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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.

44 1. Introduction

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

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

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

71 Since experimental studies have not been able to provide a general explanation to the
72 relationships observed between grassland diversity and their productivity and stability,
73 dynamical models are powerful tools for testing predictions of ecological theories. A lot of
74 mathematical models of grassland dynamics based on explicit ecological processes have been
75 developed. Some non-exhaustive reviews of grassland models are available (Snow et al.,
76 2014; Taubert et al., 2012; Wiegand et al., 2008). Grassland models published so far have
77 targeted monospecific swards (Duru et al., 2009; McCall and Bishop-Hurley, 2003;
78 Schapendonk et al., 1998), mixtures of a grass and a legume species (Lazzarotto et al., 2009;
79 Thornley, 1998), or a multispecies community constant in time (Jouven et al., 2006; Riedo et
80 al., 1998). In a review of thirteen grassland models (Taubert et al., 2012), only two considered
81 more than three different species or plant functional types: GRAS, a succession compartment
82 model (Siehoff et al., 2011) and STEPPE, a gap model of semiarid grasslands (Coffin and
83 Lauenroth, 1990); however, none of them simulate biomass. So far, very few grassland
84 models have been designed to simulate both composition and biomass changes in
85 multispecies semi-natural grasslands used as pastures or/and hayfields, a requirement for
86 understanding diversity-productivity-stability relationships. Indeed, most of current grassland
87 models focus on the impact of agricultural practices on forage production with many
88 ecophysiological and biophysical details inherited from crop models but do not consider
89 temporal changes in taxonomic and functional composition. An attempt (Lauenroth et al.,
90 1993) to couple individual-based gap models describing changes in species composition
91 (STEPPE) and ecosystem models describing nutrient cycling and biomass production
92 (CENTURY) or water balance (SOILWAT) led to the development of the ECOTONE model,

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

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

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

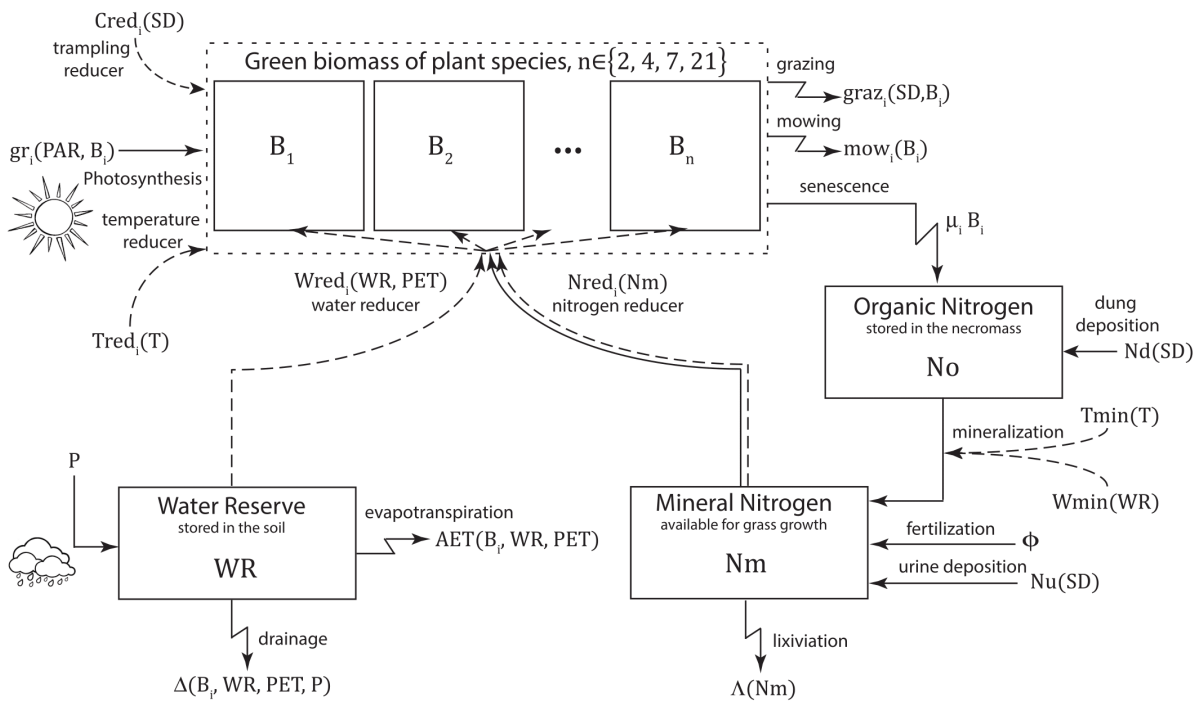
141 Thus, the first aim of the present study is to examine the consequences of increasing the
142 number of state variables (i.e. the size of the local species pool) describing plant community

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

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

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

168



169 **Fig. 1** Structure of the DYNAGRAM model. Solid lines denote flows of matter or energy and
 170 dashed lines denote reducers (mineral nitrogen acts both as a flow and as a reducer). State
 171 variables and forcing climatic variables are listed in Table 1 and a description of all
 172 parameters can be found in Tables A.1 and A.2 (Appendix A).
 173

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

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

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

207 where μ_i is a constant leaf senescence rate, as assumed in the GRAS model (Siehoff et al.,
 208 2011). A comprehensive description of DYNAGRAPH will be the subject of a next paper.
 209 Below we provide details on the three functions gr_i , mow_i and $graz_i$, useful to better
 210 understand the sensitivity analysis we performed. A complete description of all parameters is
 211 given in Tables A.1 and A.2 (Appendix A).

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

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

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

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

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

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

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

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

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

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

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

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

240 We introduced feedback loops for the two resources, available nitrogen and water reserve in
 241 the soil. The loss of green biomass due to senescence constitutes the litter, which fills a pool
 242 of organic nitrogen No stored in the soil organic matter. Depending on surface temperature
 243 $T_{min}(T)$ and soil moisture $W_{min}(WR)$, this organic nitrogen is mineralized in mineral
 244 nitrogen Nm (nitrate and ammonium) that becomes available for plant uptake. These two
 245 reducer functions affect the mineralization process and should not be confused with T_{red} and
 246 W_{red} that reduce plant growth. For each unit of biomass produced, we assumed that a fixed
 247 proportion δ_i of mineral nitrogen is consumed (Lazzarotto et al., 2009). Lixiviation $\Lambda(Nm)$
 248 limits the amount of mineral nitrogen in the soil solution. Presence of grazing animals in the
 249 pasture brings organic $Nd(SD)$ and mineral $Nu(SD)$ nitrogen restitution proportionally to the
 250 stock density SD . The mineral nitrogen pool is also filled by mineral fertilization events, Φ .

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

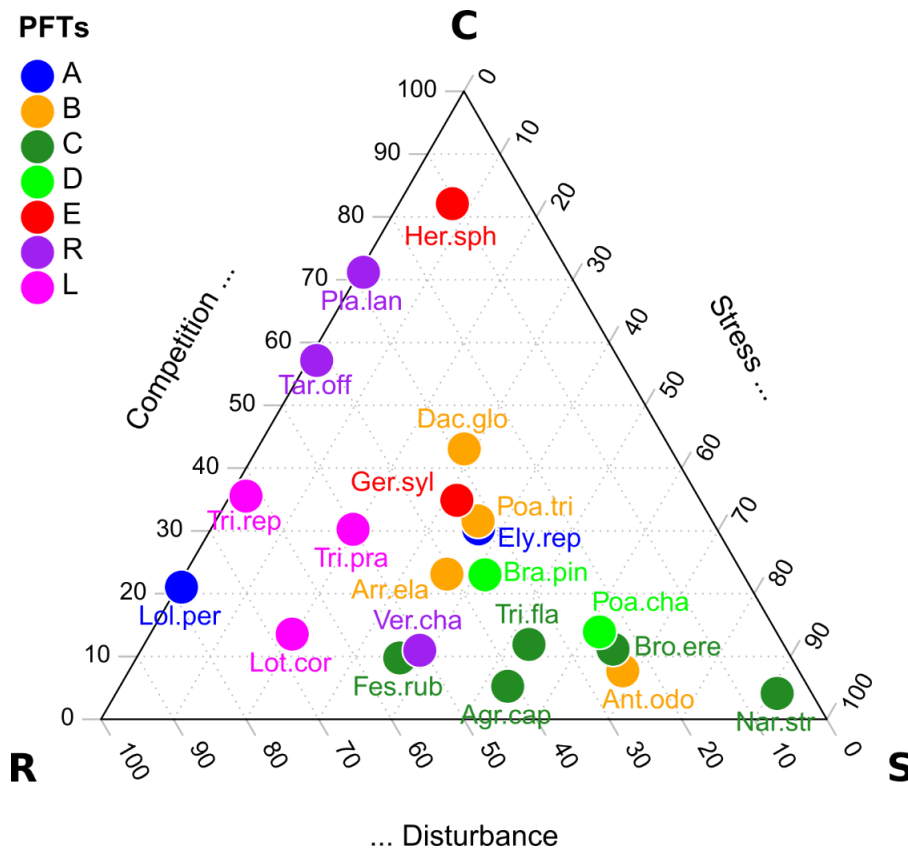
257 To summarize, if n is the size of the species pool, DYNAGRAM is defined by a system of $3 +$
 258 n ordinary differential equations associated with $3 + n$ state variables, with $9 \times n$ species-
 259 specific parameters, 31 global parameters, and 13 parameters for climatic forcing functions.

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

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

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

282 having verified that the model outputs were similar to the ones obtained with a smaller fixed
 283 or variable time step and a solver considering continuous time, such as ‘lsoda’, taking into
 284 account events (sudden changes in a state variable, e.g. mowing or fertilization).
 285



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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.

292 2.2. Choice of the biomass state variables

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

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

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

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

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

317 2.3. Selection of the key control parameters

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

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

332 We considered a management scenario that is identically repeated each year. Cattle is
 333 continuously present in the grassland during one long grazing season, from the 1st of July to
 334 the 31st of August. The first mowing event appears on the 1st of June, and a second mowing
 335 event on the 2nd of October. The amount of fertilizer, $\Phi = 90 \text{ kg N ha}^{-1}$, is split in six fractions
 336 spread on the grassland (May 1st, May 15th, June 10th, June 20th, September 1st and September
 337 15th).

338

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

342

Parameter	Category	Values in matrix \mathbf{X}			Unit	
Tm	Climate	7	9	11	$^{\circ}\text{C}$	
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	$\text{kg N ha}^{-1} \text{ a}^{-1}$
SD	Defoliation	0	0.5	1	1.5	LU ha^{-1}
$ncut$	Defoliation	0	1	2		a^{-1}

343

344 2.4. Selection of the response variables

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

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

354 \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
355 biomass values B_{tot} at day t_f , simply computed as the sum of the green biomass values of all
356 present species:

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

357 \mathbf{y}_2 is a vector of Simpson evenness values B_{eve} of the plant community at day t_f . Simpson
358 evenness is a taxonomic diversity index ranging between 0 and 1 and measuring the
359 proportion of dominant species in the community according to differences in biomass (Hill,
360 1973; Jost, 2006). A value of 1 means that all species initially introduced are equally
361 distributed in biomass in the grassland, whereas a value close to 0 means the persistence of
362 only one single species that outcompeted all others. We computed Simpson evenness by
363 dividing the inverse Simpson diversity index by n , the number of species initially present in
364 the model:

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

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

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

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

369 2.5. Assessment of the model’s response to variation in species richness

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

377 2.6. Tree-based sensitivity analysis

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

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

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

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

404 Our sensitivity analysis was based on three kinds of trees: (i) Univariate Regression Tree
405 (URT); (ii) Multivariate Regression Tree (MRT) and (iii) Dynamic Tree (DT). URT and DT
406 consider a vector \mathbf{y} containing one single synthetic variable (B_{tot} , B_{eve} , or S) contrary to MRT
407 (De'ath, 2002) that considers a matrix \mathbf{Y} including several response variables (biomass of
408 each species). URT has been used to rank a set of influential control parameters, here $\{Tm,$
409 $Pm, \theta, \Phi, SD, ncut\}$, from top to bottom, according to their impact on a single output variable
410 among the set $\{B_{tot}, B_{eve}, S\}$ for performing global sensitivity analysis (Eynaud et al., 2012;
411 Makler-Pick et al., 2011).

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

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

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

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

426 **3. Results**

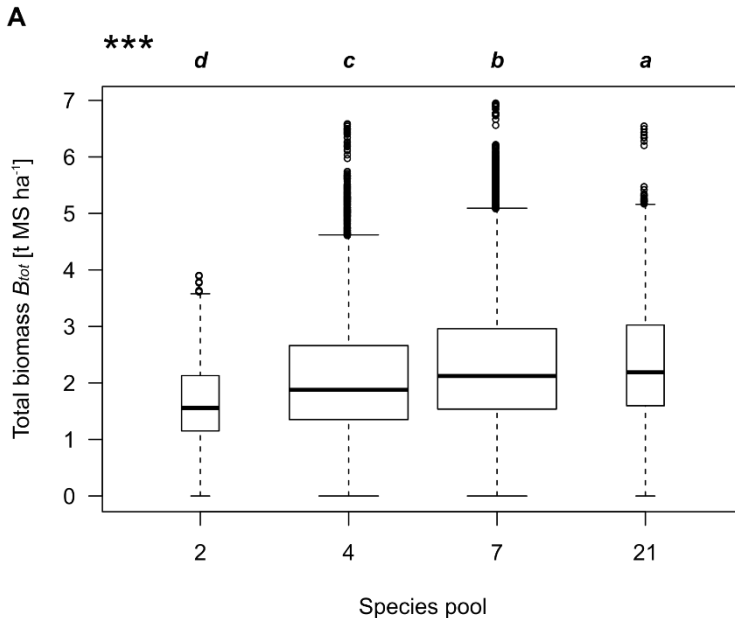
427 *3.1. Model response to variation in initial species richness*

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

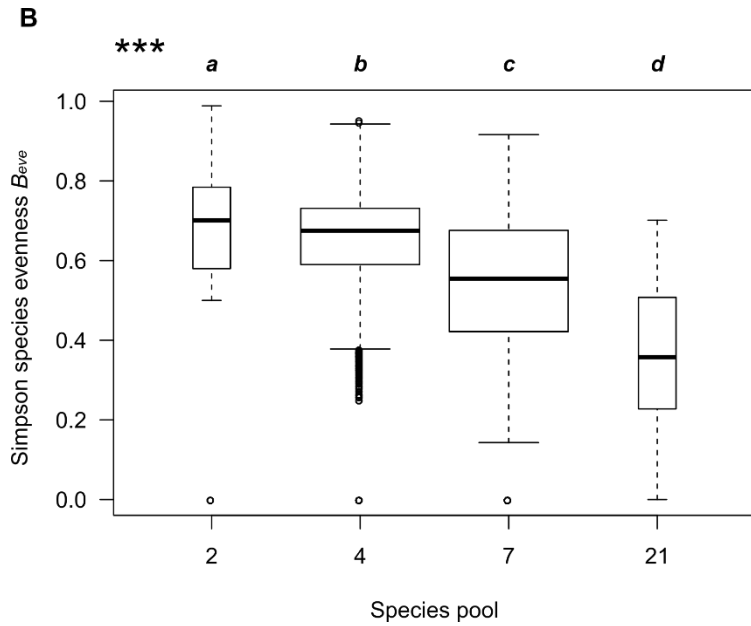
431 By contrast, Simpson evenness B_{eve} tended to decrease with initial species richness, showing
432 that the more the species pool was large, the less the final green biomass was equally
433 distributed among the species (Fig. 3B).

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

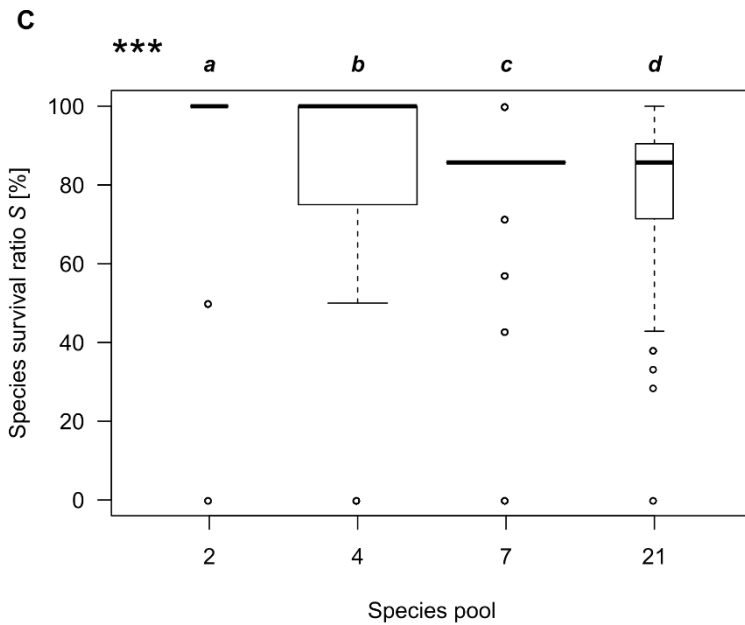
438 For 21 species in the initial species pool, the survival rate increased with the disturbance
439 intensity, which is the product of defoliation parameters SD and $ncut$ (Fig. 4A). Moreover, the
440 positive Kendall rank correlation between the disturbance intensity and the species survival
441 rate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



442



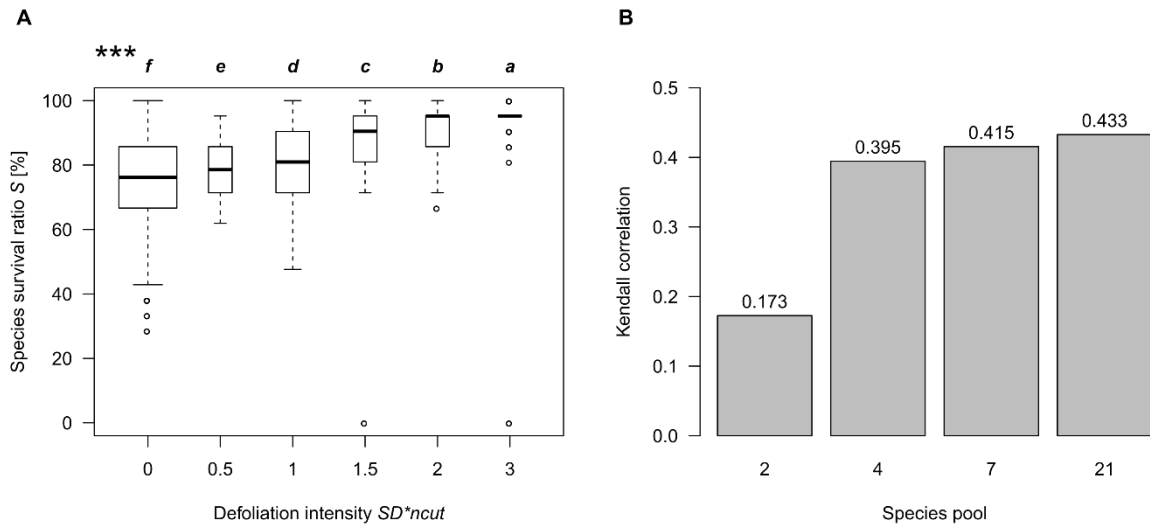
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445 **Fig. 3** Boxplots of final total biomass B_{tot} (A), Simpson species evenness B_{eve} (B) and proportion of
 446 surviving species S (C) at the end of simulations from alternative DYNAGRAM models with all
 447 combinations of control parameters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

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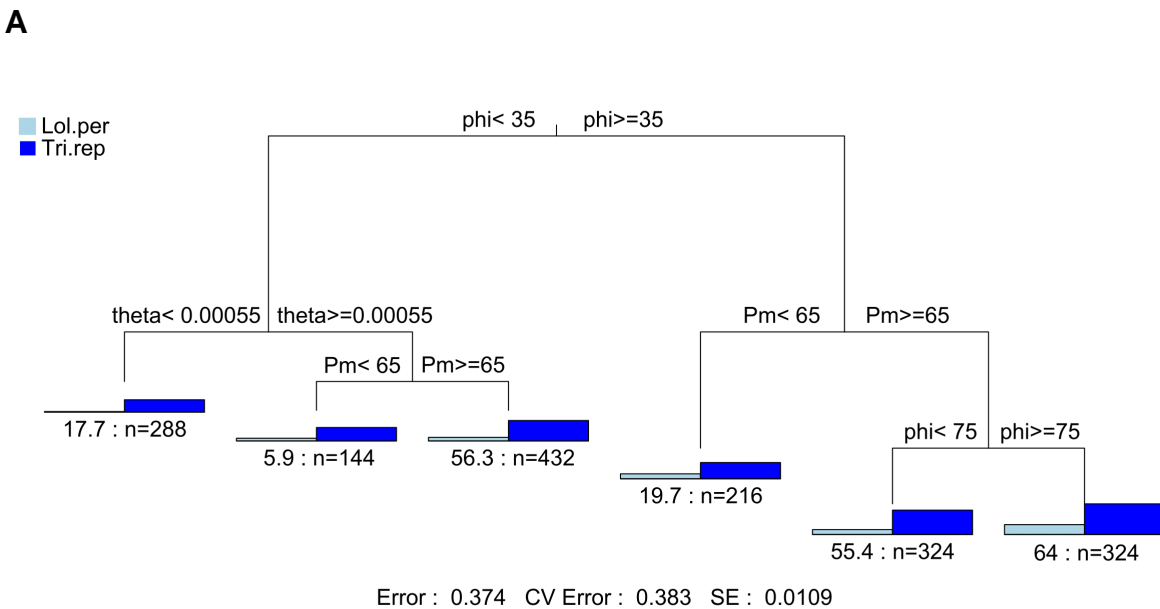
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Fig. 4 The relationship between the defoliation intensity and the species survival ratio. **A:** Boxplots of the proportion of surviving species S at the end of simulations from DYNAGRAM21 with all combinations of control parameters, in function of 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.

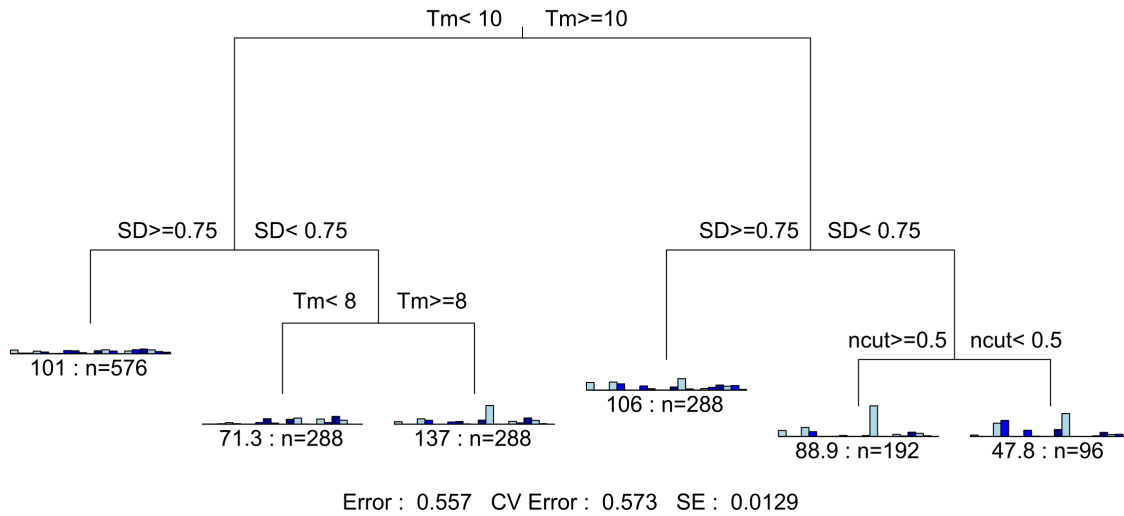
461 3.2. Sensitivity analysis of DYNAGRAM for 2 and 21 species

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

464
465



466



468

469 **Fig. 5** Multivariate regression trees of a response matrix \mathbf{Y} containing final green biomass of 2 (**A**) or
 470 21 (**B**) species explained by control parameters out of matrix \mathbf{X} . Barplots show biomass means for all
 471 species, with deviance and number of cases at each terminal node.

472

473 3.2.1. Multivariate regression trees

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

482 3.2.2. Univariate regression trees

483 Like species composition, species evenness and survival rate depended mainly on soil fertility
 484 (Φ and θ) for DYNAGRAM2, but on defoliation (SD) for DYNAGRAM21 (Table 3).

485 By contrast, the hierarchy of parameters influencing final total green biomass was
 486 independent of the size of the species pool: the first discriminant parameter was in each case
 487 fertilisation intensity Φ , followed by mineralization rate θ and mean precipitation Pm . The
 488 defoliation regime played no important role in explaining the final standing biomass of a
 489 simulated grassland made of 2 or 21 species.

490

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

498

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}

499

500 3.2.3. Dynamic trees of species evenness

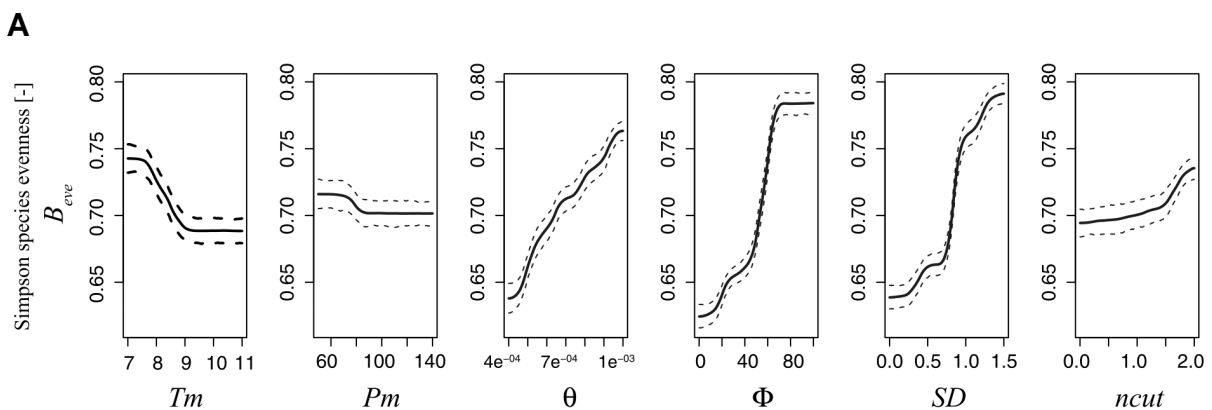
501 As the first results of the sensitivity analysis based on composition (MRT) and on Simpson
502 evenness (URT) were very similar, we will focus on this last relevant index of community
503 structure B_{eve} to investigate in more detail the main effects of the six parameters using
504 dynamic trees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

506 Dynamic trees confirmed the strong positive effect of livestock density SD on species
507 evenness with 21 species (Fig. 6B), as compared to other parameters. With two species (Fig.
508 6A), the main positive effects were also due to the amount of fertilizer Φ and the maximal
509 mineralization rate θ , which were much less influential with a large species pool. The number
510 of mowing events $ncut$ showed opposite effects on evenness: slightly positive for two species
511 and negative for 21 species. In both cases, mean temperature Tm had a negative effect on
512 evenness.

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

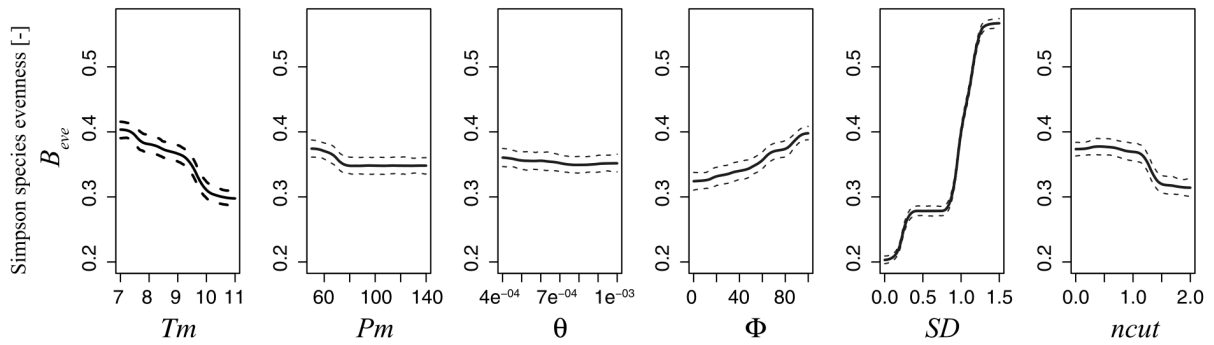
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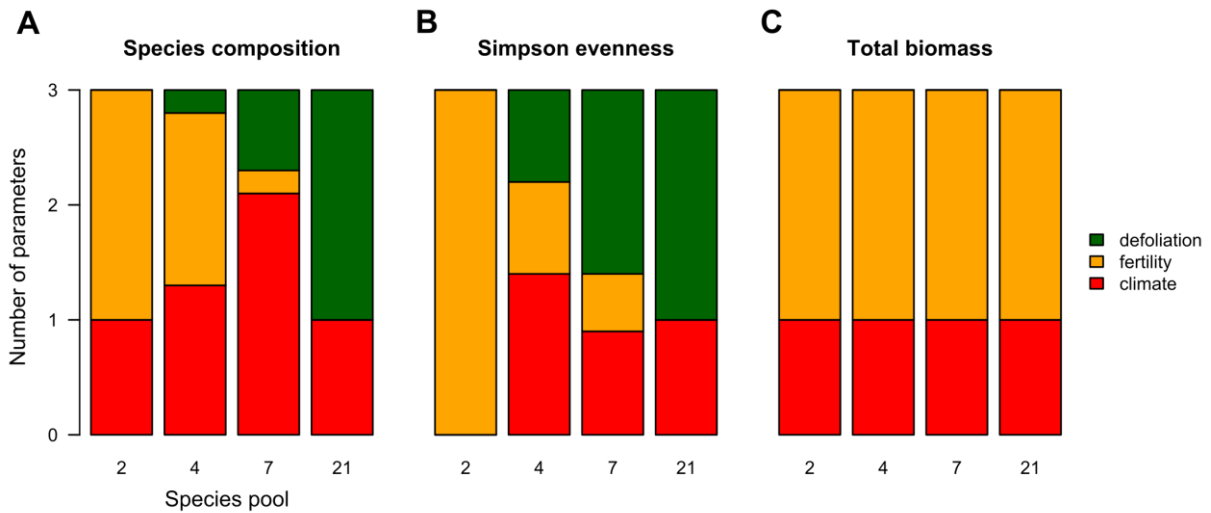
520 **B**



521
 522 **Fig. 6** Main effects of six key parameters on Simpson species evenness B_{eve} , from dynamic trees
 523 performed on DYNAGRAM2 (A) and DYNAGRAM21 (B) outputs. Climate parameters: Tm
 524 (temperature), Pm (precipitation); soil fertility parameters: Φ (fertiliser input), θ (mineralization rate);
 525 defoliation parameters: SD (livestock density), $ncut$ (mowing frequency).
 526

527 **3.3. Impact of species number on the hierarchy of influential parameters**

528 Tree-based sensitivity analysis of DYNAGRAM2 and DYNAGRAM21 suggested a shift in key
 529 parameters determining the grassland composition according to the size of the species pool.
 530 To assess the impact of species number, irrespective to species identity, on the hierarchy of
 531 the key parameters, we have to include in the comparison the results of regression trees for
 532 DYNAGRAM4 and DYNAGRAM7, each with ten random samples among the full set of 21
 533 species. Results of this comparison are summarized by bar plots (Fig. 7).
 534



535
 536 **Fig. 7** Bar plots of the three most influential control parameter categories on species composition (A),
 537 Simpson evenness (B) and total green biomass (C) at the end of simulations with 2, 4, 7 and 21
 538 species. Three key parameters were extracted from the first and second splits of each MRT (A) or
 539 URT (B, C). Results for 4 and 7 species are mean numbers from ten random species samples.
 540

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

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

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

554 **4. Discussion**

555 *4.1. Final model outputs depend on initial species richness*

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

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

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

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

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

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

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

624 4.2. A shift in key parameters across a diversity gradient

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

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

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

651 *4.3. Grassland diversity, productivity and stability*

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

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

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

673 *4.4. Simplicity or complexity?*

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

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

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

689 This issue relates to a more general problem in ecological modelling: how to keep the model
690 as simple as possible without missing key variables and processes? DYNAGRAM is simpler
691 than many other grassland models but more complex than other ones. As compared to more
692 parsimonious mechanistic models based on ODE systems (Louie et al., 2002; Siehoff et al.,
693 2011; Tilman, 1985), DYNAGRAM includes a consumption-degradation loop for nitrogen, the
694 main limiting soil nutrient, and takes into account the seasonality of plant growth and resource
695 competition (Lazzarotto et al., 2009). This added complexity was necessary to assess the
696 model's sensitivity to soil fertility, climatic conditions and defoliation.

697 As both knowledge of grassland ecosystems and computer performance progress, the
698 implementation of more and more details and processes is a general trend in grassland
699 modelling. Our choice of a minimal model complexity implies some strong assumptions. As
700 compared to more detailed models, such as MODVEGE, GEMINI or PROGRASS (Jouven et al.,
701 2006; Lazzarotto et al., 2009; Soussana et al., 2012), DYNAGRAM considers only one single
702 biomass compartment for each species without distinguishing aboveground plant structural
703 components (i.e. vegetative or reproductive, green or dead) and ignores the belowground
704 biomass (roots, rhizomes and storage organs) as well as many associated physiological
705 processes. In accordance with most grassland growth models, DYNAGRAM only simulates
706 vegetative growth and does not include seed reproduction or emergence of new species from
707 the soil seed bank or by seed dispersal.

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

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

727 **5. Conclusion**

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

735 stability of the community, measured by the proportion of surviving species after 10-year
736 simulations, and the evenness component of its diversity tend to decrease with the size of the
737 species pool, due to environmental filtering and competitive exclusion.
738 Moreover, results of our tree-based sensitivity analysis revealed an unexpected shift in the key
739 drivers of the final community structure, but not of its total biomass, when increasing the size
740 of the species pool from two to 21 species. These findings create new challenges in ecological
741 modelling to be raised through mathematical and simulation studies.

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1009 **Appendix A: Variables and parameters of DYNAGRAM**

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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

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1016 **Table A.2** List of the 21 herbaceous species to be selected in the alternative versions of
1017 DYNAGRAM, with their plant functional type (PFT), CSR strategy (Pierce et al., 2017) and
1018 species-specific parameter values: *SLA* specific leaf area (Perronne et al., 2014); λ proportion
1019 of biomass removed by a mowing event, estimated from canopy height (Perronne et al.,
1020 2014); ρ appetite for cattle (Kühn et al., 2004); σ trampling tolerance (Kühn et al., 2004); δ
1021 leaf nitrogen content (Soussana et al., 2012); k half-saturation constant of the nitrogen
1022 resource, estimated from N requirement (Julve, 2017); μ leaf senescence rate (Ryser and
1023 Urbas, 2000); T_1 lower limit of optimal growth temperature (Al Haj Khaled et al., 2005); η
1024 water requirement (Julve, 2017). In bold, the two species considered for DYNAGRAM2 and
1025 kept for defining the assemblages of DYNAGRAM4 and DYNAGRAM7. PFTs are defined by
1026 four groups of grasses and three life forms of dicots (Ansquer et al., 2004; Cruz et al., 2002):
1027 A, early and fast-growing grasses in fertile and frequently disturbed grasslands; B,
1028 competitive and productive grasses in fertile and unfrequently disturbed grasslands; C, late
1029 and slow-growing grasses in infertile and frequently disturbed grasslands; D, late and slow-
1030 growing grasses in infertile and unfrequently disturbed grasslands; E, erect forbs; R, rosette
1031 forbs; L, legumes.

1032

Symbol	Name	PFT	CSR	<i>SLA</i>	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.fla	<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

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1035 **Online Supplementary Material**

1036 The following supplementary material is available for this article.

1037

1038 **Appendix B** Preliminary identification stage of the sensitivity analysis of DYNAGRAM. This
1039 appendix details all results of the preliminary sensitivity analysis we performed to select the
1040 six key control parameters. Results stay in the three following tables:

1041 **Table B.1** Parameter sensitivity of total green biomass B_{tot} to deviations by $\pm 20\%$ from the
1042 default parameter values for DYNAGRAM2 and DYNAGRAM21. Changes were applied
1043 independently for each parameter, all other parameters keeping their default values.

1044 **Table B.2** Parameter sensitivity of species evenness B_{eve} to deviations by $\pm 20\%$ from the
1045 default parameter values for DYNAGRAM2 and DYNAGRAM21. Changes were applied
1046 independently for each parameter, all other parameters keeping their default values.

1047 **Table B.3** Ranking of parameters according to the sensitivity of total green biomass B_{tot} and
1048 of species evenness B_{eve} to variations in the default parameters for DYNAGRAM2 and
1049 DYNAGRAM21. Values were computed by both increasing and decreasing the default value of
1050 each parameter. Parameters were ranked according to the mean values of the 2 and 21 species.

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1052 **Appendix C** Main effects of key control parameters on biomass and species survival ratio.
1053 This appendix contains two figures that detail the main effects of the six parameters on total
1054 green biomass B_{tot} and species survival ratio S as revealed by dynamic trees.

1055 **Figure C.1** Main effects of six key parameters on total green biomass B_{tot} , from dynamic trees
1056 performed on DYNAGRAM2 (**A**) and DYNAGRAM21 (**B**) outputs. Climate parameters: Tm
1057 (temperature), Pm (precipitation); soil fertility parameters: Φ (fertiliser input), θ
1058 (mineralization rate); defoliation parameters: SD (livestock density), $ncut$ (mowing
1059 frequency).

1060 **Figure C.2** Main effects of six key parameters on species survival ratio S , from dynamic trees
1061 performed on DYNAGRAM2 (**A**) and DYNAGRAM21 (**B**) outputs. Climate parameters: Tm
1062 (temperature), Pm (precipitation); soil fertility parameters: Φ (fertiliser input), θ
1063 (mineralization rate); defoliation parameters: SD (livestock density), $ncut$ (mowing
1064 frequency).