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The importance of plant trait variability in grasslands: a modelling study

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Abstract

Managed grasslands play an important role in European landscapes. They are often characterized by a high productivity and a low variability of traits between species. Though the relationship between traits and productivity has been investigated by various field studies, insight is still lacking in understanding the role of species trait variability.

This study combines species-specific traits with grassland modelling to investigate how variability in grassland species influences grassland dynamics and functioning. Based on a field experiment in Central-Eastern Germany, we parameterized an individual-based grassland model. We analyzed simulations of grasslands with four grass species and compared results with observed vegetation attributes (e.g., productivity, species composition and vegetation height). In a next step, we systematically added and removed interspecific variability in traits regarding (a) photosynthetic capacity, (b) mortality, (c) plant geometry, (d) seed establishment and investigated the effect on different grassland attributes such as leaf area index and gross primary productivity.

We found that grassland dynamics are markedly influenced by species-specific differences in traits. Annual productivity was mostly driven by traits describing a plant's photosynthetic capacity and plant geometry. Some grassland attributes (like leaf area index and gross primary productivity) showed to be more sensitive to variability in plant geometric traits and traits describing seed establishment. Simulations with similar species traits resulted in a more balanced species composition, underlining the role of trait variability for interspecific competition processes. However, we showed here that different trait categories affect different attributes and functions of grasslands.

We demonstrated in this study that individual-based models can help to gain a deeper understanding of the relative importance of plant traits on community dynamics and ecosystem functions of grasslands.

Keywords: biomass dynamics, ecological modelling, managed grassland, species traits, plant measurements, Global Change Experimental Facility

1. Introduction

Grasslands play an important ecological and economic role in temperate regions since they comprise about 50% of the European land area covered by vegetation (Coyette, H.; Schenk, 2019). Most commonly found in Europe are intensively managed grasslands, which have a high biomass productivity due to a few productive grass species.

In the last decades field studies have tried to explain how functional plant traits of those grass species influence grassland productivity (Craine and Knops, 2002; Roscher et al., 2012, 2018; Sun and Frelich, 2011). Functional traits are morphological, physiological, or phenological characteristics that describe a plant's fitness by representing its ability to survive, grow and reproduce (Violle et al., 2007). Highly productive grassland plants are characterized, for example, by dense, long-lived tissue, and root traits that prevent nutrient deficiencies (Craine and Knops, 2002). Traits are also associated with productivity dynamics, e.g. the maximum height of a plant is related to the trajectory of its growth during the year (Sun and Frelich, 2011). Drawing general conclusions remains challenging, as correlations between traits and productivity can vary depending on soil conditions as well as interactions with other plant species in the community (Craine and Knops, 2002). For summarizing plant traits at the individual level to the population or community level, traits are often aggregated using the number and traits of individual plants of each species in the community in order to describe the fitness at the community level (McGill et al., 2006; Shipley et al., 2006; Violle et al., 2007). Observations in grasslands showed that "community-mean traits" (mean trait values weighted by the species relative abundances) can be linked to productivity (Roscher et al., 2012). In particular, community-mean traits that describe growth form, photosynthetic capacity and nitrogen acquisition of plants showed to explain variation in grassland productivity (Roscher et al., 2012). However, Roscher et al. (2012) also highlighted the importance of plant trait variability in grassland communities.

While earlier studies described the variability within communities mainly by the number of species (e.g., Adler et al., 2011; Mittelbach et al., 2001) the analysis of trait differences within communities reveals new opportunities for explaining grassland productivity and for gaining insights in plant interactions and their response to the environment (Gubsch et al., 2011; Hulme and Bernard-Verdier, 2018; Jung et al., 2014; McGill et al., 2006; Reich et al., 1999; Roscher et al., 2018; Zuo et al., 2017). Differences in traits can be addressed within species (intraspecific variability) and between species (interspecific variability). Focusing on interspecific variability, so called "mean trait differences" (i.e. trait differences between species in which the intraspecific variation is simplified by calculating the mean trait value per species) can help to disentangle species interactions, for instance how species compete on different resources (Gubsch et al., 2011; Roscher et al., 2018).

Community-mean traits and mean trait differences are both crucial to understand the species assembly in grassland communities. However, behind both measures can be a wide range of possible trait combinations, which is still challenging to represent by field studies.

To gain a broader picture and understanding, grassland models that incorporate plant traits are valuable tools for complementing field observations and experiments (Funk et al., 2017). Such models simulate the dynamics of grasslands based on trait parameters that describe the entire grassland community, populations or individual plants. Dependent on the conceptual design, trait-based grassland models can be applied in various ways (Snow et al., 2014; Taubert et al., 2012). For example, grassland models which assume community-mean traits are suitable for simulations of monocultures or grasslands dominated by one species (e.g., rye grass modelled by LINGRA (Schapendonk et al., 1998)). In turn, population-based models (e.g., (Duru et al., 2009; Moulin et al., 2018; Schippers and Kropff, 2001; Sitch et al., 2003)) and individual-based models (e.g., (May et al., 2009; Reeg et al., 2017; Soussana et al., 2012; Taubert et al., 2012) allow to consider trait variability within simulations.

Population and individual-based models show similarities by including traits and trait differences that refer to the growth of plants or populations dependent on light (Duru et al., 2009; May et al., 2009; Moulin et al., 2018; Reeg et al., 2017; Schippers and Kropff, 2001; Sitch et al., 2003; Taubert et al., 2020b), mortality and senescence (Duru et al., 2009; May et al., 2009; Schippers and Kropff, 2001; Sitch et al., 2003; Soussana et al., 2012; Taubert et al., 2012), the probability and time of seed germination (Duru et al., 2009; May et al., 2009; Taubert et al., 2020b), as well as traits addressing the growth form of plants (May et al., 2009; Moulin et al., 2018; Schippers and Kropff, 2001; Soussana et al., 2012; Taubert et al., 2020b). However, the description of traits can differ from one grassland model to the other and depends on the underlying modelling concept. For example, models in which plant growth is modelled as a physiological process (like leaf photosynthesis and respiration, e.g., GRASSMIND (Taubert et al., 2012)) require additional traits (e.g. maximum leaf photosynthesis rate) compared to models that include a sigmoidal function for plant growth (e.g. IBC-grass (Reeg et al., 2017)). To better asses and relate results of different modelling studies, we therefore here analyze the role of traits classified into four groups that describe a plant's a) photosynthetic capacity, b) mortality, c) seed establishment and d) geometry.

In this study, we use an individual-based model (GRASSMIND, Taubert et al.c, 2012, 2020) to analyze community-mean traits as well as mean trait differences of intensely managed grassland species. The model enables to simulate the growth of every individual plant interacting with neighboring plants dependent on their traits. We aim to answer the following questions: *(1) Can we reproduce observed aboveground productivity and species assembly using the grassland model? (2) What is the impact of* *interspecific trait variability on grassland dynamics?* (3) *Which groups of plant traits are relevant drivers for modelling grasslands (photosynthetic capacity, mortality, seed establishment or plant geometry)?*

For our analysis, we parameterized the model for a grassland experiment in Central-East Germany (Global Change Experimental Facility, GCEF, (Schädler et al., 2019)) with focus on an intensively managed grassland including four grass species (*Festulolium, Lolium perenne, Poa pratensis, and Dactylis glomerata*). Based on plant traits derived from literature, calibration and individual plant measurements, we compared simulated species assembly and grassland productivity with observations from GCEF. Furthermore, model simulations allowed to investigate effects of trait variability on grassland dynamics (e.g., gross and net primary productivity).

2. Methods and Materials

2.1 The grassland model

For our analysis we used the individual- and process-based grassland model GRASSMIND (Taubert et al., 2012). The model was developed to simulate species-rich temperate grasslands at daily time steps (Taubert et al., 2012). It enables simulations of trait-based grassland communities (Schmid et al., 2021; Taubert et al., 2020b) as well as species-mixtures (Schmid et al., 2021; Taubert et al., 2020a). In the following, we describe important plant traits and related model processes relevant in this study. For a detailed model description of GRASSMIND, see supplemental material of Taubert et al. (2012, 2020) or www.formind.org/downloads.

2.1.1 *Modelling the growth of individual plants related to their traits*

The smallest unit of the grassland model is a plant (see Fig. 1a). The plant's ability to grow is influenced by modelled processes and 20 parameters (model parameters, Table C.1) from which 12 represent species-specific mean traits (see Table 1). Those traits are classified into four groups 1) seed establishment, 2) mortality, 3) plant geometry (or growth form) and 4) photosynthetic capacity.

Every plant starts as a seed. Its probability to germinate as seedling is defined by the species-specific trait $germ_{\%}$ (%). As soon as the plant has established, it is characterized by an aboveground shoot and belowground root (described by shoot biomass B_{shoot} (in g dry matter) and root biomass B_{root} (in g dry matter)) which both can be incremented via plant growth on a daily basis (time step). After a certain amount of time, described by the species-specific trait age_{rep} (years), a plant matures and invests an additional part of their growth increment in the reproduction of new seeds (B_{Seed}). From there on, its probability to die, changes from a species-specific seedling mortality rate (trait $m_{Seedling}$ per day) to an intrinsic mortality rate (m_{basic} per day). Senescence is also part of the mortality process. In each day step, a fraction of green shoot biomass is transferred to senescent biomass with a rate defined by the reciprocal of the species-specific leaf life span (trait LLS in days).

Species-specific growth forms are considered by geometric plant traits. The shoot is modelled by a cylinder that is characterized by its height and width (referring to the outer boundaries of the plant). The distribution of biomass within the shoot is homogeneous and depends on the species-specific traits describing the biomass density per cylinder volume F (gm^{-3}) as well as the ratio between height and width Geo_{ratio} (-). Based on the biomass density F, the volume of the shoot cylinder $V_{cylinder}$ can be calculated by

$$V_{cylinder} = \frac{B_{shoot}}{F} \tag{1}$$

Further variables such as height H and width W of a plant follow then directly from the cylinder volume and the height-weight-ratio

$$W = \left(\frac{B_{shoot}}{\frac{\pi}{4} \cdot Geo_{ratio} \cdot F}\right)^{1/2} \tag{2}$$

$$H = W \cdot Geo_{ratio} \tag{3}$$

The leaf area L_{leaf} of a shoot is calculated by multiplying shoot biomass (B_{shoot}) with specific leaf area (plant trait SLA in cm^2g^{-1}). The belowground root biomass represents a fixed fraction of the overall plant biomass described by the species-specific trait B_{ratio} (-).

Within one day step, the growth of each plant in terms of its height, width, leaf area, as well as below- and above-ground plant biomass and seed biomass is updated based on the balance of a plant's photosynthesis and respiration (resulting in the net primary productivity *NPP* in gCd^{-1}). A plant's potential carbon uptake (or gross primary productivity *GPP* in gCd^{-1}) depends on its leaf area, the incoming light on the leaf surface and on traits describing its photosynthetic capacity following the light response approach of Thornely and Johnson, (1990). The incoming light on the leaf surface I_{leaf} (μmol_{photon} m^{-2} s^{-1}) is derived by the incoming irradiance on top of the plant I_s, the transmission coefficient m and the species-specific trait k describing the light extinction coefficient (Eq. 4).

$$I_{leaf} = \frac{k}{1-m} \cdot I_s \tag{4}$$

Together with species-specific traits that describe the initial slope of the light response curve α (μmol_{CO2} $\mu mol_{photons}^{-1}$) and the maximum leaf gross photosynthetic rate p_{max} (μmol_{CO2} m^{-2} s^{-1}), the photosynthetic rate of a leaf P_{leaf} is calculated (Eq. 5).

$$P_{leaf} = \frac{\alpha \cdot I_{leaf} \cdot p_{max}}{\alpha \cdot I_{leaf} + p_{max}} \tag{5}$$

By integration through the leaf area index of a plant (leaf area divided by shoot cylinder ground area; only accounting for green leaves which have not experienced turnover by senescence yet), the daily gross primary productivity GPP of a plant is calculated. Dependent on the amount of living plant biomass (shoot and root), a part of the GPP is used for respiration. Both photosynthesis and respiration can be affected by daily air temperatures (input parameter of average daily air temperature in °C). While *GPP* is reduced below 10°C, respiration continuously increases with temperature above 0° according to the approach of Schippers and Kropff, (2001). At the end of each day the remaining *NPP* is distributed in the plants shoot, root and seed components. The fraction of *NPP* allocated to the shoot biomass B_{shoot} is derived by the species-specific geometric trait $alloc_{shoot}$. The fraction $alloc_{root}$ allocated to the root biomass B_{root} follows from $alloc_{shoot}$ and the shoot-root ratio Geo_{ratio} by $alloc_{root} = \frac{alloc_{shoot}}{Geo_{ratio}}$. Finally, the remaining part of the *NPP* $(alloc_{rep} = 1 - alloc_{shoot} - alloc_{root})$ is added to the reproduction biomass B_{seed}.

2.1.2 Modelled community processes and plant interactions

Next to the processes at the individual level, the model includes processes that affect the entire grassland community. Here, we define the community as a species assembly that reacts to environmental conditions and interacts by the competition of plants for light and space resources on an area of 1 m^2 (Fig. 1b). Starting from bare ground, species-specific amounts of seeds are sown (N_{sown} in $m^{-2}d^{-1}$) at the beginning of the simulation. During the simulation, new seeds grow from a surrounding landscape into the simulated area each day related to a constant species-specific seed rain (N_{seed} in $m^{-2}d^{-1}$). The seed reproduction by individual plants (based on B_{seed}) was assumed to be dispersed outside the simulated area.

The established seedling then compete inter- and intra-specifically with other plants for light and space resources. Competition for light takes place asymmetrically by plant shading based on the approach of Monsi and Saeki, (1953). The daily amount of available light is considered using the average photosynthetic irradiance on top of the community over one day I_0 ($\mu mol_{photon}\, m^{-2}\, s^{-1}$). The plants absorb a part of the incoming radiation, so that with decreasing height from the top of the grassland community to the ground the available radiation is reduced. Large plants thereby receive more light than smaller plants (asymmetric competition), but are also exposed to self-shading (integration of Eq.6). To calculate light conditions, the aboveground space is modelled by height layers (vertical spacing of 1cm) that can be filled with plant leaf area LAI_i as the sum of the leaf area of plants in the respective height layer i. The available light I_s for each layer S can be calculated by:

$$I_s = I_0 \cdot e^{-\sum_{i>S} LAI_i} \tag{6}$$

Competition for space is considered by an increased mortality in overcrowded communities (dependent on plant width, but irrespective of plant height). If the sum of ground area of all plants' shoot cylinders exceeds the patch size of 1 m^2, a crowing mortality causes the death of plants in proportion to the exceeded area. Plant death is thereby modeled stochastically and irrespective of size.

Competition for belowground resources was not included in the simulations We assume optimal soil water and nutrient supply for all plants since the fertile soil of our study site (Haplic Chernozem) has a high water-holding capacity and was regularly fertilized with NPK-minerals (Schädler et al., 2019).

The model considers regular management by mowing. Therefore all plants of the community are cut at a specific mowing height (here, 10 cm). The associated aboveground plant biomass and leaf area are then removed from the simulated area which results in changes of light and space competition.

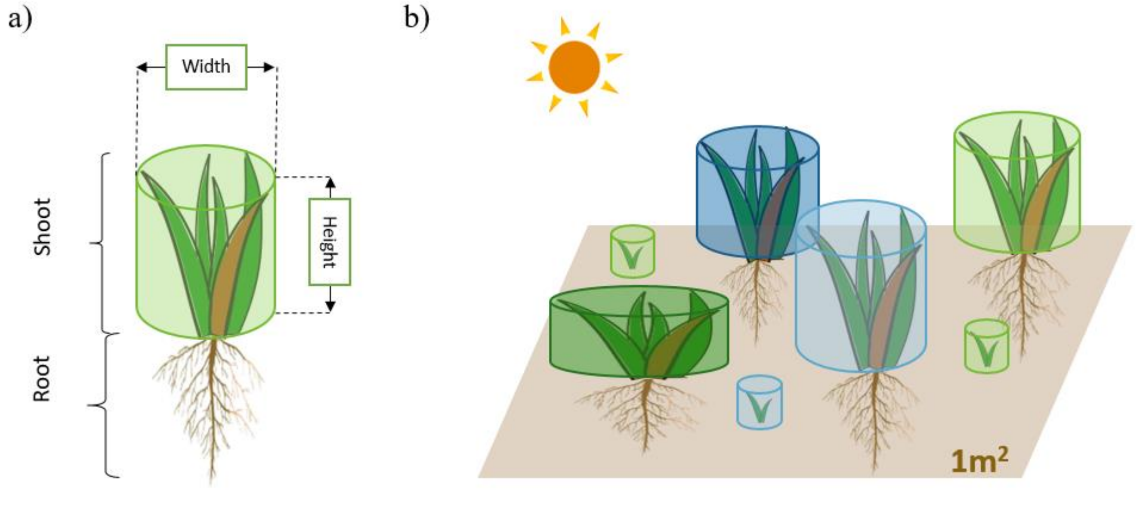

Fig. 1 Modelling concept of GRASSMIND (Taubert et al., 2012). a) A plant is characterized by two main components: the aboveground shoot and the belowground root. The shoot of a plant is encased by a cylinder that grows in in height and width according to species-specific traits. b) Plants interact on an area of 1 m² and compete for light, space, and belowground resources (here, we only focus on

aboveground resources). Plant growth is based on its species-specific traits (different species are displayed by different colors). For an overview of modelled processes see Fig. C.1. For a detailed model description see supplemental material of Taubert et al., (2012, 2020) and www.formind.org/downloads.

Table 1: Overview of the species-specific plant traits (model parameters varied in the scenario analysis).

Trait group	**Name**	**Unit**	**Description**	**Species-mean trait**				**Community-mean trait**	**Reference**
				Festulolium	*Lolium perenne*	*Poa pratensis*	*Dactylis glomerata*		
Seed Establishment[1]	age_{rep}	Years	Minimum age of mother plants for producing seeds	0.09	0.07	0.08	0.09	0.09	Calibrated
	$germ_{\%}$	-	Seed germination rate	0.3	0.7	0.75	0.7	0.68	Roscher et al., (2004) (Clay, (1987) for *L. perenne)*
Mortality	$m_{seedling}$	d^{-1}	Mortality rate of seedlings	0.2	0.27	0.24	0.12	0.14	Calibrated
	LLS	d	Leaf life span	42	33	47	44	43	Ryser and Urbas, (2000)
Plant geometry	Geo_{ratio}	-	Height-width ratio	0.85	0.65	0.71	0.71	0.72	Derived from pot experiments
	SLA	cm^{2}g^{-1}	Specific leaf area	23673	23125	20841	28673	27776	Herz et al., (2017)
	F	g cm^{-3}	Shoot biomass density	0.0010	0.0005	0.0014	0.0010	0.0010	Derived from pot experiments
	B_{ratio}	-	Shoot-root ratio of biomass	4.27	1.43	4.45	3.42	3.41	Derived from pot experiments
	$alloc_{shoot}$	-	NPP allocation of a single plant to shoot	0.49	0.42	0.70	0.77	0.73	Calibrated
Photosynthetic capacity	α	µmol$_{CO2}$ µmol$_{photons}^{-1}$	Initial slope of light response curve	0.67	0.53	0.65	0.51	0.53	Calibrated
	p_{max}	µmol$_{CO2}$ m^{-2} s^{-1}	Maximum gross leaf photosynthesis	29.4	28.8	25.5	33.5	32.7	Calibrated
	k	-	Light extinction coefficient	0.27	0.28	0.28	0.29	0.29	Calibrated

[1] Note, that whenever the trait variability in seed establishment was removed, the number of sown seeds N_{sown} as well as the species-specific seed rain N_{seed} were set to the community-weighted mean value. A detailed list of the model parameters can be found in Table C.1.

2.2 Study site and model parameterization

2.2.1 Study site and observation

We parameterized the model for a grassland located in the Central-East of Germany, which is part of a long-term experiment (Global Change Experimental Facility GCEF, Schädler et al. (2019)). The experiment was established in 2013 and includes managed grasslands and agricultural fields. In a total of 50 plots (384 m^2), different management treatments (intensive and extensive management, grazing, organic and conventional farming) as well as different climatic conditions (ambient and locally predicted future conditions) can be evaluated (Schädler et al., 2019).

In this study, we focus on five plots of intensively managed grasslands under ambient climatic conditions comprising of the following species: *Festulolium*, *Lolium perenne, Poa pratensis*, and *Dactylis glomerata*. The management of the selected plots includes regular mowing at 10 cm mowing height (four times within the growing season from late April until mid of October). Mean annual precipitation is at 489 mm and includes no artificial irrigation (Schädler et al., 2019). The grassland plots are located on fertile soil and additionally fertilized with 5 to 8 g per m^2 for three to five times per year (Schädler et al., 2019).

Measurements at GCEF include the aboveground biomasses for each species observed in 12 censuses (four censuses per year in April/May, June, August, and October shortly before the mowing dates). Therefore, all plants within a total area of 4 m^2 (8 measuring frames of 20 cm x 50 cm for each of the five plots) were cut at a height of about 3 to 5 cm above ground. The collected plant shoots were separated by species, oven dried and weighted.

Vegetation height was observed in 12 censuses (shortly before mowing) by placing a Styrofoam plate on top of the plants. We used the average value of five measurements (representing measurements at the northern, eastern, southern and western border and the center of each plot).

Next to the field measurements at GCEF, we installed pot experiments with individual plants of the four species (10 pots per species) in a cold greenhouse. We measured geometric properties of each plant (height and lateral extent) over a time period of five month (five censuses from June 2018 until October 2018).

2.2.2 Model parameterization and calibration

We parameterized the grassland model for the four grass species (*Festulolium*, *Lolium perenne, Poa pratensis*, and *Dactylis glomerata*) that were present in the intensively managed grassland plots.

The model included a set of 12 species-specific traits (per species, in total 48 parameters, see Table 1). From those, three traits per species could be found in literature (in total 12 parameters). Three traits that focus on the geometric plant characteristics were determined by measurements of pot experiments (in total 12 parameters, for details see Appendix A). For this, we calculated for each census t and species s the ratio between plant height $H_{s,t,i}$ and width $D_{s,t,i}$ (maximum of the four orthogonal measured directions) and then derived the associated GRASSMIND parameter Geo_{Ratio_s} by calculating the average over the censuses t (Eq. 7). Since measuring plant biomass is a destructive method, the fraction of biomass within the shoot's cylinder volume F_s, and the ratio of shoot to root biomass B_{ratio_s} was only measured once at the end of the growing season (last measurement in October). B_{ratio_s} was calculated by the fraction of shoot biomass B_{shoot} (as average over 10 sample pots per species s) and B_{root} (one sample for each species) (Eq. 8). F_s was derived by dividing the shoot biomass by the cylinder volume of the plant (or expansion space) that we calculated using the measured plant width and height of the last census (Eq. 9).

$$Geo_{ratio_s} = \frac{1}{5}\sum_{t=1}^{5}\left(\frac{1}{10}\sum_{i=1}^{10}\frac{H_{s,t,i}}{D_{s,t,i}}\right) \tag{7}$$

$$B_{ratio_s} = \frac{\frac{1}{10}\sum_{i=1}^{10} B_{shoot_{s,i}}}{B_{root_s}} \tag{8}$$

$$F_s = \frac{1}{10}\sum_{i=1}^{10}\frac{B_{shoot_{s,i}}}{\frac{\pi}{4}\cdot D_{s,5,i}{}^2\cdot H_{s,5,i}} \tag{9}$$

The remaining six traits per species were derived using model calibration (in total 24 parameters). Additionally to the traits, we calibrated the constant daily seed rain N_{seed} for each species (4 parameters). For this, the simulation models accounted for the daily dynamics of the grassland on a 9 m^2 area in a time period of five years starting with the sowing in September 2013 and ending in December 2017. The simulation model included the regular mowing at a height of 10 cm using the site-specific mowing dates (Schädler et al., 2019) and assumed optimal soil conditions (no limitation of soil water or nitrogen). Weather data for the model was based on daily measured air temperature and irradiance at the study site (Gründling and Vogel, 2019) . An overview of all model parameters can be found in Appendix C.1.

For the calibration of model parameters, we used the temporal measurements on vegetation height and aboveground biomass (in total and per species) of the five intensively managed grassland plots at GCEF from 2015 to 2017. We compared the observations with the simulated aboveground biomass for each species at associated points in time (simulations considered a measurement threshold above 4 cm). The simulated vegetation height was calculated as the average value of maximum plant height within the 9 simulated plots.

For the calibration, we used optimization techniques (Lehmann and Huth, 2015) that minimized differences between observations and simulations in 2,000 calibration steps (for details see Appendix D). We compared simulated and observed vegetation dynamics using the coefficient of determination R^2 (calculated by the 'lm' function of the software R (R Core Team, 2019)) and the normalized root mean square error (*nRMSE*).

2.2.3 Model analysis

To evaluate our model parameterization and calibration, we compared the simulated and observed aboveground productivity and species assembly at different time periods. The annual productivity was calculated as the sum of the harvested aboveground mown biomass of all species within one year (four mowing events per year in April/May, June, August, and October). The seasonal productivity was represented by the mown biomass in the first, second, third and fourth cut (averaged values across the years). The species composition was calculated as fractions of the biomass contributed by each species in relation to the overall biomass.

In addition, we determined Pilou's evenness (Pielou, 1966), which describes the relative contribution by different species for each vegetation attribute (here, number of plants per m², leaf area index of the grassland community, …). This index ranges from zero to one, with one indicating equal shares of all four species. Lower values reflect the dominance of few species.

2.3 Scenario analysis of trait variability

We further carried out a scenario analysis to investigate the impact of species-specific plant trait variability on grassland dynamics (Fig. 2). We compare two main approaches: First the "species-mean approach", in which the simulated grassland plants include the full interspecific trait variability and second, the "community-mean approach", where trait variability is excluded by assuming similar traits for all plants.

The species-mean approach can be seen as starting point ('baseline') representing the upper limit of interspecific trait variability (all species differ in their traits). The differences between species are addressed by species-mean traits, which differ between species, but not within species. In a next step, we carried out independent simulations in which a part of the interspecific trait variability was removed by setting the traits of different species to the community-weighted mean values (community-mean trait). For example, in the baseline scenario the height-width ratio Geo_{ratio} ranges between 0.65 and 0.85 for the four species (see Table 1). When the variability in this trait is removed, all simulated plants have a community-weighted average Geo_{ratio} of 0.72. Trait variability was removed group-wise, e.g., in the scenario “plant geometry”, all traits that describe the plant geometry ($Geo_{ratio}, SLA, F, B_{ratio}, alloc_{shoot}$) were set to the community-mean traits, while traits that describe a plant’s photosynthetic capacity, seed establishment, mortality still differed between species.

In contrast, the community-mean approach can be seen as baseline for the lower limit of trait variability (all species have similar traits) (Fig. 2b). Therefore all plants were simulated with community-weighted mean traits. Simulation scenarios then systematically added interspecific trait variability by setting each community-mean trait of a group back to the four different species-mean traits respectively.

In both approaches, four scenarios (besides the baseline) were derived according to the four groups of plant traits, for which trait differences were removed or added. Plant variability was not changed during the simulation, but from one scenario to the other. Note, that whenever the trait variability in seed establishment was removed, the number of sown seeds N_{sown} as well as the species-specific seed rain N_{seed} were set to the community-weighted mean value.

All scenarios tested in this study simulate an area of 9 m^2 over a time period of five years using daily time steps. Climate is included by daily measurements of air temperature and irradiance from 2013 to 2017 (Gründling and Vogel, 2019). The simulations included mowing (four times within the growing season from late April until mid of October) at 10 cm mowing height and assumed optimal soil conditions (no limitation of soil water or nitrogen).

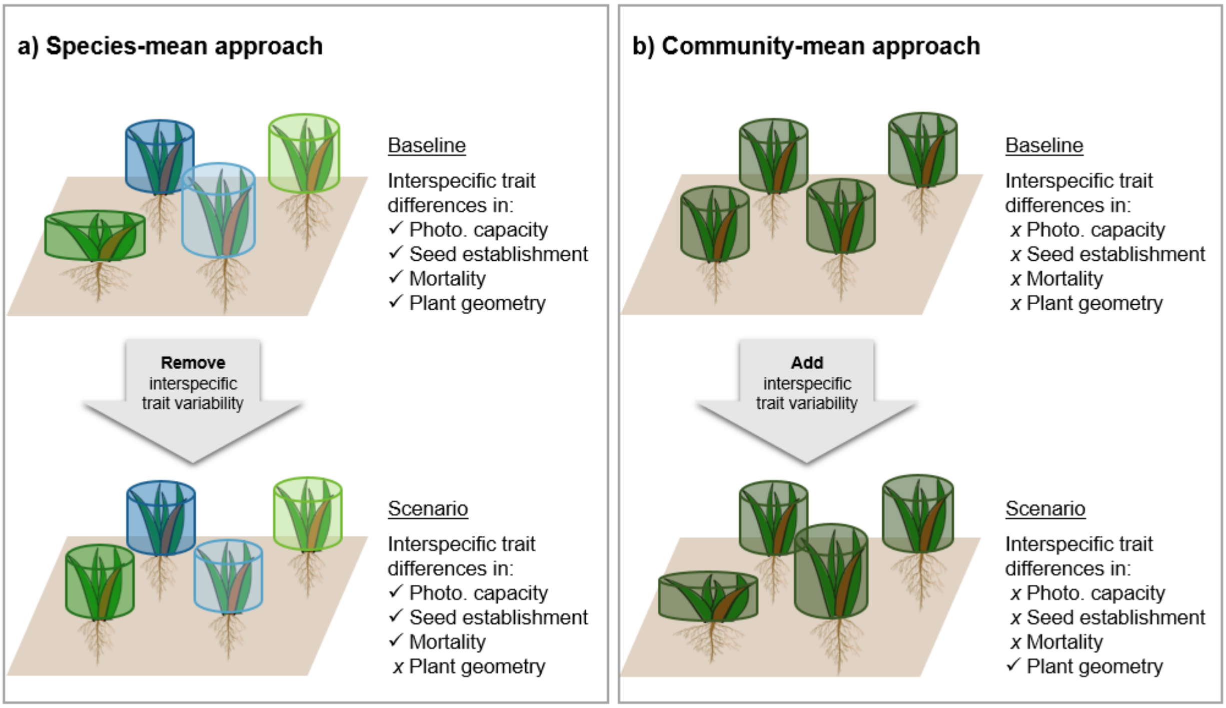

Fig. 2 Concept of simulation experiments on the example of plant geometric traits. We used two approaches to simulate scenarios with and without interspecific trait variability in grassland dynamics. a) The 'species-mean approach' is based on the full interspecific trait variability ('baseline'). Plants of the four parameterized species (indicated by different colors) differ in their growth form. For example, *Festulolium* (light blue), grows taller in height than in width compared to *Dactylis glomerata* (dark green). Four different scenarios were derived from this baseline by excluding trait variability in a specific trait group (here, plant geometric traits are set to the community-weighted mean values) while the variability of other traits remained. b) The 'community-mean approach' includes no interspecific variability ('baseline', all plants have similar community-weighted mean traits). Trait variability was then added in a specific trait group to derive four different scenarios (here, changing mean values of plant geometry traits back to the measured species-specific traits). Both approaches were carried out for each group of traits (plant's photosynthetic capacity, seed establishment, mortality, and plant geometry) separately.

We investigated the effects of trait variability on (i) the number of plants (per m²), (ii) the gross primary productivity (*GPP* in gC per m² per year), (iii) net primary productivity (NPP in g_C per m² per year), (iv) leaf area index (LAI), and (v) vegetation height (in cm). Each of these attributes was summed up for all plants and the four species, averaged across the simulated 9 m² and averaged over all simulated days of five years.

We determined deviations of the scenario simulations in comparison to the baseline of the species-mean approach or the community-mean approach, respectively. For each scenario separately, values of scenario results were subtracted from the respective baseline, and then divided by the baseline. The calculated values thereby represent the relative deviation (%) from the baseline value. Negative values show lower values of the analyzed scenario in relation to the baseline, and positive values vice versa.

3. Results

3.1 *Dynamics of aboveground biomass and species composition*

At GCEF, the observed annual biomass productivity of the intensive grassland was 1,256 g per m^2 and year with an inter-annual variation of 14 g per m^2 and year and the highest productivity in year 2016 (Fig. 3a). Pilou's evenness of the mean annual productivity was at 0.42. The grassland of all field plots was dominated by *Dactylis glomerata,* which accounts for 80% to 90% of the annual biomass productivity (Fig. 3c). The three other grass species were not able to exceed mean annual productivity values over 250 g per m^2 per year. Observed seasonal dynamics of aboveground biomass (AGB) differ between the four mowing events per year (May to October). The mean AGB per season decreases within a year from 400 ± 64 g per m^2 (in April/May) to 215 ± 84 (in October) (Fig. 3b). Again, *Dactylis glomerata* dominates in terms of biomass in all seasons (Fig. 3d).

The applied grassland model was able to reproduce the observed biomass dynamics (Fig. 3a). Across the four mowing events per year, the grassland model simulates an average annual productivity of 1,167 ± 109 g per m^2 per year (deviating less than 8% from the observed value). We found that 54% of the annual productivity develops in the first two seasons of spring and early summer similar to the observed values (60%) (Fig. 3b). The simulated inter-annual variation of AGB in August was on average higher than the observed variation (standard deviation increased by 92%). Simulated species composition (in terms of biomass) was similar to the observations (Pilou's evenness of 0.40, dominance by *Dactylis glomerata*, Fig. 3c-d).

The simulations of grasslands also reproduced observed AGB per species and census (R^2 = 87%, *nRMSE* = 0.53; Fig. E.1) as well as vegetation height for each census (R^2 = 32%, *nRMSE* = 0.39, Table D.1, Fig. E.3).

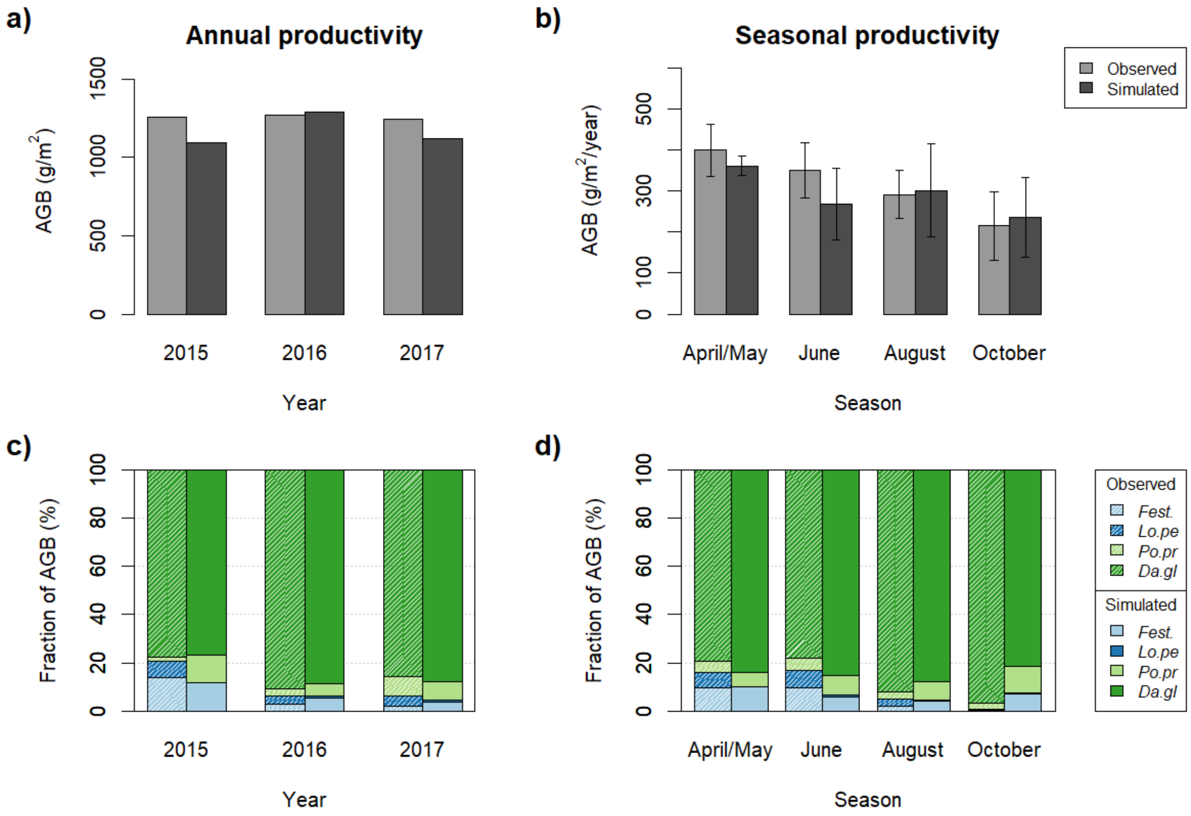

Fig. 3 Inter- and intra-annual variation in above-ground biomass (AGB) of the intensively managed grassland at GCEF. a) Observed and simulated mean annual biomass productivity. b) Mean seasonal aboveground biomass in the years 2015 to 2017 (inter-annual ranges are reflected by vertical lines). c-d) Species composition in terms of biomass compared between observations (shaded bars) and simulations (filled bars).

3.2 *Effects of trait variability on grassland dynamics*

3.2.1 *Effects on the annual productivity*

We found a marked influence of trait differences between species on the productivity of grasslands (Fig. 4). With the full interspecific trait variability, the simulated grassland shows an annual productivity of 1,167 ± 109 g per m^2 per year (Fig 4, species-mean baseline). When trait variability was removed in the four investigated trait groups (photosynthetic capacity, mortality, plant geometry and seed establishment) separately, annual productivity increased. The annual productivity was mostly affected by traits that described photosynthetic capacity (increase in annual productivity of 32%).

The species-composition (in terms of biomass) became more even when trait variability was removed. The Pilou's evenness almost doubled when differences in the plant geometric traits were missing. Results displayed that non-dominant species increase productivity. For instance, if plant geometric traits were similar, the productivity of the dominant species *Dactylis glomerata* was slightly inhibited (by -8% compared to the species composition of the baseline scenario) and in turn other species were promoted (*Poa pratensis* increased by 233%, *Lolium perenne* by 153%, and *Festulolium* by 96%). This results in a more balanced species composition (in terms of biomass).

Grasslands that were simulated without any trait variability showed a higher productivity (compared to simulations with the full variability) with almost equal shares of all four species (Fig. 4f, community-mean baseline). Small deviations in the species composition were caused by stochastic events (e.g., mortality of large plants). When trait variability was added in the simulations, we observed the associated opposing trends in species composition compared to the species-mean approach (Fig. 4 g-j). In particular, we found an increase in productivity by the dominant species and as a result a less balanced species composition. When variation was added in the geometric traits, Pilou's evenness decreased by 21%.

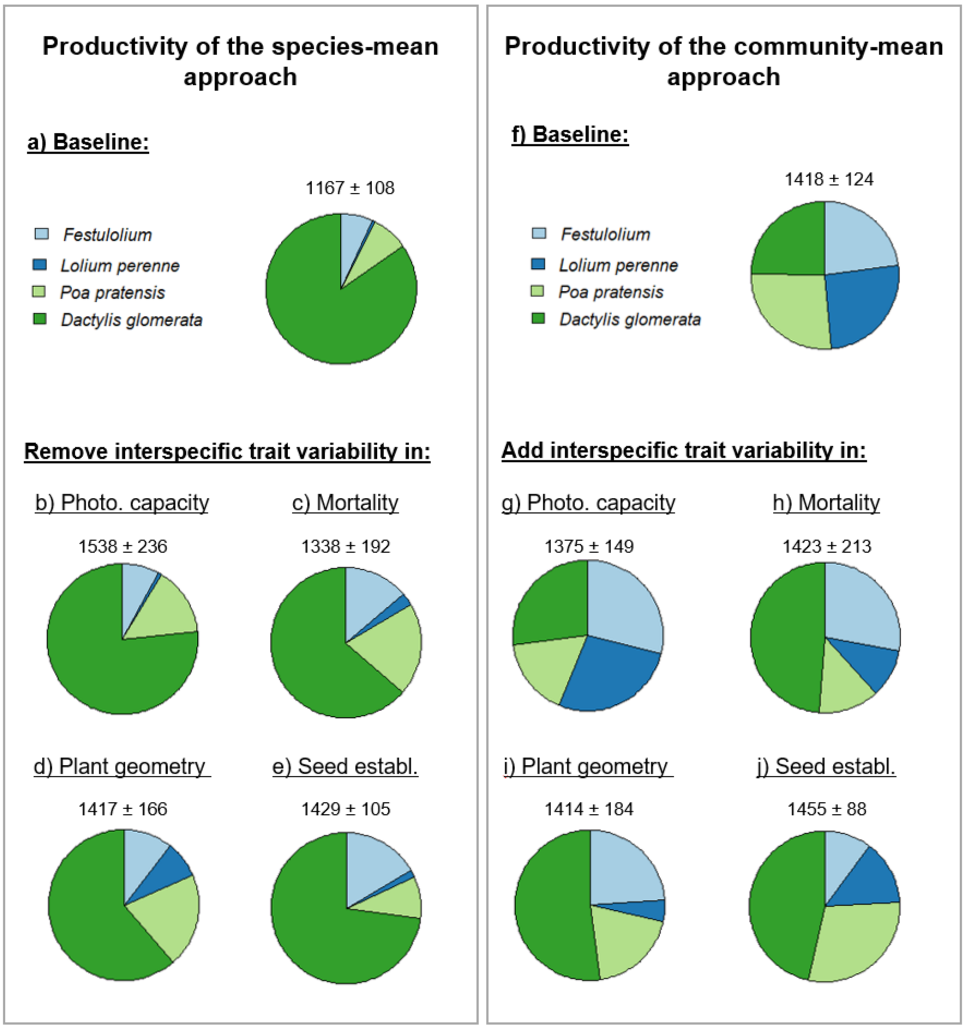

Fig. 4 Effect of trait variability on annual productivity and species composition (in terms of biomass). a) Annual productivity (g/m^2/year) (mean ± standard deviation) of the species-mean approach including all species-specific trait differences. The following lines display scenario results without variability in traits that influence a plant's b) photosynthetic capacity, c) mortality, d) geometry, or e) seed establishment. f) Annual productivity of the community-mean approach (similar traits for all species). The following lines display scenario results with added traits variability regarding the four trait groups.

3.2.2 Effects on further simulated grassland attributes

Vegetation height was sensitive to variability in seed establishment traits (with a reduction of 25% in comparison with the baseline scenario, Fig. 5b). In turn, leaf area index (LAI) and gross primary productivity (GPP) were mostly driven by plant geometric trait variability. In the absence of plant geometric differences in the species-mean approach, LAI increased by 13% (Fig. 5c) accompanied by an increase of GPP (+9%, Fig. 5d) and of net primary productivity (NPP, by +9%, Fig. 5e).

Corresponding effects were observed in the community-mean scenarios (Fig 5f-j). Again, differences in seed establishment traits increased vegetation height (by 23%, Fig. 5g), while trait differences related to a plant's geometry had the highest impact on LAI (increase by 10%, Fig. 6h).

Species composition in terms of LAI, GPP, and NPP were strongly influenced by plant geometric traits (Fig. F.2c-e). Missing trait variability resulted in more even species proportions (Fig. F.2c, reflected by an increase of the LAI-weighted Pilou's evenness by more than 60% compared to the baseline of the species-mean approach).

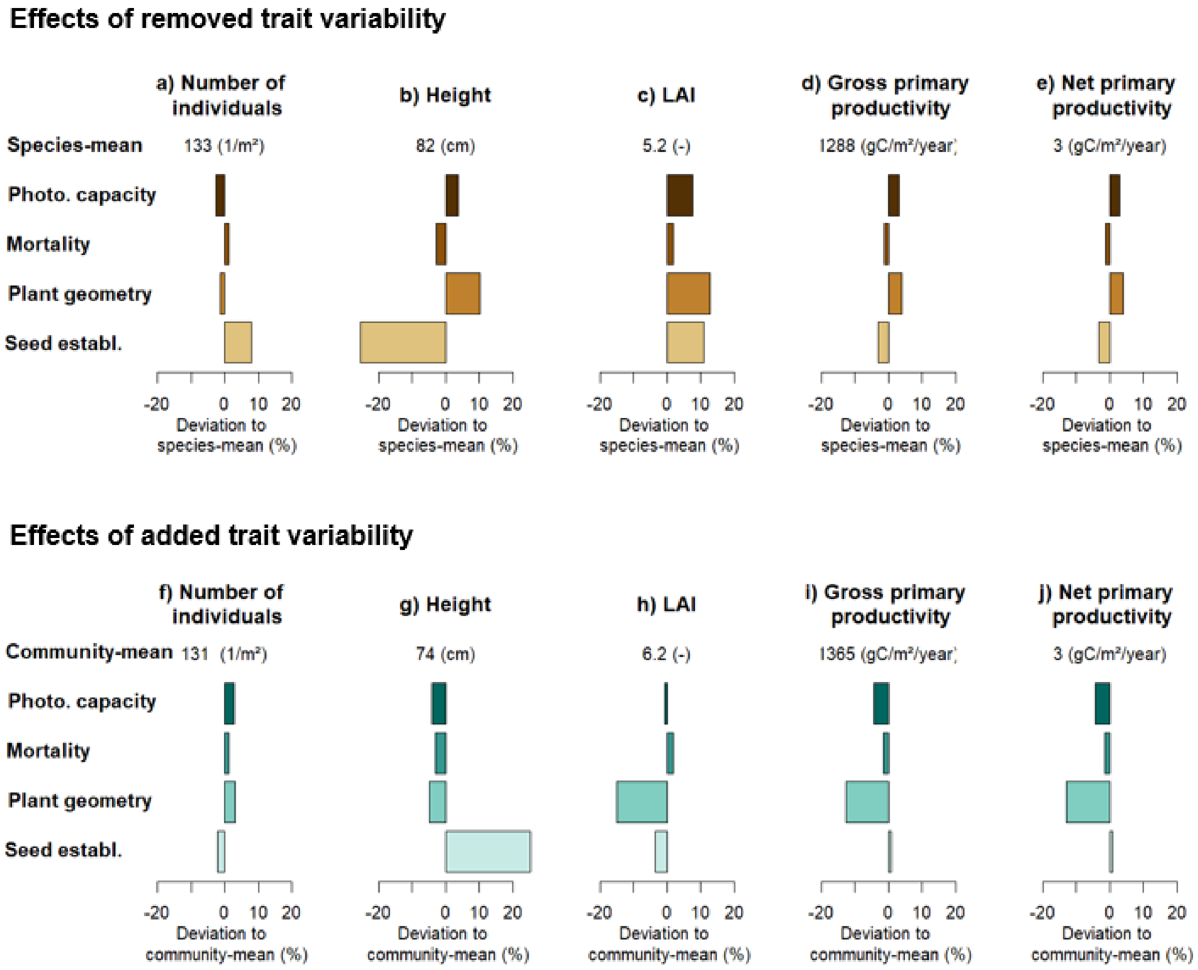

Fig. 5 Effects of plant trait variability on grassland dynamics. Shown are the average values of simulation results per m² over a time period of five years in light of a) the number of individual plants (per m²), b) vegetation height (cm), c) leaf area index, d) gross primary productivity (gC per m² per year), and e) net primary productivity (gC per m² per year). a-e). We investigated to what extent grassland dynamics including all species-specific trait differences (species-mean approach, simulated values are displayed in the first row) differ from simulations without trait differences. We analyzed the impact of traits influencing a single plant's photosynthetic capacity, mortality, geometry, and seed establishment (for a detailed traits list of each scenario see Table G.1). f-j) Effects of including trait differences in the community-mean approach. Results for the baseline simulations (having similar traits for all species) are displayed in the first row.

4. Discussion

In this study, we analyzed the effects of plant traits and their variability on grassland dynamics and species composition. The aim was to understand how trait differences among species lead to changes in grassland dynamics. Therefore, we parameterized an individual-based grassland model (GRASSMIND) for an intensively managed grassland in Germany and performed a systematic scenario analysis on the influence of plant trait variability. The focus of this study was on plant traits related to a plant's photosynthetic capacity, mortality, plant geometry, and seed establishment.

4.1 Drivers of grassland dynamics

Trait variability influences grassland dynamics strongly. We found that community-mean traits (that do not include trait differences) lead to an increase of annual productivity, and to marked changes in species composition. While the mean annual productivity was mostly affected by traits describing a plant's photosynthetic capacity, plant geometric traits are an important driver for species assembly. Our results are in line with a recent field study, which found that geometric traits (e.g., describing the growth form), traits describing the leaf photosynthetic capacity (e.g., specific leaf area and leaf nitrogen concentration), as well as species-specific differences among those traits are crucial to explain productivity and species performance (Roscher et al., 2018).

Other ecosystem functions such as gross and net primary productivity or leaf area index (and their corresponding Pilou's evenness) were influenced markedly by trait variability concerning a plant's geometry and seed establishment. Plant geometric traits in combination with the number of seedlings were also identified in field studies as an important driver for successful plant establishment in monocultures (Heisse et al., 2007). For multi-species grasslands, our simulation results suggest that missing trait variability slightly reduces the competitive advantage of the dominant species *Dactylis glomerata* and in turn notably increases the establishment of the other species.

Effects of trait differences can be related to different hypotheses. For example, the "trait hierarchy theory" states that differences in traits reflect differences in the average fitness of plants regarding their environment (Kraft et al., 2014; Kunstler et al., 2012). Field studies found that plants can be on top of the competitive hierarchy (shown by the dominance in the species assembly), e.g., if they have (geometric) traits that lead to a larger leaf size but a lower specific leaf area (Kraft et al., 2014). Our results support these findings. In the simulations the dominant species is characterized by plant geometric traits that are well adapted to plant competition for light and space which results in a high productivity. Another concept claims that trait differences lower competition on the same resource, which promotes coexistence of species ("trait difference hypothesis", Kraft et al., 2014; Mayfield and Levine, 2010). In this study, our chosen modelling design limits the opportunity to analyze this hypothesis in detail, because of the constant daily ingrowth of new seeds from the surrounding landscape into the simulated area (parameter N_{seed}). This regeneration process is explicitly modeled to prevent extinction during our scenario simulations. Thus, our model assumption allows us to focus on the effects of plant trait variability on grassland productivity and species composition only. The model parameter N_{seed} was calibrated and therefore aggregates different regeneration mechanisms in one process. Disentangling this process (i.e., seeds produced by simulated plants dispersed into the plot, combined with external seed rain by the surrounding landscape) could allow for additional analysis, but requires a further calibration of the parameter N_{seed} (Table G.1.). To draw additional conclusions about how plant traits affect plant competition, species assembly and species coexistence, future studies of grassland communities should consider detailed plant regeneration sources (Chesson, 2000; Hubbell, 2001). Larger effects found in the scenarios of the species-mean approach (with many combined trait differences) compared to the community-mean approach (with only single trait differences) indicate that especially the combination of several traits (and their variability) lead to marked shifts in species composition and grassland dynamics. This reflects that plants often include multiple trade-offs in their multi-dimensional trait space (Wright et al., 2004), and that combinations of traits might provide additional information that describe a plants functioning (Kraft et al., 2014).

4.2 Measurements of plant geometric traits

Our study further provides observations of species-specific plant geometric traits. By including measurements of plant height and a plant's lateral expansion, we determined geometric properties of grass plants that have rarely been measured so far (e.g., Kahmen and Poschlod, (2004) or F Louault *et al.*, (2005)). Based on our measurements, we found a linear relationship between plant height and width which results in a constant ratio over time (except for the early development stage of seedlings, Fig. A.1). This constant ratio reflects that as soon as plants have matured, they invest similar amounts of biomass in both, the growth of plant height and width. In the seedling stage, however, plants invest more biomass in height growth, because fast height growth at seedling stage allows an earlier start of flowering, and thereby competitive advantages in terms of reproduction (Sun and Frelich, 2011). We further observed a trade-off between the ratio of a plant's shoot and root biomass and the shoot's cylinder volume filled with biomass (Fig. B.1). By this, plants which allocate more biomass to the aboveground shoot do grow denser even though they increase height and lateral expansion proportionally (an effect also seen in field studies (Gusch et al., 2011; Heisse et al., 2007)).

In our pot experiment, plants were grown under optimal soil conditions (pots were fertilized and irrigated regularly). Note that in times of limited water or nutrient supply, plants can change their allocation and growth strategy which could result in adapted or changed traits (Roscher et al., 2018). Manually measuring a plant's geometry is time-consuming and thus, limits the amount of plants to be measured. For determining individual plant traits within grassland communities, other photo-based techniques (e.g., 'structure from motion' in combination with 'time of flight' 3D cameras (Kröhnert et al., 2018)) might be interesting. However, photo-based techniques are still challenging especially in canopies of diverse grasslands (Wachendorf et al., 2018). In order to compensate those limitations, light-field cameras (Schima et al., 2016) and other remote sensing sensors such as LIDAR, radar, and ultrasound offer interesting novel possibilities (Wachendorf et al., 2018).

4.3 Model limitations and trends found in other studies

The grassland model was able to reproduce measured time-series of aboveground biomass as well as species composition of a German field experiment on intensive grasslands with a sufficient accuracy. The annual biomass productivity was reproduced well. We found only a slight underestimation of simulated aboveground biomass in the first half of the growing season and a slight overestimation in the second half. One reason for this might be a reduction in the productivity of plants in the field due to water stress in late summer (Jansen-Willems et al., 2016) which was not included in model simulations. Seasonal grassland dynamics might be matched more closely by including additional factors in future studies, e.g. soil resource dynamics and plant competition for soil resources or species-specific differences in the response to air temperature (in respect to of plant photosynthesis and respiration). Besides the modelled effects of abiotic conditions on plants, also changes in growth strategies of plants in response to mowing could be further explored in the grassland model. Such growth changes can encompass, for example changes in the height-width ratio or the homogenous leaf distribution within the plant expansion space as well as in terms of biomass allocation to plant shoot and root. Changes in plant traits could be analyzed by including cutting events in additional pot experiments.

The model used in this study focuses on plant competition for light and space (Taubert et al., 2012, 2020). Other individual-based models which use more detailed descriptions of plant interactions in space (like IBC-grass, using the 'zone-of-influence' approach for plants of different spatial positions (May et al., 2009)) also found a sensitivity of plant geometric traits (i.e., the belowground zone-of-influence area per root mass) and in addition, traits related to a plant's ability to cope with resource stress (Weiss et al., 2014). In contrast, individual-centered models describe a population by a representative mean plant (e.g. GEMINI (Soussana et al., 2012)) and thus, do not allow for an analysis of trait differences on plant size structure and density. However, in such models community dynamics showed to be strongly dependent on leaf and root traits that determine a plants' productivity and its (geometric) relation between below- and aboveground properties (Soussana et al., 2012). Models that explicitly allow to include diverse traits for different species have the potential to extend investigations, for instance by systematically varing model parameters that represent plant traits (Funk et al., 2017).

4.4 *Implications for natural grassland*

Intensive grasslands are mainly characterized by a few grass species being more similar than the range of herbaceous species occurring in more natural grasslands. For instance, extensively managed grasslands often include besides grass species also legumes and herbs, which can differ markedly in their traits. Field studies of experimental grasslands (e.g., (Fischer et al., 2010; Weisser et al., 2017)) found a positive relationship between species-diversity and productivity (Milcu et al., 2014; Spehn et al., 2005; Tilman, 2001), but those effects diminish for species-rich ecosystems like natural grasslands (Buchmann et al., 2018; Grace et al., 2007). One reason for this is that in natural communities, productivity might be more driven by abiotic conditions like climate or soil properties and disturbances (Buchmann et al., 2018; Grace et al., 2007). Trait-based models of natural grasslands can help to disentangle the effects of abiotic conditions and trait differences. To overcome the challenging parameterization of up to 80 plant species per 4 m^2 in species-rich ecosystems (Ellenberg and Leuschner, 2010), the incorporation of trait distributions in grassland models can be a promising modelling concept as already demonstrated, for example, for species-rich forest (Sakschewski et al., 2016). Trait distribution models might also help to understand the processes that narrow the wide range of possible traits to those that can be found in the community. Observed traits for various grassland types are already available for such a comparison in global trait databases like TRY (Kattge et al., 2011).

5. Conclusions

This study demonstrated that the differences in species traits, in particular the variability of plant geometric traits, have an important influence on grassland dynamics. Detailed measurements of those traits in field studies can help to increase the accuracy in simulations and to advance further development of grassland models.

Our simulation analyses emphasize that individual-based grassland models enable a closer look at the relative importance of plant traits on community dynamics and ecosystem functions of grasslands. Here, the grassland model GRASSMIND was applied to analyze the influence of trait differences between species as observed in the corresponding field study. Such individual-based models, however, also allow to explore the effects of larger trait ranges than observed, giving the opportunity to analyze diverse species mixtures not yet studied in field experiments.

Here, we studied intensively managed grasslands consisting of four common grass species. While overall trends can be simulated with averaged trait values across species, we found that individual-based models should at least consider trait differences of plant geometry to capture species composition within simulations.

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Authors’ contributions

JH, AH and FT conceptualized the research; JH collected and prepared the data and ran analyses; JH, AH and FT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Software availability

The GRASSMIND simulation model (including parameter files and results files) and observation data of the pot experiments will be made available for free download at http://formind.org/downloads/ at the date of publication of this study.

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