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Modelling vegetation dynamics in managed grasslands: responses to drivers depend on species richness

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Abstract

In mathematical grassland models, plant communities may be represented by a various number of state variables, describing biomass compartments of some dominant species or plant functional types. The size of the initial species pool could have consequences on the outcome of the simulated ecosystem dynamics in terms of grassland productivity, diversity, and stability. This choice could also influence the model sensitivity to forcing parameters.

To address these issues, we developed a dynamic grassland model, DYNAGRAM, designed to simulate seasonal changes in both aboveground biomass production and species composition of managed permanent grasslands under various soil, climate and management conditions. We compared simulation results from alternative instances of DYNAGRAM that only differ by the identity and number of state variables describing the green biomass, here plant species. We assessed the sensitivity of each instance of the model to key forcing parameters for climate, soil fertility, and defoliation disturbances, using univariate and multivariate regression trees and dynamic trees.

Results of 10-year simulations under various climate, fertility and defoliation conditions showed that the final total biomass was tending to increase with the size of the species pool, while species evenness and the proportion of surviving species was tending to decrease. We found a positive correlation between the species survival ratio and the defoliation intensity, and this correlation increased with the initial species richness. The sensitivity to forcing parameters of community structure and species evenness differed markedly among alternative models, showing a progressive shift from high importance of soil fertility (fertilisation level, mineralization rate) to high importance of defoliation (mowing frequency, grazing intensity) as the size of the species pool increased. By contrast, the key drivers of total biomass production were independent of species richness and only linked to resource supply (nitrogen and water).

These results highlight the need to take into account the role of species diversity to explain the behaviour of grassland models.

Keywords: dynamic trees; grassland model; multivariate regression trees; plant succession; sensitivity analysis; species pool.

1. Introduction

Semi-natural permanent grasslands present important ecological, cultural and economic values, and support many ecosystem services due to their biodiversity (Gaujour et al., 2012; Mauchamp et al., 2012). Some temperate European grasslands, managed for a long time with low-intensity grazing or mowing, are the plant communities with the world records for species richness at fine scale (Wilson et al., 2012).

Various diachronic studies have revealed recent changes in the structure and composition of grassland plant communities in Europe (Gillet et al., 2016; Homburger and Hofer, 2012; Mitchell et al., 2017; Wesche et al., 2012). The causes of these changes are related to climatic (warming, extreme events) and anthropogenic (technical and socio-economic changes in management) constraints and disturbances. Land-use intensification or abandonment may lead to a severe reduction of species diversity with adverse impacts on ecosystem services. Fertilisation and defoliation regimes have been identified as the main drivers of plant species richness in productive grasslands (Gaujour et al., 2012; Mauchamp et al., 2016, 2014).

According to field observations, local species richness of temperate natural and semi-natural grasslands shows unimodal relationship with productivity, with a maximum biodiversity for intermediate productivity (Dengler et al., 2014). This questions how grassland ecosystem stability and productivity are influenced by vascular plant species richness. Field observations and experiments on semi-natural grasslands suggest that the most productive communities are the least diverse, but also the least resilient. By contrast, field experiments based on artificial species mixtures showed a positive correlation between species richness and productivity (Hector et al., 1999; Reich et al., 2012). A recent meta-analysis of experimental studies on such artificial species assemblages revealed that species richness generally improves resistance of grassland productivity to climatic extreme events, but not its recovery rate (Isbell et al., 2015). Increasing species richness in such artificial communities stabilizes whole community biomass but destabilizes the dynamics of constituent populations (de Mazancourt et al., 2013; Gross et al., 2013).

Since experimental studies have not been able to provide a general explanation to the relationships observed between grassland diversity and their productivity and stability, dynamical models are powerful tools for testing predictions of ecological theories. A lot of mathematical models of grassland dynamics based on explicit ecological processes have been developed. Some non-exhaustive reviews of grassland models are available (Snow et al., 2014; Taubert et al., 2012; Wiegand et al., 2008). Grassland models published so far have targeted monospecific swards (Duru et al., 2009; McCall and Bishop-Hurley, 2003; Schapendonk et al., 1998), mixtures of a grass and a legume species (Lazzarotto et al., 2009; Thornley, 1998), or a multispecies community constant in time (Jouven et al., 2006; Riedo et al., 1998). In a review of thirteen grassland models (Taubert et al., 2012), only two considered more than three different species or plant functional types: GRAS, a succession compartment model (Siehoff et al., 2011) and STEPPE, a gap model of semiarid grasslands (Coffin and Lauenroth, 1990); however, none of them simulate biomass. So far, very few grassland models have been designed to simulate both composition and biomass changes in multispecies semi-natural grasslands used as pastures or/and hayfields, a requirement for understanding diversity-productivity-stability relationships. Indeed, most of current grassland models focus on the impact of agricultural practices on forage production with many ecophysiological and biophysical details inherited from crop models but do not consider temporal changes in taxonomic and functional composition. An attempt (Lauenroth et al., 1993) to couple individual-based gap models describing changes in species composition (STEPPE) and ecosystem models describing nutrient cycling and biomass production (CENTURY) or water balance (SOILWAT) led to the development of the ECOTONE model,

able to simulate transitions between biomes (Peters, 2002). Several biophysical pasture models can be used to simulate growth of composite pasture types of several species under various management strategies, such as CLASS-PGM, a generic pasture growth model (Vaze et al., 2009), or DAIRYMOD and the SGS Pasture Model (Johnson, 2016), but these models are rather complex, limited to five “species” and not optimized for mowing management. GEMINI (Soussana et al., 2012) is another very detailed biophysical model of grassland ecosystems that explicitly simulates competition among any number of clonal populations for two key resources (light and nitrogen) along vertical canopy and soil profiles; plant functional traits are used to explain the response of aboveground net primary production and of plant community structure to various soil, climate and management conditions, including grazing, cutting and fertilization. Some recent mathematical models are based on stochastic differential equations adapted from the Lotka-Volterra equations to simulate changes in aboveground biomass of plant species mixtures and to explain community dynamics by environmental and demographic stochasticity (de Mazancourt et al., 2013; Lohier et al., 2016).

Taking into account the whole species diversity of grasslands in a mathematical model is quite impossible, given the large number of vascular plant species that may potentially co-occur in such ecosystems. For example, the regional species pool in permanent grasslands of the French Jura Mountains exceeds 1000 and the average number of species per local grassland is about 30, ranging from 3 to 92 (Mauchamp et al., 2012). To reduce the number of state variables describing the plant community in the model, a common solution is to consider plant functional types (PFTs) instead of individual species. PFTs can be viewed as theoretical “average species” combining parameters from a set of more or less functionally related species, such as legumes, perennial grasses or erect forbs. Typically, a PFT is a group of species with similar functional traits explaining their response to constraints and disturbances, such as management practices, and their effect on ecosystem function, such as forage production (Cruz et al., 2010, 2002; Duru et al., 2009; Graux et al., 2016). The GRAS model (Siehoff et al., 2011) simulates the succession of both dominant species and PFTs described by their cover dynamics, contrary to most agronomic grassland models, such as MODVEGE (Calanca et al., 2016; Jouven et al., 2006), which simulate seasonal changes in one or several biomass compartments, assuming a constant assemblage of species or PFTs. Individual-based, spatially explicit community grassland models such as IBC-GRASS (Weiss et al., 2014) are able to simulate metacommunities of many PFTs over hundred years, but at the price of a simplified representation of edaphic and climatic drivers. By contrast, (Confalonieri, 2014) suggested a model of plant community dynamics based on a single instance of a generic crop simulator, state variables being only simulated for the whole community. ECOHYD (Lohmann et al., 2017) is an ecohydrological model of semi-arid grasslands and savannas, able to simulate cover dynamics of a large number of PFTs, but focuses on hydrological processes and does not implement nutrient stress.

In this paper, we address a general issue that could be raised in any modelling study: the appropriate choice of the level of detail of the model, i.e. the number of state variables and associated parameters to be taken into account for describing the dynamical system, here the plant community. Although this choice is usually motivated by model objectives (e.g., with a focus on forage production or on biodiversity conservation) and by technical constraints (e.g., data availability, model performance), what are its consequences on the simulated dynamics of the virtual community in terms of grassland productivity, diversity, and stability? This question is especially relevant for permanent grasslands used for grazing or mowing and subject to seasonal changes in species composition and forage production, because of the high number of species coexisting in such ecosystems.

Thus, the first aim of the present study is to examine the consequences of increasing the number of state variables (i.e. the size of the local species pool) describing plant community

composition on model behaviour, regarding grassland productivity, diversity and stability. Specifically, we formulated four hypotheses: (H1) the inclusion of more species in the model increases its *productivity*, hence the final total biomass after ten-year simulations with various values of control parameters; (H2) the inclusion of more species in the model decreases its final species evenness, the component of community *diversity* measuring equitability in biomass and resource partitioning among species; (H3) the inclusion of more species in the model decreases its *stability*, hence the final proportion of surviving species (species survival ratio); (H4) species survival ratio increases with intensity and frequency of disturbances, and this positive correlation increases with the size of the species pool.

The second purpose is to assess the consequences of increasing the size of the species pool on the model sensitivity to key control parameters regarding climate, soil fertility and defoliation. We hypothesized that (H5) the hierarchy of influential parameters depends on species identity but not on the size of the species pool.

For these purposes, we need a simple mechanistic model in which the main ecological processes are implemented (seasonal mechanisms of plant growth, soil resource competition, response to climatic constraints and agricultural management) and in which we can vary the number and the identity of species in the initial plant community. As no such model was available, we developed DYNAGRAM, a simple and flexible dynamical model based on ordinary differential equations (ODEs), able to simulate various combinations of climate, soil and management conditions. The aim of this paper is not to present this model in detail along with results of calibration and validation with experimental data, which will be the topic of a next paper, but to use it as a tool to address two general relevant questions in ecological modelling. We simply ensured we properly modelled competition processes among species, under various forms of land use, by comparing simulated results to expert knowledge of grassland ecosystems (Cruz et al., 2010).

Fig. 1 Structure of the DYNAGRAM model. Solid lines denote flows of matter or energy and dashed lines denote reducers (mineral nitrogen acts both as a flow and as a reducer). State variables and forcing climatic variables are listed in Table 1 and a description of all parameters can be found in Tables A.1 and A.2 (Appendix A).

174

175 **2. Materials and methods**

176 *2.1. Model structure and main assumptions*

177 DYNAGRAM is a process-based succession model that simulates the aboveground vegetation
178 dynamics of a temperate grassland, both in term of composition and of forage production.
179 Using a common structure (Fig. 1), we developed four alternative versions of the model,
180 which correspond to different levels of diversity.

181 We built DYNAGRAM under some key assumptions, in the way to capture only essential
182 processes, and keeping as reduced as possible the dimension of the parameter space.
183 Grassland vegetation is described by n state variables B_i representing the green biomass
184 (leaves) for each plant species i . We did not consider the belowground biomass (roots) and the
185 reproductive parts of the plants. Hence, we assumed no seed production and no recruitment
186 from the seedbank. Two other state variables describe available resources in the soil: mineral
187 nitrogen Nm and water reserve WR (Table 1).

188 Basically, DYNAGRAM is a mechanistic model of resource competition (Tilman, 1980)
189 operating at a daily time step. We mainly based the regulation of green biomass and plant
190 competition from the standpoint of resource dynamics. A single nutrient, mineral nitrogen
191 (nitrate or ammonium), is consumed by plants for growth and is supplied by a pool of soil
192 organic nitrogen No , itself supplied by the senescence of standing biomass and litter
193 decomposition.

194 We considered four forcing climatic variables defined as simple sinusoidal functions of time
195 and acting on different processes (Table 1). This simplified formulation of the annual cycle
196 allows the manipulation of a reduced number of climatic parameters. Average daily
197 temperature T acts as a limiting factor for plant growth and litter decomposition, daily rainfall
198 P fills the soil water reserve, photosynthetic active radiation PAR is a driver of biomass
199 production by photosynthesis, and potential evapotranspiration PET determines the loss term
200 in the soil water budget equation that may cause drought stress.

201

202 **Table 1** State variables and forcing climatic variables implemented in DYNAGRAM.

203

State variables	Symbol	Description	Forcing climatic variables	Symbol	Description
Green biomass	B_i	Green biomass of plant species i	Temperature	T	Daily average air temperature acting on plant growth and mineralization rates
Organic nitrogen	No	Amount of organic nitrogen in the soil	Precipitation	P	Daily rainfall, the supply to the water reserve
Mineral nitrogen	Nm	Amount of mineral nitrogen in the soil available for plant growth	Photosynthetically active radiation	PAR	Portion of the solar radiation spectrum driving photosynthesis and determining potential growth
Water reserve	WR	Amount of water in the soil available for the plants	Potential evapotranspiration	PET	Function that determines the loss term in the water budget

204

Green biomass dynamics for each species is described by the following ODE (1). For clarity reason, we only wrote the dependence on state variables:

$$\frac{dB_i}{dt} = gr_i(B_i) Nred_i(Nm) Tred_i Wred_i(WR) Cred_i - \mu_i B_i - mow_i(B_i) - graz_i(B_i) \quad (1)$$

where μ_i is a constant leaf senescence rate, as assumed in the GRAS model (Siehoff et al., 2011). A comprehensive description of DYNAGRAM will be the subject of a next paper. Below we provide details on the three functions gr_i , mow_i and $graz_i$, useful to better understand the sensitivity analysis we performed. A complete description of all parameters is given in Tables A.1 and A.2 (Appendix A).

We assumed plant growth $gr_i(PAR, B_i)$ to be driven by an Ivlev function describing the photosynthesis process, as defined in MODVEGE (Jouven et al., 2006) and in LINGRA (Schapendonk et al., 1998). This function defines the maximal growth obtained in optimum conditions regarding resources (nutrients, water) and temperature, and in absence of disturbances (trampling). It describes the efficiency of use of solar radiation for photosynthesis and is modelled as the product of the Photosynthetically Active Radiation (PAR), the maximal Radiation Use Efficiency (RUE), which accounts for a decrease in efficiency at light intensity higher than 5 MJ m^{-2} , and an Ivlev function of the Surface Leaf Area (SLA_i) and of the plant biomass (B_i) that accounts for the proportion of light intercepted by the sward. This optimum plant growth function is given by equation (2).

$$gr_i(PAR(t), B_i(t)) = PAR(t) RUE(t) \left(1 - e^{-\alpha SLA_i \frac{B_i(t)}{10} LAM} \right) 10, \quad (2)$$

$$RUE(t) = RUE_{max} \min(1, 1 - \gamma_1(PAR(t) - \gamma_2))$$

Four reducers decrease biomass productivity. The first reducer, $Nred_i(Nm)$, is modelled by an Holling function depending on the biomass. The second reducer, $Wred_i(WR, PET)$, is a function of the water reserve and of the potential evapotranspiration. The third growth reducer, $Tred_i(T)$, depends on temperature. The fourth reducer, $Cred_i(SD)$, represents a decrease in plant growth due to trampling and is function of the livestock density, SD . Defoliation disturbances, i.e. mowing $mow_i(B_i)$ and grazing $graz_i(SD, B_i)$, act as a loss in green biomass.

The first defoliation disturbance consists on mowing events with a periodical cut of the canopy, following a pre-specified mowing schedule. All B_i variables related to green biomass are pulse-wise reduced and a proportion λ_i of all species biomass is removed. We assume this proportion to be independent of the biomass value and only depends on the species-specific canopy height. For a given mowing event, we get:

$$mow_i(B_i(t)) = \lambda_i B_i(t) \quad (3)$$

The second defoliation disturbance is due to grazing by livestock, following a predefined schedule. At every grazing day, a fixed amount κSD of standing biomass is removed by grazing. This loss of biomass is distributed among all species according to their appetite and their biomass, following a Holling type III function. During a given grazing period, we get:

$$graz_i(SD(t), B_i(t)) = \kappa SD(t) \frac{\rho_i B_i^{ng}(t)}{1 + \sum_{j=1}^n \rho_j B_j^{ng}(t)} \quad (4)$$

Soil processes are summarised by the following ODEs (5) to (7). Again, we only wrote the dependence on state variables.

$$\frac{dNo}{dt} = \sum_{i=1}^n \delta_i \mu_i B_i + Nd - \theta No Tmin Wmin(WR) \quad (5)$$

$$\frac{dNm}{dt} = \theta No T_{min} W_{min}(WR) + Nu + \Phi - \Lambda(Nm) - \sum_{i=1}^n \delta_i gr_i(B_i) N_{red_i}(Nm) T_{red_i} W_{red_i}(WR) C_{red_i} \quad (6)$$

$$\frac{dWR}{dt} = P - AET(B_i, WR) - \Delta(B_i, WR) \quad (7)$$

We introduced feedback loops for the two resources, available nitrogen and water reserve in the soil. The loss of green biomass due to senescence constitutes the litter, which fills a pool of organic nitrogen No stored in the soil organic matter. Depending on surface temperature $T_{min}(T)$ and soil moisture $W_{min}(WR)$, this organic nitrogen is mineralized in mineral nitrogen Nm (nitrate and ammonium) that becomes available for plant uptake. These two reducer functions affect the mineralization process and should not be confused with T_{red} and W_{red} that reduce plant growth. For each unit of biomass produced, we assumed that a fixed proportion δ_i of mineral nitrogen is consumed (Lazzarotto et al., 2009). Lixiviation $\Lambda(Nm)$ limits the amount of mineral nitrogen in the soil solution. Presence of grazing animals in the pasture brings organic $Nd(SD)$ and mineral $Nu(SD)$ nitrogen restitution proportionally to the stock density SD . The mineral nitrogen pool is also filled by mineral fertilization events, Φ .

The water reserve WR is filled by precipitations P and is emptied by the actual evapotranspiration $AET(B_i, WR, PET)$ and by drainage $\Delta(B_i, WR, PET, P)$. AET corresponds to the amount of water lost daily by evapotranspiration, which depends on green biomass, water reserve WR and potential evapotranspiration PET . Drainage corresponds to the loss of water by infiltration once the water reserve in the soil exceeds the water holding capacity WHC .

To summarize, if n is the size of the species pool, DYNAGRAM is defined by a system of $3 + n$ ordinary differential equations associated with $3 + n$ state variables, with $9 \times n$ species-specific parameters, 31 global parameters, and 13 parameters for climatic forcing functions.

The three primary C-S-R plant strategies defined by Grime (Grime, 1977; Pierce et al., 2017) are implicitly included in DYNAGRAM. Competitive ability (C strategy) occurs without any stress or disturbance and mainly depends on the potential growth rate of each species and their efficiency to achieve photosynthesis (parameters SLA_i , μ_i). Stress tolerance (S strategy) is represented by several species-specific parameters included in the reducers of this potential vegetative growth regarding three limiting factors (temperature, mineral nitrogen and water) and a trampling effect (parameters $T_{l,i}$, k_i , η_i , σ_i). Resistance to disturbance (R strategy) is represented by species-specific parameters concerning resistance to defoliation (mowing and grazing, which correspond to an explicit loss in green biomass; parameters ρ_i , λ_i). To show the wide diversity of life strategies and plant functional types among the 21 species considered in DYNAGRAM, we plotted their location within the CSR triangle in Fig. 2.

The DYNAGRAM model complies with five out of six criteria introduced in a recent review of grassland models (Taubert et al., 2012), by taking into account: (1) species richness, (2) resource limitation (light, nutrients, water), (3) management activities (mowing, grazing, fertilizing), (4) model simplicity, and (5) interspecific competition for resources. To keep the model simple, we did not comply with the sixth criterion concerning the representation of belowground competition processes.

We implemented DYNAGRAM in R language (R Core Team, 2017). Numerical integration of the ODE system was computed with the function 'ode()' of the R package 'deSolve' (Soetaert et al., 2010), using the Euler method and an integration time step of one day to correspond to the length of discrete management events included in the model. This choice of discrete time and difference equations was also made to reduce the simulation time in batch runs, after

having verified that the model outputs were similar to the ones obtained with a smaller fixed or variable time step and a solver considering continuous time, such as ‘lsoda’, taking into account events (sudden changes in a state variable, e.g. mowing or fertilization).

Fig. 2 Ternary plot of the CSR triangle indicating the strategy of the 21 species included in the full model (Pierce et al., 2017) and grouped into seven plant functional types (PFTs). Abbreviated names of species and PFTs refer to Table A.2.

2.2. Choice of the biomass state variables

As our aim was to capture the dynamics of the taxonomic and functional community composition and to assess the importance of community diversity, we considered various combinations of species to represent biomass state variables. In this way, we wrote four alternative versions of DYNAGRAM that only differ by the number $n \in \{2, 4, 7, 21\}$ of these state variables. We designed several assemblages containing a number n of species selected as follows among a list of 21 representative herbaceous species (Table A.2 in Appendix A).

A first model version (DYNAGRAM2) considers a mixture of two species, namely perennial ryegrass (*Lolium perenne*), a grass, and white clover (*Trifolium repens*), a legume. These two species are frequent in intensively managed grasslands and are included in several agronomic grassland models, such as PROGRASS (Lazzarotto et al., 2009), which derives from the pasture simulation model PASIM (Calanca et al., 2007; Graux et al., 2011; Riedo et al., 1998).

We selected a set of frequent and potentially dominant individual species, differing by their functional traits and ecological preferences, representative of the species pool in mid-mountain European pastures and hayfields to be included in a second version of the model

(DYNAGRAM21) with 21 plant species. As shown by Fig. 2, these species belong to various PFTs and present a wide range of CSR strategies.

Finally, for DYNAGRAM4 and DYNAGRAM7, we kept the two species present in DYNAGRAM2 (*Lolium perenne* and *Trifolium repens*), to which we added ten combinations of two or five other species, respectively, randomly selected among the 19 remaining species included in DYNAGRAM21. Thus, by keeping in all 22 alternative instances of the model (the basic DYNAGRAM2, the full DYNAGRAM21, and ten replicates of DYNAGRAM4 and DYNAGRAM7) a same grass and a same legume species we ensured a minimum common heterogeneity in the functional composition of each instance, and by our random selection of other species we avoided any subjective bias.

2.3. Selection of the key control parameters

When performing a sensitivity analysis, we look at the sensitivity of a model output $\mathbf{Y} = f(\mathbf{X})$ to variations of the control parameters in a matrix $\mathbf{X}$. Each line of the matrix $\mathbf{X}$ defines a set of parameters for which we solve the ODE system. In a first identification analysis, we assessed the sensitivity of model outputs (total biomass and species evenness) to a deviation of $\pm 20\%$ of all parameters, except species-specific parameters (Online Appendix B, Tables B.1, B.2 and B.3).

From the results of this first analysis, we selected the six most influential control parameters to be used for a more detailed sensitivity analysis, grouped in three categories: (i) *climate* parameters include mean monthly temperature Tm and mean monthly sum of precipitation Pm ; (ii) *soil fertility* parameters include the mineralization rate of organic nitrogen θ and the amount of mineral nitrogen dropped off each year on the soil as fertilizers Φ ; (iii) *defoliation* disturbance parameters include the livestock density SD during each grazing period and the number of mowing events per year $ncut$. The $\mathbf{X}$ matrix consisted of all 1728 combinations of three or four values for the six control parameters (Table 2).

We considered a management scenario that is identically repeated each year. Cattle is continuously present in the grassland during one long grazing season, from the 1st of July to the 31st of August. The first mowing event appears on the 1st of June, and a second mowing event on the 2nd of October. The amount of fertilizer, $\Phi = 90 \text{ kg N ha}^{-1}$, is split in six fractions spread on the grassland (May 1st, May 15th, June 10th, June 20th, September 1st and September 15th).

Table 2 Set of values of the selected control parameters in the matrix $\mathbf{X}$ of the sensitivity analysis. Columns of $\mathbf{X}$ correspond to the six key parameters. Lines of $\mathbf{X}$ are built from all combinations of those values, leading to $3^3 \times 4^3 = 1728$ lines. LU: livestock unit (1 LU is equivalent to a dairy cow).

Parameter	Category	Values in matrix $\mathbf{X}$				Unit
Tm	Climate	7	9	11		°C
Pm	Climate	50	80	110	140	mm month ⁻¹
θ	Soil fertility	$4 \cdot 10^{-4}$	$7 \cdot 10^{-4}$	$1 \cdot 10^{-3}$		d ⁻¹
Φ	Soil fertility	0	20	50	100	kg N ha ⁻¹ a ⁻¹
SD	Defoliation	0	0.5	1	1.5	LU ha ⁻¹
$ncut$	Defoliation	0	1	2		a ⁻¹

2.4. Selection of the response variables

The next step was thus to extract the response variables from the simulation outputs after running each alternative version of the model. Those response variables are either a matrix $\mathbf{Y}$ (if built from several output variables per simulation) or a vector $\mathbf{y}$ (if built from a single output variable).

Each line of the input matrix $\mathbf{X}$ corresponds to a set of parameters, for which we run the model and generated one response matrix $\mathbf{Y}$ and three response vectors $\mathbf{y}$ extracted from the model output at time $t_f = 3559$, that is the 1st of October at year 10 of the simulation. This day is selected just before the second yearly cut and after all other management practices having occurred in the year.

$\mathbf{Y}$ is a n -columns matrix of biomass values of all species at day t_f . $\mathbf{y}_1$ is a vector of the total biomass values B_{tot} at day t_f , simply computed as the sum of the green biomass values of all present species:

$$B_{tot}(t_f) = \sum_{i=1}^n B_i(t_f) \quad (8)$$

$\mathbf{y}_2$ is a vector of Simpson evenness values B_{eve} of the plant community at day t_f . Simpson evenness is a taxonomic diversity index ranging between 0 and 1 and measuring the proportion of dominant species in the community according to differences in biomass (Hill, 1973; Jost, 2006). A value of 1 means that all species initially introduced are equally distributed in biomass in the grassland, whereas a value close to 0 means the persistence of only one single species that outcompeted all others. We computed Simpson evenness by dividing the inverse Simpson diversity index by n , the number of species initially present in the model:

$$B_{eve}(t_f) = \frac{1}{n \sum_{i=1}^n \left(\frac{B_i(t_f)}{B_{tot}(t_f)} \right)^2} \quad (9)$$

$\mathbf{y}_3$ is a vector of the ratio S of the number of surviving species at day t_f to the initial species pool n , considering as virtually absent a species with a biomass less than 1 g DM ha⁻¹:

$$S(t_f) = \frac{\#\{B_i(t_f) > 10^{-3}\}}{n} \quad (10)$$

S represents the final proportion of surviving species, also called ‘species survival ratio’ thereafter.

2.5. Assessment of the model’s response to variation in species richness

To relate the variation of the computed indexes B_{tot} , B_{eve} and S to the size of the initial species pool, we performed Kruskal-Wallis tests with post-hoc multiple comparisons on the simulation outputs over all combinations of values for the six climate, fertility and defoliation parameters. Differences in total final biomass B_{tot} would allow to know if grassland productivity is impacted by increasing species richness in the model, whereas differences in evenness B_{eve} and survival species S would provide information about the impact on community diversity and resilience.

2.6. Tree-based sensitivity analysis

Regression tree is an iterative process of dividing the data into two partitions, and then splitting it up further on each of the branches using discriminant explanatory variables (De’ath and Fabricius, 2000). Each split corresponds to a node. A regression tree can be interpreted as

a decision tree, in which terminal leaves group records with homogenous response variables that can be explained by a series of explanatory variables (here model parameters). The homogeneity of each node is characterized by its impurity, a measure that takes the value zero for completely homogeneous nodes and increases as homogeneity decreases. Then maximizing homogeneity in a given group is equivalent to minimizing their impurity. The predicted value of the output variable for a particular node is the sample average of the output variable consisting of records included in that node. The splitting process continues until each node reaches a user-specified minimum node size and becomes a terminal node (Makler-Pick et al., 2011).

Dynamic trees were introduced to provide Bayesian inference for regression trees that change with the arrival of new observations (Taddy et al., 2011). Dynamic trees provide an efficient measure of a covariate's first-order effect, i.e. variance reduction directly attributed to splits on that variable. However, these indices are not appropriate for all applications of sensitivity analysis, as non-constant leaf prediction models, such as for linear trees. This issue has been corrected by a technique of estimation of sensitivity indices (Gramacy et al., 2013), which is model-free and can be constrained to subsets of the input space. Thus, DT computes the Sobol index associated to the sensitivity analysis (Ravalico et al., 2005), and graphically estimates how each parameter from the set of the matrix $\mathbf{X}$ impacts the output variable in vector $\mathbf{y}$.

To investigate the influence of the number of state variables describing the plant community (aboveground biomass of individual species) on the model sensitivity to key parameters (climate, soil fertility, defoliation), we performed a tree-based sensitivity analysis for each level of complexity of DYNAGRAM, with 2, 4, 7 and 21 species, based on the matrix $\mathbf{X}$ and $\mathbf{Y}$ (or vector $\mathbf{y}$) described previously.

Our sensitivity analysis was based on three kinds of trees: (i) Univariate Regression Tree (URT); (ii) Multivariate Regression Tree (MRT) and (iii) Dynamic Tree (DT). URT and DT consider a vector $\mathbf{y}$ containing one single synthetic variable (B_{tot} , B_{eve} , or S) contrary to MRT (De'ath, 2002) that considers a matrix $\mathbf{Y}$ including several response variables (biomass of each species). URT has been used to rank a set of influential control parameters, here $\{Tm, Pm, \theta, \Phi, SD, ncut\}$, from top to bottom, according to their impact on a single output variable among the set $\{B_{tot}, B_{eve}, S\}$ for performing global sensitivity analysis (Eynaud et al., 2012; Makler-Pick et al., 2011).

We applied URT and DT to assess the sensitivity of the three response variables (total biomass B_{tot} , Simpson evenness B_{eve} and survival rate S at time t_f) to the variation of the six control parameters in matrix $\mathbf{X}$.

To assess the sensitivity of species composition to the variation of the same parameters we applied MRT to the multivariate response matrix $\mathbf{Y}$ of all species biomasses, constrained by the input parameter matrix $\mathbf{X}$. To our knowledge, it is the first application of MRT to model sensitivity analysis.

We pruned each tree to plot the result with six terminal nodes. We determined the most influential parameters selected by univariate and multivariate regression trees by retaining the three discriminant parameters up to the second splits of each URT or MRT, respectively. We compared the average number of discriminant parameters of each category (climate, soil fertility or defoliation) among the four species richness levels (2, 4, 7 and 21).

All analyses were performed in the R environment (R Core Team, 2017) with the packages 'mvpart' (univariate and multivariate regression trees) and 'dynaTree' (dynamic trees).

3. Results

3.1. Model response to variation in initial species richness

Under various climate, fertility and defoliation conditions given by all combinations of the six control parameters, the final total biomass after ten years of simulation B_{tot} globally increased with the number of species in the grassland (Fig. 3A).

By contrast, Simpson evenness B_{eve} tended to decrease with initial species richness, showing that the more the species pool was large, the less the final green biomass was equally distributed among the species (Fig. 3B).

The proportion of surviving species S tended also to decrease with the size of the species pool (Fig. 3C). However, for any initial species richness, we observed that some combinations of parameter values led to cases with null values for each response variable, i.e. with the extinction of all species due to excessive stress or disturbance.

For 21 species in the initial species pool, the survival rate increased with the disturbance intensity, which is the product of defoliation parameters SD and $ncut$ (Fig. 4A). Moreover, the positive Kendall rank correlation between the disturbance intensity and the species survival rate increased with the size of the species pool (Fig. 4B).

Fig. 3 Boxplots of final total biomass B_{tot} (A), Simpson species evenness B_{eve} (B) and proportion of surviving species S (C) at the end of simulations from alternative DYNAGRAM models with all combinations of control parameters given in Table 2. All results of Kruskal-Wallis tests were highly significant (***; $P < 0.001$). Different letters indicate significant differences among groups of simulations, based on 1728 simulations for 2 and 21 species, and 10 series of 1728 simulations for different assemblages of 4 and 7 species.

Fig. 4 The relationship between the defoliation intensity and the species survival ratio. **A:** Boxplots of the proportion of surviving species S at the end of simulations from DYNAGRAM21 with all combinations of control parameters, in function of the level of defoliation intensity, with results of Kruskal-Wallis and post-hoc tests (***: $P < 0.001$); different letters indicate significant differences among levels, based on 1728 simulations for 21 species. **B:** Bar plot of the Kendall rank correlations between the size of the species pool n and the species survival ratio S , based on 1728 simulations for 2 and 21 species, and 10 series of 1728 simulations for different assemblages of 4 and 7 species.

3.2. Sensitivity analysis of DYNAGRAM for 2 and 21 species

To illustrate some details of the sensitivity analysis we performed, let us focus at first on the results of simulations with the extreme values of the species pool, i.e. 2 and 21 species.

Fig. 5 Multivariate regression trees of a response matrix **Y** containing final green biomass of 2 (**A**) or 21 (**B**) species explained by control parameters out of matrix **X**. Barplots show biomass means for all species, with deviance and number of cases at each terminal node.

3.2.1. Multivariate regression trees

The hierarchy of the most influential parameters that explained differences in final species composition differed completely between DYNAGRAM2 and DYNAGRAM21 (Fig. 5). Variations in quantitative composition of the two-species modelled grassland (Fig. 5A) were mainly driven by fertility parameters (fertilizer input Φ and mineralization rate θ converting organic N to mineral N) and by water supply Pm . By contrast, defoliation parameters (especially stock density SD) and temperature Tm played the major role in explaining the final composition of the species-rich grassland with 21 species (Fig. 5B). These results show that processes driving the assemblage may be strongly related to species richness.

3.2.2. Univariate regression trees

Like species composition, species evenness and survival rate depended mainly on soil fertility (Φ and θ) for DYNAGRAM2, but on defoliation (SD) for DYNAGRAM21 (Table 3). By contrast, the hierarchy of parameters influencing final total green biomass was independent of the size of the species pool: the first discriminant parameter was in each case fertilisation intensity Φ , followed by mineralization rate θ and mean precipitation Pm . The defoliation regime played no important role in explaining the final standing biomass of a simulated grassland made of 2 or 21 species.

Table 3 Hierarchy of key control parameters resulting from a sensitivity analysis of DYNAGRAM based on MRT and URT on the final biomass of 2 and 21 species. Response variables were individual species biomasses B_i , total biomass (B_{tot}), Simpson evenness (B_{eve}), and survival rate ratio (S) at the end of 10-year 1728 simulations for each species pool. Numbers in brackets are thresholds applied to split the tree at the first (first line, in bold) or the second level (second line). Climate parameters: Tm (temperature), Pm (precipitation); soil fertility parameters: Φ (fertiliser input), θ (mineralization rate); defoliation parameters: SD (livestock density), $ncut$ (mowing frequency).

Response variables	2 species	21 species
MRT on B_i	Φ {35} θ {5.5 10 ⁻⁴ } Pm {65}	Tm {10} SD {0.75} SD {0.75}
URT on B_{tot}	Φ {35} θ {5.5 10 ⁻⁴ } Pm {65}	Φ {35} θ {5.5 10 ⁻⁴ } Pm {65}
URT on B_{eve}	Φ {75} θ {5.5 10 ⁻⁴ } θ {5.5 10 ⁻⁴ }	SD {0.75} SD {0.25} Tm {10}
URT on S	θ {5.5 10 ⁻⁴ } Φ {35}	SD {0.75} Φ {35} Tm {10}

3.2.3. Dynamic trees of species evenness

As the first results of the sensitivity analysis based on composition (MRT) and on Simpson evenness (URT) were very similar, we will focus on this last relevant index of community structure B_{eve} to investigate in more detail the main effects of the six parameters using dynamic trees (Fig. 6). Results for total biomass and survival rate are provided as Supplementary Material (Online Appendix C, Fig. C.1 and C.2).

Dynamic trees confirmed the strong positive effect of livestock density SD on species evenness with 21 species (Fig. 6B), as compared to other parameters. With two species (Fig. 6A), the main positive effects were also due to the amount of fertilizer Φ and the maximal mineralization rate θ , which were much less influential with a large species pool. The number of mowing events $ncut$ showed opposite effects on evenness: slightly positive for two species and negative for 21 species. In both cases, mean temperature Tm had a negative effect on evenness.

Despite common trends easily explained by their common structure, the sensitivity analysis revealed strong divergences between the two alternative versions of DYNAGRAM, depending on the size of the species pool, suggesting a shift in key parameters influencing community organization.

A

B

Fig. 6 Main effects of six key parameters on Simpson species evenness B_{eve} , from dynamic trees performed on DYNAGRAM2 (A) and DYNAGRAM21 (B) outputs. Climate parameters: Tm (temperature), Pm (precipitation); soil fertility parameters: Φ (fertiliser input), θ (mineralization rate); defoliation parameters: SD (livestock density), $ncut$ (mowing frequency).

3.3. Impact of species number on the hierarchy of influential parameters

Tree-based sensitivity analysis of DYNAGRAM2 and DYNAGRAM21 suggested a shift in key parameters determining the grassland composition according to the size of the species pool. To assess the impact of species number, irrespective to species identity, on the hierarchy of the key parameters, we have to include in the comparison the results of regression trees for DYNAGRAM4 and DYNAGRAM7, each with ten random samples among the full set of 21 species. Results of this comparison are summarized by bar plots (Fig. 7).

Fig. 7 Bar plots of the three most influential control parameter categories on species composition (A), Simpson evenness (B) and total green biomass (C) at the end of simulations with 2, 4, 7 and 21 species. Three key parameters were extracted from the first and second splits of each MRT (A) or URT (B, C). Results for 4 and 7 species are mean numbers from ten random species samples.

A progressive shift from high importance of soil fertility to high importance of defoliation as the number of species increased was evidenced for both species composition (Fig. 7A) and Simpson evenness B_{eve} (Fig. 7B). A small increase in species number from 2 to 4 induced a small decrease of fertility importance in favour of defoliation and climate. Increasing further species number from 4 to 7 enhanced this trend. Finally, by including all 21 species the

influence of soil fertility parameters vanished in favour of defoliation parameters. The shift we evidenced in relative parameter influence followed a gradient only driven by the size of the species pool, whatever the species identity.

By contrast, results for total biomass B_{tot} (Fig. 7C) confirmed the absence of any trend, already observed in Table 3: parameters influencing final total green biomass were totally independent of the size of the species pool. B_{tot} always mainly depended on parameters linked to resource supply: input of Nm by soil fertilization Φ , maximal mineralization rate θ of No to Nm , and water supply by rainfall Pm .

4. Discussion

4.1. Final model outputs depend on initial species richness

The positive relationship between the size of the species pool and the final green biomass after 10 growing seasons (Fig. 3A) suggests a better overall productivity of species-rich modelled ecosystems in favourable conditions, whatever species identity. This result is in accordance with our first hypothesis and with the findings of field experiments with artificial plant communities (Hector et al., 1999; Reich et al., 2012). An analysis of these biodiversity experiments (Gross et al., 2013) suggested that interspecific competition generates compensatory dynamics in grasslands that help stabilize community biomass. This stabilizing effect of species richness on community biomass arises because increasing species richness increases mean biomass by a larger amount than it increases variance, thus increasing stability. The contrast with observations in (semi-)natural grasslands, which generally conclude to a negative correlation between species richness and productivity, can be explained by the same reasons that those given in the case of these biodiversity experiments: our simulation experiment considers artificial assemblages of a relatively small number of species (21 species is a relatively low species richness as compared to the one of semi-natural grasslands), which are not likely to coexist in extent plant communities resulting from abiotic and biotic species filtering (Lortie et al., 2004). This contrast between results of simulations or experiments and observations highlights the need to consider multi-species sward in grassland models, which was identified as one of the fifteen key challenges by a panel of European grassland modellers and experts (Kipling et al., 2016b), and a priority for further research. The simulated effect of species diversity on forage production confirms that modelling multi-species swards, along with grassland quality and the impact of management changes, requires further development (Kipling et al., 2016a; van Oijen et al., 2018).

The negative relationship between initial species richness and final species evenness (Fig. 3B) confirms our second hypothesis and the ability of our model to capture competition processes that could lead to dominance of some species. DYNAGRAM also simulates species extinction, and this diversity loss is an expression of competitive exclusion, with dominant species that outcompete some others, depending on environmental conditions.

Furthermore, we observed a decrease in the proportion of surviving species as the size of the species pool increases (Fig. 3C), confirming our third hypothesis. This trend is also in accordance with theory and experiments that suggest that increasing species richness should destabilize the dynamics of individual populations (Gross et al., 2013; Tilman, 1999). This decrease in the species survival ratio means that for high diversity levels not all species initially present can survive. However, contrary to Tilman's tradeoff-based niche theory rooted on a simple resource-reduction competition model (Tilman, 1980), which states that two different species cannot coexist on a single limiting resource, DYNAGRAM is able to simulate the persistence of more species than essential resources. In this model we considered three essential resources (mineral nitrogen, water and light) but we observed long-term

persistence of more than three species. Species coexistence could partly be explained by the cyclicity of plant growth rate due to seasonal periodic fluctuations of climatic conditions implemented in our model, allowing temporal turnover of species with different temperature optimum for growth.

Among the numerous differences with Tilman's model, we also introduced disturbances due to grassland management (defoliation by grazing and cutting), which as such could be detrimental to some intolerant species and lead to species extinction. However, according to our fourth hypothesis, disturbances are supposed to affect more competitive species and thus prevent competitive exclusion, allowing more species to coexist in the plant community. This is confirmed by our results, as the species survival ratio increased with the defoliation intensity (Fig. 4A). We report the results for 21 species, but a similar relationship was obtained for any size of the species pool (not shown). The importance of defoliation events, mowing or grazing, has also been highlighted for dynamic global vegetation models: the ORCHIDEE model better reproduces seasonal variation of LAI after integrating a management module for defoliation activities (Chang et al., 2013). It could be of interest to extend this result to other disturbances affecting grasslands, such as pest outbreaks and diseases, for which a lack of model development has been reported (Snow et al., 2014).

As expected, the positive correlation between n and S tended to increase with the size of the species pool (Fig. 4B), suggesting that disturbances play a more important stabilizing role in species-rich communities, in which non-equilibrium conditions brought by disturbances and fluctuating environment better favour species coexistence by promoting species turnover and preventing competitive exclusion of subordinate species. The relatively low correlation obtained with DYNAGRAM2 may also be explained by the identity of the selected species, *Lolium perenne* and *Trifolium repens*, which, as shown in Table A.2, are both tolerant to defoliation and trampling (Kühn et al., 2004).

These results confirm the need of taking into account the species composition of grassland vegetation to accurately estimate the leaf area index (Ben Touhami and Bellocchi, 2015). They also add to the growing evidence that increased species richness and functional diversity contribute to stabilizing biomass production and enhancing the resilience of grassland ecosystems, as shown both theoretically and experimentally (Cottingham et al., 2001; Gross et al., 2013).

4.2. A shift in key parameters across a diversity gradient

Our sensitivity analysis revealed the existence of an unexpected shift in the hierarchy of the most influential parameters on final community structure (MRT on B_i : Table 3, Fig. 5 and 7), species evenness (URT and dynamic trees on B_{eve} : Table 3, Fig. 6 and 7) and species survival ratio (URT on S : Table 3) across a gradient of species richness: as the number of state variables describing the plant community increased, the influence of soil fertility parameters related to stress tended to decline in favour of defoliation parameters related to disturbance. By considering various random combinations of species in addition to the clover-ryegrass mixture for DYNAGRAM4 and DYNAGRAM7, we showed that this general trend was independent of species identity, contrary to our fifth hypothesis.

This importance of soil nitrogen availability for a low diverse assemblage (two species) is consistent with several recent studies that specifically raised the need to model soil nutrient dynamics (Ma et al., 2014; Sándor et al., 2016; Snow et al., 2017). A sensitivity analysis of the biogeochemical grassland model COUPMODEL (Senapati et al., 2016) showed that more than half of the critical parameters, recognized as most influential on ecosystem processes, were related to nutrient dynamics. This importance of soil nitrogen availability for DYNAGRAM2 could be explained by the contrasting needs of the two species, expressed by

strong differences in species-specific parameters δ_i (leaf nitrogen concentration) and k_i (half-saturation constant for nitrogen uptake) between the grass and the legume (Table A.2). The inclusion in the model of the symbiotic fixation of atmospheric nitrogen N_2 by the legume (Lazzarotto et al., 2009) would probably have still accentuated this contrast, hence the model sensitivity to resource parameters. Conversely, a species-rich grassland, such as the one modelled by DYNAGRAM21, allows functional redundancy among species, making access to light a key factor of plant growth expressed by a strong importance of defoliation parameters. One further development could consist on taking into account the uncertainty in parameter distribution, following a method for sensitivity analysis recently proposed (Paleari and Confalonieri, 2016).

4.3. *Grassland diversity, productivity and stability*

Contrary to drivers of community structure, parameters influencing final total green biomass did not depend on the size of the species pool (Fig. 7C). Thus, the positive effect of species richness on productivity cannot be explained by changes in key drivers. For any combination of species, biomass production was mainly limited by nutrient and water availability, i.e. stress factors, while disturbances always played a minor role.

Here we assume that the green biomass at the end of the tenth growing season is proportional to the aboveground net primary productivity (ANPP) of the final plant community. We base this assumption on the observation of time series from various simulations that showed strong periodic seasonal similarities after six or seven years of repeated climate and management conditions, suggesting that the system has rapidly reached a cyclic equilibrium (results not shown). A stability analysis based on phase or bifurcation diagrams should be carried out to assess the impact of key forcing parameters, e.g. the fertilisation intensity Φ and the stock density SD , on steady states of the system (Louie et al., 2002). As we simulated seasonal dynamics, cyclic steady states are expected but this stability analysis is out the scope of the present paper.

Another possible critical choice is the date at which values of biomass state variables were kept to compare simulation outcomes. We chose the 1st of October at year 10 of each simulation, just before the second cut and after all other management practices occurred eventually in the last year, but other choices could have been possible, such as the day before the first management event, i.e. the 1st of May at year 10. This second choice led to similar results and to the same conclusions (results not shown).

4.4. *Simplicity or complexity?*

Our study highlights consequences of the chosen number of state variables on model's behaviour. In the case of our grassland model, we evidenced a shift in the hierarchy of key parameters involved in the dynamics of community structure depending on the size of the species pool. This should warn the modeller that mathematical grassland models that simplify the plant community by considering a small number of species or PFTs are likely to reveal impacts of soil fertility, whereas more complex models that include a larger species pool will be more sensitive to disturbance processes. Therefore, this result suggests some conditions in the choice of the number of species to define the hierarchy of drivers involved in plant growth, such as performed in the CoSMO sub-model that ranked disturbances as the most important drivers and nitrogen availability as the less important one (Confalonieri, 2014).

This shift of the most influential parameters follows a kind of continuum (Fig. 7). However, whereas the most influential parameters are markedly different between models with 2 and 21 species, the difference between 7 and 21 species is relatively low. Therefore, the choice of 7

species or PFTs could be a good compromise to take into account functional plant diversity with keeping the number of state variables as lower as possible.

This issue relates to a more general problem in ecological modelling: how to keep the model as simple as possible without missing key variables and processes? DYNAGRAM is simpler than many other grassland models but more complex than other ones. As compared to more parsimonious mechanistic models based on ODE systems (Louie et al., 2002; Siehoff et al., 2011; Tilman, 1985), DYNAGRAM includes a consumption-degradation loop for nitrogen, the main limiting soil nutrient, and takes into account the seasonality of plant growth and resource competition (Lazzarotto et al., 2009). This added complexity was necessary to assess the model's sensitivity to soil fertility, climatic conditions and defoliation.

As both knowledge of grassland ecosystems and computer performance progress, the implementation of more and more details and processes is a general trend in grassland modelling. Our choice of a minimal model complexity implies some strong assumptions. As compared to more detailed models, such as MODVEGE, GEMINI or PROGRASS (Jouven et al., 2006; Lazzarotto et al., 2009; Soussana et al., 2012), DYNAGRAM considers only one single biomass compartment for each species without distinguishing aboveground plant structural components (i.e. vegetative or reproductive, green or dead) and ignores the belowground biomass (roots, rhizomes and storage organs) as well as many associated physiological processes. In accordance with most grassland growth models, DYNAGRAM only simulates vegetative growth and does not include seed reproduction or emergence of new species from the soil seed bank or by seed dispersal.

Model degradation techniques can be applied to assess consequences on model performance (simulation time, prediction accuracy) of reducing the number of variables and parameters in a complex model. Applied to grassland models, they often conclude to the necessity of keeping the full complexity to ensure an acceptable goodness of fit with empirical data (Lohier et al., 2016). In this paper, our goal was more strategical than tactical: we developed DYNAGRAM to address a specific theoretical question about the response of a grassland model to climatic, edaphic and management forcings in function of the number and identity of the state variables describing the plant community. The next step will be to calibrate and to validate the model against experimental data so as to use it for the simulation of climatic and management scenarios applied to real systems. Its performance in terms of computation time as compared to more complex models makes it possible to implement DYNAGRAM as a submodel in a spatially explicit, mosaic landscape model, such as WoodPaM (Gillet, 2008; Peringer et al., 2013).

Alternatives to the development of new models may rely on re-usable components or submodels that could be coupled with generic crop simulators to simulate an assemblage of several species and reproduce plant community dynamics (Confalonieri, 2014). Another promising approach consists in comparing the performance of multiple grassland models so as to implement a multi-model ensemble prediction system in grasslands (Palareti et al., 2016; Sándor et al., 2017).

5. Conclusion

Our simulations with DYNAGRAM confirmed most of our expectations but provided new insights on the diversity-productivity-stability relationship. After reaching a cyclic equilibrium, the final structure of the grassland plant community, described by green biomass of a given set of species, depends on the size of species pool. In accordance with the insurance hypothesis (Yachi and Loreau, 1999), increasing species richness insures the ecosystem against declines in its productivity caused by climatic fluctuations and periodic anthropogenic disturbances. However, depending on species identity and environmental conditions, the

stability of the community, measured by the proportion of surviving species after 10-year simulations, and the evenness component of its diversity tend to decrease with the size of the species pool, due to environmental filtering and competitive exclusion.

Moreover, results of our tree-based sensitivity analysis revealed an unexpected shift in the key drivers of the final community structure, but not of its total biomass, when increasing the size of the species pool from two to 21 species. These findings create new challenges in ecological modelling to be raised through mathematical and simulation studies.

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1008

1009 Appendix A: Variables and parameters of DYNAGRAM

1010

1011 **Table A.1** Summary of all variables and parameters of DYNAGRAM. Values of the species-
 1012 specific parameters are given in Table A.2.

1013

Symbol	Definition	Unit	Value
<i>State variables</i>			
B_i	Green biomass of species or PFT i	kg DM ha ⁻¹	$B_i(0) = 200/n$
No	Organic nitrogen, stored in the soil organic matter	kg N ha ⁻¹	$No(0) = 5800$
Nm	Mineral nitrogen (nitrate and ammonium) in the soil solution, available for plant uptake	kg N ha ⁻¹	$Nm(0) = 20$
WR	Water reserve in the soil, available for plant uptake	mm	$WR(0) = WHC$
<i>Climatic forcing variables</i>			
T	Surface temperature	°C	function
P	Daily precipitation	mm d ⁻¹	function
PAR	Photosynthetically active radiation	MJ m ⁻² d ⁻¹	function
PET	Potential evapotranspiration	mm d ⁻¹	function
<i>Plant species-specific parameters</i>			
n	Number of species or PFTs	[count]	{2, 4, 7, 21}
SLA_i	Specific leaf area	m ² g ⁻¹	species-specific
λ_i	Proportion of biomass removed by a mowing event	d ⁻¹	species-specific
ρ_i	Appetence for feeding regime of cattle	[-]	species-specific
σ_i	Utilization indicator value for the trampling tolerance	[-]	species-specific
δ_i	Leaf nitrogen content	kg N (kg DM) ⁻¹	species-specific
k_i	Half-saturation constant: resource level at which growth rate is half its maximum	kg N ha ⁻¹	species-specific
μ_i	Basic senescence rate of leaves	d ⁻¹	species-specific
$T_{1,i}$	Lower limit of optimum of daily temperature for photosynthesis	°C	species-specific
η_i	Water stress tolerance exponent	[-]	species-specific
<i>Plant growth processes and tolerance parameters</i>			
T_0	Base temperature for light utilization and development	°C	3
T_2	Higher limit of optimum of daily temperature for photosynthesis	°C	20
T_3	Maximal temperature for light utilization and development	°C	40
RUE_{max}	Maximum radiation use efficiency	g DM MJ ⁻¹	3
LAM	Proportion of laminae in green biomass	[-]	0.68
α	Extinction coefficient	[-]	0.6
v	Holling coefficient for mineral nitrogen consumption	[-]	2
ng	Holling coefficient for green biomass removal by grazing	[-]	2
T_{tol}	Amplification exponent of the control function $f(X)$ of trampling	[-]	0.5
<i>Soil parameters</i>			
θ	Nitrogen mineralization rate	d ⁻¹	$7 \cdot 10^{-4}$
Nm_{max}	Maximal amount of Nm stored in the soil before lixiviation	kg N ha ⁻¹	120
WHC	Volumetric water content at field capacity	mm	150
PWP	Volumetric soil water content at permanent wilting point	mm	7.5
Tm_1	Critical temperature for maximal mineralization rate of No to Nm	°C	40
Tm_2	Empirical parameters describing effect of temperature on mineralization	°C	31.79
g_T	Empirical parameters describing effect of temperature on mineralization	[-]	3.36

g_{W1}	Empirical parameters describing effect of soil water on mineralization	[-]	1
g_{W2}	Empirical parameter describing effect of soil water on mineralization	[-]	6.63
g_{W3}	Empirical parameter describing effect of soil water on mineralization	[-]	-5.69
PET_{max}	Maximal measured value of PET	mm d ⁻¹	3.75
β_1	Empirical parameter for fitting f_W function of Jouven <i>et al.</i>	[-]	6.467
β_2	Empirical parameter for fitting f_W function of Jouven <i>et al.</i>	[-]	$7.623 \cdot 10^{-8}$
<i>Management parameters and auxiliary variables</i>			
SD	Livestock density, number of adult bovine units per hectare	LU ha ⁻¹	[0, SD_{max}]
SD_{max}	Maximal possible livestock density	LU ha ⁻¹	3
κ	Daily consumption of 1 adult bovine unit	kg DM LU ⁻¹ d ⁻¹	18
Φ	Yearly input of mineral nitrogen fertilizer in the soil	kg N ha ⁻¹ a ⁻¹	0
Φ_u	Rate of mineral nitrogen restitution by cattle urine deposition	kg N ha ⁻¹ d ⁻¹	0.315
Φ_d	Rate of organic nitrogen restitution by cattle dung deposition	kg N ha ⁻¹ d ⁻¹	0.236
$ncut$	Number of mowing events per year	[-]	{0, 1, 2, 3}
<i>Climatic parameters</i>			
ω	Seasonal oscillation period, conversion of radian in days	d ⁻¹	$2\pi/365$
Tm	Mean annual values of temperature T	°C	8.517
Pm	Mean annual values of sum of monthly precipitations P	mm d ⁻¹	2.056
$PARm$	Mean annual values of PAR	MJ m ⁻² d ⁻¹	5.434
$PETm$	Mean annual values of PET	mm d ⁻¹	1.93
Ta	Amplitude of T	°C	14.81
Pa	Amplitude of P	mm d ⁻¹	1.168
$PARa$	Amplitude of PAR	MJ m ⁻² d ⁻¹	7.344
$PETa$	Amplitude of PET	mm d ⁻¹	3.542
Ψ_T	Origin phase of oscillations for T	d	106.5
Ψ_P	Origin phase of oscillations for P	d	110.5
Ψ_{PAR}	Origin phase of oscillations for PAR	d	80.8
Ψ_{PET}	Origin phase of oscillations for PET	d	87.76

1014

1015

Table A.2 List of the 21 herbaceous species to be selected in the alternative versions of DYNAGRAM, with their plant functional type (PFT), CSR strategy (Pierce et al., 2017) and species-specific parameter values: SLA specific leaf area (Perronne et al., 2014); λ proportion of biomass removed by a mowing event, estimated from canopy height (Perronne et al., 2014); ρ appetite for cattle (Kühn et al., 2004); σ trampling tolerance (Kühn et al., 2004); δ leaf nitrogen content (Soussana et al., 2012); k half-saturation constant of the nitrogen resource, estimated from N requirement (Julve, 2017); μ leaf senescence rate (Ryser and Urbas, 2000); T_1 lower limit of optimal growth temperature (Al Haj Khaled et al., 2005); η water requirement (Julve, 2017). In bold, the two species considered for DYNAGRAM2 and kept for defining the assemblages of DYNAGRAM4 and DYNAGRAM7. PFTs are defined by four groups of grasses and three life forms of dicots (Ansquer et al., 2004; Cruz et al., 2002): A, early and fast-growing grasses in fertile and frequently disturbed grasslands; B, competitive and productive grasses in fertile and unfrequently disturbed grasslands; C, late and slow-growing grasses in infertile and frequently disturbed grasslands; D, late and slow-growing grasses in infertile and unfrequently disturbed grasslands; E, erect forbs; R, rosette forbs; L, legumes.

Symbol	Name	PFT	CSR	SLA	λ	ρ	σ	δ	k	μ	T_1	η
Lol.per	<i>Lolium perenne</i>	A	R/CR	0.0286	0.40	9	8	0.0182	13.00	0.0303	7.5	1.000
Ely.rep	<i>Elymus repens</i>	A	CSR	0.0233	0.70	6	7	0.0106	12.00	0.0178	9.5	1.000
Ant.odo	<i>Anthoxanthum odoratum</i>	B	S/SR	0.0283	0.70	4	5	0.0173	12.00	0.0192	11.0	1.000
Arr.ela	<i>Arrhenatherum elatius</i>	B	SR/CSR	0.0299	0.80	8	3	0.0238	11.00	0.0250	8.5	1.000
Dac.glo	<i>Dactylis glomerata</i>	B	CSR	0.0253	0.50	8	6	0.0094	11.00	0.0230	10.0	1.000
Poa.tri	<i>Poa trivialis</i>	B	CSR	0.0331	0.50	7	6	0.0224	11.00	0.0250	8.0	2.000
Agr.cap	<i>Agrostis capillaris</i>	C	SR	0.0286	0.80	5	5	0.0205	7.50	0.0205	16.0	1.000
Bro.ere	<i>Bromopsis erecta</i>	C	S/SR	0.0155	0.90	12	1	0.0105	5.15	0.0160	15.3	0.500
Fes.rub	<i>Festuca rubra</i>	C	SR	0.0164	0.90	5	6	0.0137	7.00	0.0138	13.0	1.000
Nar.str	<i>Nardus stricta</i>	C	S	0.0110	0.58	9	2	0.0175	4.85	0.0115	15.0	1.000
Tri.flu	<i>Trisetum flavescens</i>	C	SR/CSR	0.0205	0.91	5	4	0.0130	6.00	0.0212	14.0	1.000
Bra.pin	<i>Brachypodium pinnatum</i>	D	SR/CSR	0.0234	0.92	12	1	0.0202	6.25	0.0167	16.5	1.000
Poa.cha	<i>Poa chaixii</i>	D	S/CSR	0.0207	0.40	3	4	0.0175	10.00	0.0250	8.0	1.000
Ger.syl	<i>Geranium sylvaticum</i>	E	CSR	0.0315	0.82	8	3	0.0175	10.50	0.0220	8.5	2.000
Her.sph	<i>Heracleum sphondylium</i>	E	C	0.0230	0.75	6	3	0.0175	11.00	0.0176	9.0	1.000
Pla.lan	<i>Plantago lanceolata</i>	R	C/CR	0.0196	0.69	3	9	0.0191	9.00	0.0159	12.0	1.000
Tar.off	<i>Taraxacum officinale</i>	R	CR	0.0324	0.92	7	8	0.0175	9.00	0.0224	12.5	1.000
Ver.cha	<i>Veronica chamaedrys</i>	R	SR/CSR	0.0277	0.80	3	7	0.0196	9.00	0.0220	13.0	1.000
Lot.cor	<i>Lotus corniculatus</i>	L	R/SR	0.0224	0.95	9	1	0.0175	7.75	0.0173	11.5	0.707
Tri.pra	<i>Trifolium pratense</i>	L	R/CSR	0.0228	0.82	8	3	0.0196	8.00	0.0175	11.5	1.000
Tri.rep	<i>Trifolium repens</i>	L	R/CR	0.0343	0.90	9	8	0.0195	8.50	0.0234	13.0	1.000

Online Supplementary Material

The following supplementary material is available for this article.

Appendix B Preliminary identification stage of the sensitivity analysis of DYNAGRAM. This appendix details all results of the preliminary sensitivity analysis we performed to select the six key control parameters. Results stay in the three following tables:

Table B.1 Parameter sensitivity of total green biomass B_{tot} to deviations by $\pm 20\%$ from the default parameter values for DYNAGRAM2 and DYNAGRAM21. Changes were applied independently for each parameter, all other parameters keeping their default values.

Table B.2 Parameter sensitivity of species evenness B_{eve} to deviations by $\pm 20\%$ from the default parameter values for DYNAGRAM2 and DYNAGRAM21. Changes were applied independently for each parameter, all other parameters keeping their default values.

Table B.3 Ranking of parameters according to the sensitivity of total green biomass B_{tot} and of species evenness B_{eve} to variations in the default parameters for DYNAGRAM2 and DYNAGRAM21. Values were computed by both increasing and decreasing the default value of each parameter. Parameters were ranked according to the mean values of the 2 and 21 species.

Appendix C Main effects of key control parameters on biomass and species survival ratio. This appendix contains two figures that detail the main effects of the six parameters on total green biomass B_{tot} and species survival ratio S as revealed by dynamic trees.

Figure C.1 Main effects of six key parameters on total green biomass B_{tot} , from dynamic trees performed on DYNAGRAM2 (**A**) and DYNAGRAM21 (**B**) outputs. Climate parameters: Tm (temperature), Pm (precipitation); soil fertility parameters: Φ (fertiliser input), θ (mineralization rate); defoliation parameters: SD (livestock density), $ncut$ (mowing frequency).

Figure C.2 Main effects of six key parameters on species survival ratio S , from dynamic trees performed on DYNAGRAM2 (**A**) and DYNAGRAM21 (**B**) outputs. Climate parameters: Tm (temperature), Pm (precipitation); soil fertility parameters: Φ (fertiliser input), θ (mineralization rate); defoliation parameters: SD (livestock density), $ncut$ (mowing frequency).