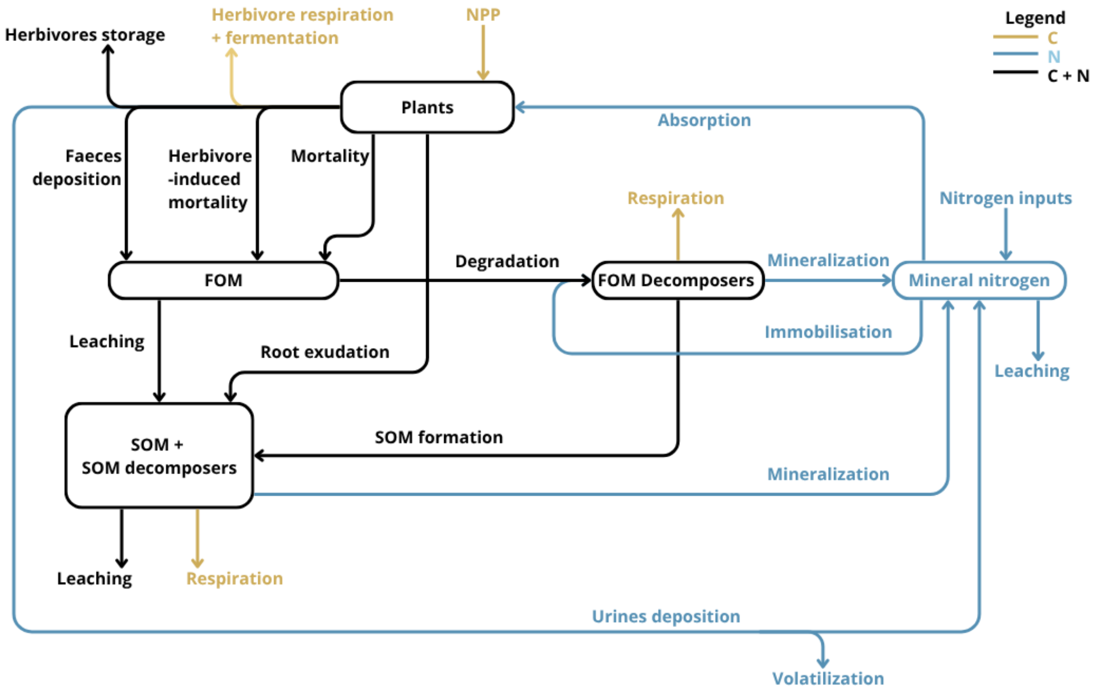
Supplementary materials



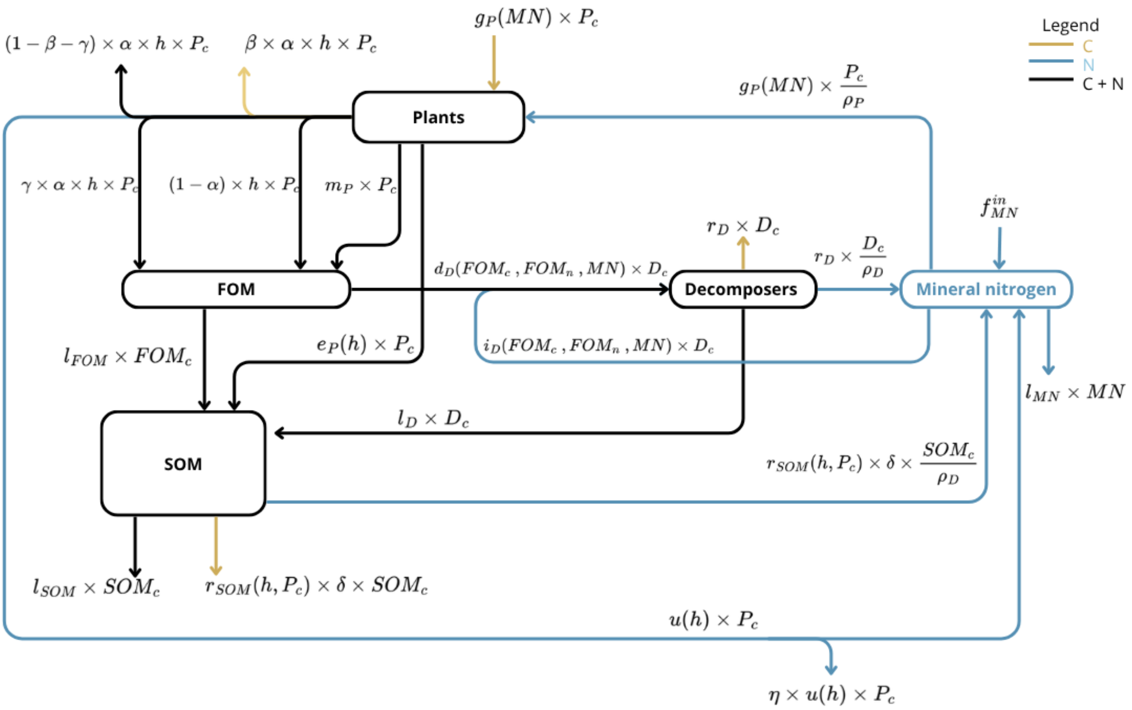


Figure S1 : Diagram of the grassland ecosystem model representing the carbon and nitrogen fluxes and their equations between plants, herbivores, FOM, decomposers, SOM and soil mineral nitrogen *Carbon fluxes are depicted in brown, nitrogen fluxes in blue, and in black are material fluxes that combine carbon and nitrogen (in biomass).*

$\rho_P > \frac{FOM_c}{FOM_n} > \rho_D$ **explanations :**

We have: $\rho_P > \rho_f > \rho_D > 0$ and so:

$$\left(\frac{m_P}{\rho_P} + \frac{(1-\alpha)\times h}{\rho_P} + \frac{\gamma\times\alpha\times h}{\rho_P}\right)\times P_c < \left(\frac{m_P}{\rho_P} + \frac{(1-\alpha)\times h}{\rho_P} + \frac{\gamma\times\alpha\times h}{\rho_f}\right)\times P_c$$

$$< \left(\frac{m_P}{\rho_D} + \frac{(1-\alpha)\times h}{\rho_D} + \frac{\gamma\times\alpha\times h}{\rho_D}\right)\times P_c$$

$$\Leftrightarrow \frac{(m_P + (1-\alpha)\times h + \gamma\times\alpha\times h)\times P_c}{\left(\frac{m_P}{\rho_P} + \frac{(1-\alpha)\times h}{\rho_P} + \frac{\gamma\times\alpha\times h}{\rho_P}\right)\times P_c}$$

$$> \frac{(m_P + (1-\alpha)\times h + \gamma\times\alpha\times h)\times P_c}{\left(\frac{m_P}{\rho_P} + \frac{(1-\alpha)\times h}{\rho_P} + \frac{\gamma\times\alpha\times h}{\rho_f}\right)\times P_c}$$

$$> \frac{(m_P + (1-\alpha)\times h + \gamma\times\alpha\times h)\times P_c}{\left(\frac{m_P}{\rho_D} + \frac{(1-\alpha)\times h}{\rho_D} + \frac{\gamma\times\alpha\times h}{\rho_D}\right)\times P_c}$$

$$\Leftrightarrow \rho_P > \frac{(m_P + (1-\alpha)\times h + \gamma\times\alpha\times h)\times P_c}{\left(\frac{m_P}{\rho_P} + \frac{(1-\alpha)\times h}{\rho_P} + \frac{\gamma\times\alpha\times h}{\rho_f}\right)\times P_c} > \rho_D$$

It means that the sum of the fluxes arriving at the FOM compartment has a C:N ratio greater than ρ_D and lower than ρ_P.

Concerning the flux leaving the FOM compartment :

- The leaching flux has the same ratio than the FOM compartment
- The decomposition flux is also leaving the FOM with the same C:N ratio as the FOM.

Then the FOM C:N ratio is determined by the fluxes entering the FOM compartment, which have a higher ratio than ρ_D and a lower ratio than ρ_P. Then $\rho_P > \frac{FOM_c}{FOM_n} > \rho_D$

Expression of the stocks at steady-state depending on parameters :

At steady-state all stock variations over time are equal to zero. The equilibrium points of the model are the values of the stocks at steady-state.

Equilibrium 1 : For $P^* = 0$

$P_c^* = 0$; $FOM_c^* = 0$; $FOM_n^* = 0$; $D_c^* = 0$; $MN^* = \frac{f_{MN}^{in}}{l_{MN}}$; $SOM_c^* = 0$; $SOM_n^* = 0$

Equilibrium 2 : For $P^* > 0$ and $D^* = 0$

P_c^* *is the smallest solution to a polynomial of degree* 2

$A \times P_c^2 * + B \times P_c * + C = 0$ with :

$$A = [\ (a_e + b_e \times h)^2 \times w \times \frac{\delta}{\rho_D} + (a_e + b_e \times h) \times w \times \delta \times$$

$$(-\mu_P \frac{MN}{MN + K_P} \times \frac{1}{\rho_P} + (1 - \eta) \times \alpha \times h \times (\gamma \times (\frac{1}{\rho_h} - \frac{1}{\rho_f}) + \frac{1}{\rho_P} - \frac{1 - \beta}{\rho_h}))\ ]$$

$$B = [\ (a_e + b_e \times h) \times w \times \frac{\delta}{\rho_D} \times l_{FOM} \times FOM_c^* + (a_e + b_e \times h) \times w \times \delta \times (f_{MN}^{in} - l_N \times MN^*)$$

$$+ l_{SOM} \times (-\mu_P \frac{MN}{MN + K_P} \times \frac{1}{\rho_P} + (1 - \eta) \times \alpha \times h \times (\gamma \times (\frac{1}{\rho_h} - \frac{1}{\rho_f}) + \frac{1}{\rho_P} - \frac{1 - \beta}{\rho_h}))\ ]$$

$$C = l_{SOM} \times (f_{MN}^{in} - l_{MN} \times MN^*)$$

$FOM_c^* = \frac{P_c * \times (m_P + (1-\alpha) \times h + \gamma \times \alpha \times h)}{l_{FOM}}$; $FOM_n^* = \frac{P_c^* \times (\frac{m_P}{\rho_P} + \frac{(1-\alpha) \times h}{\rho_P} + \frac{\gamma \times \alpha \times h}{\rho_f})}{l_{FOM}}$

$D_c^* = 0$; $MN^* = \frac{(m_P + h + a_e + b_e \times h) \times K_P}{\mu_P - m_P - h - (a_e + b_e \times h)}$

$SOM_c^* = \frac{l_{FOM} \times FOM_c^* + (a_e + b_e \times h) \times P_c^*}{l_{SOM} + (a_e + b_e \times h) \times P_c * \times w \times \delta}$;

$$SOM_n^* = \frac{l_{FOM} \times FOM_n^* + (a_e + b_e \times h) \times \frac{P_{c*}}{\rho_P} - (a_e + b_e \times h) \times P_c^* * \times w \times \frac{d}{\rho_D} \times SOM_c^*}{l_{SOM}}$$

Equilibrium 3 : For $P^* > 0$ and D* limited by N

P_c^* *is the smallest solution to a polynomial of degree* 2

$A \times P_c^2 * + B \times P_c * + C = 0$ with :

$$A = (a_e + b_e \times h) \times w \times \delta \times [\frac{m_P + (1-\alpha) \times h + \gamma \times \alpha \times h}{r_D + l_D} \times (\frac{r_D}{\rho_D} - (r_D + l_D) \times (\frac{1}{\rho_D} - \frac{FOM_n^*}{FOM_c^*})) +$$

$$(1-\eta) \times \alpha \times h \times (\gamma \times (\frac{1}{\rho_h} - \frac{1}{\rho_f}) + \frac{1}{\rho_P} - \frac{1-\beta}{\rho_h}) - \frac{m_P + h + (a_e + b_e \times h)}{\rho_P} +$$

$$\frac{1}{\rho_D} \times (\frac{l_D}{r_D + l_D} \times (m_P + (1-\alpha) \times h + \gamma \times \alpha \times h) + a_e + b_e \times h)]$$

$$B = (a_e + b_e \times h) \times w \times \delta \times [f_{MN}^{in} - l_{MN} \times MN^* + (\frac{r_D}{\rho_D} - (r_D + l_D) \times (\frac{1}{\rho_D} - \frac{FOM_n^*}{FOM_c^*})) \times \frac{-l_{FOM} \times FOM_c^*}{r_D + l_D}]$$

$$+ l_{SOM} \times [\frac{m_P + (1-\alpha) \times h + \gamma \times \alpha \times h}{\varphi + l_D} \times (\frac{r_D}{\rho_D} - (r_D + l_D) \times (\frac{1}{\rho_D} - \frac{FOM_n^*}{FOM_c^*}))$$

$$+ (1-\eta) \times \alpha \times h \times (\gamma \times (\frac{1}{\rho_h} - \frac{1}{\rho_f}) + \frac{1}{\rho_P} - \frac{(1-\beta)}{\rho_h}) - \frac{m_P + h + (a_e + b_e \times h)}{\rho_P}]$$

$$+ (a_e + b_e \times h) \times w \times \frac{\delta}{\rho_D} \times (l_D \times \frac{-l_{FOM} \times FOM_c^*}{r_D + l_D} + l_{FOM} \times FOM_c^*)$$

$$C = l_{SOM} \times [f_{MN}^{in} - l_{MN} \times MN + (\frac{r_D}{\rho_D} - (r_D + l_D) \times (\frac{1}{\rho_D} - \frac{FOM_n^*}{FOM_c^*})) \times \frac{-l_{FOM} \times FOM_c^*}{r_D + l_D}]$$

$$FOM_n^* = FOM_c^* \times \frac{\frac{m_P}{\rho_P} + \frac{(1-\alpha) \times h}{\rho_P} + \frac{\gamma \times \alpha \times h}{\rho_f}}{m_P + (1-\alpha) \times h + \gamma \times \alpha \times h} \;;$$

There is an infinite number of solutions for FOM_c^*

$$D_c * = \frac{P_c^* \times (m_P + (1-\alpha) \times h + \gamma \times \alpha \times h) - l_{FOM} \times FOM_{c^*}}{r_D + l_D} \;;$$

$$SOM_c^* = \frac{l_D \times D_c^* + l_{FOM} \times FOM_c^* + (a_e + b_e \times h) \times P_c^*}{l_{SOM} + (a_e + b_e \times h) \times P_c * \times w \times \delta} \;;$$

$$SOM_n^* = \frac{l_D \times \frac{D_c^*}{\rho_D} + l_{FOM} \times FOM_n^* + (a_e + b_e \times h) \times \frac{P_c^* *}{\rho_P} - (a_e + b_e \times h) \times P_c^* \times w \times \frac{\delta}{\rho_D} \times SOM_c^*}{l_{SOM}};$$

$$MN^* = \frac{(m_P + h + a_e + b_e \times h) \times K_P}{\mu_P - m_P - h - (a_e + b_e \times h)} \text{ et } MN^* = \frac{r_D + l_D}{a_i} \times \left(\frac{1}{\rho_D} - \frac{\frac{m_P}{\rho_P} + \frac{(1-\alpha) \times h}{\rho_P} + \frac{\gamma \times \alpha \times h}{\rho_f}}{m_P + (1-\alpha) \times h + \gamma \times \alpha \times h}\right)$$

Equilibrium 4 : For $P^* > 0$ and D* limited by C

P_c^* *is the smallest solution to a polynomial of degree* 2 , see equilibrium 3

$$D_c^* = \frac{P_c^* \times (m_P + (1-\alpha) \times h + \gamma \times \alpha \times h) - l_{FOM} \times FOM_c *}{\varphi + l_D}$$

$$FOM_c^* = \frac{r_D + l_D}{a_d} \;;\; FOM_n^* = FOM_c^* \times \frac{\frac{m_P}{\rho_P} + \frac{(1-\alpha) \times h}{\rho_P} + \frac{\gamma \times \alpha \times h}{\rho_f}}{m_P + (1-\alpha) \times h + \gamma \times \alpha \times h}$$

$$MN^* = \frac{(m_P + h + a_e + b_e \times h) \times K_P}{\mu_P - m_P - h - (a_e + b_e \times h)} \;;\; SOM_c^* = \frac{l_D \times D_c^* + l_{FOM} \times FOM_c^* + (a_e + b_e \times h) \times P_c^*}{l_{SOM} + (a_e + b_e \times h) \times P_c * \times w \times \delta} \;;$$

$$SOM_n^* = \frac{l_D \times \frac{D_c *}{\rho_D} + l_{FOM} \times FOM_n^* + (a_e + b_e \times h) \times \frac{P_c *}{\rho_P} - (a_e + b_e \times h) \times P_c * \times w \times \frac{\delta}{\rho_D} \times SOM_c^*}{l_{SOM}}$$

Table S1 : Expression of the equilibrium points of the model depending on parameters

At equilibrium 1, all the compartments are empty except the mineral nitrogen stock (MN). If plants die, herbivores can't survive without being supplemented. With no fresh organic matter (dead tissues from plants and excrements from herbivores) FOM decomposers can't survive either. Without FOM and its decomposers, the SOM stock is empty. This situation can arise if plant mortality increases sharply, due to drought or a strong grazing intensity for example.

At equilibrium 2, FOM decomposers die but none of the other compartments are empty. This equilibrium is not representative of the functioning of a grassland ecosystem, so it will not be studied in this paper.

At equilibrium 3, both FOM decomposers and plants are nitrogen limited. This equilibrium point is only valid for a specific set of parameters that are such that:

$$MN^* > 0 \;;\; P_c^* > 0 \text{ and } \frac{(m_P + h + a_e + b_e \times h) \times K_P}{\mu_P - m_P - h - (a_e + b_e \times h)} = \frac{r_D + l_D}{a_i} \times \left(\frac{1}{\rho_D} - \frac{\frac{m_P}{\rho_P} + \frac{(1-\alpha) \times h}{\rho_P} + \frac{\gamma \times \alpha \times h}{\rho_f}}{m_P + (1-\alpha) \times h + \gamma \times \alpha \times h}\right)$$

If the above equation is not respected, only plants will survive and FOM decomposers will die out. This phenomenon of exclusion-competition happens when the survival of two groups depends on a single resource.

At equilibrium 4

A condition for the existence of this equilibrium point is that the value of MN at equilibrium point is strictly positive :

$$MN^* > 0$$

$$\Leftrightarrow \mu_P - (m_P + h + e_P(h)) > 0$$

$$\Leftrightarrow \mu_P - m_P - h - a_e - b_e \times h > 0$$

$$\Leftrightarrow h < \frac{\mu_P - m_P - a_e}{b_e + 1}$$

Another condition for the existence of this equilibrium point is that the FOM decomposers are carbon limited : $a_d \times FOMc* > \frac{a_i \times MN*}{\frac{1}{\rho_D} - \frac{FOM_n*}{FOM_c*}}$

$$\Leftrightarrow a_d \times FOMc* \times \left(\frac{1}{\rho_D} - \frac{FOM_n*}{FOM_c*}\right) < a_i \times MN*$$

$$\Leftrightarrow a_d \times \frac{FOMc*}{MN*} \times \left(\frac{1}{\rho_D} - \frac{FOM_n*}{FOM_c*}\right) < a_i$$

$$\Leftrightarrow (r_D + l_D) \times \frac{\mu_P - (m_P + h + a_e + b_e \times h)}{(m_P + h + a_e + b_e \times h) \times K_P} \times \left(\frac{1}{\rho_D} - \frac{\frac{m_P}{\rho_P} + \frac{(1-\alpha) \times h}{\rho_P} + \frac{\gamma \times \alpha \times h}{\rho_f}}{m_P + (1-\alpha) \times h + \gamma \times \alpha \times h}\right) < a_i$$

Finally the value of P_c^* at equilibrium has to be strictly positive, which is the smallest solution to a polynomial of degree 2 (see equilibrium 3). This condition gives the upper value for h.

Values of the parameters

Symbol	Value	Unit	Source
ρ_P	35	$g\ C.g\ N^{-1}$	Soussana and Lemaire, 2014
a	0.006882	day^{-1}	Fu and al., 2017
K	0.324	$g\ C.m^{-2}$	calibrated
m	0.00464	day^{-1}	Perveen et al., 2014
a_e	0.00036	day^{-1}	Chari et al., 2024
l_{FOM}	0.000422868	day^{-1}	Perveen et al., 2014
μ	0.0000847	$m^2.g\ C^{-1}.day^{-1}$	Li and al., 2021 + calibrated
i	0.004*	$m^2.g\ C^{-1}.day^{-1}$	Li and al., 2021
ρ_D	11	$g\ C.g\ N^{-1}$	Manzoni et al., 2008/ Wutzler et al., 2024
φ	0.0368857	day^{-1}	Perveen et al., 2014
l_D	0.016906	day^{-1}	Perveen et al., 2014
q	0.0627704	$g\ N.m^{-2}.day^{-1}$	Perveen et al,. 2014
l_{MN}	0.00267704	day^{-1}	Perveen et al., 2014
l_{SOM}	0.00014	day^{-1}	calibrated
b_e	0.2	dimensionless	calibrated
δ	0.003	dimensionless	Perveen et al., 2014
w	0.0532	$m^2.g\ C^{-1}$	calibrated
h	7.98799×10^{-4}	day^{-1}	Perveen et al,. 2014
ρ_H	11	$g\ C.g\ N^{-1}$	Elser et al., 2000
α	0.75	dimensionless	calibrated
β	0.6	dimensionless	Soussana and Lemaire, 2014
γ	0.37	dimensionless	Soussana and Lemaire, 2014
ρ_f	25	$g\ C.g\ N^{-1}$	Lecomte et al., 2002
η	0.15	dimensionless	Selbie et al., 2015

*Arbitrary high value so that FOM decomposers are not constrained by N.

Table S2 : Definition, value, unit and reference of parameters of the model. *Most of the parameter values come from two studies (Perveen et al., 2014; Allard et al., 2007) carried out on a temperate permanent grassland, at an altitude of 1040 m in France (Laqueuille, 45°38'N, 2°44'E), with average annual precipitation of 1200 mm and an average temperature of 7 °C.*

Choice of values for the parameters

Most of the parameter values (Table S1) come from a mechanistic model called SYMPHONY (Perveen et al., 2014) which is similar to the model of this paper but does not take into account the fluxes induced by the presence of herbivores. Parameter values SYMPHONY were estimated both from published studies and specific measurements carried out on a temperate permanent grassland, at an altitude of 1040 m in France (Laqueuille, 45°38′N, 2°44′E), with average annual precipitation of 1200 mm and an average temperature of 7 °C. Regarding the other parameters, parameters e and β were calculated taking into account that 25–40% of the ingested carbon (depending on the digestibility of the grazed grasses) returns to the grassland in the form of excreta, mainly in the form of faeces (Soussana and Lemaire, 2014). Parameters μ was calculated based on a gross soil immobilization rate in grasslands of 2.7 $mg\,N.kg\,soil^{-1}.day^{-1}$ (Li et al. 2021) with a microbial biomass of 800 $mg\,C.kg\,soil^{-1}$ (Zhao et al. 2017; Rich et al., 2019). Parameter i was chosen arbitrarily high so that decomposers would not be constrained by N. Parameter z was calculated considering a root exudate C flux of $0.069\ kg\ C\ m^{-2}\ y^{-1}$ (Chari et al. 2024). Parameter m is the difference between the rate of plant carbon deposition (equal to $0.005\ day^{-1}$; Perveen and al., 2014) and the rate of root exudate z. The parameters K, α, η, s, and w were calibrated to reach at steady state, the values of stocks obtained experimentally in Perveen et al. (2014) (Table 3). The stocks reached with our model at equilibrium 4 (Table 2) for the values of parameters set of Table S1, the stocks obtained with the model SYMPHONY (Perveen and al., 2014) and the observed values given in Perveen and al. (2014) are given in Table 3.

	observed in Perveen and al. 2014	predicted with SYMPHONY	predicted with the present model	unit
P_c^*	525 ± 107	507.49	524.68	$gC.m^{-2}$
FOM_c^*	635 ± 129	634.99	635.085	$gC.m^{-2}$
MN^*	2.09 ± 0.68	2.98	2.0906	$gN.m^{-2}$
D_c^*	/	42.72	44.37	$gC.m^{-2}$

Table S3 : *Comparison of plant carbon stock (P_c^*), Fresh organic matter carbon stock (FOM_c^*), mineral nitrogen stock (MN^*) and decomposers carbon stock (D_c^*) obtained experimentally in Perveen and al. 2014, predicted with the SYMPHONY model (Perveen and al.,2014) and predicted with our model.*

With our model and the values of parameters set Table 2, the SOM carbon stock at steady state is equal to $7037.14\ gC.m^{-2}$. Then the total carbon stock of the grassland which is the sum of all the carbon stocks of the model (P_c^* , FOM_c^* , D_c^* , SOM_c^*) is equal to $8241\ gC.m^{-2}$. This result is close to the national (French) average of stocks under permanent grassland, which is $8460\ gC.m^{-2}$ (Pellerin et al. 2021).

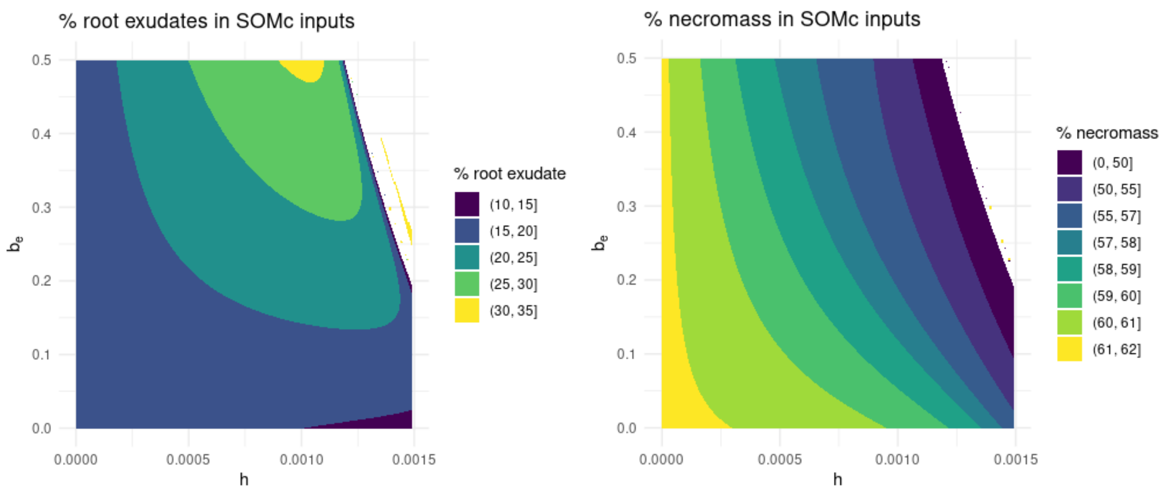


Figure S3 : Contribution of root exudates and SOMc formation by FOM decomposers to SOM_c^* input fluxes as a function of grazing intensity (h) and the herbivore-induced root exudation factor (b_e).

SOM_c formation by FOM decomposer plays a key role, accounting for more than half of the SOM_c^* input fluxes. It can even reach up to 62% of these input fluxes depending on grazing intensity.