[\frac{\mu-\delta}{\delta}m_NN_D, r_IN_I\right].\end{aligned} \tag{25}$$

Seasonal variation

We parameterized this model with data from temperate deciduous forests and grasslands. As the seasons change, the stoichiometric quality of plants oscillates periodically (Bardgett et al. 2005; Agren 2008; Cebrian 1999; Mattson 1980). Seasonal changes in plant quality and herbivore efficiency and their resultant effects on decomposition and mineralization/immobilization (Cherif and Loreau 2013) could reflect a seasonal shift between bacterial and fungal dominance (Schmidt 2007). We employ a sinusoidal function to simulate a seasonal change in plant quality and herbivore efficiency, with a period of one calendar year beginning on June 21. In this model, producer C/N ratio ranges sinusoidally from 20 to 40 (Elser 2000; Krumins 2015), and herbivore efficiency ranges sinusoidally from 0.3 to 0.8 (Krumins 2015) (Fig. 2). The equations for producer C/N ratio, α, and herbivore efficiency, e, are

$$\alpha = -10\cos\left(\frac{2\pi}{365}t\right) + 30, \text{ and}$$

$$e = 0.25\cos\left(\frac{2\pi}{365}t\right) + 0.55,$$

where t is time in days.

In general, decomposer biomass varies over time, though exact patterns and fluctuations can be complicated

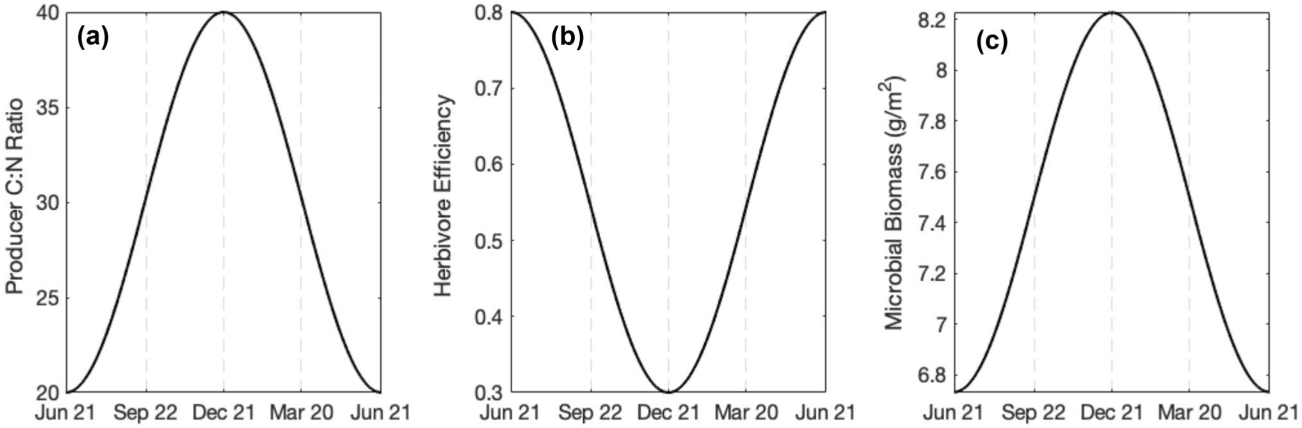

Fig. 2 (**a**) Producer C/N ratio, (**b**) herbivore efficiency, and (**c**) microbial biomass varying over the course of one calendar year

and are not captured in this model. Many grassland and forest ecosystems demonstrate little to no definite yearly pattern (Wardle 1998; Schadt 2003; Schmidt 2007). To study seasonal effects on the decomposer demand ratio and composition of the decomposer compartment as a whole, we also seasonally vary the microbial biomass (Fig. 2) as

$$N_M = -0.748 \cos\left(\frac{2\pi}{365}t\right) + 7.480.$$

For this article we chose the minimum microbial biomass to occur at the beginning of summer and the maximum to occur at the beginning of winter (Schadt 2003; Schmidt 2007). However, the function can easily be translated, or the period amended, to fit the needs of any ecosystem.

We use Eq. (16) to solve for the decomposer demand ratio δ. It is given as

$$\delta = \begin{cases} \dfrac{\mu\, m_N\, N_D}{\dfrac{dN_M}{dt} + l_M\, N_M} & \text{in C-limitation,} \\[2ex] \mu - \dfrac{\mu\, r_I\, N_I}{\dfrac{dN_M}{dt} + l_M\, N_M} & \text{in N-limitation.} \end{cases} \tag{26}$$

We now have an ODE model consisting of four coupled ODEs, representing the producer, herbivore, detritus, and inorganic N compartments, as well as an equation to determine the decomposer demand ratio. To analyze our system, we determined decomposer biomass and initial conditions for the system as outlined in Appendix C. The system was solved numerically using a fourth-order Runge–Kutta solver in MATLAB.

Results

After an initial transient period, the system stabilizes, showing a regularly oscillating microbial decomposer demand ratio that ranges from about 11.0 to 50.6 (Fig. 3e). When the producer C/N ratio begins to increase in the fall, plant quality decreases, and herbivores compensate with an increase in overall herbivory; we see that increased herbivory in the fall leads to an overall decrease in primary production in the winter (Fig. 3a). Also in the winter, inorganic N is at a high, as producer demand for inorganic N is at a low (Fig. 3d).

In the summer months, with plant C/N ratio low and herbivore efficiency at a high, the detritus C/N ratio will be at a low. Detritus coming from the producer compartment has a

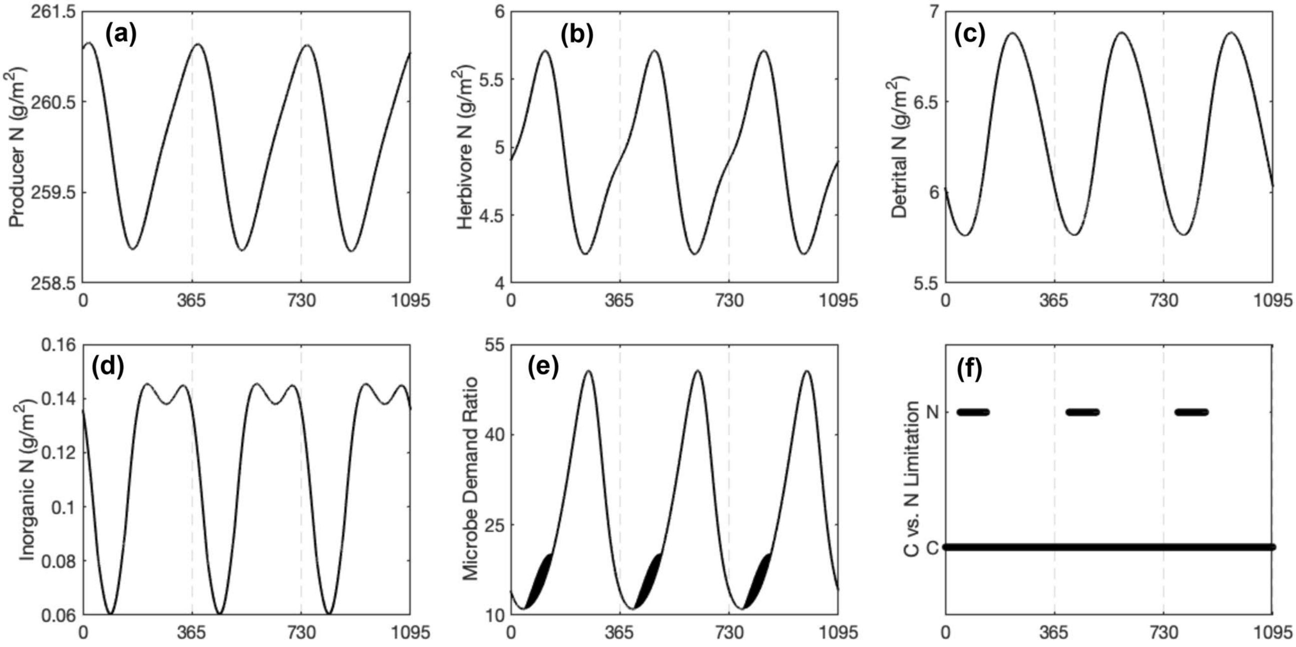

Fig. 3 (**a**) Producer N biomass, N_P, (**b**) herbivore N biomass, N_H, (**c**) detritus N, N_D, (**d**) inorganic N, N_I, (**e**) microbe demand ratio, δ, and (**f**) C vs N limitation across 3 calendar years

low C/N ratio, and biomass from the herbivore compartment has a C/N ratio that stays constant. In our forest setting, producer C/N ratios are consistently and significantly higher than herbivore C/N ratios (Elser 2000), meaning that plant quality is relatively lower, and herbivore efficiency plays a larger role in nutrient cycling (Elser 2000; Cebrian 1999). Specifically, as plant quality and inefficiency of herbivory rise, the flux of plant biomass to the detrital compartment increases, causing an overall rise in the detrital C/N ratio.

The majority of the year is spent in C limitation, with an area of switching between C and N limitation in the late summer/early fall (Fig. 3f). The darker areas in Fig. 3e show the decomposer demand ratio switching between its C-limited definition and its N-limitation definition.

We expect in the fall to see a shift to a fungally dominated decomposer compartment by the winter months. This reflects the notion that fungally dominated decomposer compartments generally mineralize nitrogen to the inorganic pool, while bacterially dominated decomposers immobilize nitrogen from the inorganic pool (Cebrian 1999; Bardgett et al. 2005; Holtkamp 2011; Schadt 2003). Mathematically, a larger demand ratio results in mineralization of excess nitrogen, while a smaller demand ratio results in immobilization of supplemental nitrogen. Our model therefore demonstrates a potential connection between seasonal oscillation of the decomposer demand ratio and fungal-bacterial dominance of the microbial compartment.

Discussion

Underlying assumptions

We have provided a brief working description of our compartment model inspired by ecological soil food webs to better understand the dynamics and relationships between producers, herbivores, and microbial decomposers. Because of the complexity of the model due to seasonal variability, certain aspects of the model have been simplified so results can be more easily analyzed and interpreted.

The system is donor-controlled, with the exception of herbivory (Cherif and Loreau 2013). Plant and microbe uptake functions are important for determining the persistence and equilibrium of the system and using donor-controlled functions often result in more stable environments. However, in most terrestrial ecosystems, the producer biomass available for consumption greatly outweighs the needs of the herbivores. This allows for a mass action term for herbivory, where herbivory is recipient-controlled and determined by both the producer biomass as well as herbivore biomass.

Producers and herbivores

We do not address producer or herbivore TER, the tipping point between C and N limitation, in this paper. Producers have constant access to unlimited carbon, and so are considered N limited. The range of values of the producer C/N ratio is much larger than the range of values of the herbivore C/N ratio, especially in terrestrial systems like ours. It is for this reason the herbivores in our model are assumed to be nitrogen limited rather than carbon limited, and so we do not address the herbivore TER (Elser 2000).

The stoichiometric quality of plant biomass can be an important selective filter upon herbivory. We define herbivore efficiency as the proportion of plant biomass that is ingested by the herbivore. When herbivores eat, they generally do not consume the entire plant due to inedible shoots and roots, or sloppy grazing, and this leftover material enters the detritus compartment as unchanged producer biomass. Therefore, herbivore inefficiency, $1 - e$, represents the percentage of plant matter removed from the plant due to herbivory that is *not* ingested by the herbivore. We define herbivore inefficiency to include plant matter not ingested due to sloppy grazing as well as inedible shoots and roots (Krumins 2015).

Plant stoichiometry will logically interact with pre-absorption mechanisms of the herbivore like selective feeding or feeding rate (Frost 2005; Gruner 2008). The implications of pre-absorption mechanisms as driven by plant quality will critically shape plant community structure as well as nutrient cycling and feedbacks to primary production (Chaudhary et al. 2020; Guernsey 2015). Pre-absorption mechanisms that may be driven by processes like allelopathy, herbivore defenses or selective feeding (Frost 2005) will underlie our efficiency parameter. Though we do not account for pre-absorption mechanisms or herbivore selection here, these mechanisms could easily be incorporated into the model by adjusting herbivore efficiency or herbivory rate.

Plants are known to increase organic input to the soil when grazed above-ground (Bardgett 1998). However, not all root exudates are sugars; many are nitrogen rich amino acids (Steinauer et al. 2016). Currently, our model includes a plant death term, but it is not tied to any seasonality. Hinsinger et al. (Hinsinger 2005) describe the temporal variability in root exudation and organic inputs to the rhizosphere. Likewise, Bardgett et al., Wardle and others (Bardgett et al. 2005; Wardle 1998; Buchkowski 2019) have eloquently described theoretical mechanisms for the feedback from herbivore via microbes back to primary production. Our model is a reliable framework in which these mechanisms can be tested. Moreover, the definition of the producer death rate could be expanded to a producer loss rate, to include tissue aborted by plants once damaged by herbivory, leaf shedding due to seasonal change, or direct-to-soil plant input.

Recalling that herbivore excretion (see Eq. 6) is given as

$$\frac{\gamma - \alpha}{\gamma} ehN_H N_P + r_H N_H,$$

then one can easily see that if the herbivore C/N ratio is greater than the producer C/N ratio ($\gamma > \alpha$), excretion is always positive. This is not the case in our ecological setting. When plant C/N greatly exceeds the herbivore C/N ratio, there are two potential scenarios. In order for excretion to be positive, the respiration rate r_H must satisfy the following inequality:

$$r_H > \frac{\alpha - \gamma}{\gamma} ehN_P.$$

This inequality demonstrates the complex relationship between herbivore respiration and our seasonally varying ecological parameters. As producer C/N (α) increases, the herbivore respires more excess carbon. However, a decrease in herbivore efficiency causes a decrease in respiration due to the increase of ingested plant matter. When the above inequality is not satisfied, excretion becomes negative, indicating immobilization of inorganic N by the herbivore. Because herbivore respiration is extremely difficult to measure (Krumins 2015), and because of the several moving pieces in the relationship between excretion and respiration rate r_H, we have chosen to use a reasonable estimated herbivore respiration rate (Krumins 2015).

Decomposers

We do not consider microbial death to detritus, following other classic decomposer models like that of (Cherif and Loreau 2013) and (Daufresne and Loreau 2001) as well as theory described by (Bardgett and Wardle 2003). Within the decomposer compartment, defining when an individual microbial decomposer is living, dormant or dead is extremely difficult; moreover, the dead biomass is labile and cycles back into the decomposer compartment through the detritus quickly, thus becoming a negligible term (Cherif and Loreau 2007; Cherif and Loreau 2013). However, some of the dead decomposer biomass is not recycled back into detritus, but instead is lost from the compartment; this is our general loss term from the decomposer pool.

The decomposer growth efficiency has the potential to vary due to several factors, such as the microbe C/N ratio, seasonal factors, or even whether the pool is bacterially versus fungally dominated (Manzoni 2008). Given a reasonable growth efficiency, the microbial C/N ratio can be directly determined from the demand ratio, or vice versa.

Sensitivity analysis

We tested the sensitivity of each variable in our model to each parameter for carbon limited microbes and for nitrogen limited microbes. The sensitivity of a variable u that depends on a parameter p is given by

$$\Upsilon_p^u = \frac{\partial u}{\partial p} \times \frac{p}{u}, \tag{27}$$

evaluated at baseline parameter values. Using Eq. (27), one can calculate the ratio of relative change of the variable u to relative change in the parameter p (Chitnis 2008). To do this, we found analytical steady states for the model, found the partial derivatives with respect to producer C/N and herbivore efficiency, and evaluated these at our baseline parameter values. For simplicity, we used the midpoint parameter values for producer C/N ratio and herbivore efficiency, $\alpha = 30$ and $e = 0.55$, and held decomposer biomass constant.

Tables 2 and 3 show that predicted seasonal changes in the producer C/N ratio (α), herbivore efficiency (e), and microbe biomass (N_M) all have a profound effect on our system, both in C and N limited environments. This indicates that modeling a realistic seasonal shift will result in changes in the movement of biomass and primary production, potentially affecting the composition of the decomposer compartment. Based on the sensitivity analysis results, we see that it may be worth investigating the role of a varying inorganic N input rate and microbial loss rate in future work.

Table 2 The sensitivity indices of the system variables for each parameter evaluated at baseline parameter values in a carbon limited environment. These indices measure the relative change of the variable to relative change in the parameter

Parameter	Variable				
	N_P	N_H	N_D	N_I	δ
α	−1	+0.599	+0.003	−0.421	+0.563
e	−1	+1.271	−0.002	+0.229	−0.623
γ	+1	−0.599	−0.003	+0.421	+0.437
u_I	0	+0.007	+0.007	−0.993	+0.006
d_P	0	−0.042	+0.00005	−0.008	+0.021
h	−1	+0.042	−0.00005	+0.008	−0.021
d_H	+0.154	−0.535	+0.002	−0.364	−0.223
r_H	+0.846	−0.507	−0.002	+0.356	+0.244
l_D	0	−0.868	−0.994	−0.839	−0.977
l_M	0	−4.840	−4.643	−4.679	−5.547
m_N	0	+0.868	−0.006	+0.839	+0.977
I_I	0	+5.882	+5.643	+5.686	+5.526
l_I	0	−0.007	−0.007	−0.007	−0.006
N_M	0	−4.840	−4.643	−4.679	−5.547

Table 3 The sensitivity indices of the system variables for each parameter evaluated at baseline parameter values in a nitrogen limited environment. These indices measure the relative change of the variable to relative change in the parameter

Parameter	Variable				
	N_P	N_H	N_D	N_I	δ
α	−1	+0.723	+0.001	−0.312	+0.691
e	−1	+1.233	−0.0008	+0.174	−0.686
γ	+1	−0.723	−0.001	+0.312	+0.309
u_I	0	+0.259	+0.003	−0.754	+0.310
d_P	0	−0.059	+0.00004	−0.008	+0.033
h	−1	+0.059	−0.00004	+0.008	−0.033
d_H	+0.154	−0.448	+0.001	−0.272	−0.106
r_H	+0.846	−0.612	−0.001	+0.264	0.139
l_D	0	0	−1	0	0
l_M	0	0	−4.665	0	+0.420
I_I	0	+1.059	+5.665	+1.008	−0.453
l_I	0	−0.0009	−0.005	−0.0008	+0.0004
r_I	0	−0.258	+0.001	−0.246	−0.310
N_M	0	0	−4.665	0	+0.420

Analysis of results

Our model remains in C limitation for most of the year, though we do see an area of switching between C and N limitation in the late summer and early fall. Recall that decomposers become N-limited only when two factors occur simultaneously: the detritus C/N ratio must be significantly larger than the decomposer demand ratio, *and* the inorganic compartment must be unable to adequately supplement needed N to the microbial pool (Cherif and Loreau 2007; Manzoni 2017). When the switching begins, inorganic nitrogen is at a minimum; however, the inorganic N begins immediately increasing, pushing the decomposer pool back to C limitation (Fig. 3d, f).

Our results suggest that seasonality with associated changes in plant quality and herbivore grazing—as well as seasonal changes in microbial biomass—could propel a transition between bacterial and fungal dominance in the decomposer compartment. In a standard producer–herbivore–microbe system, bacteria will immobilize supplemental inorganic N while fungi will mineralize excess inorganic N (Cebrian 1999; Bardgett et al. 2005; Holtkamp 2011; Schadt 2003); this is because generally, fungi have larger demand ratios than bacteria. Figure 4 shows decomposition, the flux between the microbial compartment and the inorganic nitrogen compartment, and the decomposer demand ratio across a calendar year. Decomposers are immobilizing nitrogen from the inorganic pool when the flux is greater than zero (a positive flux towards the decomposer compartment) and are mineralizing excess nitrogen when the flux is less than zero (a negative flux away from the decomposer compartment). Whether the decomposer mineralizes or immobilizes is determined by the differential between the detritus C/N ratio, μ, and the decomposer demand ratio, δ. The demand ratio is at a minimum toward the end of summer, when the system is switching between C and N limitation. Consequently, at this time there is a short period of immobilization, which could indicate a bacterially dominated decomposer compartment. Decomposition is at a maximum in the winter, resulting in a maximum of mineralization of excess nitrogen into the inorganic compartment, potentially indicating a fungally dominated decomposer compartment. Our model output accurately reflects real-world situations, as microbes immobilize nitrogen in preparation for the winter, when they retain what they need and mineralize any excess (Bardgett et al. 2005).

Decomposer communities, unlike herbivores and many plants, are capable of adapting to surroundings quickly

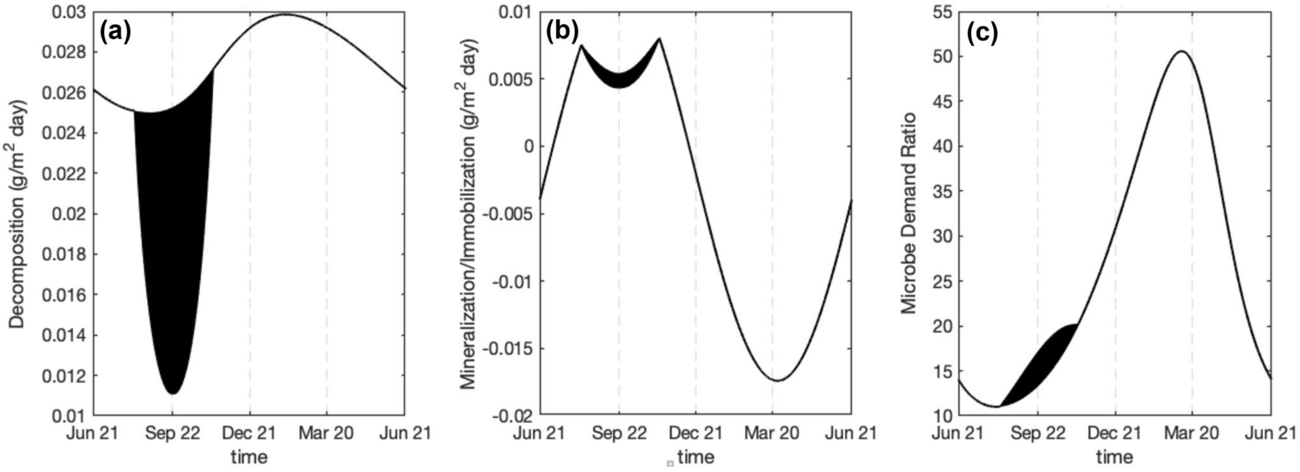

Fig. 4 (**a**) Decomposition, (**b**) mineralization/immobilization, and (**c**) microbe demand ratio over the course of one calendar year

(Schmidt 2007), so we could expect to realistically see this kind of seasonal change within the decomposer compartment. This capability of such rapid change allows us to more closely examine these types of ecosystems on a much smaller time scale. Our model is the first of its kind to specifically consider how seasonality could drive a shift between bacteria and fungi in the decomposer pool, and provides improved quantitative understanding of how a shift between a bacterially dominated decomposer compartment and a fungally dominated decomposer compartment affects the ecosystem as a whole. The model both highlights the important role of microbes in any ecological system, and provides a stepping stone to understanding the complex relationships between microbial decomposers, primary producers, and the surrounding ecosystem (Bardgett et al. 2005).

Conclusion

We have developed a novel mathematical-ecological model inspired by soil ecosystems and have studied the effect of seasonality on the producer–herbivore–microbe system. In particular, we have demonstrated how seasonal variation in plant quality and therefore soil organic matter quality, coupled with a seasonal variation in microbe biomass, has the potential to affect the degree to which fungal or bacterial communities dominate the processes of decomposition and nutrient mineralization. This is important as basic stoichiometric differences in the elemental composition of fungi and bacteria can affect the yield of mineral nutrients that are available to plant growth.

Furthermore, the consumers within either the bacterial or fungal pathways vary (Moore 2005), and their rates of decomposition and nutrient mineralization vary. This is especially the case at the lower trophic levels where herbivores may graze preferentially in either channel (McCann and Rooney 2009). Additionally, we know that the efficiency of herbivores can interact closely with the quality of organic matter to affect microbial nutrient cycling and feedbacks to plants (Krumins 2015; Cebrian 1999).

In models that describe plant and soil community interactions, there is an extremely complicated relationship between above- and below-ground communities because they exist at a range of spatial and temporal scales (Bardgett et al. 2005). Our theoretical model is important because it is the first of its kind to consider seasonal changes in plant quality, herbivore efficiency, and microbe biomass and their potential effects on the makeup of the microbial community of the rhizosphere. The model can be adapted to and parameterized for many different systems with realistic seasonal changes and can be used to make accurate predictions about the effects on overall ecosystem functioning. In addition, further analysis could explain seasonal patterns of soil respiration and could help define the mechanism through which available nitrogen is both retained and lost from the planted systems (Schmidt 2007).

Appendix A: Detritus C/N ratio, μ

The detritus C/N ratio, μ, is a function of the producer C/N ratio α and the herbivore C/N ratio γ. Since the detritus C/N ratio $\mu = C_D/N_D$, one has

$$\mu\frac{dN_D}{dt} = \frac{dC_D}{dt}.$$

Substitution of Eqs. (18)-(19) leads to

$$\begin{aligned}&\mu\Big[d_P N_P + d_H N_H + (1-e)hN_H N_P - l_D N_D\\&\quad - Min\left(m_N N_D, \frac{\delta}{\mu-\delta}r_I N_I\right)\Big]\\&= \alpha d_P N_P + \gamma d_H N_H + \alpha(1-e)hN_H N_P\\&\quad - \mu l_D N_D - \mu\cdot Min\left(m_N N_D, \frac{\delta}{\mu-\delta}r_I N_I\right).\end{aligned}$$

Simplification leads to

$$\begin{aligned}&\mu\big[d_P N_P + d_H N_H + (1-e)hN_H N_P\big]\\&= \alpha d_P N_P + \gamma d_H N_H + \alpha(1-e)hN_H N_P,\end{aligned}$$

and solving for μ one finds that

$$\mu = \frac{\alpha d_P N_P + \gamma d_H N_H + \alpha(1-e)hN_H N_P}{d_P N_P + d_H N_H + (1-e)hN_H N_P}.$$

We can rearrange the expression for μ in terms of α and γ to represent the detritus C/N ratio as a weighted average of the producer and herbivore mass as follows

$$\begin{aligned}\mu &= \alpha\left(\frac{d_p N_P + (1-e)hN_H N_P}{d_p N_P + d_H N_H + (1-e)hN_H N_P}\right)\\&\quad + \gamma\left(\frac{d_H N_H}{d_p N_P + d_H N_H + (1-e)hN_H N_P}\right).\end{aligned}$$

The coefficient α represents the percentage of detritus coming from the producers, while the coefficient γ represents the percentage coming from the herbivores.

Appendix B: C-Limited Decomposer Detritus Uptake Rate, m_N

The uptake rate m_N is based on the equation for μ so that

$$m_N = a\left(\frac{d_pN_P + (1-e)hN_HN_P}{d_pN_P + d_HN_H + (1-e)hN_HN_P}\right) + j\left(\frac{d_HN_H}{d_pN_P + d_HN_H + (1-e)hN_HN_P}\right),$$

where a is the C-limited decomposer uptake rate of plant detritus, and j is the C-limited decomposer uptake rate of herbivore detritus. Because the model is already so complex, a fixed value of m_N was used (Cherif and Loreau 2013).

Appendix C: Steady States, Decomposer Biomass, and Initial Conditions

Analytical steady states and the corresponding Jacobian matrix can be found for the original five equation model using Mathematica. However, the analytical steady states and Jacobian are extremely long and complicated and take up many pages of space. Since they are not illuminating, they are therefore not included in the article or appendices.

To numerically solve the system of equations, we must determine the decomposer biomass and initial conditions for the system. First, numerical steady states were found for the original five equation model in a C-limited state. A carbon limited state was chosen because while C-limited, it is possible for decomposers to mineralize nitrogen to the inorganic compartment or immobilize needed nitrogen from the inorganic compartment. In contrast, N-limited decomposers can only immobilize nitrogen, which could unnecessarily limit our system. We used the midpoint values for plant C/N, herbivore efficiency, and decomposer C/N, ($\alpha = 30$, $e = 0.55$, and $\beta = 7$), and herbivore respiration rate $r_H = 0.014$ (Krumins 2015). Herbivore C/N ratios can reasonably vary between 7 and 10 in a forest setting (Krumins 2015; Cherif and Loreau 2013), so a midpoint herbivore C/N ratio of $\gamma = 8.5$ was used. The numerical steady state for the decomposer N compartment gives $N_M = 7.480$.

For this value of N_M and our starting conditions on June 21 ($\alpha = 20$ and $e = 0.8$), the steady states of the mass balance equations with the exception of the decomposer equation were found numerically. These numerical steady states, shown in Table 4, are used as the initial values for the system. The system was solved numerically using a fourth-order Runge–Kutta solver in MATLAB.

Table 4 Numerically computed steady-state values used as initial conditions

Variable	Steady-state value
N_P	301.04
N_H	6.45
N_D	6.27
N_I	0.18

In the numerical solver, the system was allowed to switch between C and N limitation using Liebig's Law of the Minimum, employing a small threshold of 0.00005. Because possible decomposition values are in many cases extremely close in value, a switch between C and N limitation could occur at every time step, resulting in several switches per day, which is biologically unrealistic. Further, a switch between limitations causes discontinuities in decomposition and decomposer demand values due to the change in their definitions. The thresholding provides a realistic mechanism to determining when a switch occurs.

Acknowledgements KC was supported by National Science Foundation award CMMI-1233397 and by a Margaret and Herman Sokol Research Award. EF and LB were supported by National Science Foundation award DMS-1853610. JAK was supported by National Science Foundation award CBET-1603741. We warmly thank Leah B. Shaw for reading and commenting on an early version of the manuscript.

Author Contributions KC, EF, and JAK developed the model. KC, EF, and LB performed the analysis. All authors participated in writing the manuscript.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Consent for publication All authors gave final approval for publication.

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