Model description

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July 22, 2016

1 Purpose of the model

Plant-soil-feedbacks (PSF) are critical for understanding plant population dynamics, community structure, and ecosystem functions (Ke and Miki 2015). Usually PSF are distinguished in litter feedbacks and microbial feedbacks (Ke and Miki 2015). Whereas the first ones influence competition by changing nutrient availability, the latter have direct influence on plant growth through mutualists or antagonists/pathogens.
In the last two decades a multitude a models has been designed to simulate either litter feedbacks (e.g. Daufresne and Hedin (2005); Clark et al. (2005); Eppinga et al. (2011)) or microbial feedbacks (e.g. Bever et al. (1997); Bever (2003); Bonanomi et al. (2005); Eppinga et al. (2006); Kulmatiski et al. (2012)). A full integration of both, however, is still missing (Ke and Miki 2015).
The model presented here should be a first approach that ventures in this area. Even though the model still treats PSF as two independent processes (i.e. litter and microbial feedbacks) they can be activated in combination. This can help to improve our understanding of how PSF influence and shape plant communities.

2 Entities, state variables, and scales

Entities

The model comprises two competing plant species (further referenced as species A and B). To each species belongs a soil competitor community (Sa and Sb) that is cultivated by the species. To represent different PSF I made the simplification to divide the effects of the soil community in two groups. Here 'soil competitor' is used to represent the parts of the soil community that show mutualistic and antagonistic effects on the plant species. The parts of the soil community that govern decomposition of organic matter are summarized under the name 'soil decomposers'. This distinction is done to untangle the direct effects on plant growth and nutrient availability even though in real ecosystems they might be highly intertwined.

State variables

State variables in the model are species specific plant (B) and litter (D) biomass, available soil nitrogen (N), available light (L), the composition of the soil competitors (S_a and S_b) as well as the efficiency of the soil decomposers (Dc).

Scale

The spatial resolution of the model is approximate $1m^2$. The temporal resolution is 1 day.

3 Process overview

Primarily the model is a resource competition model *sensu* Tilman (1988) where two plant species compete for nitrogen and light. Plant growth (biomass gain) is based on species specific properties and available resources and influenced by different PSF.
The model distinguishes between plant litter feedbacks and microbial feedbacks.

Plants litter feedbacks influence plant growth in three ways. The availability of nutrients is partly determined by the quantity and quality of litter input. This input further influences the efficiency of soil decomposers. And finally the light availability is influenced by the quantity of litter.

Microbial feedbacks directly influence plant growth. Each plant species cultivates it's own soil competitors. These can have negative and/or positive feedbacks to the specie's and it's competitor's growth. The net effect for a species is simply the sum of the effect of it's own and it's competitors effects weighed by the proportional abundance of the soil competitors.
Mortality is modelled with a constant rate. However, mortality in the model does not necessarily mean the death of an individual plant but also comprises other processes like leaf turnover.

All processes are running simultaneously using ordinary differential equations.

4 Submodels

For a list with all variables and parameters see appendix A.

4.1 Biomass

Based on (Eppinga et al. 2011), biomass changes of a species are defined as:

$$\frac{dB_i}{dt} = Min\left\{g_{L,i}\frac{L}{k_{L,i}+L}, g_{N,i}\frac{N}{k_{N,i}+N}\right\}B_i - m_iB_i \tag{1}$$

Subscript i identifies the species under consideration. g_L and g_N are the maximum growth rates under light and nitrogen limitation (see eq. 8 9). These are

influenced by positive and/or negative feedback of the soil competitors, whereas the strength of the partial influence in based on the proportional abundance of the soil competitors (see eq. 8, 9, 6). Further k_L and k_N represents the light and nutrient availability at which half of g_L (g_N) is reached.
L, N represents the available Light and Nitrogen (see equation 10, 2).
Mortality in the model is implemented with a constant species specific mortality rate (m).

4.2 Nitrogen availability

Based on (Eppinga et al. 2011), nitrogen availability comprises nutrient supply, plant uptake (cf. eq 1), nutrient release from decomposition (see eq. 3) and loss from the ecosystem. Because plant density is expressed in $g\,m^{-2}$, plant uptake is also expressed per m^2. Yet, soil nitrogen availability is expressed as $mg\,kg^{-1}$. To convert plant uptake into a decrease of soil nitrogen availability the rooting depth (l_{root}) and soil bulk density (ρ) are included. We assume that rooting depth is constant and nitrogen is well mixed in this zone.

$$\begin{aligned}\frac{dN}{dt} = a(S-N) - \sum_{i=1}^{2} \frac{q_{N,i}}{\rho l_{root}} Min\left\{ g_{L,i}\frac{L}{k_{L,i}+L}, g_{N,i}\frac{N}{k_{N,i}+N} \right\} B_i \\ + \sum_{i=1}^{2} \frac{q_{N,i}^2}{Q_{N,i}\rho l_{root}} \alpha_{N,i} d_i D_i Dc\end{aligned} \tag{2}$$

Here PSF operate not only in the plant uptake (cf. eq. 1) but also in the decomposition (cf. eq. 3).

4.3 Litter mass

Based on (Eppinga et al. 2011), changes in litter mass are based on the input through mortality, as well as the decomposition of litter. Whereas the first is based on the biomass and a constant species specific mortality rate (m), the latter is influenced by the litter quantity and quality (q_N), as well as the efficiency of the soil decomposers (Dc).

$$\frac{dD_i}{dt} = m_i B_i - \frac{q_{N,i}}{Q_{N,i}} d_i D_i Dc \tag{3}$$

The efficiency of the soil decomposer itself is a function of the litter input (see eq. 4).

4.4 Soil decomposers

Soil decomposers can react in two ways on litter input. First the efficiency of the soil decomposers in not only dependent on the quality of the own litter (this is what Q_N is scaled for) but on the quantity and quality of the litter input of both species. Hence, higher quality input enhances, lower quality input deteriorates decomposition. It is to note that also this implementation is a strong simplification of real world litter dynamics. However, it has been shown that high-quality litter accelerates the decomposition of lower quality litter and vice versa (McArthur et al. 1994; Gartner and Cardon 2004).

$$\frac{dDc_a}{dt} = -\left(dc - \frac{qN_a}{QN_a}\frac{B_a}{B_a + B_b} + \frac{qN_b}{QN_b}\frac{B_b}{B_a + B_b}\right) * sccr \tag{4}$$

The second mechanism that can be incorporated is the so called home-field advantage (Ayres et al. 2009). This means litter is decomposed faster if the soil community is used to this litter. In the model the decomposition rate is coupled on Sa. Here the changes in the efficiency of the soil decomposers are defined as:

$$Dc_a = 1 + S_a * hfa \tag{5}$$

Besides these effects the soil decomposer community can react in both cases with a delay to changed conditions (see *sccr* in equations) . By creating a buffer between input and release soil decomposers can weaken the influence of the plant community on nutrient availability (Miki et al. 2010).

I chose to distinguish the effects because litter dynamics are highly complex. Effects like the home-field advantage are often, but not always to be found in ecosystems (Austin et al. 2014). For further model development a more differentiated view on litter dynamics, i.e. by coupling the two processed described here can help to represent more realistic litter dynamics in the model. Litter quality is assumed to be constant during decomposition, following e.g. Eppinga et al. (2011).

4.5 Soil competitors

Modelling of the soil competitors is based on Bever (2003). To reduce the complexity in the system, the soil competitor community is reduced to a one dimensional scale. This scale represents the proportional influence of the different soil competitors. This proportional influence is a function of the composition of the plant community. The idea behind this is that each plant species cultivates a soil competitor community. This community feedbacks to the plant species and also to the other species as described in Eq. 8, 9.

$$\frac{dS_a}{dt} = -(S_a - \frac{B_a}{B_a + B_b})) * sccr \tag{6}$$

Because the abundance of the soil competitors is a proportional value we can state that:

$$S_b = 1 - S_a \tag{7}$$

where S_a is the soil competitor community cultivated by species A and S_b the soil competitor community cultivated by species B. *sccr* defines the rate of adaptation of the soil competitors. This allows to simulate a delay in the reaction of the soil competitors.

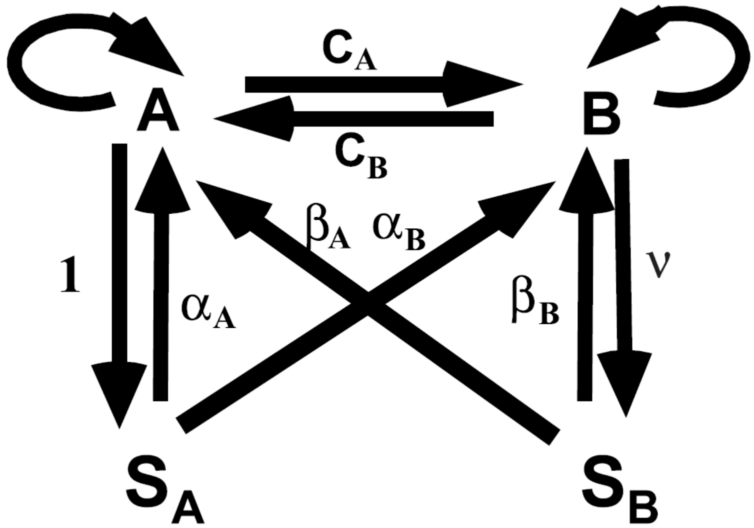

Figure 1: Depiction of the influence of the soil competitors on plant growth. Figure from Bever (2003)

4.6 Influence of soil competitors

The influence of the soil competitors is based on Bever (2003). Here we take the assumption that both the growth under light as under nitrogen limitation is affected equally by the soil competitors. The net influence is the sum of all partial influences, where *alpha* described the influences of Sa and *beta* the influences of Sb. The subscript determines the direction of the influence. E.g. $alpha_a$ is the influence of Sa on species A (see also figure 1). To avoid negative growing rates, which would happen if e.g. $\alpha_a + \beta_a > gL_a$ the minimum value for the gL and gN is 0.

$$gLi = max\{0, \alpha_i * S_a + beta_i(1 - S_a)\} \tag{8}$$

$$gN_i = max\{0, \alpha_i * S_a + beta_i(1 - S_a)\} \tag{9}$$

4.7 Light

Based on (Eppinga et al. 2011). Light availability in the model is based on light supply (L_0), plant interception, litter interception and a light loss term (L). Light input is assumed to be constant. Light interception of both vegetation and litter is based on Beer's Law. The differences in plant properties (i.e. height:mass ratio and shoot density) are respected by the species specific parameters γ and

$alpha_L$. However, also this equation is a large simplification as e.g. plant height is not explicitly considered in the model (see also Eppinga et al. (2011)).

$$\frac{1}{c_{Rate}}\frac{dL}{dt} = L_0 - \sum_{i=1}^{2}\gamma_{L,i}B_iL - \sum_{i=1}^{2}\alpha_{L,i}D_iL - L \tag{10}$$

A Model parameters and interpretation

Parameter	Interpretation	Units
$g_{L,A}$	Maximum growth rate of A under light limitation	day^{-1}
$g_{L,B}$	Maximum growth rate of B under light limitation	day^{-1}
$k_{L,A}$	Light availability at which A reaches half its maximal growth rate (if light limited)	$molm^{-2}$
$k_{L,B}$	Light availability at which B reaches half its maximal growth rate (if light limited)	$molm^{-2}$
$g_{N,A}$	Maximum growth rate of A under nitrogen limitation	day^{-1}
$g_{N,B}$	Maximum growth rate of B under nitrogen limitation	day^{-1}
$k_{N,A}$	Nitrogen availability at which A reaches half its maximal growth rate (if N limited)	$mgkg^{-1}$
$k_{N,B}$	Nitrogen availability at which B reaches half its maximal growth rate (if N limited)	$mgkg^{-1}$
m_A	Mortality rate A	day^{-1}
m_B	Mortality rate B	day^{-1}
a	Turnover rate of nutrient supply	day^{-1}
S	Nitrogen availability in absence of plants	$mgkg^{-1}$
$q_{N,A}$	Nitrogen content of tissue of A	mgg^{-1}
$q_{N,B}$	Nitrogen content of tissue of B	mgg^{-1}
ρ	Soil bulk density	gm^{-3}
l_{root}	Rooting depth of plant species	m
$\alpha_{N,A}$	Nutrient–litter feedback coefficient A	-
$\alpha_{N,B}$	Nutrient–litter feedback coefficient B	-
d_A	A litter decomposition rate	day^{-1}
d_B	B litter decomposition rate	day^{-1}
L_0	Light supply rate	$molm^{-2}day^{-1}$
$\gamma_{L,A}$	Light interception coefficient A	m^2g^{-1}
$\gamma_{L,B}$	Light interception coefficient B	m^2g^{-1}
$\alpha_{L,A}$	Light–litter feedback coefficient A	m^2g^{-1}
$\alpha_{L,B}$	Light–litter feedback coefficient B	m^2g^{-1}
$Q_{N,A}$	Nitrogen content of A litter at which ii decomposes at rate d_A	mgg^{-1}
$Q_{N,B}$	Nitrogen content of B litter at which ii decomposes at rate d_B	mgg^{-1}
c_{rate}	Parameter determining the characteristic timescale of light dynamics	day^{-1}
B_A	Aboveground living biomass of A	gm^{-2}
B_B	Aboveground living biomass of B	gm^{-2}
N	Nitrogen availability in soil	$mgkg^{-1}$
D_A	Aboveground litter mass of A	gm^{-2}
D_B	Aboveground litter mass of B	gm^{-2}
L	Light availability	$molm^{-2}day^{-1}$

t	Time	day
α_A	Influence of S_a on A	-
α_B	Influence of S_a on B	-
β_A	Influence of S_b on A	-
β_B	Influence of S_b on B	-
S_a	Proportional abundance of soil competitor community S_a	-
S_b	Proportional abundance of soil competitor community S_b	-
$sccr$	Speed with which decomposer community reacts to changes in litter quality	day^{-1}
Dc	Proportional efficiency of decomposer community compared to monoculture	-
hfa	Strength of the home field advantage	-

Table 1: Overview about parameter in the model. Table largely build on Eppinga et al. (2011) and Bever (2003)

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