The role of species traits for grassland productivity

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Abstract. The relation between species diversity and ecosystem functioning is one of the most frequently discussed topics in ecology. Experiments often revealed an increase of productivity in species-rich ecosystems. But large variations in these relationships, both on a local scale and in comparisons of sites along environmental gradients, still challenge our understanding of the role of species (with specific traits) and their interactions in ecosystems. In this study, we explored the role of species traits for ecosystem functioning. We used an individual-based mechanistic grassland model which captures intra- and interspecific competition between plants for light and soil resources. We explored how the dynamics and productivity of grasslands are influenced by species traits and analyzed in a simulation study two species, which differ only in one particular trait. Our focus was on traits that determine how species can cope with resource limitations, for which we identified their relative importance for (1) individual plant growth, (2) monoculture dynamics, and (3) species mixture dynamics. We observed diverse relationships between species traits and different vegetation attributes for the different ecosystem levels. Most traits showed positive but saturating trends of increasing trait values but the variability in these relations increased in monocultures with intraspecific plant interactions and even more pronounced in mixtures with interspecific interactions. Using a process-based grassland model, we were able to simulate overyielding even though it was not correlated with trait values or trait differences between both species. Correlations were also not found in terms of stability of vegetation dynamics. In contrast, for some traits already small differences supported the dominance of a species in the mixture in which species dynamics generally followed trade-offs. The here presented simulation study demonstrates the use of process-based models for analyzing trait-productivity relationships in grasslands. Such models can complement previous approaches in empirical and theoretical biodiversity research and can help to move closer to understanding the mechanisms governing grassland dynamics.

Key words: diversity effects; grassland model; Special Feature: Empirical Perspectives from Mathematical Ecology; species traits; trait relations.

INTRODUCTION

The relationship between species diversity and ecosystem functioning is one of the most frequently discussed topics in ecology. Biodiversity is hypothesized to strengthen an ecosystem for better coping with climate, environmental, and land use changes (Loreau et al. 2001).
Empirical studies have explored this relation for different systems such as grasslands (Tilman et al. 2001, Spehn et al. 2005, Adler et al. 2011, Weisser et al. 2017), forests (Morin et al. 2011), and aquatic and microbial systems (Kassen et al. 2000, Cardinale et al. 2005).

Early empirical studies monitored an ecosystem’s diversity in relation to its productivity like local grassland experiments that systematically manipulate the richness and assembly of plant species in monocultures and mixtures (Tilman et al. 2001, Weisser et al. 2017) and also analyses across environmental gradients and spatial scales (e.g., Nutrient Network, BioDepth). While local approaches often support a positive nonlinear relationship of productivity that saturates at high diversity levels, cross-scale analyses are still debating whether generalized relationships across environmental gradients and spatial scales (e.g., Nutrient Network, BioDepth). While local approaches often support a positive nonlinear relationship of productivity that saturates at high diversity levels, cross-scale analyses are still debating whether generalized relationships between species diversity and productivity can be confirmed (Adler et al. 2011, Fraser et al. 2015).

Species diversity can be described in different ways—from the number of single species to taxonomic or functional groups (Kinzig et al. 2002). Richness does not consider whether plant species resemble or differ in their attributes (or traits), but functional groups put plant species’ traits into focus. Herbaceous species are often classified as grasses, legumes, and forbs (Roscher et al. 2004). The latter two in particular play a decisive role for productivity increases in mixtures (i.e., overyielding; Marquard et al. 2009). Based on such analyses, the approach evolved to explore coexistence of species (Kraft et al. 2015) and ecosystem functioning in relation to species traits.

Most empirical studies, however, are constrained to a limited (regional or experimental) species pool, and thus, the considered trait space can differ across study sites and environmental gradients. Moving beyond such limitations imposes challenges for field experiments, but can be supported by modeling approaches (Loreau et al. 2001, Kinzig et al. 2002). Simple models like the Lotka-Volterra competition model (Lotka 1925, Volterra 1926) allow relating observations to an easy understandable theory of species coexistence and abundance dependent on the species’ population growth rates. Mechanistic models, in contrast, enable to explore trait effects in relation to the dynamics and processes of grasslands at multiple ecosystem levels for answering a still open question in ecology (Loreau et al. 2001, D’Andrea and Ostling 2016): Which species (having certain traits) affect which ecosystem processes in diverse communities?

Previous modeling studies not only used models of different complexity but also partly different approaches to analyze the effect of species traits on grassland productivity. Some models focused on general plant strategies (in terms of resource use) or common trait syndromes (of plant functional types) to gain an understanding of how functional traits affect ecosystem productivity (Tilman 1988, Tilman et al. 1997, May et al. 2009, Crawford et al. 2019). Several studies try to mimic empirical observations of biodiversity experiments (Soussana et al. 2012, Maire et al. 2013, Lamarque et al. 2014, Kraft et al. 2015) but parameterize only the locally occurring species (and their traits). Few studies try to expand this local view by randomly dicing out all trait values (e.g., from predefined trait distributions), for which models act then as kind of environmental filter. By this, either only successful trait combinations are able to survive on the long-term (Bohn et al. 2011, Pavlick et al. 2013) or environmental conditions shift or modify the initial trait distributions (Sakschewski et al. 2016). All approaches have in common to include multiple traits (partly also with deterministic trade-offs) of interacting species at the same time.

In this study, we aim at systematically disentangling the role of single species traits on plant growth and its interplay with intra- and interspecific interactions in monocultures and species mixtures. Our goal is to step back and to systematically learn how (and how strong) different plant traits influence different levels of grassland ecosystems (from the individual plant to the community mixture). We thereby focus on traits that govern a plant’s ability to cope with limitations of resources (light, soil water, and nitrogen) that are important for plant growth. By this, we seek to answer the following questions:

1. Which role do species traits play for the growth of plants?
2. How do species traits influence the dynamics of monocultures and mixtures?
3. Do process-based models include mechanisms to explain overyielding in species mixtures?
In a virtual simulation study, we analyzed two plant species which differ in specific traits and explored the effect of trait differences on grassland dynamics at the individual plant level, in monocultures and two species mixtures. For this, we applied a process- and individual-based grassland model, which captures explicitly demographic processes and intra- and interspecific interactions between plants for light, limited space, and soil resources (water and nitrogen). The growth of single plants is described by a balance of carbon uptake and release (driven by abiotic factors). Patterns and structures (e.g., plant density, aboveground biomass [AGB], or vegetation height) emerge at the population and ecosystem level through the interactions of individual plants— influenced by a multidimensional set of traits and stochastic demography. These features of process-based models allow to analyze multiple vegetation patterns of diverse communities at different levels (single plant, population, community) in relation to species traits.

METHODS

The grassland simulation model

The grassland model GRASSMIND combines biogeochemical cycles with biodiversity and plant–soil feedback, management, and climatic effects (Taubert et al. 2012; Appendix S1). Individual plants interact and compete for resources on one patch (1 × 1 m) without assignment of explicit spatial locations to each plant. During a year, the model simulates the daily dynamics of each single plant within the grassland based on the following processes: (1) recruitment and emergence of plant seedlings, (2) plant senescence and mortality, (3) growth of plants (based on a carbon balance of photosynthesis and respiration), which can be (4) limited by environmental conditions or reduced due to interactions between plants. Soil water, carbon, and nitrogen dynamics are modeled using the Century soil model (Parton et al. 1988).

Intra- and interspecific competition for resources encompass aboveground light and space resources as well as belowground soil water and nitrogen resources. Limitations of growth can be caused, for example, by low light intensities (e.g., shading by other plants) or by reduced soil water or soil nitrogen resources. Differences in interactions within and between species emerge from the interplay of species traits and dynamically changing plant sizes (which both drive resource demands and accessibility). By this, the model allows simulating monocultures as well as multi-species mixtures.

Simulation studies on trait–productivity relations

The here presented simulation study refers to a parameterization of GRASSMIND for a European grass species (Festuca pratensis; Appendix S2). Daily climatic conditions (precipitation, global radiation, air temperature, day length, and potential evapotranspiration) and soil properties (silty loam) represent a typical German study site (Appendix S2).

We used the parameterized grass species as a reference species and created virtual species by changing only one selected trait at a time. All other traits remain similar to the reference species. For creating a virtual species (with a selected varied trait), we used random sampling from a uniform distribution with a predefined trait value range (Table 1; Data S3). Per selected trait, we thus created 100 virtual species whereby each of them differed to the reference species by only one certain trait value. The analysis focused on traits which refer (1) to the species’ demand for light, soil water and nitrogen resources and (2) to its ability to access these resources (Table 1). In addition, we also varied traits with regard to growth strategies: shoot-root ratio (in terms of biomass) and the allocation rate (of net productivity) to aboveground shoot growth.

Simulations reflect the plant development within a 1 × 1 m area over a time period of seven years including biannual mowing. Environmental conditions and cutting regime were used similar to the field study site of the parameterized reference species (Appendix S2). We analyzed the simulations at four different levels: (1) the growth of an individual plant in the first growth year (in the absence of other plants; without cutting; Fig. 1), (2) population dynamics of monocultures, and (3) dynamics of two species mixtures in which the reference grass species interacts with a virtual species of modified traits. The latter two simulations were analyzed from the second to seventh growth year including mowing.
For each ecosystem level, we analyzed the influence of manipulated traits on the respective dynamics in terms of AGB, vegetation height, leaf area index (LAI), and green vegetation cover. Vegetation height was defined as maximum plant height in the grassland. Green vegetation cover was derived by weighting total cover with the fraction of green leaf area to total leaf area. Similar to empirical studies, we recorded each of these four vegetation attributes twice per year one day before mowing as proxies for grassland productivity (Scurlock et al. 2002; Appendix S2). For the analysis, we then calculated for each vegetation attribute the arithmetic mean and standard deviation of the 12 values (from the second to the seventh year of plant growth, e.g., in Fig. 2).

Table 1. Summary of species traits.

| Category                | Species trait         | Unit | Reference value | Sampling range |
|-------------------------|-----------------------|------|-----------------|----------------|
| Growth                  | Shoot-root ratio      |      | 2.2             | 0.1–15         |
| Growth                  | Allocation rate to shoot† |     | 0.72            | 0.01–1         |
| Light                   | Light response curve‡ | μmolCO₂/μmol photon | 0.04          | 0.01–0.5       |
| Light                   | Specific leaf area    | cm²/gODM | 164.39       | 10–500         |
| Soil water              | Water use efficiency  | gODM/kgH₂O | 6.8            | 1–15           |
| Soil water and nitrogen | Rooting depth§        |      | 0.301           | 0.01–2         |
| Soil nitrogen           | CN ratio of green leaves |     | 28              | 0.1–40         |

† The allocation rate to aboveground shoot growth refers to the net primary productivity of a plant.
‡ The light response is described by two parameters: the initial slope α at low light levels and the gross leaf photosynthesis rate at maximum light levels. We only varied here the slope of the curve.
§ Rooting depth is modeled by a power law relating a plant’s rooting depth to its aboveground biomass. We only varied here the exponent of this power law.

Fig. 1. Trait effect on height growth of a single plant. (A) Height growth of a single plant over one year (in days) without cutting. Visualized is the simulated plant height and daily height increment of a single plant (reference values). (B–E) Relationships of trait values with plant height reached at the end of one growth year (black dots) for (B) shoot-root ratio, (C) allocation rate to shoot growth, (D) specific leaf area (cm²/g), and (E) light response (μmolCO₂/μmol photon). Green dots represents traits and the respective results of the reference grass species.
In terms of AGB in mixtures of two species (reference species and one virtual species), we further calculated the relative yield (RY, Loreau and Hector 2001) for both species by relating the species’ contribution in the mixture to half of its monoculture value (assumed as expectation in the mixture). Again, we calculated the arithmetic mean and standard deviation of the resulting 12 values for each species. We then categorized simulations with regard to overyielding (both species reach higher yields in the mixture than expected), underyielding (both species reach lower yields than expected), and diverse trends (one species reaches higher yields while the other one is below its expectation). Further, we calculated the Pearson correlation coefficient (r) between the varied trait value of the virtual species and its RY (Fig. 3). For graphical purpose, outlier values (above 10) are not displayed in Fig. 3: (A) 11.8 (diverse trend); (B) 21.2, 21.1 (both diverse trend); (C) 13.0, 15.6 (both diverse trend); (E) 11.9 (overyielding); (F) 10.5, 12.1, 30.1, 11.1 (diverse trends) and 24.2, 13.4 (both overyielding); and (G) 531.9, 45.0, 19.3 (diverse trends) and 13.4, 32.2, 11.8 (overyielding).

We also analyzed species dynamics in two species mixtures by relating absolute values of the different vegetation attributes between both

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Fig. 2. Trait effect on different vegetation attributes of monocultures. Each column shows the influence of an increasing trait value of (A) shoot-root ratio, (B) allocation rate to shoot growth, (C) specific leaf area (cm²/g), (D) light response α (μmolCO₂/μmol photon) on the dynamics of a monoculture (aboveground biomass [AGB], vegetation height, leaf area index [LAI] and green vegetation cover). Vegetation cover can be larger than 100% for short time due to delayed crowding effects in the modeling approaches of the grassland model. Black dots show averages for different trait values with gray lines being the standard deviation (see Methods for details). The horizontal orange lines and orange dots represent traits of the reference species and its respective results in monocultures.
species and determined again the Pearson correlation coefficient ($r$). To give an impression on species dynamics in relation to over- or underyielding, we included in Fig. 4 the two-dimensional space covering all constant lines at which the relative yield total (RYT equal to the sum of RY of both species, Loreau 1998) of the mixture equals one (i.e., the mixture is equal to the expectation). Simulation points lying above this triangle show definite overyielding. In addition, we marked each simulation point by the coefficient of variation (CV), which relates the standard deviation of observations to its mean (two records per year from the second to the seventh growth year). Bluish points show large CV values, while reddish points indicate low CV values.

We also related vegetation attributes of the species mixture to relative trait differences of both species. Relative difference referred to the trait value of the reference species and was provided in percent. Each simulation point was additionally marked with regard to the dominance of a species. Dominance was thereby determined for that species, which was highest in the mixture in terms of the different vegetation attributes.

**RESULTS**

**Trait effects on individual plants**

Individual plant growth was strongly depending on their respective traits. In the absence of cutting, plant height followed a logistic growth curve (Fig. 1A). Plant traits influenced the slope (or rate) and the carrying capacity of this curve. For example, specific leaf area (SLA) increased plant height and damped it for decreased values (Fig. 1D). Most influential traits (from the selected ones in this study) were SLA and the
plant's response to light as well as its shoot-root ratio and allocation rate to shoot growth (Fig. 1B–E). For those traits, larger values than the reference value always resulted in an increase of plant height, with more rapid increases for SLA, light response, and the allocation rate (Fig. 1C–E) than for the shoot-root ratio (Fig. 1B). Specific leaf area, the light response, and shoot-root ratio saturated at large values (i.e., SLA > 200 cm²/g, light response α>0.1 μmol CO₂/μmol photon, shoot-root > 4). Other traits only became influential when soil resources (i.e., water and nitrogen) were limited.

**Trait effects in monocultures**

The growth of plants (having similar traits) cannot be simply scaled up from the individual to the population level (in monocultures) due to intraspecific competition for multiple resources (e.g., light, soil water, and nitrogen). For most traits, AGB, vegetation height, LAI, and green vegetation cover increased in monocultures with increasing trait values (Fig. 2A–D). Slopes (α) of the light response curve and SLA values below and above the reference traits decreased AGB and vegetation height (Fig. 2D), but in turn green vegetation cover increased stronger for SLA and α than for other traits. Most vegetation attributes saturated at high trait values (Fig. 2). Green vegetation cover showed minima at intermediate trait values of SLA and allocation rate (Fig. 2B, C). With respect to soil resources, rooting depth and water use efficiency (WUE) also affected the different vegetation attributes of grasslands (Appendix S3: Fig. S1). Vegetation cover decreased in greenness under deeper rooting.
plants but slightly increased with higher WUE (Appendix S3: Fig. S1). Variability was generally high for most analyzed vegetation attributes, except for the green vegetation cover (Fig. 2). The variability of the dynamics of monocultures was mostly influenced by a plant’s allocation rate to shoot growth, SLA, its light response, rooting depth, and WUE (Fig. 2; Appendix S3: Fig. S1).

**Trait effects in species mixtures**

When moving from monocultures to mixtures—can a species also benefit from larger trait values in competition with other species? For the simulated mixtures, the relationships obtained in monocultures remained, for example, AGB (in terms of RY), but strongly increased the variability of vegetation attributes with changing traits (Fig. 3).

We observed only for few traits a benefit for species B (with higher trait values) for increasing its productivity (Fig. 3, values above dotted line). Especially for the allocation rate, rooting depth, and SLA, we explored moderate correlations with RY (Fig. 3). All traits could enable species B to even exceed its monoculture yield although competing with another species in the mixture (Fig. 3, values of RY > 2). However, only very few trait combinations allowed for overyielding of both species (i.e., species yields in the mixture larger than expected from their monocultures, Fig. 3 green dots), especially for the light response.

Although species B was able to even exceed its monoculture productivity, this increase in productivity went to the expense of species A. Generally, the increase in abundance of species B (with varied traits) resulted in a decrease of abundance of species A (with reference traits) and vice versa (Fig. 4). Most species traits revealed such negative relationships of species dynamics (e.g., Fig. 4A–D for SLA; Appendix S3: Figs. S2, S3), except for the light response. Changes in a plant’s light response for species B predominantly resulted in benefits only for species B (in terms of AGB, height, and LAI), thus suppressing species’ A abundance. Although overyielding was rarely observed in terms of AGB and LAI, we could show that green cover and vegetation height of both species in the mixture often exceeded those values observed in the monoculture (Fig. 4B, D; Appendix S3: Figs. S2, S3). Green vegetation cover thereby was more stable over time (i.e., lower CV) than vegetation height. However, temporal stability was not correlated with trait differences.

For a few traits only, we observed significant relationships between trait differences and simulated vegetation dynamics (Fig. 4G; Appendix S3: Figs. S4, S5). The light response and SLA showed relationships with, for example, LAI and vegetation height. Dominance of a species in the mixture (e.g., in terms of abundance) was, however, not dependent on the strength of trait differences (Fig. 4E–H; Appendix S3: Figs. S4, S5). Already slightly higher trait values of species B, for example, for SLA, resulted in dominance of species B in terms of AGB, LAI, and green vegetation cover (in mixtures with species A), but rarely in terms of vegetation height (Fig. 4F). Similar results were observed for the shoot-root ratio, the allocation rate, and light response (Appendix S3: Fig. S4). Trait differences in rooting depth, CN ratio, and WUE showed no clear relationships with species dominance of the vegetation attributes (Appendix S3: Fig. S5).

**DISCUSSION**

Here, we used a process- and individual-based grassland model to analyze the impact of species diversity on ecosystem functions of grasslands. Across different ecosystem levels (individual plants, monocultures, and species mixtures), we explored the relationships of species traits on grassland dynamics based on a European grass species.

**Trait effects in grassland simulations**

We focused on traits which determine (1) resource demands of species and (2) the species’ ability to acquire resources, reflecting the modeled intra- and interspecific interactions between plants for light and soil resources. Traits associated with a plant’s demand for resources (WUE, CN ratio, and light response) can thereby be interpreted as indicators for stress tolerance. For example, species with low WUE, large CN ratios, and steep slopes of light response can cope much better with soil water and soil nitrogen limitations, as well as shading. In contrast, traits associated with a plant’s accessibility to resources
(rooting depth, SLA) rather reflect a plant’s strength when competing for resources. The shoot-root ratio and allocation rate to shoot growth, in turn, indicate a plant’s strategy whether to invest its productivity to either aboveground or belowground plant tissue, and to either growth or reproduction.

Our analysis revealed distinct trait-productivity patterns. Single plants benefit from increasing trait values (especially for SLA and light response), but tend to be suppressed by intraspecific interactions in monocultures (especially for AGB and vegetation height). In contrast, green vegetation cover of monocultures mostly increased with higher trait values. Variability in the relationships between trait values and vegetation attributes of monocultures was high but increased even more in species mixtures when interspecific interactions came into play. Nevertheless, functional relationships of traits with vegetation attributes were comparably similar in monocultures and mixtures and differed only with regard to the considered trait. Variability of trait patterns generally increased with higher trait values, except for SLA (highest variability at intermediate values) and shoot-root ratio (equally high variability across all values). Green vegetation cover showed lowest variability with trait changes, even in species mixtures. Highest stability (i.e., lowest CV) was thereby observed for intermediate levels of green cover for both species. Overyielding was in general possible to simulate with the process-based grassland model. However, overyielding and stability were not correlated with trait values, but species dominance was shown to be determined by trait differences. Our approach allows for no direct comparison to empirical observations. Here, we analyze vegetation dynamics of monocultures and two species mixtures, which differ in only one (chosen) trait value. Field studies, in turn, are often constrained by certain trait combinations of the considered species and try to filter the most relevant species traits for ecosystem productivity.

Trait–productivity patterns can further be influenced by different environmental conditions (Spehn et al. 2005, Adler et al. 2011, Fraser et al. 2015, Brun et al. 2019). Dry sandy soils, for example, could emphasize a stronger importance of a species’ rooting depth and WUE in order to support plants to better cope with water stress. Globally collected traits of plant species have therefore been analyzed in a so-called trait distributions (Wright et al. 2005, Kattge et al. 2011) and related to ecosystem productivity as well as to its environment (Wright et al. 2005, Brueelheide et al. 2018), seasonality (Orwin et al. 2018), ecosystem properties (Wright et al. 2005, van Bodegom et al. 2014), and climate change (Sakschewski et al. 2016). However, under changing environments plants may dynamically adapt to different resource conditions. Either (1) species abundances and composition can change (thus modifying strengths of intra- and interspecific competition) or (2) specific traits can vary and adapt to the changing environment within short time scales. While the first scenario is able to analyze with process-based simulation models, the latter requires model modifications and robust tests with empirical data.

**Strengths and limitations of grassland modeling**

Besides progress in empirical analyses, insights have so far also been gained in theoretical studies using phenomenological models that analyzed conditions under which species can reliably coexist or under which increases in ecosystem productivity can be expected (Tilman 1982, Hubbell 2001, Kinzig et al. 2002, Loreau 2010, Muller-Landau 2010, Kunstler et al. 2016). Theoretical concepts for explaining diversity effects range from selection by highly productive species, to complementarity of species that occupy different resource niches (Kinzig et al. 2002, Loreau 2010), to species neutrality of equivalent fitness (Hubbell 2001). Selection effects often go along with the long-term dominance of one or few productive key species. Niche and neutral theory in turn are both characterized to stabilize and maintain diversity. While niche effects are associated with differences in species traits in multiple dimensions including trade-offs (Villéger et al. 2008, Kraft et al. 2015, Wagg et al. 2017), neutrality implies no impact of trait differences on species’ fitness (Hubbell 2005). Empirical grasslands studies observed stronger support for selection or niche effects than for neutrality (Fargione and Tilman 2005, Harpole and Tilman 2006, Araya et al. 2011, Chu and Adler 2015).
systematically understand how traits influence different levels of grassland ecosystems. Species in natural grasslands or biodiversity experiments, however, differ strongly in multiple traits rather than single ones (Kattge et al. 2011, Weisser et al. 2017). Field analyses revealed a determined effect of mean trait values, trait differences, and trait plasticity in mixtures on ecosystem productivity and functioning (Roscher et al. 2018). Future extensions of our systematic simulation analysis (by including multiple varying traits and trade-off) can enable analysis and disentangling of such trait effects in a stepwise manner, up to species mixtures across all diversity levels. Such an approach can support the interpretation of diversity-productivity relations found in several field studies (Loreau et al. 2001, Tilman et al. 2001, Spehn et al. 2005, Fischer et al. 2010, Adler et al. 2011, Fraser et al. 2015, Weisser et al. 2017, Brun et al. 2019) and the disentangling of underlying processes shaping these relationships.

Further, the here chosen reference species represent a European grass species and defines by its trait values a unique strategy of the plant responding to its environment. Different combinations of multiple traits (e.g., grasses compared to forbs, Roscher et al. 2004) thus can result in different patterns of trait-productivity relations. Extended similar simulation analyses for forbs or legumes (using process-based models)—either in a stepwise manner or likewise a global sensitivity analysis—could help to broaden the picture on trait-productivity relations, intraspecific trait variation, and competitive strength of different plant functional groups commonly identified and used in grassland ecology.

Process-based grassland models provide in addition strong advantages for testing the impact of different modeling approaches (e.g., on resource competition between plants). Generally, such models allow to simplify, extend, or exchange modeling approaches on specific ecosystem processes. Important features of such models allow, among others, to include management regimes (in terms of frequency, timing, intensity, temporal, and spatial variations) and, thus, also to identify its impact on trait-productivity relations. For example, intensified management of grasslands (e.g., by regular cutting and fertilization) often goes along with decreasing species richness but an increasing productivity. In turn, regular weeding showed to frequently enable species colonization with impacts on grassland turnover and productivity (Roscher et al. 2009).

Another example comprises different modeling concepts to compare in terms of a plant’s photosynthesis, which is important to estimate the gross productivity (GPP) of grasslands (e.g., by exchanging the light response approach [Fischer et al. 2016] by the light use efficiency concept [Schippers and Kropff 2001] or the Farquhar model [Smith et al. 2001, Rolinski et al. 2018]). While keeping all other modeled process unmodified, such a comparison can firstly help to understand the sensitivity of different approaches on ecosystem functioning and secondly to unify the interpretation or even translation of model parameters. Simplification (or model upscaling) of micro-scale process-based models to meso- or macro-scale models provides the opportunity to integrate knowledge on the most important drivers of grassland dynamics (e.g., management practices) into simple models that can be applied at larger spatial scales. The use of process-based models for analyzing diversity-productivity relationships in grasslands thus complements previous attempts in biodiversity experiments, theory, and modeling with the potential to bridge the gap toward practice.

**Conclusions**

In order to deepen the understanding of the role of species traits for ecosystem functioning, we analyzed how the dynamics of grasslands are influenced by species traits using an individual-based mechanistic grassland model. We observed functional relations between traits and vegetation attributes at the individual plant level, in monocultures and mixture which mostly showed positive saturating trends but differed with regard to the considered trait. Intra- and interspecific interactions between plants, however, strongly increased the variability of trait patterns. This study demonstrates how process-based simulation models can complement previous empirical and theoretical approaches in order to broaden the picture on trait-productivity relations, intraspecific trait variation, and competitive strength of species-rich grasslands.
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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3205/full

Appendix S1: Model description of GRASSMIND.

Appendix S2: Parameterization details of reference species.

Appendix S3: Additional figures on results.

Data S1: Files of simulation results.