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Simulation of multi-species plant communities in perturbed and nutrient-limited grasslands: development of the growth model ModVege

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Abstract: Simulating the dynamics of plants species or types in grassland communities remains an open area of research for which the Community Simulation Model (CoSMo) offers novel approaches. The grassland model ModVege was first parameterised based on a functional vegetation typology, in which types "A" and "B" include fast-growing grass species with a phenology-dependent nutrient-capture strategy inherent to fertile grasslands, while the nutrient conservation strategy and late flowering characterise the other types as "b". ModVege was then coupled to the CoSMo rule set to dynamically simulate the relative abundance of plant functional types or individual species, assessed across fertilised and unfertilised, abandoned and mown conditions in a grassland site of the Massif Central of France. While for the simulation of aboveground biomass, model performance is not unambiguously linked to explicit consideration of plant diversity, the simulation of relative abundance for the whole community is satisfactory (relative root mean square error of ~13-25% when simulating functional types and ~28-52% when simulating species). This study extends previous studies by coupling CoSMo for the first time to a grassland-specific model and applying it to conditions (long-term observations, extended number of plant species, absence of fertilisation, frequent mowing and abandonment) never investigated before.

Keywords: CoSMo; grassland modelling; ModVege; multi-species-grasslands; plant functional types; relative abundance

1. Introduction

Grasslands often contain a high diversity of plants, which is of interest for wildlife conservation, for a diverse forage resource in relation to feed quality and for the resources provided to micro- and macro-fauna [1, 2]. This plant diversity can be described in different ways and studied using different approaches [3]. For instance, the number of individual species present in a grassland (species richness) informs about the ecological or patrimonial status of the communities. However, despite experimental evidence of causal relationships between species number, ecosystem productivity and carbon sequestration [4, 5], species richness is not an accurate indicator of the agronomic value of grasslands (e.g. productivity, quality, precocity). For that, herbaceous species are often classified into three taxonomic groups, namely grasses, legumes and forbs, the latter two playing a decisive role in the overgrowth of mixtures [6]. Both species richness and taxonomic diversity do not take into account whether plant species or groups of species are similar or differ in their attributes (or traits). Taxonomic-based analyses have thus evolved to explore species coexistence [7] and ecosystem functioning based on species traits (functional diversity). Functional groups highlight the traits of plant species to identify the main types of plant species present in a grassland based on biological characteristics (functional traits) that correspond to similar functioning or strategies [8]. In fact, plant functional traits mediated by plant species composition affect most key ecosystem properties, depending on the relative contribution of a given species to the total vegetation biomass [9-11]. As such, functional diversity characterises the agronomic value of grasslands, e.g. a grassland with high functional diversity can be exploited for its resilience to extreme weather events [12], and functional diversity can be an indicator of grassland ecosystem services [13, 14].

The concept of functional traits (or plant functional diversity), which provides a generic approach to characterise vegetation types [15], is attractive as a tool for inferring ecosystem processes (e.g. plant growth) through aggregated

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traits of dominant species other than weather, soil and management factors [14]. Plant traits and trait-based plant classifications thus provide a sound scientific basis for reckoning the provision of ecosystem services and guiding grassland management [16, 17]. This can be done through a typology, i.e. a set of rules to define the characteristics of an observed system (here the kind of grassland), which facilitates its classification and the assessment of the ecosystem services provided [18]. Cruz et al. [19] conceived a grass species typology with the aim to provide support to grassland advisors via a generic method facilitating the manipulation of complex information, namely on the linkage between biodiversity and grassland performance (e.g. forage production). For that, Cruz et al. [19] and Theau et al. [20] proposed a classification of perennial forage grasses based on six functional characteristics to discriminate between biomass production and fodder quality of species mixtures. This functional typology was based on 38 grass species commonly found in the upland areas of central and southern France, which were characterised under similar and controlled pedo-climatic conditions in order to obtain differences only due to their physiological/morphological peculiarities. These peculiarities include the growth strategies (capture or conservation of resources) and phenology (early- or late-growth and flowering) of the plants, which are rendered from six morphological and phenological traits [21]: leaf dry matter content, specific leaf area, leaf lifespan, leaf resistance to breakage and, for the whole plant, flowering date and maximum plant height. This functional composition, based on the identification of dominant grass species and four main types (A, B, C, D) makes it possible to create a classification according to the dates of growth peaks, and the digestibility of leaves and stems. Types A and B (fast growing, phenology-dependent nutrient-capture strategy) dominate in fertile grasslands, while the opposite is observed for types C and D (slow growing, nutrient conservation strategy, late flowering). A-type and B-type grasslands are characterised by a high nutritive value in terms of digestibility for livestock feed at the beginning of the first vegetation cycle (and a rapid decline in nutritive value with early-maturity plants) and a high biomass accumulation [22]. Conversely, types C and D species are generally characterised by low digestibility values at the beginning of the cycle (followed by a slower decline during the rest of the vegetation cycle), due to later plant maturity and lower biomass accumulation [23]. Cruz et al. [24] defined additional types to characterise tall, late-flowering species in fertile (type "b") or poor (type "d") soils. From this knowledge-based classification, it is possible to parameterise alternative grassland types for modelling purposes, aimed at predicting the dynamics of herbage biomass, structure and digestibility as a function of management practices and climate [25, 26]. Simulation models combining community traits with soil, climate and management are widely used to predict grassland productivity and biophysical/biogeochemical cycles [27, 28]. In these models, plant traits are generally considered as static inputs (i.e. model parameters) that characterise the mean vegetation of the community, which become specific and dynamic when plant diversity is taken into account. Modelling solutions linking the processes and dynamics of plant types to the processes and dynamics of communities are mostly integrated to specific models and for a limited number of species in a community [29-32]. A high detail of plant interactions can be achieved at the expense of detailed process descriptions, while niche differentiation needs to be improved to simulate the coexistence of several species [33]. DynaGraM [34] is a modelling solution addressing theoretical questions about the response of a grassland species model to climatic, edaphic and management forcing agents as a function of the state of the plant community. Conceived as a mechanistic model of resource competition [35], it is a stand-alone solution representing the regulation of green biomass and plant competition from the standpoint of resource dynamics [36], integrating eco-physiological and biophysical details inherited from ModVege [25, 26], originally developed to predict vegetation growth from permanent grasslands in central France. Another approach, the Community Simulation Model (CoSMo), provides means for incorporating plant diversity in grassland models [37]. With a set of parameter values for each plant type in a community (individual species or groups of species such as functional types), CoSMo updates the relative abundance of different plant categories (at the level of individual species or taxonomic or functional groups of species) at each time step. The characterisation of the different plant types is performed using different sets of values for the same parameters (common set of parameters for all plant categories). As the biological parameters of plant models are generally sensitive to environmental changes and farming practices, CoSMo translates these changes into a numerical framework through suitability functions (on a concept of Confalonieri et al. [38]). Competition and changes in the relative abundance of plant categories are simulated in response to hierarchical environmental drivers (biophysical and management factors, triggered or continuous), which represent the suitability of different plant categories to the conditions explored at each time step. On this basis, CoSMo derives (daily) vegetation parameter values for the plant community from the relative abundance of the different plant species or groups and the parameter values initially set to characterise the same plant species or group. These dynamically derived vegetation parameters are then used at each time step by the growth simulator (ModVege in our case). In doing so, CoSMo goes beyond the conventional assumption that the values assigned to the model parameters (by calibration, experimental measurement or from the literature) are time invariant and remain constant throughout the simulation period. The simplification of time-invariance of parameter values may be too limiting to meet the challenges facing agricultural systems, which implies that aspects related to plant diversity cannot be ignored in modelling studies [39]. Designed as a re-usable component, CoSMo was already coupled with generic crop models (CropSyst [40], WOFOST [41]) to explicitly and dynamically simulate the relative abundance of plant species in grasslands, and satisfactorily applied to annually mown grasslands in central Italy [42].

Here, the CoSMo suitability functions are exploited as a means of improving the grassland-specific model ModVege. A first approach, consistent with the level of complexity of the generic grassland simulator, dynamically models the relative abundance of functional types in a grassland community. A second approach adds complexity to ModVege to represent the dynamics of individual plant species in the community. The assessment of three modelling solutions - a grassland model in standalone, coupled versions for functional groups and individual species - was thus carried out for aboveground biomass and relative abundance of plant groups/species using multi-year field data from mown (fertilised or not) and undisturbed (abandoned) multispecies grasslands in the Massif Central of France.

2. Materials and Methods

2.1. The modelling framework

2.1.1. Generic grassland model (ModVege)

ModVege is a relatively simple process-based model that estimates herbage quantity and quality in managed, multi-species grasslands. It implements the conceptual framework originally proposed by [43, 44] to calculate the mass flow in four structural compartments of aboveground biomass on a daily time-step (Supplementary material, Figure A). The model development is based on the assumption that community behaviour can be explained by the mean traits of dominant grasses. The model addresses six basic functional groups of grasses [45] that can be combined in different proportions to simulate a wide range of grassland communities [25]. Environmental constraints are associated with water scarcity, high radiation levels and temperature extremes, within a purely source-driven model, where potential growth is expressed as a function of the photosynthetic active radiation intercepted [46]. The processes contributing to biomass turnover are growth, senescence and abscission. The onset of growth is assumed to occur when the cumulative thermal time since 1 January exceeds 200 °C-d for the first time. Water availability is related to the fractional water content, *W*=*WR*/*WHC*, where *WR* is the current water reserve and *WHC* is the water holding capacity. A simple bucket approach is used to evaluate *WR*, where precipitation is considered as an input and actual evapotranspiration (*AET*) and drainage as outputs. Drainage is assumed to occur whenever the difference between precipitation and *AET* exceeds the soil's absorption capacity, given by the difference between *WHC* and *WR*. Herbage growth is further controlled by the overall nutrient availability through a nutrient index, i.e. a relative measure of the overall nutritional status of the canopy, which can range from 0.35 in nutrient deficiency to 1.20 in heavily fertilised systems [47]. As there is no model component that simulates the nitrogen (N) cycle dynamically, the nutrition index is considered a site-specific parameter that can be reduced over time to represent the progressive depletion of N availability in unfertilised fields. Despite its simplifications, ModVege has been shown to perform well in a variety of environmental contexts and management regimes [48, 49], and is being developed [50] for application as a decision-support system [51].

2.1.2. Generic grassland model (ModVege)

CoSMo simulates plant communities through a mean parameterisation based on the relative abundance of each group/species. Its approach can be coupled with any generic grassland simulator. The relative abundance of plants species (or groups of species) depends on the hierarchical aggregation of several drivers (each one assuming values between 0 and 1), which are estimated to characterise the suitability and competitiveness of each group/species in a given context. The generic simulator community parameterisation ($y_{community}$) is updated at a daily time-step, for each simulator parameter (y) based on the relative abundance (SCP) of each group/species (i) of n simulated groups/species in a mixed cover, as follows:

$$y_{community} = \forall_y \sum_{i=1}^{n} (y_i \cdot SCP_i) \quad (1)$$

where the universal quantifier is encoded as ∀ (“for all”).

SCP_i is derived at each time step (dt), $dSCP_i(t)$, as follows:

$$\frac{dSCP_i\ (t)}{dt} = \left(\frac{Sfs_i(t) - \overline{Sfs(t)}}{I}\right) \quad (2)$$

where $Sfs_i(t)$ is the suitability factor for group/species i, $\overline{Sfs}(t)$ is the mean suitability factor for all groups/species and $80 \le I \le 120$ is an inertial replacement coefficient (suggested to be set at 100).

The term $Sfs_i(t)$ is calculated from the hierarchical suitability function of driver q for the species i, $HSf_{i,q}(t)$:

$$Sfs_i(t) = \sum_{q=1}^{z}(HSf_{i,q}(t)) \qquad (3)$$

where z is the number of drivers. In the current version, six drivers are hierarchically arranged: 1, management (cutting/grazing); 2, phenology; 3, air temperature; 4, light interception; 5, water availability; 6, N availability. They are hierarchically arranged as follows:

$$HSf_{i,q}(t) = \begin{cases} Sf_{i,q}(t) & q = 1 \\ \sqrt{HSf_{i,q-1}(t)} \cdot Sf_{i,q}(t) & otherwise \end{cases} \qquad (4)$$

Applying Eq. (3) to the case of z=6, the result is:

$$\begin{aligned} HSf_{i,1}(t) &= Sf_{i,1}(t) \\ HSf_{i,2}(t) &= \sqrt{Sf_{i,1}(t)} \cdot Sf_{i,2}(t) \\ HSf_{i,3}(t) &= \sqrt[4]{Sf_{i,1}(t)} \cdot \sqrt{Sf_{i,2}(t)} \cdot Sf_{i,3}(t) \\ HSf_{i,4}(t) &= \sqrt[8]{Sf_{i,1}(t)} \cdot \sqrt[4]{Sf_{i,2}(t)} \cdot \sqrt{Sf_{i,3}(t)} \cdot Sf_{i,4}(t) \\ HSf_{i,5}(t) &= \sqrt[16]{Sf_{i,1}(t)} \cdot \sqrt[8]{Sf_{i,2}(t)} \cdot \sqrt[4]{Sf_{i,3}(t)} \cdot \sqrt{Sf_{i,4}(t)} \cdot Sf_{i,5}(t) \\ HSf_{i,6}(t) &= \sqrt[32]{Sf_{i,1}(t)} \cdot \sqrt[16]{Sf_{i,2}(t)} \cdot \sqrt[8]{Sf_{i,3}(t)} \cdot \sqrt[4]{Sf_{i,4}(t)} \cdot \sqrt{Sf_{i,5}(t)} \cdot Sf_{i,6}(t) \end{aligned} \qquad (5)$$

The methods for estimating the suitability functions of these drivers are described in Confalonieri [37] and Movedi et al. [42]. The application within ModVege required some adaptations of the CoSMo suitability functions to the features of the generic simulator. The ModVege-based implementation of the CoSMo suitability functions is described in the Supplementary material (section 2).

2.2. Study-site and experimental design

We refer to the long-term observational system of Theix (45° 43′ N, 03° 01′ E, 880 m a.s.l.), located in the Massif Central of France (Supplementary material, Figure B). A designed experiment was established in 2005 on an area of ~3 ha, with the aim of analysing the response of permanent grasslands to changes in management practices [52] (Louault et al., 2017). The site is equipped with a meteorological station, which provides hourly values of global radiation, air temperature and precipitation, as well as soil temperature. The climate is semi-continental with a mean annual temperature of 8.7 °C and a mean yearly rainfall of 770 mm. It is essentially humid or sub-humid, according to the De Martonne-Gottmann aridity index [53], calculated annually as $b = \frac{1}{2} \cdot \left[\frac{P_y}{T_y+10} + 12 \cdot \left(\frac{p_a}{t_a+10}\right)\right]$, where P_y (mm) is total annual precipitation, T_y (°C) is the mean annual temperature, p_a (mm) is the total precipitation of the driest month, T_a (°C) is the mean monthly temperature of the driest month. The index b offers the possibility of discriminating different thermo-pluviometric conditions during the study period (Figure 1), based on the ranges of values published by Diodato and Ceccarelli [54]: b<5: extreme aridity; 5≤b<14: aridity; 15≤b<19: semi-aridity; 20≤b<29: sub-humidity; 30≤b<59: humidity; b≥59: high humidity. The highest value of the aridity index (the lowest aridity), b=46, was observed in 2010, a year with the highest rainfall (885 mm). Exceptionally, 2015 was a semi-arid year with below average rainfall (585 mm) and the aridity index b=18.

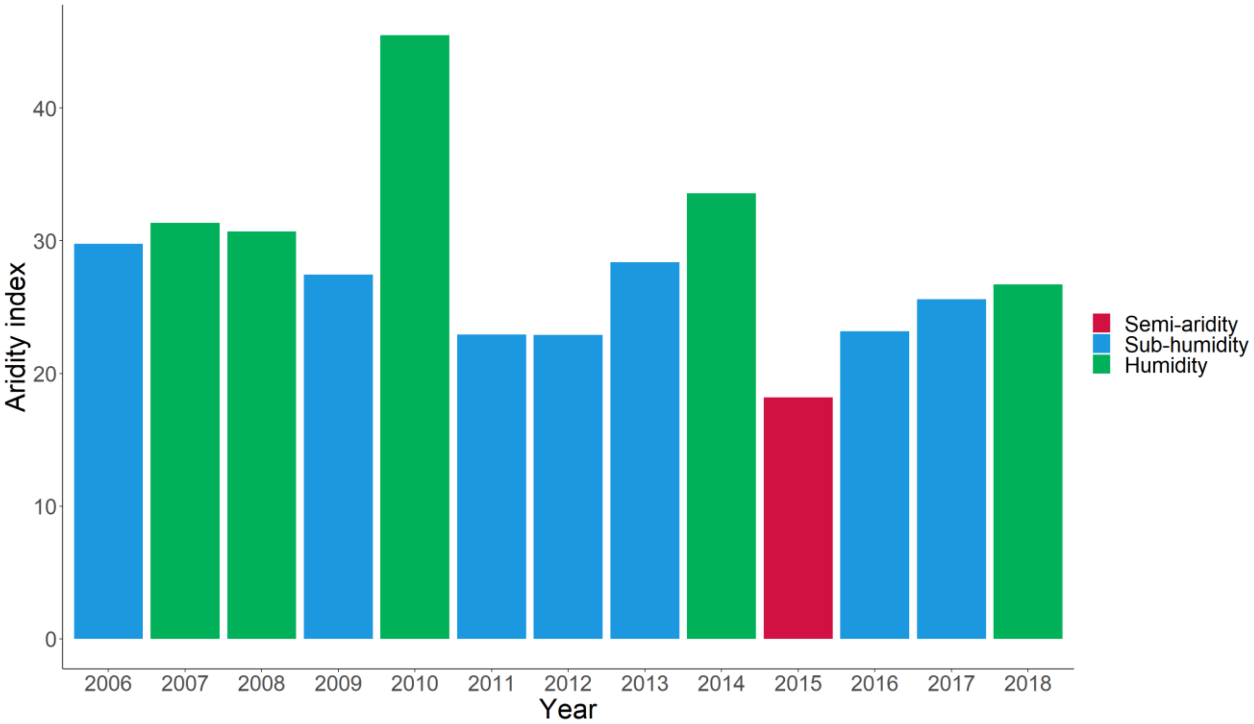

Figure 1. Thermo-pluviometric regimes of the study-site according to the De Martonne-Gottmann aridity (yearly values).

The soil developed from granitic bedrock and has different characteristics in the upper layer of the experimental site. The experimental design was thus repeated on two blocks or cambisol units, with block 1 being a eutric cambisol and block 2 being a colluvic material (heterogeneous mixture). Differences in soil characteristics (Table 1) were also observed in terms of botanical composition. At the initial stage, the most abundant species with a cumulative frequency of ~80% were, in block 1, *Cerastium glomeratum*, *Elymus repens*, *Festuca arundinacea*, *Lolium perenne*, *Poa pratensis*, *Taraxacum officinale*, i.e. six species, and in block 2, *Agrostis capillaris*, *Alopecurus pratensis*, *Holcus lanatus*, *Lolium perenne*, *Poa pratensis*, *Taraxacum officinale*, *Trifolium repens*, *Trisetum flavescens*, i.e. eight species.

Table 1. Soil properties of the grassland study-site.

Soil properties	Unit	Block 1		Block 2	
Layer thickness	m	0.10-0.20	0.20-0.40	0.10-0.20	0.20-0.40
Clay	%	19.7	17.0	23.0	25.0
Silt	%	26.9	27.4	26.1	24.2
Sand	%	53.4	55.6	51.0	50.8
Carbon content	g kg^{-1}	40.3	18.5	43.1	15.1
pH	-	5.9	6.2	6.0	6.5
Bulk density	g cm^{-3}	0.94	1.23	0.89	1.18

Management prior to 2003 consisted of a mixed regime with one to two cuts for silage or hay, with applications of mineral and organic fertilisers, followed by grazing in autumn. In the two years prior to the implementation of the experiment (2003-2004), three annual cuts were applied without fertilisation. Since 2005, treatments were applied, distinguishing between i) level of herbage utilisation by rotational grazing of cattle without fertilisation (i.e. disturbance gradient; three treatments) and ii) level of fertilisation under a fixed mowing regime (i.e. nutrient availability gradient; three treatments). Each treatment was repeated twice in each block, resulting in 28 plots. Cattle grazing treatments (not used in this study) were applied on 2200 m^2 plots while smaller plots (350-400 m^2) were either abandoned (Ab) or used for fertilisation treatments. The fertiliser application was split in early spring, after the first and after the second mowing.

Fertilisation treatments were: (1) NPK: annual addition of mineral nitrogen, phosphorus and potassium (on average 264 kg N ha^{-1}, 33 kg P ha^{-1} and 189 kg K ha^{-1}); (2) PK: annual addition of mineral phosphorus and potassium (on average 26 kg P ha^{-1} and 143 kg K ha^{-1}); (3) Null: no fertilisation. More details are in Louault et al. [52]. For the modelling, the data corresponding to the NPK, Null and Ab treatments were used as a block mean (the PK treatment was not used).

2.3. Experimental data

Aboveground standing biomass and relative abundance of plant species were determined experimentally in mown and unmown plots. Biomass was harvested from the unmown (i.e. abandoned) plots for research purposes. Aboveground biomass (AGB hereafter) was determined in four sampling areas per plot (0.3 x 0.6 m^2 in the abandonment and 0.6 x 0.6 m^2 otherwise) at ~0.055 m height, harvested up to three times a year in May, July and October, after a cleaning cut at the end of winter. The sampling area was moved within the plot at each cutting date and the aboveground biomass was removed at the beginning of the regrowth period. Herbage samples were oven dried (60 °C, 48 h). For mown plots, annual herbage production was calculated as the sum of the three sampling dates.

The relative abundance of plant species in each treatment was determined from 2006 to 2018 (all years except 2009), using 40 pinpoints regularly spaced along two to three fixed transects. Presence/absence of species was recorded at each of the 40 pinpoints. The relative abundance of each species was calculated at the plot level [55], normalised to the sum of presences of all species and expressed as a percentage.

The total number of plant species recorded at least once in blocks 1 and 2 during the study period of ~50 in the Null treatments, compared to ~35-40 with full fertilisation or abandonment (Supplementary material, Table A), reflects the positive effect of cutting and no N input on species richness [56]. In this study (and in agreement with Movedi et al. [42]), we based the modelling work on the relative abundances of dominant species or functional groups. In order to limit the uncertainties related to the initialisation and parameterisation of minor groups/species, a practical threshold of 0.04 (4%) of the mean relative abundance during the simulated period was set in order to exclude groups/species present with an abundance lower than this threshold. For modelling purposes, the relative abundances of the dominant types/species were then recalculated by relating the relative abundance of each species (Table 2) or functional types (Table 3) to the sum of the abundances. For instance, *Lolium perenne* was excluded from the list of dominant species in the block 1 treatments, with 2.0% (NPK) and 2.8% (Null), and in the block 2 abandonment, with 0.3%. On the other hand, it was included in the simulated species of the NPK and Null treatments in block 2, where its relative abundance is ~9%. Similarly, *Holcus lanatus* was excluded from the NPK treatment in block 1, where it is present at ~1%, while its presence amounts to ~8% in the same treatment in block 2, and is below the critical threshold in all other treatments except the Ab treatment in block 2, where it is at the 4% abundance threshold. We also underline that, when present, *Stellaria media* is at the 4% abundance threshold in the fertilised treatment of both blocks. It can also be seen that *Poa pratensis* is the only species present in all situations, while occasional forbs such as *Galium aparine* (block 1) and *Urtica dioica* (both blocks) are only present in the abandoned plots (about 4-7% on average and mostly absent in the first years; Table D in Supplementary material). One only legume species, *Trifolium repens*, is present above the 4% threshold (10-11%) in both the unfertilised mown treatments. The selected species have a total abundance ≥70%, and even ≥80% in the NPK treatments (Table 2).

Table 2. Relative abundances of dominant species (two blocks and three treatments). Mean values observed over the study period (Obs) were recalculated (Rec) with respect to the dominant species.

NPK			Null			Ab		
Species	**Relative abundances**		**Species**	**Relative abundances**		**Species**	**Relative abundances**	
	Obs	**Rec**		**Obs**	**Rec**		**Obs**	**Rec**
			Block 1					
Elymus repens	0.26	0.31	*Achillea millefolium*	0.04	0.06	*Alopecurus pratensis*	0.13	0.17
Festuca arundinacea	0.09	0.11	*Elymus repens*	0.05	0.07	*Arrhenatherum elatius*	0.04	0.05

Lolium multiflorum	0.07	0.09	*Festuca arundinacea*	0.09	0.13	*Dactylis glomerata*	0.04	0.05
Poa pratensis	0.15	0.17	*Holcus lanatus*	0.05	0.07	*Elymus repens*	0.27	0.35
Stellaria media	0.04	0.05	*Poa pratensis*	0.12	0.17	*Festuca arundinacea*	0.06	0.07
Taraxacum officinale	0.21	0.25	*Poa trivialis*	0.05	0.08	*Galium aparine*	0.04	0.05
			Taraxacum officinale	0.16	0.22	*Poa pratensis*	0.16	0.20
			Trifolium repens	0.14	0.29	*Urtica dioica*	0.04	0.05
Sum	0.82	1.00	Sum	0.70	1.00	Sum	0.78	1.00
Nb. of species	6		Nb. of species	8		Nb. of species	8	
				Block 2				
Achillea millefolium	0.06	0.07	*Achillea millefolium*	0.04	0.07	*Alopecurus pratensis*	0.30	0.46
Alopecurus pratensis	0.18	0.23	*Alopecurus pratensis*	0.08	0.11	*Arrhenatherum elatius*	0.06	0.08
Holcus lanatus	0.07	0.08	*Festuca arundinacea*	0.05	0.07	*Elymus repens*	0.04	0.07
Lolium perenne	0.06	0.07	*Lolium perenne*	0.09	0.13	*Holcus lanatus*	0.04	0.07
Poa pratensis	0.17	0.20	*Poa pratensis*	0.12	0.18	*Poa pratensis*	0.11	0.18
Stellaria media	0.04	0.05	*Taraxacum officinale*	0.13	0.18	*Urtica dioica*	0.09	0.14
Taraxacum officinale	0.15	0.19	*Trifolium repens*	0.11	0.15			
Trisetum flavescens	0.08	0.10	*Trisetum flavescens*	0.08	0.12			
Sum	0.80	1.00	Sum	0.70	1.00	Sum	0.72	1.00
Nb. of species	8		Nb. of species	8		Nb. of species	6	

In terms of functional grass typologies, type C was only marginally present in the unfertilised and abandoned treatments of block 2 (or absent for the rest), where the dominating groups A, B and b covered nearly 100% of abundances (Table 3).

Table 3. Relative abundances of functional groups (grass species in two blocks and three treatments). Mean values observed over the study period (Obs) were recalculated (Rec) with respect to the dominant groups.

	NPK	**Null**	**Ab**

Functional group	Relative abundances		Relative abundances		Relative abundances	
	Obs	Rec	Obs	Rec	Obs	Rec
			Block 1			
A	0.07	0.07	0.21	0.21	0.24	0.24
B	0.45	0.45	0.49	0.49	0.34	0.34
b	0.48	0.48	0.30	0.30	0.42	0.42
Sum	1.00	1.00	1.00	1.00	1.00	1.00
			Block 2			
A	0.47	0.47	0.39	0.40	0.59	0.61
B	0.33	0.33	0.32	0.32	0.27	0.28
b	0.20	0.20	0.28	0.28	0.11	0.11
Sum	1.00	1.00	0.99	1.00	0.97	1.00

Biomass yield and abundance data for plant types and species used for the modelling work are summarised in Table B and Tables C and D of Supplementary material, respectively.

2.4. Simulation design and model evaluation

Simulations were designed and model evaluation carried out to determine whether (i) CoSMo-based ModVege solutions simulated the relative abundance of plant (grass) functional types and species, and (ii) differences in simulated AGB were caused by the explicit simulation of plant diversity, by comparing the CoSMo-based and stand-alone ModVege solutions. Standalone (ModVege) and coupled (ModVege-CoSMo) modelling solutions were configured using daily weather data retrieved from the CLIMATIK database (through the INRAE portal, https://www6.paca.inrae.fr/agroclim/Les-outils) and management data as determined at the experimental site, and parameterised for each treatment of both blocks (Supplementary material). In particular, simulations were performed with common sets of ModVege and CoSMo parameters (Table E and Table H) and type- and plant-specific parameters for either ModVege (Tables F and G) or CoSMo (Tables I and J). Some ModVege parameters were extracted from published literature for (grass-based) functional types [25]. Otherwise, the datasets described in Section 2.3 were used for the calibration of models parameters. ModVege stand-alone was first run for each functional type separately (A, B and b) and then the daily community AGB was obtained as a weighted mean of the three functional types, using for each treatment the mean abundances of each type over the period 2006-2018 (Table 3) as a weighting factor. The calibration work was carried out through a trial-and-error process comparing the model estimates with observational data while ensuring biologically interpretable plant parameters by modifying their values within plausible ranges. For instance, the parameters ST1=800 °C-d and ST2=1200 °C-d of *Galium aparine* (Table G) were adapted from the ranges of values provided by Theau et al. [20], and a similar approach was adopted for the other species. For the functional types, the maximum leaf area index values (LAImax>9 $m^2\ m^{-2}$; Table I) were calibrated to the upper limit of the LAI of grasslands, which is rarely higher than 10 [57]. As well, as the canopy height varies by several folds, mainly from 0.25 to 1.50 m [58], the maximum plant height (MaxHeight) was calibrated below the upper limit of 2.0 m [59]. For specific leaf area (SLA), we used (Table G) the values provided by Bourdôt [60] for *Achillea millefolium* (0.017 $m^2\ g^{-1}$) and by Ianovici et al. [61] for *Taraxacum officinale* (0.048 $m^2\ g^{-1}$), while the SLA value used for *Urtica dioica* (0.023 $m^2\ g^{-1}$) is the one provided by Gulías et al. [62] for *Urtica atrovirens*, and for *Galium aparine* and *Trifolium repens*, 0.048 $m^2\ g^{-1}$ and 0.018 $m^2\ g^{-1}$, are within the ranges of values provided by Poorter and de Jong [63] and Nölke et al. [64], respectively. Theau et al. [20] also provided ranges of values for maximum plant heights (e.g. from <0.4 for *Taraxacum officinale*, *Stellaria media* and *Trifolium repens* to >0.9 m for *Galium aparine*, *Achillea millefolium* and *Urtica dioica*) to which we have referred for the calibrated values attributed to this CoSMo parameter (Table J). For each type/species, the first determined (and recalculated) relative abundance was used to initialise CoSMo at the start of the simulation (2006, 1 January).

The agreement between simulated and observed values of AGB and relative abundance of plant types/species (the latter only for CoSMo-based modelling solutions) was evaluated according to five commonly used metrics ($RRMSE$, $RMAE$, R^2, R, CRM) of model performance [65]. The relative root mean square error (optimum, $0 \le RRMSE\ (\%) < \infty$) and the relative mean absolute error (optimum, $0 \leq RMAE$ (%)$<\infty$) indicate how far the estimates are from the actual data: both explain this concept in relative terms (percentage over the mean), the former in square terms and the second in absolute terms. Squaring emphasises larger differences, a feature that results in giving more weight to large deviations. Algebraically, $RMAE \leq RRMSE$ (due to the influence of squaring larger values), with these metrics being approximately equal if the absolute differences are of similar magnitude. This suggests that the absolute differences are more robust (less sensitive) to large biases than squared differences. The coefficient of determination ($0 \leq R^2 \leq 1$, optimum) is the squared measure of the linear correlation coefficient ($-1 \leq R \leq 1$, optimum) between the estimates and the observations: it assesses the goodness-of-fit of the model, i.e. the proportion of the observed variance explained by the estimates. The coefficient of residual mass (*CRM*) is a measure of the tendency of the model to overestimate ($CRM<0$) or underestimate ($CRM>0$) the observations.

We also evaluated the mean values of grassland community traits as estimated on a daily basis with CoSMo-based solutions according to the relative abundance of species/types. In the absence of observations, the values of two canopy traits (maximum height and specific leaf area) were appreciated for their variation over time, compared to the constant values attributed to the corresponding parameters of the species/types composing the community.

3. Results

Results are presented via a set of performance metrics calculated separately by output, block and treatment for the whole simulation period (Supplementary material). For AGB, we compared standalone ModVege and its CoSMo-based solutions (Table K). The estimates of relative plant abundances obtained with the two CoSMo-based modelling solutions were evaluated for both functional types (Table L) and species (Table M), either taken individually or aggregated by taxonomic groups and for the whole community.

3.1. Evaluation of modelling solutions for grassland biomass production

CoSMo-based and standalone modelling solutions performed similarly (Supplementary material, Table K) with <1.2 t ha^{-1} AGB difference between simulations and observations on average ($RRMSE$~70%, $RMAE$~54% on average). In most cases, *CRM* values were negative, indicating a general model overestimation of the observed AGB (with the exception of CoSMo-based versions in the abandoned plots, with *CRM* from 0.07 to 0.12). The unfertilised (stressed and perturbed) plots were the most difficult to simulate ($RRMSE$>100%). Although error amounts were lower for abandoned plots ($RRMSE$~40%, $RMAE$<40%), with no substantial differences between modelling solutions, simulated and observed data were less correlated (R~0.4) under these stressed (unperturbed) conditions, reflected in a limited fit ($R^2 \leq 0.20$) as data points do not line up around the 1:1 identity line (Figures C, D and E in Supplementary material). Overall, all three modelling solutions accounted for the decreasing trend in biomass production (annual anomalies) over the simulation period (Figure 2). In the NPK and Null treatments, *R*-values ranged from 0.60 (with ModVege-CoSMo for functional types under NPK 1) to 0.85 (with ModVege-CoSMo for the functional types under Null 2), while the quality of the simulations of the abandoned plots was deteriorated towards the end of the simulation period. Some discrepancies between simulations and observations were also observed in the years 2008 to 2011, in the transition between mostly positive and mostly negative observed anomalies.

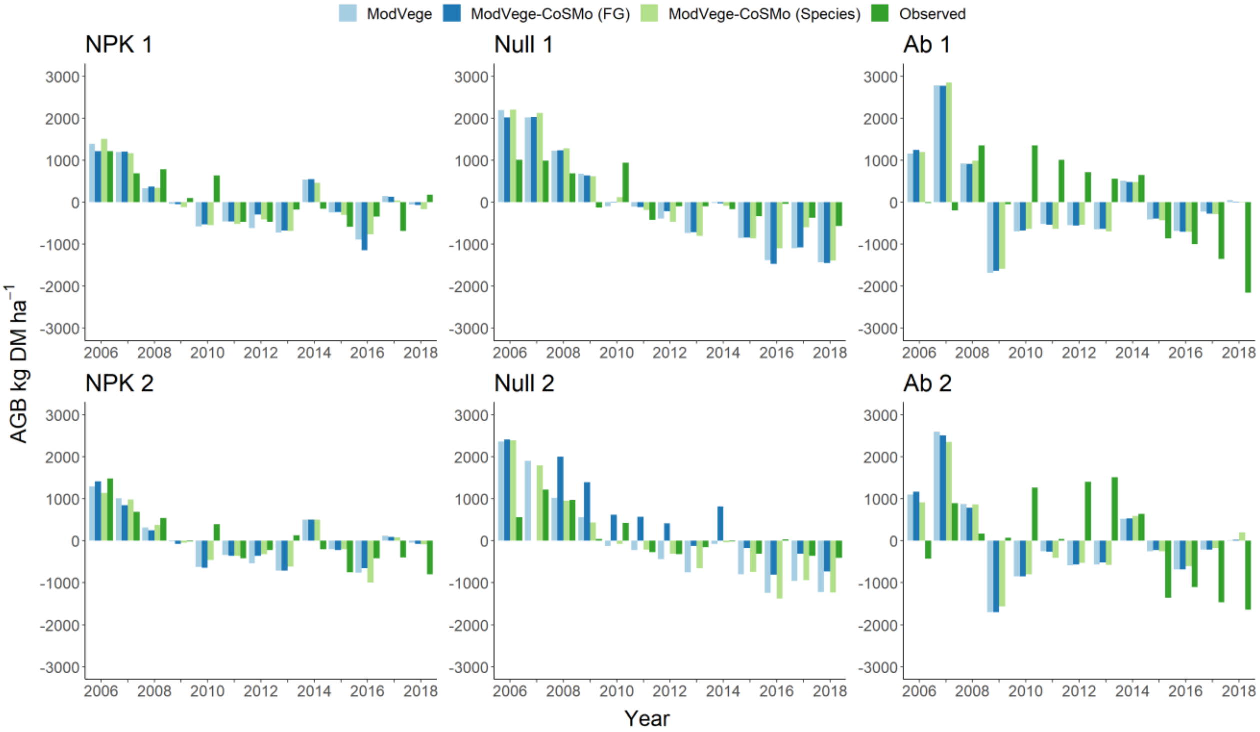

Figure 2. Annual anomalies of aboveground biomass (AGB), observed and simulated with alternative modelling solutions in three treatments (NPK: fertilised; Null: unfertilised; Ab: abandoned) and two blocks (1, 2). Annual mean values of AGB: NPK 1: 2895 kg DM ha^{-1}; NPK 2: 2477 kg DM ha^{-1}; Null 1: 1417 kg DM ha^{-1}; Null 2: 1197 kg DM ha^{-1}; Ab 1: 5245 kg DM ha^{-1}; Ab 2: 4683 kg DM ha^{-1}.

3.2. Evaluation of modelling solutions for grassland biomass production

3.2.1. Relative abundance of plant (grass) functional types

Overall, the accuracy of ModVege-CoSMo in simulating the relative abundance of plant functional types was satisfactory (Table L in Supplementary material, Figure 3). Type b had the highest correlation coefficient in block 2 NPK (*R*=0.95), and type A had the lowest in block 2 abandonment (*R*=0.04). However, the model accurately simulated the fluctuations of functional types with sufficient accuracy in all treatments, with *RRMSE* rarely >30% (i.e. types B and b in block 2 abandonment with 35.4% and 36.1%, respectively; Figure J), and <10% in fertilised treatments (i.e. type A and type b in block 2, with 9.0% and 9.2%, respectively; Figure F). The performance metrics improved at the community level (*R*>0.70 and *RRMSE*<25%).

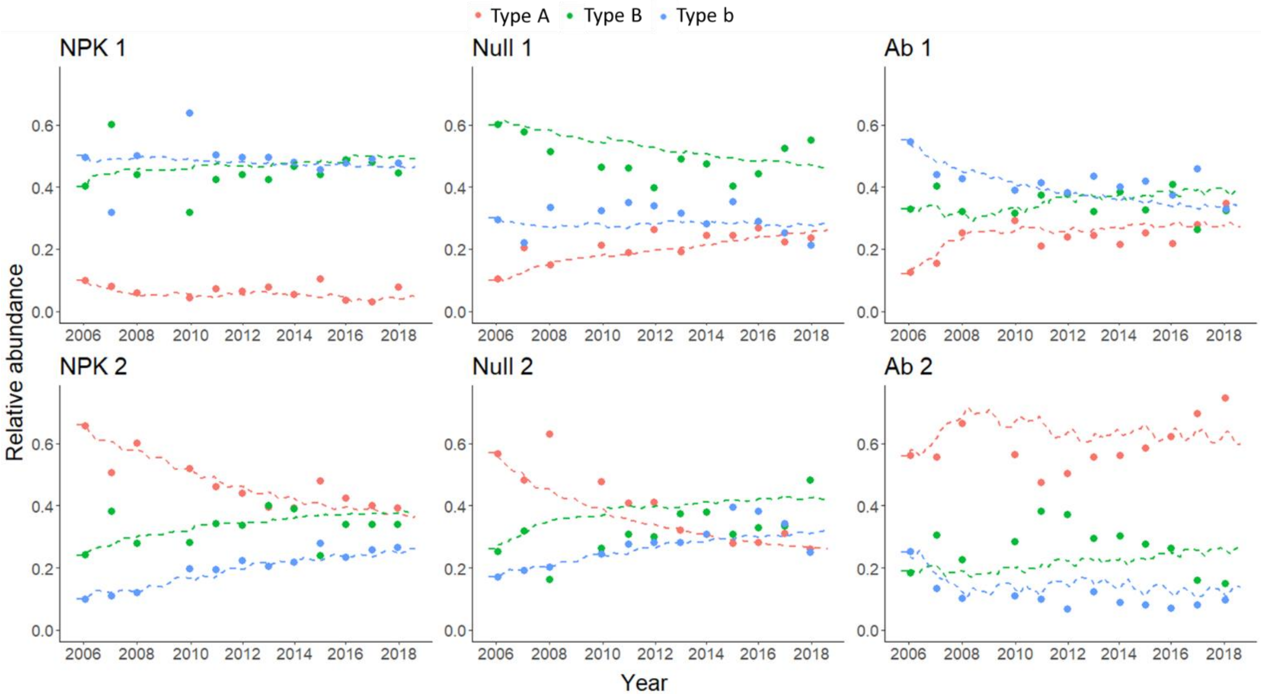

Figure 3. Observed (dots) and ModVege-CoSMo simulated (lines) fluctuations in the relative abundance of plant (grass) functional types in three treatments (NPK: fertilised; Null: unfertilised; Ab: abandoned) and two blocks (1, 2). Type A: grass species of fertile environments, small, with an early phenology and a short life span of the leaves; Type B: grass species of fertile environments, larger, with a moderately early phenology and a longer leaf life than type A; Type b: grass species preferring relatively fertile environments but differing from the two previous groups in their late phenology. Graphs of the individual plant (grass) functional types are in Supplementary material (Figures F-J).

3.2.2. Relative abundance of plant (grass) functional types

The accuracy of ModVege-CoSMo in simulating the relative abundance of plant species was generally satisfactory (Table M, Figure 4). For the grasses, i.e. the dominant taxonomic group, the mean *RRMSE* is <40% (*RMAE*<30%). Mean *RRMSE*~50% (*RMAE*~40%) calculated for forbs reflects the inaccuracies associated with two minor species (with three *RRMSE* values >100%): *Galium aparine* (block 1 abandonment; Figure O) and *Stellaria media* (NPK in both blocks; Figures K and L). While both are present at the 4% limit on average (Table 2), *Galium aparine* was notably absent in the first years of the study period (from 2006 to 2012), when the model estimated some presence of this species (Figure O). Observed and simulated means for all grasses or forbs tend to converge, with a maximum departure of 6% abundance in block 1 Ab (0.90 versus 0.84 for grasses and 0.10 versus 0.16 for forbs).

Of grass species, *Festuca arundinacea* (*RRMSE*~38-56%) and *Lolium perenne* (*RRMSE*~24-34%) had the best *R*-values, respectively in the abandoned plot of block 1 (*R*=0.91) and in the fertilised plot of block 2 (*R*=0.90). The worst *R*-value, observed for *Trisetum flavescens* in block 2 Null (*R*=0.04), reflects only a few data departing from the observations at the end of the simulation period (e.g. 2015, 2016, 2017; Figure N), which are compatible with satisfactory error amounts (*RRMSE*=36.4%, *RMAE*=27.4%). The lowest simulation errors (*RRMSE*=11.4%, *RMAE*=8.5%) were obtained with *Elymus repens* in the abandonment of block 1 (Figure O). Another dominant grass, *Poa pratensis* (Figures K-P), shows mostly *RRMSE*<30% - in NPK 1 and 2 (Figures K-L), Null 2 (Figure N) and Ab 1 (Figure O) - or *RRMSE*<50% in Null 1 (45.5%, Figure M) and Ab 2 (36.2%, Figure P). A dominant forb (absent in abandoned plots), *Taraxacum officinale*, shows *RRMSE* values <25% (*RMAE*<20%) in block 1 NPK (16.2% and 12.6%; Figure K) and Null (12.4% and 9.8%; Figure M) and in block 2 Null (22.8% and 18%; Figure N), with *RRMSE*=31.1% (*RMAE*=24.1). Overall, the dynamics of *Trifolium repens* in the unfertilised mown treatments were also reproduced (Figure M and Figure N), although some discrepant values in the most recent years (*RRMSE*~62-77%; *RMAE*~49-62%). It was then shown that changes in ModVege-CoSMo accuracy are not related with the number of plant species in the community, with community *RRMSE* values ranging from ~30% to ~46% with six species (block 1 NPK and block 2 Ab) and from ~28% (block 2 Null) to ~52% (block 1 Null) with eight species.

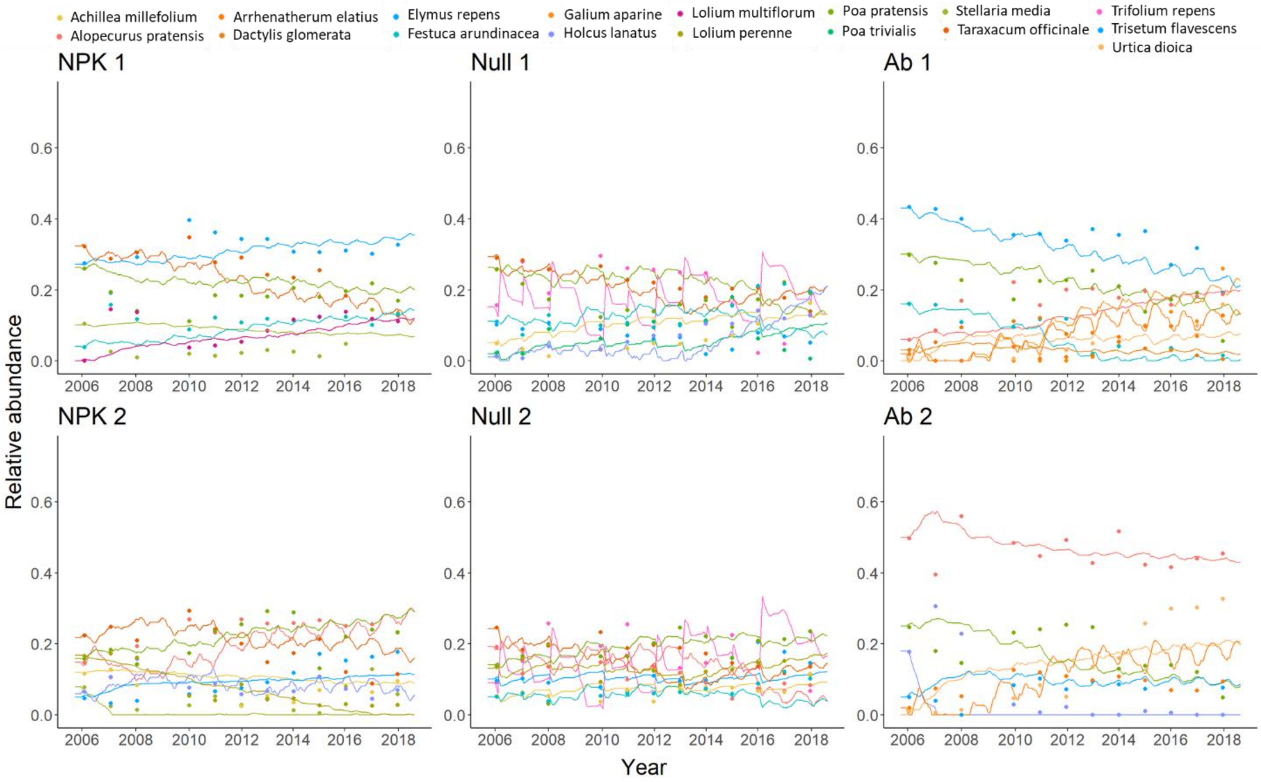

Figure 4. Observed (dots) and ModVege-CoSMo simulated (lines) fluctuations in the relative abundance of plant species in three treatments (NPK: fertilised; Null: unfertilised; Ab: abandoned) and two blocks (1, 2). Graphs of the individual plant species are in Supplementary material (Figures K-P).

The resulting feedback between plant species parameter values and modelled relative abundance of species (or types; Supplementary material, Figure Q and Figure R) permits a dynamic in defining community traits like, e.g. SLA (Figure 5) and maximum canopy height (Figure 6), whose values change during the simulation depending to the relative abundance of the species. For instance, the SLA values of the block 1 NPK community fluctuating around ~35 m^2 kg^{-1} correspond to the value assigned to *Poa pratensis* and *Elymus repens* (Supplementary material, Table F), dominant b-type grasses (with 31% and 17%, respectively; Table 2) with the environmental and management factors at work in the fertilised block 1 community. In this treatment, the modelled decline in community SLA is largely explained by the modelled (and observed) decline of *Taraxacum officinale* (Supplementary material, Figure K), a forb with high SLA (48 m^2 kg^{-1}; Supplementary material, Table G). Likewise, in block 2 NPK, dominated by the A-type grass *Alopecurus pratensis* (with 23% and SLA=44 m^2 kg^{-1}; Table 2 and Supplementary material, Table G), community SLA declines below ~35 m^2 kg^{-1} as a consequence of the decline of *Taraxacum officinale* (Supplementary material, Figure L).

With regard to the estimated values of maximum canopy height, their increase in the Ab community of block 1 reflects the (observed and simulated) increased abundance of two tall grass species, *Alopecurus pratensis* and

Arrhenatherum elatius (Supplementary material, Figure O), which have calibrated maximum heights of 1.1-1.2 m (Supplementary material, Table J).

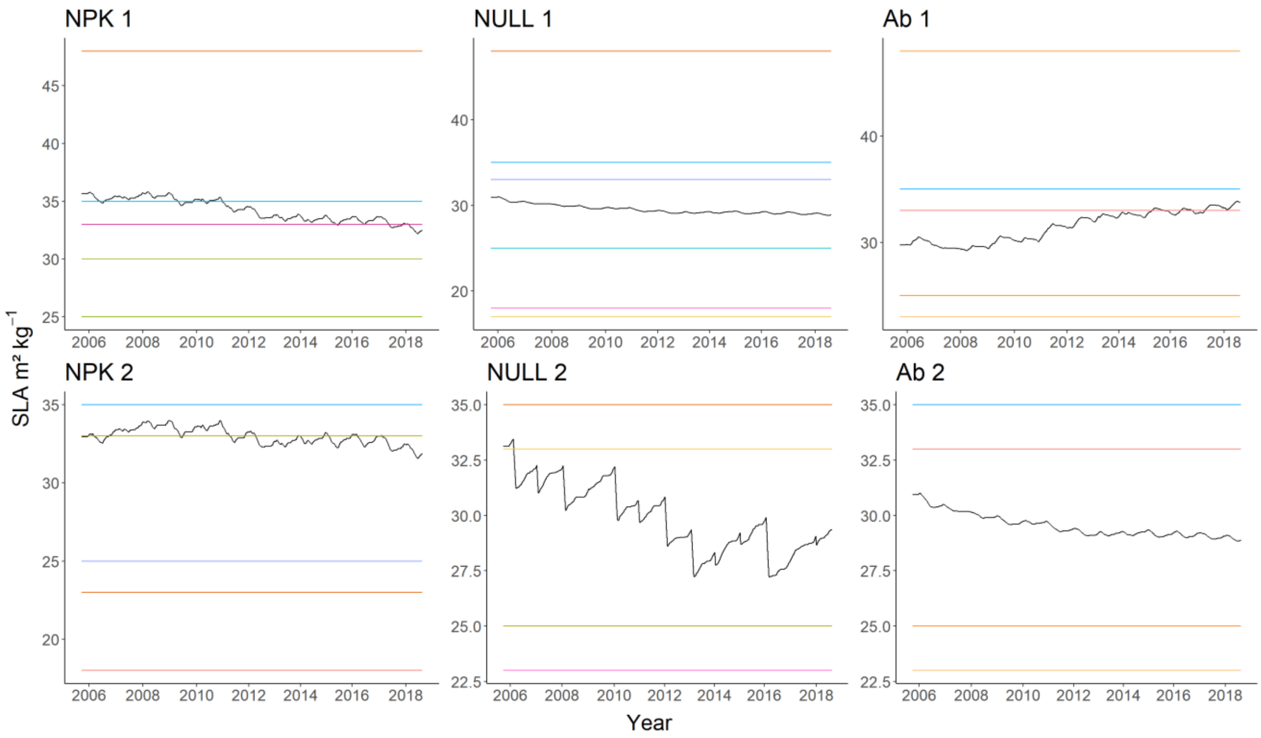

Figure 5. Daily changes in the specific leaf area (SLA) of the community during the simulation period compared to the fixed values set for the plant species (coloured lines as in Figure 4) present in the community (horizontal lines, overlapping for the same values) for three treatments (NPK: fertilised; Null: unfertilised; Ab: abandoned) and two blocks (1, 2).

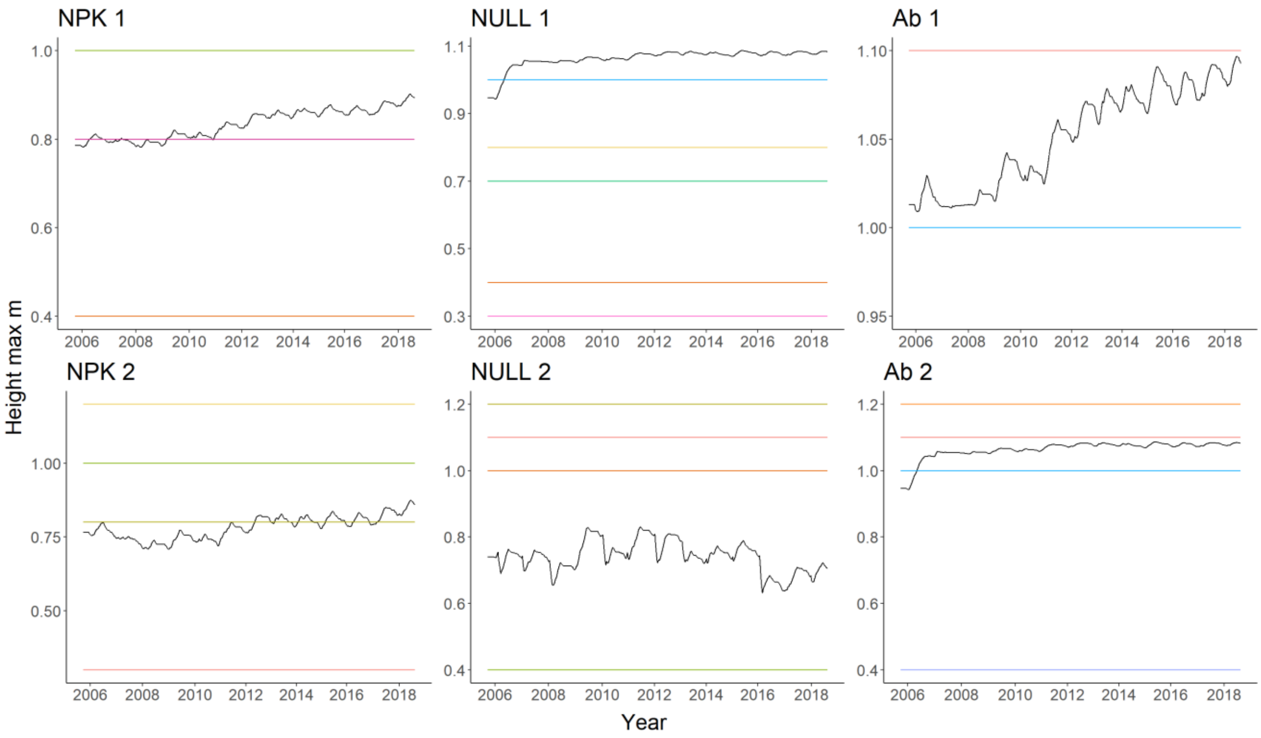

Figure 6. Daily changes in the maximum height of the community during the simulation period compared to the fixed values set for the plant species (coloured lines as in Figure 4) present in the community (horizontal lines, overlapping for the same values) for three treatments (NPK: fertilised; Null: unfertilised; Ab: abandoned) and two blocks (1, 2).

4. Discussion

4.1. Plant biomass simulation

Our results show that there is not always an adequate estimate of AGB by ModVege under different treatments, which also holds true with CoSMo-based modelling solutions. This indicates that the investigated grassland model is not yet sufficiently developed to capture the complexity of interactions between weather fluctuations, soil properties, floristic composition and the resilience of grassland communities to environmental stresses and management factors. However, discontinuous biomass measurements contain rather large uncertainties, mainly due to the spatial heterogeneity of grassland covers [66], which make model evaluation difficult [67, 68]. Even in this study, it is worth examining some issues with the experimental data, which may explain some of the discrepancies observed between the modelling solutions and the measurements. In 2008, the first biomass determination was postponed to the end of June (instead of the normal end of May; Table B in Supplementary material) because the soil was waterlogged and the harvesting machine could not be put into the field earlier (due to the reduced bearing capacity of the soil). The biomass measurements were thus carried out on a canopy that had accumulated a lot of biomass at a very early stage of reproductive development. The high biomass observed in the first determination (after the clean-up determination) of 2008 (up to ~9 t DM ha^{-1} in block 1 NPK, Table B in Supplementary material), compared to other years, is thus more likely due to a late harvest (which allowed time for biomass accumulation) than to different weather conditions. Plants experienced some dry conditions early in the growing season in subsequent years with, for instance, a total reported precipitation of 161 mm from January to May in 2011 against ~300 mm in other years (from 211 mm in 2015 to 453 mm in 2016). In particular, in 2011, precipitation data indicate a relatively dry winter and spring (309 mm of total precipitation between November 2010 and June 2011), with a water deficit in April and soil water content remaining below average during May [69]. Thus, biomass production was lower than in other years in the first determinations of 2011, which is also one of the warmest year in the time-series, with three days with maximum air temperature >35 °C detected at a nearby station [70]. This likely also reflects the lasting effects of the sequence of heatwaves that had occurred since 2009 [69].

Most problematic was the simulation of biomass in the abandonment treatment, a condition for which ModVege was not explicitly developed. Abandoned grasslands have complex vegetation structures that share environmental conditions with both open habitats and forests. At the study site, the abandoned grasslands are in an early succession stage, their vegetation structure is still more similar to open habitats than to forests, and we hypothesised that abandoned plots partly may act as managed grasslands. However, community similarity was relatively low, indicating that the dense sward found in abandoned plots created different environmental conditions (e.g. shade limiting light availability for emerging plants) compared to the mown grasslands. In particular, the vegetation cut at ground level included much of dead biomass components, which have increased along the years. The biomass sampled in summer (in July or August) was more similar to that of the mown grasslands, as it did not contain much dead biomass from the previous year's growth or that of the current growing season (which is more present in the autumn sample). The assessment at the summer sampling date (Table 4) indicates that, on average, the three modelling solutions tended to converge with the observations: <1.0 t ha^{-1} deviation down to ~0.1 t ha^{-1} with the CoSMo-based functional group solution in block 2. The simulations continue to indicate difficulties for all three modelling solutions to capture interannual variability in AGB. Deviations from observations of up to ~3.7 t ha^{-1} with ModVege standalone in 2018 in block 1 were however mitigated by the CoSMo-based solutions to ~2.8 t ha^{-1}. As well, the maximum deviation of ~3.0 t ha^{-1} observed in block 2 in 2018 with ModVege standalone was reduced to ~2.0 t ha^{-1} with CoSMo-based solutions.

Table 4. Evaluation of alternative modelling solutions for the simulation of aboveground biomass in the summer sampling of the abandoned plots (two blocks). Grey cells indicate the best performance. FG: functional groups.

Year	doy	Observed biomass	ModVege		ModVege-CoSMo FG		ModVege-CoSMo Species	
			Simulated biomass	Difference	Simulated biomass	Difference	Simulated biomass	Difference
					Block 1			
2006	200	6742	6302	-440	5509	-1233	5503	-1239
2007	213	5781	8465	2684	7581	1800	7678	1897
2008	218	8116	7955	-161	7049	-1067	7072	-1044
2009	-	-	-	-	-	-	-	-
2010	201	7734	6372	-1362	5445	-2289	5592	-2142
2011	201	5674	4736	-938	3848	-1826	3675	-1999
2012	201	8560	6934	-1626	5992	-2568	6111	-2449
2013	198	6655	6495	-160	5587	-1068	5579	-1076
2014	203	6755	6357	-398	5447	-1308	5401	-1354
2015	202	4056	3591	-465	2890	-1166	2717	-1339
2016	202	4789	6955	2166	6026	1237	6051	1262
2017	205	4498	6332	1834	5376	878	5370	872
2018	204	3005	6744	3739	5822	2817	5758	2753
Mean		6030	6437	406	5548	-483	5542	-488
Minimum		3005	3591	-1626	2890	-2568	2717	-2449
Maximum		8560	8465	3739	7581	2817	7678	2753
					Block 2			
2006	199	4576	6069	1493	5240	664	5124	548
2007	213	6822	8197	1375	7250	428	7285	463
2008	218	5832	7810	1978	6867	1035	6866	1034
2009	-	-	-	-	-	-	-	-
2010	201	8061	5982	-2079	5005	-3056	5135	-2926
2011	201	3867	5048	1181	4211	344	3945	78
2012	200	8227	6576	-1651	5664	-2563	5739	-2488
2013	198	7003	6395	-608	5494	-1509	5440	-1563
2014	203	6592	7859	1267	6948	152	5401	-1191
2015	202	3652	3911	259	3107	-545	2923	-729
2016	202	5131	6670	1539	5738	607	5786	655
2017	205	4312	6101	1789	5198	886	5169	857
2018	204	3656	6631	2975	5728	2072	5630	1974
Mean		5661	6437	776	5538	-124	5405	548
Minimum		3652	3911	-2079	3107	-3056	2910	-2926

Maximum	8227	8197	2975	7250	2072	6989	1974

Beyond the observational issues, the low modelling performance is not surprising, as simulations for grassland biomass are generally less accurate compared to cereal crops [71]. It is also a fact that the simulated biomass dynamics are essentially dissimilar between different grassland models, with shortcomings in the estimation of soil water content dynamics [72] (Sándor et al., 2017). As well, ModVege simplifies plant growth simulation, with constant ratios of the above- to below-ground biomass allocation and plant water availability linked to fractional water content through a simple bucket approach used to assess the water reserve [49]. Taken together, these simplifications affect the accuracy of simulations of transpiration and soil water content. Consequently, to improve the performance of plant water demand and consumption simulation, a more detailed hydrological model should be integrated with the growth model.

Another important limitation of ModVege is that it assumes fixed values of the nutrition index, whereas in reality the availability of N and other nutrients varies with season, environmental conditions and management. In the context of the present study, the issue is relevant because N availability is highly dependent on management. The scope of the model thus needs to be extended to include important processes that determine the nutritional status of the plant community, such as a root compartment, components to simulate mineral and organic N cycling in the soil, and a description of fertilisation [73]. Since legume fixers represent an important component of grassland communities, contributing to maintaining high productivity under low N-fertiliser supply, consideration should also be given to including a model component to simulate symbiotic N fixation [74].

In addition, drought can cause changes in grassland dynamics through physiological responses [75]. The ability of some species to resist or avoid water stress through enhanced water uptake at low soil water potentials [76, 77], which is not currently taken into account in ModVege, may be important for understanding the disparity of responses observed in field studies.

Beyond eco-physiological responses, long-term changes related to grassland-community composition should be considered [78, 79]. Here, the aim was not merely to assess the quality of AGB simulations by ModVege, but to evaluate this grassland model in comparison with solutions that introduce complexity in the modelling structure to represent plant dynamics (either species or functional types). The results are encouraging because, although the quality of the biomass simulations did not improve, it was not degraded by the complexity introduced. A pertinent point is that with CoSMo, it becomes possible for grassland simulators to obtain estimates of AGB while dynamically representing the relative abundance of plant species/types in mixed communities, a useful outcome for obtaining valuable information on a variety of ecosystem services provided by grasslands [80]. The use of a simplified plant-growth model structure, in conjunction with a plant dynamics module, proved useful as it allowed the properties of CoSMo to emerge, without interactions with the detailed biogeochemical processes of C and N cycles. CoSMo-like approaches could thus be more effective in simulating grassland biomass than in this study, as biophysical and biogeochemical issues are resolved.

4.2. Relative abundance simulation

The accuracy of ModVege-CoSMo in simulating the relative abundance of plant species in a community (*RRMSE* in the range ~28-52%; Supplementary material, Table M) was similar to that found by Movedi et al. [42] with CropSyst-CoSMo (~28-64%) and Soussana et al. [81] with GEMINI (51%), the latter (individual-centred model) being much more complex than CoSMo. The performances are also comparable to those of GRASSMIND (individual-based biogeochemical model [82]), which, however, was only applied to represent the vegetation cover a limited number of species (mixture of two grass and one forb species).

With a total of 17 species simulated (up to eight per treatment, Table 2), this study goes beyond Movedi et al. [42], where a maximum of seven species were simulated together in a simplified grassland system (once a year mowing). In our study, seven CoSMo parameters (Table I in Supplementary material) were added to 40 vegetation parameters in ModVege (24 functional type-specific parameters and 16 plant species-specific parameters; Tables F and G in Supplementary material). In comparison, the generic crop model WOFOST [41] and the grassland model GEMINI [81] would need ~100 parameters to characterise each species, and rapidly become increasingly complex as the number of species in the community increases, which obscures their interpretability and ultimately limits the applicability of the model.

Although limited to a single site, this study covers a variety of contrasting situations. They were not simulated with the same accuracy, which allows some strengths and weaknesses of the modelling framework to be identified. The satisfactory simulation of abundant grass species like *Elymus repens* and *Alopecurus pratensis*, but also *Festuca arundinacea*, *Lolium perenne* and the ubiquitous *Poa pratensis*, is important in view of modelling studies in support of agronomic and ecological objectives. Despite its classification as a weedy perennial grass for row crops, *Elymus repens* (couch grass) has in fact characteristics (erect stem growth habit, high feeding quality, vegetative reproduction through rhizomes, adaptation to a wide range of soil fertility and long seasonal growing periods) that make it an acceptable species for pastures [83], which may play a role for forage production and erosion control in northern temperate climates [84]. Its seeds are also eaten by several species of grassland birds [85]. *Alopecurus pratensis* (meadow foxtail) is also a pasture grass, usually mown before flowering to preserve its feed value, and used by some lepidopterans and other insects as a food plant [86]. *Festuca arundinacea* (tall fescue) is also an important forage crop under various fertility conditions, whose beneficial attributes for low-fertility soils are the result of a symbiotic association with an endophytic fungus, which increases soil C storage by limiting microbial and macro-faunal activity to decompose endophyte-infected organic matter inputs and by increasing C inputs through plant production [87]. *Lolium perenne* (perennial ryegrass) is an important perennial grass for turf grasses, globally one of the most important forage grasses, forming the basis of grassland production in temperate pastures as it has a low, dense vegetation with good regrowth and tillering [88]. The forage yield of *Poa pratensis* (bluegrass) is lower compared to other temperate grasses, but it has a good regrowth capacity, responds well to intensive grazing, has good nutritional quality, is a food plant for various insects and is used in mixtures with taller species [89].

The performance indices highlighting some inaccuracies in the estimates for two minor edible wild forbs, *Stellaria media* (common chickweed) and *Galium aparine* (cleavers), which are often considered as weeds, and thus of no interest for fodder crops [90]. For instance, we obtained *RRMSE* values >100% (Table M in Supplementary material) for *Stellaria media* in both fertilised plots and for *Galium aparine* in the abandoned plot of block 1, which can be explained by the presence of a few data points deviating (with small absolute differences) from the general observed trend. In fact, although the performance metrics are not entirely satisfactory, the visualisation of the simulated species dynamics shown in the time-series plots is generally consistent with that of the observations (Figures K, L and O).

Our study also confirms other findings of a change in the abundance of some dominant species as an effect of the abandonment [91, 92]. For instance, this shift of species can be seen in the abandoned block 1 plot with a decline of important grass species (i.e. *Elymus repens*, *Festuca arundinacea*, *Poa pratensis*) and an increase of the grass *Alopecurus pratensis* and forbs (i.e. *Galium aparine*, *Urtica dioica*). Here, the important point is that the model was able to reproduce these dynamics (Figure O). For the one legume species (white clover), present in unfertilised mown treatments, the spikes in the simulated lines (Figures M-N) indicate that the N provided by the symbiotic fixation option of ModVege-CoSMo coupling needs to be refined.

These satisfactory simulations also support the expression of the distribution of plant trait values at the community level by averaging the trait values weighted by the respective abundance of each species (community weighted mean by Garnier et al. [93]), which functionally characterises plant communities in different environments in order to better understand community assemblages [94]. For the SLA, for instance, the simulated trends (here estimated from the dominant species) reflect those determined by Louault et al. [52] up to 2012 for the entire set of species present in the canopy.

5. Conclusions

Based on the suitability-function rules of the Community Simulation Model (CoSMo), this study is one of the few to consider explicit and dynamic modelling of the relative abundance of plants in grassland communities. Although specific to the grassland model ModVege, it holds potential for extension to other vegetation models of similar structure, as CoSMo provides a framework for estimating the response of grassland systems with biophysical models that is more robust and comprehensive for complex vegetation covers than the mean parameterisation-based modelling paradigm. The substantial agreement between the simulations and the experimental data, obtained in a set of environmental and management options at a representative site of semi-natural grasslands of central France, demonstrates that CoSMo is an appropriate approach for estimating the dynamic behaviour of plant species (or functional or taxonomic groups) in a community. This is important because CoSMo has fewer parameters than other modelling approaches representing plant abundance, is relatively easy to calibrate and allows the use of a single instance of a generic vegetation model. We explored the parameter space of ModVege and its CoSMo-based solution under the specific climatic conditions of a single study site, under varying soil and management situations, with manual calibration to obtain a set of reference parameter values reflecting expert knowledge and simple adjustment strategies. The calibration work carried out through a trial-and-error process allowed the model estimates to be compared with observed data, and the solution obtained constitutes a satisfactory performance for two output variables (aboveground biomass and relative abundances) according to a set of metrics. By contrasting trait values for individual species to aggregated values at the community level, dynamically estimated functional traits can support predictions of community composition along environmental gradients and provide a greater understanding of changing ecosystem functioning. However, the site-specific study and the limited number of situations used for modelling raises the need for broader model evaluation work. First, this means that CoSMo-based ModVege may potentially be suitable for applications at other grassland sites if the model parameters are documented for those sites other than the one investigated here. Then, it is desirable to better understand the evolution of ecosystem functioning in the current context of global change in order to investigate whether measures of aggregate traits at the community level can be modelled at local scales, projected over the long term and upscaled across regions.

In conclusion, this study confirms that CoSMo-based solutions for grassland modelling can be easily implemented, although some background knowledge is required to parameterise each individual species/type in a grassland community. As the biophysical structure of CoSMo reflects important determinants of the functioning of grassland systems, we thus advocate its use to predict the behaviour of relevant grassland outputs, with three caveats. We first recommend further testing with grazing animals. Further tests are also required at a variety of sites, given the need to evaluate the CoSMo approach in contrasting biogeographic regions (e.g. the Mediterranean region where annual self-seeding species are dominant). Then, the present study highlights the need to orient grassland research towards the framing of dedicated functional trait measurements in the context of plant diversity and productivity observations for the CoSMo-based modelling purposes. By advancing modelling to highlight the role of plant functional diversity in grassland performance, this study is a springboard for supporting agro-ecological farming. More research on these lines can be seen as the natural evolution of this study, with the aim of developing scalable solutions open to a wide range of grassland types, while addressing the issues of re-use and interconnection of model components.

Supplementary Materials: Additional information is included in the supplementary file attached to the article.

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